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AN INTEGRATIVE APPROACH TO SPECIES-LEVEL SYSTEMATICS REVEALS THE DEPTH OF DIVERSIFICATION IN AN ANDEAN THAMNOPHILID, THE LONG-TAILED ANTBIRD

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Abstract. The geographic range of the Long-tailed Antbird (*Drymophila caudata*) extends from the Paria Mountains of Venezuela south through the Andes to northern Bolivia, a geographic and elevational distribution unique in the antbirds (Thamnophilidae). Plumage variation among most populations is not obvious, and although eight subspecies have been described, half have been synonymized. We took a multidimensional approach to reexamining the taxonomy of the complex. We identified lineages by evaluating divergence in mtDNA, and defined study groups within them to take into account previously described plumage differences. We then assessed the taxonomic status of principal lineages and study groups by comparing vocal differences among them to established taxonomic "yardsticks" for thamnophilid antbirds. Finally, we related taxa to the ecology of the regions in which they occur. The outcomes revealed substantial diversification, sufficient for recognition of four species, three restricted to the north and one widespread along the main body of the Andes extending from northwestern Colombia south to Bolivia. Speciation in Andean *Drymophila* antbirds is partially associated with elevational and environmental divergence. The results provide valuable inputs to mapping and understanding avian evolution in the Andes and demonstrate the value of a multifaceted approach in solving taxonomic problems.

Key words: Andes, Drymophila caudata*, museum specimens, niche divergence, species delimitation, phylogeography, suboscines, vocalizations*

Una Estrategia Integral para la Sistemática a Nivel de Especie Revela la Magnitud de Diversificación en un Thamnophílido Andino, *Drymophila caudata*

Resumen. La distribución geográfica de *Drymophila caudata* se extiende desde las montañas de Paria en Venezuela hacia el sur a lo largo de la cordillera de los Andes hasta el norte de Bolivia, conformando un patrón de distribución geográfico y altitudinal único en los Thamnophilidae. La variación en el plumaje entre la mayoría de las poblaciones no es obvia y a pesar de que ocho subespecies han sido descritas, la mitad han sido invalidadas. Nosotros optamos por una estrategia multidimensional para reexaminar la taxonomía del complejo. Primero, identificamos linajes con base en su divergencia en ADNmt y grupos de estudio dentro de cada linaje con base en diferencias de plumaje previamente descritas. Después, evaluamos el estatus taxonómico de cada linaje y de cada grupo de estudio mediante comparaciones de las diferencias vocales entre ellos con estándares establecidos para los thamnophílidos. Finalmente, comparamos la ecología de los taxones definidos con base en diferencias climáticas entre sus áreas de distribución. Los resultados revelan un nivel considerable de diversificación, suficiente para el reconocimiento de cuatro especies, tres de ellas restringidas a las montañas del norte y una ampliamente distribuida a lo largo de los Andes desde el noroeste de Colombia hasta Bolivia. El proceso de especiación en los thamnophílidos andinos del género *Drymophila* está parcialmente asociado con procesos de divergencia altitudinal y ambiental. Estos resultados son valiosos para entender la evolución de las aves en los Andes y demuestran el valor que tienen las estrategias multidimensionales para resolver incertidumbres taxonómicas.

INTRODUCTION

Species delimitation is an essential endeavor of systematics that aims at characterizing biodiversity and understanding its evolution (Wiens 2007, O'Meara 2010). However, establishing species boundaries among populations can be exceedingly difficult, especially for recently diverged, allopatric populations (Mayr and Ashlock 1991, Price 2007). The validation of taxonomic partitions of individuals representing lineages is crucial for phylogenetic inference (Ence and Carstens 2011). A number of methods have been developed to test for evolutionarily isolated lineages (Sites and Marshall 2003, Hart 2011) and to identify emergent properties of lineages such as distinct phenotypic and behavioral traits and ecological niche (Isler et

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al. 1998, Wiens and Graham 2005, McCormack et al. 2010). Most notably, the analysis of vocalizations of tracheophone suboscines (e.g. Rhinocryptidae, Thamnophilidae) is revolutionizing our understanding of species diversity in this group of birds with presumably innate songs and relatively conservative plumage patterns (Krabbe and Schulenberg 1997, Isler et al. 2007). The integration of multiple approaches for species delimitation from analyses of morphological, vocal, ecological, biogeographic, and genetic data is helping overcome these difficulties in birds objectively (Remsen 2005, Cadena and Cuervo 2010).

