

# The striking polyphyly of *Suiriri*: Convergent evolution and social mimicry in two cryptic Neotropical birds

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## Abstract

Two species of *Suiriri* (Aves: Tyrannidae) inhabit semi-open habitats in South America: the polytypic Suiriri Flycatcher (*S. suiriri*) and the monotypic Chapada Flycatcher (*S. affinis*). The phylogenetic relationship between these congeneric species has never been investigated in detail. Here we used molecular tools—three nuclear introns and two mitochondrial genes—to investigate the systematic position of the Chapada Flycatcher, comparing the results found with morphological and behavioral data. We found that the polytypic Suiriri Flycatcher to be monophyletic and that it is included in a clade of Elaeniini flycatchers including *Phyllomyias*, *Phaeomyias*, and *Capsiempis* among other genera. The Chapada Flycatcher, on the other hand, is a member of the Fluvicolini, sister to *Sublegatus*, and should be allocated on its own monospecific genus, which we herein describe. We suggest that social mimicry is responsible for the remarkable convergence in size, shape, plumage coloration, and behavior in the adults of the Suiriri Flycatcher and the Chapada Flycatcher.

## KEYWORDS

Cerrado, molecular systematics, *Sublegatus*, *Suiriri islerorum*, taxonomy, Tyrannidae

## 1 | INTRODUCTION

*Suiriri* is a genus of tyrant flycatcher (Aves: Tyrannidae) found in semi-open formations of South America (Fitzpatrick, 2004; Ridgely & Tudor, 2009). The taxonomy and systematics of the genus have been debated for more than a century (Allen, 1889; Hayes, 2001; Traylor, 1982; Zimmer, 1955), culminating in the description of a new cryptic species, the Chapada Flycatcher, at the very beginning of the 21st century (Zimmer, Whittaker, & Oren, 2001). Subsequently, Kirwan, Steinheimer, Raposo, and Zimmer (2014) discovered that Burmeister (1856) had previously described and named the “new” species proposed by Zimmer et al. (2001), but that Burmeister’s name was being inadvertently associated with an unnamed sympatric taxon, currently known as Burmeister’s Suiriri. The taxonomic solution found by Kirwan et al. (2014) was to propose a new scientific name for the Burmeister’s Suiriri, and to put the scientific

name of the Chapada Flycatcher, *Suiriri islerorum* Zimmer, Whittaker, and Oren, 2001, as a junior synonym. Therefore, the genus *Suiriri* (sensu Kirwan et al., 2014) includes two species, with the following taxa: (1a) *Suiriri suiriri suiriri* (Vieillot, 1818)—Suiriri Flycatcher—short-billed and white-bellied taxon with range centered in the Chaco; (1b) *Suiriri suiriri burmeisteri* Kirwan et al., 2014;—Burmeister’s Suiriri—long-billed and yellow-bellied taxon with range centered in the Cerrado; (1c) *Suiriri suiriri bahiae* (von Berlepsch, 1893)—Bahia Suiriri—taxon with intermediate bill length and yellow belly, but with some putative specimens showing white belly, with range centered in the Caatinga; and (2) *Suiriri affinis* (Burmeister, 1856)—Chapada Flycatcher—taxon with short and broad bill, yellow belly, and broader pale tips to tail feathers, with range centered in the Cerrado.

The inconvenient but inevitable consequence of such nomenclatural changes is that the names of some taxa included in *Suiriri* (sensu Kirwan et al., 2014) differ from those names adopted in all previous literature, including several papers about the natural history of two

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members of the genus (e.g., Lopes & Marini, 2005a,b, 2006). We therefore advise readers to be careful when confronting the findings of this study with previous literature.

All three subspecies of *S. suiriri* are closely related, as suggested by morphological, behavioral, vocal, and molecular data (Birdsley, 2002; Chaves, Clozato, Lacerda, Sari, & Santos, 2008; Hayes, 2001; Ohlson, Irestedt, Ericson, & Fjelds , 2013; Tello, Moyle, Marchese, & Cracraft, 2009; Zimmer, 1955). The most complete phylogenies available found *S. suiriri* to be sister to *Myiopagis*, and these are sister to *Elaenia* (Ohlson et al., 2013; Tello et al., 2009), or sister of *Phaeomyias*, *Capsiempis*, and *Phyllomyias* and near to *Myiopagis* and *Elaenia* (Ohlson, Fjelds , & Ericson, 2008), thus supporting placement among the Elaeniinae.

On the other hand, the scarce evidence available suggests that *S. affinis* is strongly differentiated genetically from members of *S. suiriri* (Zimmer et al., 2001). Bates, Zimmer, Silva, and Hunt (2001), in an unpublished Meeting Abstract, reported that molecular data suggested that *S. affinis* is not closely related to *S. suiriri*, but that it is probably related to *Sublegatus*, as cited by Fitzpatrick (2004). This supports the observation of Zimmer (1955) that the bill of *S. affinis*, if compared with *S. s. burmeisteri*, is comparatively short "but basally broad, giving an outline suggesting the bill of *Sublegatus modestus* on an enlarged scale" (see Figure 1 for pictures of some of these species).

