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SYSTEMATICS OF THE OBLIGATE ANT-FOLLOWING CLADE OF ANT BIRDS (AVES: PASSERIFORMES: THAMNOPHILIDAE)

MORTON L. ISLER,^{1,4} GUSTAVO A. BRAVO,^{2,3} AND ROBB T. BRUMFIELD²

ABSTRACT.—Results of a comprehensive molecular phylogeny of the family Thamnophilidae were consistent with earlier findings that almost all obligate army-ant-followers of the family form a monophyletic group that contains five well-supported clades and encompasses six currently recognized genera: *Phaenostictus*, *Pithys*, *Willisornis*, *Gymnopathys*, *Rhegmatorhina*, and *Phlegopsis*. A comparative analysis of seven suites of morphological, behavioral, and ecological traits within the context of the phylogeny reinforced the validity of five of these genera, but results for the sixth, *Gymnopathys*, were internally inconsistent and required the description of a new genus, *Oneillornis*. Received 22 November 2013. Accepted 5 July 2014.

Key words: antbirds, *Oneillornis*, phylogeny, systematics, Thamnophilidae.

Early naturalists in the Neotropics (e.g., Bates 1863) observed birds following army ants and capturing arthropods fleeing their onslaught. More recently, some of these species have been characterized as obligate or professional ant-followers (Willis and Oniki 1978), because the birds were dependent on ant swarms to flush prey out of the leaf litter (reviewed in Willson 2004). Almost all obligate follower species are members of the family Thamnophilidae (Willson 2004), and within the family all but one obligate species are currently considered members of five genera (*Gymnopathys*, *Rhegmatorhina*, *Phlegopsis*, *Pithys*, or *Phaenostictus*) that, along with regular ant-followers of the genus *Willisornis*, belong in a monophyletic group that has maintained this phylogenetically conserved foraging specialization for millions of years (Brumfield et al. 2007). Recent phylogenies based on DNA sequence data (Brumfield et al. 2007, Aleixo et al. 2009) suggest that generic designations in the complex are in need of reexamination. Moving in that direction, Aleixo et al. (2009) found that a previously described ant-following genus, *Skutchia* (Willis 1968), was embedded in the genus *Phlegopsis* and recommended that the species in *Skutchia* be returned to *Phlegopsis*, where it had been placed originally by Hellmayr (1907).

In a paper focused on the thamnophilid genus *Myrmeciza* (Isler et al. 2013), we considered the dilemma of setting generic limits. The choice is to establish genera solely on the basis of monophyly even though they might encompass phenotypically very different taxa—a “broad monophyly” option—or to narrow generic definitions to smaller, but more phenotypically homogeneous groups. After integrating various sources of phylogenetic, morphological, behavioral, and ecological variation in that paper, a “focused monophyly” approach was adopted as it provides recognition of phylogenetic relationships, genetic divergence, synapomorphic characters, and phenotypic distinctiveness that will best facilitate understanding and communication of relatedness of taxa among researchers, field workers and conservationists. Here, we use a similar approach to elucidate generic limits in the obligate army-ant-following antbirds. After complementing the molecular data presented by Brumfield et al. (2007) with GenBank data and newly obtained sequences, we specifically focus on assessing generic boundaries among the ant-followers by overlaying this newly obtained phylogeny with a wide variety of morphological, behavioral, and ecological characteristics, most of which were unavailable when the vast majority of existing genera were described.

METHODS

We first constructed a molecular phylogeny of the core army-ant-following genera (sensu Brumfield et al. 2007) of the Thamnophilidae including *Pithys*, *Gymnopathys*, *Rhegmatorhina*, *Phlegopsis*, *Phaenostictus*, and the closely related genus *Willisornis* (Brumfield et al. 2007). We then

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identified morphological, behavioral, and ecological characters that were found consistently among species within well-supported clades and looked for distinct gaps in these characters between each clade and its close relatives. We based decisions to recognize genera on the extent of such gaps between monophyletic groups, keeping in mind phenotypic differences among universally accepted thamnophilid genera.

Taxon Sampling and Laboratory Procedures.—Our analysis is based on DNA sequences from 57 vouchered specimens housed in accessible scientific collections (Peterson et al. 2007; Appendix 1). They represent all the currently recognized species (17) and genera (6) within the main obligate army-ant-following clade (sensu Brumfield et al. 2007), including samples of nominate populations of 16 species (only nominate *Gymnophis leucaspis* was unavailable) and type species of all genera. For outgroups we used sequences from species in other thamnophilid genera: *Euchrepomis sharpei* (LSUMZ 171313, tissue sample LSUMZ B-39086), *Myrmornis torquata* (FMNH 389880), *Microrhopias quixensis* (FMNH 321993), *Thamnophilus doliiatus* (UWBM RTB390), *Drymophila striaticeps* (LSUMZ 98339, tissue sample LSUMZ B-572), and *Hypocnemis striata* (FMNH 391408).

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), for 22 of the samples (Appendix) we amplified and sequenced three mitochondrial genes (nicotinamide dehydrogenase subunit 2 – ND2, 1,041 bp; nicotinamide dehydrogenase subunit 3 – ND3, 351 bp; cytochrome b – cytb, 1,045 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, 2,857 bp; recombination activation gene 2 – RAG2, 1,152 bp) for one individual per genus following the methods described in Groth and Barrowclough (1999) and Barker et al. (2002). For the remaining samples we obtained sequences only for ND2. Some sequences were obtained from previous publications (Brumfield et al. 2007, Aleixo et al. 2009, Moyle et al. 2009, Gómez et al. 2010, Derryberry et al. 2011, Bravo et al. 2012, Naka et al. 2012). Analyses were conducted using two concatenated six-gene alignments containing 7,001 bp; one alignment only included the

samples for which we had complete sampling of the mitochondrial genes and β F5, and the other alignment included all individuals. The motivation to have two separate alignments was to avoid potential biases resulting from missing data in the complete dataset. The reduced alignment would provide enough information to resolve the nodes informing intergeneric relationships in the obligate ant-followers and would minimize topology biases resulting from higher representation in the alignment of mtDNA than nucDNA.

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 KM260369–KM260414).

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 1,000 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). Table 1 summarizes the selected substitution model for each partition based on comparison of AIC scores. We conducted the analyses using four runs, four chains, and 2×10^7 generations with a sample frequency of 1,000, a burn-in of 20%, and chain temperature of 1.75. The “compare” and “slide” functions of

TABLE 1. Substitution model selected by MrModeltest for each of the 16 partitions included in the most informative partition strategy for both of the used alignments.

Partition	Complete alignment	Reduced alignment
RAG1-1st	GTR + I	
RAG1-2nd	GTR + I	
RAG1-3rd	HKY + Γ	
RAG2-1st	HKY + I	
RAG2-2nd	HKY + I	
RAG2-3rd	HKY + Γ	
ND2-1st	GTR + Γ + I	GTR + Γ
ND2-2nd	GTR + I	
ND2-3rd	GTR + Γ + I	
ND3-1st	HKY + Γ	K80 + Γ
ND3-2nd	GTR + Γ + I	
ND3-3rd	GTR + Γ	
cytb-1st	SYM + Γ + I	
cytb-2nd	GTR + I	
cytb-3rd	GTR + Γ	
β F5	HKY + Γ	

AWTY online (Wilgenbusch et al. 2004) were used to assess the performance of Bayesian phylogenetic inference.

