Molecular Phylogenetics and Evolution 65 (2012) 287–293

Contents lists available at SciVerse ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

DNA sequence data reveal a subfamily-level divergence within Thamnophilidae (Aves: Passeriformes)

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ARTICLE INFO

Article history:
Received 12 March 2012
Accepted 18 June 2012
Available online 1 July 2012

Keywords:
New subfamily
New genus
Avian systematics
Suboscines
Antwrens
Antbirds

ABSTRACT

The Thamnophilidae is a diverse radiation of insectivorous passerine birds that comprises nearly 220 species and is mostly restricted to the lowlands and lower montane forests of the Neotropics. Current classification within Thamnophilidae relies primarily on morphological variation, but recent incorporation of molecular and vocal data has promoted changes at various taxonomic levels. Here we demonstrate that the genus *Terenura* is polyphyletic because *Terenura callinota*, *T. humeralis*, *T. spodioptila*, and *T. sharpei* are phylogenetically distant from the type species of the genus, *Terenura maculata*. More importantly, the former four species are not particularly closely related to any other thamnophilids and represent a clade that is sister to all other members of the family. Because no genus name is available for this previously undetected lineage in the Thamnophilidae, we describe the genus *Euchrepomis* for *callinota*, *humeralis*, *spodioptila*, and *sharpei*, and erect the subfamily Euchrepomidinae. We discuss the taxonomic and evolutionary significance of this divergent lineage. This study highlights the importance of taxonomic coverage and the inclusion of type taxa to redefine classifications to reflect accurately evolutionary relationships.

1. Introduction

The Thamnophilidae is a diverse radiation of insectivorous passerine birds that comprises approximately 220 species and is mostly restricted to the lowlands and lower montane forests of the Neotropics (Zimmer and Isler, 2003). Traditional classification within the family is based primarily on comparisons of plumage and morphometric proportions of external features such as bill, tail, wings, and tarsi (Cory and Hellmayr, 1924; Peters, 1951; Ridgway, 1911; Sclater, 1890). Examination of internal morphological features (e.g. the sound producing organ in birds, the syrinx) suggested that members of the family Thamnophilidae are diagnosable anatomically from other passerine families (Ames, 1971). Furthermore, molecular phylogenetic studies have shown that the family Thamnophilidae is a monophyletic group, that their closest relatives are other lineages of Neotropical suboscine passerines in the furnariid radiation, and that phylogenetic reconstructions are not entirely congruent with traditional taxonomic classification (Bravo et al., 2012; Brumfield et al., 2007; Irestedt et al., 2004; Moyle et al., 2009; Sibley and Ahlquist, 1990).

Molecular phylogenetic analyses coupled with analyses of variation of their innate songs have promoted a reappraisal of the evolutionary diversity of the Thamnophilidae with numerous taxonomic consequences. Most such changes are descriptions of new species or reassessments of species limits (e.g. Cháves et al., 2010; Isler and Whitney, 2011; and references therein). However, few studies have evaluated traditional classifications at deeper taxonomic levels (Aleixo et al., 2009; Bravo et al., 2012; Isler et al., 2006; Moyle et al., 2009) due primarily to incomplete taxonomic sampling. Moyle et al. (2009) recognized two subfamilies, Myrmornithinae and Thamnophilinae, with the former consisting of the monotypic genera *Myrmornis*, *Pygiptila*, and *Thamnistes*, and the latter comprising all remaining genera in the family except the genus *Terenura*, which they left unassigned to subfamily. Traditional linear classifications place *Terenura* near *Epinecrophylla*, *Isleria*, *Myrmotherula*, *Microrhopias*, *Herpsilochmus*, *Formicivora*, *Drymophila*, and *Hypocnemis*, with which *Terenura* shares small body size, small thin bills, and in some species, black and white streaking on the head and neck. As far as we can determine, the monophyly of the genus *Terenura* and its relationships to the adjacent genera in linear sequences have never been formally questioned. Recently, however, *Terenura sharpei* and *T. humeralis* were shown to be the sister group to all other Thamnophilidae (Bravo et al., 2012; Brumfield and Edwards, 2007; Irestedt et al., 2004; Moyle et al., 2009), but lack of samples of the type species of the genus, *T. maculata*, impeded certainty about the phylogenetic placement of *Terenura*.

