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ARTICLE

# A new species of *Formicivora* Swainson, 1824 (Thamnophilidae) from the state of São Paulo, Brazil

**Dante Renato Corrêa Buzzetti[1], Ricardo Belmonte-Lopes[2,3,4], Bianca Luiza Reinert[2, 5], Luís Fábio Silveira[6], and Marcos Ricardo Bornschein[2, 7, 8]**

[1] Centro de Estudos Ornitológicos, Rua Álvaro Rodrigues 139, sala 4, CEP 04582-000, São Paulo, Brasil.
[2] Mater Natura – Instituto de Estudos Ambientais, Rua Lamenha Lins 1080, CEP 80250-020, Curitiba, Paraná, Brasil.
[3] Laboratório de Dinâmica Evolutiva e Sistemas Complexos, Departamento de Zoologia, Universidade Federal do Paraná, Centro Politécnico, Jardim das Américas, CEP 81531-990, Curitiba, Paraná, Brasil.
[4] Programa de Pós-Graduação em Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná, CEP 81531-990, Curitiba, Paraná, Brasil.
[5] Laboratório de Biodiversidade, Conservação e Ecologia de Animais Silvestres, Departamento de Zoologia, Universidade Federal do Paraná, Centro Politécnico, Jardim das Américas, CEP 81531-990, Curitiba, Paraná, Brasil.
[6] Seção de Aves, Museu de Zoologia da Universidade de São Paulo (MZUSP), Caixa Postal 42494, CEP 04218-970, São Paulo, Brasil.
[7] Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, CEP 81531-990, Curitiba, Paraná, Brasil.
[8] Corresponding author: bornschein.marcao@gmail.com

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**ABSTRACT:** *Formicivora paludicola* sp. nov. (São Paulo Marsh Antwren) is described from 13 specimens (nine males and four females) collected in the municipalities of Mogi das Cruzes, Salesópolis, and São José dos Campos, near the city of São Paulo, in the east of the state of São Paulo, southeastern Brazil. Males of the new species are distinct from those of *F. acutirostris* (Marsh Antwren), its sister species, by their black underparts and thighs, very dark grayish brown upperparts, and smaller exposed culmen. Females can be distinguished from those of *F. acutirostris* by the color of the upperparts and flanks, which are also very dark grayish brown, and by the smaller exposed culmen. Mitochondrial DNA sequences also distinguish these two species and the analysis of their vocalizations also showed differences, mainly in the frequency in which certain phrases of the vocal repertoire are used. São Paulo Marsh Antwren inhabits marshes where the vegetation is high (*ca*. 60–250 cm). The species was found in 15 small and isolated areas, at the headwaters of the rivers Tietê and Paraíba do Sul, at altitudes between 600 and 760 m a.s.l. One of these areas was later flooded by the construction of a dam. Most of the marshes where the new species was found are heavily degraded by sand mining, housing developments, fish farming, drainage for cattle raise and agricultural activities, invasion by exotic plants and fire. We propose urgent measures for the protection of this new species.

**KEY-WORDS:** conservation; Marsh Antwren; marshes; *Stymphalornis*, taxonomy.

## INTRODUCTION

The systematics and taxonomy of Thamnophilidae have experienced a great improvement during the last two decades as result of the description of new taxa in several different genera, the elevation of some subspecies to full species status and the reorganization of genus-level taxonomy on the basis of both morphological and molecular analyses (*e.g.*, Isler *et al.* 2007, Moyle *et al.* 2009, Belmonte-Lopes *et al.* 2012). Increased fieldwork and improvement in the design and performance of vocal and molecular analyses are enhancing our understanding of the taxonomic diversity of this family. Progress in alpha taxonomy has been followed by advances in the knowledge of phylogenetic relationships, primarily based on molecular studies (Brumfield *et al.* 2007, Moyle *et al.* 2009, Isler & Whitney 2011).

Among the 49 genera currently recognized in the family, the genus *Formicivora* Swainson, 1824 is among those that have undergone the most taxonomic changes in the last 20 years. Currently, the genus *Formicivora* included eight species: *F. grisea*, *F. serrana*, *F. littoralis*, *F. melanogaster*, *F. rufa*, *F. grantsaui*, *F. erythronotos*, and *F. acutirostris* (Gonzaga 2001, Gonzaga *et al.* 2007). A large number of taxa have been described for this genus recently, an unexpected scenario considering that most *Formicivora* species are very vocal and conspicuous birds, found in open, even disturbed areas, and are easily detected in the field. Gonzaga (2001) performed the first phylogenetic analysis of the genus and, based on vocal and morphological characters, suggested the monophily of *Formicivora* with the inclusion of *Stymphalornis acutirostris* and the exclusion of *F. iheringi*, placed in its own genus *Neorhopias* Hellmayr, 1920. More recently Hilty (2003) suggested that *F. grisea*

*intermedia* could represent a valid species (see also Ridgely & Tudor 2009), and Gonzaga *et al.* (2007) described a new species from the Chapada Diamantina, northeastern Brazil. Finally, Firme & Raposo (2011) suggested that *F. littoralis* is not a valid biological species, and that this taxon and *F. serrana interposita* could be considered as subspecies of *F. serrana*, as originally described by Gonzaga & Pacheco (1990). Recent molecular studies of the genus corroborate Gonzaga (2001), and also suggest that the monophily of *Formicivora* depends on the exclusion of *F. iheringi* and inclusion of *Stymphalornis* Bornschein, Reinert & Teixeira, 1995 (Bravo 2012, Belmonte-Lopes 2013).

During field work on 6 October 2004 DRCB heard, tape recorded and observed, at an extensive marsh dominated by *Typha domingensis* and *Schoenoplectus californicus* in Mogi das Cruzes, São Paulo state, at 625 m a.s.l., a female and a subadult male of an antwren at first glance attributable to *F. acutirostris* (Marsh Antwren). This species inhabits the coastal marshes in the states of Paraná, Santa Catarina, and Rio Grande do Sul, in southern Brazil, from sea-level up to about 10 m a.s.l. (Reinert *et al.* 2007, Bencke *et al.* 2010). Believing this might be a new species, DRCB returned to the area the next day, saw an adult male with black underparts and collected a pair of this antwren (see *Formicivora* sp. nov. photos # 6 and 7 in Minns *et al.* [2009]).

LFS, learning (through Luiz Pedreira Gonzaga) of the discovery of the *Formicivora* at Mogi das Cruzes, made visits to an area at Biritiba-Mirim in February 2005 and found there another population of this *Formicivora*. Since this area was to be flooded by a dam (Barragem do Paraitinga 2), LFS invited BLR to help in an evaluation of the size of the population which would be affected by the dam. On obtaining an estimate of about 100 individuals in the area, a project was developed by a group, which included MRB, RB-L and other ornithologists to capture and transfer the antwrens to other areas. After capturing the first individuals, MRB recognized the antwren as different from *F. acutirostris*, and collected and prepared specimens for further studies. The authors initiated detailed analyses to confirm the first impressions that the São Paulo birds represent a new species, described herein.

## MATERIAL AND METHODS

### Morphology

The specimens of *Formicivora* sp. nov. that were collected are housed at the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, in the state of São Paulo, the Museu de História Natural "Capão da Imbuia" (MHNCI), Curitiba, in the state of Paraná, and the Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre, in the state of Rio Grande do Sul. For comparison with the new species, we examined specimens of *F. acutirostris* and other *Formicivora* (see list of specimens in appendix 1).

We took measurements with calipers to the nearest 0.1 mm of the length of the exposed culmen, bill length, bill depth, and bill width (the last three measurements from the proximal edge of the nares to the bill tip), wing length (chord), tail length (from the insertion of the central rectrices to their tip), and tarsus length. These measurements were taken from specimens, as well as from several live birds mist-netted for ongoing studies, of both *Formicivora* sp. nov. and *F. acutirostris*. We took measurements of the birds' total length (according to Sick 1997) and wing-span with a ruler to the nearest 0.1 cm. We did not measure tail length when the longest rectrix was damaged and when both central rectrices were absent. Tarsus lengths were measured in skins according to Sick (1997), but measurements of mist-netted birds were taken differently: the bird's toes were bent backwards and the measurement was taken from the distal part of the leg (dorsal side) to the toe pad near the base of the hallux. The measurements of mist-netted individuals were tested for normal distribution, and then compared using the t test or the Mann-Whitney test (for the measurements that did not present a normal distribution). Birds were weighed with a Pesola spring balance with a 30 g scale. We checked the pterylosis and the number of wing feathers in the collected specimens. The number of tail feathers was noted, both in the study skins and the mist-netted specimens. Carcasses of collected birds were preserved in ethanol 80% v/v, and muscular tissue in ethanol 100% v/v. Colors follow Munsell (1994) and geographic coordinates were taken in the field with a Garmin GPS.

### Vocalizations

We recorded vocalizations with Sony TCM 5000EV analogue tape recorders, a Sound Devices 722 digital audio recorder and a Sony PCM50 digital recorder, with Sennheiser ME66 and ME67 microphones. DRCB's recordings are housed in the Arquivo Sonoro Dante Buzzetti (ASDCB), mantained by the first author. Copies of these recordings were or will be deposited at Arquivo Sonoro Prof. Elias P. Coelho, Universidade Federal do Rio de Janeiro (ASEC – UFRJ), and at the Arquivo Sonoro do Museu de Zoologia da Universidade de São Paulo (MZUSP). Additional vocalizations were obtained from a published DVD-ROM (Minns *et al.* 2009) and from the online collection xeno-canto (www.xeno-canto.org) (Appendix 2). All recordings of *F. acutirostris* made by the authors were of spontaneous vocalizations.

Analogue tape recordings were digitalized at 44.1 kHz, 16-bit, and digital recordings were made with the same parameters. Spectrograms were produced in Raven

1.2.1 using a Blackman window type, with a resolution of 1024 bands and overlap of 96%. The vocal variables were measured from the fundamental harmonics using screen cursors on the spectrograms. The variables measured were: total phrase duration, duration of the interval between the notes, note length, minimum frequency, maximum frequency or peak frequency (*sensu* Isler *et al.* 1998), and frequency amplitude (band-width) of the first and second notes. Descriptions of note shape were made from spectrograms at the same scale as that of the respectives figures which appear in the text. We applied the statistical tests proposed by Isler *et al.* (1998) and Patten & Unitt (2002) despite the low sample size, but as the results were not significant they are not presented.

### Molecular analysis

We obtained muscular tissue of *F. acutirostris* from specimens collected and feather material of this species from individuals banded; for *Formicivora* sp. nov. we used tissue from individuals collected. We obtained sequences from four individuals of the first species and of three individuals of the second species for the mitochondrial genes cytochrome b (CYB, 1,045 base pairs – b.p.), nicotinamide dehydrogenase subunit 2 (ND2, 1,041 b.p.), nicotinamide dehydrogenase subunit 3 (ND3, 351 b.p.), and for one autossomal nuclear intron, the $\beta$-fibrinogen intron 5 ($\beta$F5, 563 b.p.). The sequences' GenBank accession numbers are given in Appendix 3.

Genomic DNA was extracted from 25 mg of pectoral muscle or 2-5 slices (0.2 mm) of the feather cannon from 2-3 contour feathers using the Qiagen DNeasy kit and following the manufacturer's protocol. The DNA extracted was subjected to polymerase chain reactions performed using the protocols of Brumfield *et al.* (2007), and each gene region was bidirectionally sequenced to verify accuracy. Additional sequences from a previous publication (Brumfield *et al.* 2007) available at GenBank were also used. Sequences for each gene were aligned using the program MAFFT v. 6 (Katoh *et al.* 2002) and manually edited in BioEdit (Hall 1999) so to include the largest number of homologous positions in all sequences. To select between the possible partition schemes, we performed Bayesian inference analyses for five different partition schemes under a GTR+G model of nucleotide substitution using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). We compared the likelihood values of all partition schemes tested by Bayes Factors using Tracer 1.5 (Rambaut & Drummond 2009) to select the most adequated partition scheme. All analyses were performed with four chains, 2,000,000 generations (sampled at each 1,000), and two replicates. Bayes factors were calculated as marginal likelihood estimates following the method of Newton & Raftery (1994) with the modifications proposed by Suchard *et al.* (2001). We used the guidelines of Kass & Raftery (1995) for interpreting the values of $\log_{10}(B_{10})$. The scheme selected through Bayes Factors was one with the mitochondrial genes grouped and coded by codons, in addition to a partition for $\beta$F5 (scheme IV in Table 5; total of four partitions).