Taxonomic Assessment.—Principal well-supported clades recovered in the phylogenetic analyses provided the foundation upon which we assessed phenotypic differences to make generic recommendations. To make trait comparisons and establish diagnosability of the identified groups, we used a recent compilation of thamnophilid information (Zimmer and Isler 2003) to extract plumage, behavioral, and ecological data whose original sources may be obtained from the publication. We supplemented these data by more recent sources cited herein and by measuring 10 morphological 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 82 individuals (Appendix 2). 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 diagnosability among clades, we compared mean values of ecomorphological variation among clades, and conducted discriminant function analyses (DFA) using log-transformed measurements for all individuals in currently recognized genera as well as potentially new genera.

RESULTS

Molecular Analysis.—Maximum-likelihood and Bayesian analyses of both datasets (i.e., all individuals vs. individuals with complete gene sampling only) produced similar topologies indicating with high support that the core clade of obligate army-ant-followers (henceforth, the complex) contains five well-supported clades within it (Figs. 1, 2). Among currently recognized genera, only *Gymnopathys* was recovered as non-monophyletic. The only discrepancies between maximum-likelihood and Bayesian inference trees are: (1) the position of *Willisornis*; the former places it as sister to a clade containing *Phlegopsis*, *Gymnopathys*, and *Rhegmatorhina*, whereas the latter recovers it as sister to a clade containing only *Gymnopathys* and *Rhegmatorhina*. and (2) the relationships among clades identified on the figures as *Gymnopathys* 1, *Gymnopathys* 2, and *Rhegmatorhina*, the basal node of which is unresolved in both cladograms.

From here on, principal clades are identified by the genera they include and subclades by the oldest name among their constituent species. The clades (numbered following Figs. 1, 2) include: (1) the *Phaenostictus* clade; (2) the *Pithys* clade; (3) the *Willisornis* clade; (4) the *Phlegopsis* clade that includes three subclades: (4a) the *erythroptera* clade; (4b) the *borbae* clade; and (4c) the *nigromaculata* clade; and (5) the *Gymnopathys/Rhegmatorhina* clade that also include three subclades: (5a) the *rufigula* clade containing *Gymnopathys leucaspis* and *G. rufigula*; (5b) the *lunulatus* clade containing *G. lunulatus* and *G. salvini*; and (5c) the *gymnops* clade, which contains five species in the genus *Rhegmatorhina*.

Morphological Variation among Obligate Army-Ant-Following Birds.—All clades differed diagnostically in plumage (Table 2). On the other hand, the ant-followers share many morphometric similarities (Tables 3, 4). Component measurements (e.g., wing length) are in most cases proportional to size. Clades differ principally in size and bulk as reflected in the ratio between weight and body length, for which every clade differs from its closest relative except for the *rufigula* and *gymnops* clades. Remaining differences in morphometric proportions (Table 4) primarily involve bill measurements. Because bill length is similar across all clades regardless of size, larger species exhibit significantly smaller ratios of bill size to total length. However, bill proportions were consistent across all clades except for the

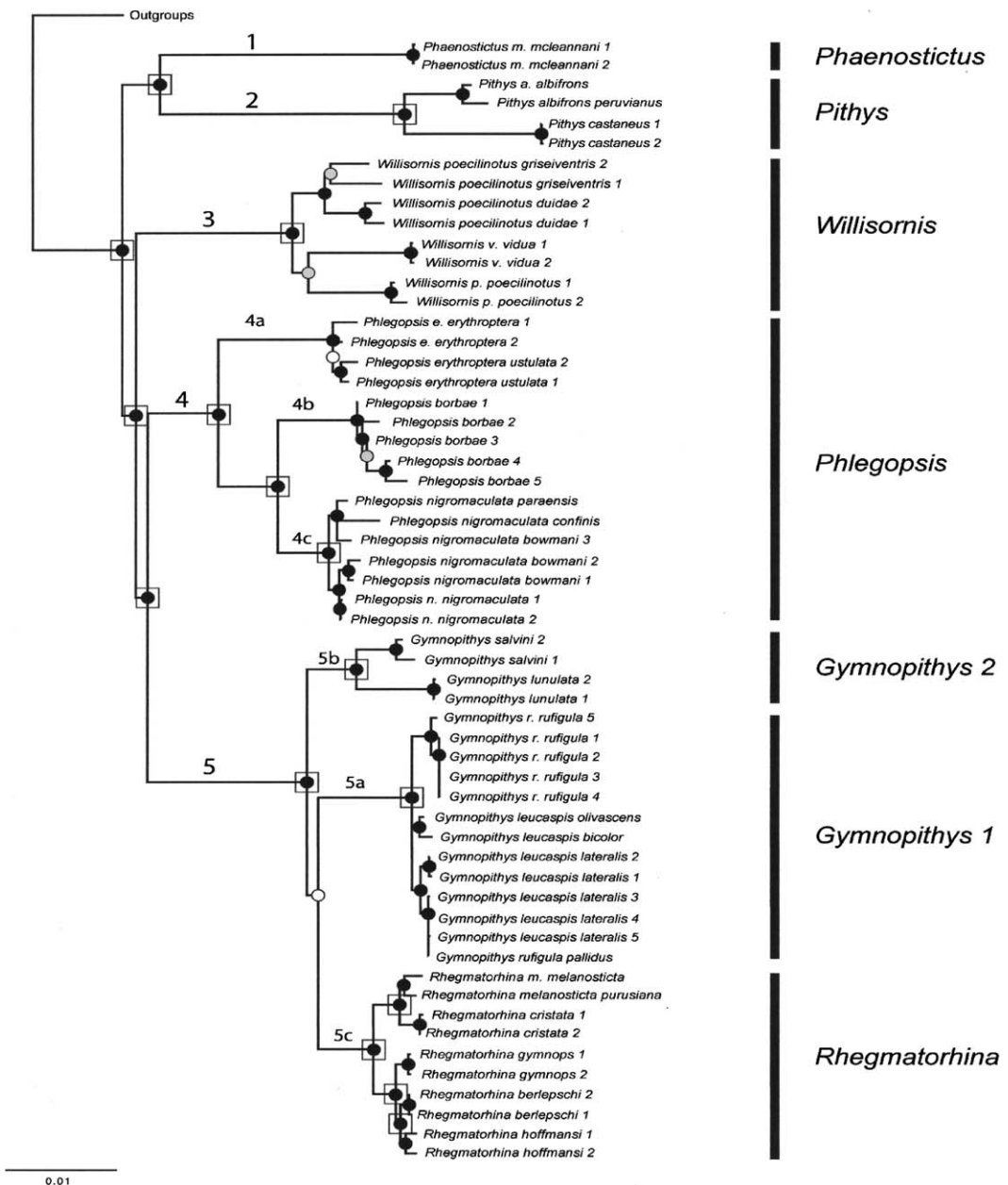


FIG. 1. Maximum-likelihood tree of the core obligate-army-ant-following thamnophilids, showing that they represent a monophyletic group. All genera, with the exception of *Gymnopathys*, represent monophyletic groups. The color of the circles at nodes indicates bootstrap support values, >70% (black), 50–70% (gray), <50% (white). Hollow squares around some nodes represent highly supported nodes (>70%) in the analysis performed using samples with no missing mtDNA and $\beta F5$ data.

relatively deeper bills of the *nigromaculata* and *erythroptera* clades. The proportionately longer tail of the *Phaenostictus* clade was the only other significant difference.

