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Genetic and morphological data support placement of *Myrmotherula gularis* (Spix) in the monotypic genus *Rhopias* Cabanis and Heine (Aves: Passeriformes: Thamnophilidae)

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Abstract

Recent DNA-based phylogenetic analyses of the family Thamnophilidae have shown that the genus *Myrmotherula* is polyphyletic. Traditional plumage-based taxonomy has been misleading in terms of identifying independently evolving lineages within the complex. Here, we integrate a molecular phylogeny with morphometric information and ancestral reconstruction of syringeal character states of the *Musculus vocalis ventralis*, to investigate the taxonomic position of *M. gularis*, a species for which phylogenetic affinities have long been uncertain. We show that *M. gularis* represents a long branch in the tribe Thamnophilini that is not closely related to any other member of the *Myrmotherula* complex. Its relationships within the tribe remain uncertain because of the lack of phylogenetic resolution at the base of the tribe. *M. gularis* shares a derived character state of the *M. vocalis ventralis* with *Taraba*, *Hypoedaleus*, and *Mackenziaena*, which supports a close relationship between *M. gularis* and the large antshrikes. *M. gularis* can be diagnosed from *Myrmotherula* and *Epinecrophylla* by this condition of its *M. vocalis ventralis*, and from *Isleria* by plumage and other morphological traits. The phylogenetic and morphological distinctiveness of *M. gularis* does not warrant merging it into any other genus. We propose that this species be placed in a monotypic genus, for which the available name *Rhopias* applies.

Key words: Antwren, *Musculus vocalis ventralis*, phylogeny, syrinx, Atlantic Forest

Introduction

The genus *Myrmotherula* Sclater, 1858, as traditionally recognized, was one of the most species-rich avian genera in the New World (Meyer de Schauensee, 1966; Sibley & Monroe, 1990; Zimmer & Isler, 2003). The traditional plumage-based taxonomy of the genus was considered problematic by earlier authors (i.e., Cory & Hellmayr, 1924; Peters, 1951), and several subsequent studies indicated that *Myrmotherula* is polyphyletic (Hackett & Rosenberg, 1990; Gonzaga, 2001; Irestedt *et al.*, 2004; Brumfield *et al.*, 2007; Bravo *et al.*, 2012). Recently, the genus *Epinecrophylla* Isler and Brumfield, 2006 (Isler *et al.*, 2006) was described for eight species referred to as the “stipple-throated” antwrens, and the genus *Isleria* Bravo, Chesser and Brumfield, 2012 was erected for *M. hauxwelli* Sclater and *M. guttata* Vieillot.

Despite the description of these two new genera, taxonomic problems in the *Myrmotherula* complex (sensu Zimmer & Isler, 2003) remain. The phylogenetic position of *M. gularis* (Spix, 1825) is unclear, but earlier analyses

of plumage, morphometrics, vocalizations and syringeal anatomy (Gonzaga, 2001), and DNA-based phylogenetic reconstructions (Isler *et al.*, 2006; Bravo *et al.*, 2012) suggest that it is not closely related to *Myrmotherula*, *Epinecrophylla* or *Iseria*.

Here, we evaluate the generic status of *M. gularis* by integrating a subset of a comprehensive molecular phylogeny of the Thamnophilidae (Bravo *et al.*, unpubl. data) with analyses of morphometric data and ancestral reconstruction of states of the *Musculus vocalis ventralis*, a feature of syringeal morphology previously used in phylogenetic inference in the family (Gonzaga, 2001).

Methods

Molecular analyses. We used a subset of a densely sampled molecular phylogeny of the Thamnophilidae (only six of the 224 species are missing) (Bravo *et al.*, unpubl. data) to evaluate the phylogenetic placement of *M. gularis*. We used sequences of three mitochondrial genes (*cytochrome b*—*cytb*, 1,045 bp; *NADH dehydrogenase subunit 2*—ND2, 1,041 bp; and *NADH dehydrogenase subunit 3*—ND3, 351 bp), one autosomal nuclear intron (*b-fibrinogen intron 5*— β F5; 568 bp), and two coding nuclear genes (*recombination activation gene 1*—RAG1, 2,872 bp; *recombination activation gene 2*—RAG2, 1,152 bp). Taxon sampling (Table 1) for this subset includes 57 individuals representing 52 species and 30 genera (23% and 59% of the family, respectively), and included samples of *Myrmotherula brachyura* Hermann (2 individuals), *M. axillaris* Vieillot (2), *M. gularis* (4), *Epinecrophylla haematonota* Sclater (1), *E. erythrura* Sclater (1) and *Iseria hauxwelli* (1). Note that the type species of *Myrmotherula* is *Muscicapa pygmaea* Gmelin, a synonym of *Myrmotherula brachyura*, a taxon represented in our sampling (see above). The samples from *M. gularis* covered the extremes of its distribution. The phylogeny was outgroup-rooted using sequences of nine species of non-thamnophilid suboscines: *Pipra* spp. Linnaeus (Pipridae; LSUMZ B-18078/AMNH DOT-3872), *Furnarius rufus* (Gmelin) (Furnariidae; AMNH DOT-10431), *Chamaeza campanisona* (Lichtenstein) (Formicariidae; UWBM KGB14), *Liosceles thoracicus* (Sclater) (Rhinocryptidae; FMNH 390080), *Hylopezus berlepschi* (Hellmayr) (Grallariidae; FMNH 322345), *Pittasoma* spp. Cassin (Conopophagidae; LSUMZ B-2285/B-11863), and *Melanopareia elegans* (Lesson) (Melanopareidae; LSUMZ B-5245/5246).

Total DNA was extracted from 25 mg of pectoral muscle using the Qiagen DNeasy kit following the manufacturer's protocol, and polymerase chain reactions were performed using the protocols of Brumfield *et al.* (2007) for *cytb*, ND2, ND3, and β F5, and of Groth and Barrowclough (1999) and Barker *et al.* (2002) for RAG-1 and RAG-2. Each gene region was bidirectionally sequenced to verify accuracy. Additional sequences from our previous work (Brumfield & Edwards, 2007; Brumfield *et al.*, 2007; Moyle *et al.*, 2009; Gómez *et al.*, 2010; Bravo *et al.*, 2012) that were available on GenBank were also used.

Analyses were conducted using a concatenated six-gene 7,029 bp alignment produced in the program MAFFT v. 6 (Katoh *et al.*, 2002). To avoid phylogeny over-parameterization, we ran ML analyses for six different partition schemes under the GTR+G model of nucleotide substitution using RAxML 7.2.7 (Stamatakis, 2006) on the Cipres Science Gateway V 3.1 (Miller *et al.*, 2010). We used the obtained likelihood values to calculate the Akaike Information Criterion (AIC) (Akaike, 1974) for each partition and established that the most informative partition scheme was the one with 16 partitions (the nuclear intron and each codon position for each coding gene are treated separately). Using this partitioning scheme, we estimated the phylogeny via maximum likelihood using RAxML and assessed nodal confidence by performing 1,000 bootstrap replicates.