Here, we investigate the systematic position of *S. affinis*, which has never been thoroughly evaluated into a phylogenetic context, comparing the results found with morphological and behavioral data. Although available phylogenies have included samples from all three

subspecies of *S. suiriri*, none has ever included samples of *S. affinis* (e.g., Birdsley, 2002; Chaves et al., 2008; Ohlson et al., 2008, 2013; Rheindt, Norman, & Christidis, 2008; Tello et al., 2009).

## 2 | MATERIALS AND METHODS

### 2.1 | Sampling

We obtained tissue samples of three specimens of *S. affinis* and three specimens of *S. suiriri* from four localities in South America (Table 1). Specimen vouchers of all tissue samples are deposited in the Centro de Cole es Taxonomicas da Universidade Federal de Minas Gerais (DZUFMG) and Museu de Zoologia da Universidade de S o Paulo (MZUSP). We also included one sample each of *Sublegatus modestus*, and of *S. obscurior*, with vouchers specimens deposited in the Museu Paraense Em lio Goeldi (MPEG).

DNA was extracted from the liver or pectoral muscle tissues of specimens. DNA was extracted using a phenol–chloroform–isoamyl alcohol protocol (Chaves et al., 2008). All new sequences were deposited in GenBank, accession numbers: MF497835 to MF497867 (Table S1).

We used sequences of the two protein-coding mitochondrial genes to infer relationships of *S. affinis* and *S. suiriri*: *NADH dehydrogenase subunit 2* (ND2) and *cytochrome b* (Cyt-*b*). We also used three nuclear introns: *myoglobin intron 2* (Myo), *glyceraldehyde-3-phosphate dehydrogenase intron 11* (G3PDH), and *ornithine decarboxylase introns 6 and 7 along with the intercepting exon 7* (ODC). The following



**FIGURE 1** (a) *Suiriri suiriri burmeisteri* (Photo: Rafael Fortes, Minas Gerais, Brazil, WA 741587); (b) *Suiriri affinis* (Photo: Eduardo Patrial, Maranh o, Brazil, WA 953039); (c) *Sublegatus modestus* (Photo: Jarbas Mattos, Rio Grande do Sul, Brazil, WA 1135409); and (d) *Sublegatus obscurior* (Photo: S lvia F. Linhares, Mato Grosso, Brazil, WA 1762284)

**TABLE 1** Specimens and localities of a collection of the samples sequenced in this study

Sample ID	Taxon	Locality
MZUSP 79709	<i>Suiriri suiriri burmeisteri</i>	ESEC Serra Geral do Tocantins, Tocantins, Brazil
DZUFMG 5829	<i>Suiriri suiriri burmeisteri</i>	Estrada para Água Fria, Chapada dos Guimarães, Mato Grosso, Brazil
DZUFMG 4970	<i>Suiriri suiriri burmeisteri</i>	Fazenda Brejão, Brasilândia de Minas, Minas Gerais, Brazil
DZUFMG 5828	<i>Suiriri affinis</i>	Estrada para Água Fria, Chapada dos Guimarães, Mato Grosso, Brazil
MZUSP 79715	<i>Suiriri affinis</i>	Mata do Rio Galhã, Mateiros, Tocantins, Brazil
DZUFMG 4965	<i>Suiriri affinis</i>	Fazenda Brejão, Brasilândia de Minas, Minas Gerais, Brazil
MPEG 58065	<i>Sublegatus obscurior</i>	Ilha do Marajó, Chaves, 4 km S, Pará, Brazil
MPEG 57708	<i>Sublegatus modestus</i>	Fazenda Passo Formoso, Rodovia do Estanho, Manicoré, Amazonas, Brazil