Cabanis and Heine (1859–1860) named the genus *Terenura* for the species *Myiothera maculata* (Wied, 1831) of southeastern

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http://dx.doi.org/10.1016/j.ympev.2012.06.016

Brazil, which had been placed in *Formicivora* by Sclater (1858). Cabanis and Heine did not provide a diagnosis or description of their new genus, but *Terenura* translates as "soft tail" in Greek (Jobling, 2010). The species *Formicivora callinota* (Sclater, 1855) was subsequently included in *Terenura* by Taczanowski and von Berlepsch (1885) without comment, but perhaps because Sclater noted in his original description of *callinota* that "it [*callinota*] must be placed next to the Brazilian *Formicivora maculata* . . . with which it agrees in form and style of plumage." This rationale apparently led to the association of *callinota* with *maculata*. Subsequent classifications continued to place both in *Terenura*, along with three additional species described later, all noted as close relatives of *callinota* and all described in *Terenura*: *T. humeralis* (Sclater and Salvin, 1880), *T. spodioptila* (Sclater and Salvin, 1881), and *T. sharpei* (von Berlepsch, 1901). The classification of *Terenura* as containing five species remained stable until the addition of a sixth, newly discovered species: *T. sicki* (Texeira and Gonzaga, 1983). At least two phenotypic groups have been recognized within the genus based on plumage differences: the "streaked-headed" group consisting of *T. maculata* and *T. sicki*, and the "standard" *Terenura* consisting of the remaining four species (Ridgely and Tudor, 1994). The "streaked-headed" *Terenura* are restricted to the Atlantic Forest, whereas the "standard" *Terenura* are found through much of Amazonia, the Guianan shield, and mid-elevations in the Andes and southern Central American mountains (Zimmer and Isler, 2003).

Here, we present results of morphological and DNA-based phylogenetic analyses to test the monophyly of the genus *Terenura* and assess its phylogenetic position within the family. We demonstrate that *Terenura* is polyphyletic and that a subset of its members, not including the type species *T. maculata*, represents the sister clade to the rest of the Thamnophilidae. This subset of species must be placed in a separate genus for which no name is available, and they deserve to be treated as a separate subfamily. We describe a new genus for these species, place them in a new subfamily, and discuss its phylogenetic, morphological, and evolutionary distinctiveness among the Thamnophilidae.

2. Materials and methods

2.1. Taxon sampling and laboratory procedures

Our analysis is based on DNA sequences from 37 samples with physical voucher specimens housed in accessible scientific collections (Peterson et al., 2007; Table 1). They represent 31 species and 23 genera (14% and 48% of family, respectively), including samples of nominate populations of *Terenura macul*ata (3; type species), *T. callinota* (2), *T. humeralis* (2), *T. sharpei* (2), and *T. spodioptila* (1). Samples of *T. sicki* were not available to us. For outgroups we used sequences from *Pipra* spp. (Pipridae; LSUMZ B-18078/AMNH DOT-3872), *Furnarius rufus* (Furnariidae; AMNH DOT-10431), *Chamaeza campanisona* (Formicariidae; UWBM KGB14), *Hylopezus berlepschi* (Grallariidae; FMNH 322345), *Lioscelles thoracicus* (Rhinocryptidae; FMNH 390080/322412), *Pittasoma* spp. (Conopophagidae; LSUMZ B-2285/B-11863), and *Melanopareia elegans* (Melanopareiidae; LSUMZ B-5245/5246),

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 (nicotinamide dehydrogenase subunit 2 – ND2, 1041 bp; nicotinamide dehydrogenase subunit 3 – ND3, 351 bp; cytochrome b – cytb, 1045 bp) and one autosomal nuclear intron (β-fibrinogen intron 5 – βF5, 554 bp). We also amplified two coding nuclear genes (recombination activation gene 1 – RAG1, 2875 bp; recombination activation gene 2 – RAG2, 1152 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 (Bravo et al., 2012; Brumfield and Edwards, 2007; Brumfield et al., 2007; Derryberry et al., 2011; Gómez et al., 2010; Moyle et al., 2009). Analyses were conducted using a concatenated six-gene alignment containing 7025 bp.

We edited sequences using Sequencher 4.7 (Gene Codes Corporation, Ann Arbor, MI) and checked that protein-coding sequences did not include stop codons or anomalous residues. We aligned sequences using the program MAFFT v. 6 (Katoh et al., 2002), and obtained a concatenated dataset using Geneious Pro v5.5 (Drummond et al., 2011). Newly obtained sequences were deposited in GenBank (Accession numbers JX213474–JX213578).

2.2. Phylogenetic analyses

We conducted ML analyses for six 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; each codon position for each coding gene, and the nuclear intron for separate partitions). To evaluate nodal support of the fully partitioned dataset, we conducted a rapid bootstrap analysis in RAxML using 1000 bootstrap replicates under the GTR + Γ model of nucleotide substitution, following recommendations by the author in RAxML manual.

Using the same partition strategy followed in the likelihood analysis (16 partitions), we also performed a Bayesian analysis as implemented in Mr. Bayes 3.1.2 (Huelsenbeck and 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 comparison of AIC scores for each partition, we determined that: the GTR + Γ + I model was the best fit for the first codon position of ND2, cytb, and RAG1, and the second codon position of ND2, ND3, and RAG1. GTR + Γ provided the best fit for the third codon position of ND2, ND3, cytb, and RAG1, and for the nuclear intron BF5. GTR + I was the best fit for the second codon position of cytb and RAG2; SYM + Γ provided 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 third codon position of RAG2. We conducted the analysis using 4 runs, 4 chains, and 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" and "slide" functions of AWTY online (Wilgenbusch et al., 2004) were used to assess the performance of Bayesian phylogenetic inference.