We conducted a Bayesian analysis using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001) on the University of Oslo Biportal (Kumar *et al.*, 2009). For each partition we evaluated 24 finite-sites substitution models with MrModeltest 2.3 (Nylander, 2004) based on likelihood scores from PAUP* (Swofford, 2003). We identified the best substitution model via comparison of AIC values. We performed our analysis with four runs and four MCMC chains, using 20,000,000 generations with a sample frequency of 1,000, a chain temperature of 1.75, and a burn-in of 20%. The results of the Bayesian inference were analyzed for convergence using the compare splits and the slide window analyses implemented at AWTY (Wilgenbusch *et al.*, 2004; Nylander *et al.*, 2008). Both approaches demonstrated that the chains reached convergence adequately.

Morphological analyses. To examine the position of *M. gularis* in the morphometric space occupied by the Thamnophilini (*sensu* Moyle *et al.*, 2009), we performed a principal components analysis (PCA) on log-

transformed morphometric measurements of tail, wing, and tarsus using R v2.13 (R Development Core Team, 2011). A total of 96 specimens was measured, including at least four individuals of each species (except for *Frederickena fulva*, $n = 3$) included in the phylogenetic analyses (Appendix 1). To capture variation in both size and shape across species, measurements were not corrected for body size or weight.

We also examined the syringeal morphology of 65 species of Thamnophilidae from 28 genera (total of 88 specimens) (Appendix 2) because it has been shown to be a phylogenetically informative trait in suboscines (e.g. Ames, 1971; Prum, 1990; Galvão & Gonzaga, 2011). Specifically, we examined the pair of Musculi vocales ventrales (Mm. v. ventrales) of each species for the presence or absence of two previously described character states (Gonzaga, 2001). In one state the cranial ends of the Mm. v. ventrales meet at the ventral surface of the syrinx, forming a continuous arch. In the other, a large gap separates its cranial ends, with each muscle being, or tending to be, restricted to the ventrolateral surface of the syrinx (Fig. 1). Syringes were obtained from dissected study specimens, stained with iodine, and analyzed in stereoscopic microscopes using the 20-60X objectives. Because syringeal material of *E. haematonota* was unavailable, we examined material of its close relative *E. spodionota* (Sclater & Salvin), and used the observed state as representative of the genus *Epinecrophylla* in the ancestral state reconstructions. Additional data were obtained from Bornschein *et al.* (1995) and Gonzaga (2001). Because syringeal data were unavailable for some species included in the phylogenetic analyses, we used a smaller subset of species to reconstruct ancestral character states of the Mm. v. ventralis in the Thamnophilidae. Ancestral character states were reconstructed using unordered parsimony and maximum-likelihood under an Mk1 model (Lewis, 2001) in Mesquite 2.75 (Madison & Madison, 2011). We used the default settings of Mesquite to allow states to be parsimoniously placed at each node (most parsimonious reconstructions set; see Swofford & Maddison, 1987; Maddison & Maddison, 2000) instead of attempting to resolve ambiguous nodes via optimization criteria.

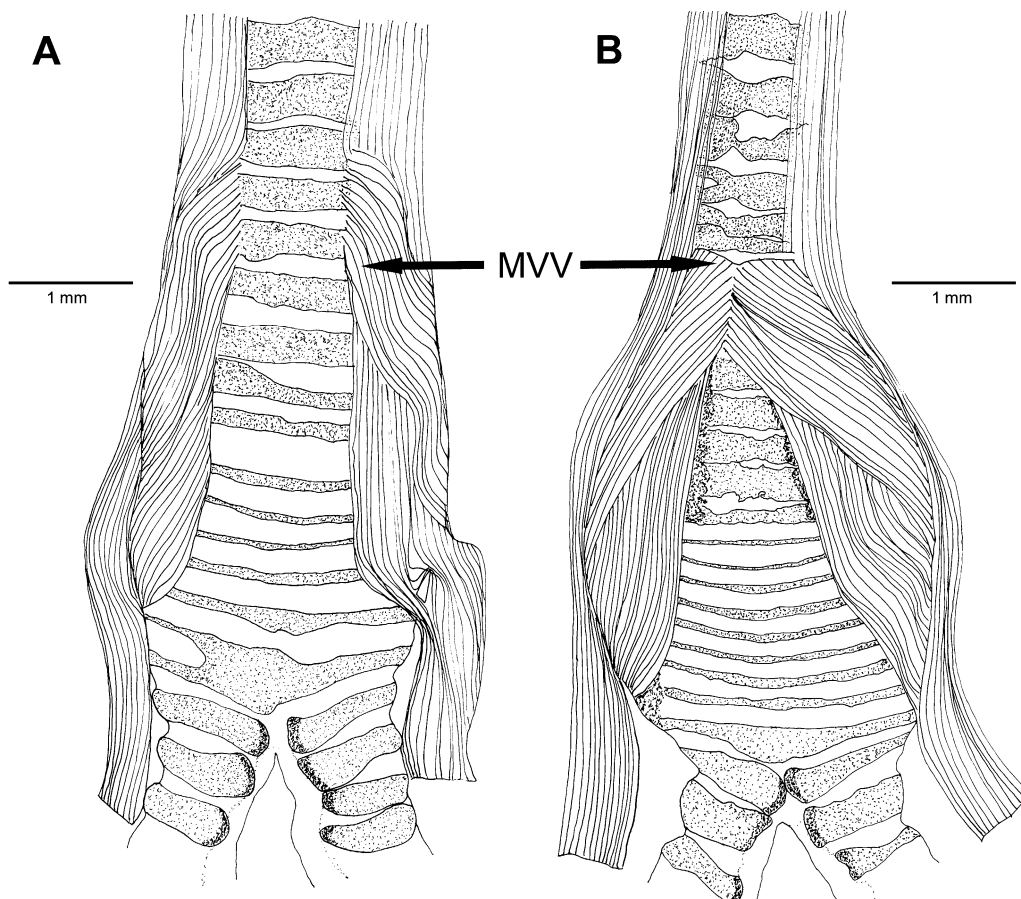


FIGURE 1. Different conditions of the Musculus vocalis ventralis (MVV) found in the Thamnophilidae. A. Cranial ends of the Mm. v. ventrales separated by a large gap on the ventral side of the syrinx in *Myrmotherula axillaris* (MCP 3134); this morphology was found in other *Myrmotherula* species examined, as well as in *Epinecrophylla* and other taxa (see Fig. 5 and Appendix 2). B. Cranial ends of the Mm. v. ventrales meet on the ventral side of the syrinx of *Myrmotherula gularis* (MCP 1724), forming an arch; this morphology was found in *Iseria* and several other taxa (see Fig. 5 and Appendix 2).

Results

Molecular analyses. The maximum likelihood and Bayesian analyses (Figs. 2 and 3) confirmed that *M. gularis* is not a close relative of *Myrmotherula*, *Epinecrophylla*, or *Isleria*. As previously suggested, *Myrmotherula* belongs in the tribe Formicivorini (sensu Moyle *et al.*, 2009), *Epinecrophylla* in the tribe Microrhopiini (Moyle *et al.*, 2009), and *Isleria* and *M. gularis* in the tribe Thamnophilini (Bravo *et al.*, 2012). *M. gularis* represents a highly distinctive lineage with relatively low intraspecific variation, but some genetic structure. The phylogenetic position of *M. gularis* within the Thamnophilini remains unresolved. *Myrmotherula gularis*, *Dichrozona cincta* (Pelzeln), and *Megastictus margaritatus* (Sclater) represent genetically distinctive lineages with long branches and poorly supported phylogenetic positions. With very low support, both methods of phylogenetic analysis suggest that *M. gularis* might be sister to a clade containing the large antshrikes in the genera *Cymbilaimus* Gray, *Batara* Lesson, *Taraba* Lesson, *Hypoedaleus* Cabanis and Heine, *Mackenziaena* Chubb, and *Frederickena* Chubb. Results of the Bayesian analysis (Fig. 3) suggest, with low support, that *M. gularis* might also be sister to *Dichrozona* Ridgway, but this could be an artifact of long-branch attraction.