primers were used for PCR and/or sequencing reactions: H6313 5'-CTCTTATTTAAGGCTTTGAAGGC-3', L5216 5'-GGCCCATACCCC GRAAATG-3' (Sorenson, Ast, Dimcheff, Yuri, & Mindell, 1999), L5758 5'-GGNGGNTGRRBHGGNYTDAAYCARAC-3', and H5766 5'-DGADGARAADGCYARRAYTTDCG-3' (Brumfield & Edwards, 2007) for *ND2* gene, amplifying a segment of 1140 bps; L14841 5'-CCATCCAACATCTCAGCATGATGAAA-3' (Kocher et al., 1989) and H16065 5'-AACTGCAGTCATCTCCGGTTACAAGAC-3' (Lougheed, Freeland, Handford, & Boag, 2000) for *Cyt-b*, amplifying a segment of 1,100 bps; Myo2 5'-GCCACCAAGCACAAGATCCC-3' (Slade, Moritz, Heideman, & Hale, 1993), Myo3 5'-CGGAAGAGCTC CAGGGCCTT-3', and Myo3F 5'-TTCAGCAAGGACCTTGATAAT GACTT-3' (Heslewood, Elphinstone, Tiedemann, & Baverstock, 1998) for *Myo*, amplifying a segment of about 750 bps; G3P-13b 5'-TCCACCTTTGATGCGGGTGCTGGCAT-3', G3P-14b 5'-AAGTCCA CAACACGGTTGCTGTA-3' and G3PintL1 5'-GAACGACCATTTTGT CAAGCTGGTT-3' (Fjeldså, Zuccon, Irestedt, Johansson, & Ericson, 2003) for *G3PDH*, amplifying a segment of about 380 bps; and OD6 5'-GAC TCCAAAGCAGTTTGTCTCAGTGT-3', OD8R 5'-TCTTACAGGCCAGGGAAGCCACCAAT-3' (Allen & Omland, 2003), and ODintF 5'-ATGCCCGCTGTGTGTTG-3' (Ericson et al., 2006) for *ODC*, amplifying a segment of about 700 bps. Amplifications were carried out in 15- $\mu$ L reactions containing 0.5 U of *Taq* polymerase (Invitrogen), 1 $\times$  buffer with 1.5 mM MgCl<sub>2</sub> (Invitrogen), 200  $\mu$ M dNTPs 0.5  $\mu$ M each primer, and 2  $\mu$ L of genomic DNA (~40 ng). PCRs of *ND2* were performed under the following conditions: 94°C for 2 min, 35 cycles of 94°C for 30 s, 63°C for 40 s, 72°C for 2 min, and a final extension of 10 min at 72°C. *Cyt-b* amplification followed 94°C for 2 min, 35 cycles of 94°C for 30 s, 50°C for 45 s, 72°C for 1 min, and a final extension of 10 min at 72°C. *ODC* and *Myo* amplification followed 95°C for 2 min, 40 cycles of 95°C for 1 min, 63°C for 30 s, 72°C for 1 min, and a final extension of 7 min at 72°C. *G3PDH* amplification followed 94°C for 5 min, 40 cycles of 94°C for 40 s, 58°C for 40 s, 72°C for 1 min, and a final extension of 7 min at 72°C.

The amplification products were purified by precipitation in PEG 8000 (20% polyethylene glycol, 2.5 M NaCl) and dissolved in ultra-pure water. The purified PCR products were sequenced using the BigDye v3.1 terminator sequencing reaction mix following the manufacturer's protocols (Applied Biosystems, USA), electrophoresed on

an ABI3130xl sequencer. Each gene region was bidirectionally sequenced to verify accuracy.

High-quality sequences were aligned and checked for quality and accuracy using SeqScape v2.6 to visualize and check manually all chromatograms. For the three nuclear introns, heterozygous positions were identified by visual inspection of chromatograms data. We codified double peaks present in both strands as ambiguous sites according to the IUPAC code. The alignments of the consensus sequences for all individuals and species were built using the program MUSCLE v3.6 (Edgar, 2004) using default settings, available in MEGA v6 software (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013).

