

A new species of *Epinecrophylla* antwren from the Aripuanã-Machado interfluvium in central Amazonian Brazil with revision of the “stipple-throated antwren” complex

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Early in the focused investigation of the avifauna of the Aripuanã-Machado interfluvium (2000–2003), BMW determined that a form of *Epinecrophylla*⁴ (then *Myrmotherula*) *haematonota* was restricted to this “speciation block,” later termed a “mini-interfluve” (Cohn-Haft *et al.* 2007), and was apparently isolated from the nearest other members of the *haematonota* complex by the formidable barrier of the Rio Madeira. The loudsong of this population was audibly distinct from that of *E. h. amazonica* on the opposite bank of the Madeira and differed even more conspicuously from those of relatively distant *E. h. haematonota* and *E. h. pyrrhonota*, across the Rio Solimões/Marañón and in upper Amazonia. Analysis of a sufficiently robust sample of recordings to document these observed vocal distinctions in concert with results of morphological and DNA-based phylogenetic analyses showing appreciable differentiation in some of these parameters has convinced us that this restricted Aripuanã-Machado population is most appropriately introduced at the species level within a revised *E. haematonota* complex. We propose to name it:

Epinecrophylla dentei

Roosevelt Stipple-throated Antwren

Choquinha-do-rio-roosevelt (Portuguese)



Holotype.— Museu de Zoologia da Universidade de São Paulo (MZUSP) 80591, adult female from Brazil: Amazonas; left bank of the Rio Roosevelt in the municipality of Novo Aripuanã at “Esperança trail” (08°29’00”S/60°59’22”W); elevation about 110 m; collected 26 September 2007 by Vítor de Q. Piacentini and Luís Fábio Silveira, prepared by Emerson Boaventura. Voice not recorded. Pectoral muscle tissue preserved in ethanol (MZUSP 80591), field number 106. Hologenotype (Chakrabarty 2010) sequences of the mitochondrial gene NADH subunit 2 (ND2, 1041 bp) deposited in GenBank (KC768944).

Diagnosis: Morphology.— Alphanumeric color designations determined through direct comparison with Munsell soil color charts (1994); colors in quotation marks are chart designations. Adult females of *E. dentei* are readily distinguished from adult *E. h. amazonica* by the buffy (“very pale brown” [10YR 8/2]) contour feathers of the throat *contra* white in *E. h. amazonica*. Both taxa present black in the basal (non-contour) feathers of the throat, producing the distinctly streaked pattern, which is lacking or inconspicuous in females of *E. h. pyrrhonota*. Adult females have belly “yellowish brown” (10YR 5/6), notably distinct from the paler and grayer “very pale brown” (10YR 7/3) of adult female *E. h. amazonica* from the left bank of the upper Rio Madeira, but females from the region of the Rio Juruá appear to be indistinguishable by color of the posterior underparts. Males may be weakly distinguished from those of *E. h. amazonica* by tail more nearly concolor with the upperparts (*contra* olive-gray and contrasting more strongly with the reddish upperparts in *E.*

h. amazonica); and weakly from *E. h. pyrrhonota* by the overall paler upperparts. **Voice.**— The loudsong differs diagnostically (Isler *et al.* 1998) in pace from those of other taxa in the *E. haematonota* complex and individual note structure is nearly 100% diagnostic (described below). Selected audio files for inter-taxon comparisons, including those used for spectrograms in Krabbe *et al.* (1999) and this paper, are archived at the Internet Bird Collection (IBC) website. **Genetic divergence.**— Separated from its sister-taxon *E. haematonota amazonica* by approximately 3.1% uncorrected sequence divergence in the mitochondrial gene ND2. Also, ND2 uncorrected sequence divergence from all other members of the *haematonota* complex is 5–6.3% (see *Phylogenetic relationships*, below).