2.3. Ecomorphological analyses

We measured 10 ecomorphological variables (wing length, primary 10 length, tail length, rectrix 1 width, secondary 1 length, bill length from nostril to tip, bill width at nostrils, bill depth at nostrils, tarsus length, hallux length) from 243 individuals (Appendix) representing antwrens in the genera, *Epinecrophylla*, *Isleria*, *Myrmotherula*, *Microrhopias*, *Herpsilochmus*, *Formicivora*, *Stymphalornis*, *Terenura*, *Stymphalornis,* and *Terenura*. All measurements were taken to the nearest 0.01 mm with a Mitutoyo Digimatic Point Caliper by G.A.B. Details of how they were taken can be found elsewhere (Baldwin et al., 1931; Derryberry et al., 2011). To assess how diagnosable *Terenura* is with respect to all other antwrens in ecomorphological space, we conducted a discriminant function

Table 1
Ingroup taxa used in this study with tissue collection voucher number. Tissue collections: LSUMZ—Louisiana State University Museum of Natural Science, Baton Rouge; UWBM—University of Washington Burke Museum, Seattle; USNM—United States National Museum of Natural History – Smithsonian Institution, Washington; AMNH—American Museum of Natural History, New York City; FMNH—Field Museum of Natural History, Chicago; MPEG—Museu Paraense Emílio Goeldi, Belém, Brazil; IAvH—Instituto Alexander von Humboldt, Villa de Leyva, Colombia.

Species	Subspecies	Tissue no.	Locality
Cymbilaimus lineatus	*intermedius*	LSUMZ B-18168	Bolivia: Santa Cruz
Frederickena fulva	nominate	LSUMZ B-4281	Peru: Loreto
Thamnophilus doliatus	*radiatus*	UWBM RTB390	Bolivia: Santa Cruz
Dysithamnus mentalis	*emiliae*	FMNH 392443	Brazil: Pernambuco
Thamnomanes caesius	*glaucus*	USNM B-9482	Guyana: Barima-Waini
Epinecrophylla haematonota	nominate	LSUMZ B-4579	Peru: Loreto
Myrmotherula brachyura 1	monotypic	LSUMZ B-20305	Brazil: Amazonas
Myrmotherula brachyura 2	monotypic	LSUMZ B-4889	Peru: Loreto
Myrmotherula surinamensis	monotypic	USNM B-11838	Guyana: Upper Takutu-Upper Essequibo
Myrmotherula multostriata	monotypic	LSUMZ B-12968	Bolivia: Santa Cruz
Myrmorchilus strigilatus	nominate	FMNH 392862	Brazil: Sergipe
Herpsilochmus sticturus	monotypic	USNM B-5228	Guyana: Cuyuni-Mazaruni
Microrhopias quixensis	*albicauda*	FMNH 321993	Peru: Madre de Dios
Formicivora grisea	nominate	LSUMZ B-15217	Bolivia: Santa Cruz
Formicivora melanogaster	nominate	LSUMZ B-6675	Bolivia: Santa Cruz
Formicivora rufa	*chapmani*	FMNH 391399	Brazil: Amapá
Drymophila genei	monotypic	FMNH 432972	Brazil: Minas Gerais
Hypocnemis striata	*affinis*	FMNH 391408	Brazil: Pará
Terenura maculata 1	monotypic	LSUMZ B-25885	Paraguay: Caaguazú
Terenura maculata 2	monotypic	LSUMZ B-25886	Paraguay: Caaguazú
Terenura maculata 3	monotypic	MPEG 64833	Brazil: Paraná
Terenura callinota 1	nominate	LSUMZ B-2198	Panama: Panamá
Terenura callinota 2	nominate	IAvH BT-7518	Colombia: Huila
Terenura humeralis 1	nominate	LSUMZ B-7029	Peru: Loreto
Terenura humeralis 2	nominate	LSUMZ B-7044	Peru: Loreto
Terenura sharpei 1	monotypic	LSUMZ B-39086	Bolivia: Cochabamba
Terenura sharpei 2	monotypic	LSUMZ B-22813	Bolivia: La Paz
Terenura spodioptila	nominate	USNM B-5113	Guyana: Cuyuni-Mazaruni
Cercomacra tyrannina	nominate	LSUMZ B-2273	Panama: Darién
Pyriglena leuconota	hellmayri	FMNH 334469	Bolivia: Santa Cruz
Sclateria naevia	nominate	FMNH 391418	Brazil: Amapá
Myrmeciza pelzelni	monotypic	LSUMZ B-7523	Venezuela: Amazonas
Myrmornis torquata	nominate	FMNH 389880	Brazil: Rondônia
Pithys albifrons	nominate	FMNH 391430	Brazil: Amapá
Gymnopithys rufigula	*pallida*	LSUMZ B-7512	Venezuela: Amazonas
Hylophylax naevioides	nominate	LSUMZ B-2230	Panama: Darién
Phaenostictus mcleannani	nominate	LSUMZ B-2135	Panama: Darién

analysis (DFA) using log-transformed measurements for all individuals in the data set and three grouping units: "streaked-headed" *Terenura*, "standard" *Terenura*, and all other antwrens.