## 2.2 | Phylogenetic inferences

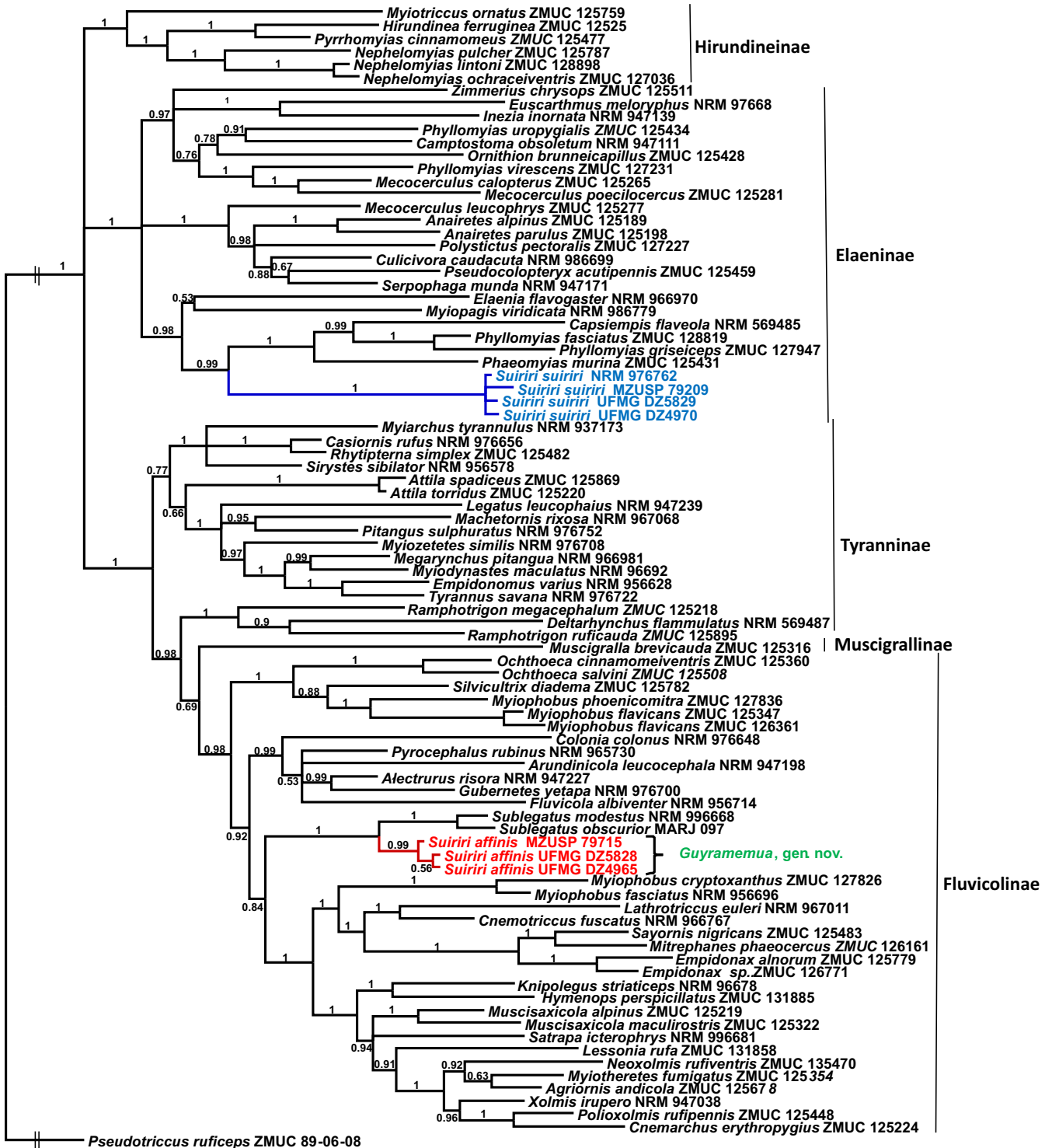
We used sequence data available in GenBank, in addition to our own data, to draw phylogenetic reconstructions. We followed the classification proposed by Ohlson et al. (2013) for the family Tyrannidae, and we used *Pseudotriccus* (Rhynchocyclidae) as an out-group in the analyses. We then conducted the analyses with partitioned output for the three nuclear introns and with two distinct datasets for mtDNA markers. The bulk of our dataset for mtDNA sequences was downloaded from GenBank and come from several articles (Table S1), and consequently, several specimens had only one of two genes sequenced. Therefore, the *ND2* and *Cyt-b* phylogenetic reconstructions we reanalyzed independently, because our dataset did not allow a satisfactory concatenated analysis. Concatenating these two genes would lead to large missing data for one or another marker, which would greatly impair the support of nodes and the fidelity of phylogenetic relationships between species.

We also inspected gene alignments in MEGA v6 to identify unreversed molecular synapomorphies for *Suiriri affinis* within Fluvicolinae across each of the five genes analyzed. We inspected nucleotide substitutions of 39 species of Fluvicolinae available for *ODC*, *G3PDH*, and *Myo*, and 20 species for *Cyt-b* and *ND2*. The molecular synapomorphies were numbered by their position in each gene alignment.

To avoid phylogeny over-parameterization in inference of topology, we used PARTITIONFINDER v1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) to choose the best partitioning scheme for nuclear

and mtDNA datasets, performing nucleotide substitution model selection for each partition selection. The nuclear introns and each codon position for each coding gene (or exon) were treated separately. After this, we conducted Bayesian inferences in MRBAYES v3.2.6 (Ronquist et al., 2011) on the CIPRES SCIENCE PORTAL (Miller, Pfeiffer, & Schwartz, 2010) to estimate the phylogenetic

relationships using the selected partition scheme and models of nucleotide substitution according to the Bayesian information criterion (BIC) method (Schwarz 1978), which often outperform other commonly used criteria (Luo et al., 2010). The posterior probabilities for model parameters, tree, and branch lengths were obtained with a Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) sampler.



**FIGURE 2** 50% majority-rule Bayesian consensus tree of some selected Tyrannidae based on 3674 base pairs of a scheme of four partitions of nuclear introns Myo, G3PDH, and ODC. Branch support values are presented as Bayesian posterior probabilities

Four chains were run for two independent runs with 20 million generations each of four MCMCMCs each, with trees sampled every 500 generations. The trees sampled during the 20% burn-in phase were discarded. Parameter estimates and tree distributions were examined with Tracer v1.6 (Rambaut, Suchard, Xie, & Drummond, 2014) for convergence and to assess whether the MCMCMC analysis had run long enough.

## 2.3 | Morphological, behavioral, and breeding comparisons

Morphological comparisons were based on the visual examination of plumage coloration and body shape of study skins of all species of Fluvicolinae housed in DZUFMG and MZUSP, as well as on consultation on the color plates and text descriptions of all species of tyrant flycatchers (Fitzpatrick, 2004). Behavioral and breeding comparisons were made after twenty years of fieldwork conducted throughout Brazil, and the examination of the nest and egg collection of the Coleção Ornitológica Marcelo Bagno da Universidade de Brasília, Brasília (COMB), supplemented by literature data.

