Reassessment of the systematics of the widespread Neotropical genus *Cercomacra* (Aves: Thamnophilidae)

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A comprehensive molecular phylogeny of the family Thamnophilidae indicated that the widespread neotropical genus *Cercomacra* Sclater, 1858 is polyphyletic. Two non-sister clades in putative *Cercomacra* were uncovered: (1) the ‘*nigricans*’ clade (*Cercomacra sensu stricto*), formed by *manu*, *brasiliana*, *cinerascens*, *melanaria*, *ferdinandi*, *carbonaria*, and *nigricans*; and (2) the ‘*tyrannina*’ clade formed by *nigrescens*, *laeta*, *parkeri*, *tyrannina*, and *serva*. *Sciaphylax* was sister to the ‘*tyrannina*’ clade and this group was sister to a clade formed by *Drymophila* and *Hypocnemis*. This whole major clade then was sister to *Cercomacra sensu stricto*. Further work is needed to resolve the phylogenetic placement of *brasiliana* and *cinerascens* within *Cercomacra*, and the relationships within the ‘*tyrannina*’ clade. Because the group of species referred to as the ‘*tyrannina*’ clade does not have an available name, we erect a new genus that recognizes the monophyly and distinct nature of this group. A molecular time scale for the evolution within *Cercomacra sensu lato* is proposed.


INTRODUCTION

Our ability to understand the evolution of the high biological diversity of the Neotropics relies on accurate systematics and taxonomy. The ability to use molecular data to assess phylogenetic relationships is leading to new insights that are overturning relationships in many lineages of Neotropical organisms. One of these lineages, the typical antbirds (Thamnophilidae), comprises the largest group within the tracheophone assemblage of New World suboscines (Irestedt et al., 2002, 2004; Brumfield et al., 2007; Moyle et al., 2009; Ohlson et al., 2013). This highly diverse Neotropical family includes 220 species in at least 48 genera of insectivorous forest birds distributed from southern Mexico to Paraguay and northern Argentina (Zimmer & Isler, 2003; Remsen et al., 2013). Antbirds represent a significant portion of avian diversity in most Amazonian and Atlantic forests, with as many as 40 species recorded at a single site (Terborgh et al., 1990; Blake, 2007).
The monophyly of the Thamnophilidae is well supported by both morphology (Ames, 1971; Welsh, 1977) and molecular data (Sibley & Ahlquist, 1990; Irestedt et al., 2004; Brumfield et al., 2007; Moyle et al., 2009; Ohlson et al., 2013). Evolutionary relationships within this family were poorly understood until recent molecular studies focusing on intergeneric relationships were completed (Irestedt et al., 2004; Brumfield et al., 2007; Moyle et al., 2009; Bravo et al., 2012b; Ohlson et al., 2013). These studies have corroborated previous suggestions on the polyphyly of several antbird genera (e.g. Hackett & Rosenberg, 1990; Ridgely & Tudor, 1994; Bates, Hackett & Goerck, 1999; Zimmer & Isler, 2003), and the resurrection or recognition of several new thamnophilid genera in recent years (Bornschein, Reinert & Teixeira, 1995; Isler et al., 2006; Isler & Whitney, 2011; Belmonte-Lopes et al., 2012; Bravo, Chesser & Brumfield, 2012a; Bravo et al., 2012b; Isler, Bravo & Brumfield, 2013). Monophyly of other genera remains to be assessed. The genus *Cercomacra*, the subject of this study, has also been suggested to be non-monophyletic (Zimmer & Isler, 2003).

*Cercomacra* includes medium-sized birds generally with black, grey or brownish plumage. Males can be distinguished from those of most other Thamnophilid genera by possessing a combination of uniform black or grey plumage, relatively long tails, and small white dots in the greater wing coverts and sometimes at the tips of the rectrices. As with other speciose Thamnophilid genera, *Cercomacra* represents a taxonomically difficult group for defining species limits because of similarity in plumage coloration among populations and species (Bierregaard, Cohn-Haft & Stotz, 1997; Zimmer & Isler, 2003). Proof of this is the recent discovery of two cryptic species overlooked by traditional taxonomy (*laeta* and *parkeri*; Bierregaard et al., 1997; Graves, 1997). Males, in general, look very similar to one another while female plumage may vary considerably, a trend called ‘heterogyny’ (Hellmayr, 1929). Thus, females exhibit the majority of plumage characters one may use to assess relationships within the genus based on morphology (Fitzpatrick & Willard, 1990; Silva, 1992).

As currently defined, *Cercomacra* contains 12 species and 20 subspecies of mid-sized insectivorous antbirds found throughout the continental Neotropics (Peters, 1951; Ridgely & Tudor, 1994; Stotz et al., 1996; Bierregaard et al., 1997; Graves, 1997; Zimmer & Isler, 2003) (Fig. 1). They occur in forest understorey and borders of lowland and montane humid forest, secondary woodlands, deciduous and gallery woodlands, bamboo thickets, and shrubby clearings in tropical lowlands from Paraguay to Mexico (Ridgely & Tudor, 1994), with highest diversity in Amazonia. A set of species occurs in drier gallery forests or other marginal habitats around the Amazonian periphery (Fitzpatrick & Willard, 1990; Silva, 1992; Ridgely & Tudor, 1994) following a circum-Amazonian distribution (Remsen et al., 1991) (Fig. 1A).