Distribution.— Restricted to central Amazonian Brazil on the right bank of the Rio Madeira in the Aripuanã-Machado interfluvium: from the left bank of the Rio Aripuanã upriver to its confluence with the Rio Roosevelt, from which point upriver it is known only from the left bank of the Roosevelt in the state of Amazonas and extending into northwest Mato Grosso south and west to the right bank of the Rio Machado (or Ji-Paraná) in the state of Rondônia; southern range limits unknown (Fig. 1).

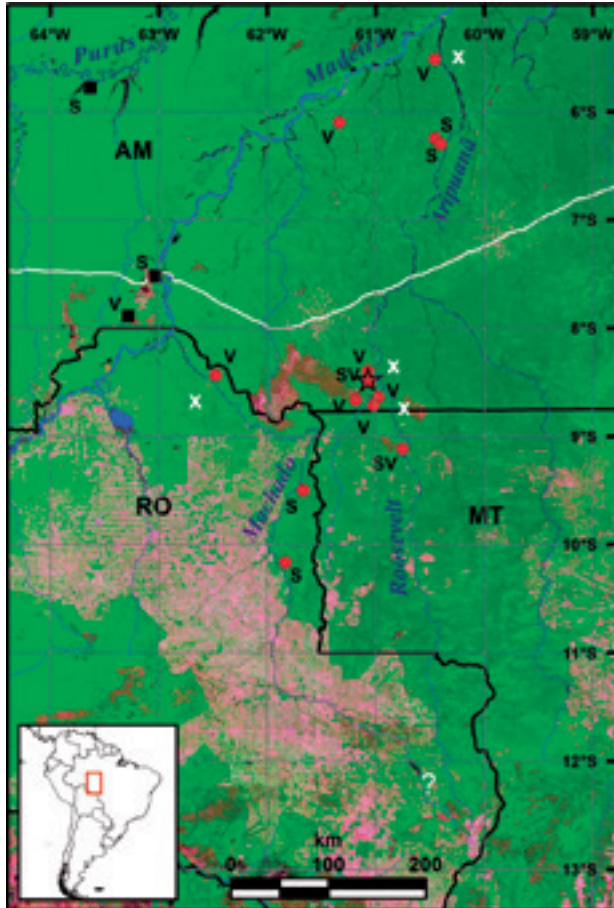
Description of holotype.— See color illustration. Several photos (Fig. 2) and some high-definition video of both sexes in the hand and are archived at the MZUSP. Alphanumeric color designations determined through direct comparison with Munsell soil color charts (1994); colors in quotation marks are chart designations. Plumage fresh and unworn, tail and wing not in molt; skull 100%

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⁴ Genus *Epinecrophylla* - new genus (Isler *et al.* 2006), split from *Myrmotherula* 8: 577.



ossified. Crown slightly redder than “dark yellowish brown” (10YR 3/4) with tiny feathers at base of bill and above eye slightly buffier; facial and auricular region mottled slightly paler, contrasting with crown. Nape slightly redder than crown but contrasting strongly with uniformly “dark red” (brighter than 2.5YR 4/8) mantle, scapulars, back, rump, and uppertail coverts; innermost secondaries (overlying folded wing) washed with this same color but slightly browner overall and narrowly tipped paler. Tail and primary stack concolor with crown, thus contrasting equally strongly with red upperparts; central rectrices ever so slightly paler tipped. Tail graduated, outer rectrices 6.4 mm shorter than central pair. Main color of throat about the same as facial region, slightly whiter than “very pale brown” (10YR 8/2) and marked with five 1.5 mm wide black streaks formed almost entirely by contrasting basal feathering (i.e., contour feathers are essentially unmarked), the central streak about 19 mm long and about 10 mm longer than the shortest, outermost ones. Breast becoming slightly darker and browner than throat, nearest “light yellowish brown” (10YR 6/4) blending to darker “yellowish brown” (10YR 5/6) through the posterior underparts. Upperwing coverts nearest “very dark brown” (10YR 2/2) with more olivaceous bases, each feather marked with a bold, yellowish-buff (nearest 10YR 7/8) spot at the tip encompassing both webs about equally. Alula and tiny feathers at bend of wing blackish with narrow but sharply contrasting buff-white margins on distal webs becoming slightly wider toward the feather tip. Primary coverts blackish with minute reddish tips. Underwing coverts plain whitish blending toward color of breast at their margins. **Soft part colors:** bill dark gray; tarsus and feet gray; iris gray. **Standard measurements:** total length (just before specimen preparation) 108 mm; bill (culmen from base at skull) 14.6 mm; bill from anterior edge of nares 9.6 mm; bill width at anterior edge of nares 3.5 mm; bill depth at anterior edge nares 3.9 mm; wing (chord) 50.3 mm; tail 36.7 mm; tarsus 15.5 mm; mass 9.0 g.

