Article

Taxonomic revision of the Scaled Antbird *Drymophila squamata* (Aves: Thamnophilidae) reveals a new and critically endangered taxon from northeastern Brazil

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Abstract

The Scaled Antbird *Drymophila squamata* is a suboscine passerine endemic to the Atlantic Forest of eastern Brazil. Two subspecies, putatively diagnosed by the presence/absence of white spots on the crown, have traditionally been recognized: the nominate, ranging from Pernambuco to Bahia in northeastern Brazil, and *D. squamata stictocorypha*, from Minas Gerais to Santa Catarina in southeastern and southern Brazil. Here we combine morphological, acoustic, and genetic data to examine geographic variation in and revise the taxonomy of *D. squamata*. We show that there are two separately evolving population lineages in *D. squamata*, one south and the other north of the São Francisco River. The latter is unnamed and is thus described herein. We found that crown variation is not as geographically structured as previously thought, and thus we suggest that *D. squamata stictocorypha* is not a valid taxon. Finally, we also provide evidence of clinal variation in the species' vocalizations and underscore the importance of broad geographic sampling when assessing species limits using vocalizations.

Key words: Antbirds, Atlantic Forest, clinal variation, Pernambuco Center of Endemism, São Francisco River

Introduction

The Scaled Antbird *Drymophila squamata* (Lichtenstein, 1823) is a sedentary, sexually dichromatic suboscine passerine endemic to the Atlantic Forest of eastern Brazil (Zimmer & Isler 2003). Two subspecies, putatively diagnosed by the number of white spots on the crown, have been widely recognized—the nominate ranging from Pernambuco to Bahia in northeastern Brazil, and *D. squamata stictocorypha* (Boucard & Berlepsch, 1892) from Minas Gerais to Santa Catarina (Cory & Hellmayr 1924; Zimmer & Isler 2003). The nominate form was described as *Myiothera squamata* Lichtenstein, 1823, based on trade skins from the northeast Brazilian state of Bahia, and *D. squamata stictocorypha* was originally described as *Formicivora stictocorypha* Boucard & Berlepsch, 1892, based on a specimen from the southeast Brazilian state of Rio de Janeiro that differed from typical *squamata* by having spots on the crown. After examining specimens collected in the state of Bahia, Pinto (1935) found that some specimens from this state also had spots on the crown. The observation that variation in the crown pattern was not as geographically structured as previously thought led him to synonymize *D. squamata stictocorypha* with

D. squamata squamata in his catalogs of the birds of Brazil (Pinto 1938, 1978), a decision widely followed in the subsequent literature (Naumburg 1939; Peters 1951). However, based on an unpublished molecular analysis of the genus that suggested genetic differences between the two putative subspecies (Goerck 1999), Zimmer & Isler (2003) resurrected the subspecies *stictocorypha*, and this treatment has been followed in most recent literature (Grantsau 2010; Dickinson & Christidis 2014; del Hoyo 2020).

In the course of a phylogeographic study of *D. squamata* (Fazza 2015), we found a genetically and morphologically distinctive population north of the São Francisco River in northeastern Brazil, for which there is no name available. Here, we describe this unnamed taxon and revise the taxonomy of *D. squamata* through a detailed study of geographic variation in morphological, acoustic, and genetic traits. Based on the largest and most geographically comprehensive sample of specimens examined to date, we corroborate Pinto's (1935) suspicion that *D. squamata stictocorypha* is not valid, and we show that populations exhibit discrete geographic variation in another plumage tract, elucidating the existence of a new taxon endemic to the Pernambuco Center of Endemism (PCE) in northeastern Brazil.