A discriminant function analysis of 10 log-corrected ecomorphological features showed that all five principal clades identified solely on the basis of monophyly are diagnosable (Wilks'

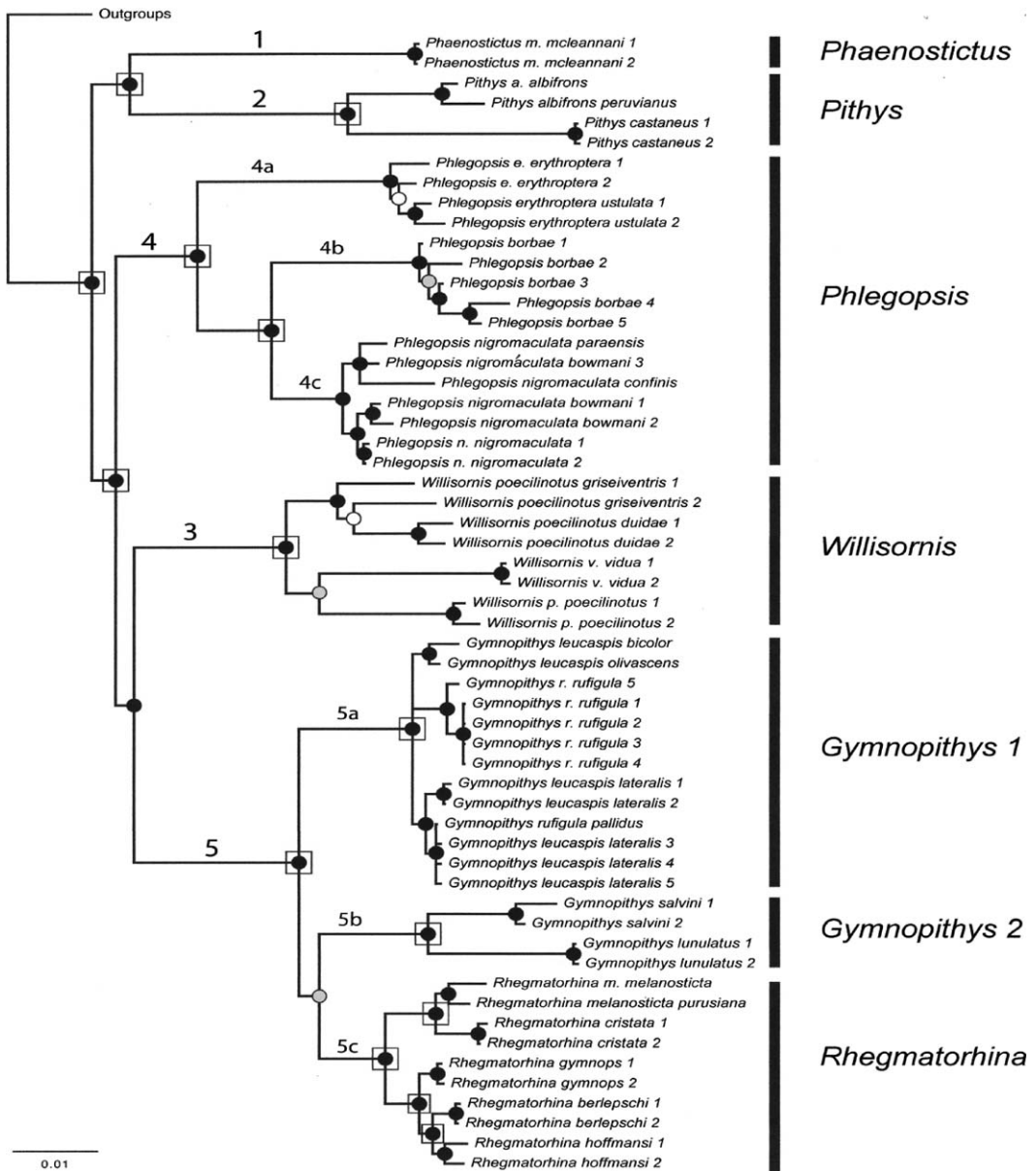


FIG. 2. Fifty percent majority-rule Bayesian consensus tree of the core obligate-army-ant-following thamnophilids, showing that they represent a monophyletic group. All genera, with the exception of *Gymnopathys*, represent monophyletic groups. The color of the circles at nodes indicates posterior probability values, >0.95 (black), 0.95–0.75 (gray), <0.75 (white). Hollow squares around some nodes represent highly supported nodes (>0.95) in the analysis performed using samples with no missing mtDNA and β F5 data.

lambda = 0.005, $F_{4,77} = 20.4$, $P < 0.0001$). All individuals were correctly assigned in their clade (Fig. 3). The first discriminant function separated groups primarily on differences in length of the first secondary remige and tarsus (LD1 = 67.1%), whereas the second function discriminated groups

based on differences in wing, tarsus, and tail length (LD2 = 17.4%).

Loudsong Variation among Obligate Army-Ant-Following Birds.—As can be seen in Figure 4, loudsongs of species in the *Willisornis* (Fig. 4A), *Phaenostictus* (Fig. 4B), and *Pithys* (Fig. 4C; *P.*

TABLE 2. Plumage description of clades and subclades identified within the obligate army-ant-following birds.

Clade/subclade	Name	Plumage description
1	<i>Phaenostictus</i>	Monomorphic. Black head surmounted by a large blue periorbital patch, olive-gray crown, and rufous nape; body feathers above and below with large black subterminal spots edged cinnamon-buff; and a blackish-brown tail
2	<i>Pithys</i>	Monomorphic. Extensive rufous-chestnut body coloration and a contrasting black head with white throats and feather tufts or periocular patch; tarsi and feet orange
3	<i>Willisornis</i>	Dimorphic. Males are gray and black and females predominantly brown. Males show extensive white or whitish edges to the wing coverts and lower back. Females either have a wing covert pattern similar to the male or gray underparts.
4a	<i>erythroptera</i>	Dimorphic. Males predominantly black with whitish edges in upper back, and rufous wing coverts and remiges. Females predominantly brown with whitish wing coverts. Both sexes have a red periorbital patch.
4b	<i>borbae</i>	Monomorphic. Predominantly brown with elongated white feathers on forehead and lores, and with barred black and white band across upper belly.
4c	<i>nigromaculata</i>	Monomorphic. Head and neck down to belly black. Upperparts and wing coverts predominantly light olive, covered with black spots of varying size and edgings. Remiges primarily rufous.
5a	<i>rufigula</i>	Monomorphic except for interscapular patches in some taxa. Blue periorbital patch with upperparts predominantly brown and lighter to with lower parts. No scaling or barring is found.
5b	<i>lunulatus</i>	Dimorphic. Males predominantly gray with supercilium, chin, and throat white. Females predominantly brown with barred tail.
5c	<i>gymnops</i>	Dimorphic. Both sexes share a fairly prominent crest, light periorbital patches, and plain brownish tail. Males with upper parts predominantly brown. Females with lower parts predominantly brown. Dark masks are common in both sexes. A scaling pattern in back is common in females.

albifrons, the note of *P. castaneus* ascends) clades are structurally distinct from the remaining clades whose series of notes primarily descend in frequency. Loudsongs of the three sub-clades in the *Phlegopsis* clade are simple descending series (Fig. 4D–F). Notes in loudsongs of species in the *Gymnopathys/Rhegmatorhina* clade typically rise in frequency or are flat before falling (Fig. 4G–I), although notes of *Gymnopathys salvini* (Fig. 4J) simply descend like loudsongs in the *Phlegopsis* clade. Note that the two species in the *lunulatus* clade differ structurally. Note peaks of *lunulatus*

rise and fall in frequency as notes lengthen, whereas the longer notes of *salvini* descend while remaining similar in duration. These are the only structurally inconsistent loudsongs within any of the clades.