To date, no study has formally addressed the relationships of all members of *Cercomacra*, although some studies have partially examined relationships within the genus (Fig. 2), and all were done before *laeta* and *parkeri* were described. Based on comparisons of female plumage patterns and vocalizations, Fitzpatrick & Willard (1990) suggested two species groups, ‘tyrannina’ (tyrannina, serva, nigrescens, brasiliana) and ‘nigricans’ (nigricans, carbonaria, ferdinandi, melanaria, manu), and left cinerascens in an undetermined position. They suggested *C. brasiliana*, from the Atlantic Forest, to belong in the ‘tyrannina’ group based on female plumage coloration,
but vocalizations of this species were not known. Within the 'nigricans' group, they suggested a close relationship between melanaria and manu, and a group formed by nigricans, carbonaria, and Ferdinandi. Cercomacra cinerascens was suggested to be close to the 'nigricans' group, but relationships within the 'tyrannina' group were not suggested (Fig. 2A). A phylogenetic analysis of the 'nigricans' group based on a small set of plumage and vocal characters suggested that this group is monophyletic, and that Cinerascens is sister to this group (Silva, 1992; Fig. 2B). In contrast to Fitzpatrick and Willard's hypothesis, Silva did not find nigricans, Ferdinandi, and carbonaria to be closely related, but recovered manu and melanaria as sister taxa. Silva's (1992) coding of characters for the 'nigricans' group has been questioned especially with respect to the inferred relationship between melanaria and manu. Zimmer, Whittaker & Stotz (1997) suggested that characters that support this relationship (i.e. similar female plumages and narrower white tips in rectrices of both sexes) might be ancestral, and proposed that melanaria was sister to a group formed by nigricans, carbonaria, and Ferdinandi, and that manu was sister to this clade (Fig. 2C). In sum, differences among existing phylogenetic hypotheses are related to the placement of manu and the existence of a nigricans–carbonaria–Ferdinandi clade. Relationships within the 'tyrannina' group have not been thoroughly assessed and the group is now thought to include the newly described C. laeta (Birregaard et al., 1997) and C. parkeri (Graves, 1997). It has been suggested that C. brasiliana is related to C. cinerascens based on male plumage similarities (Cory & Hellmayr, 1924), but similarities in female plumage coloration and ecology suggest a relationship to the 'tyrannina' group (Fitzpatrick & Willard, 1990; Ridgely & Tudor, 1994), and vocalizations suggest it to be closer to the 'nigricans' group together with cinerascens (Zimmer & Isler, 2003). The monophyly of Cercomacra has been questioned on the basis of differences in nests and vocalizations between the 'nigricans' and 'tyrannina' groups, suggesting that morphological characters used to unite these antbirds in Cercomacra might be convergent (Zimmer & Isler, 2003). In this study, we test the monophyly of Cercomacra using phylogenetic analyses of mitochondrial and nuclear data for all species and suitable outgroups. The results show that the traditional Cercomacra is not monophyletic and is composed of divergent clades, requiring a formal description and designation of a new genus.


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**Figure 2.** Hypotheses of relationships for the *Cercomacra* 'nigricans' group: A, Fitzpatrick & Willard (1990); B, Silva (1992); C, Zimmer et al. (1997).
MATERIAL AND METHODS

TAXON SAMPLING AND DNA SEQUENCING

Our taxon sampling for Cercomacra included 20 individuals representing all 12 traditionally recognized species (Appendix). We sequenced 13 individuals, representing ten Cercomacra taxa and three thamnochroïd outgroups (Cymbilaimus, Sciaphylax, Sake-sphorus) (Appendix). The other ten Cercomacra sequences came from our previous work on thamnochroïd relationships (Brumfield et al., 2007; Gomez et al., 2010) (Appendix). To examine the monophyly of Cercomacra, we also included published sequences of 29 of the 48 recognized thamnochroïd genera (Irestedt et al., 2004; Brumfield et al., 2007; Moyle et al., 2009; Ohlson et al., 2013; Remsen et al., 2013) and three non-thamnochroïd outgroups (Appendix).

We followed standard methods for DNA extraction, PCR and DNA sequencing for three mitochondrial gene regions, NADH dehydrogenase subunit 2 (ND2), NADH dehydrogenase subunit 3 (ND3), and cytochrome b (CYTB); and one nuclear intron, β-fibrinogen intron 5 (FIB5) (for detailed description of the methods, see Supporting Information File S1). All sequences were deposited in GenBank (Appendix). Mitochondrial sequences were aligned to the ND2, ND3, and CYTB sequences of chicken (Desjardins & Morais, 1990) using Sequencher (version 4.1; Gene Codes) and checked by eye. FIB5 sequences were aligned with each other and checked by eye to identify gap locations in the intron sequences and to find areas of ambiguous alignments in the nuclear data set (as in Brumfield et al., 2007).

PHYLOGENETIC ANALYSES

We conducted phylogenetic analyses using Bayesian inference (BI) and maximum-likelihood (ML) methods. Prior to the analysis, we determined the best-fit substitution model for each data partition setting with jModelTest (Posada, 2008) according to the Akaike information criterion (AIC). We did this for the concatenated and separate data sets, and for 17 different partitions of the data based on gene regions and codon positions (data not shown).

We performed BI analyses (Rannala & Yang, 1996; Yang & Rannala, 1997) using MrBayes 3.2 (Huelsenbeck & Ronquist, 2001; Ronquist, Huelsenbeck & Teslenko, 2011). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) sampling was performed, depending on the analysis, with one cold and three or five incrementally heated chains, starting from a random tree; chains were run for ten million generations using the default temperature parameter and default priors as starting values for the model parameters. Trees were sampled every 100th generation. Bayesian posterior probabilities were obtained from the 50% majority-rule consensus of all trees retained after a 10% burn-in. Posterior probability values were considered statistically significant when $P \geq 0.95$. Every analysis was repeated twice (each starting from different, randomly chosen trees) to check for appropriate mixing of MCMCMC sampling. Independent analyses were considered to have converged if their log-likelihood values approached similar mean values. Finally, visual comparisons of the posterior probabilities of the independent runs were done to ensure congruence of the analyses.

We performed ML searches in Garli 2.0 (Zwickl, 2006). Support for the tree was examined using 100 bootstrap replicates (Felsenstein, 1985). Parameters for each of the four genes and the combined data sets were estimated from the ML tree using PAUP*, version 4.0b10 (Swofford, 2002).

For both BI and ML inference, we performed five independent analyses of the concatenated data using different partitioned model settings. The best partitioning strategy was selected based on Bayes factors (Kass & Raftery, 1995; Nylander et al., 2004) for BI analysis and AIC for ML. We also performed BI and ML analyses of each mitochondrial gene data set with codon positions in each gene treated as independent partitions. For the FIB5 analysis, we used a single-partition setting, and combined all mitochondrial genes in a single dataset using a three-model partition setting.

Prior to undertaking concatenated phylogenetic analyses, we used the incongruence length difference (ILD) test (Farris et al., 1995a, b) implemented in PAUP*, and an assessment of topological incongruences (see below) to search for conflicting phylogenetic signal among individual partitions and between the mtDNA and FIB5 data sets.

CONGRUENCE AMONG MAJOR DATA PARTITIONS AND PHYLOGENETIC METHODS

We examined congruence between major data partitions (mitochondrial vs. nuclear intron) by inspecting posterior probabilities $\geq 0.95$ and bootstrap values $\geq 70\%$ resulting from the separate BI and ML analyses (Mason-Gamer & Kellogg, 1996). We considered nodes with posterior probabilities $\geq 0.95$ and/or bootstrap support $\geq 70\%$ supporting different phylogenetic relationships for different partitions as a potential incongruence between partitions (Hillis & Bull, 1993).