3. Results

3.1. Phylogenetic analyses

The resulting maximum-likelihood and Bayesian phylogenetic trees produced identical topologies indicating that *T. callinota*, *T. humeralis*, *T. spodioptila*, and *T. sharpei* form a clade that is sister to the rest of the family, and that they are not closely related to *T. maculata* (Fig. 1). All four runs of the Bayesian analyses exhibited highly similar levels of convergence and subsamples of the chains were sampling trees in proportion to their posterior probability. Therefore, the phylogenetic hypothesis produced with Bayesian methods was satisfactory. We found that *Terenura maculata*, the type species of the genus, belongs in the subfamily Thamnophilinae and that it is closely related to members of the genus *Myrmotherula*.

3.2. Ecomorphological variation

A discriminant function analysis of 10 log-corrected ecomorphological features showed that *Terenura* comprises two morphologically distinct groups based primarily on differences in wing dimensions (Fig. 2). One group corresponds to *T. maculata* (streaked-headed), whereas the other includes *T. callinota*, *sharpei*, *humeralis*, and *spodioptila* (standard). Both groups are also diagnosable from other antwrens in morphologically similar genera (Wilks' lambda = 0.46, $F_{20,462} = 10.82$, $P = 0.00$). All *T. maculata* specimens were correctly predicted as *T. maculata*, and all "standard" *Terenura* specimens were correctly predicted as such.

3.3. New genus

No valid genus name exists for *T. callinota*, *T. humeralis*, *T. spodioptila*, and *T. sharpei* (Cory and Hellmayr, 1924); therefore, we erect the new genus:

Euchrepomis genus nov.
Type species. *Formicivora callinota* Sclater, 1855.
Included taxa. *Euchrepomis callinota* (Sclater, 1855), *Euchrepomis humeralis* (Sclater and Salvin, 1880), *Euchrepomis spodioptila* (Sclater and Salvin, 1881), *Euchrepomis sharpei* (von Berlepsch, 1901) with all of their currently named subspecies.
Diagnosis and definition. Small (7–8 g) antbirds with brightly colored (orange-rufous or yellow) rumps and lower backs that contrast strongly with the rest of the upperparts and (males) black crowns. Differs from all other Thamnophilidae in that the males have the lesser coverts in the bend of wing area bright yellow or bright orange-rufous, contrasting strongly with the rest of the wing. Also differs from all other Thamnophilidae in having the combination of brightly colored rumps and lower backs, with unstreaked upperparts and crowns. Three of the

