



Taxonomic revision of *Myrmeciza* (Aves: Passeriformes: Thamnophilidae) into 12 genera based on phylogenetic, morphological, behavioral, and ecological data

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Abstract

A comprehensive molecular phylogeny of the family Thamnophilidae indicated that the genus *Myrmeciza* (Gray) is not monophyletic. Species currently assigned to the genus are found in three of the five tribes comprising the subfamily Thamnophilinae. Morphological, behavioral, and ecological character states of species within these tribes and their closest relatives were compared to establish generic limits. As a result of this analysis, species currently placed in *Myrmeciza* are assigned to *Myrmeciza* and eleven other genera, four of which (*Myrmelastes* Sclater, *Myrmoderus* Ridgway, *Myrmophylax* Todd, and *Sipia* Hellmayr) are resurrected, and seven of which (*Ammonastes*, *Ampelornis*, *Aprositornis*, *Hafferia*, *Inundicola*, *Poliocrania*, and *Sciaphylax*) are newly described.

Key words: antbirds, *Myrmeciza*, phylogeny, systematics, Thamnophilidae

Introduction

Historically, the 22 species currently (American Ornithologists' Union 1998, Zimmer & Isler 2003, Remsen *et al.* 2013) comprising the genus *Myrmeciza* (Gray) have been placed in a multiplicity of genera accompanied by uncertainty and controversy. Notable attempts at generic classification were made by Hellmayr in Cory and Hellmayr (1924), who consolidated the species into two genera; by Todd (1927), who placed the species in five genera, two newly described; by Zimmer (1932), who considered Todd's five genera "unsatisfactory" and recommended calling all the species *Myrmeciza*; by Peters (1951), who placed them into three of Todd's genera; and finally by Meyer de Schauensee (1970), who apparently followed Zimmer's recommendation and placed all the species into *Myrmeciza*. The decision to consolidate has since been followed by various authors (e.g. Sibley & Monroe 1990, Ridgely & Tudor 1994, Zimmer & Isler 2003) who, however, indirectly or directly expressed doubt that *Myrmeciza* represented a monophyletic group. Subsequently, polyphyly was confirmed by genetic studies (Irestedt *et al.* 2004, Brumfield *et al.* 2007, Moyle *et al.* 2009, Belmonte-Lopes *et al.* 2012), but monophyly has never been formally tested using complete taxon (species level) sampling. Therefore, our objective has been to test the monophyly of *Myrmeciza* and provide a genus-level taxonomic classification for species currently placed in this genus.

An inherent dilemma in making generic recommendations for a large number of taxa, such as currently placed in *Myrmeciza*, is whether to place species that are phenotypically very different in large genera solely on the basis of monophyly (a "broad monophyly" option) or to revive, and if needed describe, smaller morphologically, ecologically, and behaviorally distinct genera by combining phylogenetic information with other lines of information (a "focused monophyly" option). Both options have limitations with regard to their information content. Large inclusive genera (the current *Myrmeciza* is an example) may provide no insights into the relationship among species within morphologically and behaviorally distinct clades. On the other hand, basing genera on smaller clades may lead to a multitude of genera, some of which will be monotypic and therefore also provide little insight into relationships.

Because consistency is an important principle of classification at all levels, we approached the problem of defining genera with the “focused monophyly” option in mind. This option provides recognition of phylogenetic relationships, synapomorphic characters, and phenotypic distinctiveness that will best facilitate understanding and communication of relatedness of taxa among analysts, field workers and conservationists. Our procedure, therefore, is to overlay a wide variety of morphological, behavioral, and ecological characteristics on a newly completed molecular phylogeny, and then to assess the degree of differentiation and diagnosability of different clades that could be treated as genera. Historically, thamnophilid genera typically have been defined solely by morphological characters. In the last fifty years, an enormous amount of natural history knowledge has been obtained for thamnophilid taxa previously only known from specimens. Now, we can use a wide variety of morphological, behavioral, and ecological characteristics within a framework of DNA-based phylogenetic relationships to define and allocate species into genera.

Methods

Procedurally, we initially constructed a molecular phylogeny to identify those well-supported clades in which members of *Myrmeciza* are placed and then looked for distinct gaps in morphological, behavioral, and ecological characters between those clades and their close relatives. We based decisions to recognize genera on the extent of such gaps including comparisons with phenotypic differences among universally accepted thamnophilid genera. In the Results and Discussion section, we first examine, discuss, and make generic recommendations for each clade, and in a final section all the results are arrayed to test for consistency across clades and provide a reference point for replication.

Molecular analysis. To evaluate the phylogenetic relationships of *Myrmeciza* antbirds, we used a subset of a densely sampled molecular phylogeny of the Thamnophilinae containing 218 of the 224 species (Bravo 2012). We used sequences of three protein-coding 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 (*β-fibrinogen intron 5*—*βF5*; 593 bp), and two protein-coding nuclear genes (*recombination activation gene 1*—RAG1, 2,875 bp; *recombination activation gene 2*—RAG2, 1,152 bp). Taxon sampling (Table 1) for this subset includes 97 individuals representing 75 species and 32 genera (33% and 63% of the family, respectively), and two samples of all currently recognized species of *Myrmeciza* except for *Myrmeciza palliata* (Todd) ($n = 1$). Samples were unavailable for *Pyriglena atra* (Swainson), although its sister relationship to *P. leucoptera* (Vieillot) has been demonstrated elsewhere (Maldonado-Coelho 2012), and *Schistocichla caurensis*. Our samples of the type species of *Myrmeciza*, *M. longipes* (Swainson), corresponded only to subspecies *panamensis* because no tissue samples of the nominate subspecies were available to us; we assumed that the samples are suitable representatives of *Myrmeciza longipes*. The phylogeny was outgroup-rooted using sequences we generated or downloaded from GenBank: *Acanthisitta chloris* (Acanthisittidae; ROM UV RIF001/RIF002; GenBank GQ140172, AY325307), *Smithornis sharpei/capensis* (Eurylaimidae; LSUMZ B-21171; GenBank AF090340), *Tyrannetes stolzmanni* (Pipridae; AMNH DOT-2997), *Pipreola whitelyi* (Cotingidae; FMNH 339665), *Geositta poeciloptera* (Furnariidae; LSUMZ B-13968), *Furnarius rufus* (Furnariidae; AMNH DOT-10431), *Dendrocolaptes sanctithomae* (Furnariidae; AMNH DOT-3689), *Chamaeza campanisona* (Formicariidae; UWBM KGB14), *Liosceles thoracicus* (Rhinocryptidae; FMNH 390080), *Hyllopezus berlepschi* (Grallariidae; FMNH 322345), *Pittasoma michleri/rufopileatum* (Conopophagidae; LSUMZ B-2285/B-11863), and *Melanopareia elegans* (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 *βF5*, and of Groth and Barrowclough (1999) and Barker *et al.* (2002) for RAG-1 and RAG-2. Each gene region was sequenced bidirectionally 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) were also used.

Analyses were conducted on a concatenated six-gene 7,057 bp alignment obtained using the program MAFFT v. 6 (Katoh *et al.* 2002). To avoid over-parameterization, we ran ML analyses for six different partition schemes under the GTR+ Γ 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 these 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.

TABLE 1. Ingroup taxa used in this study and their respective tissue collection catalog number. Tissue collections: LSUMZ—Louisiana State University Museum of Natural Science, Baton Rouge; AMNH—American Museum of Natural History, New York City; ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia; COP—Colección Ornitológica Phelps, Caracas, Venezuela; FMNH—Field Museum of Natural History, Chicago; IAvH—Instituto Alexander von Humboldt, Villa de Leyva, Colombia; INPA—Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; KU—University of Kansas Natural History Museum, Lawrence; LGEMA—Laboratório de Genética e Evolução Molecular de Aves Universidade de São Paulo, São Paulo, Brazil; MCP— Coleção de Ornitologia do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MZUSP—Museu de Zoologia Universidade de São Paulo, São Paulo, Brazil; UAM—University of Alaska Museum, Fairbanks; USNM—United States National Museum of Natural History - Smithsonian Institution, Washington; UWBM—University of Washington Burke Museum, Seattle.

Species	Subspecies	Locality	Museum	Tissue No.
<i>Cymbilaimus lineatus</i>	<i>intermedius</i>	Bolivia: Santa Cruz	LSUMZ	B-18168
<i>Hypoedaleus guttatus</i>	<i>monotypic</i>	Argentina: Misiones	UWBM	DHB1805
<i>Batara cinerea</i>	<i>argentina</i>	Bolivia: Santa Cruz	UWBM	RTB520
<i>Mackenziaena leachii</i>	<i>monotypic</i>	Argentina: Misiones	USNM	B-5986
<i>Thamnophilus doliatus</i>	<i>radiatus</i>	Bolivia: Santa Cruz	UWBM	RTB390
<i>Thamnophilus praecox</i>	<i>monotypic</i>	Ecuador: Sucumbíos	ANSP	B-3190
<i>Neotantes niger</i>	<i>monotypic</i>	Peru: Cuzco	FMNH	321806
<i>Thamnistes anabatinus</i>	<i>rufescens</i>	Peru: San Martín	LSUMZ	B-5467
<i>Dysithamnus mentalis</i>	<i>emiliae</i>	Brazil: Pernambuco	FMNH	392443
<i>Thamnomanes caesius</i>	<i>glaucus</i>	Guyana: Barima-Waini	USNM	B-9482
<i>Epinecrophylla haematonota</i>	<i>nominata</i>	Peru: Loreto	LSUMZ	B-4579
<i>Myrmotherula brachyura</i>	<i>monotypic</i>	Brazil: Amazonas	LSUMZ	B-20305
<i>Myrmotherula axillaris</i>	<i>nominata</i>	Suriname: Sipaliwini	LSUMZ	B-55209
<i>Myrmotherula menetriesii</i>	<i>nominata</i>	Bolivia: Pando	LSUMZ	B-9759
<i>Myrmorchilus strigilatus</i>	<i>nominata</i>	Brazil: Sergipe	FMNH	392862
<i>Herpsilochmus sticturus</i>	<i>monotypic</i>	Guyana: Cuyuni-Mazaruni	USNM	B-5228
<i>Microrhophias quixensis</i>	<i>albicauda</i>	Peru: Madre de Dios	FMNH	321993
<i>Drymophila ferruginea</i>	<i>monotypic</i>	Brazil: São Paulo	LSUMZ	B-37217
<i>Drymophila genei</i>	<i>monotypic</i>	Brazil: Minas Gerais	FMNH	432972
<i>Hypocnemis ochrogyna</i>	<i>monotypic</i>	Bolivia: Santa Cruz	LSUMZ	B-15122
<i>Hypocnemis striata</i>	<i>affinis</i>	Brazil: Pará	FMNH	391408
<i>Euchrepomis humeralis</i>	<i>monotypic</i>	Peru: Loreto	LSUMZ	B-7029
<i>Euchrepomis sharpei</i>	<i>monotypic</i>	Bolivia: Cochabamba	LSUMZ	B-39086
<i>Cercomacra tyrannina</i>	<i>nominata</i>	Panama: Darién	LSUMZ	B-2273
<i>Cercomacra laeta</i>	<i>sabinoi</i>	Brazil: Pernambuco	FMNH	392376
<i>Cercomacra parkeri</i>	<i>monotypic</i>	Colombia: Antioquia	IAvH	BT-4962
<i>Cercomacra nigrescens</i>	<i>approximans</i>	Brazil: Rondônia	FMNH	389848
<i>Cercomacra serva</i>	<i>hypomelaena</i>	Peru: Loreto	LSUMZ	B-27609
<i>Pyriglena leuconota</i>	<i>hellmayri</i>	Bolivia: Santa Cruz	FMNH	334469

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TABLE 1. (Continued)