TEST OF MONOPHYLY

We used a likelihood-based test using parametric bootstrapping and an a posteriori significance test
(SOWH test; Goldman, Anderson & Rodrigo, 2000) to test for the monophyly of Cercomacra. The SOWH test evaluates the significance of the differences between the ML tree (which recovered Cercomacra as polyphyletic, see below) and a constraint tree forcing the genus to be monophyletic. We used the program Seq-Gen v1.3.3 (Rambaut & Grassly, 1997) to produce a null distribution using a resampling/reanalysis approach, accomplished by simulating 100 sequence alignments under the null topology (i.e. the constraint tree); we then calculated the likelihood scores of the constraint and ML topology given the simulated alignments in PAUP*, Due to computational constraints, we used a reduced set of taxa (N = 18) including all studied traditional species of Cercomacra and selected outgroups for the SOWH test.

**Estimating divergence times**

We used an uncorrelated lognormal relaxed-clock model implemented in the program BEAST (Drummond et al., 2012) to estimate divergence times in Cercomacra. The analysis was conducted using the mitochondrial data partitions (ND2, ND3, and CYTB), each with individual models of molecular evolution chosen by jModelTest. To calibrate the tree, we used the CYTB substitution rate of 2.1% sequence divergence per million years (0.0105 substitutions/site/year; Weir, Bermingham & Schluter, 2008; Weir, Bermingham & Schluter, 2009). We linked the tree model and left the clock and site models unlinked and used a Yule tree prior. Two independent runs of ten million generations were performed, sampling one tree in every 1000 in BEAST 1.7.2. Node posterior probabilities were computed across the sampled trees after a 10% burn-in. We examined marginal probabilities of all samples in Tracer 1.5 (Rambaut & Drummond, 2007) to verify an effective sample size (ESS) exceeding 200 for all parameters. Intervals of divergence times were associated with their respective geological time periods following Gradstein et al. (2004).

**RESULTS AND DISCUSSION**

**Data characteristics**

The final alignment of the combined mitochondrial and nuclear intron data totalled 3018 bp (mtDNA = 2437 bp; FIB5 = 581 bp) (Table S1). Within Cercomacra, the length of the nuclear sequences showed marked differences between two groups corresponding to the ‘nigricans’ group (540–541 bp, seven species, including cinerascens and brasiliana) and the ‘tyrannina’ group (547–552 bp, five species). In outgroups, the length of the nuclear sequences varied from 545 bp in Lioseles thoracicus to 564 bp in Euchrepomis humeralis. From the aligned sequences we found a total of 36 indel regions that varied from 1 to 13 bp. Although we found no obvious regions of ambiguous alignment in this data set (and therefore we treated indels as missing data in the phylogenetic analyses), a visual examination of the indels showed that members of the ‘nigricans’ group present an 11-bp deletion at position 135, which is not found in members of the ‘tyrannina’ group. Within this later group, we found a 3-bp deletion at position 273 that was present in serva, tyrannina, nigrescens, and parkeri, but not in laeta.

Although limited by our taxon sampling, our estimates of intraspecific sequence divergence suggest significant genetic structure within two species in the ‘nigricans’ group (cinerascens and manu) and four species in the ‘tyrannina’ group (nigrescens, tyrannina, serva, and laeta). Thus, some of these traditional species may constitute species complexes containing geographical structure that needs more study (Table S2). A full report of data characteristics and DNA sequence variation between and within study taxa is available in Supporting Information File S1.

**Phylogenetic analyses**

*Concatenated analyses:* In the BI analyses, visual comparisons of tree log-likelihoods and Bayes factors of the runs of different data partition model settings found that the ten-partition model had the best fit to the data. A four-partition model performed significantly better than the three-partition model, the four-partition model with unlinked parameters, and the single-partition model including all data, but was outperformed by the ten-partition model (Table 1). The BI majority rule tree of the best model recovered 14 nodes that uncover Cercomacra relationships (Fig. 3, nodes 1–14), with 93% of them having ≥ 0.95 posterior probability support. In the ML analyses, visual comparisons of tree log-likelihoods and the AIC scores of the runs of different data partition models found that the single-partition model had the best fit to the data (Table S3). The ML tree had 86% similarity in nodal congruence to the BI tree. The ML tree recovered 11 nodes (excluding outgroup taxa), 55% of which had ≥ 70% bootstrap support. Differences with the BI tree were due to five highly supported nodes (BP ≥ 0.95) on the Bayesian tree that were not found on the ML tree, and three poorly supported nodes (< 70%) on the ML tree not found on the BI tree.

*Separate analyses:* With the exception of ND3 (41.4%), the other Bayesian mitochondrial gene trees (Figs S2–S4, Table S1) recovered either higher (73%, ND2)
or relatively similar (62%, CYTB) proportions of supported nodes (posterior probabilities ≥0.95) than the FIB5 (68%) tree (Fig. 4B). The mitochondrial tree (Fig. 4A) had 67% of nodes supported, while the Bayesian concatenated tree had 79% (Fig. 3). CYTB and ND2 trees had the greatest proportion of their nodes congruent with the Bayesian concatenated tree (62 and 60%, respectively). The mitochondrial tree had 72% of congruent nodes and the FIB5 tree 51%; thus, mitochondrial genes contributed the most to the overall topology of the Bayesian concatenated tree. Topological incongruence between the FIB5 tree and the mitochondrial tree was found within the ‘tyrannina’ group. The incongruence was caused by three highly supported nodes, one in the mitochondrial tree (Node 15, Fig. 4A) and two in the FIB5 tree (Nodes 11, 12, Fig. 4B).

Based on these results, we used the majority-rule consensus tree and posterior probabilities of the ten-partition Bayesian model to represent the overall topology of the study taxa (Fig. 3), with the exception of three nodes that were involved in the incongruence between the mitochondrial and the FIB5 data sets (see discussion below).

**THE POLYPHYLY OF CERCOMACRA**

Our BI/ML concatenated tree did not recover Cercomacra as monophyletic (Fig. 3). This tree

### Table 1. Summary of Bayes factor tests showing the effects of different data partitions on model likelihood

<table>
<thead>
<tr>
<th>Model* (number of partitions)</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>1: Single partition (1)</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2: 1st mtDNA, 2nd mtDNA, FIB5 (3)</td>
<td>-3133.79†</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3: 1st mtDNA, 2nd mtDNA, 3rd mtDNA, FIB5 (4)</td>
<td>-3457.59</td>
<td>-323.81</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4: ND2, ND3, CYTB, FIB5 (4)</td>
<td>-1097.17</td>
<td>+2036.62</td>
<td>+2360.43</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>5: 1st ND2, 2nd ND2, 3rd ND2, 1st ND3, 2nd ND3, 3rd ND3, ...</td>
<td>-3461.15</td>
<td>-327.37</td>
<td>-3.56</td>
<td>-2363.99</td>
<td>0</td>
</tr>
</tbody>
</table>

The row models are labelled M₀ and positive values in the cells indicate support for the column model (M₁).