## 3 | RESULTS

### 3.1 | Phylogenetics

We generated final alignments with 767 base pairs (bps) of *Myo*, 677 bps of *G3PDH*, and 2230 bps of *ODC*, totaling 3674 bps of concatenated sequences for nuclear introns (Data S1). We also obtained 1014 bps of *ND2* and 996 bps of *Cyt-b* for mtDNA genes (Data S2 and S3). Table S2 synthesizes the molecular synapomorphies for *Suiriri affinis* within Fluvicolinae, where we also identified 11 unreversed molecular synapomorphies across four genes for it.

For the nuclear *MYO-G3PDH-ODC* dataset, the PARTITIONFINDER selected a partitioning scheme composed of four subset partitions (partitions 1–4) that was further preferred overall using the greedy search algorithm. In partition 1, the K80+ G model was the best fit for the first codon position of *Myo* exon 2; the first codon position of *ODC* exon 7; and *ODC* introns 6 and 7. In partition 2, the K80+ G model was the best fit for the second codon position of *Myo* exon 2; *Myo* intron 2; the first and second codon positions of *ODC* exon 6; and the third codon position of *ODC* exon 8. In partition 3, the JC model was the best fit for the third codon position of *Myo* exon 2; the first, second, and third codon positions of *Myo* exon 3; the third codon position of *ODC* exon 6; the second and third codon positions of *ODC* exon 7; and the first codon position of exon 8. Finally, in partition 4, the K80+ G model also was the best fit for the intron *G3PDH* and the second codon position of *ODC* exon 8. For the mtDNA *ND2* dataset, the PARTITIONFINDER selected a partitioning scheme composed of three subset partitions, one for each codon position. The GTR + I + G model was the chosen for the first and second codon positions, and the GTR + G model was the chosen for the third codon position. For the mtDNA *Cyt-b* dataset, the PARTITIONFINDER selected also a partitioning scheme composed of three subset partitions. The

SYM + I + G, HKY + I + G, and GTR + G models were chosen for the first, second, and third codon positions, respectively.

Bayesian analyses produced well-resolved trees with strong support for most nodes in the three sets of data analyzed. See Figure 2 for partitioned *Myo-G3PDH-ODC* nuclear introns, and Fig. S1 for *ND2* and Fig. S2 for *Cyt-b* mitochondrial genes, respectively.

*Suiriri affinis* was sister to members of the genus *Sublegatus* with strong support in all analyses (Figures 2, Figs S1, and S2). On the other hand, the systematic position of *S. suiriri* was ambiguous, varying between datasets. *Suiriri suiriri* occupied a basal branch sister to the clade containing *Phaeomyias*, *Phyllomyias*, and *Capsiempis* with strong support for introns (Figure 2). However, with *ND2* marker, the phylogenetic relationships of *S. suiriri* with *Phaeomyias*, *Phyllomyias*, and *Capsiempis* showed a low Bayesian support (Fig. S1), and with *Cyt-b* marker, *S. suiriri* occupied a basal branch with a low Bayesian support sister to the clade including *Mecocerculus*, *Anairetes*, *Culicivora*, *Pseudocolopteryx*, *Polystictus*, and *Serpophaga* (Fig. S2).

## 4 | DISCUSSION

### 4.1 | Taxonomy and nomenclature

Data obtained confirmed the striking polyphyly of *Suiriri*, showing the taxon *affinis* to be sister to the genus *Sublegatus*, forming a clade with high support. Therefore, the Chapada Flycatcher should be removed from the genus *Suiriri*, which can be done in two different ways, moving the Chapada Flycatcher into *Sublegatus*, or placing it in a monotypic genus. We favored the second option for three main reasons: (i) the Chapada Flycatcher is much larger and shows distinct color patterns in tail, rump, upper tail coverts, and throat when compared to the three species of *Sublegatus*, which are homogeneous in color and size (detailed below); (ii) songs of the Chapada Flycatcher are complex and elicited during ritualized sex-specific displays, while all three species of *Sublegatus* are shy and quiet birds, whose main vocalizations are thin, whistled calls; and (iii) the significant large genetic distance between the Chapada Flycatcher and the three species of *Sublegatus*. Because no generic name is available for the Chapada Flycatcher, here we describe a new genus for it.