Etymology.—Emílio Dente (1919-1995) certainly was one of the most important collectors and specimen preparators in the history of Brazilian ornithology. He worked in several different research institutions, including the Department of Zoology of the Secretary of Agriculture (today the Museum of Zoology of the University of São Paulo) and the Adolfo Lutz Institution in São Paulo, collecting mostly ornithological material in many different regions of Brazil, mainly in Amazonia. Outstanding among the many collections made by Dente were the thousands of specimens secured on the Rio Capim in Pará and in the state of Roraima, all assiduously prepared and labeled with his im-

peccable penmanship. With the name of this antwren we honor Emilio Dente not only for having been a productive collector, but also for his highly refined specimen preparation technique for both birds and mammals, a talent that he shared with many up-and-coming taxidermists in Brazil, leaving a legacy in this field, and for being the upright, honest person he always was. Dente died in Itapetinga, São Paulo, at the age of 76.

The English and Portuguese names reference the type locality of *E. dentei* on the Rio Roosevelt, which forms the southeastern distributional barrier.

REMARKS

Type series.—The allotype of *Epinecrophylla dentei* is MZUSP 80589, adult male from the same locality as the holotype. Remaining paratypes of *E. dentei* are the following twenty-seven specimens: MZUSP 80587 male, 80588 male, 80590 male, and 80592 female (all from the type locality); 92307 female and 92308 male (MT, left bank Rio Roosevelt); Museu Paraense Emílio Goeldi (MPEG) 30864 male (AM, right bank Rio Madeira, km 969 on Jacareacanga-Humaitá highway, Rio 9 de Janeiro); 58721 male, 58722 female, 58723 female, 58724 female, 58725 male, 58726 male, and 58728 male (AM, Humaitá [right bank Rio Madeira], Parintintin Indigenous Territory); 59023 male and 59024 female (AM, Humaitá [right bank Rio Madeira], Ipixuna Indigenous Territory); 71105 male and 71141 female (RO, Machadinho d’Oeste, right bank Rio Ji-Paraná); Instituto Nacional de Pesquisas da Amazônia (INPA) 707 female and 751 male (AM, left bank rio Aripuanã, rio Arauazinho, igarapé Três Jacus, 127 km south Novo Aripuanã); 1829 male and 1831 female (AM, left bank rio Aripuanã, igarapé Arauazinho, 130 km south Novo Aripuanã); 1788 male (RO, REBIO Jaru, right bank rio Ji-Paraná [Machado], mouth of igarapé Tarumã); 1789 male (RO, REBIO Jaru, right bank rio Ji-Paraná, “trilha da torre”). Louisiana State University Museum of Natural Science (LSUMNS) 182832 male, 182833 male, and 182834 female (MT, left bank Rio Roosevelt).

There is no appreciable variation in the series of adult females, but it appears that immatures have plainer throats (i.e., less obvious streaked pattern). Males show some variation in the extent of black and white in the throat feathers, especially those toward the posterior edge of the patterned patch: some individuals appear darker-throated owing to less extensive white tips on individual feathers. It appears that iris color of adult females is clear grayish or pale beige, and that of adult males, a much darker brownish-red; bill shapes of the sexes may also differ slightly but this requires further investigation (Fig. 2). Immature males (skull ossifications less than 50%) have grayish eyes.