After selecting the partition scheme, we used jModelTest (Posada 2008) to determine the best fit model of DNA substitution for each partition using the Bayesian Information Criterion (Schwarz 1978), given that this method has been shown to often outperform other commonly used criteria (Luo *et al.* 2010). After this we conducted Bayesian analysis using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001) using the selected partition scheme and models of DNA substitution. We performed our analysis with four runs and four MCMC chains, using 4,000,000 generations with a sample frequency of 1,000, and a burn-in of 20%, with these analyses being performed on the Cipres Science Gateway version 3.1 (Miller *et al.* 2010). The results of the Bayesian inference were analyzed for convergence using the compare splits and the slide window analyses implemented at AWTY (Wilgenbusch *et al.* 2004, Nylander *et al.* 2008), and also in Tracer and by Bayes Factors. Both approaches demonstrated that the runs converged, and we combined the trees from all runs (except for the burn-in) and used them to estimate a 50% majority rule consensus tree. We also estimated a phylogenetic hypothesis via maximum likelihood under a GTR+G model of nucleotide substitution in RAxML 7.2.7 (Stamatakis 2006), with branch support being obtained through 1,000 bootstrap replicates. Additionally, we estimated the genetic distances between the samples under the Tamura-Nei model of DNA substitution, with the variance being estimated through 1,000 bootstrap replicates using MEGA 5.05 (Tamura *et al.* 2011). The chicken mitochondrial genome (GenBank accession NC 001323.1) was used as reference sequence to define the position number of sites of CYB, ND2, and ND3. Additionally, we inferred a Bayesian chronogram for a larger set of taxa of the genus *Formicivora* with a calibration rate of 2.1% per million years for CYB (Weir & Schluter 2008) and a log-normal relaxed clock using BEAST 1.74 (Drummond & Rambault 2007) (RB-L *et al*. unpublished data) to obtain an estimate of the age of the split between the Marsh Antwrens.

## RESULTS

The comparison of 13 specimens collected in São Paulo state with 13 of *F. acutirostris*, the handling of additional mist-netted birds (37 individuals from São Paulo, and 69 of *F. acutirostris*), and the additional data from vocalizations and genetics showed certain differences which lead us to describe the bird from São Paulo as a distinct species, here named:

***Formicivora paludicola*** sp. nov.

São Paulo Marsh Antwren

Bicudinho-do-brejo-paulista

Figures 1, 2, and 3

*Holotype*. MZUSP 78787: adult male (Figure 1), skull ossified, testes partially enlarged (5 mm); collected by DRCB on 07 October 2004 at Córrego Taboão do Parateí (23°24'27"S, 46°13'35"W; 630 m a.s.l.), municipality of Mogi das Cruzes, São Paulo state, Brazil; prepared by LFS. Tissue sample and carcass preserved. No molt; light yellow fat; 10 rectrices.

**FIGURE 1.** From the top, holotype (male, MZUSP 78787) and paratype (female, MZUSP 78788) of São Paulo Marsh Antwren *Formicivora paludicola* sp. nov., and a pair of Marsh Antwren *F. acutirostris* (male, MZUSP 78797, and female, MZUSP 78798). Plate by Eduardo Brettas.

*Paratypes*. MZUSP 78788: adult female (Figure 1), skull ossified, ovarium partially developed (10 mm x 5 mm); other data as the holotype. MZUSP 78789: adult male, skull ossified, testes minute (1.5 x 1.0 mm); collected by MRB, BLR, RB-L, C. O. A. Gussoni, P. Lopes and G. A. Benedicto on 17 March 2005 at Rio Paraitinga (23°31'S, 45°55'W; 760 a.s.l.), Barragem do Paraitinga 2, municipality of Salesópolis, São Paulo state, Brazil; prepared by MRB. Tape recorded. Tissue sample and carcass preserved. No brood patch; molting feathers on body, wing and tail; small amount of light yellow fat in the body; 10 rectrices. MHNCI 6587 (ex MZUSP 78790): adult male, skull ossified, testes minute (1.0 x 1.0 mm); collected on 18 March 2005; other data as MZUSP 78789. MCP 3265 (ex MZUSP 78791): adult male, skull ossified, testes minute (1.0 x 0.5 mm); collected on 19 March 2005. Not tape recorded; orange fat in the body and skin; other data as MZUSP 78789. MHNCI 6725 (ex MZUSP 78792); adult female, skull ossified, ovarium inactive (5.0 x 3.0 mm); other data as MZUSP 78789. MZUSP 78793: subadult female, skull not fully ossified; ovarium inactive (3.0 x 1.0 mm); collected on 19 March 2005. Not tape recorded; orange fat in the body and skin; other data as MZUSP 78789.

*Diagnosis - morphology*. Males of *F. paludicola* can be distinguished from other Thamnophilidae outside the *Formicivora* genus by the presence of 10 rectrices and by the combination of dark grayish brown upperparts, black underparts and a long black tail. Females of *F. paludicola* can be distinguished from other Thamnophilidae that do not belong to the *Formicivora* genus by having 10 rectrices, unstreaked dark grayish brown upperparts, long black tail, and white underparts, heavily marked with black streaks. A recent molecular study including all species of *Formicivora* showed that the two taxa with 10 rectrices (*F. acutirostris* and *F. paludicola*) are sister species (Bravo 2012, Belmonte-Lopes 2013), so within the genus we diagnosed the new species only with respect to *F. acutirostris*.

Adult males of *F. paludicola* can be distinguished from adult males of *F. acutirostris* by their black (1: 2.5/N) instead of dark gray (1: 4/N) cheeks, auriculars, throat, belly and thighs (see Figures 1, 2, and 3). Males of *F. paludicola* also have the crown, upperparts and upper tail coverts dark grayish brown (2.5Y/4/2), as opposed to the dark brown (10YR/3/3) of males of *F. acutirostris*. Moreover, males of *F. paludicola* have a smaller exposed culmen in comparison with males of *F. acutirostris* (Table 1; see also Table 2). Females of *F. paludicola* can be distinguished from females of *F. acutirostris* by their brown (10YR4/3) crown, upperparts and upper tail coverts and dark grayish brown (10YR/4.2) flanks, and also by the smaller exposed culmen (Table 1; see also Table 2). Females of *F. acutirostris* have dark grayish brown (10YR/4/2) upperparts and dark brown (10YR/3/3) flanks (Figure 1).

**FIGURE 2.** Males of São Paulo Marsh Antwren *Formicivora paludicola* sp. nov. in comparison with a male of Marsh Antwren *F. acutirostris* (in the center). From left to right *F. paludicola* MZUSP 78789 and MZUSP 78787 (holotype), *F. acutirostris* MZUSP 78797, and *F. paludicola* MZUSP 78796 and MZUSP 85428.


**FIGURE 3.** Males of São Paulo Marsh Antwren *Formicivora paludicola* sp. nov. (A) and Marsh Antwren *F. acutirostris* (B) in the wild. Photos by Robson Silva e Silva and RB-L.

*Diagnosis - genetics*. Based on the specimens sequenced, *F. paludicola* can be diagnosed from *F. acutirostris* by differences in their mitochondrial DNA. For CYB, the new species differs in one transition (position 15,231 of *Gallus gallus* mitochondrial genome, from adenine in *F. acutirostris* to guanine in the the new species), and two transversions (positions 15,120 and 15,519; from thymine in *F. acutirostris* to cytosine in *F. paludicola*, and from adenine in *F. acutirostris* to cytosine in *F. paludicola*, respectively). For ND2, they differ in two transitions (positions 5,624 and 5924; respectively, from thymine in *F. acutirostris* to cytosine in *F. paludicola*, and from guanine to adenine) and one transversion (position 5828, from adenine in *F. acutirostris* to thymine in *F. paludicola*). For ND3, they differ in three transitions (positions 10,862, 10,913, and 11,114; respectively, from thymine in *F. acutirostris* to cytosine in *F. paludicola*, from cytosine to thymine, and from adenine to guanine). The uncorrected genetic distance between *F. paludicola* and *F. acutirostris* was between 0.004-0.011 according to

CYB, between 0.003-0.006 according to ND2, between 0.011-0.017 according to ND3, and between 0-0.002 according to βF5.

*Description of holotype*. See figure 1. Crown, back, mantle and upper tail coverts dark grayish brown (2.5Y/4/2). Forehead gray (1: 5/N) and lores black. A discrete white superciliary stripe. Auriculars, throat and underparts black (1: 2.5/N). Thighs, undertail coverts and tail black, with fourth and fifth pair of rectrices tipped white. Lesser wing coverts white, and medium and large coverts black with white tips, with the exception of the proximal part of the latter two coverts, which are dark grayish brown (2.5Y/4/2). Underwing coverts white, tipped black. Primaries and secondaries are very dark brown (10YR/2/2) with white inner vane, tertials with a dark grayish brown (2.5Y/4/2) stripe on the outer vane. Irides brown, tarsi and toes dark bluish gray (2: 5/1/5GB), nails gray, and bill black.

**TABLE 1.** Measurements (mm) and weight (g) of live specimens of *Formicivora paludicola* sp. nov. and *F. acutirostris.* The values presented are range, mean ± standard deviation (in parentheses) and sample size. All *p* values were obtained using the Mann-Whitney test, except when indicated by *, when the t test was used.

| Measurements | *F. paludicola* Males | *F. acutirostris* Males | | *F. paludicola* Females | *F. acutirostris* Females | |
|---|---|---|---|---|---|---|
| Exposed culmen | 10.9-13.5 (12.44 ± 0.55) n = 31 | 14.3-14.9 (14.69 ± 0.21) n = 7 | $p < 0.01$ | 11.4-12.9 (12.32 ± 0.4) n = 35 | 13.8-14.7 (14.33 ± 0.29) n = 10 | $p < 0.01$ |
| Bill depth[1] | 3.0-3.7 (3.33 ± 0.14) n = 30 | 3.1-3.6 (3.33 ± 0.15) n = 59 | $p > 0.05$* | 3.0-3.6 (3.27 ± 0.16) n = 34 | 3.0-4.1 (3.27 ± 0.20) n = 61 | $p > 0.05$* |
| Bill width[1] | 3.1-3.9 (3.51 ± 0.24) n = 30 | 3.1-3.7 (3.4 ± 0.18) n = 61 | $p < 0.05$ | 3.3-3.8 (3.53 ± 0.13) n = 34 | 3.1-3.7 (3.4 ± 0.18) n = 61 | $p < 0.01$ |
| Wing[2] | 47.0-52.6 (49.46 ± 1.3) n = 31 | 45.2-51.7 (48.52 ± 1.23) n = 58 | $p < 0.01$ | 41.6-49.8 (47.11 ± 1.64) n = 34 | 44.4-49.9 (47.31 ± 1.2) n = 61 | $p > 0.05$ |
| Tail[3] | 55.5-66.9 (62.61 ± 3.05) n = 13 | 53.7-67.5 (60.52 ± 3.27) n = 29 | $p < 0.05$ | 58.1-63.6 (60.45 ± 1.59) n = 10 | 54.9-67.9 (59.97 ± 2.86) n = 23 | $p > 0.05$ |
| Tarsus[4] | 22.8-25.3 (24.03 ± 0.54) n = 31 | 24.0-26.0 (24.86 ± 0.46) n = 39 | $p < 0.01$ | 22.8-24.4 (23.68 ± 0.49) n = 34 | 22.9-25.8 (24.63 ± 0.54) n = 60 | $p < 0.01$ |
| Weight | 8.3-10.5 (9.29 ± 0.53) n = 35 | 8.5-11.5 (9.96 ± 0.6) n = 69 | $p < 0.01$* | 8-10 (9.16 ± 0.53) n = 37 | 8.5-12 (9.75 ± 0.76) n = 65 | $p < 0.01$* |

1 From the proximal edge of nares to bill tip.

2 Chord.

3 From the central rectrices insertion to their tip.

4 From the distal part of leg (dorsal side) to the toepad near the base of the hallux (with the bird fingers flexed backwards).