*Commas indicate unlinked parameters among partitions.
†Values are twice the log of the Bayes Factors in the comparison between models M₁ and M₀ (2logB₁₀).
Figure 4. Resulting phylograms of the Bayesian consensus trees of Cercomacra from the separate analyses of concatenated mitochondrial (A) and FIB5 (B) data sets. A, phylogram of Bayesian consensus tree from the concatenated mitochondrial nine-partition model analysis (1st ND2 [GTR+G], 2nd ND2 [TVM+I+G], 3rd ND2 [HKY+G], 1st ND3 [SYM+G], 2nd ND3 [TIM3+I+G], 3rd ND3 [TIM1+G], 1st CYTB [GTR+I+G], 2nd CYTB [TIM2+I+G], 3rd CYTB [GTR+I+G]). B, phylogram of Bayesian consensus tree from the FIB5 single-partition model analysis (TIM3+G). Support values correspond to Bayesian posterior probabilities and ML bootstrap values, respectively. Numbered nodes represent those also found in the concatenated analysis. Incongruent nodes between the mitochondrial (node 15) and FIB5 (nodes 11 and 12) trees are marked with asterisks.
recovered two well-supported non-sister groups: (1) the ‘nigricans’ clade, including carbonaria, nigricans, ferdinandi, melanaria, cinerascens, brasiliana, and manu; and (2) the ‘tyrannina’ clade, including serva, tyrannina, nigrescens, parkeri, and laeta. In the ‘nigricans’ clade, carbonaria and nigricans are sister to ferdinandi, and this group is sister to melanaria. This whole clade is sister to a weakly supported clade formed by cinerascens and brasiliana. Cercomacra manu is sister to all the other members of the ‘nigricans’ clade. In the ‘tyrannina’ clade, laeta is sister to a clade formed by parkeri, nigrescens, serva, and tyrannina. In this latter clade, serva and tyrannina form a clade sister to nigrescens, and this whole clade is sister to parkeri. Sciaphylax is sister to the ‘tyrannina’ clade, forming a group sister relationship to a clade formed by Drymophila and Hypocnemis. All but one of the 14 nodes that concern ‘Cercomacra’ relationships (see Fig. 3) are supported by high Bayesian posterior probabilities. ML bootstrap values, by contrast, were more conservative and only imply high support for six of the 14 nodes (Fig. 3).

Within the ‘tyrannina’ group, the mtDNA tree strongly supported nigrescens (0.99/79) basal to a clade formed by laeta, parkeri, tyrannina, and serva (Fig. 5A), while the FIB5 tree, which has the same topology as the Bayesian concatenated tree, strongly supported laeta (1.00/78) basal to a clade formed by parkeri, nigrescens, tyrannina, and serva (Fig. 5B). These incongruent placements may not be related to saturation present in the mtDNA, because the levels of genetic divergence observed within the tyrannina clade [8.3 ± 0.4% (1.8–10.7)] were below the range of saturated positions (see Fig. S1). An additional examination of this node showed that the observed incongruence was caused by four FIB5 substitutions supporting the FIB5 topology (Fig. 5B) and no FIB5 changes supporting the alternative mtDNA topology (Fig. 5A). The mitochondrial data supported the mtDNA topology with 53 substitutions and the FIB5 topology with 29 substitutions (Fig. 5). We found the substitutions supporting these alternative topologies to be evenly distributed throughout the studied sequences, and thus it is unlikely that the mitochondrial and nuclear characters supporting either topology are the product of a particular mitochondrial or nuclear region of high mutation rate. The observed incongruence between markers supporting a different topology could be influenced by short internodes separating laeta, parkeri, serva, and tyrannina (see Fig. 4), as well as the slower evolutionary rate and smaller total number of characters of the FIB5 compared with the mitochondrial genes. Thus, we suggest that the mitochondrial tree must represent the correct basal split within this group.

The results of our BI/ML concatenated analyses show that Cercomacra, as traditionally defined, is polyphyletic. Differences in log-likelihoods between the ML tree and the constraint tree in which

Figure 5. Trees showing incongruent topologies within the ‘tyrannina’ clade. The number of mitochondrial and nuclear substitutions supporting those topologies is showed below the branches. Numbers above the branches represent Bayesian posterior probabilities and maximum-likelihood bootstraps.

Cercomacra was forced to be monophyletic were statistically significant (SOWH test, \( P \leq 0.05 \)) (Fig. 6).

**Morphological, Behavioural, and Ecological Differences Between the 'Nigricans' and 'Tyrannina' Clades**

The non-monophyly of Cercomacra is consistent with some plumage, behavioural, and ecological differences between these two clades. Regarding plumage, the species in the 'tyrannina' clade lack, in both sexes, the conspicuous white tips on the rectrices present in all species of the 'nigricans' clade (Zimmer & Isler, 2003). Also, females of the 'tyrannina' clade are predominantly warm buffy-brown or orange buff, whereas females of the 'nigricans' clade are grey to olive-grey except for C. cinerascens in which females are dull greyish brown. Vocal differences among species of the 'nigricans' and 'tyrannina' clades are well known. Species in the 'nigricans' clade ('croakers') engage in complex duets in which female vocal cues are given during the course of the male’s loudsong, causing the male to change its vocalization and to begin a synchronized duet (with the exceptions of cinerascens and brasiliana that perform a more imperfectly synchronized duet). Among the species in the 'tyrannina' clade ('whistlers'), males and females have very distinctive loudsongs that overlap in timing of delivery, but the female loudsongs start while males are singing (Zimmer & Isler, 2003). Differences in nest architecture also give support for these clades: species in the 'tyrannina' clade for which nest data are available all build deep pouch-shaped nests with oblique entrances, whereas species in the 'nigricans' clade build cup-nests with horizontal entrances, with the exception of C. manu which builds a pouch-type nest (Kratter, 1998; Zimmer & Isler, 2003; Batista De Pinho et al., 2006). Species in the 'nigricans' clade are found mostly occupying the midstory to canopy strata of tropical evergreen interior forest, forest edges, and mid-canopy vine-tangles, whereas those from the 'tyrannina' clade are mostly inhabitants of the understory of forest edge and secondary growth (Stotz et al., 1996; Zimmer & Isler, 2003).