Morphological analysis. The PCA analysis of morphometric measurements of genera in the Thamnophilini (Fig. 4) showed that the overall body structure of *M. gularis* is distinctive within the tribe. PC1 reflected overall size variation associated primarily with tail length, and explained 91.8% of the variance. Differences in PC2 and PC3 scores had low explanatory power and are not discussed further.

The condition of the Mm. v. ventrales in *M. gularis* corresponds to the character state in which the muscles meet in the ventral surface of the syrinx, forming a continuous arch (Fig. 1B; Appendix 2). This character state was found in all tribes except for Formicivorini, which contains the genera *Myrmotherula* and *Formicivora* Swainson. The character state in which the cranial ends of the Mm. v. ventrales are separated by a large gap (Fig. 1A) is widely distributed in the analyzed subset of the Thamnophilidae.

The ancestral reconstruction of morphological states of the M. vocalis ventralis was not entirely congruent between parsimony and ML methods. The parsimony reconstruction on the Bayesian topology was mostly equivocal, whereas the ML reconstruction on the Bayesian topology was congruent with results of both methods on the ML topology. All reconstructions were congruent regarding the character condition in the ancestor of the *Myrmotherula* type-species clade. Therefore, we only present results based on the ML topology (Fig. 5). Bayesian reconstructions are available upon request.

Both reconstructions under the ML topology recovered the condition in which the cranial ends of the Mm. v. ventrales are separated by a large gap as the most likely plesiomorphic condition in the family. The condition in which the Mm. v. ventrales forms a continuous arch is homoplastic, having evolved at least five times independently. Reconstructions by unordered parsimony and maximum likelihood produced concordant results regarding the ancestral state of Mm. v. ventrales in the tribe Formicivorini (Fig. 1A, Fig. 5). *Myrmotherula* species exhibited a Mm. v. ventrales separated by a large gap (Fig. 1A) and differed from the observed character state in *M. gularis* (Fig. 1B).

Discussion

Molecular and morphological analyses showed that *M. gularis* is not a close relative of other *Myrmotherula* (including the assemblage that contains the type species), *Epinecrophylla*, or *Isleria*, providing support for previous findings that *Myrmotherula sensu lato* is polyphyletic (Hackett & Rosenberg, 1990; Gonzaga, 2001; Irestedt *et al.*, 2004; Isler *et al.*, 2006; Brumfield *et al.*, 2007; Gomez *et al.*, 2010; Bravo *et al.*, 2012). Because the closest relatives of *M. gularis* remain uncertain, merging this taxon with any other genus would potentially violate the principle of monophyly. Given the high levels of ecological and phenotypic divergence between *M. gularis* and its putative closest relatives, it would also create an exceptionally heterogeneous taxon (see below). Therefore, we consider that *M. gularis* must be placed in a monotypic genus. The following name has priority (see Cory & Hellmayr, 1924) and is resurrected for this taxon:

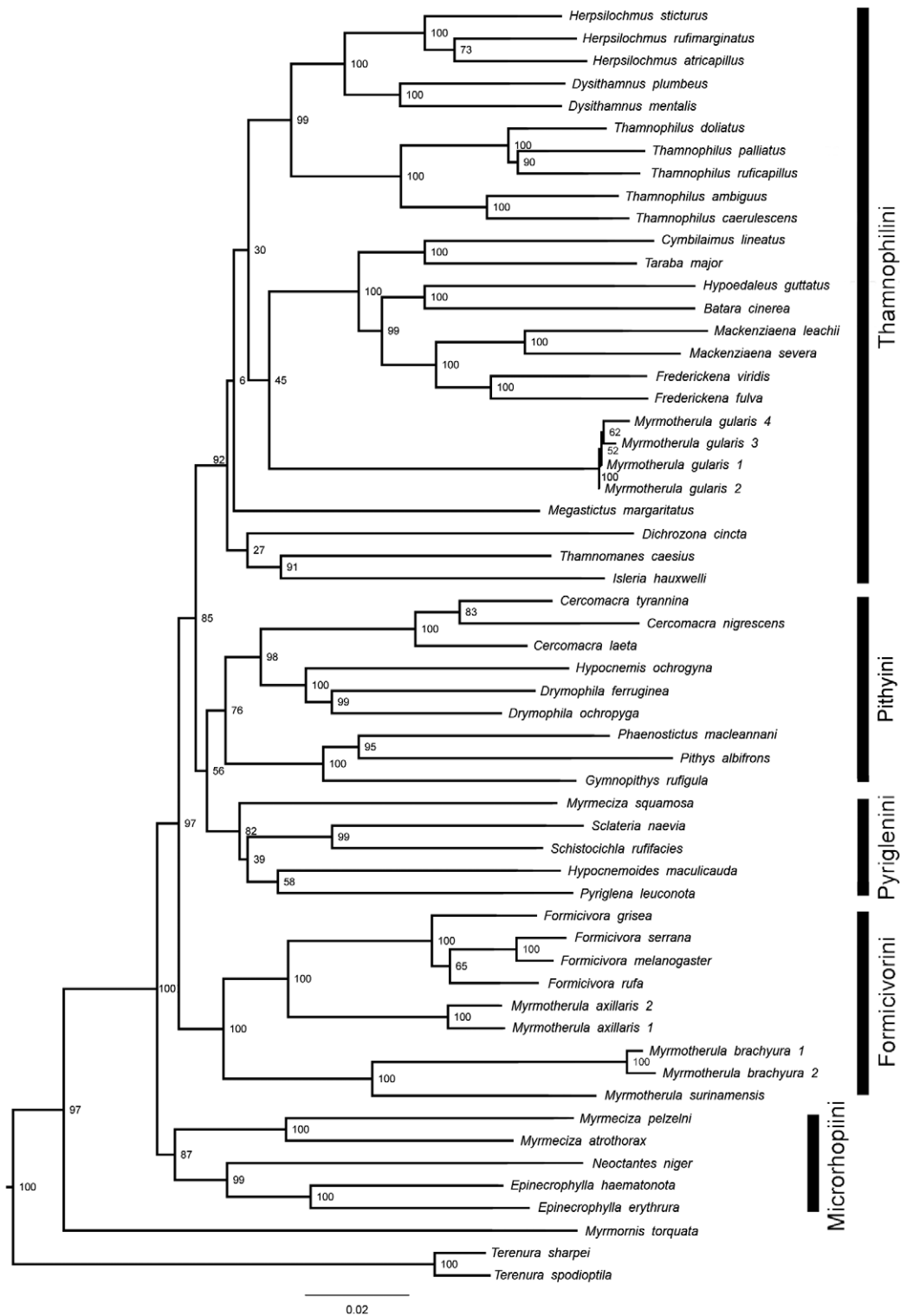


FIGURE 2. Maximum-likelihood phylogeny of a subset of the Thamnophilidae showing that *M. gularis* is not closely related to *Myrmotherula*, *Epinecrophylla*, or *Iseria*. Numbers at each node indicate bootstrap support based on 1000 maximum likelihood replicates.