**TABLE 2.** Measurements (mm) and weight (g) of collected specimens of *Formicivora paludicola* sp. nov. and *F. acutirostris*. The values presented are range, mean ± standard deviation (in parentheses) and sample size.

| Measurements | *F. paludicola* Males | *F. acutirostris* Adult males | *F. acutirostris* Subadult males[1] | *F. paludicola* Females | *F. acutirostris* Females |
|---|---|---|---|---|---|
| Bill length[2] | 9.9-11.4 (10.61 ± 0.50) n = 7 | 11.4-12.4 (11.85 ± 0.36) n = 6 | 11.2; 11.4 n = 2 | 10.0-11.0 (10.57 ± 0.51) n = 3 | 11.0-12.2 (11.50 ± 0.53) n = 4 |
| Bill depth[2] | 3.0-3.4 (3.25 ± 0.14) n = 6 | 3.0-3.5 (3.34 ± 0.16) n = 7 | 2.9 n = 1 | 3.1-3.3 (3.20 ± 0.10) n = 3 | 2.9-3.2 (3.07 ± 0.15) n = 3 |
| Bill width[2] | 3.3-3.7 (3.60 ± 0.15) n = 7 | 3.7-3.9 (3.79 ± 0.09) n = 7 | 3.9 n = 1 | 3.5-3.6 (3.53 ± 0.06) n = 3 | 3.4-3.9 (3.67 ± 0.25) n = 3 |
| Wing[3] | 48.4-51.2 (49.77 ± 0.95) n = 7 | 49.2-51.1 (50.19 ± 0.61) n = 7 | 49.0; 51.7 n = 2 | 48.0-50.4 (48.80 ± 1.39) n = 3 | 48.1-52.7 (49.73 ± 2.03) n = 4 |
| Tail[4] | 57.9-64.3 (62.23 ± 2.93) n = 4 | 58.2-63.0 (61.07 ± 1.88) n = 7 | 59.7; 60.4 n = 2 | 55.7-61.3 (59.23 ± 3.07) n = 3 | 59.0-60.4 (59.70 ± 0.99) n = 2 |
| Tarsus[5] | 19.8-21.4 (20.79 ± 0.65) n = 7 | 20.3-21.7 (21.06 ±0.48) n = 7 | 21.3 n = 1 | 18.9-20.5 (19.80 ± 0.82) n = 3 | 19.3-21.7 (20.73 ± 1.01) n = 4 |
| Total lenght[5] | 145-153 (148.75 ± 3.50) n = 4 | 143-152 (147.43 ± 3.41) n = 7 | 140; 145 n = 2 | 139.0-143.0 (140.67 ± 2.08) n = 3 | 146.0; 147.0 n = 2 |
| Wing span | 160-167 (163.33 ± 3.20) n = 6 | 163-167 (165.0 ± 1.41) n = 7 | 165.0; 165.0 n = 2 | 155.0; 162.0 n = 2 | 152.0-167.0 (159.25 ± 6.60) n = 4 |
| Weight | 8.5-11.0 (9.57 ± 0.79) n = 9 | 9.5-10.9 (9.96 ± 0.52) n = 7 | 10.0; 11.0 n = 2 | 8.0-9.6 (8.73 ± 0.66) n = 4 | 9.0-10.2 (9.70 ±0.53) n = 4 |

[1] One with plumage like female, and the other still with considerable amount of white on underparts.

[2] From proximal edge of nares to bill tip.

[3] Chord.

[4] From the central rectrices insertion to their tip.

[5] Follows Sick (1997).

*Measurements of holotype*. Total length 147.0 mm; exposed culmen 13.7 mm; bill length 11.4; bill width 3.5; wing 49.7 mm; tail 64.3 mm; tarsus 21.1 mm; weight 8.9 g.

*Variation in type series*. Male specimens do not show significant variation in the plumage, except in the amount of white in the rectrices, which varies slightly between birds (Table 3). The males MZUSP 78794 and 78795 have some whitish feathers on the ventral surface, particularly on the sides of the body, reminiscent of the earlier plumage similar to the female plumage (see below in Discussion). Females have a distinct plumage, described below.

*Description of the female*. See figure 1. The female MZUSP 78788 has the crown, back, mantle and upper tail coverts dark grayish brown (10YR4/3). Forehead and lores gray (1: 5/N). A discrete white superciliary stripe. Auriculars gray, throat and underparts white with black spots. Thighs black with white tips, undertail coverts and tail black, with fourth and fifth pair of rectrices tipped white. Lesser wing coverts white, medium and large coverts black with white tips, with the exception of the proximal part of the latter two coverts, where the innermost part is dark grayish brown (10YR4/3), the middle is dark grayish brown (10YR4/3) with a white apical spot, and the remaining becoming increasingly black with white apical spots. Underwing coverts white. Primaries and secondaries are very dark brown (10YR/2/2) with white inner vane, tertials with a dark grayish brown (2.5Y/4/2) stripe on the outer vane. Irides brown, tarsi and toes dark bluish gray (2: 5/1/5GB), nails gray, and bill black. Other females (MZUSP 78792 and 78793) show the throat and belly less heavily spotted black. In other features, they do not show significant variation in the plumage, except in the amount of white in the rectrices (Table 3).

**TABLE 3.** Amount of white (mm) in the rectrices ventral surface tip in *Formicivora paludicola* sp. nov.[1] We presents only the largest measurement when the amount of white differed between the feathers of a pair. Abbreviation: m = male; f = female. Acronyms: MZUSP - Museu de Zoologia da Universidade de São Paulo; MHNCI - Museu de História Natural "Capão da Imbuia"; MCP - Museu de Ciências e Tecnologia da Pontifícia, Universidade Católica do Rio Grande do Sul.

| Specimen | Sex | Pair of rectrices | | | | |
|---|---|---|---|---|---|---|
| | | 1st | 2s | 3rd | 4th | 5th |
| MZUSP 78787 | m | 0.0[2] | 0.0[2] | 0.0[2] | 1.5 | 1.6 |
| MZUSP 78789 | m | 0.0[2] | 0.3 | ? | ? | ? |
| MZUSP 78794 | m | 0.2 | 0.8 | 0.9 | 1.6 | 2.6 |
| MZUSP 78795 | m | 0.0 | 0.0 | ? | 0.0 | 1.2 |
| MZUSP 78796 | m | 0.0 | 0.0 | 0.2 | 1.5 | 1.9 |
| MHNCI 6587 | m | 0.2 | ? | 1.2 | 1.8 | 2.2 |
| MCP 3265 | m | 0.2 | 0.2 | 0.4 | 1.7 | 2.1 |
| MZUSP 78788 | f | 0.0[2] | 0.0[2] | 0.0[2] | 0.9 | 1.6 |
| MZUSP 78793 | f | 0.0[2] | 0.0[2] | 0.0[2] | 1.0[2] | 1.0[2] |
| MHNCI 6725 | f | 0.0[2] | 0.5 | 0.7 | 2.1 | 2.3 |

[1] Amount of white measured in the feather rachis, even if the white is expanded in the vanes.

[2] Feathers worn (white tips may have disappeared or decreased).

*Additional material (non-type material)*. MZUSP 78794: adult male, skull not fully ossified, testes minute (1.0 x 1.0 mm left testes; 0.5 x 0.5 mm right testes); collected by MRB, BLR and RB-L on 05 April 2005 at Córrego Taboão do Parateí (23°24'27"S, 46°13'35"W; 630 m a.s.l.), municipality of Mogi das Cruzes, São Paulo state, Brazil; prepared by MRB. Not tape recorded. Tissue sample and carcass preserved. No brood patch; molting feathers on body, wing and tail; small amount of light orange fat in the body; 10 rectrices; nine secondary remiges. MZUSP 78796: adult male, skull ossified, testes minute (1.5 x 1.0 mm left testes; 1.0 x 1.0 mm right testes). Tape recorded. Other data as MZUSP 78794. MZUSP 78795: subadult male, skull not fully ossified, testes minute (1.0 x 0.5 mm left testes; 0.5 x 0.5 mm right testes); collected by MRB, BLR, RB-L, LFS, C. O. A. Gussoni, E. Machado and F. Schunck on 10 April 2005 at Rio Paraitinga (23°31'S, 45°55'W; 760 a.s.l.), Barragem do Paraitinga 2, municipality of Salesópolis, São Paulo state, Brazil; other data as MZUSP 78794. MZUSP 85428: adult male; collected by LFS and É. Machado on 21 November 2009 at Usina da Light (23°34'S, 45°49'W), municipality of Salesópolis, São Paulo state, Brazil. MZUSP 85429: adult female. Other data as MZUSP 85428. MZUSP 91700: adult male; collected by LFS, Gláucia del Rio and Marco Antônio Rego on 06 January 2011 at Fazenda Montes Claros (23°04'S, 46°02'W), municipality of São José dos Campos, São Paulo state, Brazil.

*Distribution. Formicivora paludicola* is known from 15 localities in the municipalities of Biritiba-Mirim, Mogi das Cruzes, Salesópolis, Santa Isabel, and São José dos Campos, São Paulo state, southeastern Brazil (Figure 4, Appendix 4), at altitudes ranging from 600 to 760 m a.s.l. These localities lie at the headwaters of the Tietê and Paraíba do Sul river basins. Since the species' discovery in 2004, we have conducted searches in more than 50 marshes to the south of the known distribution of *F. paludicola*, from sea level (municipalities of Bertioga, Santos, Cubatão, and Itanhaém) to 900 m (in municipalities surrounding the known localities) but have found no evidence of its presence at those sites.

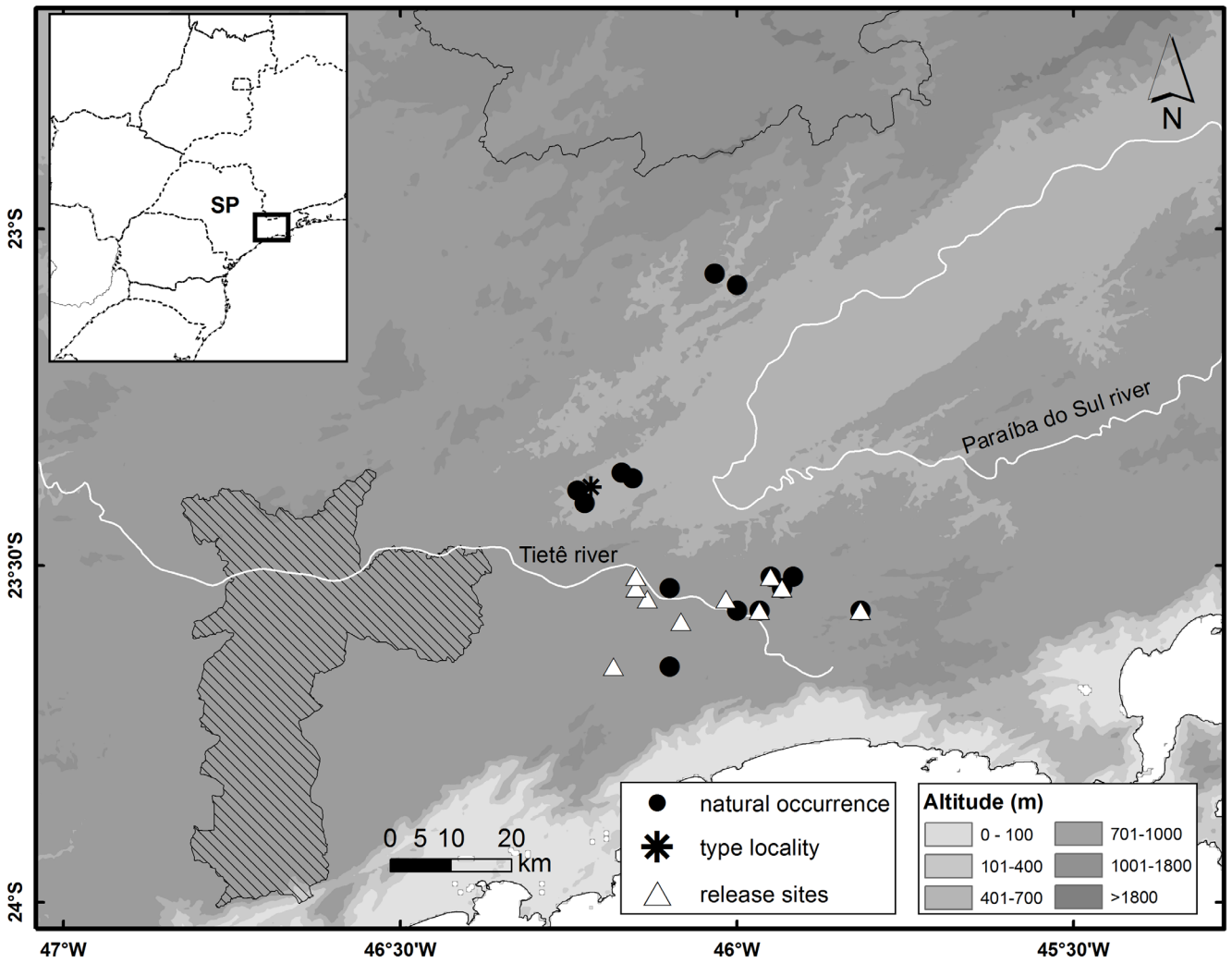


**FIGURE 4.** Distribution of São Paulo Marsh Antwren *Formicivora paludicola* sp. nov., São Paulo state, southeastern Brazil. Hatched area represents the city of São Paulo. The black line at the top of the figure represents the border between the states of São Paulo and Minas Gerais.