**Nomenclature and Description of a New Genus**

Cercomacra, as traditionally defined, has a complex nomenclatural history. Through the years, its species were included in different genera, including Formicivora and Pyriglena, until Sclater (1858) unified them under Cercomacra. When describing this new genus, Sclater (1858: 244), used specimens from Rio de Janeiro that were previously misidentified as Myrmothera caerulescens Vieillot, 1817 by Ménétriés (1835, who changed the name to Formicivora caerulescens). Additionally, among the specimens that Sclater (1890) identified as Cercomacra caerulescens there were specimens from south-eastern Brazil, as well as Pará. Because no known species of Cercomacra occurs both in south-eastern Brazil and in Pará, it can be deduced that Sclater’s series included more than one species. Sclater’s use of the name Myrmothera caerulescens was incorrect because it referred to a different taxon (possibly Willisornis poecilinotus Cabanis, 1847). Later, Hellmayr (1905) pointed out...
that specimens of Cercomacra caerulescens (Sclater, 1858) did not match those of Myrmothera caerulescens Vieillot, 1817, and proposed a new name for Sclater’s species, Cercomacra brasiliana, listing six specimens from south-eastern Brazil as syntypes. A direct implication of Hellmayr introducing the name Cercomacra brasiliana is the series used by Sclater (1890: 264) to designate his C. caerulescens, and not the specimens Hellmayr (1905) pointed out later. This complex nomenclatural history involves at least four species, as well as the actual definition of the genus Cercomacra, a problem that will be fully addressed in a future publication (M. Raposo et al., in preparation). Here we opt to adopt the proposition of Cory & Hellmayr (1924, p. 213), which considers C. brasiliana as the type species of Cercomacra and, simultaneously, we consider that the name is applicable to the south-eastern Brazilian populations of this genus, first called Formicivora caerulescens Ménetriés, 1835 and then Cercomacra caerulescens Sclater, 1858.

Based on the results of the phylogenetic analyses, the genus Cercomacra is therefore applicable to the species: Cercomacra brasiliana Hellmayr, 1905; Cercomacra nigricans Sclater 1858; Cercomacra carbonaria Sclater & Salvin, 1873; Cercomacra cinerascens (Sclater, 1857); Cercomacra ferdinandi Snethlage, 1928, Cercomacra melanaria (Ménétriés, 1835), and Cercomacra manu Fitzpatrick and Willard, 1990.

Because the group of species referred to as the ‘tyrannina’ clade does not have an available name, we erect a new genus that recognizes the monophyly and distinct nature of this group.

**Cercomacroides J. G. Tello & M. A. Raposo, gen. nov.**

*Type species*: Cercomacroides tyrannina (Sclater, 1855), comb. nov., Dusky Antbird (= Cercomacra tyrannina [Sclater], 1855).

*Other included species*: Cercomacroides laeta (Todd, 1920), comb. nov., Willis’s antbird; Cercomacroides serva (Sclater, 1858), comb. nov., black antbird; Cercomacroides nigrescens (Cabanis & Heine, 1859), comb. nov., blackish antbird; Cercomacroides parkeri (Graves, 1997), comb. nov., Parker’s antbird.

*Diagnosis*: Comparisons in the diagnosis are only between Cercomacroides and Cercomacra because a previous study (Isler et al., 2013) has already reported comparisons between the tyrannina clade (= Cercomacroides) and the other genera (Sciaphylax, Drymophila, and Hypocnemis) in the larger Thamnophilid clade (Fig. 3). Cercomacroides can be distinguished from Cercomacra by the lack of conspicuous white tips on the rectrices of both sexes; by the predominantly warm buffy-brown or orange buff plumage in females; by the whistling loudsongs and non-synchronized vocal duets; and by building deep pouch-shaped nests with oblique entrances.

*Etymology*: The Latin suffix -oides, taken from ancient Greek ‘eidos’ means ‘having the likeness of’. Our choice of the name Cercomacroides is an allusion to the great shape and plumage similarity among the species of Cercomacroides and those of the genus Cercomacra, probably as a result of convergence.

We recommend the following placement and provisional classification of Cercomacra and Cercomacroides, based on our phylogeny and the proposed classification of Furnariidés by Moyle et al. (2009) and Ohlson et al. (2013):

**FAMILY** Thamnophilidae

**TRIBE** Pithyini

Cercomacra

Cercomacroides, Sciaphylax

Drymophila, Hypocnemis

**Cercomacra Sclater, 1858**

Cercomacra manu (Fitzpatrick & Willard, 1990)

Cercomacra brasiliana (Hellmayr, 1905), type of Cercomacra

Cercomacra cinerascens (Sclater, 1857)

Cercomacra melanaria (Ménétriés, 1835)

Cercomacra ferdinandi (Snethlage, 1928)

Cercomacra carbonaria (Sclater & Salvin, 1873)

Cercomacra nigricans (Sclater, 1858)

**Cercomacroides gen. nov.**

Cercomacroides nigrescens (Cabanis & Heine, 1859)

Cercomacroides laeta (Todd, 1920)

Cercomacroides parkeri (Graves, 1997)

Cercomacroides tyrannina (Sclater, 1855), type of Cercomacroides

Cercomacroides serva (Sclater, 1858)

**Relationships within Cercomacra**

Cercomacra comprises manu, brasiliana, cinerascens, melanaria, ferdinandi, carbonaria, and nigricans (Fig. 3). Cercomacra manu is sister to the rest of Cercomacra, which comprises two clades: one clade formed by the circum-Amazonian taxa (melanaria, ferdinandi, carbonaria, and nigricans), in which carbonaria and nigricans are sister to ferdinandi, and then to melanaria; and a second clade formed by the Amazonian cinerascens and the south-eastern...
Atlantic Forest brasiliana. All nodes received high posterior probability and ML bootstrap support, with the exception of the node uniting cinerascens and brasiliana (Fig. 3). Resolution of this latter node has important biogeographical implications (see below) and needs to be investigated further. Vocal similarities between cinerascens and the circum-Amazonian taxa support a close relationship between these taxa (Fitzpatrick & Willard, 1990; Zimmer et al., 1997; Isler & Whitney, 2002), as supported (albeit weakly) by the mtDNA tree (Fig. 4A).

Contrasting with previous hypotheses (Fig. 2), our molecular analyses found that the ‘nigricans’ group, as delimited by Fitzpatrick & Willard (1990), Silva (1992), or Zimmer et al. (1997), does not constitute a natural group, because brasiliana and cinerascens are embedded within this clade (Fig. 3). Similarity in vocalizations, i.e. a two-element call of males and a single element in the female call during the duet, supports the inclusion of cinerascens and brasiliana within Cercomacra senso stricto (Vielliard, 1995; Isler & Whitney, 2002; Zimmer & Isler, 2003). The phylogenetic results also agree with the previous suggestion of a close relationship between carbonaria, nigricans, and ferdinandi (Fitzpatrick & Willard, 1990; Zimmer et al., 1997; Fig. 2A, C). The species in this subclade possess plumage (heavy streaking on throat of females) and vocal (male–female duet song pattern) similarities that support their close relationship, particularly between nigricans and carbonaria (Fitzpatrick & Willard, 1990; Zimmer et al., 1997; Isler & Whitney, 2002; Zimmer & Isler, 2003). Our results confirm Zimmer et al.’s (1997) conclusion that characters suggesting a close relationship between melanaria and manu (Fitzpatrick & Willard, 1990; Silva, 1992), i.e. the overall similarity in female plumages, are probably due to sharing ancestral or convergent features within the group.