Rhopias Cabanis and Heine, 1859–1860

Type-species: *Thamnophilus gularis* Spix, 1825

Type-locality: Rio de Janeiro (designated by Cory & Hellmayr, 1924)

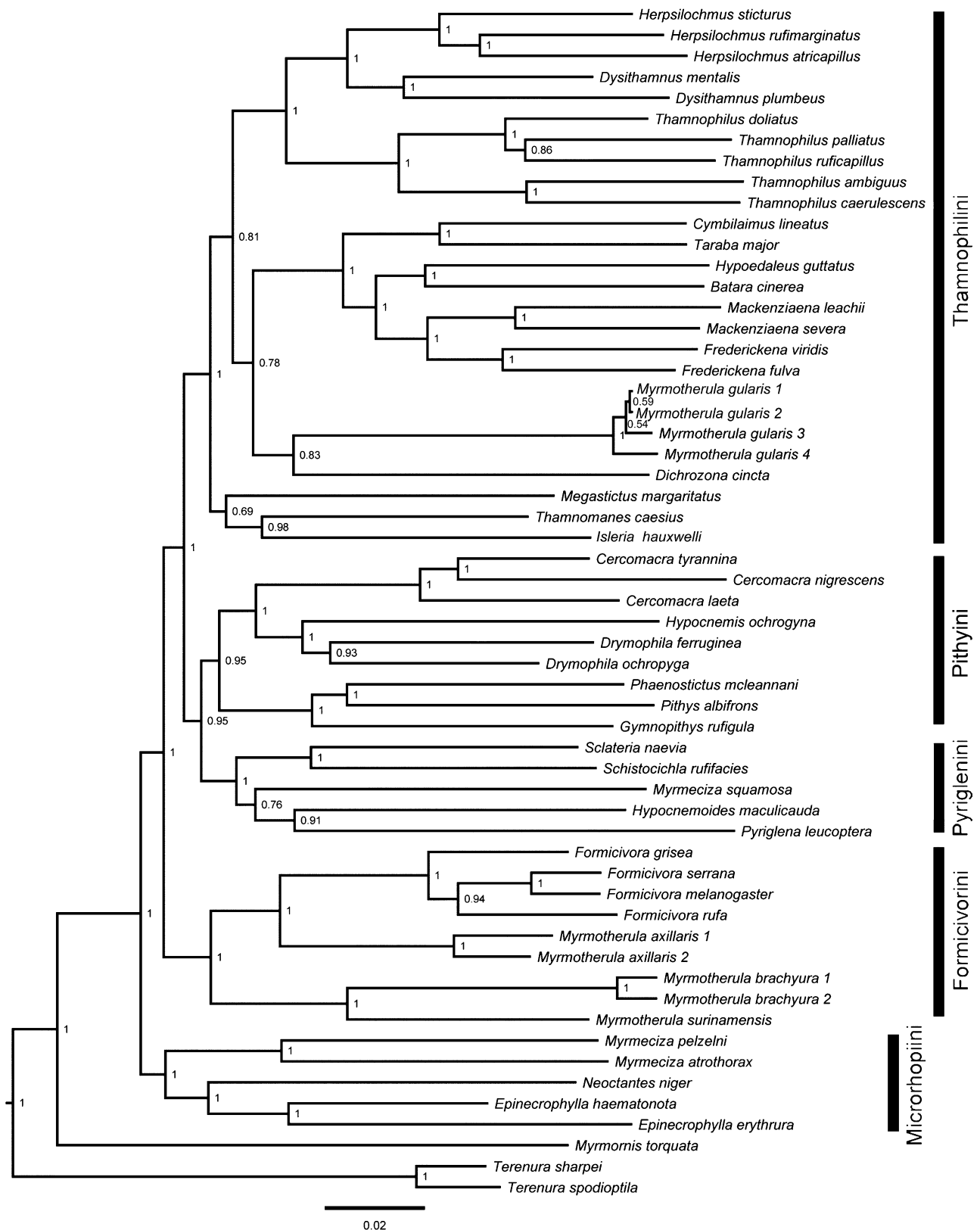


FIGURE 3. 50% Majority-rule Bayesian consensus tree of a subset of the Thamnophilidae showing that *M. gularis* is not closely related to *Myrmotherula*, *Epinecrophylla*, or *Isleria*. Numbers at each node indicate posterior probability values.

Included species: *Rhopias gularis* (Spix, 1825)

Diagnosis: Small thamnophilid, member of the tribe Thamnophilini (sensu Moyle *et al.* 2009) as indicated by phylogenetic inference based on molecular data. Measures 8.5–9.5 cm and weighs 10–13 g, with short tail (51.8%

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of wing length) and relatively long tarsi (38.1% of wing length). *Rhopias* has a tracheophone syrinx, with the cranial ends of the Mm. v. ventrales meeting in the ventral surface of the syrinx and forming a continuous arch. This condition of the M. vocalis ventralis diagnoses the genus from all species currently placed in *Myrmotherula* and other species in the tribe Formicivorini, all of which have the cranial ends of the Mm. v. ventrales separated by a large gap on the ventral side of the syrinx. *Rhopias* can be diagnosed from the clade of the large antshrikes and the other genera in the Thamnophilini (except for *Dichrozona* and *Iseria*) by its shorter tail and longer tarsi in relation to wing length. *Rhopias* can be diagnosed from *Iseria* by its relatively longer tail (45.5% of wing length in *Iseria*), and from *Dichrozona* by its smaller wings, relatively longer tail (41% of wing length in *Dichrozona*), and by its condition of the M. vocalis ventralis.