Material and Methods

Genetic analysis. We sampled 16 specimens from 10 locations scattered across the species' distribution (Fig. 1), obtained either from museum or university collections or from our own field expeditions (Table S1). We extracted genomic DNA from these samples following the protocol described by Bruford *et al*. (1992) and sequenced one mitochondrial and two nuclear genes: NADH dehydrogenase subunit 2 (ND2); β-fibrinogen intron 7 (FIB7); and glyceraldehyde 3-phosphate dehydrogenase intron 11 (G3PDH). We used the primers L5215 (Hackett 1996) and H6313TRP (Sorenson *et al.* 1999) for ND2, FIB-BI7U and FIB-BI7L (Prychitko & Moore 1997) for FIB7, and G3PL890 and G3PH950 (Friesen *et al.* 1997) for G3PDH. Nuclear genes were sequenced at Macrogen Inc. (Rockville, MD, USA) and the mitochondrial gene was sequenced at Universidade de São Paulo with an ABI3730 DNA Analyzer (Applied Biosystems). Sequences generated in this study are deposited in GenBank (accession numbers OR232974–OR233021).
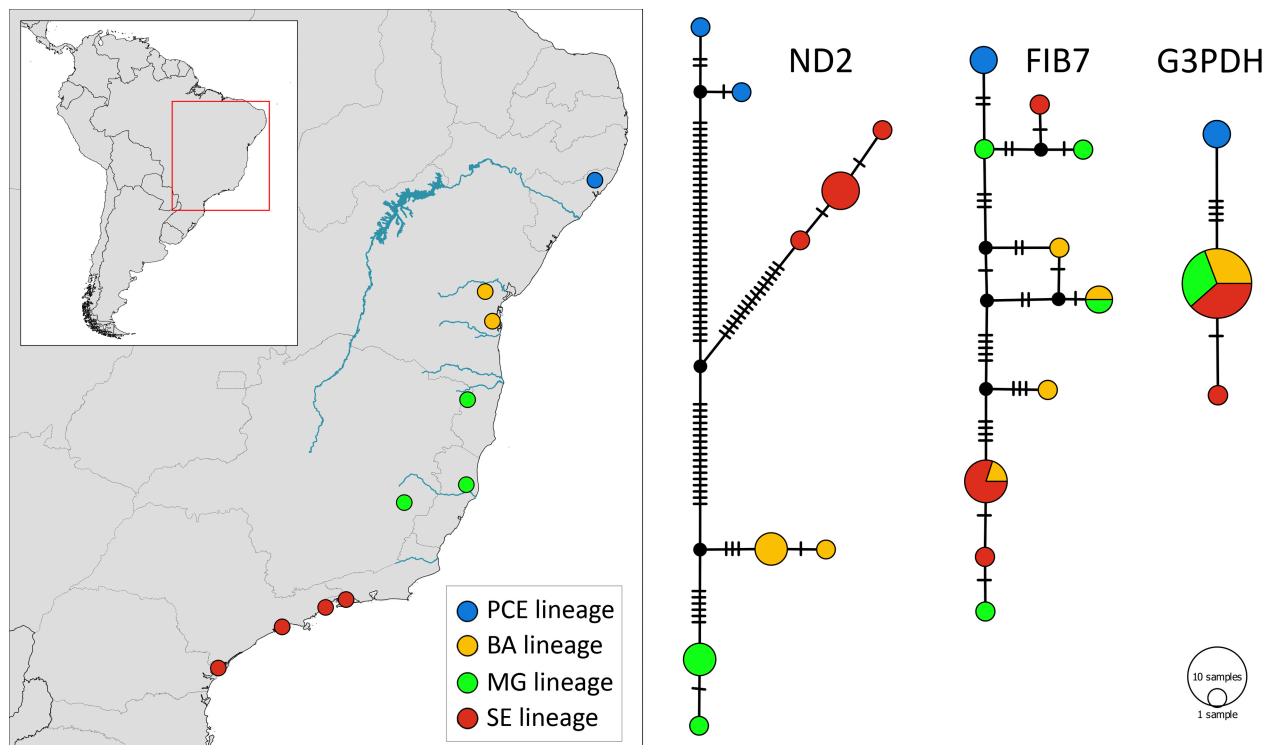

FIGURE 1. Genetic population structure in *Drymophila squamata* inferred by variation of the mitochondrial gene ND2 and the nuclear genes FIB7 and G3PDH. Circles in haplotype networks represent unique haplotypes with size proportional to their relative frequency. Different colors correspond to the four phylogeographic lineages recovered in the ND2 haplotype network, referred to as the "PCE" (blue symbols), "BA" (yellow symbols), "MG" (green symbols), and "SE" (red symbols) lineages.

We aligned sequences with the MUSCLE algorithm (Edgar 2004) implemented in GENEIOUS v.9.1.8 (Kearse *et al*. 2012), and we excluded short sequences and trimmed the matrices to exclude positions with missing data. The resulting alignments had 1032 bp for the ND2 gene, 849 bp for the FIB7 gene, and 416 bp for the G3PDH gene. Then, we estimated genetic population structure in *D. squamata* using TCS haplotype networks (Clement *et al*. 2000) as implemented in POPART (Leigh & Bryant 2015). Phylogenetic and demographic analyses, and other estimates of genetic population structure, will be presented in a separate study with denser sampling (Fazza *et al*., in prep.).

Morphological analysis. We examined 273 museum skins held at the following collections: Academy of Natural Sciences of Drexel University (ANSP), Philadelphia, USA; American Museum of Natural History (AMNH), New York, USA; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; Museu Nacional (MNRJ), Rio de Janeiro, Brazil; and Universidade Federal da Bahia (UFBA), Salvador, Brazil. We visually compared specimens both to assess geographic plumage variation and to test putative plumage differences proposed in subspecies descriptions. In subsets of the examined specimens, we coded specimens for the presence of spots on the crown (three character states: no white spots, few white spots, or many white spots; 141 adult males coded) and for the shape of markings on the back (two character states: teardrop-shaped or crescent-shaped; 145 adult males coded) (Fig. 2). Geographic coordinates were taken from the specimen labels, when available, or from ornithological gazetteers (Paynter & Traylor 1991; Vanzolini 1992). Table S2 lists all specimens examined.