Nest Variation among Obligate Army-Ant-Following Birds.—Forty-five nests have been described for nine of the 17 species included. All nests were supported from below (not hung from branches) and were cup-shaped (not domed) although a few were so shallow as to barely resemble a cup. However, substrate placement of

TABLE 3. Morphometrics. Body length = Total length – Tail length. All measurements in mm except weight in g.

Clade/subclade	Total length	Body length	Weight	Wing length	Primary length	Secondary length	Tail length	Tail width	Bill length	Bill width	Bill depth	Tarsus length	Hallux length
1 <i>Phaenostictus</i>	192	108	50	88	62	79	84	14.8	13.8	5.3	6.7	32.6	19.9
2 <i>Pithys</i>	130	84	26	74	55	64	46	10.1	11.6	4.7	4.8	23.4	15.4
3 <i>Willisornis</i>	125	84	17	66	46	57	41	8.9	11.2	4.6	4.4	23.2	16.5
4a <i>erythroptera</i>	182	117	58	92	66	85	65	15.6	12.4	5.0	5.9	33.9	20.7
4b <i>borbae</i>	170	116	43	85	63	79	54	16.1	12.1	4.8	6.5	31.4	19.9
4c <i>nigromaculata</i>	170	115	47	87	62	80	55	11.8	11.4	4.7	5.8	31.4	20.5
5a <i>rufigula</i>	130	86	27	74	53	67	46	10.4	11.6	5.0	4.9	27.0	17.1
5b <i>lunulatus</i>	132	88	24	71	50	65	44	9.9	12.2	4.9	4.7	25.5	16.9
5c <i>gymnops</i>	144	93	29	77	55	70	51	10.6	12.3	4.8	5.0	27.4	17.3

TABLE 4. Morphometric proportions.

Clade/subclade	Weight/ body length	Wing length/ total length	Wing length/ body length	Primary length/ secondary length	Tail length/wing length	Tail width/tail length	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
1 <i>Phaenostictus</i>	0.46	0.46	0.81	0.78	0.95	0.18	0.072	0.38	0.49	0.61	0.42	0.17	0.44
2 <i>Pithys</i>	0.31	0.57	0.88	0.86	0.62	0.22	0.089	0.40	0.41	0.66	0.50	0.18	0.35
3 <i>Willisornis</i>	0.20	0.53	0.79	0.81	0.62	0.22	0.090	0.41	0.39	0.71	0.48	0.19	0.33
4a <i>erythroptera</i>	0.50	0.51	0.79	0.78	0.71	0.24	0.063	0.44	0.52	0.61	0.34	0.19	0.38
4b <i>borbæ</i>	0.37	0.50	0.73	0.80	0.64	0.30	0.071	0.40	0.54	0.63	0.39	0.19	0.32
4c <i>nigromaculata</i>	0.41	0.51	0.76	0.78	0.63	0.22	0.067	0.41	0.51	0.65	0.36	0.19	0.32
5a <i>rufigula</i>	0.31	0.57	0.86	0.79	0.62	0.23	0.089	0.43	0.42	0.63	0.43	0.21	0.35
5b <i>lunulatus</i>	0.27	0.54	0.81	0.77	0.62	0.22	0.092	0.40	0.38	0.66	0.48	0.19	0.33
5c <i>gymnops</i>	0.31	0.54	0.83	0.77	0.66	0.21	0.085	0.39	0.41	0.63	0.45	0.19	0.35

nests varied. Most commonly, 20 nests for seven species were placed in hollow stumps within a few meters of the ground. Alternative nest sites for these seven species were hollows formed at the base of palm fronds (six nests for three of the species), cavities in live trees (two species), and in litter at the base of a tree (one species). Substrate placement differed for nests of the two remaining species. Eleven recently described *Phaenostictus mcleannani* nests (Buehler et al. 2004, Class and Chaves-Campos 2009) were placed between tree buttresses on the ground (although one was slightly elevated). The smaller sample (four nests) of *Pithys albifrons* were all placed atop live vegetation (two atop small palms, one in sedge, and one in a clump of tuberous plants). Although nests of species in all clades were bottom-supported cups, differences in substrate placement appear relevant to generic considerations.

Other Considerations.—Other than morphology, loudsongs, and nest architecture, no intrinsic or supporting behavioral or ecological traits provide distinctions among clades relevant to distinguishing obligate ant-follower genera. Tail movement, an intrinsic trait distinguishing other thamnophilid clades (Isler et al. 2013), was consistent in all clades. Foraging behavior, diet (Chesser 1995), and habitat, which often provide supporting evidence of generic distinctions, were also found to be almost entirely consistent, the exception being that species in the *Willisornis* clade are considered regular rather than obligate ant-followers.

Hybridization between species may provide another insight in generic considerations. Especially noteworthy is a specimen originally described as a species but later shown to be a hybrid between species in the *erythroptera* and *nigromaculata* sub-clades (Graves 1992). Curiously, although hybridization among thamnophilid species is rare (Graves 1992), hybrids have also been found between species within the *gymnops* clade (*Rhegmatorhina berlepschi* and *R. hoffmannsi* hybridize extensively in the upper Madeira-Tapajós interfluvium, and genetic introgression between them is currently under study; B. M. Whitney, pers. comm.) and the *rufigula* clade (individual identified as *Gymnopathys rufigula pallidus* in Naka et al. 2012 and in Figs. 1, 2).