RELATIONSHIPS WITHIN CERCOMACROIDES

The new genus Cercomacroides comprises nigrescens, laeta, parkeri, tyrannina, and serva. In the concatenated tree, all internal nodes within Cercomacroides received high posterior probability support, but low or no ML bootstrap support (Fig. 3). An incongruent signal between the mitochondrial and nuclear markers was uncovered in this group, and the concatenated tree was biased toward the FIB5 signal (see discussion above and Figs 3–5). The main difference between these two topologies is regarding the identity of the taxon sister to the rest of the group: nigrescens in the mtDNA tree, and laeta in the FIB5 tree (Fig. 5). Both major data sets supported a close relationship between serva and tyrannina (although support in the mitochondrial tree was low; Fig. 4A), which was not expected due to the great plumage similarity between tyrannina and parkeri (Graves, 1997). Overall similarities in male and female vocalizations (based on the analysis of vocalizations from Isler & Whitney, 2002) and plumage coloration (Graves, 1997; Zimmer & Isler, 2003) suggest that parkeri is closer to tyrannina and serva than to laeta or nigrescens, but do not provide clear evidence for the phylogenetic placement of laeta and nigrescens. Full resolution of the internal relationships within Cercomacroides may require the addition of more nuclear markers.

DIVERGENCE ESTIMATES OF CERCOMACRA AND CERCOMACROIDES

Posterior rate estimates (parameter ‘meanRate’ in BEAST) ranged from 0.30 to 0.42% s s⁻¹ Mya⁻¹ for FIB5, 1.92 to 2.16% for CYTB, 1.82 to 2.40% for ND3, and 2.24 to 2.86% for ND2. According to this tree (Fig. 7), the age of the roots of Cercomacra and Cercomacroides clades ranged from the late Miocene through the early Pliocene between 9.3 and 4.2 Mya (Cercomacra, mean = 6.7 Mya (9.3–4.5 Mya); Cercomacroides, mean = 6.2 Mya (8.6–4.2 Mya)). Subsequent major splits within the Cercomacra and Cercomacroides clades all are estimated to have occurred between the Late Miocene and Late Pleistocene (9.3–0.3 Mya within Cercomacra; and 8.6–3.3 Mya within Cercomacroides). The separation of Cercomacroides from Scaphylas was estimated to have occurred c. 9.6 Mya (13.2–6.4 Mya), and this latter clade separated from the Hypocnemis–Drymophila clade c. 11.0 Mya (15.0–7.5 Mya). Finally, the Cercomacroides–Scaphylas–Hypocnemis–Drymophila clade separated from Cercomacra at approximately 11.6 Mya (15.9–7.9 Mya).

The ancestral Cercomacra lineage split from its most recent common ancestor in the mid to late Miocene (see above). Cercomacra manu, the taxon diverging first from the rest of the genus, split in the late Miocene to early Pliocene between 9.3 and 4.5 Mya. The phylogenetic position of brasiliana and cinerascens is not yet resolved. Cercomacra brasiliana is either sister to cinerascens (Figs 3, 4B) or sister to the cinerascens–circum-Amazonian clade (melanaria, ferdinandi, carbonaria, and nigricans) (Fig. 4A). Alternatively, it may be sister to the circum-Amazonian clade (although this relationship was not recovered in any of the analyses). Internal branches separating these three major clades are short and divergence of all three occurred within 1 Mya (Figs 4A, 7). The mitochondrial tree suggests that brasiliana is sister to the cinerascens–circum-Amazonian clade, and that divergence occurred in the late Miocene to early Pliocene between 8.0 and 3.9 Mya. The mitochondrial topology shows that
cinerascens is sister to the circum-Amazonian clade, diverging in the late Miocene to early Pliocene between 7.6 and 3.7 Mya. Within the circum-Amazonian clade, the split of melanaria from the rest of the taxa took place between 6.0 and 2.8 Mya. Subsequent splits in Cercomacra took place in the Pleistocene and included the separation of ferdinandi from the carbonaria–nigricans clade between 0.9 and 2.1 Mya, and the separation of carbonaria and nigricans between 0.8 and 0.3 Mya.

The ancestral Cercomacroides lineage split from its most recent common ancestor in the middle to late Miocene between 13.2 and 6.4 Mya. The lack of resolution of the internal nodes in the Cercomacroides tree due to data incongruence prevents us from determining the order in which internal splits took place. However, the mitochondrial topology suggests that the earliest split took place sometime in the late Miocene to early Pliocene between 8.6 and 4.2 Mya, and involved the basal divergence between nigrescens and the laeta–tyrannina–parkeri–serva clade. The order of splits that separated these four taxa is unknown, but based on the mitochondrial tree estimates, we can suggest that they took place not far from each other sometime between 6.8 and 3.3 Mya (Fig. 7).

Cercomacra and Cercomacroides constitute two independent lineages of similar age distributed in several major areas of endemism (Table S4), whose relationships can provide important insights on the biogeography of the Neotropical lowlands. Both genera originated sometime between the late Miocene and early Pliocene. This range of time, particularly between 3 and 7 Mya, coincides with molecular estimates of the time of origin of several Neotropical avian genera (e.g. Lovette, 2004; Pereira & Baker, 2004; Barker, 2007; Miller et al., 2008; Ribas, Miyaki & Cracraft, 2009; Antonelli et al., 2010; Patel et al., 2011). Diversification in the late Miocene to early Pliocene coincides with a time period of dynamic geomorphological activity in the region (Antonelli et al., 2010; Hoorn et al., 2010a; Wesselingh et al., 2010). During this period, the completion of present-day patterns of river systems and drainage divides in South America began to be achieved (Campbell, Frailey & Romero-Pittman, 2006; Figueiredo et al., 2009; Hoorn et al., 2010b; Latrubesse et al., 2010). A combination of tectonics (Andean uplift) and sea transgressions, due to sea-level rise, led to the formation of structural arches, palaeorivers, and ancient lakes that may have contributed to diversification of biota (Lundberg et al., 1998; Hoorn et al., 2010a; Wanderley-Filho et al., 2010). Diversification during the late Pliocene coincides with a time period of strong global cooling and the formation of the first glacial period at the end of the Pliocene (van der Hammen & Hooghiemstra, 2000), with subsequent effects on the vegetation cover, structure, and species composition of the region (Colinvaux et al., 1996; Haffer, 1997, Colinvaux & De Oliveira, 2001; Haffer & Prance, 2001; Behling, Bush & Hooghiemstra, 2010). This also coincides with the presence of an extensive wetland system occupying the western Amazonian basin (Klammer, 1984; Frailey, 1988; Marroig & Cerqueira, 1997; Hoorn et al., 2010b). The palaeogeographical conditions at that time (arches, river basins, etc.) that start forming at the late Miocene, together with climate fluctuations that characterized the late Pliocene to late Pleistocene, may have contributed to the origination of current Neotropical avian diversity (Haffer, 1997; Aleixo & Rossetti, 2007; Antonelli et al., 2010).