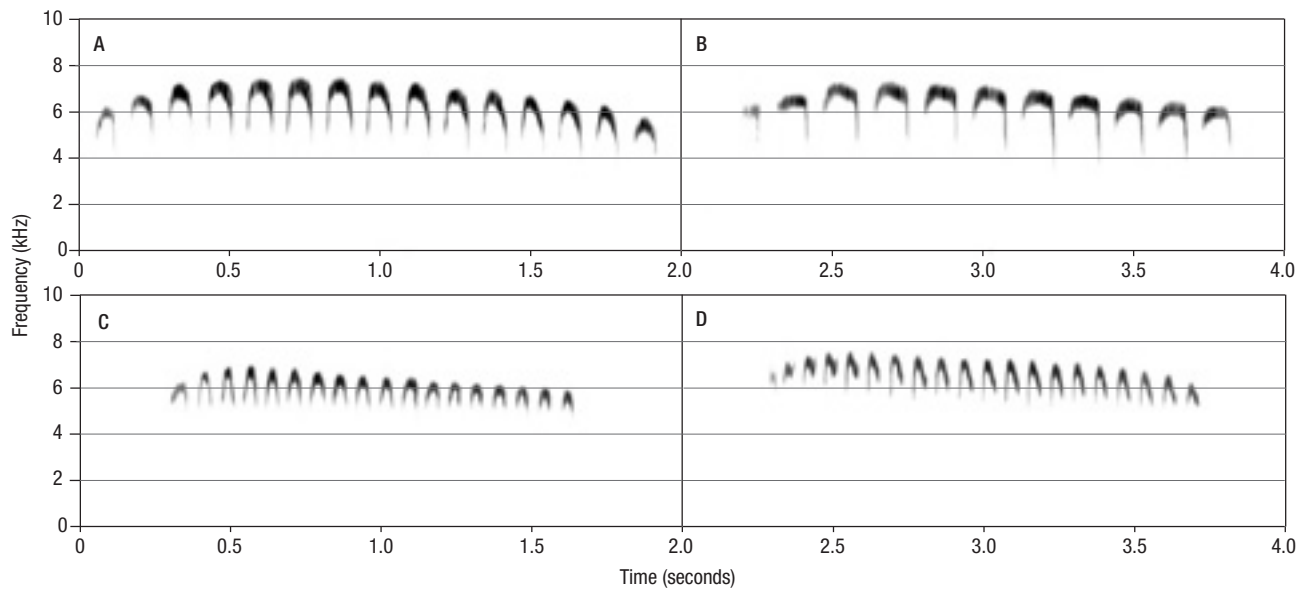
Ecology and behavior.—*Epinecrophylla dentei* is, like all other members of the genus, a dead-leaf foraging specialist as defined by Rosenberg (1990); specific foraging behavior closely matches that described in detail for *E. spodionota* by Whitney (1994). One interesting difference in its foraging behavior is an apparent association with *Megastictus margaritatus* (Pearly Antshrike), interpreted by Whittaker (2009) as *Epinecrophylla* following *Megastictus*, but perhaps only seasonally. The asso-



Figure 1. Geographic distribution of specimens examined in the *Epinecrophylla haematonota* complex in south-central Amazonian Brazil. Red dots = *E. dentei*. Red star = type locality of *E. dentei* on the left bank of the Rio Roosevelt. Black squares = *E. amazonica*. Adjacent letters provide documentation: S = specimen; V = vocal recording. A white X marks places where BMW has searched for *E. dentei* and is confident that it is absent although it occurs immediately across the Aripuanã/Roosevelt or Machado rivers at these points; a white ? in the narrow headwaters region of the Machado and Roosevelt marks an area that has not been inventoried where the species is expected to occur and range limits need to be determined. Black lines mark the boundaries of Brazilian states as indicated by their official abbreviations: AM = Amazonas; RO = Rondônia; MT = Mato Grosso. The federal highway BR-230 (“Transamazônica”) is shown in white.