DISCUSSION

The integration of modern genetic studies with traditional phenotypic data provides a powerful

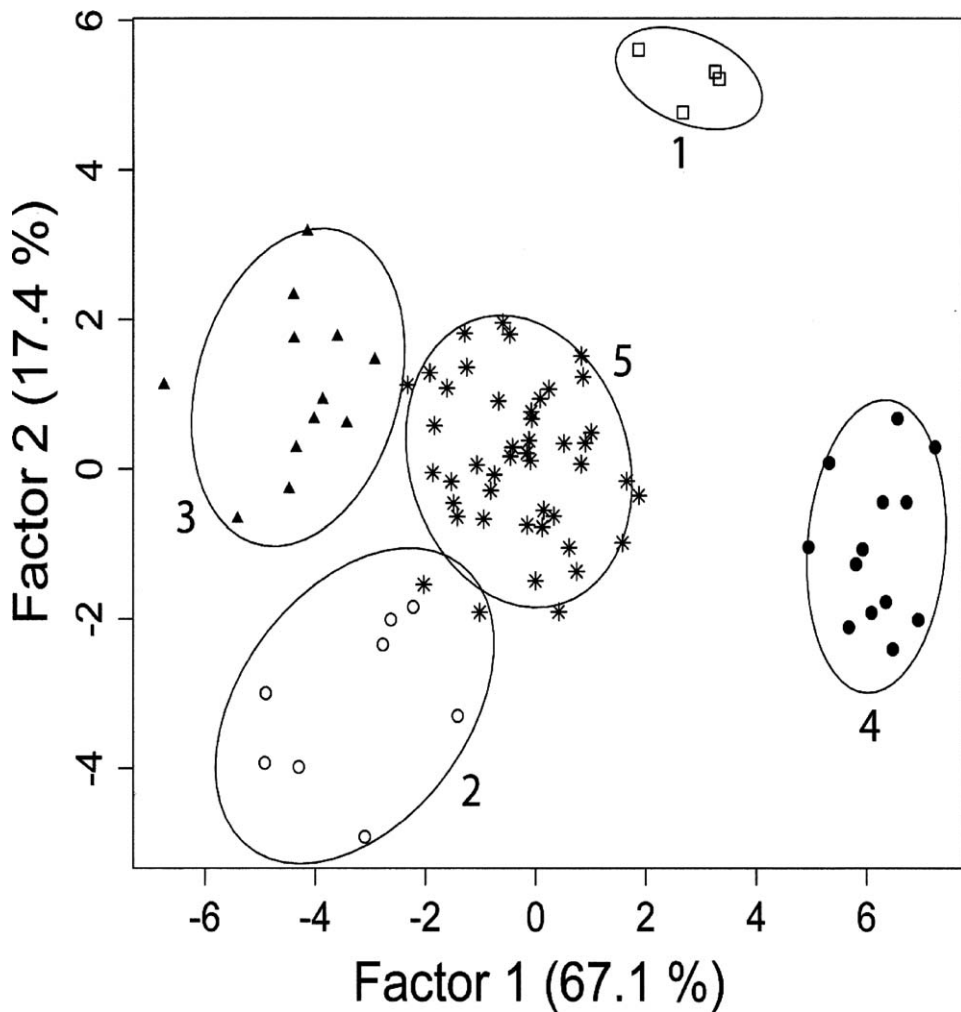


FIG. 3. Discriminant factors of ecomorphological variation of the core obligate-army-ant-following thamnophilids following a plausible genus-level classification scheme based solely on the monophyly of the main clades in the group. Positive values of Factor 1 represent longer secondary 1 feathers and longer tarsi. Positive values of Factor 2 represent longer tails and longer tarsi. Ellipses represent 95% confidence intervals. Numbers next to ellipses indicate clades they represent. (1) *Phaenostictus*; (2) *Pithys*; (3) *Willisornis*; (4) *Phlegopsis*; and (5) *Gymnophithys/Rhegmatorhina*.

new tool to overcome the difficulties of generic designations, especially problems of homoplasy. Instances of homoplasy are prevalent in obligate ant-followers, in which a variety of morphological characters (e.g., black-spotted back feathers) are found in the plumages of otherwise morphologically distinct taxa (Aleixo et al. 2009). Evolutionary relationships uncovered in molecular-based phylogenies provide the structure, unavailable to earlier systematists, for a taxonomic classification that reflects the evolutionary history of the group.

The molecular phylogeny identified five principal clades of ant-followers. Three of these clades are restricted currently to species placed in a single genus: (1) *Phaenostictus*; (2) *Pithys*; and (3) *Willisornis*. Our results were consistent with the maintenance of these three genera, finding that they are distinguished by plumage, by morphometric measurements related to differences in size and bulk, and by the structure of their loudsongs. Behavioral support includes apparently distinct nest placement in *Phaenostictus* and regular rather than obligate ant-following

