



Isleria, a new genus of antwren (Aves: Passeriformes: Thamnophilidae)

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Abstract

A comprehensive molecular phylogenetic analysis of the family Thamnophilidae indicated that the genus *Myrmotherula* is not monophyletic. The clade composed of *M. guttata* and *M. hauxwelli* is only distantly related to other members of the genus and should be removed from *Myrmotherula*. The phenotypic distinctiveness of the clade argues against merging it with its sister group *Thamnomanes* and no generic name is available for the *guttata-hauxwelli* clade. Consequently, we describe the genus *Isleria* for these two species, and designate *Myrmothera guttata* as its type species.

Key words: *Myrmotherula*, *Isleria*, phylogeny, Thamnophilidae, antwrens

The genus *Myrmotherula* Sclater is one of the most species-rich avian genera in the New World (Ridgely & Tudor, 1994; Stotz *et al.*, 1996). Up to 35 species have been recognized (Zimmer & Isler, 2003) and additional species likely remain undescribed (e.g. Krabbe *et al.*, 1999). All species of *Myrmotherula* are small, short-tailed antwrens, but ecological, behavioral, and plumage differences among species have led to the recognition of different species assemblages within the genus (Hackett & Rosenberg, 1990; Ridgely & Tudor, 1994; Zimmer & Isler, 2003). Recent phylogenetic studies demonstrated conclusively that the traditional genus *Myrmotherula* did not represent a monophyletic group, suggesting that the recognized assemblages represent distinct evolutionary lineages that may have converged on similar morphotypes (Hackett & Rosenberg, 1990; Irestedt *et al.*, 2004; Isler *et al.*, 2006; Brumfield *et al.*, 2007). A subset of eight species, known as the “stipple-throated assemblage,” was recently placed in a new genus, *Epinecrophylla*, based on molecular, morphological, vocal, ecological, and behavioral evidence (Isler *et al.*, 2006).

A comprehensive molecular phylogeny of the Thamnophilidae shows that the polyphyly of *Myrmotherula* is more pervasive than previously acknowledged (Bravo *et al.* unpubl. data; Figs. 1, 2), which emphasizes the necessity of a thorough taxonomic revision of the genus. Here, we present phylogenetic results that illustrate the polyphyly of *Myrmotherula* (*sensu* Isler *et al.* 2006), the type species of which is *M. brachyura* (Hermann, 1783), and demonstrate that *M. guttata* (Vieillot, ca. 1825) and *M. hauxwelli* (Sclater, 1857) should be placed in a new genus. Neither of these species is the type of a previously erected genus (Cory & Hellmayr, 1924); consequently, we describe a new genus, as follows:

Isleria gen. nov.

Type species. *Myrmothera guttata* Vieillot, ca. 1825.

Included species. *Isleria guttata* (Vieillot, ca. 1825) *comb. nov.*, Rufous-bellied Antwren; *Isleria hauxwelli* (Sclater, 1857) *comb. nov.*, Plain-throated Antwren.

Diagnosis, morphology. Small birds of the family Thamnophilidae typically 8.5–11g and 8.5–9.5 cm long (Zimmer & Isler, 2003); rectrix 1 length 22–24.5 mm; rectrix 1 width 5.3–6.3 mm; wing chord 50–53 mm; primary

10 length 33–37 mm; secondary 1 length 43–46.5 mm; bill length from nares to tip 8.5–9.5 mm; bill width at nares 3–4 mm; bill depth at nares 3.3–3.8 mm; tarsus length 18–20 mm; hallux length 11.5–13 mm (measurements from LSUMZ 84823, 109924, 109926, 161753, 165714; MPEG 45899, 45900, 51034). Sexually dimorphic in plumage, males predominantly gray and females brown. Distinguished from all other small antwrens primarily by the presence of conspicuous white or buffy distal markings on the tertiary feathers of both males and females. The lack of any plumage markings on the head, underparts, and upperparts of either sex also makes *Isleria* fully diagnosable from *Myrmotherula gularis* Spix, the stipple-throated antwren assemblage (*Epinecrophylla*), and the streaked antwren assemblage (*Myrmotherula*, sensu Isler *et al.* 2006). *Isleria* species have longer and larger tarsi, feet, and toes than other species of *Myrmotherula* except *M. gularis*, and shorter tails than all other antwrens except those in the streaked assemblage. The lack of markings on the breast and back makes *Isleria* diagnosable from other small antbirds with conspicuous distal spots on the tertiaries, such as *Hylophylax* Ridgway and *Dichrozona* Ridgway, and its smaller size distinguishes *Isleria* from *Megastictus* Ridgway (18–21 g; Zimmer & Isler, 2003).