Vocalization analysis. We examined 110 individual vocalization recordings obtained from the Macaulay Library (ML), xeno-canto (XC), and WikiAves (WA). All these recordings were used in visual analysis, and 90 of them with sufficient quality were used for measurements (Table S3). Prior to analysis, all recordings were standardized into mono-channel WAV files with 44.1 kHz and 16 bits using GoldWave v.6.52. Following the results of our genetic analysis, we categorized recordings into three groups for vocal comparisons: one comprising recordings from southeastern Brazil, from Santa Catarina to Rio de Janeiro (SE); one comprising recordings from Espírito Santo, Bahia, and northeastern Minas Gerais (BA+MG); and one comprising recordings from north of the São Francisco River in Alagoas and Pernambuco (PCE). A concern that vocalizations of males and females might differ, as in some other antbirds (*e.g.*, Isler *et al*. 2007, 2012), suggests that recordings of males and females ideally should be compared separately. However, most recordings did not identify sex and, in preliminary inspections of recordings, we also did not identify any major differences that could suggest sexual dimorphism in vocalizations of *D. squamata*. Thus, we analyzed all recordings together without controlling for possible sex differences.

We first produced spectrograms of each recording and labeled every vocalization as to type. We identified five distinct types of vocalizations, which we termed loudsongs, long calls, medium calls, short calls, and rattles (Fig. 3). Loudsongs consist of a clear introductory whistle (rarely two or none) followed by a descending series of high-pitched, increasingly raspy notes (Fig. 3A). Long calls are similar to loudsongs, but lack the introductory whistle and have longer, flatter notes (Fig. 3B). Medium calls consist of a short series of M- or inverted-U-shaped notes descending in frequency (Fig. 3C–E). Short calls are short series of two or three high-pitched notes that usually do not descend in frequency (Fig. 3F). Finally, rattles are a rapid succession of short sharp notes (Fig. 3G–I). We measured recordings of all these vocalization types except long calls, for which too few recordings with sufficient quality for measurements were available. Long calls were thus assessed only visually through spectrograms. Also, no short call recordings with sufficient quality for measurements were available for the PCE population, and so quantitative comparisons of this vocalization were restricted to the other two populations. Tables 1–4 provide selected measurements of loudsong, medium call, short call, and rattle variables.

We then visually assessed variation in note shape and measured variation in number of notes, total duration of the vocalization, pace (number of notes divided by the duration from the beginning of the first note to the beginning of the last note), note duration, duration of intervals between notes, and maximum and minimum frequency of each note (detailed descriptions of each of these characters are available in Isler *et al.* 1998). Whenever possible, we measured more than one vocalization (range 1–3) for each recording to account for within-individual variation. Measurements of multiple vocalizations of individuals were averaged to provide means for individuals before inclusion in the analysis. Spectrograms and measurements were made in Raven Pro v.1.6.4 using a Blackman window, with size of 1024 samples, 3 dB bandwidth of 154 Hz, 90% overlap, and a discrete Fourier transform of 1024 samples, yielding time and frequency measurement precision of 0.0005 s and 46.9 Hz, respectively (Charif *et al.* 2010). Time was measured in seconds and frequency in Hertz.

TABLE 1. General measurements of loudsong variables of populations of *Drymophila squamata* (mean ± SD / range). Time variables are in seconds, frequency variables in hertz. Sample sizes reflect number of individual birds, not number of vocalizations measured.

Population	*n*	Number of notes	Duration	Pace	Maximum frequency	Minimum frequency
SE	13	5.87 ± 1.19	4.06 ± 0.90	0.58 ± 0.06	5764 ± 504	3397 ± 408
		4–7	2.8–5.61	2.8–5.6	4932–6511	2673–4172
BA+MG	10	5.86 ± 0.77	3.77 ± 0.80	0.54 ± 0.06	5799 ± 327	3051 ± 608
		5–7	2.81–5.92	2.81–5.92	5195–6251	1976–3859
PCE	5	6.75 ± 1.49	4.08 ± 0.79	0.54 ± 0.05	5615 ± 288	3275 ± 150
		5–9	3–5.2	3–5.16	5205–6002	3119–3523

TABLE 2. General measurements of medium call variables of populations of *Drymophila squamata* (mean ± SD / range). Time variables are in seconds, frequency variables in Hertz. Sample sizes reflect number of individual birds.

Population	*n*	Number of notes	Duration	Pace	Maximum frequency	Minimum frequency
SE	13	6.57 ± 1.4	0.74 ± 0.13	0.1 ± 0.01	4150 ± 275	2188 ± 243
		5–9	0.53–1.01	0.09–0.12	3604–4643	1652–2520
BA+MG	8	6.12 ± 1.13	0.62 ± 0.07	0.09 ± 0.01	4327 ± 360	1874 ± 307
		5–8	0.53–0.73	0.08–0.11	3877–4894	1404–2445
PCE	9	5 ± 1.05	0.5 ± 0.08	0.09 ± 0.01	4705 ± 245	2136 ± 338
		3–7	0.37–0.63	0.08–0.11	4326–5044	1649–2510

TABLE 3. General measurements of short call variables of populations of *Drymophila squamata* (mean ± SD / range). Time variables are in seconds, frequency variables in Hertz. No recordings of sufficient quality for measurements were available for the PCE population. Sample sizes reflect number of individual birds.