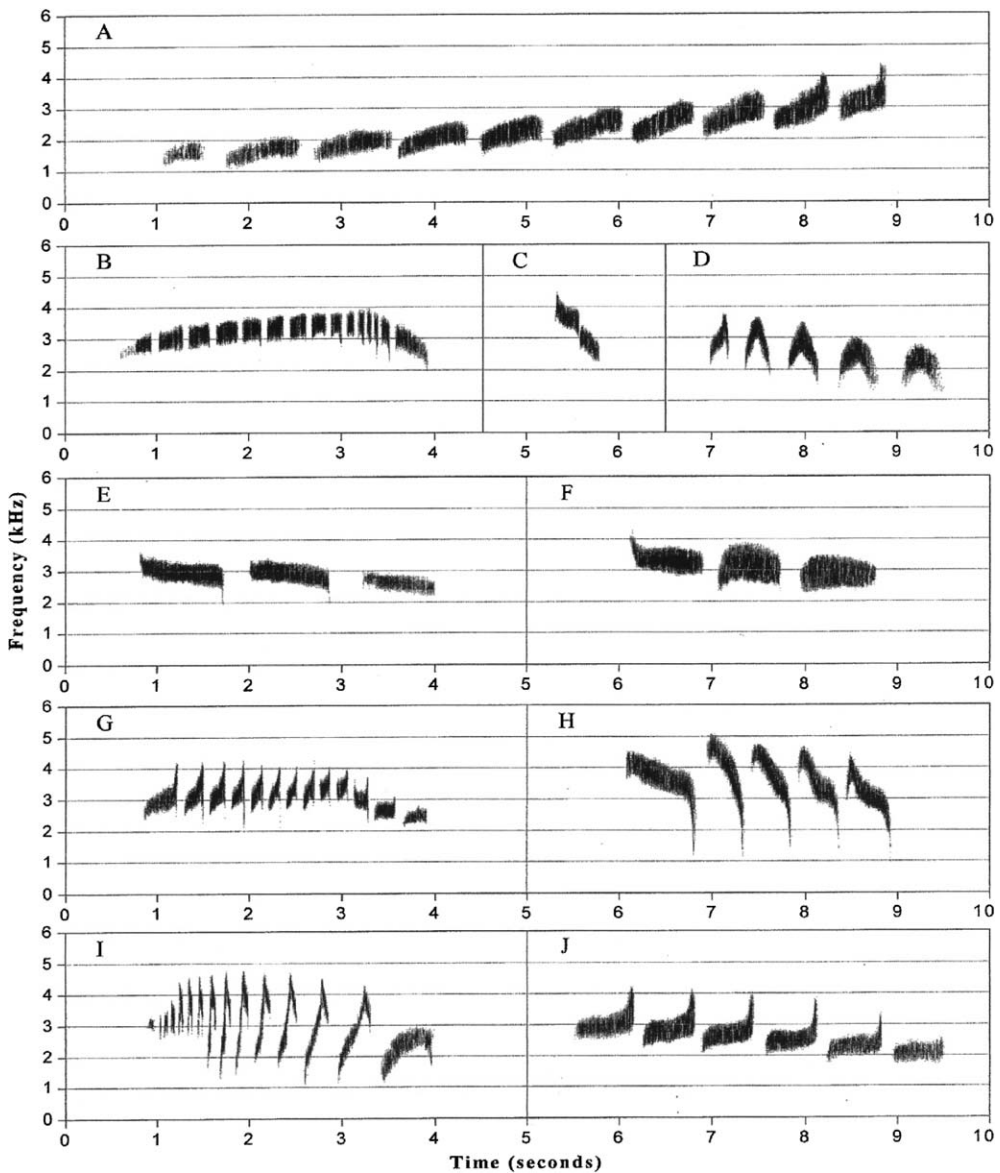


FIG. 4. Loudsongs of representative species of ant-following thamnophilids showing note structure characteristic of clades. Loudsongs of both *Gymnophithys lunulatus* and *G. salvini* are shown because structurally they are inconsistent. A. *Willisornis poecilinotus* (Clade 3) São Gabriel da Cachoeira, Amazonas, Brazil (Whitney ISL-BMW.79:08). B. *Phaenostictus mcleannani* (Clade 1) Kuna Yala Indian Reserve, San Blas, Panama (Whitney ISL-BMW.17:33). C. *Pithys albifrons* (Clade 2) Quebrada Sucusari, Loreto, Peru (Parker/Budney MLNS 34305). D. *Phlegopsis erythroptera* (Clade 4a) Libertad, Loreto, Peru (Parker MLNS 29314). E. *Phlegopsis borbae* (Clade 4b) Borba, Amazonas, Brazil (Whitney ISL-BMW.190:29). F. *Phlegopsis nigromaculata* (Clade 4c) Serra dos Carajás, Pará, Brazil (Whitney ISL-BMW.63:16). G. *Gymnophithys rufigula* (Clade 5a) El Palmar, Bolívar, Venezuela (Schwartz MLNS 62174). H. *Rhegmatorhina gymnops* (Clade 5c) Rio São Benedito, Pará, Brazil (Whitney ISL-BMW.176:06). I. *Gymnophithys lunulatus* (Clade 5b example 1) Liborio, Loreto, Peru (Whitney ISL-BMW.93:116). J. *Gymnophithys salvini* (Clade 5b example 2) Explorer's Inn, Madre de Dios, Peru (Parker MLNS 23814).

in *Willisornis*. Species limits within *Willisornis* should be assessed further, because the relationship between its two currently recognized species, *W. poecilinotus* and *W. vidua*, remains unresolved. This was not unexpected based on a previous morphological and vocal analysis (Isler and Whitney 2011).

The phylogeny identified subclades within each of the remaining two principal clades. The *Phlegopsis* clade (4) includes the *erythroptera*, *borbae*, and *nigromaculata* subclades. Plumage differences had led to the placement of *borbae* in a monotypic genus (*Skutchia*) and the others in *Phlegopsis*, but an earlier phylogenetic study (Aleixo et al. 2009) showed that this treatment rendered *Phlegopsis* paraphyletic and concluded that plumage differences among the three clades and sexual dimorphism in *erythroptera* were insufficient to relegate the clades to three genera. The phylogenetic results and phenotypic comparisons of the present study are consistent with the earlier recommendations (Cory and Hellmayr 1924, Aleixo et al. 2009) to maintain all three subclades in *Phlegopsis*.

The final principal clade (5) includes the *rufigula*, *lunulatus*, and *gymnops* subclades. Although the basal node of the *lunulatus*, *gymnops*, *rufigula* clade is not resolved, and species limits within *rufigula* seem unresolved, our results as well as those of Brumfield et al. 2007 indicate that the *rufigula*, *lunulatus*, and *gymnops* subclades represent distinct lineages. The *rufigula* and *lunulatus* subclades are currently placed in *Gymnopathys* and the *gymnops* subclade in *Rhegmatorhina*. Given the substantial distinctions between them in plumage, consolidating *Gymnopathys* and *Rhegmatorhina* into a single genus (*Gymnopathys* has priority) is inconsistent with the “focused monophyly” approach. However, if the genus *Rhegmatorhina* is recognized, the *rufigula* and *lunulatus* subclades cannot be maintained in the same genus under the principle of monophyly. We conclude that *Rhegmatorhina* should be maintained, that *Gymnopathys* be restricted to the *rufigula* subclade, and that a new genus must be erected for the *lunulatus* subclade.

Taxonomic recommendations.—We recommend that species in the obligate ant-follower clade be maintained in seven genera, six of which are recognized, and one of which requires a new name. The following diagnoses are placed in context of the phylogeny. Consequently, pheno-

typic comparisons are primarily of sister clades. English names follow Remsen et al. (2013).

***Phaenostictus* Ridgway, 1909**

Type species.—*Phlogopsis mcleannani* Lawrence, 1837.

Included species.—*Phaenostictus mcleannani* (Lawrence 1837) OCELLATED ANTIBIRD.

Diagnosis.—Both sexes distinguished by a combination of plumage characters including black sides of head and throat, a large blue periorbital patch, olive-gray crown, and rufous nape; body feathers above and below with large black subterminal spots edged cinnamon-buff; and a blackish-brown tail. Morphometrically distinguished from all genera in the complex by an unusually long tail and from its close relatives by its large size and weight. Loudsong a long rapid series that rises and falls in pitch, structurally unique in complex.

***Pithys* Vieillot, 1818**

Type species.—*Pipra albifrons* Linnaeus, 1766.

Included species.—*Pithys albifrons* (Linnaeus 1766) WHITE-PLUMED ANTIBIRD.

Pithys castaneus (Berlioz 1938) WHITE-MASKED ANTIBIRD.

Diagnosis.—Distinguished in both sexes by extensive rufous-chestnut body coloration and contrasting black head with white throat and feather tufts or pericocular patch; tarsi and feet orange. Morphometrically distinguished from closest relative (*Phaenostictus*) by its smaller size (length and weight) and shorter tail (relative to total length and wing length). Loudsong a single whistle, structurally unique in complex.

***Willisornis* Agne and Pacheco, 2007**

Type species.—*Hypocnemis poecilinota* Cabanis, 1847.

Included species.—*Willisornis poecilinotus* (Cabanis 1847) COMMON SCALE-BACKED ANTIBIRD.

Willisornis vidua (Hellmayr 1905) XINGU SCALE-BACKED ANTIBIRD.

Diagnosis.—Distinguished from all in complex except *Oneillornis* by the combination of gray and black male plumage and predominantly brown female plumage. Males differ from *Oneillornis* by extensive white or whitish edges to the wing coverts and lower back reflected in their vernacular name. Females differ from *Oneillornis* either by a wing covert pattern similar to the male or by gray underparts. Morphometrically slighter (weighs less) than all others in complex. Loud-

songs a slow series rising in pitch, structurally unique in the complex.

Phlegopsis Reichenbach, 1850

Type species.—*Myothera nigro-maculata* d'Orbigny and Lafresnaye, 1837.

Included species.—*Phlegopsis nigromaculata* (d'Orbigny and Lafresnaye, 1837) BLACK-SPOTTED BARE-EYE.

Phlegopsis borbae Hellmayr, 1907 PALE-FACED BARE-EYE.