Species	Subspecies	Locality	Museum	Tissue No.
<i>Pyriglena leucoptera</i>	<i>monotypic</i>	Paraguay: Caaguazú	LSUMZ	B-25922
<i>Myrmoborus leucophrys</i>	<i>nominate</i>	Bolivia: Pando	LSUMZ	B-9286
<i>Myrmoborus lugubris</i>	<i>berlepschi</i>	Peru: Loreto	LSUMZ	B-7269
<i>Myrmoborus myotherinus</i>	<i>ochrolaema</i>	Brazil: Pará	FMNH	391406
<i>Myrmoborus melanurus</i>	<i>monotypic</i>	Peru: Loreto	LSUMZ	B-43056
<i>Hypocnemoides melanopogon</i>	<i>nominate</i>	Guyana: Potaru-Siparuni	KU	1334
<i>Hypocnemoides maculicauda</i>	<i>monotypic</i>	Brazil: Rondônia	MCP	2614
<i>Gymnocichla nudiceps</i>	<i>nominate</i>	Panama: Darién	LSUMZ	B-2228
<i>Sclateria naevia</i>	<i>nominate</i>	Brazil: Amapá	FMNH	391418
<i>Percnostola rufifrons</i>	<i>jensoni</i>	Peru: Loreto	LSUMZ	B-7011
<i>Percnostola arenarum</i>	<i>ssp. nov.</i>	Peru: Loreto	LSUMZ	B-42715
<i>Percnostola lophotes</i>	<i>monotypic</i>	Bolivia: Pando	LSUMZ	B-9499
<i>Schistocichla schistacea</i>	<i>monotypic</i>	Peru: Loreto	LSUMZ	B-4686
<i>Schistocichla leucostigma</i>	<i>nominate</i>	Suriname: Sipaliwini	LSUMZ	B-55190
<i>Schistocichla humaythae</i>	<i>nominate</i>	Bolivia: Pando	LSUMZ	B-8922
<i>Schistocichla brunneiceps</i>	<i>monotypic</i>	Peru: Madre de Dios	FMNH	433483
<i>Schistocichla rufifacies</i>	<i>monotypic</i>	Brazil: Rondônia	FMNH	389929
<i>Schistocichla saturata</i>	<i>monotypic</i>	Guyana: Cuyuni-Mazaruni	KU	3895
<i>Myrmeciza longipes</i> 1	<i>panamensis</i>	Panama: Panamá	LSUMZ	B-46533
<i>Myrmeciza longipes</i> 2	<i>panamensis</i>	Panama: Panamá	LSUMZ	B-46534
<i>Myrmeciza exsul</i> 1	<i>niglarus</i>	Panama: Panamá	UAM	20240
<i>Myrmeciza exsul</i> 2	<i>occidentalis</i>	Costa Rica: Puntarenas	LSUMZ	B-16088
<i>Myrmeciza ferruginea</i> 1	<i>nominate</i>	Suriname: Sipaliwini	LSUMZ	B-55285
<i>Myrmeciza ferruginea</i> 2	<i>nominate</i>	Brazil: Amazonas	LSUMZ	B-20403
<i>Myrmeciza ruficauda</i> 1	<i>soror</i>	Brazil: Pernambuco	FMNH	392445
<i>Myrmeciza ruficauda</i> 2	<i>soror</i>	Brazil: Alagoas	FMNH	399262
<i>Myrmeciza loricata</i> 1	<i>monotypic</i>	Brazil: Minas Gerais	MZUSP	85430
<i>Myrmeciza loricata</i> 2	<i>monotypic</i>	Brazil: Minas Gerais	MZUSP	85433
<i>Myrmeciza squamosa</i> 1	<i>monotypic</i>	Brazil: São Paulo	LSUMZ	B-16940
<i>Myrmeciza squamosa</i> 2	<i>monotypic</i>	Brazil: São Paulo	LGEMA	1526
<i>Myrmeciza laemosticta</i> 1	<i>monotypic</i>	Panama: Coclé	LSUMZ	B-52919
<i>Myrmeciza laemosticta</i> 2	<i>monotypic</i>	Costa Rica: Cartago	LSUMZ	B-72189
<i>Myrmeciza palliata</i>	<i>palliata</i>	Colombia: Antioquia	IAvH	BT-8455
<i>Myrmeciza nigricauda</i> 1	<i>monotypic</i>	Ecuador: Esmeraldas	LSUMZ	B-11775
<i>Myrmeciza nigricauda</i> 2	<i>monotypic</i>	Ecuador: Esmeraldas	LSUMZ	B-11717
<i>Myrmeciza berlepschi</i> 1	<i>monotypic</i>	Ecuador: Esmeraldas	LSUMZ	B-12026
<i>Myrmeciza berlepschi</i> 2	<i>monotypic</i>	Ecuador: Esmeraldas	LSUMZ	B-29981
<i>Myrmeciza pelzelni</i> 1	<i>monotypic</i>	Venezuela: Amazonas	LSUMZ	B-7523
<i>Myrmeciza pelzelni</i> 2	<i>monotypic</i>	Colombia: Caquetá	IAvH	BT-573
<i>Myrmeciza hemimelaena</i> 1	<i>nominate</i>	Peru: Ucayali	UAM	20237
<i>Myrmeciza hemimelaena</i> 2	<i>pallens</i>	Bolivia: Santa Cruz	LSUMZ	B-18271
<i>Myrmeciza castanea</i> 1	<i>centuculorum</i>	Peru: Loreto	LSUMZ	B-42168

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TABLE 1. (Continued)

Species	Subspecies	Locality	Museum	Tissue No.
<i>Myrmeciza castanea</i> 2	<i>nominata</i>	Peru: San Martín	LSUMZ	B-44678
<i>Myrmeciza atrothorax</i> 1	<i>obscurata</i>	Peru: Madre de Dios	FMNH	322209
<i>Myrmeciza atrothorax</i> 2	<i>nominata</i>	Brazil: Roraima	INPA	A-1079
<i>Myrmeciza melanoceps</i> 1	<i>monotypic</i>	Peru: Loreto	LSUMZ	B-43013
<i>Myrmeciza melanoceps</i> 2	<i>monotypic</i>	Peru: Loreto	LSUMZ	B-42878
<i>Myrmeciza goeldii</i> 1	<i>monotypic</i>	Bolivia: Pando	LSUMZ	B-9293
<i>Myrmeciza goeldii</i> 2	<i>monotypic</i>	Peru: Madre de Dios	LSUMZ	B-21212
<i>Myrmeciza hyperythra</i> 1	<i>monotypic</i>	Peru: Loreto	LSUMZ	B-7342
<i>Myrmeciza hyperythra</i> 2	<i>monotypic</i>	Brazil: Amazonas	LSUMZ	B-35684
<i>Myrmeciza fortis</i> 1	<i>nominata</i>	Peru: Ucayali	UAM	20533
<i>Myrmeciza fortis</i> 2	<i>nominata</i>	Peru: Loreto	LSUMZ	B-4704
<i>Myrmeciza zeledoni</i> 1	<i>nominata</i>	Panama: Bocas del Toro	UAM	20534
<i>Myrmeciza zeledoni</i> 2	<i>macrorhyncha</i>	Ecuador: Esmeraldas	LSUMZ	B-12004
<i>Myrmeciza immaculata</i> 1	<i>nominata</i>	Colombia: Norte de Santander	IAvH	BT-92
<i>Myrmeciza immaculata</i> 2	<i>nominata</i>	Venezuela: Táchira	COP	JM1059
<i>Myrmeciza disjuncta</i> 1	<i>monotypic</i>	Colombia: Vichada	IAvH	BT-8017
<i>Myrmeciza disjuncta</i> 2	<i>monotypic</i>	Colombia: Vichada	IAvH	BT-8031
<i>Myrmeciza griseiceps</i> 1	<i>monotypic</i>	Peru: Tumbes	LSUMZ	B-66366
<i>Myrmeciza griseiceps</i> 2	<i>monotypic</i>	Peru: Tumbes	LSUMZ	B-66571
<i>Myrmornis torquata</i>	<i>nominata</i>	Brazil: Rondônia	FMNH	389880
<i>Pithys albifrons</i>	<i>nominata</i>	Brazil: Amapá	FMNH	391430
<i>Gymnopithys rufigula</i>	<i>pallidus</i>	Venezuela: Amazonas	LSUMZ	B-7512
<i>Hylophylax naevioides</i>	<i>nominata</i>	Panama: Darién	LSUMZ	B-2230
<i>Hylophylax naevius</i>	<i>nominata</i>	Suriname: Sipaliwini	LSUMZ	B-55298
<i>Willisornis poecilinotus</i>	<i>griseiventris</i>	Bolivia: La Paz	FMNH	391148
<i>Phaenostictus mcleannani</i>	<i>nominata</i>	Panama: Darién	LSUMZ	B-2135

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.

Morphological, behavioral, and ecological data We used two principal sources of data in the comparisons: (1) a morphometric data set assembled by GAB and supplemented by data from Zimmer and Isler (2003); and (2), plumage, behavioral, ecological, and distributional data from a compilation of information on thamnophilids (Zimmer and Isler 2003). Original sources for the data from Zimmer and Isler (2003) may be obtained from the publication; these have been supplemented by more recent sources which are cited herein. In making comparisons, we maintained phenotypically similar species in a sub-clade when the phylogeny indicated that they were sister species and branch lengths were short. Comparisons within and between clades are presented in the following format:

Phylogenetic relationships.—Describes how taxa are related to each other and defines names employed in the results.

Biogeography.—Provides as background a brief summary of distribution and spatial relationships among taxa, including an identification of geographic range overlaps.

Plumage.—Summarizes plumage characters that distinguish genera. This does not include diagnoses of individual species.

Morphometrics.—Provides original weight data and 10 ecomorphological variables representing the size and shape of the bill, wing, tail, tarsus, and feet. These were taken from museum specimens of 245 individuals of 62 species. For most species, we obtained measurements from at least two adult males and two adult females; eleven species were represented by fewer than four measured specimens (1, $n=4$; 2, $n=4$; 3, $n=3$). Measurements obtained were bill length, bill width and depth at the level of the anterior border of the nostrils, wing length to the longest primary, wing length to the tenth primary, length to the first secondary feather, tail maximum length, central rectrix maximum width, tarsus length, and hallux length. All measurements were taken with a Mitutoyo Digimatic Point Caliper by GAB and details of how they were taken can be found elsewhere (Baldwin *et al.* 1931; Derryberry *et al.* 2011). Additional weight and total length data were obtained from Zimmer and Isler (2003). “Body length” was estimated by subtracting tail length from total length. Because total length and body length are approximations, they were only used in ratios with other measurements rather than as independent characters in making generic recommendations. Ratios comparing morphological structures (e.g., wing length/total length, tail length/wing length) that have been used historically (e.g., Ridgway 1911) to define genera were then calculated for every species. Because no standard exists, we set a twenty percent differential of values obtained as a conservative yardstick of a diagnostic difference between populations.

Loudsongs.—Provides descriptions that are limited to general characteristics differentiating clades. For example, species in one clade may deliver uncountable trills of notes whereas loudsongs in another might be a countable series of distinct notes. “Countable” is defined as the human ability to count notes at normal loudsong speed.

Habitat.—Describes differences and commonalities.

Foraging behavior.—Emphasizes height above the ground, substrates searched, and attack behavior (following Remsen & Robinson 1990).

Tail and wing movements.—Identifies differences in tail movements that Willis in a series of papers (e.g. Willis 1985) concluded distinguished thamnophilid genera. These were supplemented and extended to wing movements described in Zimmer and Isler (2003).

Nest architecture.—Includes data from a recent review of *Myrmeciza* nests (Greeney *et al.* 2013).

Discussion.—Identifies and discusses treatment options on the basis of supporting evidence.

Taxonomic Recommendations.—Draws conclusions regarding the number of genera appropriate for the clade and the distribution of species among them on the basis of principles and procedures described in the following section. We describe new genera as necessary and provide new diagnoses for existing genera. English names of included species follow Remsen *et al.* (2013).

Taxonomic assessment. The obtained phylogeny of *Myrmeciza* provided the main framework for our generic recommendations. First, we identified those clades of *Myrmeciza* species that were found to violate the principle of monophyly, and hence, required further assessment of their generic placement. Next, for each of those clades, we compared the morphological, behavioral, and ecological features described above with those of their well-supported sister groups. If relationships among clades were not resolved with high support or various generic rearrangements were possible the comparison was conducted including all possible clades.

We then determined the presence or absence of diagnostic traits between clades. In addition to plumage and morphometrics, traits considered intrinsic and therefore relevant to defining genera in the Thamnophilidae included loudsongs (Baptista & Kroodsma 2001), tail and wing movements (Willis 1985), and nest architecture (Sheldon & Winkler 1999, Zyskowski & Prum 1999). If one or more of these traits differed diagnostically between a species-group and its relatives, we considered recommending generic status under the “focused monophyly” option described in the introduction. No rule is available, however, for setting how many traits need differ to recommend generic status. Consequently, we employed four considerations. First, diagnostic differences among multiple traits were considered supportive of generic distinction. Second, generic status was enhanced by strong differences within traits (e.g., multiple morphometric differences compared to one). Third, generic designation was supported if the extent of diagnostic differences was similar to distinctions between universally-accepted existing genera (e.g., between *Pyriglena* and *Percnostola*) in the major clade under study. Fourth, although not considered intrinsic, the presence of diagnostic differences in habitat and foraging behavior were deemed supportive.

In a final section, we array our recommendations to examine their consistency and provide a benchmark for replication. To provide additional perspective, genera are compared to the relative ages of clades in a time-calibrated phylogeny of the entire family that has been presented elsewhere (Bravo 2012).

Results and discussion

Molecular analysis. Maximum-likelihood (Fig. 1) and Bayesian (Fig. 2) phylogenetic trees produced identical topologies, indicating with high support that *Myrmeciza* is not monophyletic and that its members are placed in three of the five tribes of the Thamnophilidae proposed by Moyle *et al.* (2009). *Myrmeciza atrothorax* (Boddaert), *M. pelzelni* Sclater, and *M. disjuncta* Friedmann belong in the Microrhopiini, *M. hemimelaena* Sclater and *M. castanea* (Zimmer) belong in the Pithyini, and the remaining species are found in the Pyriglenini. The type species of the genus, *M. longipes*, belongs in the latter tribe and is not sister to any other member of the genus.

Morphological, behavioral, and ecological data and taxonomic assessment. Given the well-supported and substantial genetic distances among the tribes, comparisons of morphological, behavioral, and ecological character states were limited to clades within tribes in establishing generic limits of species currently placed in *Myrmeciza*. In presenting and discussing our results, we give each clade the name of a genus or species at its base.

