

***Epinecrophylla*, a new genus of antwrens (Aves:
Passeriformes: Thamnophilidae)**

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Abstract.—We offer a new generic name for the stipple-throated assemblage of antwrens (Thamnophilidae) currently placed in the genus *Myrmotherula*. Molecular studies demonstrated that *Myrmotherula* is polyphyletic, with the stippled-throated group forming a clade that is not sister to any other currently recognized *Myrmotherula* species. The stipple-throated assemblage is distinguished morphologically by at least one sex having a black throat stippled white or buffy white combined with a comparatively long, unmarked tail, although three populations considered subspecies have lost one of these characters. The distinct evolution of this assemblage is supported by diagnostic behavioral characters derived from foraging behaviors, vocal repertoires, and nest architecture.

In a pioneering isozyme-derived phylogeny of antwrens (Thamnophilidae: *Myrmotherula*), Hackett & Rosenberg (1990) identified a grouping whose species shared an obvious plumage feature, the presence of numerous pale spots on a black throat of one sex or, rarely, both sexes. They termed this clade the “checker-throated” *Myrmotherula* group. Earlier, Gradwohl & Greenberg (1984) and Remsen & Parker (1984) identified three members of the group as “dead-leaf specialists” that foraged almost entirely by searching for insects in curled dead

leaves suspended above the ground. More recently, the group, now termed the “stipple-throated” assemblage, was found to possess a distinct type of vocalization used in ritualized confrontations (Zimmer & Isler 2003). A recent molecular phylogeny of the Thamnophilidae (Irestedt et al. 2004) that included two species from the stipple-throated assemblage found that those species were probably not closely related to the genus *Myrmotherula*.

A name for the stipple-throated assemblage does not exist (Cory & Hellmayr 1924). Here, we erect a genus that recognizes the monophyly and distinct nature of this assemblage.

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Epinecrophylla M. L. Isler & Brumfield,
new genus

Type species.—*Formicivora haematonota* Sclater, 1857.

Diagnosis, morphology.—Small birds of the family Thamnophilidae, typically (a few individual measurements fell outside these ranges) 9–11 cm long (flattened skin); mass 8–11 g; tail length 33–45 (mostly 38–44) mm; wing chord 47–54 mm; tarsus 15–17 mm; bill length (from nares) 8–10 mm; bill width (at nares) 3.5–4.3 mm; bill depth (at nares) 3.5–4.3 mm. All species, except *E. ornata*, are primarily brown (anterior underparts gray in most males, posterior upperparts red in some populations), lacking distinguishing markings on the crown or above the eye but with male having chin and part or all of throat black covered with small white spots (“stippling”). Both sexes have dark brown to black wing coverts whose apexes are typically marked with conspicuous white or buffy spots. Tail unmarked; irides typically pale (white, buffy, pale red); tarsi gray. The stipple-throated assemblage is distinguished from all other small antwrens, except *Myrmotherula gularis* (see Discussion), by having a stippled black throat combined with unstreaked brown plumage, contrasting dark wing coverts spotted pale, tail long and unmarked, and bill long.

Molecular analysis.—Two molecular studies (Hackett & Rosenberg 1990, Irestedt et al. 2004) that included species of both *Myrmotherula* and *Epinecrophylla* showed that they comprise at least two distinct clades that are not each others closest relative. In their isozyme study, Hackett & Rosenberg (1990) included five *Epinecrophylla* species (including representatives from four populations of *E. haematonota*), 13 *Myrmotherula* species, and eight additional thamnophilid species from eight other genera. Although the phenogram reconstructed from the isozyme data included the anomalous placement of *Pygiptila stellaris* within the

stippled-throated assemblage, a relationship not verified by Irestedt et al. (2004) or an ongoing study (Brumfield et al. in prep.), Hackett & Rosenberg’s (1990) phenogram illustrated both that the *Epinecrophylla* species grouped together and that the genus was not sister to *Myrmotherula*. Irestedt et al. (2004) included two *Epinecrophylla* species and six *Myrmotherula* species (the *Myrmotherula* tally includes *Formicivora* and *Myrmochanes*, which were found to be closely related to *Myrmotherula*). Their combined-data phylogeny provided support for the monophyly of *Epinecrophylla* and their myoglobin data suggested the genus is more closely related to *Neoctantes*, *Microrhopias*, and *Myrmorchilus* than to *Myrmotherula*.