### 4.2 | *Guyramemua*, gen. nov.

Type species: *Suiriri affinis* (Burmeister, 1856)

#### 4.2.1 | Diagnosis

*Guyramemua affinis* comb. nov., the only species in the genus, is distinguished from all other Fluvicolinae genera by its unique tail pattern, with brownish-black rectrices showing pale base and tips. *Guyramemua* can be distinguished from *Sublegatus*, its sister genus, also by its larger size; rump and uppertail coverts contrastingly paler than the upperparts (concolor in *Sublegatus*); and throat contrastingly white. *Guyramemua* can be distinguished from the syntopic and morphologically very similar *Suiriri suiriri burmeisteri* by its broad pale

terminal fringe to tail and by the bill entirely black and distinctly short, but relatively broad. *Guyramemua* shows derived molecular characters apomorphic for Fluvicolinae across four genes. These are for *ND2*: H345G, A415G, and A934G; for *Cyt-b*: Y3G, H174G, M381G, Y588G, and H925G; for *G3PDH*: A163G, and T581C; for *ODC*: G2014A. The genus *Sublegatus* can be distinguished from *Guyramemua* by 12 unreversed molecular synapomorphies within Fluvicolinae across five genes (Table S2). These are for *ND2*: H480T and C1014A; for *Cyt-b*: C531T, A720G, and B925A; for *G3PDH*: G569C; for *ODC*: G1521A; and for *Myo*: C1T, T17C, G26A, C27T, and A28G. For *Myo*, we also identified a deletion of four nucleotides (TGTG) at position 78–81 of alignment for *Guyramemua* and *S. modestus*; however, *S. obscurior* does not have this deletion (Table S2).

#### 4.2.2 | Etymology

The generic name is derived from Tupi, an indigenous South American language: from *gúyra* (bird) and *memûã* (cheater, trickster) (Barbosa, 1970; Navarro, 2006). We specify that the name is gender neutral attending to Article 30.2.2 of the ICZN (1999), because Tupi was a genderless language (Barbosa, 1956). We choose this name for the genus because its only species “tricked” ornithologists three times before we could clarify its specific name, taxonomy, and systematic position. The first trick was hiding in plain sight as ornithologists failed to recognize that two similar-looking species occurred side by side in the Cerrado, even though there was evidence of this since Allen (1889). The second time was when Zimmer et al. (2001), after accurately pointing out that two cryptic species occur syntopically in the Cerrado, missed the chance to correctly use the name proposed by Burmeister. The third time was when the Chapada Flycatcher was inadvertently included in the genus *Suiriri*. One and a half decades of additional research was necessary for the Chapada Flycatcher to be correctly classified.

*Guyramemua* and *Sublegatus* have significant genetic distances between them, comparable to the genetic distances observed between other well-established genera, such as *Alectrurus* and *Gubernetes*, *Mitrephanes* and *Sayornis*, and *Agriornis*, *Neoxolmis*, and *Myiotheretes* for nuDNA; and also between *Aphanotriccux* and *Lathrotriccus*, and *Empidonax* and *Contopus* for mtDNA. Levels of genetic distance alone are a poor justification for the demarcation of a genus in avian systematics, because there is no standard benchmark genetic distance. For example, some congeneric species of *Muscisaxicola* and *Phyllomyias*, for example, shown genetic distance within the range between the Chapada Flycatcher and *Sublegatus* (Figure 2). On the other hand, the genetic distance between the Chapada Flycatcher and the three species of *Sublegatus* is similar, or even larger, than that observed between several undisputed sister genera of Tyrannidae, such as *Casiornis* and *Rhytipterna* (Figure 2; Ohlson et al., 2013). This does not mean that genetic distance is a useless systematic character, but that any decision regarding the generic allocation of a species should rely “not by one character, but by a group of carefully chosen characters” (Winston, 1999).

None of the newly published phylogenies of the Tyrant Flycatchers and allied families has conducted a thorough revision of the genus-level classification of the whole group. Some obvious splits were made in separate papers (e.g., Ohlson, Fjeldsã, & Ericson, 2009), but other generic changes, not so obvious, are still waiting for a more detailed study. The lack of a thorough revision of genus-level classification accompanying complete phylogenies is a common practice in ornithology. A remarkable exception to this rule was the study of Burns, Unitt, and Mason (2016), which conducted a revision of the genus-level classification of the family Thraupidae. This study resulted in a generic rearrangement of an entire family, including the description of eleven new genera and the resurrection of several generic names. We have no doubt that a similar study is necessary for the Tyrannidae and allied families and that it would result in profound generic rearrangements of this entire group. Therefore, many Tyrannidae genera require systematic revision and, much probably, splits.

#### 4.3 | Phylogenetics

The topologies we obtained agree with the most recent phylogenies available, which found strongly supported *S. suiriri* (*Muscicapa suiriri* Vieillot, 1818, is by tautonymy the type of the genus *Suiriri* d'Orbigny, 1840) to be closely related to *Phaeomyias*, *Phyllomyias*, and *Capsiempis* and forming a clade sister to the clade containing *Myiopagis* and *Elaenia*, thus among the Elaeniini (Chaves et al., 2008; Ohlson et al., 2008, 2013; Tello et al., 2009). We also confirmed that *S. s. suiriri* and *S. s. burmeisteri* are closely related and that *G. affinis* is sister to *Sublegatus*, as previously suggested (Bates et al., 2001; Fitzpatrick, 2004).