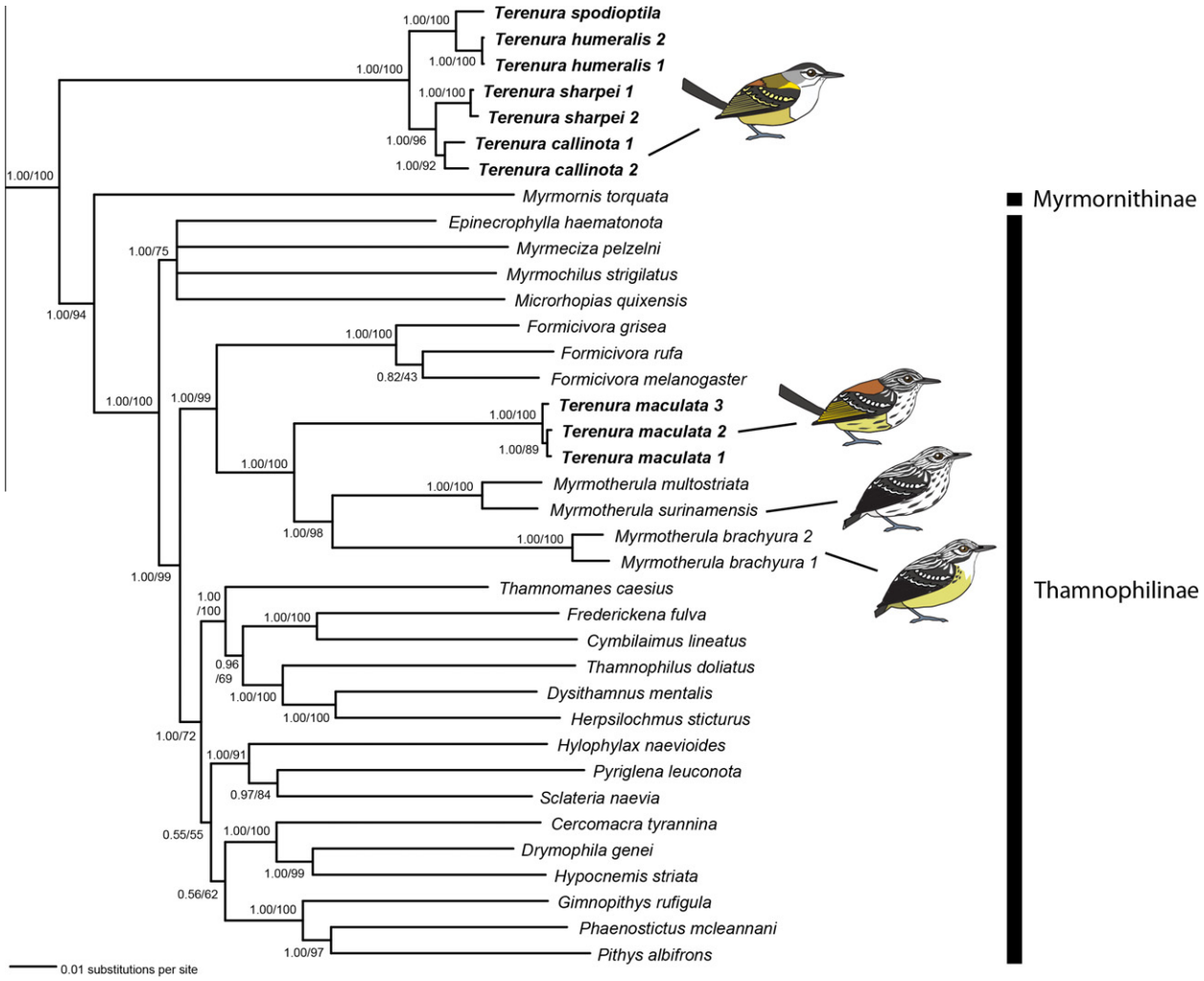

Fig. 1. 50% Majority-rule Bayesian consensus tree topology of a subset of the Thamnophilidae showing that *Terenura callinota*, *T. humeralis*, *T. spodioptila*, and *T. sharpei* are not closely related to *T. maculata*. Numbers at each node indicate posterior probability values (left) and bootstrap support values based on 1000 maximum-likelihood replicates (right). Outgroups not shown.

four species are the only species in the Thamnophilidae with bright greenish backs and margins of the remiges; these are gray in *spodioptila*, although the taxon *meridionalis*, currently treated as a subspecies of spodioptila, has distinctly olive margins of remiges (Snethlage, 1925).

Etymology. Feminine generic name derived from the Greek *euchrôs* (ruddy, bright-colored) and *epômis* (point of the shoulder). This refers to the bright yellow or bright orange-rufous coloration of the lesser secondary coverts of males; a character that, within Thamnophilidae, is unique to the members of the genus.

3.4. New subfamily

Moyle et al. (2009) divided the Thamnophilidae into two subfamilies, Myrmornithinae for *Myrmornis*, *Pygiptila*, and *Thamnistes*, and Thamnophilinae for everything else except *Terenura*, and found that *Terenura* (here *Euchrepomis*) *sharpei* was sister to all other thamnophilids. With more extensive taxon sampling, we are compelled to recognize this new genus as a separate subfamily:

Euchrepomidinae, *subfam. nov*.

Type genus. *Euchrepomis* genus nov.

Diagnosis and definition. The degree of genetic differentiation between Euchrepomidinae and the other subfamilies in the Thamnophilidae is substantial. For instance, members of *Euchrepomis* differ in sequence divergence from any other genus in the family by no less than 13.4% in cytochrome b and 18.4% in ND2 (uncorrected p-distances). Also, their level of divergence in a slowly evolving nuclear gene such as RAG1 (2.0–2.9%) is similar to that exhibited in other subfamily-level comparisons in the Furnariides (e.g. 2.1–3.0% between Rhinocryptinae and Scytalopodinae; and 2.7–2.9% among Sclerurinae, Dendrocolaptinae, Furnariinae). Also, species of *Euchrepomis* possess several morphological and behavioral distinctions. The presence of brightly colored lesser coverts is unique in the family. Conspicuous fluffing or expansion of the brightly colored feathers of the upperparts, including these bright feathers of the lesser upperwing coverts, is the principal component of apparently aggressive or territorial interactions between males. Finally, no other thamnophilid group is so restricted to foraging in the canopy, at the periphery of crowns of trees. Several other small "antwrens" in the genera *Myrmotherula* and *Herpsilochmus*, as well as the two members of true *Terenura*, regularly forage in the canopy, but all of these also range regularly into the subcanopy, which is rare for species in *Euchrepomis*.