Etymology. We take great pleasure in naming this genus after Morton and Phyllis Isler in recognition of their outstanding contributions to the knowledge of the taxonomy and systematics of Neotropical birds, especially antbirds of the family Thamnophilidae. Their milestone syntheses of tanager biology (Isler & Isler, 1987), antbird vocalizations (Isler & Whitney, 2002), and antbird biology (Zimmer & Isler, 2003) have provided solid foundations for the advancement of scientific knowledge of these groups. In addition, their numerous studies of vocal variation in antbirds (e.g. Isler *et al.*, 1997, 1999, 2001, 2005, 2007; Isler & Whitney, 2011) have not only improved our understanding of species limits within the group, but have provided methodological guidelines to incorporate vocal and geographic data to better understand taxonomy, systematics, and evolutionary processes in the family (Isler, 1997; Isler *et al.*, 1998). The Islers' enthusiasm to learn, collaborate, and share their extraordinary knowledge of bird biology has become their trademark, and made them role models for upcoming generations of ornithologists. The name *Isleria* is feminine in gender.

Molecular analyses. Here, we present a subset of taxa from a densely sampled molecular phylogeny of the Thamnophilidae (including 214 of 220 species) to show that *I. guttata* and *I. hauxwelli* are only distantly related to the *Myrmotherula* clade. Taxon sampling (Table 1) for this subset includes 39 individuals representing 28 species and 19 genera (13% and 40% of the family, respectively), and includes samples of the following species included in or recently split from *Myrmotherula*: *M. brachyura* (2; type species), *M. multostriata* Sclater (1), *M. axillaris* Vieillot (2), *M. menetriesii* Orbigny (1), *M. gularis* (2), *Epinecrophylla haematonota* Sclater (1; type species), *E. erythrura* Sclater (1), *Isleria guttata* (5), and *I. hauxwelli* (5). Samples of *Isleria* cover the full extent of the distribution of both species and represent all subspecies currently recognized. For outgroups we used *Chamaeza campanisona* Lichtenstein (Formicariidae; UWBK KGB14), *Hylopezus berlepschi* Hellmayr (Grallariidae; FMNH 322345), and *Melanopareia elegans* Lesson (Melanopareidae; LSUMZ B-5245/5246), and the tree was rooted between ingroup and outgroup.

Total DNA was extracted from 25 mg of pectoral muscle using the Qiagen DNeasy kit, following the manufacturer's protocol. Based on the methods described in Brumfield *et al.* (2007) we amplified and sequenced three mitochondrial genes (NADH dehydrogenase subunit 2 – ND2, 1041 bp; NADH dehydrogenase subunit 3 – ND3, 351 bp; cytochrome *b* – cytb, 842 bp) and one autosomal nuclear intron (β -fibrinogen intron 5 – β F5, 554 bp). We also amplified two coding nuclear genes (*recombination activation gene 1* – RAG1, 2872 bp; *recombination activation gene 2* – RAG2, 1142 bp) following the methods described in Groth and Barrowclough (1999) and Barker *et al.* 2002. Additionally, some sequences were obtained from previous publications of our own work (Brumfield & Edwards, 2007; Brumfield *et al.*, 2007; Moyle *et al.*, 2009; Gómez *et al.*, 2010). Analyses were conducted using a concatenated six-gene alignment containing 6802 bp.

To avoid the risk of over-parameterizing our estimate of phylogeny, 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 then calculated the Akaike Information Criterion (AIC) for each partition and established that the most informative scheme is the fully partitioned dataset (16 partitions; the nuclear intron and each codon position for each coding gene are treated separately). To evaluate nodal support of the fully partitioned dataset we conducted a rapid bootstrap analysis in RAxML using 1000 bootstrap replicates. The resulting maximum-likelihood tree indicates that *Isleria* is not closely related to *Myrmotherula* or *Epinecrophylla*, but instead is sister to *Thamnomanes* Cabanis (Fig. 1).