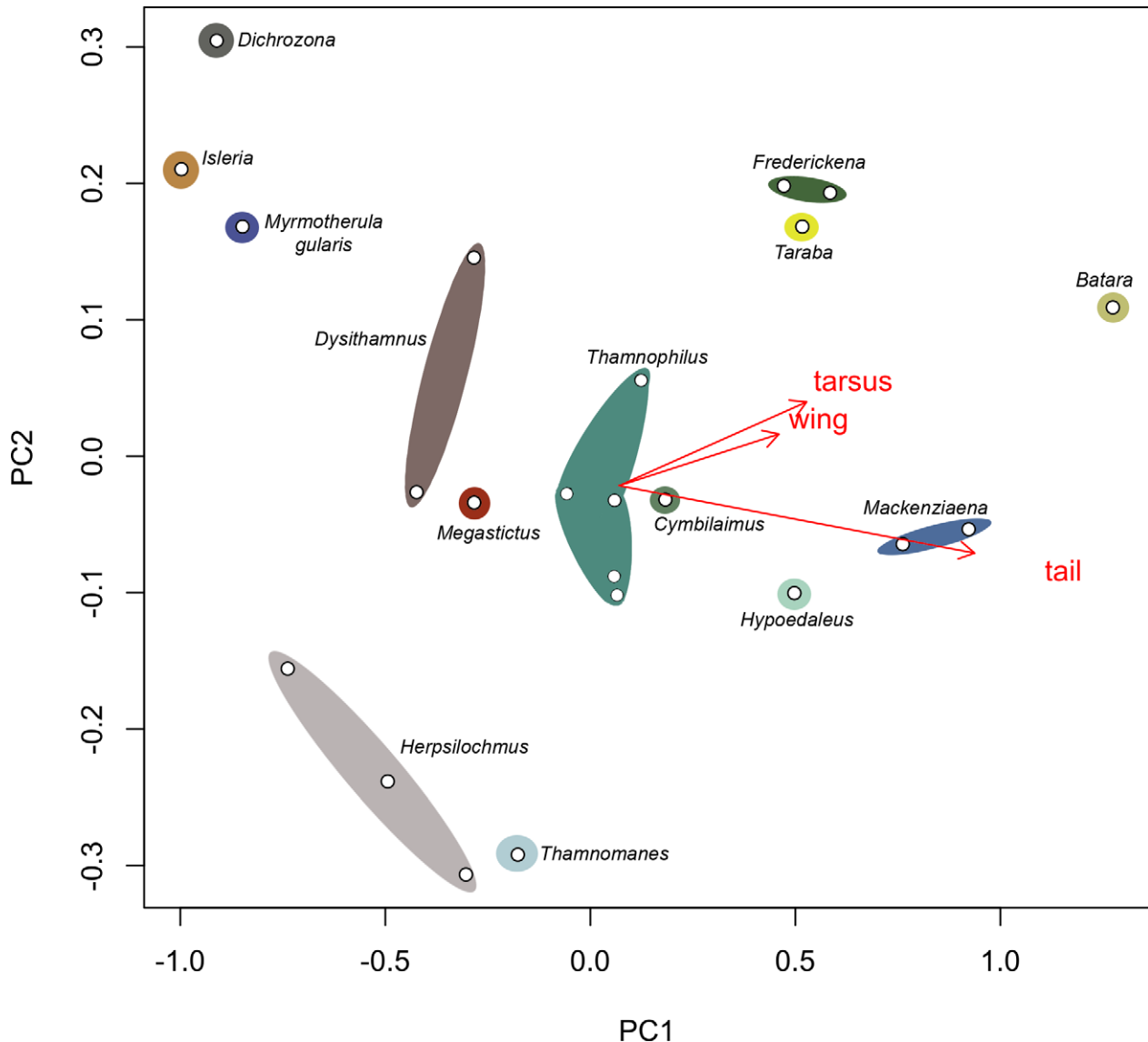


FIGURE 4. PCA analysis of wing, tail, and tarsus length for the genera of the tribe Thamnophilini.

Rhopias gularis, the only species of the genus, has reduced sexual dimorphism: both sexes have gray underparts and rufescent brown upperparts, lower flanks, and crissum. Both sexes present a forehead grizzled with gray, black throat with white spots (spots larger in the female), wing-coverts blackish with buff tips forming two wing-bars, and a white (males) or a buff (females) patch on the leading edge of the wing at the wrist. *Rhopias* differs from the clade containing *M. brachyura* (streaked antwren assemblage), the clade containing *M. axillaris* (grey antwren assemblage), and the clade containing *M. unicolor* (plain-winged *Myrmotherula* group) (sensu Zimmer & Isler, 2003) by having a stippled black-throat with unstreaked brown and grey plumage instead of streaked, mostly grey, or plain-winged plumage pattern, and also by a smaller bill and tail (see Cory & Hellmayr,

1924). *Rhopias* can be diagnosed from *Isleria* by the absence, in both sexes, of conspicuous white or buff markings on tertiary feathers (Bravo *et al.*, 2012). Plumage features are shared in *Rhopias* and *Epinecrophylla*, but *Rhopias* has a considerably shorter tail, and species in the two genera exhibit consistent ecological differences (Isler *et al.*, 2006; see below). *Rhopias* can also be diagnosed from *Epinecrophylla* by its Mm. v. ventrales, which forms a continuous arch rather than being separated by a large gap, and by its dark-colored iris (black or dark brown), which differs from the more light-colored irides found in *Epinecrophylla*.

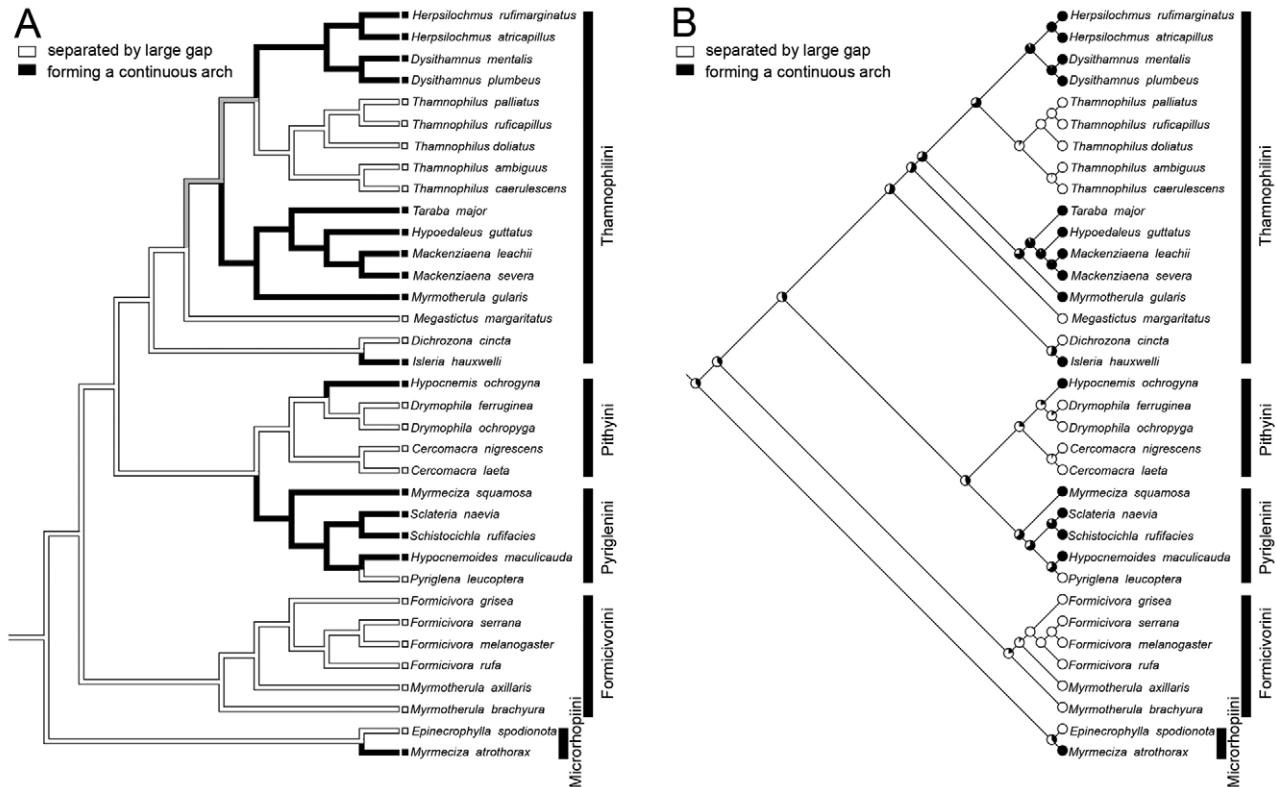


FIGURE 5. Reconstructions of character states of the *Musculus vocalis ventralis* in a reduced subset of the family Thamnophilidae derived from the phylogenetic analyses (see Fig. 2 and 3). A. Unordered parsimony reconstruction, gray color indicates equivocal ancestral states under the most parsimonious reconstructions set. B. Maximum likelihood reconstruction.