Probably the first record of a bird now known as *F. paludicola* dates of 4 November 1945, when Hélio Camargo collected a female of "*Formicivora rufa rufatra*" (Camargo 1946:158) at Boracéia Biological Station (23°38'S, 45°52'W), municipality of Salesópolis, eastern São Paulo state (see Cavarzere *et al.* 2010). Unfortunately, this specimen was severely damaged by the shot and was not prepared for the collection. Curiously, this record from outside the normal range of *F. rufa*, Rusty-backed Antwren, was not recognized as anomalous by later authors, except by Willis & Oniki (2003), who considered it to be a mistake. Boracéia Biological Station lies in montane Atlantic Forest and the nearest record of *Formicivora rufa* is about 200 km west. LFS did not found marshes in this location during recent searches and probably this habitat has disappeared from the reserve.

*Etymology*. *Paludicola*, from the Latin, means native to or inhabitant of marshes. This species is restricted to this habitat, and our intention in choosing the specific name *paludicola* is to focus attention on the conservation of the marshes of southern and southeastern Brazil.

## Vocalizations

The name of each kind of vocalization in the vocal repertoire in any species is subjective. We have tried to name each different vocalization according to the context in which it is used by *F. paludicola* and by its sister species, *F. acutirostris*. We consider that all vocalizations described below for the two species are homologous.

*Loudsong*. The loudsoung (*sensu* Willis 1967) of *F. paludicola* (Figure 5) is a sequence of rapidly but evenly repeated two-note phrases, like that of *F. acutirostris*, and unlike the loudsongs of other *Formicivora* species, that consist of a repetition of a single or bipartite song note (Gonzaga 2001). The number of phrase repetitions and the interval between each sequence is highly variable in *F. paludicola* and *F. acutirostris*, and depends very much on

**TABLE 4.** Measurements of phrases of the loudsong (*sensu* Willis 1967) of *Formicivora paludicola* sp. nov. and *F. acutirostris*. The values presented are range and mean ± standard deviation (in parentheses).

| Variable | *Formicivora paludicola* (6 individuals, 124 phrases) | *Formicivora acutirostris* (5 individuals, 107 phrases) |
|---|---|---|
| Phrase duration (s) | 0.240-0.338 (0.277 ±0.028) | 0.240-0.430 (0.293 ± 0.041) |
| Length note 1 (s) | 0.047-0.070 (0.057 ± 0.004) | 0.045-0.072 (0.057 ± 0.004) |
| Max. freq. note 1 (kHz) | 2.1-3.7 (2.9 ± 0.2) | 2.6-3.8 (3.2 ± 0.4) |
| Low. freq. note 1 (kHz) | 1.2-1.9 (1.7 ± 0.2) | 1.4-2.1 (1.7 ± 0.1) |
| Freq. amplitude note 1 (kHz) | 0.8-2.4 (1.3 ± 0.3) | 0.8-2.3 (1.5 ± 0.5) |
| Length note 2 (s) | 0.017-0.052 (0.028 ± 0.006) | 0.023-0.068 (0.037 ± 0.007) |
| Max. freq. note 2 (kHz) | 2.9-4.6 (3.7 ± 0.4) | 2.8-4.7 (3.7 ± 0.3) |
| Low. freq. note 2 (kHz) | 1.4-2.3 (1.9 ± 0.1) | 1.9-2.7 (2.3 ± 0.2) |
| Freq. amplitude note 2 (kHz) | 0.9-2.7 (2.1 ± 0.7) | 0.9-2.3 (1.5 ± 0.2) |
| Interval between notes (s) | 0.144-0.257 (0.191 ± 0.020) | 0.143-0.347 (0.200 ± 0.042) |

the level of excitement of the bird (BLR *et al.*, unpub. data). For this reason, the number of phrase repetitions and the interval between them were not considered. Measurements of loudsongs of *F. paludicola* and *F. acutirostris* are given in Table 4. For *F. paludicola* the interval between the notes represents about 69% of the phrase duration, with the first note of the phrase presenting a sharp descending frequency modulation, as does the second, although the latter often ends in a short duration frequency modulation slight upward or horizontal. For *F. acutirostris* the interval between the notes represents about 68% of the phrase duration, with the first note also presenting a sharp descending frequency modulation, as does the second, although the latter ends in a small upward and downward modulation (Figure 5, F and H).

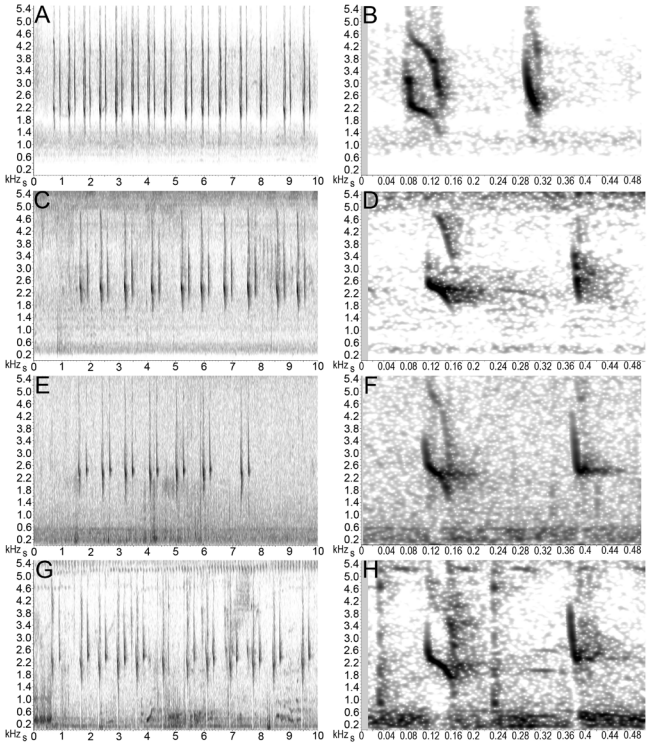


**FIGURE 5.** Loudsongs of *Formicivora paludicola* sp. nov. and *F. acutirostris*. A. Female of *F. paludicola* recorded at Bairro Rio Acima, municipality of Biritiba-Mirim, São Paulo state (recorded by A. Whittaker). B. Detail of a phrase of A. C. Male of *F. paludicola* recorded at Bairro Rio Acima (recorded by J. C. Minns). D. Detail of a phrase of C. E. Male of *F. acutirostris* recorded at Jundiaquara Island, municipality of Guaratuba, Paraná state (recorded by BLR). F. Detail of a phrase of E. G. A different male of *F. acutirostris* recorded at Jundiaquara Island (recorded by MRB). H. Detail of a phrase of G.

*Alarm call*. This call type (Figure 6) is known from *F. paludicola*, *F. acutirostris*, *F. rufa*, and *F. grantsaui*, supposedly being homologous to the call with a similar structure given by *F. grisea* (Gonzaga 2001, Gonzaga *et al.* 2007). In *F. paludicola* and *F. acutirostris* this call consists of a two note phrase emitted by birds alone and in duet, with a phrase repetition rate depending on the bird's level of excitement. In *F. paludicola* the alarm call phrases (n = 3 individuals and 44 phrases) had a total duration ranging from 0.194-0.355 s (0.275 ± 0.071 s), with the interval between the notes ranging from 0.113-0.342 s (0.178 ± 0.058 s), which represents 65% of the phrase duration. The first alarm call note has a duration ranging between 0.022-0.063 s (0.032 ± 0.011 s), with a minimum frequency of 2.3-3.7 kHz (3.0 ± 0.5 kHz), a maximum frequency between 2.8-4.5 kHz (3.8 ± 0.4 kHz), and a frequency amplitude ranging from 0.5-1.5 kHz (0.8 ± 0.2 kHz). The second alarm call note lasts between 0.049-0.106 s (0.067 ±0.014 s), with a minimum frequency of 0.7-1.8 kHz (1.3 ± 0.2 kHz), a maximum frequency between 3.1-4.5 kHz (3.8 ± 0.3 kHz), and a frequency amplitude ranging from 1.8-3.7 kHz (2.5 ± 0.4 kHz).

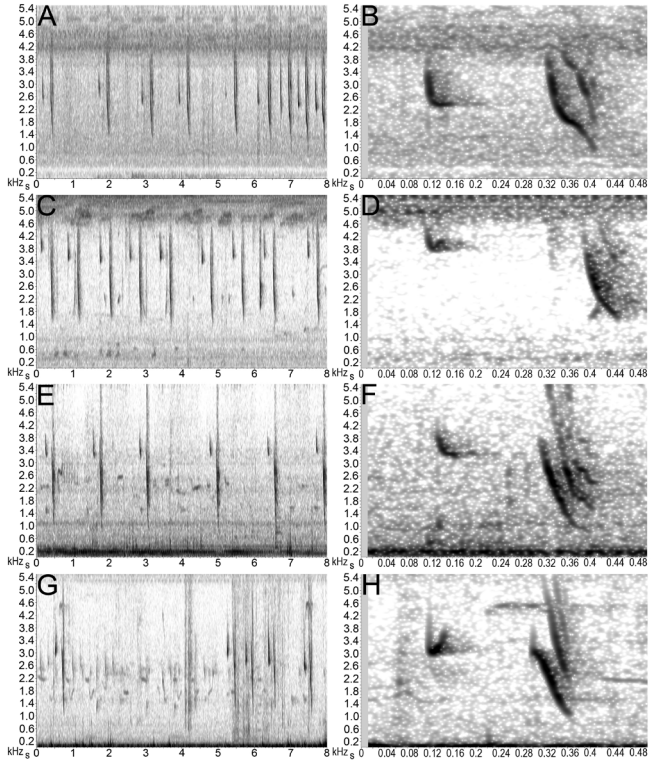


**FIGURE 6.** Alarm calls of *Formicivora paludicola* sp. nov. and *F. acutirostris*. A. Male of *F. paludicola* recorded at Estrada do Rio Acima, municipality of Biritiba-Mirim, São Paulo state (recorded by LFS). B. Detail of A. C. Female of *F. paludicola* recorded at Rio Paraitinga, Barragem do Paraitinga 2, municipality of Salesópolis, São Paulo state (recorded by BLR). D. Detail of C. E. Male of *F. acutirostris* recorded at Jundiaquara Island, municipality of Guaratuba, Paraná state (recorded by RB-L). F. Detail of E. G. Female of *F. acutirostris* recorded at Jundiaquara Island (recorded by BLR). H. Detail of G.

*Contact call*. The contact calls of *F. paludicola* and *F. acutirostris* (Figure 7) have a similar note shapes to those that Gonzaga *et al.* (2007) described as a "territorial duet calls" of *F. rufa*. However, in the former two taxa, they can also be produced by birds vocalizing alone, following other vocalizations or as an isolated series of calls. In *F. paludicola* and *F. acutirostris* this vocalization consists of a single note repeated in short sequences or alone, with the

note presenting a sharp descending frequency followed by a small ascending modulation that ends with a small plateau. The contact call note of *F. paludicola* (n = 2 individuals and 34 notes) had a duration of about 0.031-0.049 s (0.041 ± 0.001 s), with a minimum frequency of 1.6-2.1 kHz (1.8 ± 0.1 kHz), a maximum frequency between 3.4-4.8 kHz (4.1 ± 0.01 kHz), and a frequency amplitude ranging from 1.7-3.1 kHz (2.3 ± 0.1 kHz). In *F. acutirostris* the final part of the note after the plateau presents a small downward frequency modulation that can reach half of the amplitude of the ascending modulation of the note.

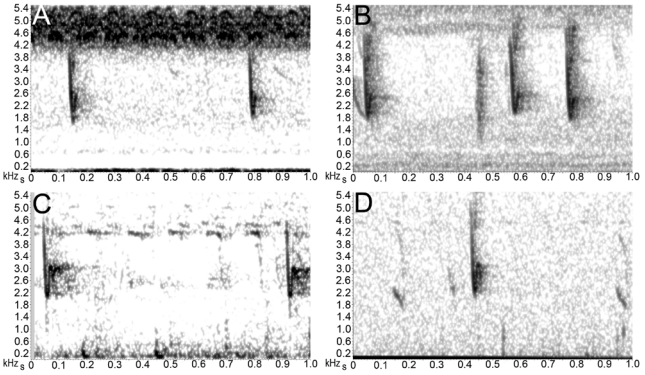


**FIGURE 7.** Contact call of *Formicivora paludicola* sp. nov. and *F. acutirostris*. A. Male of *F. paludicola* recorded at Estrada da Casa Grande, municipality of Biritiba-Mirim, São Paulo state (recorded by LFS). B. Pair of *F. paludicola* recorded at Rio Paraitinga, Barragem do Paraitinga 2, municipality of Salesópolis, São Paulo state (recorded by MRB). The first two calls were from one individual and the third from the other. C. Male of *F. acutirostris* recorded at Jundiaquara Island, municipality of Guaratuba, Paraná state (recorded by RB-L). D. Another male of *F. acutirostris* recorded at Jundiaquara Island (recorded by BLR).