Population	*n*	Number of notes	Duration	Pace	Maximum frequency	Minimum frequency
SE	13	2.13 ± 0.35	0.30 ± 0.07	0.10 ± 0.02	5323 ± 310	2096 ± 555
		2–3	0.25–0.48	0.09–0.14	4923–6274	1106–2856
BA+MG	5	2.20 ± 0.45	0.33 ± 0.05	0.12 ± 0.01	4799 ± 75	2017 ± 335
		2–3	0.29–0.42	0.11–0.13	4685–4873	1767–2665

TABLE 4. General measurements of rattle variables of populations of *Drymophila squamata* (mean ± SD / range). Time variables are in seconds, frequency variables in Hertz. Sample sizes reflect number of individual birds.

Population	*n*	Number of notes	Duration	Pace	Maximum frequency	Minimum frequency
SE	4	9.75 ± 3.4	0.57 ± 0.18	0.055 ± 0.007	5692 ± 392	1779 ± 64
		7–14	0.37–0.73	0.048–0.061	5114–5964	1714–1846
BA+MG	5	9.2 ± 1.1	0.52 ± 0.07	0.052 ± 0.003	5527 ± 665	1633 ± 570
		8–11	0.41–0.61	0.047–0.056	4755–6429	1150–2484
PCE	5	8 ± 2	0.4 ± 0.11	0.045 ± 0.004	5943 ± 399	2057 ± 440
		6–11	0.30–0.54	0.040–0.050	5353–6312	1660–2776

We were interested in identifying diagnostic vocal characters (*i.e.*, discrete, non-overlapping character states), rather than in testing for differences between means or medians in the measured characters. Thus, ranges of discrete variables (*e.g.*, number of notes) had to be non-overlapping to be considered diagnostic character states, visual differences in note shape were considered diagnostic when they could be used unequivocally to identify every (or almost every) spectrogram, and ranges of continuous variables had both to be non-overlapping and to meet Isler *et al.*'s (1998) test to estimate that ranges would not overlap with larger sample sizes:

$$X_a + t_a SD_a \leq X_b - t_b SD_b$$

where *X* are means and SD are standard deviations of the populations with the smaller (*a*) and the larger (*b*) set of measurements, and t_i is the *t*-score at the 97.5 percentile of the *t* distribution for *n* – 1 degrees of freedom.

Results

Genetic population structure. Haplotype networks recovered 9 unique haplotypes in the 16 ND2 sequences, 10 in the 16 FIB7 sequences, and 3 in the 16 G3PDH sequences. The ND2 mitochondrial gene haplotype network was considerably more geographically structured than haplotype networks of nuclear markers (Fig. 1). Mitochondrial haplotype variation separated *D. squamata* into four groups: one north of the São Francisco River in Alagoas (hereafter PCE; blue in Fig. 1); one in Bahia (hereafter BA; yellow in Fig. 1); one from eastern Minas Gerais to Espírito Santo (hereafter MG; green in Fig. 1); and one in southeastern Brazil from southern Rio de Janeiro to northern Paraná (hereafter SE; red in Fig. 1). In both the ND2 and G3PDH networks, the PCE population was recovered as the most genetically differentiated population, separated from all the others by > 50 and 4 mutational steps, respectively. In both the FIB7 and G3PDH nuclear gene haplotype networks, a unique haplotype was recovered for the PCE population, whereas populations south of the São Francisco River exhibited no clear pattern of structure (Fig. 1).
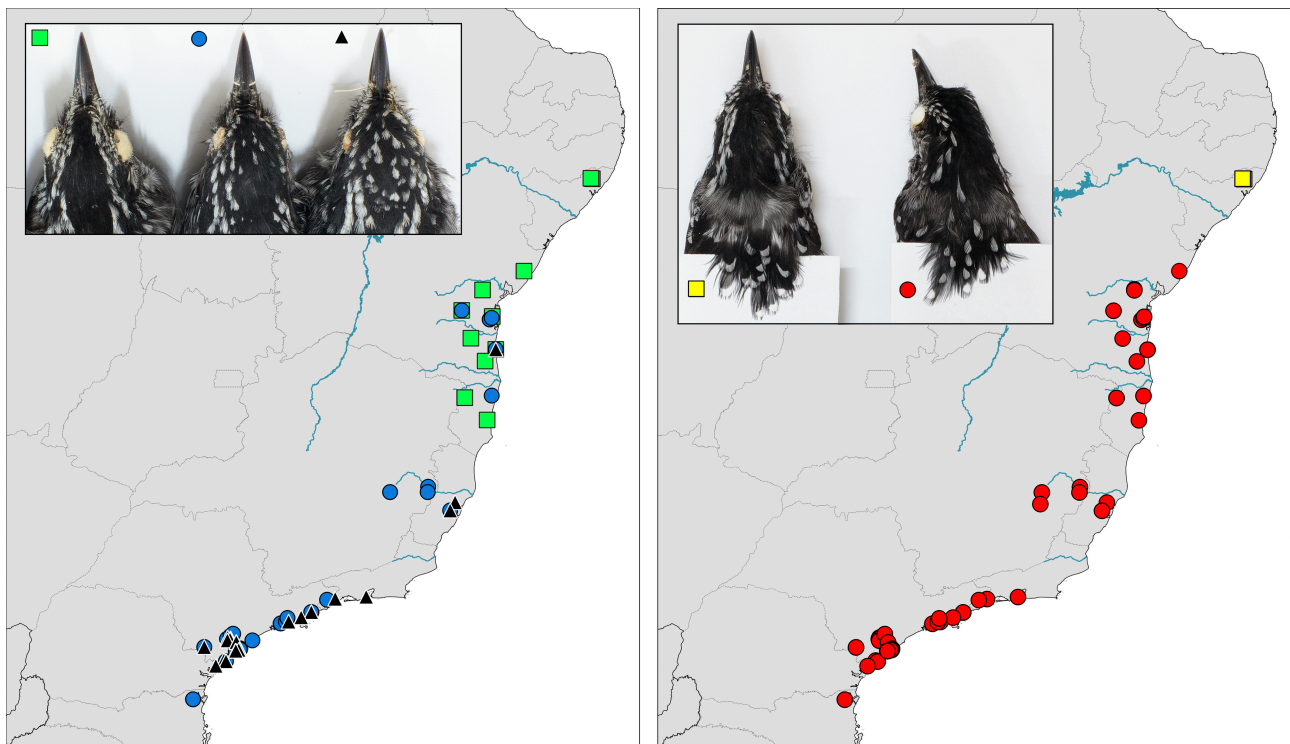