Figure 2. *Epinecrophylla dentei* female (left) and male captured in a mist-net on the left bank of the Rio Roosevelt in Mato Grosso, Brazil. Note the different iris colors and bill shapes of the sexes. Further sampling will be required to confirm whether this apparent sexual dimorphism is constant in the species. Photo by Fabio Schunck (11 August 2011).

Figure 3.
Loudsongs of taxa in the *Epinecrophylla haematonota* complex. (A) *E. dentei*: Brazil: Mato Grosso; left bank Rio Roosevelt (Whitney BMW C 0462 in Isler inventory). (B) *E. amazonica*: Bolivia: Pando; Río Abuña (Parker TAP 034 006). (C) *E. pyrhoneota*: Venezuela: Bolívar; Río Caura (Whitney BMW 071 005). (D) *E. haematonota*: Brazil: Amazonas; Reserva Natural Palmarí (Whitney BMW 185 041). See Krabbe et al. (1999) for a representative spectrogram of the loudsongs of *E. spodionota* and *E. h. fjeldsaai*.



ciation of these two thamnophilids has been observed by BMW on a number of occasions in several different months of the year, and it has not been clear who is following whom. It seems plausible that they both benefit, the antwren taking advantage of the vigilance of the much more sedentary antshrike to avoid predation while investigating complex dead-leaf structures, and the watchful, “sit-and-wait” foraging strategy of the antshrike (Whitney and Rosenberg 1993) perhaps aided by the antwren’s invasive foraging behavior flushing arthropods from hiding in dead foliage. Over the course of many years of fieldwork, this association has never been observed by BMW anywhere a member of the *haematonota* complex occurs together with *Megascictus* outside the range of *E. dentei*, and it seems to be a behavioral characteristic of both species unique to Aripuanã-Machado populations. BMW suspects that the overlap of widespread and ecologically almost identical *E. leucophthalma* (White-eyed Antwren) with *E. dentei* throughout the range of the latter in forest habitat with little heterogeneity in the understory may have driven *dentei* to minimize niche overlap by associating less with mixed-species flocks, where accompanied by vigilant *Thamnomanes* antshrikes, and more with non-flocking *Megascictus*. In other regions of overlap of *Epinecrophylla leucophthalma* and *E. haematonota*, such as southern Amazonia west of the Madeira, greater habitat heterogeneity (in particular, the abundance of bamboo and fluvially perturbed forest) seems to account for their slight segregation (Zimmer and Isler 2003, BMW *pers. obs.*). No genetic mixing has been observed or is to be expected between these two *Epinecrophylla* antwrens; they are in sister-clades (GAB *pers. obs.*) and have highly differentiated songs (BMW *pers. obs.*). Thus, previously established reproductive barriers have been operative in fostering their overlap in secondary contact despite essentially identical foraging ecologies. The stomach of one male (MZUSP 92308) contained only insects, including fragments of Hymenoptera (Formicidae), Orthoptera, and larvae of either Coleoptera or Lepidoptera. The nest and eggs of *E. dentei* remain unknown. High-definition video of *Epinecrophylla dentei* in habitat may be viewed at IBC.