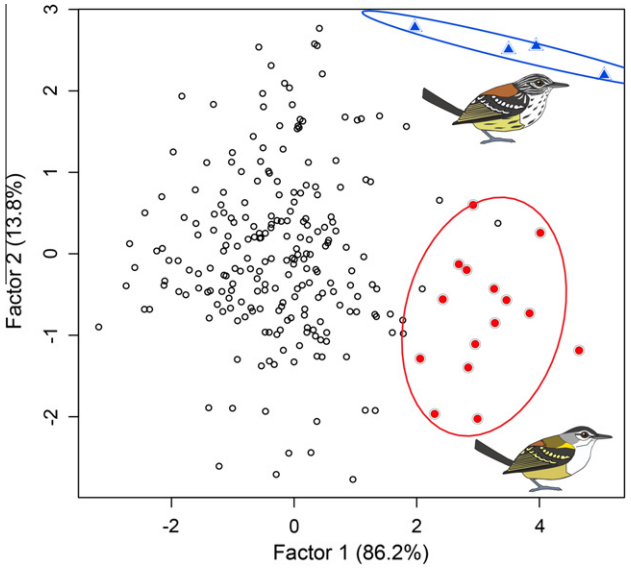

Fig. 2. Discriminant factors of ecomorphological variation of antwrens in the genera *Epinecrophylla*, *Isleria*, *Myrmotherula*, *Microrhopias*, *Herpsilochmus*, *Formicivora*, *Stymphalornis*, *Terenura*, and *Euchrepomis*. Positive values of Factor 1 represent shorter secondary 1 feathers. Positive values of Factor 2 represent shorter wings. Triangles represent specimens of *Terenura*. Solid circles represent specimens of *Euchrepomis*. Ellipses represent 95% confidence intervals.

4. Discussion

Levels of genetic divergence between *Euchrepomis* and other members of the Thamnophilidae are comparable to those between traditionally recognized subfamilies in the Furnariides. Therefore, based on Moyle et al.'s (2009) classification of the Furnariides, which was primarily based on genetic divergences and the principle of monophyly, we consider that *Euchrepomis* is not only a separate, fully diagnosable genus, but also deserves recognition as a separate subfamily (Euchrepomidinae). Although levels of morphological, ecological, and behavioral divergence seem subtler, they support the idea of *Euchrepomis* as a fully diagnosable taxonomic and evolutionary unit. We propose that the genus *Terenura* be placed in the subfamily Thamnophilinae, and based on close ecological and phenotypic similarities and their distributions, we predict that *T. sicki* will prove to be sister to *T. maculata* once sequence data become available.

Because phenotypic evolution in the family is subject to different evolutionary processes that can lead to overall morphological similarity among distant relatives (Brumfield et al., 2007; Gómez et al., 2010; Seddon, 2005; Tobias and Seddon, 2009), traditional taxonomy does not reflect phylogenetic history of the family (e.g. Bravo et al., 2012; Isler et al., 2006). In fact, morphological similarities between members of *Euchrepomis* and *Terenura* explain why the new genus has been overlooked previously. Sclater's, 1855 comment that *callinota* must be related to *maculata* is understandable; they do indeed share general shape similarities and plumage features, i.e., orange-rufous on lower back and rump, similar markings on wing coverts, yellowish flanks, and black and gray head. However, other phenotypic and ecological characteristics are consistent with the idea that *Euchrepomis* represents a unique, diagnosable unit in the family, and support a close relationship between *Terenura* and the "streaked antwrens" in the genus *Myrmotherula*.

Euchrepomis does not have the streaked plumage pattern exhibited by *Terenura maculata* and *T. sicki*, a pattern widespread among the "streaked antwrens" in the genus *Myrmotherula*. Salvin and Godman noted that the membranous nasal operculum in *maculata* mentioned by Sclater is not present in *callinota* (Salvin and Godman, 1879–1904), which exhibits open nostrils without any overhanging membrane. We noted that specimens of *callinota*, *sharpei*, and *humeralis* housed at LSUMZ and MZUSP also lack a