All these factors may have played some role in the diversification of Cercomacra and Cercomacroides lineages. Today, the distributions of members of these two lineages present an interesting contrast to the majority of currently documented biogeographical patterns for Amazonian birds. These birds exhibit a great degree of range overlap that exists within related lineages of different ages. Cercomacra includes divergent overlapping Amazonian taxa, including the more restricted manu and the widespread Amazonian cinerascens along with the circum-Amazonian lineage, one of which (carbonaria) has a distribution completely within the range of cinerascens (Fig. 1). Ecological differences between these species are significant (e.g. manu is a bamboo specialist, carbonaria a gallery forest species and cinerascens a mid-canopy, vine tangle specialist). The ecological differences between the broadly overlapping members of Cercomacroides (serva and nigrescens; laeta and tyrannina) are less obvious and offer an interesting system to investigate the co-occurrence of comparatively young and ecologically similar lineages in Amazonia.

CONCLUSIONS

Phylogenetic analyses of mitochondrial and nuclear intron data documented phylogenetic relationships between and among putative Cercomacra lineages. The analyses of concatenated and separated data sets identified phylogenetic incongruence between the mitochondrial and nuclear intron data at some intermediate nodes, which are probably caused by the smaller number of nuclear compared with mitochondrial characters, and the presence of short internodes separating those relationships.

Two non-sister clades in putative Cercomacra were uncovered by this study and one received a new generic description: (1) Cercomacra sensu stricto, formed by manu, brasiliana, cinerascens, melanaria, ferdinandi, carbonaria, and nigricans; and (2) Cercomacroides gen. nov., formed by nigrescens, laeta, parkeri, tyrannina, and serva. Sciaphylax was sister to Cercomacroides and this group was sister to a clade formed by Drymophila and Hypocnemis. This whole major clade then was sister to Cercomacra. Further work is needed to resolve the phylogenetic placement of brasiliana and cinerascens within Cercomacra, and the relationships within Cercomacroides.

This study provides an initial historical framework to begin reconstructing the biogeographical history.
of these lineages. Cercomacra and Cercomacroides belong to one of the most specious families in the Neotropics, and thus historical patterns of diversification derived from these genera are potentially representative of the evolutionary history of a good portion of the Neotropical lowland forest avifauna. Both from taxonomic and from biogeographical perspectives, these two genera constitute broadly informative Neotropical case studies.

ACKNOWLEDGEMENTS

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REFERENCES


J. G. TELLO 560


Latrubesse EM, Cozzuol M, da Silva-Caminha SA,


Welsh CJ. 1977. Phylogeny of the antbirds (Formicariidae and Thamnophilidae) based on hindlimb myology and plumage. PhD, University of Pittsburgh, Pittsburgh.


SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

File S1. Supplementary text including materials and methods, results and discussion.

Figure S1. Comparison of uncorrected percentage sequence divergence between mtDNA and FIB5. The slope is represented by the regression equation. Black circles represent comparisons within the ‘nigricans’ group; light grey circles represent comparisons within the ‘tyrannina’ group; grey circles represent comparisons between the ‘nigricans’ and ‘tyrannina’ groups; and white circles represent comparisons with the outgroups.

Figure S2. Phylogram of Bayesian consensus tree from the ND2 three-partition model analysis (1st[GTR+G], 2nd[TVM+I+G], 3rd[HKY+G]). Support values correspond to Bayesian posterior probabilities and ML bootstrap values, respectively.

Figure S3. Phylogram of Bayesian consensus tree from the ND3 three-partition model analysis (1st[SYM+G], 2nd[TIM3+I+G], 3rd[TIM1+G]). Support values correspond to Bayesian posterior probabilities and ML bootstrap values, respectively.

Figure S4. Phylogram of Bayesian consensus tree from the CYTB three-partition model analysis (1st[GTR+I+G], 2nd[TIM2+I+G], 3rd[GTR+I+G]). Support values correspond to Bayesian posterior probabilities and ML bootstrap values, respectively.

Table S1. Properties of three mitochondrial genes and one nuclear intron based on maximum-parsimony, maximum-likelihood, and Bayesian inference.

Table S2. Uncorrected pairwise percentage sequence divergence (p) at different taxonomic levels for three mitochondrial genes and one nuclear intron (mean ± SE, range in parentheses).

Table S3. Summary of AIC scores showing the effects of different data partitions on model likelihood.

Table S4. Geographical distribution in major area(s) of endemism for Cercomacra and Cercomacroides taxa.
### APPENDIX