FIGURE 2. Geographic plumage variation in *Drymophila squamata*. (A) Variation in crown pattern, from entirely black (green squares), to moderately white-spotted (blue circles), to entirely white-spotted (black triangles). (B) Markings of the back are either crescent-shaped white markings (yellow squares) or teardrop-shaped white markings (red circles). The specimen marked with a yellow square is the holotype of the new subspecies described herein. See Figure S1 for a complete dorsal view in comparison with other specimens.

Geographic plumage variation. We found geographic variation in two plumage tracts: crown pattern and the shape of markings on the back. Crown pattern varied from entirely black to moderately white-spotted to entirely white-spotted (Fig. 2). The character state "entirely black crown" was restricted to the PCE, BA, and MG lineages, and birds with variably spotted crowns ranged from Bahia to the southern limit of the species' range (Fig. 2). With the largest number of specimens examined to date, we corroborate Pinto's (1935) suspicion that absence of white spots on the crown is not diagnostic for the BA population, because birds with spotted crowns also occur there. Variation in the markings of the back was more geographically structured, allowing the identification of two diagnostically distinct, allopatric populations: one with crescent-shaped markings north of the São Francisco River, and the other with teardrop-shaped markings south of this river (Fig. 2). Despite some individual variation in the shape and size of the white markings on the back within these two groups, all birds north of the São Francisco River had crescent-shaped markings, whereas all birds south of this river had teardrop-shaped markings (Fig. S1).