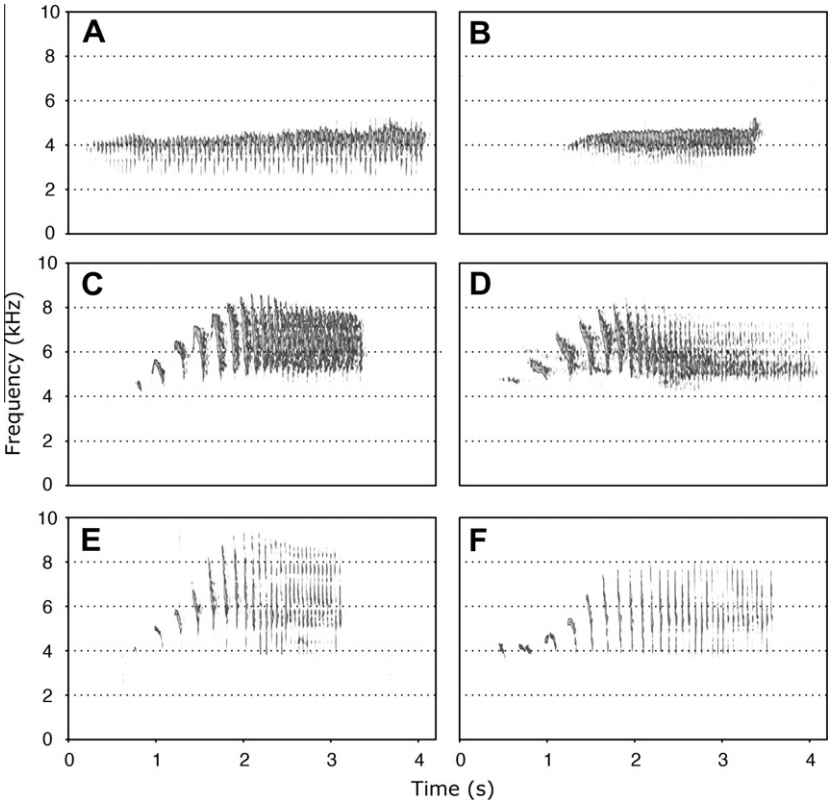

Fig. 3. Examples of loudsongs of *Terenura* (A – *maculata*; B – *sicki*) and *Euchrepomis* (C – *callinota*; D – *sharpei*; E – *humeralis*; F – *spodioptila*). Both genera are characterized by remarkably high similarity of loudsongs among all of their respective species. Recordings obtained from Isler and Whitney (2002).

membranous operculum, supporting observations by Salvin and Godman. However, we could not observe any kind of covering on *maculata* either. Also, direct examination of specimens at MZUSP revealed that tails of *Terenura maculata* specimens are softer than those of *Euchrepomis* specimens (M.A. Rego, personal communication), consistent with the meaning of the name *Terenura*.

Euchrepomis is the only genus in the family that exhibits conspicuous and contrasting orange-rufous or yellow rumps and shoulders that are actively displayed during aggressive interactions between males. Although males of both species of *Terenura* exhibit bright coloration in the upperparts, we have never observed either of them actively fluffing or otherwise displaying these feathers, even after considerable playback. *Euchrepomis* represents the only genus in the family entirely associated with the canopy and it is widely allopatric to *Terenura*.

Intrageneric similarity of loudsongs of both *Terenura* and *Euchrepomis* is remarkably high. In contrast, loudsongs show only weak intergeneric similarity. Although both possess high-pitched trills (Fig. 3), the peak frequencies of *Euchrepomis* loudsongs (5.2–6.6 kHz) are higher than those of *Terenura* (4.3–4.4 kHz), and paces of *Euchrepomis* loudsongs (9–13 notes/s) are slower than those of *Terenura* (19–22 notes/s). Given the importance of vocalizations in the diversification of the family (Seddon, 2005), these differences are not only relevant for diagnosing both genera, but suggest that these two genera have experienced distinct evolutionary histories.

Finally, this study represents another example of how traditional taxonomy based on morphological similarities can be incongruent with DNA-based phylogenetic classifications (e.g. Bledsoe, 1988; Raposo do Amaral et al., 2009). Although it had been previously suggested that *Terenura sensu lato* represented two distinct groups based on plumage differences (Ridgely and Tudor, 1994), only complete sampling with the inclusion of the type species, *T. maculata*, allowed testing the evolutionary and taxonomic validity of these groups. This highlights the importance of including samples of type taxa in both systematic and taxonomic studies.

Acknowledgments

We are grateful to curators and collection managers of the Field Museum of Natural History (FMNH), United States National Museum of Natural History (USNM), University of Washington's Burke Museum (UWBM), American Museum of Natural History (AMNH), Museu de Zoologia Universidade de São Paulo (MZUSP), Museu Paraense Emílio Goeldi (MPEG), Instituto Alexander von Humboldt (IAvH), and Instituto de Ciencias Naturales (ICN). A.M. Cuervo provided sequences for one specimen housed at Banco de Tejidos – Instituto Alexander von Humboldt (IAvH). N. Aristizábal assisted in obtaining sequences. This research was supported by grants from the Frank Chapman Memorial Fund – AMNH, the American Ornithologists' Union, the LSUMNS Big Day Fund, and LSU Biograds to GAB, NSF grants DEB-0841729 and DBI-0400797 to RTB, and DEB-1011435 to GAB. We thank N. David for his expertise in constructing new genus and subfamily names, and J.A. Chaves for his great assistance designing and executing the antbird illustrations. This manuscript was greatly improved thanks to valuable comments provided by A.M. Cuervo and two anonymous reviewers.

Appendix A

Antwren specimens measured at scientific collections. Louisiana State University Museum of Natural Science (LSUMZ); Museu Paraense Emílio Goeldi (MPEG); Museu de Zoologia Universidade de Zoologia (MZUSP); Instituto de Ciencias Naturales (ICN); American Museum of Natural History (AMNH); United States National Museum of Natural History (USNM); Instituto Alexander von Humboldt (IAvH).