Phlegopsis erythroptera (Gould 1855) RED-DISH-WINGED BARE-EYE.

Diagnosis.—Distinguished morphometrically from *Oneillornis*, *Gymnopathys*, and *Rhegmatorhina* by large size; bill short compared to body length and deep compared to bill length. Loudsong a short series of simple notes descending in pitch, structurally unique in the complex except for *Oneillornis salvini*.

Oneillornis new genus

Type species.—*Pithys lunulata* Sclater and Salvin, 1873.

Included species.—*Oneillornis lunulatus* (Sclater and Salvin 1873) *comb. nov.* LUNULATED ANTBIRD.

Oneillornis salvini (Berlepsch, 1901) *comb. nov.* WHITE-THROATED ANTBIRD.

Diagnosis.—Distinguished from *Gymnopathys* by plumage being sexually dimorphic and from *Gymnopathys* and *Rhegmatorhina* by lack of periorbital skin patches and by males being predominantly gray rather than brown. Females differ from females of both genera by having strongly marked tails.

Etymology.—We are pleased to name this genus for our friend and colleague John Patton O'Neill, whose pioneering field work in South America led to the discovery of dozens of new avian species and helped propel the Louisiana State University Museum of Natural Science into becoming one of the great ornithology collections in the world, whose paintings grace our lives and provide keys for field study, and, especially, whose intense love of ornithological exploration and appreciation for the value of museum specimens has been passed on to a multitude of students, one by one, for five decades. The name *Oneillornis* is masculine in gender.

Gymnopathys Bonaparte, 1857

Type species.—*Turdus rufigula* Boddaert, 1783.

Included species.—*Gymnopathys rufigula* (Boddaert 1783) RUFOUS-THROATED ANTBIRD.

Gymnopathys leucaspis (Sclater 1854) BICOLOR-ED ANTBIRD.

Diagnosis.—Distinguished from *Rhegmatorhina* and *Oneillornis* by sexes being alike in plumage (except presence and color of interscapular patch in some taxa). Distinguished from *Oneillornis* by males primarily brown rather than gray, by females lacking conspicuous tail markings, and by both sexes having periorbital skin patches. Loudsong a series of short notes flat in pitch, then descending sharply.

Rhegmatorhina Ridgway, 1888

Type species.—*Rhegmatorhina gymnops* Ridgway, 1888.

Included species.—*Rhegmatorhina gymnops* Ridgway, 1888. BARE-EYED ANTBIRD.

Rhegmatorhina cristata (Pelzeln, 1869). CHEST-NUT-CRESTED ANTBIRD.

Rhegmatorhina melanosticta (Sclater and Salvin 1880). HAIRY-CRESTED ANTBIRD.

Rhegmatorhina berlepschi (Snethlage 1907). HARLEQUIN ANTBIRD.

Rhegmatorhina hoffmannsi (Hellmayr 1907). WHITE-BREASTED ANTBIRD.

Diagnosis.—Distinguished by shaggy crests. From *Gymnopathys* by sexually dimorphic plumages; females (except *R. gymnops*) with black spotted upperparts. From *Oneillornis* by male plumage primarily brown rather than gray, by females lacking conspicuous tail markings, and by both sexes having large periorbital skin patches. Loudsong a long note followed by shorter notes starting at a higher pitch and going down scale.

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APPENDIX 1. Ingroup taxa used in this study and their respective tissue collection catalog number. Sample numbers followed by an asterisk identify samples used in all analyses; remaining specimens were sequenced only for ND2. For museum acronyms see acknowledgements.

Sample	Species	Locality	Voucher	Tissue
1*	<i>Pithys a. albifrons</i>	Brazil: Amapá	FMNH 391430	FMNH 391430
2	<i>Pithys albifrons peruvianus</i>	Brazil: Amazonas	INPA MA439	INPA A-1138
3*	<i>Pithys castaneus 1</i>	Peru: Loreto	MUSM KE157	LSUMZ B-42817
4	<i>Pithys castaneus 2</i>	Peru: Loreto	LSUMZ 177297	LSUMZ B-42901
5*	<i>Gymnopathys leucaspis bicolor</i>	Panama: Darién	LSUMZ 108844	LSUMZ B-2096
6	<i>Gymnopathys leucaspis olivascens</i>	Panama: Bocas del Toro	CUMV 51302	STRI JTW268
7*	<i>Gymnopathys leucaspis lateralis 1</i>	Peru: Loreto	LSUMZ 115499	LSUMZ B-4136
8	<i>Gymnopathys leucaspis lateralis 2</i>	Peru: Loreto	LSUMZ 115502	LSUMZ B-4290
9	<i>Gymnopathys leucaspis lateralis 3</i>	Brazil: Amazonas	INPA ITM108	INPA A-1997
10	<i>Gymnopathys leucaspis lateralis 4</i>	Brazil: Amazonas	INPA ITM98	INPA A-1942
11	<i>Gymnopathys leucaspis lateralis 5</i>	Brazil: Amazonas	INPA MFT98	INPA A-1137
12*	<i>Gymnopathys rufigula pallidus</i>	Venezuela: Amazonas	FMNH 319276	LSUMZ B-7512
13	<i>Gymnopathys r. rufigula 1</i>	Suriname: Sipaliwini Distrikt	LSUMZ 178459	LSUMZ B-55217
14	<i>Gymnopathys r. rufigula 2</i>	Brazil: Amazonas	INPA GAB209	INPA A-1599
15	<i>Gymnopathys r. rufigula 3</i>	Brazil: Roraima	INPA MASJR30	INPA A-1073
16	<i>Gymnopathys r. rufigula 4</i>	Brazil: Amazonas	INPA LNN300	INPA A-1232
17	<i>Gymnopathys r. rufigula 5</i>	Brazil: Amazonas	INPA MA464	INPA A-1200
18*	<i>Gymnopathys salvini 1</i>	Bolivia: La Paz	FMNH 391147	FMNH 391147
19	<i>Gymnopathys salvini 2</i>	Brazil: Amazonas	MPEG 55232	LSUMZ B-35718
20*	<i>Gymnopathys lunulata 1</i>	Peru: Loreto	LSUMZ 161783	LSUMZ B-27384
21	<i>Gymnopathys lunulata 2</i>	Peru: Loreto	MUSM JAA96	LSUMZ B-42895
22*	<i>Rhegmatorhina gymnops 1</i>	Brazil: Pará	MPEG 54707	LSUMZ B-35336
23*	<i>Rhegmatorhina gymnops 2</i>	Brazil: Pará	MPEG 54687	LSUMZ B-35298
24*	<i>Rhegmatorhina berlepschi 1</i>	Brazil: Pará	MPEG 20350	MPEG 20350
25*	<i>Rhegmatorhina berlepschi 2</i>	Brazil: Pará	MPEG 20404	MPEG 20404
26*	<i>Rhegmatorhina hoffmannsi 1</i>	Brazil: Rondônia	FMNH 389933	FMNH 389933
27	<i>Rhegmatorhina hoffmannsi 2</i>	Brazil: Rondônia	MPEG 55001	LSUMZ B-36786
28*	<i>Rhegmatorhina cristata 1</i>	Brazil: Amazonas	INPA LNN261	INPA A-1136
29	<i>Rhegmatorhina cristata 2</i>	Brazil: Amazonas	INPA MFT99	INPA A-1139
30*	<i>Rhegmatorhina m. melanosticta</i>	Peru: Loreto	LSUMZ 115512	LSUMZ B-4248
31	<i>Rhegmatorhina melanosticta purusiana</i>	Bolivia: Pando	LSUMZ 132987	LSUMZ B-9734
32	<i>Willisornis p. poecilinotus 1</i>	Brazil: Roraima	INPA LNN234	INPA A-1060
33	<i>Willisornis p. poecilinotus 2</i>	Brazil: Roraima	INPA LNN427	INPA A-1790
34	<i>Willisornis poecilinotus duidae 1</i>	Brazil: Amazonas	INPA CLB65	INPA A-655

APPENDIX 1. Continued.