TABLE 1. Ingroup taxa used in this study with frozen tissue collection voucher number. Tissue collections: LSUMZ—Louisiana State University Museum of Natural Science, Baton Rouge; USNM—United States National Museum of Natural History, Smithsonian Institution, Washington; FMNH—Field Museum of Natural History, Chicago; UWBM—University of Washington Burke Museum, Seattle; AMNH—American Museum of Natural History, New York City; INPA—Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

Species	Subspecies	Tissue No.	Locality
<i>Cymbilaimus lineatus</i>	<i>intermedius</i>	LSUMZ B-18168	Bolivia: Santa Cruz
<i>Mackenziaena leachii</i>	monotypic	USNM B-5986	Argentina: Misiones
<i>Taraba major</i>	<i>melanurus</i>	FMNH 321773	Peru: Madre de Dios
<i>Thamnophilus doliatus</i>	<i>radiatus</i>	UWBM RTB390	Bolivia: Santa Cruz
<i>Megastictus margaritatus</i>	monotypic	LSUMZ B-6836	Peru: Loreto
<i>Neotantes niger</i>	monotypic	FMNH 321806	Peru: Cusco
<i>Dysithamnus mentalis</i>	<i>emiliae</i>	FMNH 392443	Brazil: Pernambuco
<i>Thamnomanes ardesiacus</i>	nominate	LSUMZ B-6896	Peru: Loreto
<i>Thamnomanes saturninus</i>	nominate	FMNH 389947	Brazil: Rondônia
<i>Thamnomanes caesius</i>	<i>glaucus</i>	USNM B-9482	Guyana: Barima-Waini
<i>Thamnomanes schistogynus</i>	nominate	LSUMZ B-992	Bolivia: La Paz
<i>Epinecrophylla haematonota</i>	nominate	LSUMZ B-4579	Peru: Loreto
<i>Epinecrophylla erythrura</i>	<i>septentrionalis</i>	LSUMZ B-5474	Peru: San Martín
<i>Myrmotherula brachyura</i> 1	monotypic	LSUMZ B-4889	Peru: Loreto
<i>Myrmotherula brachyura</i> 2	monotypic	LSUMZ B-20305	Brazil: Amazonas
<i>Myrmotherula multostriata</i>	monotypic	LSUMZ B-12968	Bolivia: Santa Cruz
<i>Myrmotherula gularis</i> 1	monotypic	LSUMZ B-16938	Brazil: São Paulo
<i>Myrmotherula gularis</i> 2	monotypic	FMNH 330815	Brazil: São Paulo
<i>Myrmotherula axillaris</i> 1	<i>luctuosa</i>	FMNH 392444	Brazil: Pernambuco
<i>Myrmotherula axillaris</i> 2	nominate	LSUMZ B-55209	Suriname: Sipaliwini
<i>Myrmotherula menetriesii</i>	nominate	LSUMZ B-9759	Bolivia: Pando
<i>Isleria hauxwelli</i> 1	nominate	LSUMZ B-10787	Peru: Ucayali
<i>Isleria hauxwelli</i> 2	<i>clarior</i>	FMNH 392044	Brazil: Mato Grosso
<i>Isleria hauxwelli</i> 3	<i>clarior</i>	LSUMZ B-36639	Brazil: Rondônia
<i>Isleria hauxwelli</i> 4	<i>suffusa</i>	LSUMZ B-4270	Peru: Loreto
<i>Isleria hauxwelli</i> 5	<i>hellmayri</i>	FMNH 391378	Brazil: Pará
<i>Isleria guttata</i> 1	monotypic	USNM B-14413	Guyana: East Berbice-Corentyne
<i>Isleria guttata</i> 2	monotypic	FMNH 391375	Brazil: Amapá
<i>Isleria guttata</i> 3	monotypic	AMNH DOT-3042	Venezuela: Amazonas
<i>Isleria guttata</i> 4	monotypic	INPA A-1258	Brazil: Amazonas
<i>Isleria guttata</i> 5	monotypic	INPA A-1766	Brazil: Roraima
<i>Dichrozona cincta</i>	monotypic	FMNH 391144	Bolivia: La Paz
<i>Herpsilochmus sticturus</i>	monotypic	USNM B-5228	Guyana: Cuyuni-Mazaruni
<i>Terenura sharpei</i>	monotypic	LSUMZ B-39086	Bolivia: Cochabamba
<i>Cercomacra tyrannina</i>	nominate	LSUMZ B-2273	Panama: Darién
<i>Sclateria naevia</i>	nominate	FMNH 391418	Brazil: Amapá
<i>Myrmeciza pelzelni</i>	monotypic	LSUMZ B-7523	Venezuela: Amazonas
<i>Myrmornis torquata</i>	nominate	FMNH 389880	Brazil: Rondônia
<i>Phaenostictus mcleanmani</i>	nominate	LSUMZ B-2135	Panama: Darién