As part of a larger study of thamnophilid phylogenetic relationships (Brumfield et al. in prep.), DNA sequences from mitochondrial and nuclear genes were collected from 104 thamnophilid species including six species from the stipple-throated group (*E. gutturalis*, *E. fulviventris*, *E. leucophthalma*, *E. spodionota*, *E. haematonota*, and *E. erythrura*) and 14 *Myrmotherula* species. Consistent with earlier studies, the analysis supported a tree in which the stipple-throated assemblage was monophyletic but not sister to the assemblage of *Myrmotherula* species. Especially significant was the finding that *Myrmotherula gularis*, a species that has sometimes been associated with the Stipple-throated group and which was omitted in the two prior molecular studies, was not a member of either the *Epinecrophylla* or *Myrmotherula* clades. Detailed methodologies on molecular data collection and analysis are available from R.T.B. and will be found in a forthcoming publication on the molecular systematics of the Thamnophilidae (Brumfield et al. in prep.).

Vocal analysis.—A distinct behavioral difference between *Epinecrophylla* and *Myrmotherula* species is the presence/

absence of a song type and related display. In ritualized confrontations, individuals of *Epinecrophylla* species face each other about 30 cm apart, lower the head, fluff out the back plumage, and pivot from side to side, incessantly delivering a vocalization that is distinct from the loudsong (Zimmer & Isler 2003). This type of behavior and associated vocalization is not known to occur in repertoires of *Myrmotherula* species. Other vocal differences were sought in an analysis of loudsongs (terminology following Willis 1968). A loudsong for the eight *Epinecrophylla* species was measured and compared to a loudsong of each of 25 *Myrmotherula* species and six additional populations that were selected to reflect intraspecific vocal variation in three species. One hundred and four vocal characters were derived from spectrogram measurements and from ratios of measurements. Following decision rules set out in earlier papers (e.g., Isler et al. 1998, 1999), diagnostic vocal differences between loudsongs of species of the two genera were found solely in frequency levels; *Epinecrophylla* species loudsongs were delivered at higher frequencies. In particular, when values were sorted in ascending order, there was no overlap between the two groups of species in the frequency measurement taken at the point of maximum intensity. Arrays of other measures of frequency (e.g., frequencies at highest point of individual notes) were consistent with that finding, except for values for *Myrmotherula minor* whose apparent loudsong is highly aberrant.

Nest architecture.—Nest architecture provides another invaluable clue to evolutionary history (Sheldon & Winkler 1999). The value of nest characters in reconstructing avian relationships has been demonstrated in the Furnariidae, a closely related suboscine family (Zyskowski & Prum 1999). Though not yet subject to a similarly rigorous phylogenetic analysis, preliminary organization of

nest descriptions for the Thamnophilidae suggests that nest architecture in this family also offers insights into phylogeny (Zimmer & Isler 2003). Nests known for three *Epinecrophylla* species are domed- or oven-shaped nests with oblique or side entrances; nests of the remaining five species are unknown. Of the 14 *Myrmotherula* species for which nests have been described (nests of 13 species are unknown), all are deep cups, with the depth often approaching the width (Zimmer & Isler 2003). Although nests of fewer than half of the *Epinecrophylla* species are known, this apparent major difference in nest architecture provides supporting evidence for the separation of species into the two genera.

Foraging behavior.—Curled dead leaves suspended in the vegetation are abundant in many Neotropical forests and provide a specialized opportunity for avian foraging, thus adding to species diversity (Terborgh 1980). Testing this concept in an elevational transect in Bolivia, Remsen & Parker (1984) identified a number of dead-leaf searchers which they grouped into three categories: Specialists (>75% of observations), Regular Users (25–75% of observations), and Occasional Users (<25% of observations). The two *Epinecrophylla* species in the area were among the Specialists. Rosenberg (1990a, 1990b, 1997) extended these studies further in three locations and showed that what separated dead-leaf Specialists, including three *Epinecrophylla* species, from other birds that inspected dead leaves less often was their highly stereotyped manipulation of the dead leaves with their bills or feet. Numerous other studies (e.g., Greenberg & Gradwohl 1997, Stotz 1990, other papers listed in Zimmer & Isler 2003) also reported that all eight *Epinecrophylla* species forage almost exclusively at isolated dead-leaf clusters. In contrast, *Myrmotherula* species typically perch-glean or sally-glean arthropods from a variety of surfaces including live leaves,