Geographic acoustic variation. We found geographic variation in only a few vocal characters, namely medium call duration, rattle between-note interval durations, and short call maximum frequency. Southern birds tended to deliver longer medium calls than northern birds (Table 2). However, variation was not discrete. Rather, a strong negative correlation between medium call duration and latitude (Pearson's correlation: $r = -0.7$, $p < 0.001$; Fig. S2) suggests clinality in this character. The SE and PCE populations differed diagnostically in the duration of most intervals between notes in rattles, and differences passed Isler *et al.*'s (1998) test. However, these differences seem to be just the ends of clinal gradients connected by the BA+MG population (Fig. S3). We also found strong negative correlations between rattle between-note interval durations and latitude ($r < -0.7$, $p < 0.01$ in all cases), also suggesting that these characters change clinally. Finally, short call maximum frequency ranged from 4685 to 4873 Hz in the BA+MG population, and from 4923 to 6274 Hz in the SE population. This discrete difference passed Isler *et al.*'s (1998) test. However, we had no short call recordings from the PCE population to assess whether it also represents just the extreme of a geographic cline. Several other vocal characters (*e.g.*, note shapes of medium calls; Fig. 3) varied individually, not geographically.
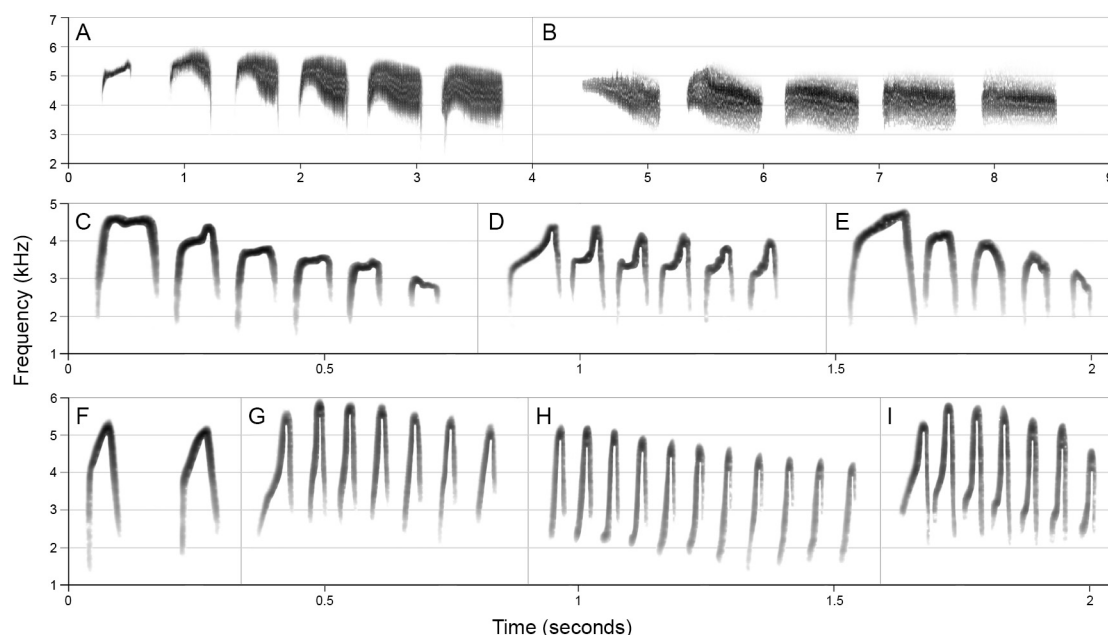

FIGURE 3. Vocalizations of *Drymophila squamata*. Spectrograms A and B illustrate the loudsong and long call, respectively. Spectrograms C–E illustrate variations of the medium call, spectrogram F illustrate the short call, and spectrograms G–I illustrate variations of the rattle call. Representative spectrograms were selected to reflect the range of variation in vocalizations. The duration of intervals between notes in rattles varied geographically and changed gradually from north to south, being shorter in northern birds and longer in southern ones. Differences in note shape and frequency in both medium calls and short calls, however, represent individual, not geographic, variation. The following annotations include the location and catalog number of each sound recording used to produce spectrograms: (A) Loudsong from Parque Estadual da Serra do Conduru, Bahia, XC 618874. (B) Long call from Murici, Alagoas, ML 128004. (C) Medium call from Ubatuba, São Paulo, XC 80164. (D) Medium call from Reserva Biológica de Sooretama, Espírito Santo, ML 113317. (E) Medium call from Murici, Alagoas, ML 128038. (F) Short call from Ubatuba, São Paulo, XC 80168. (G) Rattle from Ubatuba, São Paulo, XC 80164. (H) Rattle from Reserva Biológica de Sooretama, Espírito Santo, ML 113333. (I) Rattle from Murici, Alagoas, XC 550478. See Table S3 for further information on recordings.

Taxonomy. Given the genetic and plumage distinctiveness of the birds north of the São Francisco River, we believe this population is best treated as a distinct taxon, which we here name:

Drymophila squamata selenosticta **subsp. nov.** Piacentini, Lima & Fazza
Crescent-backed Antbird (Pintadinho-do-nordeste in Portuguese)

Holotype: MZUSP 98322, adult male (skull 100% ossified, testes 2 x 3.5 mm) with molting tail feathers, from Fazenda Bananeiras, Murici Ecological Station, municipality of Murici, state of Alagoas, Brazil (9°13'16" S, 35°52'45" W); collected on 26 November 2012 by H. Batalha-Filho, M. Maldonado-Coelho, C. Assis, and A. C. Fazza; prepared as a study skin by V. Q. Piacentini (Fig. S1). Pectoral muscle preserved at the MZUSP (98322) and LGEMA (15912) tissue collections, and carcass preserved in ethanol at MZUSP.

Paratypes: MZUSP 98323, adult male from the same locality as the holotype, collected on 28 November 2012 (Fig. S1); MNRJ 32046, adult male from Fazenda Pedra Branca (currently part of the Murici Ecological Station), Murici, Alagoas, Brazil, collected on 6 February 1979 by L. P. Gonzaga, D. M. Teixeira, and F. M. Oliveira; MNRJ 34996, adult female from Serra Branca (currently part of the Murici Ecological Station), Murici, Alagoas, Brazil, collected on 24 January 1987 by D. M. Teixeira and colleagues.

Diagnosis: All individuals of *D. squamata selenosticta* can be distinguished from their counterparts of all other populations of *D. squamata* by having crescent-shaped white markings on the back.

Distribution: Known historically from seven localities in the Atlantic rainforest of Pernambuco and Alagoas (Table 5), of which it persists only at the Murici Ecological Station.