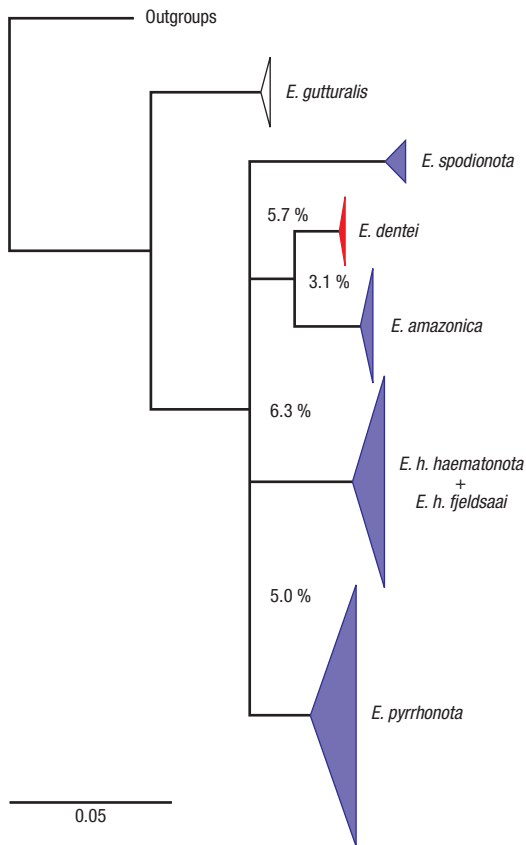
Vocalizations.— Our sample of 141 recordings of members of the *Epinecrophylla haematonota* complex was segregated into four study populations: (1) *pyrrhoneota* north of the Rio Napo and Amazon; (2) *haematonota* south of the Napo and Amazon south to the Abujao region of Ucayali in Peru east to the Rio Juruá in Amazonas and Acre in Brazil; (3) *amazonica* in the Juruá-Madeira interfluvium in Brazil extending northeast to the Purús-Madeira interfluvium just south of the Amazon and extending southwest to the Río Manu region of Peru and Pando, Bolivia; and (4) *dentei* in the region east of the Rio Madeira between the Rio Aripuanã/Roosevelt and the Rio Machado. Although we employed the names of subspecies to refer to these populations, the distributions of them are only partially consistent with cur-

rent subspecies’ range descriptions. We determined that the type of *amazonica* was collected on the right bank of the Rio Juruá (Ihering 1904, Pinto 1945).

All members of the complex deliver a large number of types of vocalizations for a small thamnophilid, and nearly all of them are consistent across populations. The only vocalization with sufficient samples that differed diagnostically was the loudsong (Fig. 3), which differed significantly (following Isler *et al.* 1998, 2007) in pace. Thus, *haematonota* ($n = 15$) and *pyrrhoneota* ($n = 22$) loudsongs were delivered at the fastest pace (means 13.0 notes/sec and 16.2 notes/sec, respectively); *amazonica* ($n = 14$) at the slowest pace (5.6 notes/sec); and the pace of *dentei* loudsongs ($n = 15$) was intermediate (7.9 notes/sec). Except for *pyrrhoneota* and *haematonota*, the average pace of the four populations differed significantly. Differences in note and interval length between *amazonica* and *dentei* barely failed the more stringent Isler *et al.* (1998) test that values would not be likely to overlap with larger samples, and note shapes (rounded crowns in *dentei*, flat tops in *amazonica*) also separated *dentei* and *amazonica* loudsongs almost perfectly in “blind tests” of spectrograms. The different note shapes are, no doubt, responsible for the subtly different auditory quality of the songs of these two. “Call-series” were a second vocal type with potential to differ substantially between some of the populations, but sample sizes were so minimal as to make them a concern only for future recording efforts.

Phylogenetic relationships and taxonomy.— DNA sequence data for the mitochondrial gene NADH subunit 2 (ND2, 1041 bp) were obtained for 50 individuals in the genus *Epinecrophylla*, representing the eight currently recognized species, and all known forms within the *E. haematonota* complex (see SI for a list of ingroup and outgroup taxa).

Phylogenies by maximum-likelihood and Bayesian inference methods (see details in SI) showed that all individuals of *E. dentei* (east of the Rio Madeira) belong, with high support, in a clade that is sister to all individuals identified as *E. h. amazonica* (west of the Madeira; Fig 4). Moreover, this clade is embedded within a well-supported larger clade containing three other genetically distinctive lineages. The first is *E. spodionota* (Andean foothills); the second contains *E. h. haematonota* with embedded *E. fjeldsaai* (south of the Rio Napo south to the Rio Maraón/Solimões); and the third *E. h. pyrrhoneota* (north of the Rio Napo and Rio Solimões). Relationships among these lineages are not well resolved, which supports the idea that *E. haematonota* is paraphyletic and genetically diverse (Fig. 4). As described by Zimmer (1932), these taxa are clearly distinguished by plumage differences which, when combined with the substantial levels of genetic diversity and some significant levels of vocal differentiation, support raising them to the species level. We suggest that the most satisfactory classification for these lineages is