Our Bayesian tree built with introns recovered a moderately supported clade containing *Guyramemua* + *Sublegatus* on the basal branch to all species in Tribes Contopini and Xolmiini, as in Ohlson et al. (2008). However, Ohlson et al. (2013), after analyzing a dataset including two other nuclear gene regions (RAG-1 and RAG-2), found with high support the genus *Sublegatus* in a basal branch of another Fluvicolinae group, including part of the Tribe Fluvicolini with *Pyrocephalus*, *Fluvicola*, *Arundinicola*, *Gubernetes*, and *Alectrurus*. The same arrangement was found in Tello et al. (2009). Meanwhile, mitochondrial *Cyt-b* marker joined *Guyramemua* + *Sublegatus* with a strong support clade with *Colonia*, *Fluvicola*, and *Gubernetes*, and for mtDNA *ND2* marker with a low support with *Colonia* (note: *Fluvicola* and *Gubernetes* *ND2* sequences lack in the dataset).

The genus *Sublegatus* includes three species of small tyrant flycatchers (~12–16 g) (Dunning, 2008) found in dry arid scrub, light open woodland, mangroves, and borders of forests and clearings (Fitzpatrick, 2004; Haverschmidt, 1970; Restall, Rodner, & Lentino, 2006; Ridgely & Tudor, 1994; Wetmore, 1972). It is worth mentioning that the genus *Sublegatus* needs revision, because it is known to harbor paraphyletic species as Rheindt, Christidis, and Norman (2008), as can be seen here in Fig. S1 for *S. arenarum*. *Guyramemua affinis*, which is much larger (~20 g, Lopes & Marini, 2006), favors shrubby savannas and light open woodlands (Fitzpatrick, 2004;

Lopes & Marini, 2006), presenting habitat requirements similar to those of *S. modestus* (with which *G. affinis* was found in syntopy in several sites surveyed by us) and *S. arenarum* (*S. obscurus* inhabits more mesic habitats). Behavioral and breeding data might provide additional evidence about the correct systematic position of *G. affinis*, but these data need to be subject to a thorough cladistic analysis, what is out of the scope of this study. In the following paragraphs, we summarize available information as a contribution to subsequent studies.

Remarkable differences between the nests, eggs, nestlings, and juveniles of *Guyramemua affinis* and *Suiriri s. burmeisteri* were first described by Lopes and Marini (2005a). The eggs of *S. s. burmeisteri* are white (Lopes & Marini, 2005a), similar to that of *S. s. suiriri*, which is a relatively uncommon pattern among Tyrannidae that built open nests (Narosky & Salvador, 1998; de la Peña, 2013; Skutch, 1997). Eggs of members of *Myiopagis* and *Elaenia*, genera closely related to *Suiriri*, are usually marked with dark blotches, forming a wreath around its thicker end (Narosky & Salvador, 1998; de la Peña, 2013). In a similar way, eggs of *Guyramemua* also present a wreath of small brown blotches around its blunt end, a pattern also observed in *Sublegatus* and in almost all related genera of Fluvicolini that build open nests, such as *Pyrocephalus*, *Myiophobus*, *Ochthoeca*, and *Coloramphus* (Narosky & Salvador, 1998; de la Peña, 2013), but not in *Gubernetes*, which lays white eggs (Heming, Gressler, Russell, & Marini, 2016). Therefore, egg coloration seems not to be informative of the systematic position of *S. suiriri* or *G. affinis*.

Young nestlings (~3 days old) of *Guyramemua* have blackish skin, exhibiting short and whitish plumes (Lopes & Marini, 2005a), a pattern similar to that of other Fluvicolini, such as *Sublegatus* and *Pyrocephalus* (de la Peña, 2006, 2013; LEL pers. obs.). Young nestlings of *Suiriri*, on the other hand, have greyish brown skin and exhibit comparatively longer, greyish plumes (Lopes & Marini, 2005a), more similar to that of closely related Elaeniini (de la Peña, 2006, 2013; LEL pers. obs.).

Juveniles of *Guyramemua* are similar to the adults of the species, while juveniles of *S. s. suiriri* and *S. s. burmeisteri* (juveniles of *S. s. bahiae* are unknown) are markedly distinct from the adults, exhibiting the head, back, and wing coverts largely tipped white (Lopes & Marini, 2005a; de la Peña, 2013), an unusual pattern of plumage coloration in Tyrannidae (Ridgely & Tudor, 1994). Surprisingly, juveniles of *Sublegatus* also exhibit plumage largely tipped white, superficially resembling that of *S. suiriri* (Lopes & Marini, 2005a; Wetmore, 1972). Nevertheless, a closer look reveals distinct patterns of white markings on feathers of these species, suggesting that this pattern of plumage coloration evolved independently. Freshly plumaged juveniles of *Suiriri* show contour feathers of the entire upperparts marked with a small white drop-like spot in the center of the tip of each contour feather (see a color picture in <http://www.wikiaves.com.br/816045>). These white markings disappear with feather wear from several feather tracts. On the other hand, freshly plumaged juveniles of *Sublegatus* show contour feathers of the entire upperparts marked with a discrete white fringe along the entire tip of each contour feather (<http://www.wikiaves.com.br/280304>).