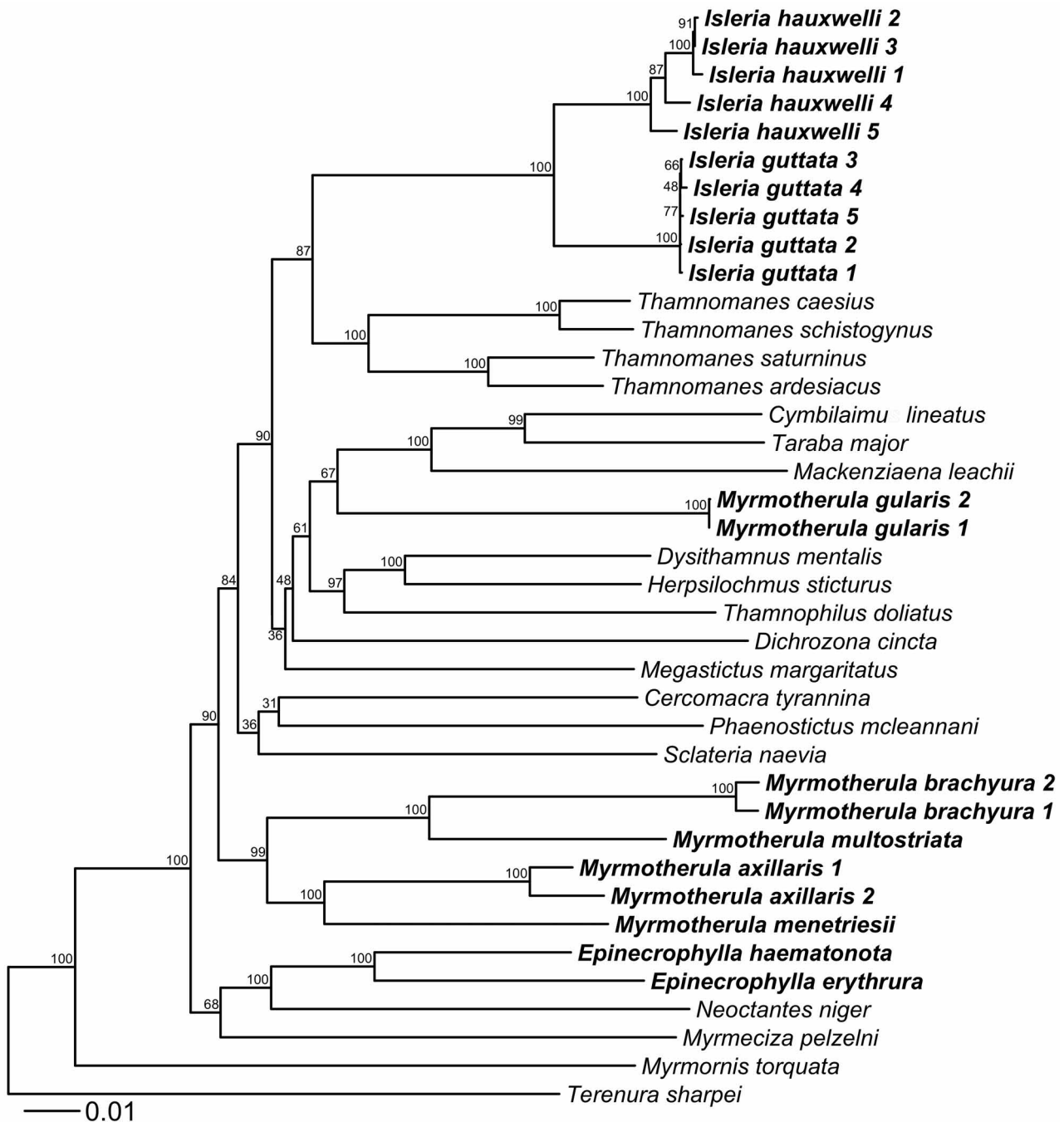


FIGURE 1. Maximum-likelihood phylogeny of a subset of the Thamnophilidae showing that *Isleria* is not closely related to *Myrmotherula* or *Epinecrophylla*. Numbers at each node indicate bootstrap support based on 1000 maximum-likelihood replicates.