Sample	Species	Locality	Voucher	Tissue
35	<i>Willisornis poecilinotus duidae</i> 2	Brazil: Amazonas	INPA MA460	INPA A-1193
36*	<i>Willisornis poecilinotus griseiventris</i> 1	Bolivia: La Paz	FMNH 391148	FMNH 391148
37*	<i>Willisornis poecilinotus griseiventris</i> 2	Brazil: Rondônia	MCP 2362	MCP 2362
38*	<i>Willisornis v. vidua</i> 1	Brazil: Pará	MPEG 53293	LSUMZ B-16954
39*	<i>Willisornis v. vidua</i> 2	Brazil: Pará	MPEG 53292	LSUMZ B-16956
40	<i>Phlegopsis n. nigromaculata</i> 1	Peru: Loreto	LSUMZ 110203	LSUMZ B-2813
41	<i>Phlegopsis n. nigromaculata</i> 2	Brazil: Acre	MPEG 59868	MPEG 59868
42*	<i>Phlegopsis nigromaculata bowmani</i> 1	Brazil: Rondônia	FMNH 389842	FMNH 389842
43	<i>Phlegopsis nigromaculata bowmani</i> 2	Brazil: Pará	MPEG 58133	MPEG 58133
44	<i>Phlegopsis nigromaculata bowmani</i> 3	Brazil: Pará	MPEG 56103	MPEG 56103
45	<i>Phlegopsis nigromaculata confinis</i>	Brazil: Pará	MPEG 55694	MPEG 55694
46	<i>Phlegopsis nigromaculata paraensis</i>	Brazil: Pará	MPEG 58980	MPEG 58980
47	<i>Phlegopsis e. erythroptera</i> 1	Brazil: Amazonas	MPEG 59609	MPEG 59609
48	<i>Phlegopsis e. erythroptera</i> 2	Peru: Loreto	LSUMZ 110219	LSUMZ B-2707
49*	<i>Phlegopsis erythroptera ustulata</i> 1	Bolivia: Pando	LSUMZ 133046	LSUMZ B-9617
50	<i>Phlegopsis erythroptera ustulata</i> 2	Brazil: Amazonas	MPEG 57142	MPEG 57142
51*	<i>Phlegopsis borbae</i> 1	Brazil: Mato Grosso	MZUSP 96631	LGEMA P44
52	<i>Phlegopsis borbae</i> 2	Brazil: Amazonas	MPEG 58755	MPEG 58755
53	<i>Phlegopsis borbae</i> 3	Brazil: Amazonas	MPEG 57694	MPEG 57694
54	<i>Phlegopsis borbae</i> 4	Brazil: Amazonas	MPEG 57691	MPEG 57691
55	<i>Phlegopsis borbae</i> 5	Brazil: Amazonas	MPEG 57693	MPEG 57693
56*	<i>Phaenostictus m. mcleannani</i> 1	Panama: Darién	LSUMZ 108372	LSUMZ B-2135
57	<i>Phaenostictus m. mcleannani</i> 2	Panama: Darién	LSUMZ 104693	LSUMZ B-1390

APPENDIX 2.

The following list identifies specimens measured in this study. For museum acronyms see acknowledgements. *Pithys albifrons* (LSUMZ 116931, ♂; MPEG 59533, ♀; MPEG 64725, ♂; MPEG 65800, ♀), *Pithys castaneus* (LSUMZ 172973, ♀; LSUMZ 172975, ♂; LSUMZ 172974, ♀; LSUMZ 172977, ♂), *Gymnopathys leucaspis* (LSUMZ 180750, ♂; LSUMZ 112584, ♂; LSUMZ 164166, ♂; LSUMZ 108359, ♀; LSUMZ 83240, ♀; MPEG 59538, ♀; MPEG 42708, ♂; LSUMZ 110147, ♀; LSUMZ 116946, ♂), *Gymnopathys rufigula* (LSUMZ 68553, ♂; MPEG 43772, ♂; MPEG 66153, ♀; LSUMZ 178461, ♀; LSUMZ 178459, ♀; LSUMZ 175423, ♀), *Gymnopathys salvini* (LSUMZ 132956, ♂; MPEG 54997, ♂; MPEG 49484, ♀; LSUMZ 78519, ♀), *Gymnopathys lunulatus* (LSUMZ 161784, ♀; LSUMZ 110124, ♂; LSUMZ 161783, ♂; LSUMZ 172980, ♀), *Rhegmatorhina gymnops* (USNM 120960, ♀; MPEG 65697, ♂; MPEG 59153, ♂; MPEG 67657, ♀; MPEG 59152, ♀), *Rhegmatorhina berlepschi* (AMNH 286932, ♂; MZUSP 76331, ♀; MZUSP 76333, ♀; MZUSP

76332, ♂), *Rhegmatorhina hoffmannsi* (AMNH 491345, ♂; MPEG 39791, ♂; MPEG 57682, ♂; MPEG 39808, ♀; MPEG 57686, ♀), *Rhegmatorhina cristata* (LSUMZ 104957, ♀; MPEG 55865, ♀; MPEG 42724, ♂; MPEG 42725, ♀), *Rhegmatorhina melanosticta* (LSUMZ 115512, ♂; MPEG 52172, ♀; MPEG 60021, ♂; LSUMZ 132982, ♀), *Willisornis poecilinotus* (MPEG 65805, ♀; LSUMZ 110185, ♂; MPEG 59581, ♂; MPEG 59579, ♀; MPEG 58216, ♂; MPEG 57264, ♀; MPEG 56232, ♂; MPEG 55666, ♀), *Willisornis vidua* (MPEG 61128, ♂; MPEG 61125, ♀; LSUMZ 67352, ♂; LSUMZ 67349, ♀), *Phlegopsis nigromaculata* (LSUMZ 137280, ♂; MPEG 57368, ♀; MPEG 51986, ♂; LSUMZ 110205, ♀), *Phlegopsis erythroptera* (LSUMZ 110211, ♂; MPEG 59607, ♀; MPEG 60731, ♂; MPEG 57146, ♀), *Phlegopsis borbae* (AMNH 491993, ♂; MZUSP 84827, ♂; MZUSP 84826, ♀; MZUSP 84825, ♂; MZUSP 80544, ♀), *Phaenostictus mcleannani* (LSUMZ 163606, ♀; LSUMZ 104693, ♀; LSUMZ 177738, ♂; LSUMZ 108372, ♂).