The dramatic wing-lifting displays that accompany male–female duets in *Guyramemua* is also shared with other Fluvicolini, such as *Gubernetes yetapa* (whose displays were considered “remarkably similar” by Zimmer et al., 2001) and the less dramatic *Fluvicola nengeta*, which generally does not lift wings above head (pers. obs.). Even though no member of *Sublegatus* seems to regularly exhibit any wing display during duets, Edson Endrigo (pers. com.) reported to us that he once observed a pair of *S. modestus* lifting their wings after the playback of the typical voice of the species (see a picture of a possible display in <http://www.wikiaves.com.br/1212515>). Furthermore, nestlings of *S. modestus* sometimes perform rhythmic movements with both wings (“a veces los pichones chicos realizan movimientos acompasados de las alas,” de la Peña, 2013), what might be interpreted as a reminiscence of the wing display. On the other hand, to the best of our knowledge, members of no genus closely allied to *Suiriri* seem to exhibit any wing display while duetting.

Both *G. affinis* and *S. suiriri burmeisteri* “periodically wagged its tail downward in a relaxed manner when foraging, particularly after perch changes” (Zimmer et al., 2001). It is amazing how a very characteristic behavior like this can be shared by species that are only distantly related. To the best of our knowledge, no other Elaeniini shows this behavior, which is also shared by at least one species of Fluvicolini, the Vermilion Flycatcher *Pyrocephalus rubinus* (Zimmer et al., 2001). The remarkable convergence in morphology and behavior between the two species studied here deserves further comments.

#### 4.4 | Convergent evolution and social mimicry

Convergence in body size and shape, as well as in plumage coloration and pattern, can be produced by natural and sexual selection in the absence of any interspecific social interactions or mimicry (Prum, 2014). Classic examples are Eastern Meadowlarks *Sturnella magna* (Icteridae) of the New World and Yellow-throated Longclaws *Macronyx croceus* (Motacillidae) of Africa, and Phainopeplas *Phainopepla nitens* (Ptiliogonatidae) of North America and Crested Black-Tyrants *Knipolegus lophotes* (Tyrannidae) of South America (Prum, 2014; Willis, 1976). Nevertheless, given that *G. affinis* is regularly found in syntopy with *S. s. burmeisteri* and that these species even associate in mixed-species flocks (Lopes, 2005), their remarkable similarity, which includes not only their morphology, but also the downward dip of the tail, is unlikely to have evolved by chance. Although a deep examination of this phenomena is out of the scope of this study, we suspect that some kind of social mimicry is a possible explanation for the observed convergence, a hypothesis that remains to be tested.

Several alternative and not mutually exclusive mechanisms might be responsible for character convergence in these species, including: (i) economy of communication, which avoids wasting time and energy during unnecessary displays and interpretation during interspecific communication, resulting in mutual economy (Moynihan, 1968, 1981); and (ii) antipredator device, reducing oddity and causing visual predator confusion, making it difficult to select a potential prey item among a mixed-species flock (Barnard, 1979, 1982;

Willis, 1989). This last hypothesis, even though very difficult to test, gains additional support by field observations of a third species, which usually associates with the two tyrant flycatchers in mixed-species flock (*Veniliornis mixtus* was recorded in about 30% of the mixed-species flocks studied by Lopes (2005)). This species is the Checkered Woodpecker *Veniliornis mixtus*, a distinct species in the genus that was until quite recently classified in the genus *Picoides* (Moore, Weibel and Agius 2006). Although this woodpecker is obviously very distinct from a Tyrant Flycatcher when perched, it is similar (general size and plumage color) to them when seen flying from behind, as experienced by LEL when studying the foraging behavior of birds associated with mixed-species flocks in central Brazil (Lopes, 2005) and by LFS when fieldworking in the northern part of the Cerrado.

A third alternative mechanism, interspecific social dominance mimicry, is highly unlikely, because in this kind of mimicry, model species are always "larger in body mass than mimic species, and socially dominant over them" (Prum, 2014; Prum & Samuelson, 2012), which is not the case. Body size (Zimmer et al., 2001) and weight (Lopes & Marini, 2006) are quite similar and overlapping between *S. s. burmeisteri* and *G. affinis*. Furthermore, despite the high overlap in the home range of these species, agonistic encounters between them are rare and restricted to the environs of the nest of the aggressor species (Lopes & Marini, 2006).

Although the Elaeniini-like appearance of *G. affinis* might at first glance suggest that it is mimicking *S. s. burmeisteri*, the scarce evidence available suggests that this is not the case. This because all members of *Sublegatus* exhibit a superficial morphological resemblance to the Elaeniini, which led the genus to be traditionally included among the Elaeniini based on plumage coloration and body shape, being only recently transferred to the Fluvicolini based on molecular evidence (Chaves et al., 2008; Ohlson et al., 2008; Tello et al., 2009). Furthermore, the downward dip of the tail shared by both species seems to be a character associated with the Fluvicolini, as discussed above for *P. rubinus*. Therefore, we believe that both *G. affinis* and *S. s. burmeisteri* converged in appearance and behavior to share the benefits from morphological similarity.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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