Tribe Microrhopiini

Phylogenetic relationships.—Three species currently placed in *Myrmeciza* (*atrothorax*, *pelzelni*, and *disjuncta*) and *Myrmorchilus strigilatus* (Wied) form a well-supported clade (henceforth the *Myrmorchilus* clade) within the Microrhopiini (Figs. 1 and 2).

Biogeography.—*Myrmorchilus strigilatus* comprises two disjunct populations in NE Brazil and the Chaco of Bolivia, Paraguay, and Argentina; *disjuncta* is restricted to the upper Rio Orinoco and the upper and mid Rio Negro in Venezuela, Colombia, and Brazil; *atrothorax* is discontinuously distributed throughout Amazonia; and *pelzelni* is confined to the headwaters region of the Rio Negro and nearby locations in Colombia and Venezuela. Ranges of *disjuncta*, *atrothorax*, and *pelzelni* overlap in the upper Rio Negro region.

Plumage.—Differs substantially among all four species of the *Myrmorchilus* clade. Outstanding characters include stripes and black patches in *strigilatus*; contrasting blackish tails and gray unmarked facial pattern in *atrothorax*; plain, mostly unmarked plumage in *disjuncta*; and boldly scaled facial pattern and spotted wing coverts in *pelzelni*. No major plumage character is shared by all four species, and only a few characters by portions of the group. Unspotted tails are shared by both sexes of *disjuncta*, *atrothorax*, and *pelzelni*. Males of *strigilatus*, *pelzelni*, and *atrothorax* share a narrow black throat patch that broadens into the breast. Females of *disjuncta* and *atrothorax* share reddish-yellow-brown underparts.

Morphometrics.—Although *strigilatus* is longer and heavier compared to the three *Myrmeciza* species (Table 2), morphometric proportions are similar among the four species (Table 3), except that the long bill of *disjuncta* (bill length/total length) and the short hallux of *strigilatus* (hallux length/tarsus length) differ diagnostically.

Loudsongs.—Loudsongs of species in the *Myrmorchilus* clade have almost nothing in common, and those of *strigilatus* and *disjuncta* are unique in the Thamnophilidae. Loudsongs of *pelzelni* and *atrothorax* both consist of series of notes rising in pitch but are dissimilar in their duration, note shape, pace, and change of pace.

Habitat.—*Myrmorchilus strigilatus* occurs in deciduous woodlands and scrub, especially those with terrestrial bromeliads; *disjuncta* is found in stunted, extremely dense bushy woodland and more open bush-covered fields (*monte cerrado* in Venezuela; bushy *campina* in Brazil), both growing on sandy soils (recent additions: Borges 2004, Naka *et al.* 2006); *atrothorax* is an edge species occupying a variety of habitats from light gaps in evergreen forest to river-edge thickets and ridge tops; and *pelzelni* is found in evergreen forest growing on white sandy soils.

Foraging Behavior.—*Myrmorchilus strigilatus* forages mostly on the ground in leaf litter and terrestrial bromeliads; both *disjuncta* and *atrothorax* forage on the ground in leaf litter or near the ground on vertical perches, often shifting back and forth between ground and perches; and *pelzelni* forages almost entirely on the ground in leaf litter, occasionally sallying up to the undersides of substrates.

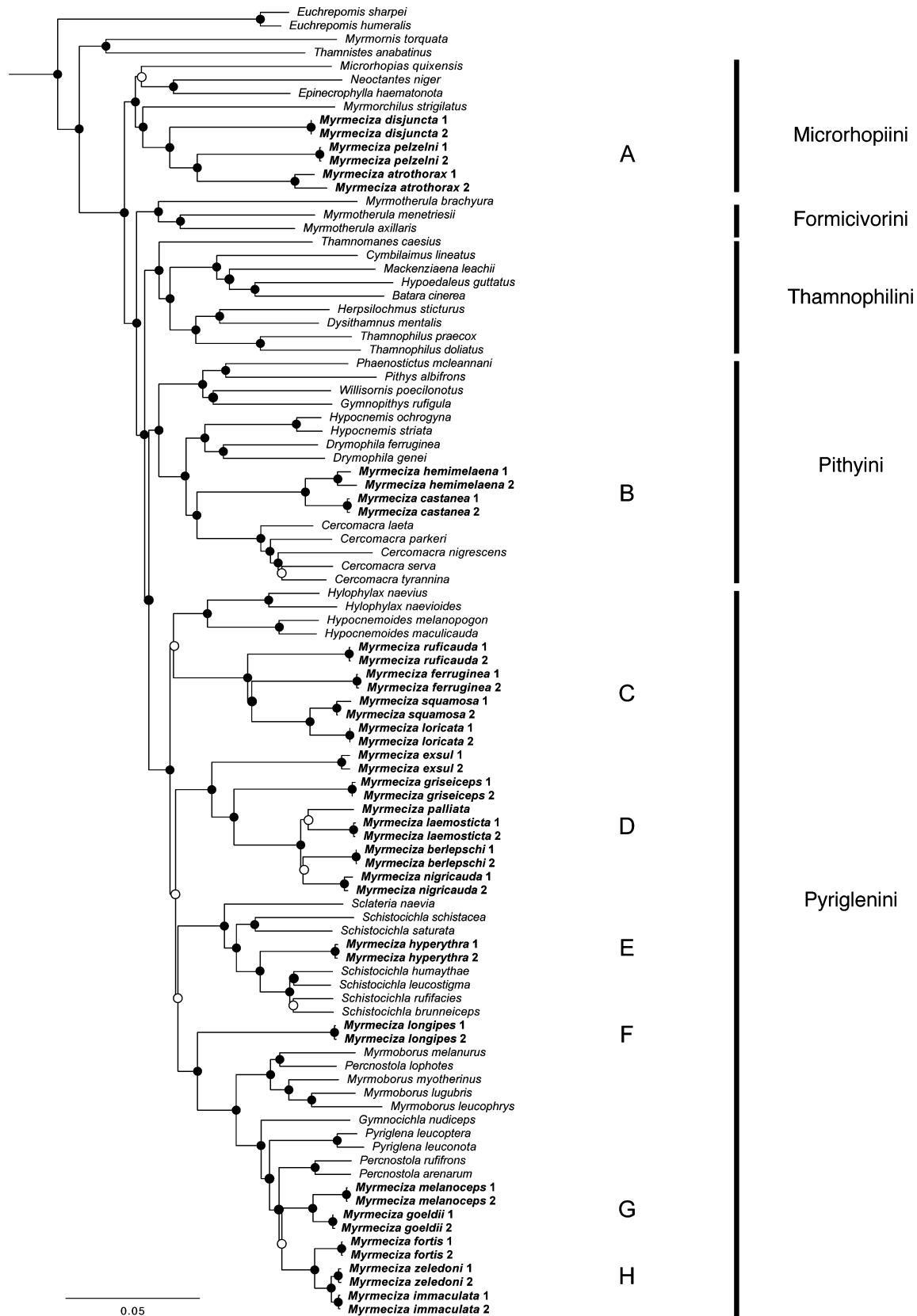


FIGURE 1. Maximum-likelihood tree of a subset of the Thamnophilinae, showing that *Myrmeciza* is polyphyletic (species names in these clades are emboldened). Members of *Myrmeciza* are placed in eight different well-supported clades in the Microrhopiini, Pithyini, and Pyrglenini. The color of the circles at nodes indicates bootstrap support values, > 70% (black), 50-70% (gray), < 50% (white).

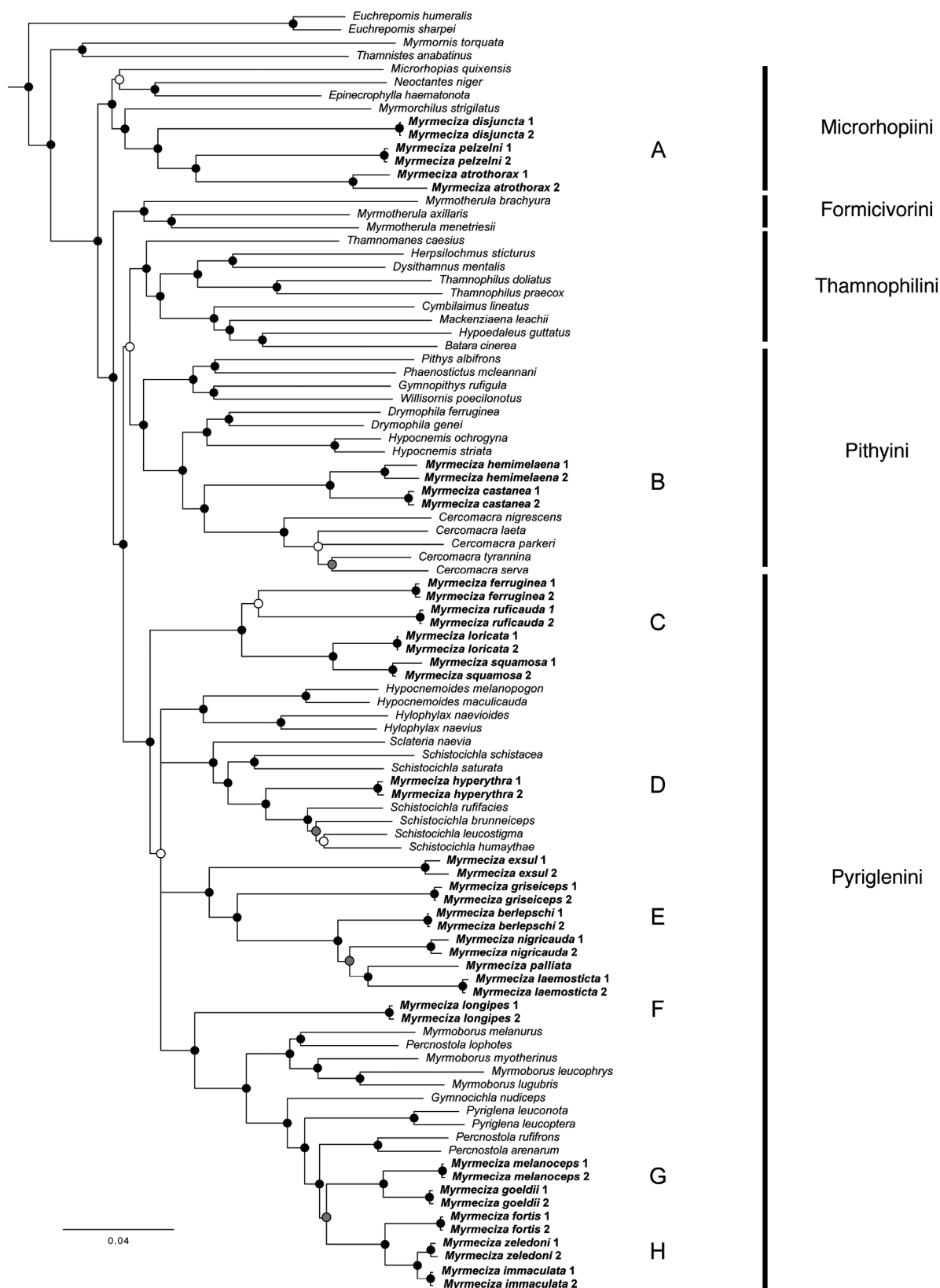


FIGURE 2. Bayesian consensus tree of a subset of the Thamnophilinae, showing that *Myrmeciza* is polyphyletic (species names in these clades are emboldened). Members of *Myrmeciza* are placed in eight different well-supported clades in the Microrhopiini, Pithyini, and Pyriglenini. The color of the circles at nodes indicates posterior probability support, > 0.95 (black), 0.95–0.75 (gray), < 0.75 (white).

Tail and wing movements.—Tail movements of *strigilatus* have been described as “swings tail over the back— frequently at an angle of 90°” (Wetmore 1926). Typically *disjuncta* flicks its tail up and down in a shallow 10° arc, but more rarely *disjuncta* lowers its tail slowly below body level and flicks it up rapidly or wags tail sideways, also flicks its wings in and out of synchrony with its tail movements. Movements of *atrothorax* and *pelzelni* appear similar and involve frequent wagging of the tail, first slowly downward and then rapidly upward, also repeated wing twitching.

Nest architecture.—The nest of *strigilatus* is a cup placed on the ground (recent addition: Lima *et al.* 2008); the only known nest of *atrothorax* was a cup built in a clump of sedge over water. Nests of *pelzelni* and *disjuncta* are unknown.

Discussion.—The question is whether the members of the *Myrmorchilus* clade should be united, placed into separate genera, or placed in two or three genera. The four species differ in almost every aspect of morphology and behavior. Virtually no plumage character unites them as reflected in their current discontinuous placement in the taxonomic sequence, nor do morphometrics provide support for uniting them. For example, near equality of wing and tail length, the principal character that Todd (1927) used to describe a genus for *atrothorax*, is only shared with *strigilatus*. The constituent species share a ground or near-ground foraging behavior, and three of the four species prefer sandy soil habitats. Otherwise, behavioral attributes of the four species are inconsistent, and in the case of their loudsongs, extremely diverse.