Using the same partition strategy followed in the likelihood analysis, we also performed a Bayesian analysis as implemented in Mr. Bayes 3.1.2 (Huelsenbeck & Ronquist, 2001) on the Cipres Science Portal (Miller *et al.*, 2010). To determine the best nucleotide substitution model for each partition, we used PAUP* (Swofford, 2003) to obtain likelihood values for the 24 substitution models featured in MrModeltest 2.3 (Nylander, 2004). Based on the comparison of the AIC scores for each partition, we determined that the GTR + Γ + I model was the best fit for all codon positions of ND2 and the second codon position of ND3. GTR + Γ provided the best fit for the third codon position of RAG1 and RAG2, the third codon position of ND3 and *cytb*, and the nuclear intron BF5. GTR + I was the best fit for the second codon position of *cytb*; SYM + Γ + I provided the best fit for the first codon position of *cytb*; SYM + Γ was the best fit for the first codon position of ND3; HKY + Γ + I was the best fit for the first codon

position of RAG2; and HKY + I was the best model for the second codon position of RAG1 and RAG2 and the first codon position of RAG1. We ran our analysis using 4 runs, 4 chains, 2×10^7 generations with a sample frequency of 1000, a burn-in of 20%, and chain temperature of 1.75. The use of the “compare” function of AWTY online (Wilgenbusch *et al.*, 2004) informed us that in all four runs we obtained highly similar levels of convergence. In addition, through the “slide” command we were able to establish that subsamples of the chains were sampling trees in proportion to their posterior probability. These two tests suggest that our phylogenetic hypothesis via Bayesian methods was satisfactory. The topology of the phylogenetic tree is virtually identical to that of the tree obtained through maximum-likelihood and also supports the separation of *Iseria* from *Myrmotherula* or *Epinecrophylla* (Fig 2).