*Distress call*. The distress call of *F. paludicola* (Figure 8) is similar to those described for *F. acutirostris*, *F. grisea*, *F. serrana*, *F. littoralis*, *F. rufa*, *F. grantsaui*, *F. melanogaster*, *Neorhopias iheringi*, *Myrmotherula axillaris*, and *M. longipennis* (Gonzaga 2001, Gonzaga *et al.* 2007). The distress calls of both Marsh Antwrens consist of a constant repetition of the same harmonic rich fundamental note, which can show a highly variable shape, but never turns into a trill as described for *F. rufa* (Gonzaga *et al.* 2007). In *F. paludicola* the general note shape can be described as an upward modulation followed by a descending modulation (inverted "u" or "v" shape"), but the midpoint between the ascending and descending part of the note is not always centered (it may be displaced to the left or right), and the downward part can show small plateaus while descending in frequency. Alternatively, it may start with a small upward frequency modulation followed by a almost vertical ascending modulation, then forming a plateau or descending slowly until a almost vertical downward modulation followed by a slow downward modulation at the end of the note (Figure 8, E); or the notes may even show an initial sharp downward frequency modulation followed by a modulation similar to the one found in the inverted "u" notes (Figure 8, G).

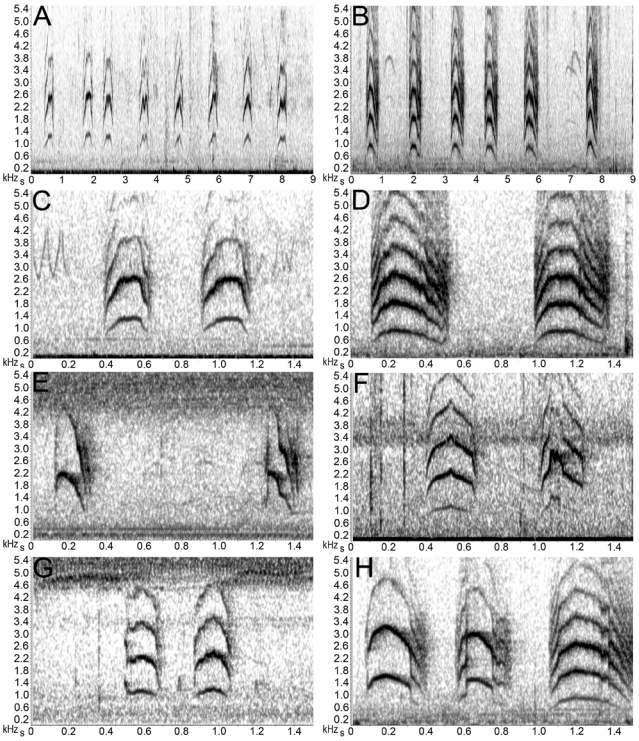


**FIGURE 8.** Distress calls of *Formicivora paludicola* sp. nov. and *F. acutirostris*. A. Female of *F. paludicola* recorded at Estrada da Casa Grande, municipality of Biritiba-Mirim, São Paulo state (recorded by LFS). B. Female of *F. acutirostris* recorded at Rio São João near the Folharada Island, municipality of Guaratuba, Paraná state (recorded by RB-L). C. Detail of A. D. Detail of B. E. Female of *F. paludicola* recorded at Rio Paraitinga, Barragem do Paraitinga 2, municipality of Salesópolis, São Paulo state (recorded by BLR). F. Male of *F. paludicola* recorded at Sitio do Caleb, municipality of São José dos Campos, São Paulo state (recorded by LFS). G. Female of *F. paludicola* (same individual of E). H. Male (first two notes) and female (third note, same individual of B) of *F. acutirostris* recorded at the Rio São João (recorded by RB-L).

In *F. paludicola* the duration of the fundamental note of the distress call (n = 5 individuals and 51 calls) ranged from 0.110-0.295 s (0.186 ± 0.049 s), with its minimum frequency ranging from 0.6-1.3 kHz (0.9 ± 0.2 kHz), the maximum frequency between 1.0-1.9 kHz (1.4 ± 0.3 kHz), and the frequency amplitude ranging from 0.2-0.7 kHz (0.5 ± 0.1 kHz). The duration of the first harmonic note ranged from 0.142-0.315 s (0.232 ± 0.059 s), with its minimum frequency going from 0.9-2.0 kHz (1.4 ± 0.3 kHz), the maximum frequency between 1.9-3.5 kHz (2.7 ± 0.5 kHz), and the frequency amplitude ranging from 0.6-1.8 kHz (1.2 ± 0.1 kHz).

*Display call*. The display calls of *F. paludicola* and *F. acutirostris* are different from those described by previous authors for all other *Formicivora* species (Gonzaga 2001, Gonzaga *et al.* 2007). The typical notes are composed of

two linked ascending and descending modulations, but birds sometimes emit only half of the note (one upward and downward frequency modulation; Figure 9). There are also some other variations found in the display call of *F. paludicola* and *F. acutirostris* (Figure 10), but these variants were found in only one individual of each species. The display call notes of *F. paludicola* (n = 5 individuals and 51 calls) had a duration between 0.110-0.295 s (0.186 ± 0.049 s), with its minimum frequency going from 0.6-1.3 kHz (0.9 ± 0.2 kHz), a maximum frequency between 1.0-1.9 kHz (1.4 ± 0.3 kHz), and a frequency amplitude ranging between 0.2-0.7 kHz (0.5 ± 0.1 kHz).

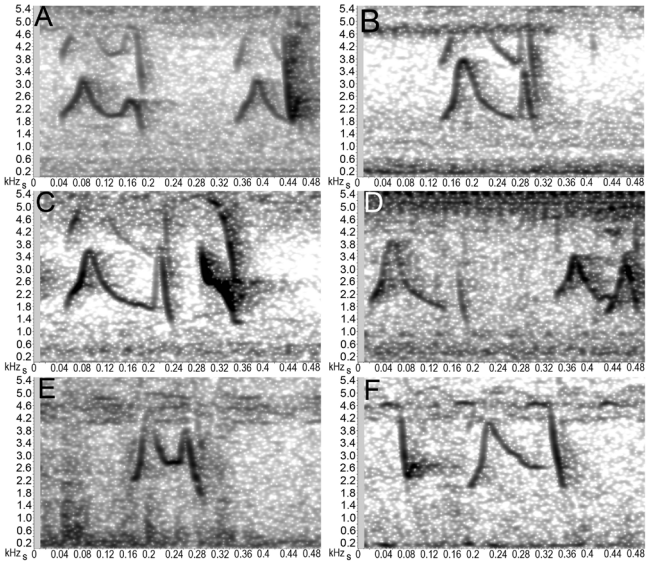


**FIGURE 9.** Display calls of *Formicivora paludicola* sp. nov. and *F. acutirostris*. A. Pair of *F. paludicola* recorded at Rio Paraitinga, Barragem do Paraitinga 2, municipality of São Paulo state (recorded by MRB). The two display calls are by the female, one note complete and the other being half of a note, with the male responding with a contact call. B. Another example of recording A by the same female. C. A third example from same recording A. In this example the display call is by the male, and the second note is the first note of a phrase of the song of the female. D. A fourth example from the same recording A. The first note and the first modulation up and down seemed to be emitted by the male, whereas the second up and down modulation seemed to be emitted by the female. E and F. Pair of *F. acutirostris* recorded at Jundiaquara Island, municipality of Guaratuba, Paraná state (recorded by RB-L). In F, the first note is a contact call by one individual and the second is the display call by the other.

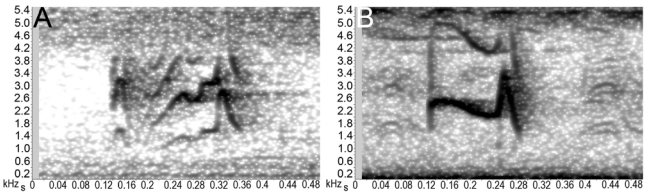


**FIGURE 10.** Variations of the display calls found in *Formicivora paludicola* sp. nov. and *F. acutirostris*. A. Female of *F. paludicola* recorded at Rio Paraitinga, Barragem do Paraitinga 2, municipality of Salesópolis, São Paulo state (recorded by BLR). B. Female of *F. acutirostris* recorded at Rio Claro, municipality of Guaratuba, Paraná state (recorded by BLR).

*Foraging call*. This vocalization is uttered by birds while foraging, being found in *F. paludicola* and *F. acutirostris*. Most of the time this one note call of low intensity is almost inaudible, and can only be heard at very close quarters, although sometimes the voice is loud enough to be heard at up to 2 m. The notes of *F. paludicola* ranged from 0.025-0.047 s (0.037 ± 0.008 s), with a minimum frequency of 2.1-2.3 kHz (2.2 ± 0.1 kHz), a maximum frequency between 2.4-2.8 kHz (2.6 ± 0.2 kHz), and a frequency amplitude ranging from 0.3-0.6 kHz (0.4 ± 0.1 kHz).

*Aggressive call*. This vocalization was heard and tape recorded at the type locality, and at three other areas in its vicinity. It was emitted by four different females of *F. paludicola* after playback of the loudsong, almost always when the male was issuing the loudsong. *Formicivora acutirostris* also emits this vocalization, which is used in the same context. In *F. paludicola* this vocalization is generally repeated once or in short sequences of up to nine emissions between other vocalizations (n = 4 individuals and 48 calls). For *F. acutirostris* we heard up to four repeats of this vocalization, but were only able to record single emissions (n = 2 individuals and 2 calls) of this call by this species.

This call lasts from 0.042-0.144 s (0.114 ± 0.006 s), and is composed of two notes, the first one more variable in form, but normally resembling an inverted "u", and the second consisting of an abrupt descending note with a inflection upward and then downward. The first note varies in shape from an inverted "u" to flatter or almost pulse-like emissions. The fundamental of this note lasted from 0.013-0.036 s (0.020 ± 0.004 s), with a minimum frequency of 0.9-2.2 kHz (1.3 ± 0.2 kHz), a maximum frequency between 1.6-4.0 kHz (2.0 ± 0.4 kHz), and a frequency amplitude ranging from 0.3-2.4 kHz (0.7 ± 0.2 kHz). The fundamental of the second note lasted from 0.025-0.050 s (0.039 ± 0.003 s), with a minimum frequency of 1.3-1.7 kHz (1.6 ± 0.1 kHz), a maximum frequency between 3.4-4.6 kHz (3.9 ± 0.3 kHz), and a frequency amplitude ranging from 1.8-3.0 kHz (2.5 ± 0.2 kHz). The aggressive call of the two species overlaps in frequency and time, and there are small variations in the shape of the two notes of this call.

## Molecular analysis

The comparison by Bayes Factors (Table 5) showed that the two replicates of the runs used for the partitioning test converged. The comparison between different partitioning schemes by Bayes Factors (Table 5) shows that the models that treated each codon position separately received very strong support over the others. Between the codon partition schemes there are no significant differences between the full partitioned scheme (10 partitions, each

mitochondrial gene separately partitioned into different codon positions, and βF5 treated separately) and the scheme considering three codon positions (independently of the mitochondrial gene) and βF5 separately (four partitions). Due to this aspect, the second partition scheme was used for further analysis.

The trees obtained by the two different methods presented the same topology, and both analyses indicated with high support that *F. paludicola* and *F. acutirostris* represent distinct clades, with samples of each of these taxa representing reciprocally monophyletic groups (Figure 11). The combined mitochondrial genetic distance between *F. acutirostris* and *F. paludicola* ranged between 0.005-0.009 (0.006 ± 0.001) (Table 6). The variability within *F. paludicola* was of 0-0.001 (0.001 ± 0.000), and within *F. acutirostris* was of 0-0.003 (0.002 ± 0.001). Except for one individual of *F. paludicola*, all other sequences of both species of Marsh Antwrens for the βF5 presented the same base composition.