Taxonomic Recommendations.—Because of the extensive differences among these four species in plumage and other phenotypic attributes, we recommend that *Myrmorchilus* be maintained and that *disjuncta*, *atrothorax*, and *pelzelni* each be placed in a monotypic genus. *Myrmophylax* Todd is available as a generic name for *atrothorax*. New names are needed for *disjuncta* and *pelzelni*.

***Myrmorchilus* Ridgway, 1909**

Type species. *Myiothera strigilata* Wied, 1831.

Included species. *Myrmorchilus strigilatus* (Wied). STRIPE-BACKED ANTBIRD.

Diagnosis. Distinguished from other genera in *Myrmorchilus* clade by black streaked upperparts combined with black anterior underparts (males) or streaked black (females), black patch formed by wing coverts and bases of primaries, and black and rufous tails. Hallux short relative to tarsus length. Loudsongs structurally distinct. Tail “swings” over back unique in clade as is bromeliad-laden habitat. Ground nest differs from that of *Myrmophylax*.

***Myrmophylax* Todd, 1927**

Type species. *Formicarius atrothorax* Boddaert, 1783.

Included species. *Myrmophylax atrothorax* (Boddaert). BLACK-THROATED ANTBIRD.

Diagnosis. Distinguished from other genera in *Myrmorchilus* clade by blackish unmarked tail and gray unmarked ocular region and ear coverts (both sexes), by male dark olive brown above and dark gray below with extensively black foreparts, and by small white wing coverts spots (most subspecies). Loudsongs structurally distinct. Lowers tail slowly and flicks it up rapidly, differing from *Myrmorchilus* and *Aprositornis*. Affinity for edge habitats unique in clade. Cup nest differs from that of *Myrmorchilus*.

***Aprositornis* Isler, Bravo, and Brumfield gen. nov.**

Type species. *Myrmeciza disjuncta* Friedmann, 1945.

Included species. *Aprositornis disjuncta* (Friedmann) *comb. nov.* YAPACANA ANTBIRD.

Diagnosis. Distinguished from other genera in *Myrmorchilus* clade by relatively unmarked plumage dark gray above with a suggestion of white superciliary and white (male) or light reddish-yellow brown (female) below; small white wing covert spots (male) and interscapular patch; pinkish legs; and long bill compared to its overall length. Loudsongs structurally distinct. Tail flicking unique in clade. Impenetrable sandy soil habitat.

Etymology. The feminine generic name is taken from the Greek *aprositos* (unapproachable, hard to get at) and *ornis* (bird), referring to its preference for impassable bushy habitats, which seems to explain why it was so poorly known until recently.

***Ammonastes* Bravo, Isler, and Brumfield gen. nov.**

Type species. *Myrmeciza pelzelni* Sclater, 1890.

Included species. *Ammonastes pelzelni* (Sclater) *comb. nov.* GRAY-BELLIED ANTBIRD.

Diagnosis. Distinguished from other genera in *Myrmorchilus* clade by upperparts reddish-yellow brown, by underparts with broad black throat and breast patch (male) white edged black-edged spots (female) becoming reddish-yellow brown posteriorly, and by boldly scaled facial pattern and spotted wing coverts. Loudsongs structurally distinct. Tail lowered slowly and flicked up rapidly, differing from *Myrmorchilus* and *Aprositornis*. Forest floor habitat.

Etymology. The masculine generic name is taken from the Greek *amos* (sand) and *nastes* (inhabitant), referring to its preference for habitats growing on white sand soil.

Tribe Pithyini

Phylogenetic relationships.—In the Pithyini (Figs. 1 and 2), *Myrmeciza hemimelaena* and *M. castanea*, recently distinguished cryptic species (Isler et al 2002), form a well-supported clade (henceforth the *hemimelaena* clade) sister to the *tyrannina*-group (following Fitzpatrick & Willard 1990) of *Cercomacra*. In the following comparisons the *tyrannina* clade includes *Cercomacra tyrannina* (Sclater), *C. serva* (Sclater), *C. nigrescens* (Cabanis and Heine), *C. laeta* (Todd), and *C. parkeri* Graves.

Biogeography.—Both clades occur in Amazonia (*hemimelaena* clade primarily south of the Amazon) with populations extending into the Andes (*hemimelaena* clade to 1350 m; *tyrannina* clade to 2200 m). The *tyrannina* clade also has a trans-Andean distribution that extends into the Chocó, the Colombian inter-Andean valleys, and Middle America. Species in the two clades are sympatric principally south of the Amazon.

Plumage.—The two clades differ in a number of plumage features. Males in the *hemimelaena* clade are posteriorly chestnut, anteriorly gray above and black below extending to breast; wing coverts are mostly black with chestnut edges and broad white tips. Males in the *tyrannina* clade are gray with white interscapular patches and narrow white wing covert tips, some with narrow white tips to the rectrices. Females of the *hemimelaena* clade resemble males except that the throat and breast are reddish yellow-brown. Females of the *tyrannina* clade are mostly olive brown above, variably tinged gray or rufous, with unmarked wing coverts, and tawny buff to cinnamon below.

Morphometrics.—Species in the *hemimelaena* clade have shorter and narrower tails than those of the *tyrannina* clade (Table 2) which produce substantial differences in morphological proportions involving tail measurements (Table 3).

Loudsongs.—Both clades share two characteristics: (1) male and female loudsongs differ, and (2) loudsongs of both sexes are short (almost all <2 sec). Because of substantial variation among species within each clade, no vocal characters distinguish the clades.

Habitat.—Members of both clades primarily inhabit evergreen forest although regional populations of each appear to be restricted to various microhabitats.

Foraging behavior.—Members of the *hemimelaena* clade forage mostly <1 m off the ground, hopping deliberately while rummaging in leaf piles on the ground and picking prey off low substrates. Members of the *tyrannina* clade forage higher although mostly within 5 m of the ground; methodically perch-gleaning prey from leaf surfaces and other substrates.

Tail and wing movements.—Members of both clades twitch tails from side to side and flick wings frequently.

Nest architecture.—Nests of the *hemimelaena* clade (known only for *hemimelaena*) are an open cup placed close to the ground. One nest was supported by palm leaves and attached to surrounding substrates on one side. Nests of the *tyrannina* clade (known for *tyrannina* and *laeta*) are a deep pensile pouch with an opening near the top, suspended from the tips of vines and drooping branches within 3 m of the ground.

TABLE 2a. Morphometrics (part 1 of 2). Body length = Total length—Tail length. All measurement in cm. except Weight in g.

Tribe or major clade	Species or species group	Total length	Body Length	Weight	Wing Length	Primary Length	Secondary Length
Microrhopiini	<i>strigilatus</i>	155	95	23	63	48	60
	<i>disjuncta</i>	135	86	14	59	40	55
	<i>atrothorax</i>	135	83	17	55	36	51
	<i>pelzelni</i>	135	89	17	56	41	53
Pithyini	<i>hemimelaena</i> clade	115	79	16	54	37	51
	<i>tyrannina</i> clade	140	81	17	61	40	57
<i>ferruginea</i> clade	<i>ferruginea</i>	145	92	24	64	45	59
	<i>ruficauda</i>	145	95	19	66	47	60
	<i>loricata</i>	145	79	17	60	40	55
	<i>squamosa</i>	145	82	18	58	40	54
<i>Hylophylax</i> clade	<i>Hypocnemoides</i> species	115	81	13	60	44	53
	<i>Hylophylax</i> species	110	76	13	59	42	53
<i>exsul</i> clade	<i>exsul</i>	140	97	26	64	45	59
	<i>griseiceps</i>	130	76	15	57	37	56
	<i>berlepschi</i>	140	98	26	67	44	58
	<i>laemosticta</i> group	135	90	24	63	43	58
<i>Sclateria</i> clade	<i>schistacea</i> group	150	98	23	66	45	60
	<i>hyperythra</i>	170	111	41	78	55	75
	<i>caurensis</i>	185	111	39	84	57	78
	<i>naevia</i>	150	100	24	68	45	63
<i>longipes</i> clade	<i>longipes</i>	150	98	28	66	48	63
	<i>myotherinus</i> -group	125	85	20	65	45	59
	<i>lophotes</i>	145	91	31	73	51	69
	<i>nudiceps</i>	155	97	32	75	51	68
	<i>Pyriglena</i> species	170	96	31	76	51	70
	<i>Percnostola</i> species	145	92	25	69	47	62
	<i>immaculata</i> clade	175	103	44	80	55	74
	<i>melanoceps</i> clade	170	106	43	87	61	82

TABLE 2b. Morphometrics (part 2 of 2). All measurements in cm.

Tribe or major clade	Species or species group	Tail Length	Tail width	Bill Length	Bill Width	Bill Depth	Tarsus Length	Hallux Length
Microrhopiini	<i>strigulatus</i>	60	10.7	10.8	3.6	4.1	31.8	14.4
	<i>disjuncta</i>	49	13.4	12.4	4.2	3.9	25.4	15.6
	<i>atrothorax</i>	51	11.1	9.6	4.0	3.9	24.6	14.3
	<i>pelzelni</i>	46	9.5	10.3	3.9	3.7	23.6	13.6
Pithyini	<i>hemimelaena</i> clade	36	7.1	9.3	4.0	3.7	23.5	14.5
	<i>tyrannina</i> clade	59	11.2	10.6	4.7	4.4	22.8	14.7
<i>ferruginea</i> clade	<i>ferruginea</i>	54	9.4	12.3	4.2	4.4	26.3	14.8
	<i>ruficauda</i>	50	9.7	10.9	4.0	4.5	24.0	16.1
	<i>loricata</i>	66	9.5	9.1	3.7	3.5	24.7	15.9
	<i>squamosa</i>	63	9.7	8.7	3.6	3.5	27.0	16.6

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TABLE 2b. (Continued)

Tribe or major clade	Species or species group	Tail Length	Tail width	Bill Length	Bill Width	Bill Depth	Tarsus Length	Hallux Length
<i>Hylophylax</i> clade	<i>Hypocnemoides</i> species	34	8.2	11.0	4.2	3.4	23.3	13.8
	<i>Hylophylax</i> species	34	7.3	10.1	4.9	4.0	19.7	13.2
<i>exsul</i> clade	<i>exsul</i>	43	10.2	11.6	4.7	4.8	27.8	16.5
	<i>griseiceps</i>	54	8.7	10.4	3.8	3.4	23.8	14.7
	<i>berlepschi</i>	42	8.5	12.6	5.0	5.4	25.9	16.1
	<i>laemosticta</i> group	45	9.7	11.4	4.7	4.6	26.6	15.5
<i>Sclateria</i> clade	<i>schistacea</i> group	52	11.2	11.0	4.5	4.8	26.4	15.6
	<i>hyperythra</i>	59	11.9	13.9	5.3	6.2	29.6	17.9
	<i>caurensis</i>	74	14.3	14.3	5.3	6.1	29.2	17.6
	<i>naevia</i>	50	11.0	14.9	4.2	4.4	25.3	16.0
<i>longipes</i> clade	<i>longipes</i>	52	9.4	11.9	4.3	4.4	29.5	16.1
	<i>myotherinus</i> -group	40	8.8	11.0	4.9	4.8	26.0	16.4
	<i>lophotes</i>	54	11.2	12.0	5.2	5.8	30.7	19.7
	<i>nudiceps</i>	58	13.2	12.6	5.3	5.2	30.2	19.2
	<i>Pyriglena</i> species	74	16.3	10.9	4.5	4.9	31.0	18.2
	<i>Pernostola</i> species	53	10.8	12.0	5.0	5.2	28.4	17.8
	<i>immaculata</i> clade	72	13.8	13.3	5.4	6.3	33.6	19.1
	<i>melanoceps</i> clade	64	13.4	13.9	5.8	6.4	32.9	21.2

Discussion.—The extensive differences between the two clades in morphology, nest architecture and foraging behavior indicate that they should be placed in different genera. *Cercomacra* species are the subject of an extensive ongoing study (J. Tello *et al.* in prep). Consequently, we have described attributes of the *tyrannina* clade solely for comparison purposes without making a taxonomic recommendation.

Taxonomic Recommendations.—We recommend that the *hemimelaena* clade be given generic recognition which we are prepared to name as no name is available.

Sciaphylax Bravo, Isler, and Brumfield gen. nov.

Type species. *Myrmeciza hemimelaena* Sclater, 1857.

Included species. *Sciaphylax hemimelaena* (Sclater) *comb. nov.* CHESTNUT-TAILED ANTBIRD.

Sciaphylax castanea (Zimmer) *comb. nov.* ZIMMER'S ANTBIRD.

Diagnosis. Distinguished from *Cercomacra tyrannina* clade by deep yellowish-red-brown posterior coloration, including tail, and bold wing covert pattern; by short, narrow tail and related proportions (tail length/total length, tail length/wing length); and by cup nest; supported by near-ground foraging behavior.

Etymology. The feminine generic name is taken from the Greek *skia* (shade, shadow) and *phylax* (a watcher, a guardian), meaning “a guardian of the shade,” reflecting habitat preference and conspicuous singing behavior.