stems, twigs, moss, and vines (Zimmer & Isler 2003). No *Myrmotherula* species is a dead-leaf Specialist. Although *M. guttata*, *M. hauxwelli*, *M. behni*, *M. urosticta*, *M. snowi*, and *M. longipennis* are Regular Users and probe dead leaves with their bills, they do not manipulate them in the manner of *Epinecrophylla* species. In addition, *M. iheringi* is a Regular User in bamboo, and a number of other species (*M. longicauda*, *M. gularis*, *M. axillaris* outside southeastern Brazil, *M. schisticolor*, *M. sunensis*, *M. minor*, *M. menetriesii*, *M. assimilis*) probe dead-leaf clusters occasionally. Interestingly, in southeastern Brazil, where no *Epinecrophylla* species occurs, *M. axillaris luctuosa* is a Regular User but strikes the dead-leaf clusters with its bill to dislodge insects rather than manipulating them in the manner of *Epinecrophylla* species. The distinctive foraging specialization of *Epinecrophylla* species further supports their placement in a distinctive genus.

Etymology.—The feminine generic name is taken from the Greek *epi* (on), *necro* (dead) and *phyllo* (leaf), meaning “on the dead leaf,” reflecting the strong predilection of members of the genus to search for insects on dead hanging leaves.

Discussion

Placement of the new genus within the taxonomic sequence of the Thamnophilidae awaits further study, especially molecular analyses. Both Irestedt et al. (2004) and the ongoing study (Brumfield et al. in prep.) support a sister relationship between *Epinecrophylla* and *Neotantes*. The following species, following the sequence and English names of Remsen et al. (31 January 2006) are included in the genus:

Epinecrophylla fulviventris (Lawrence, 1862) Checker-throated Antwren
Epinecrophylla gutturalis (Sclater & Salvin, 1881) Brown-bellied Antwren

Epinecrophylla leucophthalma (Pelzeln, 1869) White-eyed Antwren
Epinecrophylla haematonota (Sclater, 1857) Stipple-throated Antwren
Epinecrophylla fjeldsaai (Krabbe, Isler, Isler, Whitney, Alvarez, & Greenfield, 1999) Brown-backed Antwren
Epinecrophylla spodionota (Sclater & Salvin, 1880) Foothill Antwren
Epinecrophylla ornata (Sclater, 1853) Ornate Antwren
Epinecrophylla erythrura (Sclater, 1890) Rufous-tailed Antwren

Populations of *E. ornata* differ from the other seven *Epinecrophylla* species in the following ways: male throat solid black; female throat black spotted white except in *E. o. hoffmannsi* in which the female lacks this feature; more extensively gray plumage in *E. o. atrogularis* and *E. o. meridionalis*; shorter tail (33–38 mm); and rectrices tipped white in the nominate form and in *E. o. saturata*.

In our considerations, we paid particular attention to *Myrmotherula gularis*, a species endemic to southeastern Brazil that superficially bears resemblance to members of the stipple-throated assemblage, in having a black throat spotted white (male) or a black and white spotted throat (female), extensively brown plumage, and dark wing coverts apically tipped white. Our molecular study found *M. gularis* not to be a member of the stipple-throated clade nor sister to it. In addition, other morphological and behavioral characteristics of *M. gularis* were inconsistent with those of *Epinecrophylla* species. The tail of *M. gularis* is considerably shorter (25–28 mm) than any *Epinecrophylla* species, its vocal repertoire lacks the agonistic song typical of *Epinecrophylla* repertoires; its nest is a deep cup rather than a dome; and it typically perch-gleans and sally-gleans in live vegetation near the ground rather than foraging in hanging dead leaves (Zimmer & Isler 2003). The evidence clearly demonstrates that the

stippled throat of *M. gularis* is an example of homoplasy and that *M. gularis* is not a member of the stipple-throated assemblage. The generic placement of *M. gularis* awaits further results of molecular studies now underway.

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