Etymology: the name *selenosticta* is formed from the Greek words σεληνη *selēnē*, meaning "moon," and στικτος *stiktos*, meaning "spotted, marked," thus alluding to the diagnostic dorsal markings shaped like a crescent moon.

TABLE 5. Localities with records of *Drymophila* s*quamata* s*elenosticta*. Sources: 1—specimen NHMUK 1968.66.192; 2—Roda (2003); 3—Barnett *et al*. (2005); 4—Teixeira *et al.* (1986); 5—Teixeira (1987); 6—Multiple records on the Macaulay Library; 7—Multiple sound recordings on xeno-canto; 8—Multiple photographs and sound recordings on WikiAves; 9—Multiple sound recordings deposited in Fonoteca Neotropical Jacques Vielliard; 10—Multiple sound recordings in deposited in Arquivo Sonoro Elias Coelho; 11—J. F. Pacheco & F. Olmos, personal communication.

Locality	Coordinates	Time-span of records	Sources
1. São Lourenço da Mata, PE	*c*. 7°59'55" S, 35°02'34" W	1903	1
2. Mata de Maria Maior, Canhotinho, PE	8°59'24" S, 36°07'25" W	< 2003	2
3. Frei Caneca Reserve, Jaqueira, PE	8°43'12" S, 35°49'48" W	2003–2008	3, 7
4. Murici Ecological Station, Murici, AL	09°12'49" S, 35°52'31" W	1979–present	4, 5, 6, 7, 8, 9, 10
5. Engenho Coimbra, Ibateguara, AL	09°00'14" S, 35°50'44" W	< 2003	2
6. Mata do Pinto, São José da Lage, AL	8°58'12" S, 36°06'00" W	< 2003	2
7. Fazenda Santa Maria, União dos Palmares, AL	9°09'00" S, 35°52'48" W	2004	11

Discussion

Geographic variation and taxonomy. Results from our genotypic and phenotypic analyses together indicate the existence of two separately evolving population lineages in *D. squamata*, one north and the other south of the São Francisco River. Given their fixed plumage and genetic differences, these lineages are easily recognizable as distinct species under both the General Lineage (de Queiroz 1998) and Phylogenetic (Cracraft 1983) species concepts. Under the Biological Species Concept (Mayr 1942; Coyne & Orr 2004), on the other hand, we consider that these lineages are best treated as members of a polytypic species. Our acoustic trait analysis revealed no significant non-clinal vocal differences among lineages of *D. squamata*, and plumage differences between them are minimal. In the family Thamnophilidae, vocal differences are thought to play a central role as premating isolating barriers, whereas plumage differences are thought to be of minor importance. Many sympatric antbirds are weakly distinct in plumage but exhibit marked vocal differences (Zimmer & Isler 2003), indicating that acoustic signaling traits, possibly along with postmating isolating mechanisms (Cronemberger *et al.* 2020), play a substantially more important role in reproductive isolation than do visual signaling traits. Even minor vocal differences often drive behavioral discrimination and assortative mating between pairs of closely related antbird taxa (Seddon & Tobias 2010; Macedo *et al.* 2019), whereas even obvious plumage differences seem to be ineffective in maintaining species boundaries in this group (*e.g.*, Del-Rio *et al.* 2022). In line with this, acoustic trait divergence has been widely used to establish species limits in the family (Isler *et al.* 1997, 1998, 1999, 2007, 2012; Isler & Maldonado-Coelho 2017; Isler & Whitney 2018). Thus, given the lack of vocal differences between the separately evolving lineages we identified north and south of the São Francisco River, we consider that *selenosticta* is best recognized as a subspecies of *D. squamata* under the Biological Species Concept.

The inferred pattern of mitochondrial variation suggests considerable population structure south of the São Francisco River (Fig. 1). The major phylogeographic break, between the BA+MG and SE lineages, is somewhat consistent with results from our morphological analysis, which showed that birds from the state of Bahia have a plumage character state (entirely black crown) that is absent in the SE lineage (Fig. 2). However, some birds from Bahia exhibit white-spotted crowns (Fig. 2), and so none of the mitochondrial lineages south of the São Francisco River are diagnostically distinct from one another by plumage. Although one could probably make a case for recognizing the BA+MG mitochondrial lineage with a subspecies label on the basis of mitochondrial DNA diagnosability alone (in which case the name *stictocorypha* could be applied), we consider that this genotypic differentiation in mitochondrial DNA is best interpreted as genetic population structure below the taxonomic level, and we agree with Pinto (1935) that the whole population south of the São Francisco River is best treated as a single taxon. Importantly, from a phenotypic perspective, *stictocorypha* falls well below the commonly accepted lower boundary for defining a valid subspecies. Of 30 specimens from the BA+MG mitochondrial lineage, 14 had an entirely black crown, 13 had a moderately-white-spotted crown, and 3 had an entirely-white-spotted crown. Thus, only 47% (14 of 30) of the specimens of the BA+MG mitochondrial lineage were morphologically separable from birds of the SE lineage, meaning that *stictocorypha* could not be recognized as diagnostically distinct even if one employs relaxed thresholds of diagnosability such as the "75% rule" (Amadon 1949; Patten & Unitt 2002).