Tribe Pyriglenini

The remaining *Myrmeciza* species are distributed among four of the five major clades within the Pyriglenini (Figs. 1 and 2) uncovered by the molecular analysis, although low support at the basal nodes of the tribe makes relationships of these clades uncertain. However, genera within the Pyriglenini are well defined phylogenetically and phenotypically as expressed in the diagnoses that follow. For that reason and to simplify the presentation, comparisons are principally made within major clades, but unique attributes within the Pyriglenini are also noted. All clades of Pyriglenini, including one not containing a *Myrmeciza* species, are examined.

TABLE 3a. Morphometric proportions (part 1 of 2).

Tribe or major clade	Species or species group	Weight/ Body length	Wing length/ Total length	Wing length/ Body length	Primary length/ Secondary length	Tail length/ Wing length	Tail width/ Tail length
Microrhopiini	<i>strigulatus</i>	0.24	0.41	0.67	0.80	0.95	0.18
	<i>disjuncta</i>	0.16	0.44	0.69	0.73	0.84	0.27
	<i>atrothorax</i>	0.20	0.41	0.66	0.70	0.94	0.22
	<i>pelzelni</i>	0.19	0.42	0.63	0.78	0.82	0.21
Pithyini	<i>hemimelaena</i> clade	0.20	0.47	0.68	0.73	0.70	0.20
	<i>tyrannina</i> clade	0.21	0.44	0.76	0.71	0.95	0.19
<i>ferruginea</i> clade	<i>ferruginea</i>	0.26	0.44	0.69	0.75	0.84	0.18
	<i>ruficauda</i>	0.20	0.46	0.70	0.79	0.75	0.19
	<i>loricata</i>	0.21	0.41	0.76	0.73	1.10	0.14
	<i>squamosa</i>	0.22	0.40	0.71	0.73	1.08	0.15
<i>Hylophylax</i> clade	<i>Hypocnemoides</i> species	0.16	0.52	0.74	0.83	0.57	0.24
	<i>Hylophylax</i> species	0.17	0.54	0.78	0.79	0.58	0.21
<i>exsul</i> clade	<i>exsul</i>	0.27	0.46	0.66	0.76	0.67	0.24
	<i>griseiceps</i>	0.20	0.44	0.75	0.67	0.95	0.16
	<i>berlepschi</i>	0.27	0.48	0.68	0.75	0.64	0.20
	<i>laemostieta</i> group	0.27	0.47	0.71	0.73	0.71	0.22
<i>Sclateria</i> clade	<i>schistacea</i> group	0.23	0.44	0.67	0.75	0.78	0.22
	<i>hyperythra</i>	0.37	0.46	0.70	0.73	0.76	0.20
	<i>caurensis</i>	0.35	0.46	0.76	0.73	0.88	0.19
	<i>naevia</i>	0.24	0.45	0.68	0.71	0.73	0.22
<i>longipes</i> clade	<i>longipes</i>	0.27	0.44	0.68	0.76	0.79	0.18
	<i>myotherinus</i> -group	0.23	0.52	0.76	0.76	0.62	0.22
	<i>lophotes</i>	0.34	0.50	0.80	0.74	0.74	0.21
	<i>nudiceps</i>	0.33	0.48	0.77	0.75	0.77	0.23
	<i>Pyriglena</i> species	0.32	0.45	0.79	0.73	0.97	0.22
	<i>Percnostola</i> species	0.27	0.48	0.75	0.76	0.77	0.20
	<i>immaculata</i> clade	0.43	0.46	0.78	0.74	0.90	0.19
	<i>melanoceps</i> clade	0.41	0.51	0.82	0.74	0.74	0.21

TABLE 3b. Morphometric proportions (part 2 of 2).

Tribe or major clade	Species or species group	Bill length/ Total length	Bill width/ Bill length	Bill depth/ Bill length	Hallux length/ Tarsus length	Bill length/ Tarsus length	Tarsus length/ Total length	Tail length/ Total length
Microrhopiini	<i>strigulatus</i>	0.070	0.33	0.38	0.45	0.34	0.20	0.39
	<i>disjuncta</i>	0.092	0.34	0.32	0.61	0.49	0.19	0.36
	<i>atrothorax</i>	0.071	0.41	0.40	0.58	0.39	0.18	0.38
	<i>pelzelni</i>	0.076	0.38	0.36	0.58	0.44	0.17	0.34
Pithyini	<i>hemimelaena</i> clade	0.081	0.43	0.40	0.62	0.40	0.20	0.31
	<i>tyrannina</i> clade	0.076	0.44	0.41	0.64	0.46	0.16	0.42

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TABLE 3b. (Continued)

Tribe or major clade	Species or species group	Bill length/ Total length	Bill width/ Bill length	Bill depth/ Bill length	Hallux length/ Tarsus length	Bill length/ Tarsus length	Tarsus length/ Total length	Tail length/ Total length
<i>ferruginea</i> clade	<i>ferruginea</i>	0.085	0.34	0.36	0.56	0.47	0.18	0.37
	<i>ruficauda</i>	0.075	0.37	0.41	0.67	0.45	0.17	0.34
	<i>loricata</i>	0.063	0.41	0.38	0.64	0.37	0.17	0.45
	<i>squamosa</i>	0.060	0.41	0.40	0.61	0.32	0.19	0.44
<i>Hylophylax</i> clade	<i>Hypocnemoides</i> species	0.096	0.38	0.31	0.59	0.47	0.20	0.30
	<i>Hylophylax</i> species	0.092	0.48	0.40	0.67	0.51	0.18	0.31
<i>exsul</i> clade	<i>exsul</i>	0.083	0.41	0.41	0.59	0.42	0.20	0.31
	<i>griseiceps</i>	0.080	0.36	0.33	0.62	0.44	0.18	0.42
	<i>berlepschi</i>	0.090	0.40	0.43	0.62	0.49	0.18	0.30
	<i>laemosticta</i> group	0.084	0.42	0.41	0.58	0.43	0.20	0.33
<i>Sclateria</i> clade	<i>schistacea</i> group	0.073	0.41	0.44	0.59	0.42	0.18	0.35
	<i>hyperythra</i>	0.082	0.38	0.44	0.60	0.47	0.17	0.35
	<i>caurensis</i>	0.077	0.37	0.43	0.60	0.49	0.16	0.40
	<i>naevia</i>	0.099	0.28	0.29	0.63	0.59	0.17	0.33
<i>longipes</i> clade	<i>longipes</i>	0.079	0.36	0.37	0.55	0.40	0.20	0.35
	<i>myotherinus</i> -group	0.088	0.45	0.44	0.63	0.42	0.21	0.32
	<i>lophotes</i>	0.083	0.43	0.48	0.64	0.39	0.21	0.37
	<i>nudiceps</i>	0.081	0.42	0.41	0.64	0.42	0.19	0.37
	<i>Pyriglena</i> species	0.064	0.41	0.45	0.59	0.35	0.18	0.43
	<i>Percnostola</i> species	0.083	0.42	0.43	0.63	0.42	0.20	0.37
	<i>immaculata</i> clade	0.076	0.41	0.47	0.57	0.40	0.19	0.41
	<i>melanoceps</i> clade	0.082	0.42	0.46	0.64	0.42	0.19	0.38

ferruginea clade

Phylogenetic relationships.—*Myrmeciza ferruginea* (Müller), *M. ruficauda* (Wied), *M. loricata* (Lichtenstein), and *M. squamosa* (Pelzeln), henceforth the *ferruginea* clade, form a well-supported clade. Relationships within the clade are not well resolved except for the sister relationship between *loricata* and *squamosa* (Figs. 1 and 2).

Biogeography.—Three species, *ruficauda*, *loricata*, and *squamosa*, are confined to the Atlantic Forest of Brazil; *ferruginea* is found in the Guianan region and south of the Rio Amazon in the Madeira–Tapajós interfluvium. They mainly occur in lowlands except that *loricata* is restricted to foothills. The three Atlantic Forest species are allopatric or parapatric, although *ruficauda* and *loricata* may overlap in Espírito Santo.

Plumage.—The three Atlantic Forest species are similar. They share some striking features, particularly black wing coverts broadly tipped white or buff, black ear patches (gray in female *ruficauda*) contrasting with brown upperparts, and light brown or white underparts which are scalloped with black feathers edged white in males. The fourth species, *ferruginea* has a large black breast patch and bare blue periorbital skin, but shares the conspicuous wing covert pattern, black ear patch, and contrasting brown plumage.

Morphometrics.—Although total lengths are similar (Table 2), the essentially identical *loricata* and *squamosa* have longer tails than *ferruginea* and *ruficauda* and hence smaller bodies. Consequently, *loricata* and *squamosa* have greater tail/wing length ratios (Table 3). In addition, bill lengths of *ferruginea* and *ruficauda* are long relative to tarsus length.

Loudsongs.—Loudsongs of *loricata*, *ferruginea*, and *squamosa* are short (6–7 notes), countable series of doublets whose peaks descend in frequency. The loudsong of *ruficauda* is also delivered in doublets but given so

rapidly that individual notes can barely be discriminated. Only in *ferruginea* does the loudsong of females differ appreciably from that of the male.

Habitat.—The three Atlantic Forest species prefer sandy soil forests, drier forests, or steep slopes (*loricata*) with a high density of slender saplings and broad-leaved plants in the understory; *ferruginea* also occurs in sandy soil forests but is also found around light gaps and treefalls in humid forest.

Foraging behavior.—All four species are highly terrestrial, foraging on the ground and less often jumping up to low perches. All glean prey from leaf litter or substrates within 1 m of the ground. Only *ferruginea* is known to follow army ants regularly.

Tail and wing movements.—*Myrmeciza ferruginea* flicks its tail up and down in a shallow arc and flicks its wings; *ruficauda* slowly dips its tail and raises it more rapidly; *loricata* and *squamosa* flick their tails (normally slightly cocked) upward before lowering them slowly and flick their wings.

Nest architecture.—Nests of *ferruginea*, *ruficauda*, and *loricata* are open cups placed on the ground, or slightly elevated on a platform of debris, among and often partially covered by dead leaves, branches, and small plants (recent addition: Buzzetti & Barnett 2003). The only nest known for *squamosa* is similar but based on the unclear description may be placed among exposed roots of a tree.

Discussion.—Morphometric distinctions lend support to maintaining two genera (*ferruginea/ruficauda* and *loricata/squamosa*). Inconsistencies in wing and tail movements and aspects of *ferruginea* plumage lend weight to a three genus solution (*ferruginea*, *ruficauda*, and *loricata/squamosa*). On the other hand, commonalities of most aspects of morphology (especially plumage) and behavior (loudsongs, habitat, foraging behavior, and nest architecture) indicate that the species should be placed in a single genus.

Taxonomic Recommendations.—Given the numerous phenotypic consistencies among the species, we recommend that the four species be considered congeneric. Available names include *Myrmoderus* Ridgway (1909), which has priority over *Myrmedestes* Todd (1927).

***Myrmoderus* Ridgway, 1909**

Type species. *Myiothera loricata* Lichtenstein, 1823.

Included species. *Myrmoderus ferrugineus* (Müller). FERRUGINOUS-BACKED ANTBIRD.

Myrmoderus loricatus (Lichtenstein). WHITE-BIBBED ANTBIRD.

Myrmoderus ruficauda (Wied). SCALLOPED ANTBIRD.

Myrmoderus squamosus (Pelzeln). SQUAMATE ANTBIRD.

Diagnosis. Distinguished from other genera in Pyriglenini by scalloped underparts of males (solid black in *ferruginea*), black ear covert patches, extensively rufous brown plumage, and broadly tipped blackish wing coverts. Open cup nests on ground, loudsongs consisting of doublets, and flicking tail movements distinguish *Myrmoderus* from other clades in Pyriglenini except *Hylophylax* clade. Proportionately long tail and slender bill identified by Ridgway as generic characters apply only to *loricatus* and *squamosus*.

***Hylophylax* clade**

Phylogenetic relationships.—The *Hylophylax* clade (Figs. 1 and 2) consists of two well-supported genera, *Hylophylax* and *Hypocnemoides*. The following comparisons examine distinctions between them and identify synapomorphies for later use in comparisons to other clades in the Pyriglenini. *Hylophylax* includes *H. naevioides* (Lafresnaye), *H. naevius* (Gmelin), *H. punctulatus* (Des Murs). *Hypocnemoides* includes *H. melanopogon* (Sclater), and *H. maculicauda* (Pelzeln).

Biogeography.—Representatives of *Hylophylax* and *Hypocnemoides* occur throughout Amazonia. One *Hylophylax* species is trans-Amazonian.

Plumage.—The two genera are distinctive in plumage. *Hypocnemoides* species are gray above with white edges to blackish wing coverts; males have a black throat and gray underparts; females underparts are primarily white. Species of *Hylophylax* are yellowish brown but boldly patterned; most species have black throats or malars, white spots on posterior upperparts, black spots on anterior underparts, and black wing coverts with large spots on tips.

Morphometrics.—The two genera are similar morphometrically except for bill proportions (Tables 2 and 3)

Loudsongs.—Loudsongs of *Hypocnemoides* species consist of a long, rapidly delivered series of ascending and descending notes; those of *Hylophylax* species consist of a series of doublets, varying in duration and frequency pattern by species, but readily identifiable as *Hylophylax* loudsongs.