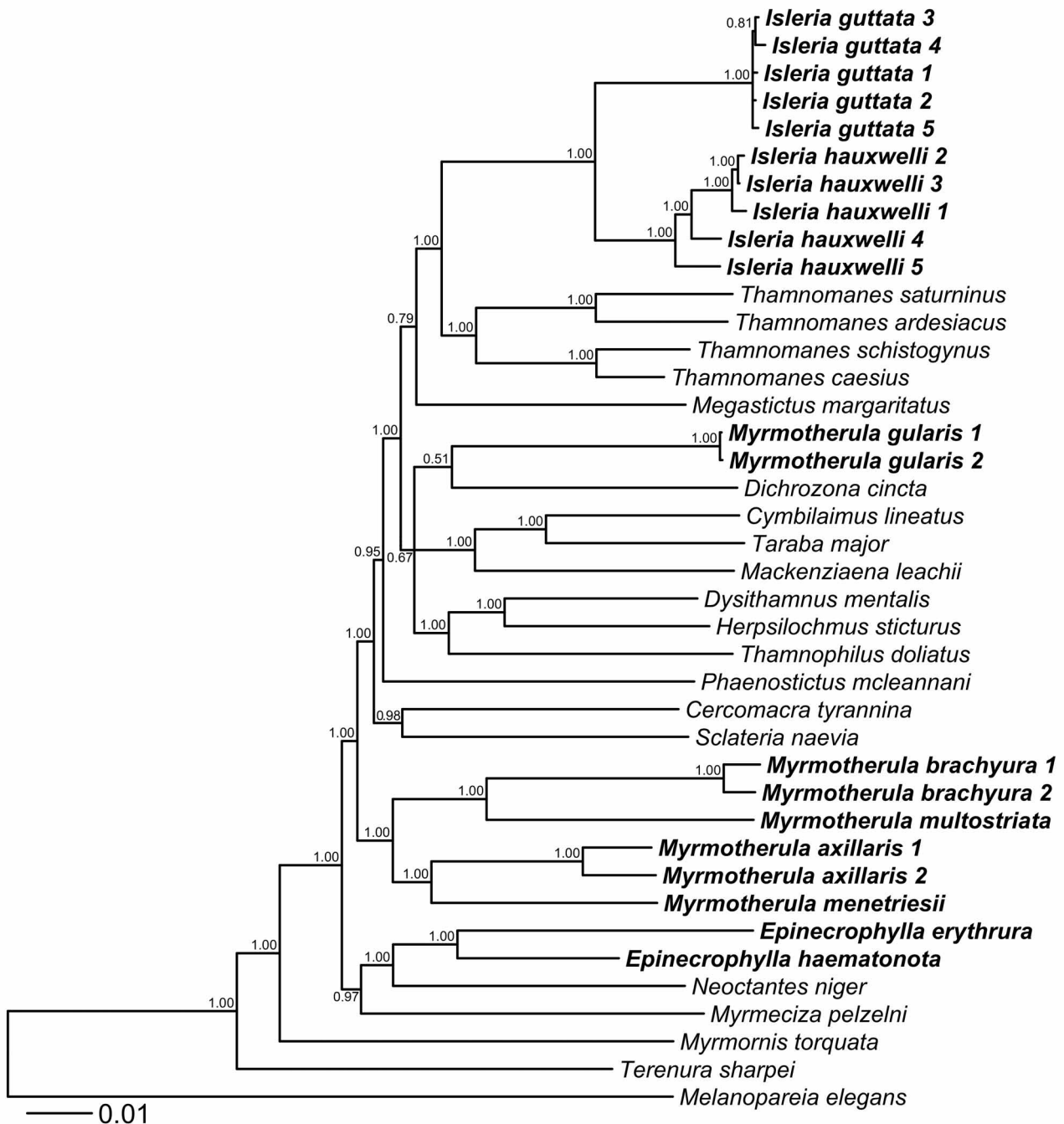


FIGURE 2. 50% Majority-rule Bayesian consensus tree of a subset of the Thamnophilidae showing that *Iseria* is not closely related to *Myrmotherula* or *Epinecrophylla*. Numbers at each node indicate posterior probability values.

Both analyses indicated that *I. guttata* and *I. hauxwelli* are sister species and that they are distantly related to *Myrmotherula* and *Epinecrophylla*. *Iseria* and the genus *Thamnomanes* form sister groups embedded within a

larger clade that contains a variety of morphologically, ecologically, and behaviorally distinctive genera such as *Sclateria* Oberholser, *Phaenostictus* Ridgway, *Dichrozona*, *Thamnophilus* Vieillot, *Herpsilochmus* Cabanis, *Dysithamnus* Cabanis, *Taraba* Lesson, and others. This result confirms that previously recognized assemblages (Zimmer & Isler, 2003) within *Myrmotherula* represent independent evolutionary units and are not necessarily closely related. In this case, it had already been suggested that *I. guttata* and *I. hauxwelli* not only constitute a different assemblage (Ridgely & Tudor, 1994) but could represent a separate evolutionary unit because of differences in plumage, vocalizations, ecology, and foraging behavior (Zimmer & Isler, 2003).

An alternative treatment for the species placed in *Iseria* would be to merge them into *Thamnomanes*, but morphological, behavioral, vocal, and ecological differences do not warrant such taxonomic treatment. First, species of *Thamnomanes* lack markings on the apexes of wing coverts, tertials, and tail, whereas such markings are conspicuous in both species of *Iseria*. Second, both species of *Iseria* are much smaller (8.5–12 g) than species of *Thamnomanes* (16–21 g; Zimmer & Isler, 2003). Third, all species of *Thamnomanes* are known to be active sentinel participants in mixed-species flocks that forage in the understory and midstory (mostly up to 8 m above ground), whereas species of *Iseria* usually forage away from mixed-flocks and mostly below 3 m (Pearson, 1977; Munn & Terborgh, 1979; Schulenberg, 1983; Stotz, 1990; Rosenberg, 1993; Zimmer & Isler, 2003). Finally, loudsongs of species of *Thamnomanes* are long series of notes that fall in pitch at the end before dropping into a final rattle or raspy note, whereas *Iseria* loudsongs are simpler and composed of repetitive whistles that become shorter at the end of the song (Isler & Whitney, 2002; Zimmer & Isler, 2003). This level of differentiation is similar to that observed between other sister genera in the Thamnophilidae, and supports the separation of *Thamnomanes* and *Iseria*. Therefore, our decision to create a new genus (*Iseria*) is supported by the non-monophyly of the genus *Myrmotherula*, morphological, behavioral, and ecological differences with *Thamnomanes*, and the lack of an available genus name for *I. guttata* and *I. hauxwelli*.

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