Distribution and ecology. *Rhopias gularis* is endemic to the Atlantic Forest of eastern Brazil, where it occurs from sea level to 1550 m, primarily above 300 m (Zimmer & Isler, 2003) although in the southernmost Brazilian states the species is common below this altitude (MRB unpub. data). It occurs from the southern coast of the state of Bahia to the northeastern part of the state of Rio Grande do Sul, Brazil; it also extends westward into the state of Paraná (Sick, 1997; Zimmer & Isler, 2003). It is not sympatric with any species of *Epinecrophylla* or *Isleria*.

Rhopias gularis is commonly found in pairs or small family groups. The species favors tangles and dense vegetation, especially shaded ravines in mountainous areas and sluggish streams in the lowlands (Ridgely & Tudor, 1994; Zimmer & Isler, 2003). It tends to forage near the ground away from mixed-species flocks, in contrast to many species of *Myrmotherula* and *Epinecrophylla* (e.g., Skutch, 1946, 1969; Pearson, 1977; Munn & Terborgh, 1979; Stotz, 1990; Whitney, 1994; Stotz *et al.*, 1996; Sick, 1997; Develey & Peres, 2000; Develey & Stouffer, 2001). The vocal repertoire of *Rhopias* does not include the song type used in ritualized confrontations of *Epinecrophylla* (Isler *et al.*, 2006).

The nest of *R. gularis* is briefly described as cup-shaped and is supported from below or placed on a branch fork (Zimmer & Isler, 2003). It is not clear whether it differs from nests constructed by members of the streaked-antwren group (including *M. brachyura*), which have pouch or deep cup nests (Zimmer & Isler, 2003; Isler *et al.*, 2006). However, it differs from the nests of *Epinecrophylla*, which are domed or oven shaped with oblique or side entrances (Sick, 1997; Isler *et al.*, 2006). The nest of *R. gularis* resembles those of *Isleria* and those of some members of the gray assemblage (Zimmer & Isler, 2003), although some species of the latter group apparently construct open cup nests attached at rim (Sick, 1997).

TABLE 1. Ingroup taxa used in this study and their respective tissue collection catalog number. Tissue collections: AMNH—American Museum of Natural History, New York City; FMNH—Field Museum of Natural History, Chicago; KU—The University of Kansas Natural History Museum, Lawrence; LSUMZ—Louisiana State University Museum of Natural Science, Baton Rouge; MCP—Coleção de Ornitologia do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MZUSP—Museu de Zoologia Universidade de São Paulo, São Paulo; USNM—United States National Museum of Natural History—Smithsonian Institution, Washington; UWBM—University of Washington Burke Museum, Seattle.

Species	Subspecies	Country and political subregion	Museum	Tissue No.
<i>Cymbilaimus lineatus</i>	<i>intermedius</i>	Bolivia: Santa Cruz	LSUMZ	B-18168
<i>Hypodaleus guttatus</i>	<i>guttatus</i>	Argentina: Misiones	UWBM	DHB1805
<i>Batara cinerea</i>	<i>argentina</i>	Bolivia: Santa Cruz	UWBM	RTB520
<i>Mackenziaena leachii</i>	monotypic	Argentina: Misiones	USNM	B-5986
<i>Mackenziaena severa</i>	monotypic	Paraguay: Itapúa	KU	3729
<i>Frederickena viridis</i>	monotypic	Guyana: Barima-Waini	USNM	B-9259
<i>Frederickena fulva</i>	monotypic	Peru: Loreto	LSUMZ	B-4281
<i>Taraba major</i>	<i>melanurus</i>	Peru: Madre de Dios	FMNH	321773
<i>Thamnophilus doliatus</i>	<i>radiatus</i>	Bolivia: Santa Cruz	UWBM	RTB390
<i>Thamnophilus palliatus</i>	<i>puncticeps</i>	Bolivia: Santa Cruz	UWBM	MAB2
<i>Thamnophilus ambiguus</i>	monotypic	Brazil: Bahia	LSUMZ	B-35569
<i>Thamnophilus caerulescens</i>	<i>caerulescens</i>	Brazil: São Paulo	FMNH	395426
<i>Thamnophilus ruficapillus</i>	<i>cochabambae</i>	Bolivia: Santa Cruz	UWBM	RTB347
<i>Megastictus margaritatus</i>	monotypic	Peru: Loreto	LSUMZ	B-6836
<i>Neotantes niger</i>	monotypic	Peru: Cuzco	FMNH	321806
<i>Dysithamnus mentalis</i>	<i>emiliae</i>	Brazil: Pernambuco	FMNH	392443
<i>Dysithamnus plumbeus</i>	monotypic	Brazil: Bahia	MZUSP	BA192
<i>Thamnomanes caesioides</i>	<i>glaucus</i>	Guyana: Barima-Waini	USNM	B-9482
<i>Epinecrophylla haematonota</i>	<i>haematonota</i>	Peru: Loreto	LSUMZ	B-4579
<i>Epinecrophylla erythrura</i>	<i>septentrionalis</i>	Peru: San Martín	LSUMZ	B-5474
<i>Myrmotherula brachyura</i>	monotypic	Brazil: Amazonas	LSUMZ	B-20305
<i>Myrmotherula brachyura</i>	monotypic	Peru: Loreto	LSUMZ	B-4889
<i>Myrmotherula surinamensis</i>	monotypic	Guyana: Upper Takutu-Upper Essequibo	USNM	B-11838
<i>Isleria hauxwelli</i>	<i>suffusa</i>	Peru: Loreto	LSUMZ	B-4270
<i>Myrmotherula gularis</i>	monotypic	Brazil: São Paulo	LSUMZ	B-16938
<i>Myrmotherula gularis</i>	monotypic	Brazil: São Paulo	FMNH	330815
<i>Myrmotherula gularis</i>	monotypic	Brazil: Bahia	MCP	1724
<i>Myrmotherula gularis</i>	monotypic	Brazil: Paraná	MCP	1726
<i>Myrmotherula axillaris</i>	<i>luctuosa</i>	Brazil: Pernambuco	FMNH	392444
<i>Myrmotherula axillaris</i>	<i>axillaris</i>	Suriname: Sipaliwini District	LSUMZ	B-55209
<i>Dichrozona cincta</i>	monotypic	Bolivia: La Paz	FMNH	391144
<i>Herpsilochmus atricapillus</i>	monotypic	Bolivia: Santa Cruz	LSUMZ	B-6632
<i>Herpsilochmus sticturus</i>	monotypic	Guyana: Cuyuni-Mazaruni	USNM	B-5228
<i>Herpsilochmus rufimarginatus</i>	<i>frater</i>	Venezuela: Bolívar	FMNH	339650
<i>Formicivora grisea</i>	<i>grisea</i>	Bolivia: Santa Cruz	LSUMZ	B-15217
<i>Formicivora serrana</i>	<i>serrana</i>	Brazil: Minas Gerais	MZUSP	85431
<i>Formicivora melanogaster</i>	<i>melanogaster</i>	Bolivia: Santa Cruz	LSUMZ	B-6675
<i>Formicivora rufa</i>	<i>chapmani</i>	Brazil: Amapá	FMNH	391399
<i>Drymophila ferruginea</i>	monotypic	Brazil: São Paulo	LSUMZ	B-37217
<i>Drymophila ochropyga</i>	monotypic	Brazil: Rio de Janeiro	LSUMZ	B-37221
<i>Hypocnemis ochrogyna</i>	monotypic	Bolivia: Santa Cruz	LSUMZ	B-15122
<i>Terenura sharpei</i>	monotypic	Bolivia: Cochabamba	LSUMZ	B-39086
<i>Terenura spodioptila</i>	<i>spodioptila</i>	Guyana: Cuyuni-Mazaruni	USNM	B-5113
<i>Cercomacra tyrannina</i>	<i>tyrannina</i>	Panama: Darién	LSUMZ	B-2273
<i>Cercomacra laeta</i>	<i>sabinoi</i>	Brazil: Pernambuco	FMNH	392376
<i>Cercomacra nigrescens</i>	<i>approximans</i>	Brazil: Rondônia	FMNH	389848
<i>Pyriglena leucoptera</i>	monotypic	Paraguay: Caaguazú	LSUMZ	B-25922
<i>Hypocnemoides maculicauda</i>	monotypic	Bolivia: Santa Cruz	LSUMZ	B-12660
<i>Sclateria naevia</i>	<i>naevia</i>	Brazil: Amapá	FMNH	391418
<i>Schistocichla rufifacies</i>	monotypic	Brazil: Rondônia	FMNH	389929
<i>Myrmeciza squamosa</i>	monotypic	Brazil: São Paulo	LSUMZ	B-16940
<i>Myrmeciza pelzelni</i>	monotypic	Venezuela: Amazonas	LSUMZ	B-7523
<i>Myrmeciza atrothorax</i>	<i>obscurata</i>	Perú: Madre de Dios	FMNH	322209
<i>Myrmornis torquata</i>	<i>torquata</i>	Brazil: Rondônia	FMNH	389880
<i>Pithys albifrons</i>	<i>albifrons</i>	Brazil: Amapá	FMNH	391430
<i>Gymnopathys rufigula</i>	<i>pallidus</i>	Venezuela: Amazonas	LSUMZ	B-7512
<i>Phaenostictus mcleannani</i>	<i>mcleannani</i>	Panama: Darién	LSUMZ	B-2135