Habitat.—*Hypocnemoides* species are closely associated with streams and other water related habitats. *Hylophylax punctulatus* primarily inhabits seasonally flooded evergreen forest. The remaining *Hylophylax* species inhabit the understory of evergreen forest, both *terra firme* and *várzea*, and mature second growth.

Foraging behavior.—Species of *Hylophylax* often fly among vertical perches < 2 m from the ground while sallying to substrates, and they accompany mixed flocks or follow army ants regularly. *Hypocnemoides* species hop through branches and vines mostly < 2 m from the surface, often (but not always) over water, sally to substrates including water surfaces, and occasionally join mixed flocks or follow army ants.

Tail and wing movements.—*Hylophylax* species hold their tails below the plane of the body, flick them upward to just above plane of body, and then lower them slowly. *Hypocnemoides* species hold their tails up over plane of body, frequently flicking them up even higher while flicking wings constantly.

Nest architecture.—*Hylophylax* nests are hanging cups slung from between two horizontal branches or a branch fork close to ground (known for 2 spp.; recent addition: Greeney 2007). The nest of *Hypocnemoides* (known for *melanopogon*) is a pouch with its entrance near the top, placed over water and slung from a variety of surfaces.

Discussion.—These well-marked genera have not been associated historically. Their common heritage appears to be reflected only in similarities of morphometrics (other than bill shape) and aspects of foraging behavior.

Taxonomic Recommendations.—*Hylophylax* and *Hypocnemoides* should be maintained as distinct genera based on differences in plumage, bill proportions, loudsongs, nests, and tail and wing movements, and supported by habitat differences.

***Hypocnemoides* Bangs and Penard, 1918**

Type species. *Hypocnemis melanopogon* Sclater, 1857.

Included species. *Hypocnemoides melanopogon* (Sclater). BLACK-CHINNED ANTBIRD.

Hypocnemoides maculicauda (Pelzeln). BAND-TAILED ANTBIRD.

Diagnosis. Distinguished from sister group *Hylophylax* and all other genera in the Pyriglenini by plumage, restricted to black, white, and shades of gray. Nest unique in Pyriglenini. Distinguished from *Hylophylax* by narrower bill width and depth compared to bill length, loudsong, and tail movements; habitat and foraging behavior differences are supportive.

***Hylophylax* Ridgway, 1909**

Type species. *Conopophaga naevioides* Lafresnaye, 1847.

Included species. *Hylophylax naevioides* (Lafresnaye). SPOTTED ANTBIRD.

Hylophylax naevius (Gmelin). SPOT-BACKED ANTBIRD.

Hylophylax punctulatus (Des Murs). DOT-BACKED ANTBIRD.

Diagnosis. Distinguished from *Hypocnemoides* and all other genera in Pyriglenini by boldly patterned plumage. Distinguished from *Hypocnemoides* by broader bill width and depth compared to bill length, loudsong, nest, and tail movements; habitat and foraging behavior differences are supportive.

***Sclateria* clade**

Phylogenetic relationships.—*Sclateria naevia* (Gmelin) is sister to species currently placed in the genus *Schistocichla*, among which *Myrmeciza hyperythra* (Sclater) is nested (Figs. 1 and 2). In the following morphological analysis, data for *Sclateria naevia*, *Myrmeciza hyperythra*, and *Schistocichla caurensis* (Hellmayr)

are separated because of their larger size, but given their similarity, the plumage and morphometrics of *Schistocichla leucostigma* Pelzeln, *S. saturata* (Salvin), *S. humaythae* (Hellmayr), *S. brunneiceps* (Zimmer), *S. rufifacies* (Hellmayr), and *S. schistacea* (Sclater) are combined as the *schistacea* group. Until recently (Isler *et al.* 2007) *leucostigma*, *humaythae*, *brunneiceps*, and *rufifacies* were considered conspecific.

Biogeography.—Together *leucostigma*, *humaythae*, *brunneiceps*, and *rufifacies* cover much of Amazonia along with *naevia* with which they are sympatric. Ranges of *schistacea* and *hyperythra* are limited to western Amazonia where they are sympatric with *subplumbea* and *naevia*, and *caurensis* is restricted to the tepuis region.

Plumage.—Males of all species are gray with white wing covert spots; *hyperythra* has a pale blue periorbital skin patch and *naevia* a whitish supercilium (variable in intensity) and underparts variably streaked white or extensively white. Females of the *schistacea* group and *caurensis* are reddish brown (paler below) with cinnamon tinged wing spots and head variably gray. The underparts of females of *hyperythra* are similar, but their upperparts are gray, and they have white wing spots and periorbital skin patches like the males. Females of *naevia* have a supercilium and underparts pattern similar to that of the males, but their upperparts are grayish-brown.

Morphometrics.—The size (Table 2) and proportions (Table 3) of *naevia* are similar to those of the *schistacea* group, but its long slender bill is unique among the Pyriglenini. Except for tail length, *hyperythra* and *caurensis* are similar to one another in measurements and proportions, and their proportions are similar to the smaller *schistacea* group.

Loudsongs.—All species deliver long trills except for *schistacea*, whose loudsong is a short countable series of clear notes, and *caurensis*, whose loudsong is a slightly longer countable series of buzzy notes.

Habitat.—The *schistacea* group inhabits evergreen terra firme forest in lowlands and foothills. Others in the clade occupy more specialized habitats: *naevia* is found in seasonally flooded forest and sluggish streams in *terra firme*; *hyperythra* in seasonally flooded and transitional forests; and *caurensis* on boulder-strewn tepui slopes.

Foraging behavior.—All species forage on the ground and on low substrates mostly <1 m, hop deliberately, rummage in leaf piles on the ground, and pick prey off low substrates. Specialized foraging behavior includes *naevia* picking prey off water and *caurensis* probing in boulder mosses and litter.

Tail and wing movements.—All species except *naevia* flick their tails up and drop them to ca 30° below horizontal; *naevia* jerks its tail from side to side. In an earlier publication (Zimmer & Isler 2003) *hyperythra* was said to pound its tail downward, but video documentation (K. J. Zimmer, pers. comm.) shows that its tail movements are the same as those of other species in the group except *naevia*.

Nest architecture.—Few nests are known for species in this clade. Conflicting accounts for *leucostigma* include an open cup (Belcher & Smooker 1936; Greeney *et al.* 2013) and a nest under a log (O. Tostain pers. comm.). The only nest reported for *naevia* was an open cup over a stream (David & Londoño 2011). Two nests described for *hyperythra* were open cups, one attached to a spiny palm and the other to ferns (Londoño 2003).

Discussion.—The first issue is whether to maintain *Sclateria* as a monotypic genus. Its sister relationship with the rest of the clade is well supported in the molecular analysis. Its maintenance as a monophyletic genus is buttressed by plumage distinctions and bill morphology unique among the Pyriglenini. Differences in tail movements between *Sclateria* and the remaining species in the clade strongly indicate they should not be considered congeneric, a position supported by the specialized foraging behavior of *Sclateria*.

The second issue is whether to place in the same genus three subsequent clades consisting of *schistacea/saturata*, *hyperythra*, and *rufifacies/brunneiceps/leucostigma/humaythae* and presumably *caurensis*. The principal consideration is that *hyperythra* is nested in the phylogenetic tree between two clades of species currently placed in *Schistocichla*, some of which are similar morphologically and have been considered conspecific. The pale blue periorbital skin of *hyperythra* occurs in multiple thamnophilid clades and should not necessitate generic distinction. Otherwise, outside of the more extensive gray upperparts of the female, *hyperythra* is a large version of the *Schistocichla* species morphologically. Behavioral characteristics of *hyperythra* are also consistent with those of *Schistocichla* species although more needs to be known of nest architecture. The evidence points to placing *Schistocichla* species and *hyperythra* in the same genus.

Taxonomic Recommendations.—We recommend that *Sclateria* be maintained as a monotypic genus and that *hyperythra* and species currently placed in *Schistocichla* be merged. *Myrmelastes* Sclater 1858a has priority for this reconstituted genus. Thus, *Schistocichla* becomes a junior synonym of *Myrmelastes*.

Sclateria Oberholser, 1899

Type species. *Sitta naevia* Gmelin, 1788.

Included species. *Sclateria naevia* (Gmelin). SILVERED ANTBIRD.

Diagnosis. Distinguished from other genera in Pyriglenini by whitish supercilium and white-streaked underparts (reduced in some subspecies) and by bill proportions (bill width and depth compared to length). Distinguished from *Myrmelastes* by tail movements; habitat and foraging behavior differences are supportive.

Myrmelastes Sclater, 1858a

Type Species. *Thamnophilus hyperythrus* Sclater, 1855.

Included species. *Myrmelastes saturatus* (Salvin). RORAIMAN ANTBIRD.

Myrmelastes schistaceus (Sclater). SLATE-COLORED ANTBIRD.

Myrmelastes hyperythrus (Sclater). PLUMBEOUS ANTBIRD.

Myrmelastes rufifacies (Hellmayr). RUFIOUS-FACED ANTBIRD.

Myrmelastes brunneiceps (Zimmer). BROWNISH-HEADED ANTBIRD.

Myrmelastes humaythae (Hellmayr). HUMAITA ANTBIRD.

Myrmelastes leucostigma (Pelzeln). SPOT-WINGED ANTBIRD.

Myrmelastes caurensis (Hellmayr). CAURA ANTBIRD.

Diagnosis. Males distinguished from all other genera in Pyriglenini by plain gray plumage with darker wing coverts and white wing covert spots combined with absence of white interscapular patch. Female plumage similar to *Sclateria* but distinguished by gray on head or upperparts (except *humaythae*) and lack of pale superciliary. Differs from *Sclateria* in bill proportions (bill width and depth compared to length) and tail movements.

exsul clade

Phylogenetic relationships.— This clade of species currently placed in *Myrmeciza* includes *M. exsul* (Sclater) as sister to the rest, and *M. griseiceps* (Chapman) as sister of a well-supported, although internally unresolved, clade consisting of *M. berlepschi* (Hartert), *M. nigricauda* (Salvin and Godman); *M. palliata* (Todd) and *M. laemosticta* Salvin (Figs. 1 and 2; Chaves *et al.* 2010). Until recently, *nigricauda*, *palliata*, and *laemosticta* were considered conspecific, and, given their morphological similarity, their plumage and morphometric data are combined as the *laemosticta* group.

Biogeography.—The *exsul* clade is trans-Andean. Species occur from Nicaragua to the western slopes of the Andes in extreme northwest Peru; *exsul* and *berlepschi* inhabit lowlands and the remaining species mostly foothills although *griseiceps* ranges to 3000 m. *Myrmeciza exsul* and *berlepschi* are sympatric in Colombia; *exsul* and *nigricauda* overlap elevationally; *berlepschi* and *nigricauda* appear to be elevationally parapatric. All other species are allopatric.

Plumage.—Except for the black *berlepschi*, the clade is gray anteriorly and brown (typically dark reddish-brown) posteriorly with wing coverts tipped white in at least one sex (except some subspecies of *exsul*) and white interscapular patches (small in *exsul*). Females in the *laemosticta* group are distinguished by black throats spotted white. Male *griseiceps* has a large black breast patch and graduated tail tipped white; the female has a white throat and breast streaked pale gray. Bare blue periorbital skin distinguishes *exsul*. Male *berlepschi* lacks white wing covert spots that are present in the female, which also has white spots from throat to upper belly.

Morphometrics.—Although the tail of *berlepschi* is slightly shorter and its bill slightly longer, species in the clade are similar in their measurements except for *griseiceps* (Table 2). *Myrmeciza griseiceps* is smaller except its tail is longer which creates a high ratio between tail length and wing and total length. In addition, its bill is thinner which produces a low bill depth/bill length ratio (Table 3).

Loudsongs.—The structure of male loudsongs of *laemosticta*, *berlepschi*, *nigricauda*, and *palliata* are similar: a countable series of abrupt notes shaped like a sharply peaked chevron. Female loudsongs of all four species can readily be distinguished from those of males, especially by their longer and flatter notes. Loudsongs of *griseiceps*

(a rapid trill) and *exsul* (two-noted) differ from those of *berlepschi* and the *laemosticta* group as well as from one another, and their female songs are more similar to those of their respective males.

Habitat.—All species inhabit dense, tangled vegetation, the type of vegetation varying with conditions within their ranges: *exsul* in dense, tangled vegetation in humid lowland forest and mature second growth, sometimes in areas with more open undergrowth; *griseiceps* in patches of dense montane forest especially bamboo patches; *berlepschi* in heavily vegetated lowland forest, especially at borders and light gaps, and dense second growth; the *laemosticta* group in wet forest in foothills, often in ravines and steep slopes with tangled treefalls and landslides.

Foraging behavior.—All species except *griseiceps* forage primarily on the ground, hopping up to low substrates mostly <1 m (although *nigricauda* and *berlepschi* are poorly known). In contrast, *griseiceps* forages mostly 2–7 m up.

Tail and wing movements.—All species pound their tails down and raise them back slowly.

Nest architecture.—*Myrmeciza exsul* builds a bulky bottom-supported cup placed on a foundation of plants and debris < 0.4 m off the ground. The nest of *laemosticta* is a rim-supported cup built with flexible fibers and placed on shrubs 30–50 cm off the ground (Greeney *et al.* 2013). One minimally described nest, likely to be *palliata* given the record's locality, was said to be a cup placed low in a shrub.