Collection data and voucher information for tissue samples used in this study.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Locality</th>
<th>Museum Code</th>
<th>GenBank Accession Numbers</th>
</tr>
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<tr>
<td><strong>C. brasiliana</strong></td>
<td>Brazil: Rio de Janeiro: Fazenda Bela Vista, Cordeiro, 22° 02′ S, 42° 18′ W, 337 m elev.</td>
<td>MNRJ 44251</td>
<td>HM637230, HM637271, HM637136, HM637183</td>
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<td><strong>C. carbonaria 1</strong></td>
<td>Brazil: Rondônia: Fazenda Santa Cecilia, E bank Rio Branco, across from Boa Vista.</td>
<td>FMNH 389250</td>
<td>HM637234, HM637276, HM637141, HM637188</td>
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<td><strong>C. carbonaria 2</strong></td>
<td>Brazil: Rondônia: Fazenda Santa Cecilia, E bank Rio Branco, across from Boa Vista.</td>
<td>FMNH 389251*</td>
<td>KF826071, KF826030, KF826043, KF826057</td>
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<td><strong>C. cinerascens (selateri) 1</strong></td>
<td>Peru: Loreto: 79 km WNW Contamana, 7° 08′ S, 75° 41′ W, 400 m elev.</td>
<td>LSUMNS B28057</td>
<td>HM637229, HM449834, HM637135, HM637184</td>
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<td><strong>C. cinerascens (cinerascens) 2</strong></td>
<td>Peru: Loreto: 1 km N Rio Napo, 157 km by river NNE Iquitos.</td>
<td>LSUMNS B2859*</td>
<td>KF826073, KF826031, KF826045, KF826059</td>
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<td><strong>C. ferdinandi</strong></td>
<td>Brazil: Tocantins: Parque Estadual do Cantão, 09° 15′ 53″ S, 50° 00′ 39″ W.</td>
<td>MZUSP 79871*</td>
<td>KF826072, KF826044, KF826057, KF826062</td>
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<td><strong>C. laeta (sabinoi) 1</strong></td>
<td>Brazil: Pernambuco: Timbaúba.</td>
<td>FMNH 392376</td>
<td>HM637231, HM637272, HM637137, HM637184</td>
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<td><strong>C. manu 1</strong></td>
<td>Brazil: Pará: 126 km NW Alta Floresta S bank Rio São Benedito</td>
<td>LSUMNS B35304</td>
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<td><strong>C. manu 2</strong></td>
<td>Bolivia: Pando: Nicolás Suarez; 12 km by road S of Cobija, 8 km W on road to Mucden.</td>
<td>LSUMNS B9100*</td>
<td>KF826074, KF826032, KF826046, KF826060</td>
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<td><strong>C. melanaria 1</strong></td>
<td>Bolivia: El Beni: Laguna Suarez, 5 km sw Trinidad, 230 m elev.</td>
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<td><strong>C. melanaria 2</strong></td>
<td>Paraguay: Alto Paraguay: W bank Rio Negro, ca. 8 km above mouth, 20° 06′ S, 58° 08′ W.</td>
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<td><strong>C. nigrescens (fuscicauda) 2</strong></td>
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<td><strong>Dichrozona cincta</strong></td>
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<td><em>Formicivora rufa</em></td>
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<td><em>Microchroia quinxensis</em></td>
<td>Perú: Madre de Dios: Hacienda Amazonia.</td>
<td>FMNH 321993</td>
<td>EF639895, EF640027,</td>
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<td><em>Myrmophylax athorithorax</em></td>
<td>Perú: Madre de Dios: Hacienda Amazonia.</td>
<td>FMNH 322209</td>
<td>EF639896, EF640028,</td>
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<td><em>Sciaphlyax hemimelaena</em></td>
<td>Perú: Ucuyali: Lower Urubamba: Centro Pucaní 10° 40.5′ S 73° 32.7′ W.</td>
<td>STRI MJM796*</td>
<td>KF826083, KF826041,</td>
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<td><em>Myrmodorus myotherinus</em></td>
<td>Brazil: Pará: Serra dos Carajás.</td>
<td>FMNH 391406</td>
<td>KF826055, KF826069</td>
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<td><em>Myrmorchilus arctothericus</em></td>
<td>Brazil: Sergipe: Canindé do São Francisco, Curituba, Fazenda Mirama.</td>
<td>FMNH 392862</td>
<td>EF639902, EF640035,</td>
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<td><em>Myrmornis torquata</em></td>
<td>Brazil: Rondónia: Cachoeira Nazaré, W bank Río Jiparaná, 100 m elev.</td>
<td>FMNH 389880</td>
<td>EF640102, EF639968</td>
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<td><em>Myrmotherula axillaris</em></td>
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<td>FMNH 392444</td>
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<td><em>Neoctantes niger</em></td>
<td>Perú: Cuzco: Tono.</td>
<td>FMNH 321806</td>
<td>EF640104, EF639970</td>
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<td><em>Percnostola lophotes</em></td>
<td>Perú: Madre de Dios: Moskititas, 13.4 km N NW Atalaya, left bank of Alto Madre de Dios River.</td>
<td>FMNH 433492</td>
<td>EF639908, EF640042,</td>
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<td><em>Phegeopsis nigromaculata</em></td>
<td>Brazil: Rondónia: Cachoeira Nazaré, W bank Río Jiparaná, 100 m elev.</td>
<td>FMNH 389842</td>
<td>EF40109, EF639975</td>
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<td><em>Pithys albifrons</em></td>
<td>Brazil: Amapá.</td>
<td>FMNH 391430</td>
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<td><em>Pygiptila stellaris</em></td>
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<td>FMNH 389931</td>
<td>EF639912, EF640046,</td>
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<td>EF640113, EF639979</td>
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<td><em>Pyriglena leucnota</em></td>
<td>Bolivia: Santa Cruz: San José-San Ignacio Road, Km 69.</td>
<td>FMNH 334469</td>
<td>EF639913, EF640047,</td>
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<td><em>Rhegmatorhina hoffmannsi</em></td>
<td>Brazil: Rondónia: Cachoeira Nazaré, W bank Río Jiparaná, 100 m elev.</td>
<td>FMNH 389933</td>
<td>EF639914, EF640048,</td>
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<td><em>Rhegmania luctuosus</em></td>
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<td>FMNH 389938*</td>
<td>EF640115, EF639981</td>
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<td><em>Sclateria naevia</em></td>
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<td>FMNH 391418</td>
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<td><em>Taraba major</em></td>
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<td>FMNH 321773</td>
<td>EF639916, EF640050,</td>
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<td><em>Teremura humeralis</em></td>
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<td>FMNH 389942</td>
<td>EF640117, EF639983</td>
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<td><em>Thamnomanes saturninus</em></td>
<td>Brazil: Rondónia: Cachoeira Nazaré, W bank Río Jiparaná, 100 m elev.</td>
<td>FMNH 389947</td>
<td>KF826084, KF826042,</td>
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APPENDIX  Continued

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<th>Taxon</th>
<th>Locality</th>
<th>Museum Code(^a)</th>
<th>GenBank Accession Numbers(^b)</th>
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<td><em>Thamnophilus</em></td>
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<td><em>aethiops</em></td>
<td>Brazil: Alagoas: Ibateguara, Engenho Coimbra,</td>
<td>FMNH 399223</td>
<td>EF639924, EF640058, EF640125, EF639991</td>
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<td>Usina Serra Grande.</td>
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<td><em>Willisornis</em></td>
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<td><em>poecilinotus</em></td>
<td>Bolivia: La Paz: T.C.O Campamento Araona,</td>
<td>FMNH 391148</td>
<td>EF639888, EF640020, EF640087, EF639953</td>
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<td>‘Palmasola’, Río Manupari.</td>
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\(^a\)Indicate sequences added to GenBank for this study.

\(^b\)Museum abbreviations: MNRJ = Museu Nacional da Universidade Federal do Rio de Janeiro; FMNH = Field Museum of Natural History; LSUMNS = Louisiana State University Museum of Natural Science; MZUSP = Museum of Zoology of the University of São Paulo; UKMNHN = University of Kansas Museum of Natural History; IAvH-CT = Colección de Tejidos, Instituto Alexander von Humboldt; AMNH = American Museum of Natural History; STRI = Smithsonian Tropical Research Institute.

\(^b\)BF5, ND2, ND3, CYTB.