Phylogenetic affinities. Cabanis and Heine (1859–1860) suggested the inclusion of the species now classified as *Epinecrophylla haematonota*, *E. ornata*, *Isleria guttata*, and *I. hauxwelli* in the genus *Rhopias*. None of our results or those from other studies (Isler *et al.*, 2006; Bravo *et al.*, 2012) support the placement of any of these species with *Rhopias*; despite high degrees of phenotypic similarity, our results showed that these species are not closely related to *R. gularis*. Although our molecular results show that *Rhopias* does not belong in the same tribe as *Myrmotherula*, its placement in the Thamnophilini was unexpected. The shared syrinx morphology between *Rhopias* and the large thamnophilid antshrikes, as well as other genera such as *Herpsilochmus* and *Dysithamnus*, also supports the placement of *Rhopias* in the tribe. Further studies are needed to unravel the phylogenetic affinities of *Rhopias* within the Thamnophilini.

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APPENDIX 1.

List of measured specimens and voucher numbers. Skin collections: Louisiana State University Museum of Natural Science—LSUMZ; Museu de Zoologia da Universidade de São Paulo—MZUSP; Museu Paraense Emílio Goeldi—MPEG.

Cymbilaimus lineatus (LSUMZ 67236; 164137; 109816; 119691); *Hypoedaleus guttatus* (LSUMZ 69110; 101779; MZUSP 6359; 28289); *Batara cinerea* (LSUMZ 68019; 68255; 153725; MZUSP 34022); *Mackenziaena leachii* (LSUMZ 62957; MZUSP 31034; 34351; 36446); *Mackenziaena severa* (LSUMZ 71406; MZUSP 24126; 70194; 75666); *Frederickena fulva* (LSUMZ 70899; 109823; 115168); *Frederickena viridis* (LSUMZ 165707; 178432; MPEG 59490; 65409); *Taraba major* (LSUMZ 124101; 124106; 156455; 177725); *Thamnophilus ruficapillus* (LSUMZ 65169; 98320; 169877; MPEG 27603); *Thamnophilus palliatus* (LSUMZ 37679; 162662; 179658; MPEG 60367); *Thamnophilus ambiguus* (LSUMZ 70441; MZUSP 2838; 28281; 28284); *Thamnophilus caerulescens* (LSUMZ 74065; 124145; MPEG 47255; 87013); *Thamnophilus doliatus* (LSUMZ 11403; 116220; 124115; 127131; 175398; 178080); *Dysithamnus plumbeus* (MZUSP 25086; 33379; 34538; 37863); *Dysithamnus mentalis* (LSUMZ 27196; 92348; 104686; 128508; 175404; 179012; MZUSP 75515); *Herpsilochmus atricapillus* (LSUMZ 124185; MZUSP 31766; 83300; 84393); *Herpsilochmus rufimarginatus* (LSUMZ 68025; 153373; MZUSP 25652; 73351; 76222); *Herpsilochmus sticturus* (LSUMZ 128512; MPEG 64995; 64996; 65432); *Myrmotherula gularis* (LSUMZ 52761; MZUSP 81160; 81489; 81490); *Dichrozona cincta* (LSUMZ 115337; 132757; MPEG 52512; 52861); *Iseria hauxwelli* (LSUMZ 84823; 109924; 109926; 161753); *Megastictus margaritatus* (LSUMZ 109854; 115200; 115202; 115203); *Thamnomanes caesius* (LSUMZ 109866; 109882; 153350; 153352).

Appendix 2. Specimens examined for morphology of the *Musculus vocalis ventralis*. Source column indicates literature reference or voucher number from examined specimens. When more than one uncatalogued specimen was examined the number of individuals is indicated in parenthesis. Museum Collections: LSUMZ – Louisiana State University Museum of Natural Science; MCP – Coleção de Ornitologia do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul; MHNCI – Museu de História Natural “Capão da Imbuia”; MZUSP – Museu de Zoologia da Universidade de São Paulo; MPEG – Museu Paraense Emílio Goeldi.