## Habitat

*Formicivora paludicola* is found only in marshes where cattails *Typha domingensis* (Typhaceae) and bulrush *Schoenoplectus californicus* (Cyperaceae) are abundant (Figure 12), and their height ranges from 60 to 250 cm. The vegetation is also composed of other Cyperaceae (*e.g.*, *Rhynchospora globosa*, *Rhynchospora* sp.), and Poaceae (*e.g.*, *Brisa* sp.). Some bushes can be found among the main vegetation, such *Eupatorium* spp., *Baccharis semiserrata*, *B. illinita*, *Baccharis* sp. (Asteraceae), *Tibouchina gracilis*, *T. ursina* (Melastomataceae), *Siphocampilus verticillatus* (Campanulaceae), *Leucothoe* sp. (Ericaceae), *Rapanea parvifolia* (Myrsinaceae) and *Eupatorium bupleurifolium* (Asteraceae), the latter being most abundant. Grasses such *Eriochrysis* sp., *Panicum* sp., and ferns are also observed. At the type locality, the area of the marsh comprises almost 13 ha, and when *F. paludicola* was discovered in 2004, almost 70% of the area was dominated by *T. domingensis* and 30% by *S. californicus*. Further observations were conducted by DRCB in the same area in 2010, and at that time, *T. domingensis* had expanded its area to occupy almost 80% of the marsh, while *S. californicus* occupied less than 15%, the balance consisting mainly of the exotic grass *Melinis minutiflora* (Poaceae). The marshes inhabited by the São Paulo Marsh Antwren occur as patches of different sizes located along small rivers or on river flood plains. Along the course of

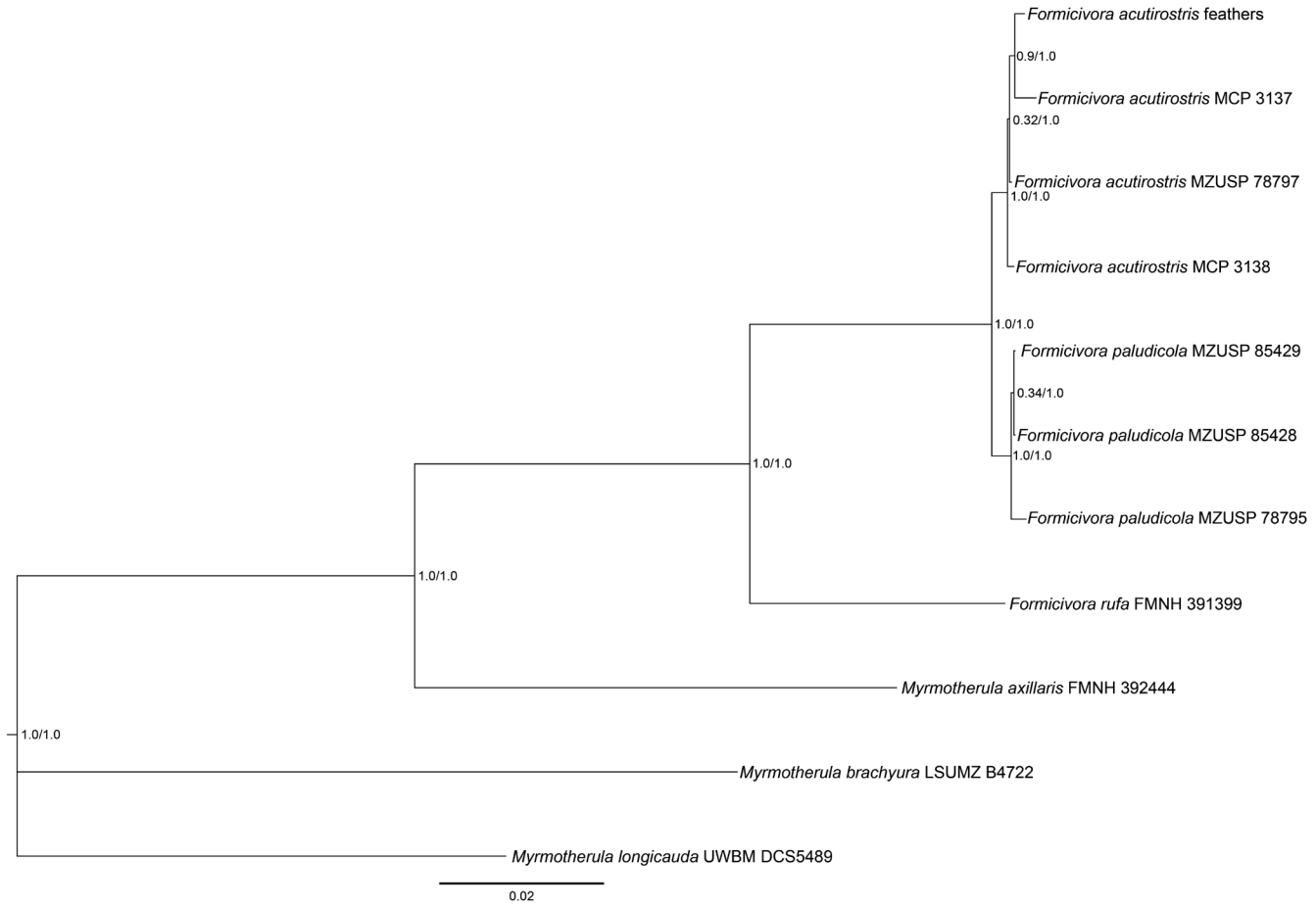


**FIGURE 11.** Phylogenetic tree obtained by Bayesian inference and maximum likelihood. Small values at the nodes are posterior probabilities and the bootstrap support. Specimen acronyms are detailed in appendix 3.

**TABLE 5.** Comparison by Bayes Factors of the likelihood of different partition schemes estimated using MrBayes. The roman numbers indicates the different partition schemes and the letters a and b the two replicates. The guidelines of Kass & Raftery (1995) for interpreting the values of $\log_{10}(B_{10})$ suggests that values ≤ 3 over not worth more than a bare mention, values from 3 to 20 suggest positive evidence against $H_0$, values from 20 to 150 suggests strong evidences against $H_0$, and values > 150 suggests very strong evidence against $H_0$. MIT (contatenated mitochondrial genes) refers to all mitochondrial genes together, and $_{codon}$ refers to the use of a codon partitioning (all codon positions analyzed separately. βF5 = intron 5 of the β fibrinogen; CYB = cytochrome b; ND2 = nicotinamide dehydrogenase subunit 2; ND3 = nicotinamide dehydrogenase subunit 3.

| Partition scheme | | lnP (model\|data) | S.E. | $B_{10}$ | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Ia | Ib | IIa | IIb | IIIa | IIIb | IVa | IVb | Va | Vb |
| no partitions (I) | Ia | -7688.921 | 0.503 | - | -0.70 | -13.05 | -13.34 | -13.62 | -13.51 | -159.98 | -160.02 | -160.99 | -161.13 |
| | Ib | -7687.304 | 0.347 | 0.70 | - | -12.35 | -12.63 | -12.92 | -12.81 | -159.28 | -159.31 | -160.29 | -160.43 |
| MIT+βF5 (II) | IIa | -7658.872 | 0.434 | 13.05 | 12.35 | - | -0.29 | -0.57 | -0.46 | -146.93 | -146.97 | -147.94 | -148.08 |
| | IIb | -7658.213 | 0.357 | 13.34 | 12.63 | 0.29 | - | -0.29 | -0.17 | -146.64 | -146.68 | -147.66 | -147.80 |
| CYB+ND2+ND3+βF5 (III) | IIIa | -7657.551 | 0.449 | 13.62 | 12.92 | 0.57 | 0.29 | - | 0.12 | -146.35 | -146.39 | -147.37 | -147.51 |
| | IIIb | -7657.820 | 0.481 | 13.51 | 12.81 | 0.46 | 0.17 | -0.12 | - | -146.47 | -146.51 | -147.48 | -147.63 |
| $MIT_{codon}$+βF5 (IV) | IVa | -7320.560 | 0.429 | 159.98 | 159.28 | 146.93 | 146.64 | 146.35 | 146.47 | - | -0.04 | -1.01 | -1.16 |
| | IVb | -7320.472 | 0.472 | 160.02 | 159.31 | 146.97 | 146.68 | 146.39 | 146.51 | 0.04 | - | -0.98 | -1.12 |
| $CYB_{codon}$+$ND2_{codon}$ +$ND3_{codon}$+βF5 (V) | Va | -7318.224 | 0.481 | 160.99 | 160.29 | 147.94 | 147.66 | 147.37 | 147.48 | 1.01 | 0.98 | - | -0.14 |
| | Vb | -7317.901 | 0.377 | 161.13 | 160.43 | 148.08 | 147.80 | 147.51 | 147.63 | 1.16 | 1.12 | 0.14 | - |

**TABLE 6.** Combined mitochondrial genetic distances for several taxa of the tribe Formicivorini calculated under the Tamura-Nei model of DNA substitution, with the variance (upper diagonal) estimated with 1,000 bootstrap replicates. The bold type values indicates comparisons between *Formicivora paludicola* sp. nov. and *F. acutirostris*.

| | Specimen | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Myrmotherula longicauda* UWBM DCS5489 | | 0.014 | 0.020 | 0.021 | 0.021 | 0.021 | 0.021 | 0.020 | 0.020 | 0.020 | 0.021 |
| 2 | *Myrmotherula brachyura* LSUMZ B4722 | 0.173 | | 0.019 | 0.020 | 0.020 | 0.020 | 0.020 | 0.020 | 0.020 | 0.020 | 0.020 |
| 3 | *Myrmotherula axillaris* FMNH 392444 | 0.224 | 0.215 | | 0.015 | 0.015 | 0.015 | 0.015 | 0.015 | 0.014 | 0.014 | 0.015 |
| 4 | *Formicivora rufa* FMNH 391399 | 0.225 | 0.239 | 0.160 | | 0.008 | 0.008 | 0.009 | 0.009 | 0.008 | 0.008 | 0.008 |
| 5 | *Formicivora acutirostris* MZUSP 78797 | 0.218 | 0.231 | 0.172 | 0.079 | | 0.000 | 0.001 | 0.001 | 0.001 | 0.001 | 0.002 |
| 6 | *Formicivora acutirostris* MCP 3138 | 0.220 | 0.232 | 0.173 | 0.080 | 0.000 | | 0.001 | 0.001 | 0.001 | 0.001 | 0.002 |
| 7 | *Formicivora acutirostris* MCP 3137 | 0.224 | 0.237 | 0.178 | 0.083 | 0.003 | 0.003 | | 0.001 | 0.002 | 0.002 | 0.002 |
| 8 | *Formicivora acutirostris* feathers | 0.219 | 0.233 | 0.176 | 0.082 | 0.002 | 0.002 | 0.004 | | 0.002 | 0.002 | 0.002 |
| 9 | *Formicivora paludicola* MZUSP 85428 | 0.223 | 0.234 | 0.175 | 0.079 | **0.005** | **0.005** | **0.008** | **0.006** | | 0.000 | 0.001 |
| 10 | *Formicivora paludicola* MZUSP 85429 | 0.223 | 0.234 | 0.175 | 0.079 | **0.005** | **0.005** | **0.008** | **0.006** | 0.000 | | 0.001 |
| 11 | *Formicivora paludicola* MZUSP 78795 | 0.226 | 0.236 | 0.178 | 0.081 | **0.006** | **0.006** | **0.009** | **0.008** | 0.001 | 0.001 | |

the upper Tietê river we found several narrow strips of marsh dominated by *Panicum* sp. (possibly *P. mertensii*) between the forest and the water, but we not found *F. paludicola* in this habitat.

*Formicivora paludicola* shares its habitat with typical marsh species such as *Laterallus melanophaius*, *L. leucopyrrhus*, *Pardirallus nigricans*, *P. sanguinolentus*, *Phacellodomus ferrugineigula*, *Certhiaxis cinnamomeus*, *Pseudocolopteryx sclateri*, *Donacobius atricapilla*, *Agelasticus cyanopus*, and *Sporophila bouvreuil*.

### Behavior

*Formicivora paludicola* is found in pairs or family groups of four birds, moving by small leaps and short flights through the vegetation in the lower strata of the marshes. The birds do not leave the marshes and their flight is short and heavy, not exceeding *ca*. 25 m in a straight line. The species spends most of the time looking for insects such as mosquitoes, mantises, and caterpillars. Pairs stay very close together, giving short, weak foraging calls. They do not vocalize very much, and are heard mostly in the early morning or afternoon. Their territories are defended aggressively by both sexes, and the birds are readily responsive to playback.

The first pair of the species found in October 2004 consisted of a subadult male and a female, indicating that subadult males can start to breed before they acquire full adult plumage (see below). A male and female collected in early October (MZUSP 78787 and 78788) had incubation patches, indicating reproductive activity and participation by the male in incubation, as is observed for almost all the Thamnophilidae (Zimmer & Isler 2003). Copulations were recorded in October 2006, and young birds, whose plumage is like that of the adult female (see below), were recorded in January, February, and March.