Discussion.—The issue is whether to consolidate these six species in a single genus or to place *exsul*, *griseiceps*, and the *laemosticta* group and *berlepschi* in three genera. The question is complicated by *griseiceps* whose unique morphology led Hellmayr to conclude that the species “is extremely puzzling in its affinities.” (Cory and Hellmayr 1924). The phylogeny embeds *griseiceps* between *exsul* and the clade consisting of *berlepschi*, *nigricauda*, *palliata* and *laemosticta*. These four species evidence similar morphology and behavior. *Myrmeciza exsul* is close to this group in morphology and behavior, as was suggested earlier by Robbins and Ridgely (1991). However, nest architecture supports distinguishing *exsul* from the *laemosticta* clade.

Taxonomic Recommendations.—Differences in plumage, morphometrics, foraging behavior, and loudsong structure between *griseiceps* and other members of the *exsul* clade require that *griseiceps* be placed in a monotypic genus. Despite the similarities between *exsul* and *berlepschi* and the *laemosticta* group, *exsul* then must be placed in a monotypic genus to avoid paraphyletic genera; differences in plumage, vocalizations, and nest architecture also support such treatment. We recommend that *berlepschi* and the *laemosticta* group be considered congeneric. The appropriate name for this genus is *Sipia*. New generic names are needed for *exsul* and *griseiceps*.

***Poliocrania* Bravo, Isler, and Brumfield gen. nov.**

Type species. *Myrmeciza exsul* Sclater, 1858b.

Included species. *Poliocrania exsul* (Sclater) *comb. nov.* CHESTNUT-BACKED ANT BIRD.

Diagnosis. Distinguished from *Ampelornis* and *Sipia* by blue periorbital patch, by lack of spots or streaks on throat or underparts of female, and by loudsong structure. Differs from *Ampelornis* in numerous morphometric measures and proportions such as tail/wing length ratio; differences in foraging behavior supportive. Nest architecture differs from *Sipia*.

Etymology. The feminine generic name is taken from the Greek *polios* (ashy-gray) and *kranion* (skull, head), reflecting the gray head of the type species.

***Ampelornis* Isler, Bravo, and Brumfield, new genus**

Type species. *Myrmoderus griseiceps* Chapman, 1923.

Included species. *Ampelornis griseiceps* (Chapman) *comb. nov.* GRAY-HEADED ANT BIRD.

Diagnosis. Distinguished from *Poliocrania* and *Sipia* by morphometric measures, such as tail length/wing length ratio and bill depth/bill length ratio, resulting from relatively longer tail and thinner bill; by female's streaked underparts; and by loudsong structure; differences in foraging behavior supportive.

Etymology. The masculine generic name is taken from the Greek *ampelos* (vine) and *ornis* (bird), reflecting the viny habitat often occupied by this species.

Sipia Hellmayr, 1924

Type species. *Pyriglena berlepschi* Hartert, 1898.

Included species. *Sipia berlepschi* (Hartert). STUB-TAILED ANTBIRD.

Sipia nigricauda (Salvin and Godman). ESMERALDAS ANTBIRD

Sipia laemostieta (Salvin). DULL-MANTLED ANTBIRD.

Sipia palliata (Todd). MAGDALENA ANTBIRD.

Diagnosis. Distinguished from *Ampelornis* and *Poliocrania* by female throat spots and loudsong structure. Further distinguished from *Poliocrania* by nest structure and lack of blue periorbital patch and from *Ampelornis* by numerous morphometric measures, such as tail length/wing length ratio; differences in foraging behavior supportive.

longipes clade

Phylogenetic relationships.—The phylogeny located *Myrmeciza longipes* (hereafter *longipes*) at the base of a large clade with the *Myrmoborus* clade and the *Gymnocichla* clade as subsequent sisters (Figs. 1 and 2). The *Myrmoborus* clade consists of *Percnostola lophotes* Hellmayr and Seilern and four *Myrmoborus* species including *M. melanurus* (Sclater and Salvin), *M. myotherinus* (Spix), *M. leucophrys* (Tschudi), and *M. lugubris* (Cabanis). Data for the morphologically similar *Myrmoborus* species are combined as the *myotherinus* group. *Percnostola lophotes* is identified by its specific name. The *Gymnocichla* clade includes *Gymnocichla nudiceps* (Cassin) (hereafter *nudiceps*); the genus *Pyriglena* including *P. leuconota* (Spix), *P. leucoptera* (Vieillot), and presumably (Maldonado-Coelho 2012) *P. atra* (Swainson); the genus *Percnostola* including *P. rufifrons* (Gmelin) and *P. arenarum* Isler, Alvarez, Isler, and Whitney; and two clades currently placed in *Myrmeciza*—the *immaculata* clade including *M. immaculata* (Lafresnaye), *M. zeledoni* Ridgway, and *M. fortis* (Sclater and Salvin), and the *melanoceps* clade including *M. melanoceps* (Spix) and *M. goeldii* (Snethlage). Relationships among *Percnostola*, the *immaculata* clade, and the *melanoceps* clade are not resolved with high support. Although not included in our analysis, *Rhopornis ardesiacus* (Wied) is also a member of the *longipes* clade (Bravo et al. in prep.).

Biogeography.—Most species are Amazonian in distribution. However, *longipes* is patchily distributed west of the Andes and east of the Andes north of the Amazon, *nudiceps* and *immaculata* are trans-Andean, and the ranges of *Pyriglena* species extend to both Pacific slope of the Andes and the Atlantic coast of Brazil south to northern Argentina. Most species have limited geographic ranges and are allopatric within clades except *myotherinus* and *leucophrys* whose ranges are extensive and overlap most other cis-Andean species. Also, *longipes* is sympatric only with *leucophrys* in the Guianan region; *fortis* is sympatric with the *melanoceps* clade; and *immaculata* is only narrowly sympatric with *nudiceps*, as are *Pyriglena* and *Percnostola* species with *fortis*, *melanoceps*, and *goeldii*.

Plumage.—*Pyriglena*, *Percnostola*, and *Myrmoborus* species exhibit distinctive plumage features. Males of all species are black, gray, and white although plumages of some *Pyriglena* subspecies also include dark chestnut. Males of *Pyriglena* species have bright red eyes and white interscapular patches. The gray males of the two *Percnostola* species have distinctive black throats and dark crowns. The gray males of most species in the *Myrmoborus* clade have a distinctive face and throat patch edged with a white or pale gray superciliary although those of *melanurus* and *lophotes* are altogether black or blackish. Females are primarily brown with the following features: *Pyriglena* species have blackish tails; females of *Percnostola* species are gray or cinnamon-gray above; most females in the *Myrmoborus* clade have black or blackish lores and ear-coverts forming a distinctive patch although these are lacking in one *lugubris* subspecies and *lophotes*. The distinct plumage of *longipes* is distinguished by a number of characters including the rufous upperparts of males and the black subapical spots on wing coverts of females and most male subspecies. Males of *nudiceps* and the *immaculata* and *melanoceps* clades are black or blackish with bare bluish periorbital patches (extending to the forecrown in *nudiceps*); the presence of white patches differs among species except that *immaculata* and *fortis* share mostly concealed white patch at the bend of wing. Females of *nudiceps* and the *immaculata* and *melanoceps* clades are yellowish-brown to reddish-brown with bare bluish periorbital patches and pale wing covert edges (variable), the presence and extent of black or gray differing among species.

Morphometrics.—The most notable differences in measurements are the large sizes of species in the

immaculata and *melanoceps* clades (Table 2). However, these two clades differ in opposing directions in wing and tail lengths, leading to a large difference in tail/wing ratio (Table 3). Other noteworthy differences in size involve the relatively short bills and long tails of *Pyriglena* species which result in significant differences in bill length/total length and tail length/wing length ratios with the *myotherinus* clade, *mudiceps*, *Percnostola* species, and the *melanoceps* clade.

Loudsongs.—Loudsongs of all species are structurally similar, consisting of a 2–4 second series of similar notes (typically an inverted V or U shape, less often down-slurred) that are repeated in a regular pattern (only species in the *immaculata* clade show a slight shift in pattern).

Habitat.—The most distinct types of habitat are occupied by *longipes* which is found in semideciduous and gallery forest, second growth woodland, and shrubby borders. Other species principally occur in evergreen forests, although some *Pyriglena leuconota* subspecies occupy deciduous forests. Nearly all species in the *longipes* clade show a predilection for dense tangles and thickets, especially in forest openings and borders. Specialties include water-related habitats for some *Myrmoborus* species, sandy soil forest for *Percnostola* species, and floodplain and transitional forest for the *melanoceps* clade and *lophotes*.

Foraging behavior.—All species forage primarily on the ground and on low substrates mostly within 1–2 m of the ground. All species, except perhaps for *lophotes* and *arenarum*, follow army ant swarms to some extent. Most are considered “regular” ant-followers, and *fortis* is considered an obligate follower.

Tail and wing movements.—All species (*arenarum* unknown) pound the tail downward and slowly raise it to horizontal or slightly higher.

Nest architecture.—Except for *longipes* all species (*arenarum* unknown) build domed or partially domed nests atop leaf litter on the ground or to 1 m off the ground among fallen limbs or leaf rachides of understory palms (recent additions: Greeney et al. 2004, Lebbin et al. 2007). *Myrmeciza longipes* builds an open cup just off the ground; said to be placed on supports rather than slung from them.

Discussion.—Consistency of behavioral characteristics, including loudsong structure, tail and wing movements, and foraging behavior, reinforces the molecular finding of common ancestry for species in the *longipes* clade. An exception is *Myrmeciza longipes* which differs from other species in the clade in its nest architecture and habitat preferences. Existing genera within the group, *Gymnocichla*, *Myrmoborus*, *Pyriglena* and *Percnostola*, have, however, long been recognized as distinct in plumage and morphometrics from each other and from *longipes*, and placing them in a single genus is clearly inappropriate. This leaves questions of *lophotes* and the *immaculata* and *melanoceps* clades. Regarding *lophotes*, the phylogeny places it within *Myrmoborus*, and its plumage resemblance to *Myrmoborus melanurus* (not noted previously in the literature) became obvious after the genetic study showed that they are sisters. The morphologically similar *immaculata* and *melanoceps* clades form a polytomy with *Percnostola* (Figs. 1 and 2) and, therefore, cannot be placed in the same genus. The two clades differ principally in tail length and wing length and consequently in wing/tail proportions. Given the choice of uniting the *immaculata* and *melanoceps* clades with the morphologically dissimilar *Percnostola* or recommending that they be placed in three genera, the latter course is most consistent with previous generic decisions in the Thamnophilidae, such as the purely morphological basis for the maintenance of *Gymnocichla* and *Pyriglena*.

Taxonomic Recommendations.—We recommend that *Myrmeciza longipes* be maintained in a monotypic genus, that *Gymnocichla*, *Myrmoborus*, *Pyriglena*, and *Percnostola* be maintained as genera, and that *Percnostola lophotes* be transferred to the genus *Myrmoborus*. We also recommend that species in the *immaculata* and *melanoceps* clades be considered distinct from the foregoing and that they be placed in different genera given their uncertain phylogenetic relationship and the morphometric characters that distinguish them.

***Myrmeciza* Gray, 1841**

Type species. *Drymophila longipes* Swainson, 1825.

Included species. *Myrmeciza longipes* (Swainson). WHITE-BELLIED ANTBIRD.

Diagnosis. Distinguished from other genera in the *longipes* clade by plumage including rufous upperparts and black anterior underparts bordered gray of males and black subapical spots on wing coverts of females and most male subspecies. Open cup nest off the ground unique in *longipes* clade. Habitat distinctions are supportive.

***Myrmoborus* Cabanis and Heine, 1859**

Type species. *Pithys leucophrys* Tschudi, 1844.

Included species. *Myrmoborus melanurus* (Sclater and Salvin). BLACK-TAILED ANTBIRD.

Myrmoborus lophotes (Hellmayr and Seilern). WHITE-LINED ANTBIRD.

Myrmoborus myotherinus (Spix). BLACK-FACED ANTBIRD.

Myrmoborus leucophrys (Tschudi). WHITE-BROWED ANTBIRD.

Myrmoborus lugubris (Cabanis). ASH-BREASTED ANTBIRD.

Diagnosis. Distinguished from other genera in the *longipes* clade by plumage. Males all blackish with white wing covert edges or gray with distinctive black mask; most females with similar mask. Bill wide relative to length. Differs from *Pyriglena* in tail length and bill length proportions. Domed-shaped nest differs from nest of *Myrmeciza*.

***Gymnocichla* Sclater, 1858a**

Type species. *Myiothera nudiceps* Cassin, 1850.

Included species. *Gymnocichla nudiceps* (Cassin). BARE-CROWNED ANTBIRD.

Diagnosis. Distinguished from other genera in *longipes* clade by plumage. Extensive bare crown of male and mostly unmarked black male and brown female plumages distinctive. Differs from *Pyriglena* in tail length and bill length proportions. Domed-shaped nest differs from nest of *Myrmeciza*.