An interesting additional finding of our study was evidence of clinal vocal variation in *D. squamata*. In a study of vocal variation in Andean populations of the Variable Antshrike *Thamnophilus caerulescens* Vieillot, 1816, Isler *et al.* (2005) demonstrated that the loudsong pace varies clinally in the Andean portion of the species' range, showing for the first time that vocal characters can vary clinally in suboscine passerines. Clinal variation was also recently found in the loudsongs of another group of antbirds, the *Pyriglena* fire-eyes (Maldonado-Coelho *et al.* 2023). Here, we demonstrate another case of this phenomenon, which may be more common than previously thought. Clines usually arise as a result of primary differentiation along environmental gradients or hybridization upon secondary contact of lineages that diverged in allopatry (Endler 1977; Barton & Hewitt 1989). Although not yet formally tested, the latter scenario seems a more likely explanation for the clinal vocal variation of *Drymophila squamata*, as there is no obvious environmental gradient along the species' range and also because many Atlantic Forest lineages are known to have been repeatedly geographically isolated during climate fluctuations in the Pleistocene (Carnaval & Moritz 2008). Overall, our finding of clinality in vocalizations of *D. squamata* reinforces the importance of broad geographic sampling when assessing species limits using vocalizations (Remsen 2005; Cicero *et al.* 2021; Donald 2021). Without samples of the clinal intermediates, the geographic ends of the cline could be erroneously considered diagnostically distinct in these acoustic traits.

Conservation. *Drymophila squamata* is typically fairly common throughout most of its range (Zimmer & Isler 2003). In the PCE, the species was repeatedly reported as very common at Murici between the 1980s and early 2000s (Teixeira *et al.* 1986; eBird checklist S64422055 by T. S. Schulenberg & R. S. Ridgely in October 1987; C. Marantz [pers. comm.] in March 2001). Today, however, it seems to be almost as scarce as the critically endangered Alagoas Antwren *Myrmotherula snowi* Teixeira & Gonzaga, 1985, with only 22 individuals of *D. squamata selenosticta* captured during more than ten years of mist-netting at the Murici Ecological Station (October 2010–March 2021; Lima *et al.* 2022). In addition to Murici, the species was earlier recorded in six other localities in the states of Alagoas and Pernambuco (Table 5). In the latter state, the first record was a single individual collected by Alphonse Robert on 26 July 1903 in the lowland forests of São Lourenço da Mata (NHMUK 1968.66.192), and the last one was a male recorded in 2008 at the Frei Caneca Reserve (WA 1369365; C. Albano). Despite recent searches using playback at the latter site (RDL in 2017–2019), the species has never been recorded there again. Currently, it is known only from the Murici Ecological Station.

The Atlantic rainforest north of the São Francisco River has been virtually extirpated over the last 500 years to make way for sugarcane fields and cattle ranches, and the few forest remnants are extremely fragmented and degraded (Ranta *et al.* 1998; Silva & Tabarelli 2000; Silveira *et al.* 2003; Tabarelli *et al.* 2006). With less than 2–5% of its original forest remaining, the so-called Pernambuco Center of Endemism holds one of the greatest concentrations of critically endangered bird taxa in the Americas (Teixeira 1986; Brooks & Balmford 1996; Lees *et al.* 2014; Pereira *et al.* 2014; Develey & Phalan 2021). In addition to deforestation, hunting, and other ills that plague the region's biota, many Atlantic Forest bird species have their northern geographic range edge in the Pernambuco Center of Endemism, where they often exist at their niche limits and are thus more sensitive to disturbance (Orme *et al.* 2019). Also, understory insectivorous birds such as *Drymophila squamata* are among the most sensitive to forest fragmentation (Bierregaard & Lovejoy 1989; Stouffer & Bierregaard 1995; Aleixo 1999; Laurance 2004; Laurance *et al.* 2004). All these factors together put *D. squamata selenosticta* on the brink of extinction, a situation that requires urgent conservation measures.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Figure S1. Individual variation in the shape and size of the white markings on the back. From left to right: MZUSP 98322 from Murici, Alagoas (holotype of *Drymophila squamata selenosticta* **subsp. nov.**); 98323 from Murici, Alagoas (paratype of *Drymophila squamata selenosticta* **subsp. nov.**); 33401 from Ilhéus, Bahia; 76215 from Porto Seguro, Bahia; 100644 from Prado, Bahia; 94350 and 94353, both from Santa Maria do Salto, Minas Gerais; 47946 from Rio Ipiranga, São Paulo.

Figure S2. Clinal variation in duration of medium calls.

Figure S3. Clinal variation in the duration of intervals between notes of "rattle" calls. Pearson's correlation coefficients varied from -0.65 to -0.87, and linear models' R^2 from 0.37 to 0.73. All p values were ≤ 0.01.

Table S1. Genetic samples.

Table S2. Museum skins.

Table S3. Sound recordings.