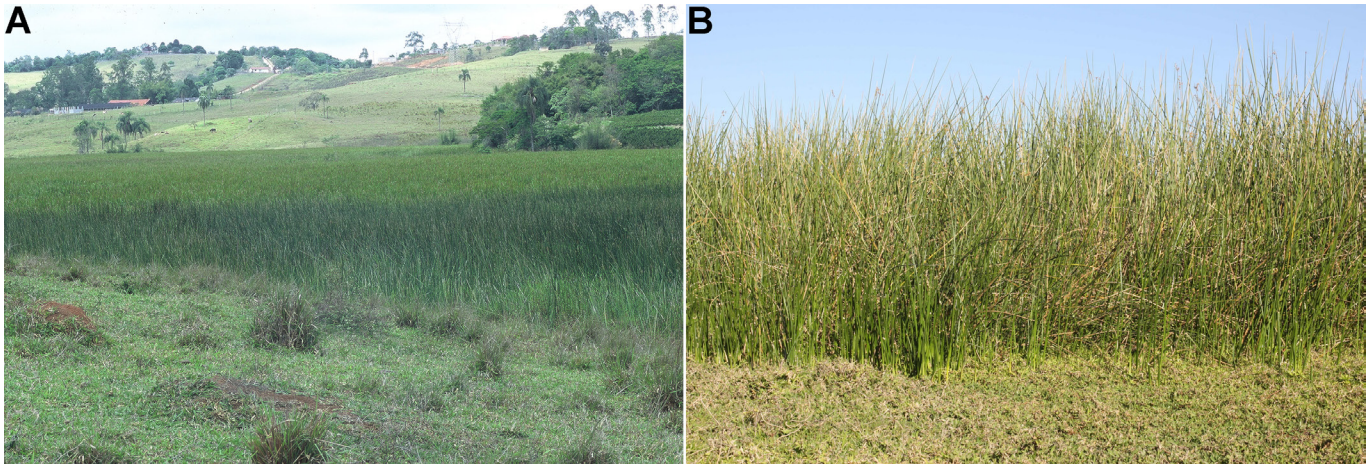


**FIGURE 12.** Habitat of the São Paulo Marsh Antwren *Formicivora paludicola* sp. nov. at its type locality, Córrego Taboão do Parateí, municipality of Mogi das Cruzes, São Paulo state, Brazil. A. General view of the marsh, with the domain of cattails *Typha domingensis* in the light green area, and the domain of bulrush *Schoenoplectus californicus* in the darker green area. B. Close-up of bulrush. Photos by DRCB.

## DISCUSSION

### Plumage

We observed and banded individuals of *F. paludicola* with plumage similar to that of the females, as described above, but with some gray rather than black on the breast, and in some cases also with a lesser amount of white on the breast. This plumage is similar to that of the male of *F. acutirostris* described in Bornschein *et al.* (1995), which was later recognized to be a young bird (Reinert & Bornschein 1996; see also Reinert 2008). Because *F. paludicola* and *F. acutirostris* are sister species, we believe that plumage succession of young males of *F. paludicola* follows that of young males of *F. acutirostris*, with a temporary plumage pattern (immature plumage) similar to that of the female before acquisition of adult plumage, as in several other thamnophilids (Zimmer & Isler 2003).

In several banded males of *F. paludicola* we observed one or a few white feathers on the breast or flanks, a remainder of the immature plumage. Remainders of immature plumage are also found in *F. acutirostris*, but in a different pattern. The immature males of the latter species change at an age of about seven months to a subadult plumage characterized by gray or dark gray underparts, with the presence of several ventral feathers with white margins (Reinert 2008). Thus, *F. paludicola* and *F. acutirostris* exhibit distinct patterns in their subadult plumage. We do not discard the possibility that the white feathers amid the black ventral plumage of *F. paludicola* are maintained as a neotenic characteristic, due to the abundance of individuals with this characteristic.

## Vocalizations

The vocalizations of *F. paludicola* and *F. acutirostris* that were analysed do not meet the diagnosticability criteria proposed by Isler *et al.* (1998) because of the extensive overlap in the range of the continuous variables of these two taxa. Despite this overlap, the second note of the loudsong of *F. paludicola* tends to present a shorter duration and greater frequency amplitude than that of *F. acutirostris* (Figure 5), and the contact call note of *F. paludicola* seems to lack the final downward modulation found in *F. acutirostris* (Figure 7). The differences in the number of repetitions of the aggressive calls between *F. paludicola* and *F. acutirostris* can also be indicative of a ongoing divergence process.

In this context it is worth mentioning the example of *Terenura maculata* and *T. sicki*, species with evident plumage differences, with the latter replacing the former in the northern Atlantic Forest, but which do not fit the diagnostic criteria proposed for vocalizations by Isler *et al.* (1998) (see Minns *et al.* 2009), as in the case of *F. paludicola* and *F. acutirostris*. Although we have analysed seven different vocalizations of the Marsh Antwrens, the vocal repertoire of a Thamnophilidae can include up to 16 vocalizations (*Gymnopythis leucaspis*) (Willis 1967). This suggests the need for additional knowledge and recordings of the complete accoustic repertoire of *F. paludicola* and *F. acutirostris* to analyse the possibility of divergence in other types of vocalization not contemplated here.

## Molecular analysis

Although the mitochondrial genetic distances between *F. paludicola* and *F. acutirostris* were low, the phylogenetic analyses showed that all individuals of *F. paludicola* formed a monophyletic clade that was sister to another clade formed by all samples of *F. acutirostris* (i.e., reciprocal monophyly in mtDNA was achieved). The low genetic distances suggests a recent divergence between *F. paludicola* and *F. acutirostris*. The estimated Bayesian chronogram (not show) suggests that the divergence between these two species can be estimated to have occurred between 250,000 to 640,000 years before the present (median of 420,000 years before the present).

## Biogeography

Considering the small dispersal capability of *F. acutirostris* and other thamnophilids (Reinert *et al.* 2007, Lees & Peres 2009, Woltmann *et al.* 2012), which also seems to be the case for the *F. paludicola* (see Results, and below), the Serra do Mar escarpment appears to be a insurmountable physical and ecological barrier between the two species at the present time. The Serra do Mar reaches about 1,000 m a.s.l. on the latitude of Mogi das Cruzes and Biritiba-Mirim, where *F. paludicola* is found, and almost all the area of Serra do Mar is covered by forests. However, there are records of neotectonic activity (≤ 1,2 million years) in the Paraíba do Sul river valley and specially at the headwaters of the Tietê river basin (Saadi *et al.* 2002, Ribeiro *et al.* 2006), the area to which *F. paludicola* is restricted.

Biogeographic models described for eastern Brazil freshwater fishes (Ribeiro 2006) propose mechanisms that could at first sight be involved in the present relationships and distribution of the two Marsh Antwren species (see below). Ribeiro (2006) identified three biogeographic patterns for freshwater fishes, related to different taxonomic units with different ages. Pattern "A" dates back to the Cretaceous period, and involves large clades at familial and subfamilial levels; pattern "B" dates back to the Tertiary period, and involves sister group relationships between genera; and pattern "C" involves recent species-level fauna interchange between uplands and coastal rivers due to stream capture and neotectonics (Ribeiro 2006). Although these models were proposed to explain fish distributions, they should be considered for the Marsh Antwrens because of the fact that the present day species occur in habitats associated with water, distributed along water bodies and flood plains.

Considering the time estimated for the divergence of the two Marsh Antwrens (250,000 - 640,000 years before present), the divergence between these species could be related to the pattern "C" of Ribeiro (2006). Ribeiro (2006) suggests that part of the fish fauna of the upper Tietê river could be the result of the capture of the lowland biota of coastal drainages by an uplift, but does not give the precise timing of this event. If it occurred in the last one million years, it could be related to the split between the Marsh Antwrens, in which case it would be expected that the ancestor of the Marsh Antwrens ocurred at the coast and was captured together with the fish fauna. The separation of the Marsh Antwrens could also be related to a stream capture event, as in the case of some fishes of the Guaratuba River basin at Boracéia Ecologial Station and its coastal affluents (Ribeiro *et al.* 2006).

However, as one species occurs in the Paraíba do Sul river drainage and the other on the coast, is possible that the Marsh Antwrens' ancestor occupied the whole drainage and also marshes in the lowlands. The Paraíba do Sul River valley is an old geological feature, which has seen the formation of several paleolakes (*e.g.* Petri & Fúlvaro 1983, Zanão *et al.* 2006), and therefore the existence of marshes in this valley over a long time is to be expected. Recent studies suggest that on the coast of southeastern and southern Brazil the colonization by the mangrove *Rhizophora mangle* started after the Quaternary Glaciation (Pil *et al.* 2011), and the area occupied today by mangroves could have been occupied by marshes before the mangrove expansion. Mangroves

are a habitat that occupies tidal flats in tropical areas, being replaced by salt marshes in temperate zones (Doody 2001), and salt marshes are the core area for *F. acutirostris* (MRB *et al.*, unpubl. data). In this scenario of an ancestor with a continous population in the Paraíba do Sul drainage and on the coast, the marked changes in sea levels in the Pleistocene (Haq *et al.* 1987) and the respective environmental changes could have isolated the populations in the valley from the ones on the coast and at the same time extinguished the populations intermediary to the present day distribution of the species.

Sea level fluctuations are also implied in the present distribution of *F. acutirostris* as isolated populations in Paraná and Santa Catarina coast (Reinert *et al.* 2007). The hypothesis of a continuous population would be supported by the occurrence of populations of *F. paludicola* in the medium and lower course of the Paraíba do Sul River. Independently of the biogeographical events involved in the speciation between *F. paludicola* and *F. acutirostris*, we consider that, in spite of present day climatic change and the predicted rise in sea level (Church & White 2006, IPCC 2007), there is no possibility of expansion in the ranges of *F. paludicola* and *F. acutirostris* and contact between them in the near future. Under an evolutionary and conservationist view, *F. paludicola* represents a distinct evolutionary lineage from *F. acutirostris*, and as so it should be a target for conservation action.

## Habitat

At the type locality of *F. paludicola*, *T. domingensis* was a localy invasive plant to the detriment of *S. californicus* (even though both are native plants to Brazil). In the headwaters of the Taboão do Parateí stream, many signs of degradation were observed, with the expansion of *T. domingensis* and the disappearance of *S. californicus* in the sedimented areas. *Typha domingensis* is also an invasive plant in highland marshes around the city of Curitiba in the state of Paraná in southern Brazil (*ca.* 900 m a.s.l.), the habitat of the Marsh Tapaculo (*Scytalopus iraiensis*) (Bornschein *et al.* 1998). We believe that the original habitats of *F. paludicola* were marshes dominated by *S. californicus*. Reinert (2008) highlights that areas dominated solely by *S. californicus* were never used for nesting by *F. acutirostris*, but where associated with other plants *S. californicus* supplies fibers for nest building and support for nest attachment (Reinert *et al.* 2012). Nevertheless, *F. paludicola* seem to have adapted to *T. domingensis*, as suggested by the number of pairs using this vegetation at the type locality (DRCB, unpubl. data). We are not aware of the presence of marshes dominated by *S. californicus* at other sites in the Paraíba do Sul or Tietê river basins, except for small areas at Cunha, Mairiporã and Atibaia (DRCB, unpubl. data), which could support populations of *F. paludicola*.

On a visit in 2004 to a marsh of about 4 ha near the type locality, the species was not found in the area despite hours of search with playback. The locals informed that the marsh appeared only three years previously, due to changes in the topography and natural drainage that led to the establishment of *T. domingensis*. The area was located less than 1 km from the type locality, which indicates the low dispersal capabilities of *F. paludicola*, and the need for marsh corridors for its dispersal.

## Conservation

The conservation of open areas in Brazil is highly problematic (Bornschein *et al.* 1998). Environmental legislation protects mainly forests and open areas such as natural savannas, and marshes are treated as less important habitats (Bornschein *et al.* 1998). Most of the marshes where the new species was found are heavily degraded by sand mining, housing developments, fish farming, drainage for cattle raising and agricultural activities, fire, and invasion by exotic plants. Exotic plants include the grasses *Urochloa arrecta* (or *Brachiaria subquadripara*) and *Melinis minutiflora*, and *Hedychium coronarium* (Zingiberaceae). Invasion by *U. arrecta* is one of the main factors that threaten populations of *F. acutirostris* (Reinert *et al.* 2007).

Geological evaluation of the subsoil at the type locality of *F. paludicola* revealed a layer of pure sand almost 15 m deep below the area (Luis A. Kaimoto, pers. comm.). This suggests that many areas where *F. paludicola* occurred in the past have been affected by sand mining, which has been carried out for more than 100 years ago by the companies of one family (Luis A. Kaimoto, pers. comm.). Sand mining causes continual changes in the landscape where marshes occur, creating an environment where even *T. domingensis* is not able to establish itself. Many other marshes may be associated with the presence of sand deposits, and therefore could be affected by future sand mining projects. Sand mining is also a threat to the habitats of its sister species, *F. acutirostris* (Reinert *et al.* 2009).

Other areas where *F. paludicola* might occur have been affected by the construction of dams in several rivers. The species was found by LFS in the area of the Paraitinga dam while it was filling, which prompted a project to rescue and relocate the birds. During a period of about 15 days, BLR, MRB, RB-L, LFS, and other ornithologists captured 72 individuals at the dam, and relocated them in other nearby marshes. In a search three years after the release, most of these individuals were found, and some of them were accompanied by young birds, indicating successful breeding (Érika Machado and Gláucia del Rio *et al.*, unpubl. data).