***Pyriglena* Cabanis, 1847**

Type species. *Turdus leucopterus* Vieillot, 1818

Included species. *Pyriglena leuconota* (Spix). WHITE-BACKED FIRE-EYE.

Pyriglena leucoptera (Vieillot). WHITE-SHOULDERED FIRE-EYE.

Pyriglena atra (Swainson). FRINGE-BACKED FIRE-EYE.

Diagnosis. Distinguished from other genera in *longipes* clade by brilliant red eyes and by plumage and morphometrics. Males with large white interscapular patches; females with blackish tails. Distinguished from *Myotherinus*, *Gymnopithys*, *Percnostola*, and *Inundicola* by short bills and long tails and by bill length/total length and tail length/wing length ratios. Domed-shaped nest differs from nest of *Myrmeciza*.

***Percnostola* Cabanis and Heine, 1859**

Type species. *Turdus rufifrons*. Gmelin, 1789.

Included species. *Percnostola rufifrons* (Gmelin). BLACK-HEADED ANTBIRD.

Percnostola arenarum Isler, Alvarez, Isler, and Whitney. ALLPAHUAYO ANTBIRD.

Diagnosis. Distinguished from other genera in *longipes* clade by plumage. Gray males differ from all but *Myrmoborus* from which distinguished by black throats and dark crowns. Females distinguished from *Myrmoborus* by dark or contrasting crown and either lack of dark face mask or white in underparts. Differs from *Pyriglena* in tail length and bill length proportions. Domed-shaped nest differs from nest of *Myrmeciza*. Sandy soil forest habitat preference supportive.

***Hafferia* Isler, Bravo, and Brumfield gen. nov.**

Type species. *Thamnophilus immaculatus* Lafresnaye, 1845.

Included species. *Hafferia fortis* (Sclater and Salvin) *comb. nov.* SOOTY ANTBIRD.

Hafferia immaculata (Lafresnaye) *comb. nov.* BLUE-LORED ANTBIRD.

Hafferia zeledoni (Lafresnaye) *comb. nov.* ZELEDON'S ANTBIRD.

Diagnosis. Distinguished from other genera in *longipes* clade except *Pyriglena* and *Inundicola* by plumage. Male black or grayish black; female brown or brown and gray, both lacking wing covert spots. Differs from *Pyriglena* by having bare periorbital patch and lacking white interscapular patch. Differs from *Inundicola* by longer tail and shorter wings resulting in substantially larger tail length/wing length ratio. Domed-shaped nest differs from nest of *Myrmeciza*.

Etymology. We are pleased to name this genus for the late Jürgen Haffer, whose seminal contributions to Neotropical ornithology are summed up elsewhere (Winkler 2011) and whose brilliant mind and willingness to share enriched us personally over the years. The name *Hafferia* is feminine in gender. If *Hafferia* and *Inundicola* are united, we would afford priority to *Hafferia*.

***Inundicola* Bravo, Isler, and Brumfield gen. nov.**

Type species. *Thamnophilus melanoceps* Spix, 1825.

Included species. *Inundicola melanoceps* (Spix) *comb. nov.* WHITE-SHOULDERED ANTBIRD.

Inundicola goeldii (Sneathlage) *comb. nov.* GOELDI'S ANTBIRD.

Diagnosis. Distinguished from other genera in *longipes* clade except *Pyriglena* and *Hafferia* by plumage. Male black; female brown or brown and black, both lacking wing covert spots. Differs from *Pyriglena* by having bare periorbital patch and in tail length and bill length proportions. Differs from *Hafferia* by shorter tail and longer wings resulting in substantially smaller tail length/wing length ratio. Domed or partially-domed nest differs from nest of *Myrmeciza*.

Etymology. The masculine generic name is taken from the Latin *inundo* (deluge, flood) and *cola* (dwelling in), reflecting the habitat preference of the included species for seasonally flooded (*várzea*) and river-edge forest.

Overview of recommendations

The objectives of this final section are to compare recommendations to test for consistency and to provide a benchmark for replication. It is widely recognized that no specific criteria exist to delimit genera. To provide a point of reference for replication of our results, however, this section makes explicit how character states affected recommendations and incorporates additional perspective of the divergence among the proposed genera based on a time-calibrated phylogeny of the Thamnophilidae presented elsewhere (Bravo 2012).

TABLE 4. Diagnostic differences of traits within and between clades. 0 = no differences between genera; 1 = some genera differ; 2 = all genera differ. “Song” = loudsong. The Result column identifies the number of genera recommended and whether they exist or are new. “New” includes any changes from the existing (Remsen *et al.* 2013) classification, and thus includes revived as well as new names. See text for definitions of clades and genera.

Comparison	Plumage	Morpho metrics	Song	Habitat	Foraging	Tail/wing	Nest	Result
within <i>Myrmorchilus</i> clade	2	1	2	2	0	1	1	1 existing, 3 new
<i>hemimelaena</i> clade and sister clade	2	2	0	0	2	0	2	1 existing, 1 new
<i>ferruginea</i> clade and sister clade	2	0	1	0	0	1	2	1 new
within <i>Hylophylax</i> clade	2	2	2	0	0	2	2	2 existing
within <i>Sclateria</i> clade	2	2	0	0	2	2	0	1 existing 1 new
within <i>exsul</i> clade	2	1	2	0	1	0	0	3 new
<i>Myrmeciza longipes</i> and sister clade	2	0	0	2	0	0	2	1 existing
<i>Myrmoborus</i> clade and sister clade	2	1	0	0	0	0	0	1 existing
<i>Gymnocichla</i> and sister clade	2	1	0	0	0	0	0	1 existing
<i>Pyriglena</i> and sister clade	2	1	0	0	0	0	0	1 existing
<i>Percnostola</i> and sister clade	2	1	0	1	0	0	0	1 existing
<i>immaculata</i> and <i>melanoceps</i> clades	0	2	0	0	0	0	0	2 new

Table 4 compares differences found in seven traits. Difference in plumage characters is most consistent in the diagnoses. The comparison between the *immaculata* and *melanoceps* clades is the only exception. The second most common is morphometrics. Morphometric differences were commonly used in earlier generic descriptions, but they were typically imprecise. The fewer morphometric differences compared to plumage differences in Table 4 undoubtedly reflect our more severe threshold for distinguishing morphometric differences.

The currently recognized genera of *Myrmoborus*, *Gymnocichla*, and *Pyriglena* are distinguished from all the Pyriglenini only by plumage although also from some genera in the tribe by morphometrics and from *Myrmeciza* by nest architecture and habitat (Table 4). These genera have had a solid history of recognition, so plumage distinctions may be said to reflect a minimum threshold for acceptance. At the other extreme, the recommended genera in the *Myrmorchilus* clade differ to some extent in all traits except foraging. The two genera in the *Hylophylax* clade (both currently recognized) are the next most differentiated. Except for those provided for the *immaculata* and *melanoceps* clades, newly recommended genera are distinguished not only by plumage but also by characters in at least one of three categories—nest architecture, tail/wing movements, and song structure—that we consider intrinsic. Characteristics relating to habitat and foraging behavior are less clearly intrinsic, and in our diagnoses we describe differences in them as supporting characters.

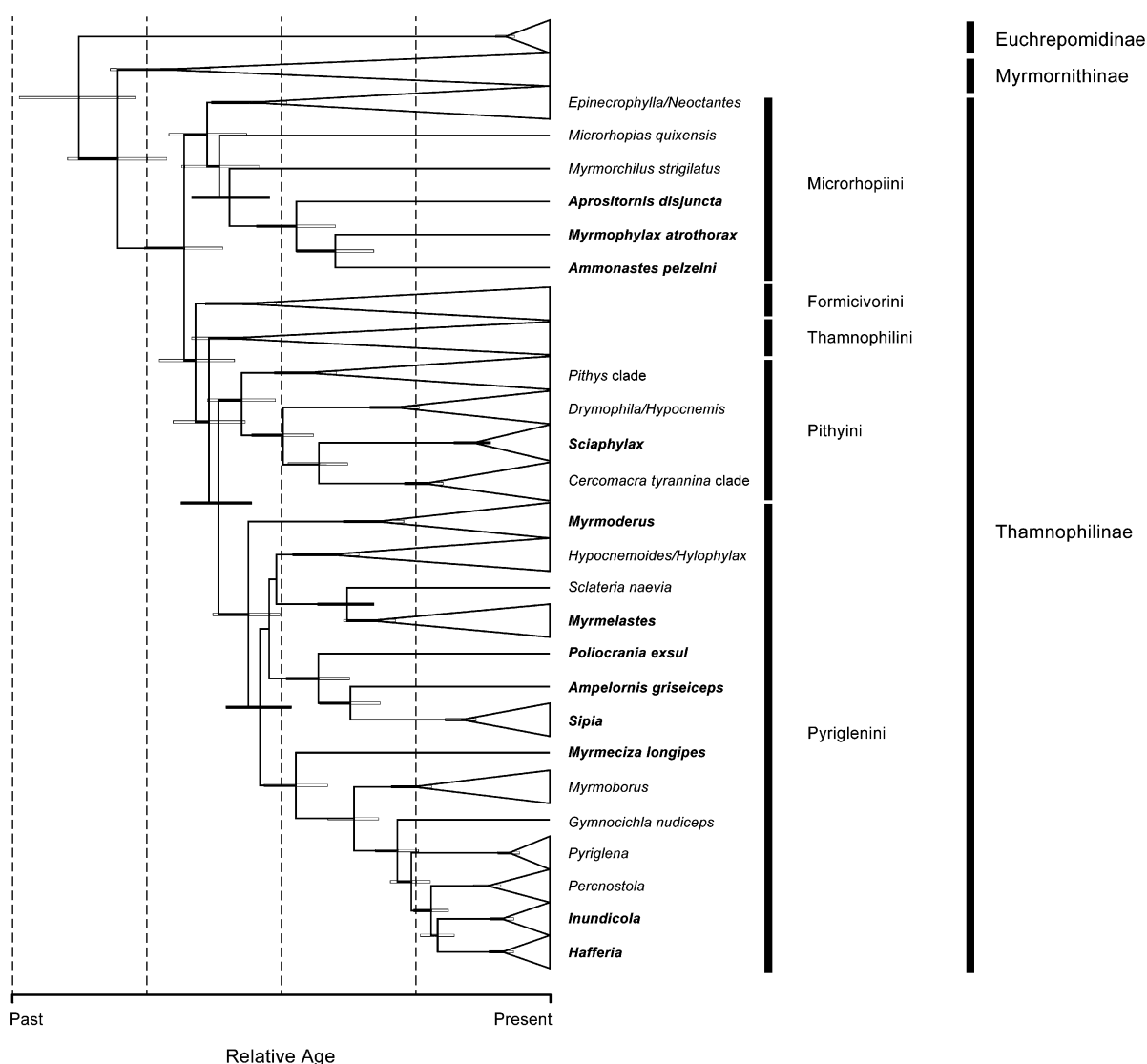


FIGURE 3. Simplified time-calibrated chronogram of the Thamnophilidae showing relative ages of former members of the genus *Myrmeciza* and the main radiations in the family. Estimated stem ages of newly designated monotypic genera suggest that they diverged long ago from their closest relatives and provide additional support for their phenotypic, ecological, and behavioral distinctiveness. Bars at nodes indicate the 95% highest posterior density for the inferred divergence time estimates (Bravo 2012).

To provide additional perspective on the recommendations, the extent of diagnostic differences among genera was compared to the relative age of different clades in a time-calibrated species-level phylogeny of the entire family (Bravo 2012; Fig. 3). The two clades that resulted in various monotypic genera are old, especially the one containing *Myrmorchilus*-*Aprositornis*-*Myrmophylax*-*Ammonastes*. The estimated crown age of this clade overlaps with the crown age range estimated for the entire subfamily Thamnophilinae (ca. 215 species), and is similar to that of the principal tribes included therein. This explains why these genera are extremely different from each other and from the rest of the family. Likewise the estimated split of *Poliocrania* from *Ampelornis* and *Sipia* is quite old; its age is estimated as half of that of the family. The most recent age of partitioning of recommended genera involves the unresolved split of *Percnostola*, *Hafferia*, and *Inundicola*. As can be seen in Table 4, of all the recommended genera, *Hafferia* and *Inundicola* are distinguished by the fewest phenotypic characters. Future studies may find strong support for their sister relationship in which case they could be united under *Hafferia*. The estimated age of their divergence, however, is similar to that of other well-established genera in the family.

Of the 21 genera diagnosed, nine are monotypic. As stated in the introduction, we recognize the drawback of monotypic genera. When merited, however, a monotypic genus has value in identifying birds that do not have an extant close relative and that differ from others in morphology and behavior. As shown on Table 4, multiple diagnostic characteristics distinguish the nine monotypic genera, and recommendations are supported by their age relative to that of the family and its main radiations. In addition, because species limits in the Thamnophilidae are in need of reassessment (Remsen 2005), they actually may not represent monotypic taxa. At least three monotypic genera (*Myrmophylax*, *Sclateria*, and *Myrmeciza*) are highly likely to consist of multiple species. New information on ecology and behavior, in conjunction with increased morphological and phylogeographic data, will facilitate our continuing quest for accurate and informative thamnophilid genera.

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