to recognize five species within the complex: *E. haematonota* (Napo Stipple-throated Antwren), *E. pyrrhonota* (Negro Stipple-throated Antwren), *E. amazonica* (Madeira Stipple-throated Antwren), *E. dentei* (Roosevelt Stipple-throated Antwren), and *E. spodionota* (Foothill Stipple-throated Antwren).

Our analysis of ND2 revealed that *E. fjeldsaai* (2 specimens from proximate localities whose identity was confirmed by Krabbe *et al.* [1999]) is embedded within *haematonota* (0.5–1.2 % sequence divergence between *fjeldsaai* and closer *haematonota*), notwithstanding that we had no samples of *haematonota* from very near the range of *fjeldsaai* (see SI). We do not have a sufficient sample of loudsongs of *fjeldsaai* to determine whether it is diagnosable from that of *haematonota*. However, in its distinctive brown mantle, *fjeldsaai* presents obvious phenotypic differentiation that suggests a potential, as-yet unrecovered genetic signature. Three distinct scenarios might explain this observed pattern. First, it is possible that *fjeldsaai* and *haematonota* are not reproductively isolated and that there is substantial gene flow between them. Therefore, *fjeldsaai*'s distinctive phenotype would not represent a discrete change in plumage variation and intermediate phenotypes would be expected along their contact zone. At the time of description of *fjeldsaai* as a species, very few specimens (and no genetic analysis) were available. Second, *fjeldsaai* and neighboring *haematonota* met in secondary contact, probably across most of *fjeldsaai*'s eastern distributional margin, before achieving complete reproductive isolation but after attaining phenotypic differentiation, and now introgression is taking place. Finally, it is possible that *fjeldsaai* and *haematonota* speciated quite recently and became more or less reproductively isolated but now are showing shared ancestral polymorphism in mitochondrial genes that obscures their recent history. Genetic divergences in the autosomal nuclear intron (β fibrinogen intron 5 – β F5, 554 bp) between *fjeldsaai* and *haematonota* also show that they are genetically indistinguishable (0.1–0.4 % uncorrected sequence divergence; Bravo and Brumfield unpubl. data). At this time, because of the high similarity in mitochondrial and nuclear haplotypes between *fjeldsaai* and *haematonota*, we suggest that *fjeldsaai* is most appropriately ranked as a subspecies of *E. haematonota*.

A robust analysis of population dynamics, including assessment of the potential influence of sexual selection for brown-

backed males in the range of *fjeldsaai* acting to stem introgression, will permit a much better-informed interpretation of their evolutionary history and destiny. With acceptance of the above, novel taxonomy would come a shift in English names; we propose the above to highlight significant distributional attributes of species within the stipple-throated antwren complex. We recommend information-rich English names that unambiguously identify monophyletic lineages, even if they require as many or more syllables as does the scientific name. "Roosevelt Antwren", for example, strips away much of the utilitarian aspect of the name in the sole interest of speaking/writing fewer syllables.

Conservation.— There are no imminent threats to the survival of *Epinecrophylla dentei*, but the lack of protection of forest in the narrow headwaters of the Machado/Roosevelt/Aripuanã rivers, and the urgent need to secure adequate samples of specimens from this region expressed by Whitney *et al.* (2013) in the description of *Hypocnemis rondoni* (this volume) is echoed here.

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Figure 4. Maximum-likelihood tree topology of the *Epinecrophylla haematonota* complex within which *E. dentei* is sister to *E. amazonica*, and *E. fjeldsaai* is embedded within *E. haematonota*. Relationships among the four distinct lineages in the complex remain poorly resolved. All resolved nodes have bootstrap support values based on 1000 replicates >70 and posterior probability values >0.95.

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