Over the last three years we have unsuccessfully searched for this species in marsh habitats in more than 50

localities surrounding the known areas, but *F. paludicola* seem to be restricted to the higher regions of the Tietê and Paraíba do Sul rivers. Auditory and visual censuses of marshes within the species known range indicate an estimated population of 250-300 individuals. *Formicivora paludicola* has been considered as "Critically Endangered" in the state of São Paulo even before its formal description (Silveira 2010), but the species is not yet classified as threatened neither by the Brazilian government, nor by the World Conservation Union.

The new species has not been found in any conservation unit until the present, and there is a clear need to create protected areas including large populations of the São Paulo Marsh Antwren. There is also a need to restrict economic activities (*e.g.* agriculture and sand mining) and increase surveillance over marsh areas, as some of the areas where the species occurs should be preserved according to Brazilian law, but in practice there is no protection and many sites are being exploited commercially. Urgent action is needed on these issues to prolong this species' survival in the face of imminent extinction. This is the third species of bird to be described in the last 20 years that lives exclusively in the marshes of southern and southeastern Brasil. The discovery of this shy and severely threatened bird less than 50 km from the center of the largest and still growing city in South America (with more than 13 million inhabitants) makes the remark in Zimmer & Isler (2003:450) sound prophetic: "...how much remains to be discovered about birds in South America, even in relatively well-studied and heavily populated regions".

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## APPENDIX 1.

Material analyzed of *Formicivora* spp. (all skins from Brazil).

*Formicivora acutirostris*. **Paraná**. Antonina: MHNCI 4884-5. Morretes: MHNCI 5748. Guaratuba: MN 42978-80, MZUSP 78797-8, MCP 3137-8, 3799. Matinhos: MN 39458 (holotype), 39457 (paratype). The specimens at MZUSP were previously housed in Louisiana State University Museum of Natural Sciences respectively under numbers LSUMZ 161021 and 161020 (ex MHNCI 4883 and 4882, respectively).

*Formicivora erythronotos*. **Rio de Janeiro**. Mambucaba: MZUSP 76678-9.

*Formicivora grantsaui*. **Bahia**. Mucugê: MZUSP 76676-7 (paratypes), MCP 3151, 3163.

*Formicivora grisea*. **Pará**. Conceição do Araguaia: MZUSP 42371; Fordlândia: MZUSP 70509; Santana do Araguaia: MZUSP 82139, 90074-5. **Mato Grosso**. Pontes e Lacerda: MZUSP 78071. **Bahia**. São Francisco do Conde: MCP 3145, 3154.

*Formicivora littoralis*. **Rio de Janeiro**. Cabo Frio: MZUSP 73506-7 (paratypes).

*Formicivora melanogaster*. **Piauí**. MZUSP 77741-2. **Pernambuco**. Agrestina: MZUSP 63492, 63525. **Alagoas**. Palmeira dos Índios: MZUSP 37419. **Bahia**. Bonito: MCP 3158; Ibicoara: MCP 1899; Mucugê: MZUSP 76450, Muquém do São Francisco: MZUSP 81536. **Tocantins**. Conceição do Tocantins: MZUSP 84399-401. **Goiás**. Colinas do Sul: MZUSP 74116. **São Paulo**. Avanhandava: MZUSP 4446.

*Formicivora rufa*. **Pará**. Santana do Araguaia: MZUSP 90073. **Rondônia**. Cerejeiras: MCP 2622. **Rio de Janeiro**. Campos dos Goytacazes: MZUSP 78861; Cardoso Moreira: MZUSP 26906-7. **São Paulo**. Bebedouro: MZUSP 4675; Franca: MZUSP 8021, 8081-2; Itapura: MZUSP 5035; Jaboticabal: MZUSP 1157; Lins: MZUSP 26662-4; Presidente Venceslau: MZUSP 32670; Rincão: MZUSP 1675.

*Formicivora serrana*. **Minas Gerais**. Almenara: MZUSP 85997; Brumal: MZUSP 85432; Coronel Fabriciano: MZUSP 25243; Marliéria: MZUSP 10385; Poté: MZUSP 87032-3.

## APPENDIX 2.

Vocalizations of *Formicivora paludicola* sp. nov. and *F. acutirostris* examined (all recordings from Brazil). Unless stated otherwise, the recordings listed here were obtained by the authors. When recordings were associated with collected specimens, the latter's label number is given in brackets. For each set of recording, general localities are followed by the name of municipalities. Abreviation: XC = recording available at Xeno-Canto collection.

*Formicivora paludicola*. **São Paulo**. Bairro Rio Acima (23°32'S, 45°05'W), including "Estrada do Rio Acima", municipality of Biritiba-Mirim: loudsong (n = 49 phrases from two or three individuals, recorded by J. C. Minns and A. Whittaker; in Minns *et al.* [2009]; n = 30 phrases from one individual); alarm call (n = 28 calls from one individual); distress call (n = 27 calls from one individual). Córrego Taboão do Parateí (23°24'27"S, 46°13'35"W), municipality of Mogi das Cruzes: loudsong (n = 4 phrases from one individual, recorded by N. Athanas, XC 6432); alarm call (n = 1 calls from one individual, recorded by N. Athanas, XC 6433); distress call (n = 12 calls from one individual, recorded by N. Athanas, XC 6434); aggressive call (n = 39 calls from 3 individuals). Estrada da Casa Grande (23°34'S, 46°00'W), municipality of Biritiba-Mirim: contact call (n = 11 calls from one individual); distress calls (n = 1 call from one individual). Jardim Guanabara (23°22'14"S, 46°09'18"W), municipality of Mogi das Cruzes: aggressive call (n = 9 calls from one individual). Rio Paraitinga (23°31'S, 45°55'W), Barragem do Paraitinga 2, municipality of Salesópolis: loudsong (n = 41 phrases from 2 individuals); alarm call (n = 15 phrases from one individual); contact call (n = 34 calls from 2 individuals); distress call (n = 8 calls from 2 individuals); display call (n = 12 calls from at least 2 individuals); foraging call (n = 6 calls from at least 2 individuals). Sitio Caleb (23°05'S, 46°00'W), municipality of São José dos Campos: distress call (n = 4 calls from one individual).

*Formicivora acutirostris*. **Paraná**. Jundiaquara Island (25°52'24"S, 48°45'32"W), municipality of Guaratuba: loudsong (n = 87 phrases from 7 individuals, one of them recorded by D. D. Sobotka); alarm call (n = 54 calls from 5 individuals); contact call (n = 13 calls from 3 individuals); display call (n = 10 calls from 2 individuals); foraging call (n = 3 calls from one individual); aggressive call (n = 3 calls from 2 individuals). Rio Claro (25°52'22"S, 48°45'38"W), municipality of Guaratuba: foraging call (n = 18 calls from one individual). Rio São João near the Folharada Island (25°51'26"S, 48°44'19"W), municipality of Guaratuba: distress call (n = 105 calls from 2 individuals). Road from Garuva to the north (25°57'06"S, 48°48'52"W), municipality of Guaratuba: loudsong (n = 30 phrases from one individual, recorded by A. Whittaker, in Minns *et al.* [2009]). **Santa Catarina**. RPPN Volta Velha (26°04'57"S, 48°38'27"W), municipality of Itapoá: loudsong (n = 22 phrases from one individual) (see Minns *et al.* 2009).

## APPENDIX 3.

Taxa used in the phylogenetic study, including *Formicivora paludicola* sp. nov., with voucher number and GenBank accession numbers for sequences of the mitochondrial genes cytochrome b (CYB), nicotinamide dehydrogenase subunit 2 (ND2), nicotinamide dehydrogenase subunit 3 (ND3), and the autossomal nuclear intron 5 of $\beta$-fibrinogen ($\beta$F5). Acronyms: FMNH - Field Museum of Natural History; LSUMZ - Louisiana State University Museum of Natural Sciences; MCP - Museu de Ciências e Tecnologia da Pontifícia, Universidade Católica do Rio Grande do Sul; MZUSP - Museu de Zoologia da Universidade de São Paulo; UWBM - University of Washington Burke Museum.

| Specimen | Voucher | Origin | CYB | ND2 | ND3 | $\beta$F5 |
|---|---|---|---|---|---|---|
| *Myrmotherula brachyura* | LSUMZ B4722 | Peru: Loreto | EF639973.1 | EF640040.1 | EF640107.1 | --- |
| *Myrmotherula longicauda* | UWBM DCS5489 | Bolivia: Cochabamba | EF639974.1 | EF640041.1 | EF640108.1 | EF639907.1 |
| *Myrmotherula axillaris* | FMNH 392444 | Brazil: Pernambuco | EF639972.1 | EF640039.1 | EF640106.1 | EF639906.1 |
| *Formicivora rufa* | FMNH 391399 | Brazil: Amapá | EF639946.1 | EF640013.1 | EF640080.1 | EF639881.1 |
| *Formicivora acutirostris** | MZUSP 78797 | Brazil: Paraná | KJ151919* | KJ151926* | KJ151933* | KJ151940* |
| *Formicivora acutirostris** | MCP 3138 | Brazil: Paraná | KJ151920* | KJ151927* | KJ151934* | KJ151941* |
| *Formicivora acutirostris** | MCP 3137 | Brazil: Paraná | KJ151921* | KJ151928* | KJ151939* | KJ151942* |
| *Formicivora acutirostris** | feathers | Brazil: Paraná | KJ151922* | KJ151929* | KJ151935* | KJ151943* |
| *Formicivora paludicola** | MZUSP 85428 | Brazil: São Paulo | KJ151923* | KJ151930* | KJ151936* | KJ151944* |
| *Formicivora paludicola** | MZUSP 85429 | Brazil: São Paulo | KJ151924* | KJ151931* | KJ151937* | KJ151945* |
| *Formicivora paludicola** | MZUSP 78795 | Brazil: São Paulo | KJ151925* | KJ151932* | KJ151938* | KJ151946* |

* This study.

## APPENDIX 4.

Gazetteer of localities of *Formicivora paludicola* (all in the São Paulo state, southeastern Brazil; see Figure 4).

**Natural occurrence**. **Municipality of Biritiba-Mirim**. Avenida Presidente Castelo Branco com Estrada do Rio Acima (23°32', 46°06'W); Bairro Rio Acima (23°32'S, 45°05'W); Barragem de Ponte Nova (23°23'S, 46°13'W); Estrada da Casa Grande (23°34'S, 46°00'W). **Municipality of Mogi das Cruzes**. Barragem do Rio Biritiba 1 (23°39'S, 46°06'W); Córrego Taboão do Parateí (23°24'27"S, 46°13'35"W); Jardim Guanabara (23°22'14"S, 46°09'18"W); Jardim Itapeti (23°21'42"S, 46°10'17"W). **On the border of the municipalities of Mogi das Cruzes and Santa Isabel**. Fazenda Taboão (23°23'19"S, 46°14'15"W). **Municipality of Salesópolis**. Barragem do Paraitinga 1 (23°32'S, 45°56'W); Distrito Nossa Senhora dos Remédios (23°31'S, 45°57'W); Rio Paraitinga (23°31'S, 45°55'W), Barragem do Paraitinga 2; Usina da Light Estrada dos Mirandas (23°34'S, 45°49'W). **Municipality of São José dos Campos**. Fazenda Montes Claros (23°04'S, 46°02'W); Sítio Caleb (23°05'S, 46°00'W).

**Release sites** (from individuals captured in an area to be flooded by a dam [Barragem do Paraitinga 2] and relocated). **Municipality of Biritiba-Mirim**. Barragem de Biritiba Mirim (23°34'S, 46°04'W); Barragem de Ponte Nova (23°34'S, 45°58'W); Barragem do Rio Biritiba 2 (23°35'S, 46°05'W); Pomar do Carmo (23°33'S, 46°01'W). **Municipality of Mogi das Cruzes**. Barragem do Rio Jundiaí / Taiaçupeba (23°39'S, 46°11'W); Cocuera (23°33'S, 46°08'W); Condomínio Toyama (23°31'S, 46°09'W); Kimberly-Clark (23°32'S, 46°09'W); Linhão Vila Oliveira (23°31'S, 46°09'W); Ponte dos Vilares (23°31'S, 46°09'W). **Municipality of Paraibuna**. "Nascente do Tietê" (23°34'S, 45°44'W). **Municipality of Salesópolis**. Barragem do Paraitinga 2 (23°32'S, 45°56'W); Rio Paraitinga a jusante do eixo da Barragem do Paraitinga 2 (23°31'S, 45°57'W); Usina da Light Estrada dos Mirandas (23°34'S, 45°49'W).

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