Epinecrophylla fulviventris (LSUMZ 163587, 163589, 178011); *E. gutturalis* (LSUMZ 53090, MPEG 66252, 66254, 66258); *E. leucophthalma* (LSUMZ 52029, 137147, 150759, 172928); *E. haematonota* (LSUMZ 109932, 109934, 109938, 132702); *E. fjeldsaai* (LSUMZ 83109); *E. spodionota* (LSUMZ 87968, 87969, 116881, 116883); *E. ornata* (LSUMZ 92379, 157127, MPEG 53893, 61345, 61346); *E. erythrura* (LSUMZ 78457, 83126, 87970, 116880); *Isleria guttata* (LSUMZ 165714, MPEG 45899, 45900, 51034); *I. hauxwelli* (LSUMZ 84823, 109924, 109926, 161753); *Myrmotherula brachyura* (LSUMZ 102097, MZUSP 84846, 84847, 84848); *M. obscura* (LSUMZ 109908, 109916, 109917, 156501); *M. ignota* (LSUMZ 162115, 164145, 178016, 178017); *M. ambigua* (MPEG 53081); *M. sclateri* (LSUMZ 132665, MPEG 39992, 39995, 39997); *M. surinamensis* (MPEG 20262, 20264, 21102, 21103); *M. multostriata* (LSUMZ 115269, 115270, 116332, 137133); *M. pacifica* (LSUMZ 108320, 108321, 177733, ICN 31097, 31576); *M. cherriei* (ICN 37229, 37230); *M. klagesi* (LSUMZ 165771, B-25560, B-25561, MCH470/471); *M. longicauda* (LSUMZ 102100, 102101, 173982, 173983); *M. gularis* (LSUMZ 52761, MZUSP 81489, 81490, 81160); *M. axillaris* (MPEG 56945, LSUMZ 115305, 132726, 108334, 177734, 156522, 156519, 178447); *M. schisticolor* (LSUMZ 108330, 116897, 138712, 173985); *M. sunensis* (LSUMZ 83141, 83142, 83145, 83146); *M. minor* (MZUSP 5477, 28292, 60794, 70595); *M. longipennis* (LSUMZ 109965, MPEG 35222, 53675, 59604); *M. urosticta* (LSUMZ 113494, MZUSP 76217, 76218, 76219); *M. iheringi* (LSUMZ 98334, MZUSP 76979, MPEG 60199, 60200); *M. grisea* (LSUMZ 90719, 90721, 179663, 179664); *M. unicolor* (LSUMZ 68022, MPEG 34454, MZUSP 2188, 67316, 79957); *M. behni* (LSUMZ 175410); *M. menetriesii* (LSUMZ 109978, 153368, 161758, MPEG 38067, 38212); *M. assimilis* (LSUMZ 109982, 119767, MPEG 56696, 56697); *Herpsilochmus sellowi* (MZUSP 80770, 83298, MPEG 54039, 54040, 57350); *H. pileatus* (MZUSP 76468, 76469, 76470, MPEG 54042, 54043); *H. atricapillus* (LSUMZ 124185, MZUSP 31766, 83300, 84393); *H. motacilloides* (LSUMZ 106002, 106003, 128513, 128514); *H. parkeri* (LSUMZ 116902, 116903, 116906, 116908); H. sticturus (MPEG 64995, 64996, 65342); *H. dugandi* (LSUMZ 92402, 128512); *H. stictocephalus* (MPEG 64992, 62993, 64994); *H. gentryi* (LSUMZ 172933, 172935, 172938, 172939); *H. dorsimaculatus* (LSUMZ 53111, MPEG 53110, 56389, 64711); *H. roraimae* (LSUMZ 175411); *H. pectoralis* (LSUMZ 71677, MPEG 52474, MZUSP 2848, 6836, 14256); *H. longirostris* (LSUMZ 150769, 150770, 150771, MPEG 55927); *H. axillaris* (LSUMZ 84851, 87989, 169888, 179675); *H. rufimarginatus* (LSUMZ 68025, 153373, MZUSP 25652, 73351, 76222); *H.* sp. nov. 1 (LSUMZ B-25578, LSUMZ B-25579); *H.* sp. nov. 2 (LSUMZ 179661); *Microrhopias quixensis* (LSUMZ 119771, 132764, 163580, MPEG 56388); *Formicivora iheringi* (AMNH 243055, MZUSP 7639); *F. grisea* (LSUMZ 150778, 150780, 175413, MPEG 53486); *F. serrana* (LSUMZ 65176, MZUSP 10385, 25243); *F. littoralis* (MPEG 46318, 46320, 73507); *F. melanogaster* (LSUMZ 124196, MZUSP 81536, 83297, 84396); *F. rufa* (LSUMZ 124198, MZUSP 79625, 79626, 79627); *F. grantsaui* (MZUSP 76677, MPEG 60420, 60419); *Stymphalornis acutirostris* (MZUSP 78797); *S.* sp. nov. (MZUSP 78797, 78788, 78790); *Terenura maculata* (MZUSP 49910, 49912, 62534, USNM 515966); *Euchrepomis callinota* (LSUMZ 84862, 87995, 108346, 173966); *E. humeralis* (LSUMZ 119769, 132786, 170889, MPEG 63205); *E. sharpei* (LSUMZ 90722, 90723, 162682, 171313); *E. spodioptila* (MPEG 53109, IAvH 11286, USNM 625209).

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