Species	Source	Country and political subregion	<i>Musculi vocales</i>	
			<i>ventrales</i> separated	continuous
<i>Hypoedaleus guttatus</i>	MCP 3127, MCP 3130, MCP uncatalogued	Brazil: Bahia, Paraná, Santa Catarina		x
<i>Mackenziaena severa</i>	MCP 2553, MCP uncatalogued	Brazil: Paraná		x
<i>Mackenziaena leachii</i>	MCP uncatalogued	Brazil: Rio Grande do Sul		x
<i>Taraba major</i>	MCP 2620	Brazil: Rondônia		x
<i>Sakesphorus cristatus</i>	MCP 3134	Brazil: Bahia	x	
<i>Thamnophilus doliatus</i>	MCP uncatalogued (3)	Brazil: Paraná	x	
<i>Thamnophilus ruficapillus</i>	MCP uncatalogued	Brazil: Rio Grande do Sul	x	
<i>Thamnophilus torquatus</i>	MCP uncatalogued	Brazil: Bahia	x	
<i>Thamnophilus palliatus</i>	Gonzaga (2001)	Brazil: Rio de Janeiro	x	
<i>Thamnophilus schistaceus</i>	MCP 3168	Brazil: Rondônia	x	
<i>Thamnophilus pelzelni</i>	MCP uncatalogued	Brazil: Paraná	x	
<i>Thamnophilus ambiguus</i>	Gonzaga (2001)	Brazil: Rio de Janeiro	x	
<i>Thamnophilus caeruleus</i>	MCP uncatalogued (2)	Brazil: Paraná, Rio Grande do Sul	x	
<i>Thamnophilus amazonicus</i>	MCP uncatalogued	Brazil: Rondônia	x	

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Species	Source	Country and political subregion	<i>Musculi vocales</i>	
			separated	continuous
<i>Megastictus margaritatus</i>	LSUMZ 114428	Peru: Loreto	x	
<i>Dysithamnus stictothorax</i>	MCP 3149	Brazil: Paraná		x
<i>Dysithamnus mentalis</i>	MCP 2577	Brazil: Santa Catarina		x
<i>Dysithamnus xanthopterus</i>	MCP 3164	Brazil: Paraná		x
<i>Dysithamnus plumbeus</i>	MCP 3131, MCP 3132	Brazil: Bahia		x
<i>Isleria hauxwelli</i>	LSUMZ 117911	Ecuador: Pastaza		x
<i>Pygoptila stellaris</i>	MCP 2148	Brazil: Rondônia	x	
<i>Epinecrophylla spodionota</i>	LSUMZ 83751	Peru: San Martín	x	
<i>Myrmotherula brachyura</i>	Gonzaga (2001)	Brazil: Roraima	x	
<i>Myrmotherula gularis</i>	MCP 1724, MCP 1725, MCP 1726, MCP 1727, Gonzaga (2001)	Brazil: Bahia, Rio de Janeiro, Paraná		x
<i>Myrmotherula axillaris</i>	MCP 3134, MCP 3139, MCP 3159, Gonzaga (2001)	Brazil: Rondônia, Maranhão, Bahia, Rio de Janeiro	x	
<i>Myrmotherula minor</i>	MCP 3155	Brazil: Bahia	x	
<i>Myrmotherula longipennis</i>	Gonzaga (2001)	Brazil: Maranhão	x	
<i>Myrmotherula urosticta</i>	MCP 3153	Brazil: Bahia	x	
<i>Myrmotherula unicolor</i>	MCP 2506, MCP 3150, MCP uncatalogued	Brazil: Paraná, Santa Catarina	x	
<i>Myrmotherula menetriesii</i>	Gonzaga (2001)	Brazil: Pará, Maranhão	x	
<i>Dichrozona cincta</i>	LSUMZ 114441	Peru: Loreto	x	
<i>Myrmorchilus strigilatus</i>	MCP 3161	Brazil: Bahia		x

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Species	Source	Country and political subregion	<i>Musculi vocales</i>	
			separated	continuous
<i>Herpsilochmus sellowi</i>	MCP 3140, MCP 3146, Gonzaga (2001)	Brazil: Bahia		x
<i>Herpsilochmus pileatus</i>	MPEG 54042, MPEG 54043, MCP uncatalogued	Brazil: Bahia		x
<i>Herpsilochmus atricapillus</i>	Gonzaga (2001)	Brazil: Bahia		x
<i>Herpsilochmus longirostris</i>	MCP uncatalogued	Brazil: Paraná		x
<i>Herpsilochmus rufimarginatus</i>	Gonzaga (2001)	Brazil: Rio de Janeiro		x
<i>Microrhopias quixensis</i>	Gonzaga (2001)	Brazil: Amazonas	x	
<i>Formicivora iheringi</i>	MCP 3142, MCP 3157, Gonzaga (2001)	Brazil: Bahia	x	
<i>Formicivora erythronotos</i>	Gonzaga (2001)	Brazil: Rio de Janeiro	x	
<i>Formicivora grisea</i>	Gonzaga (2001)	Brazil: Espírito Santo	x	
<i>Formicivora serrana</i>	Gonzaga (2001)	Brazil: Minas Gerais	x	
<i>Formicivora littoralis</i>	Gonzaga (2001)	Brazil: Rio de Janeiro	x	
<i>Formicivora melanogaster</i>	MCP 3158, MCP uncatalogued (2), Gonzaga (2001)	Brazil: Bahia, Minas Gerais	x	
<i>Formicivora rufa</i>	MCP 2622, Gonzaga (2001)	Brazil: Rondônia, Espírito Santo, Rio de Janeiro	x	
<i>Stymphalornis acutirostris</i>	MCP 3137, MCP 3138, MHNCI 4884, MHNCI 4885, Bornschein <i>et al.</i> (1995), Gonzaga (2001)	Brazil: Paraná	x	
<i>Stymphalornis</i> sp.	MZUSP 78789, MCP uncatalogued	Brazil: São Paulo	x	

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Species	Source	Country and political subregion	<i>Musculi vocales</i>	
			<i>ventrales</i> separated	continuous
<i>Drymophila ferruginea</i>	MCP 1710, MCP uncatalogued, Gonzaga (2001)	Brazil: Rio de Janeiro, São Paulo, Paraná	x	
<i>Drymophila genei</i>	MCP 2015	Brazil: Minas Gerais		x
<i>Drymophila ochropyga</i>	MCP 1718, Gonzaga (2001)	Brazil: Minas Gerais, Paraná	x	
<i>Drymophila malura</i>	MCP 1712, MCP 1713, MCP uncatalogued (5)	Brazil: Paraná, Santa Catarina	x ¹	x ²
<i>Drymophila squamata</i>	MCP 3141, Gonzaga (2001)	Brazil: Bahia, Rio de Janeiro, São Paulo	x	
<i>Hypocnemis ochrogyna</i>	MCP 2618, MCP 3177	Brazil: Rondônia		x
<i>Cercomacra brasiliana</i>	MCP uncatalogued (2)	Brazil: Rio de Janeiro	x	
<i>Cercomacra laeta</i>	Gonzaga (2001)	Brazil: Maranhão	x	
<i>Cercomacra nigrescens</i>	MCP 2623	Brazil: Rondônia	x	
<i>Pyriglena leucoptera</i>	MCP uncatalogued	Brazil: Rio Grande do Sul	x	
<i>Myrmoborus leucophrys</i>	MCP 2149, MCP uncatalogued	Brazil: Rondônia	x	
<i>Hypocnemoides maculicauda</i>	MCP 2614, MCP 2616	Brazil: Rondônia		x
<i>Sclateria naevia</i>	MCP 2508	Brazil: Rondônia		x
<i>Schistocichla ruffifacies</i>	MCP 3170	Brazil: Rondônia		x
<i>Myrmeciza squamosa</i>	MCP uncatalogued	Brazil: Paraná		x
<i>Myrmeciza atrothorax</i>	MCP 3175	Brazil: Rondônia		x
<i>Hylomyphylax punctulatus</i>	MCP uncatalogued	Brazil: Rondônia	x	
<i>Willisornis poecilinotus</i>	MCP 2362, MCP 2363	Brazil: Rondônia	x	

¹State observed in three individuals of *Drymophila malura*.

²State observed in two individuals of *Drymophila malura*.