The Long-tailed Antbird, *Drymophila caudata* (Sclater, 1854). is unique among typical antbirds (Thamnophilidae) in having a lengthy latitudinal range from the coastal mountains of Venezuela through the Andes to northern Bolivia and a wide (800 to 3150 m) elevational range, occurring in *Chusquea* bamboo stands and shrubby tangles along the humid forest belt (Zimmer and Isler 2003). The linear geographic distribution of *D. caudata* is fragmented by low-elevation gaps and high-elevation ridges and includes unsampled regions that may or may not represent true distributional gaps (Fig. 1). Bates et al. (1999) reported moderate genetic differentiation in *D. caudata* between two sites in the eastern Andes of Peru where dry valleys bisect the species' distribution. Most Andean birds with linear and fragmented distributions exhibit marked geographic variation in plumage patterns (Remsen 1984, Graves 1988, Brumfield and Remsen 1996, Gutiérrez-Pinto et al. 2012), but plumage differences among populations of *D. caudata* are subtle and confounded by individual variation. As a result, of the eight subspecies of *D. caudata* described, four (*striaticeps, occidentalis, peruviana,* and *boliviana*) have been synonymized with the nominate form (Cory and Hellmayr 1924, Zimmer 1931). Preliminary analyses of vocalizations and phylogeography pointed to the need for a rigorous integrative reexamination of the taxonomy of *D. caudata* (Cuervo and Brumfield, unpubl. data; Zimmer and Isler 2003).

In this study, we take an integrative approach to identify and evaluate evolutionarily isolated lineages across the range of *Drymophila caudata.* First, we use DNA sequences of three mitochondrial loci to identify independent lineages within *D. caudata*, investigate genetic structure across its distributional range, and infer evolutionary isolation. Second, we establish study groups within principal lineages to take into account previously described subspecies defined by plumage. Third, we assess diagnosability in songs and calls to infer divergence among and within the principal lineages and evaluate species status by a "yardstick" method for suboscine passerines (Isler et al. 1998, Remsen 2005). Fourth, we use elevational and environmental data to examine whether ecological divergence accompanies population differentiation. Finally, we integrate the results of these approaches to propose a taxonomic revision of *D. caudata*.

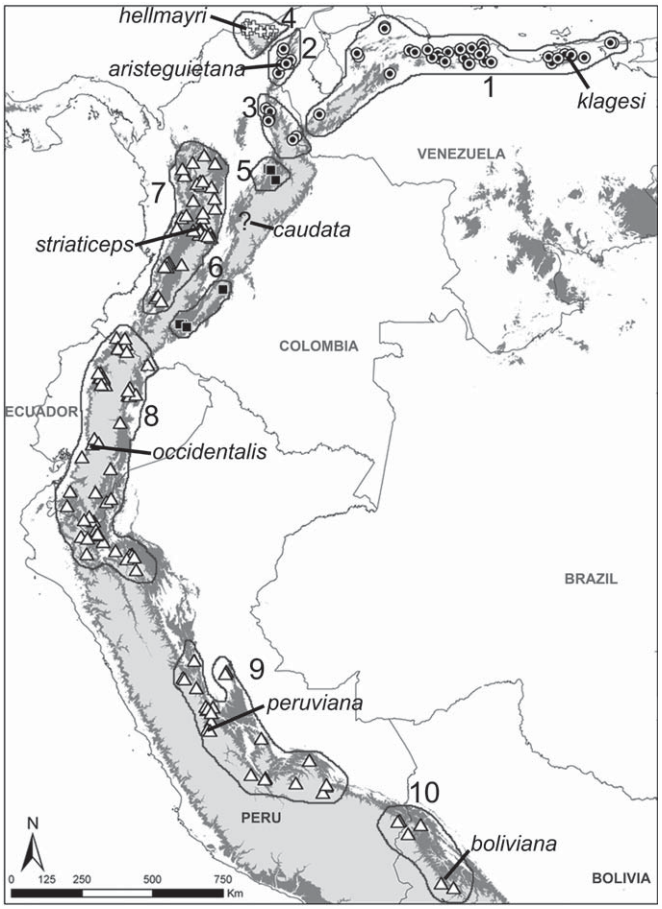

FIGURE 1. Distribution of the *Drymophila caudata* complex. Symbols represent records of occurrence of the four species we define: circles = *D. klagesi*, crosses = *D. hellmayri*, squares = *D. caudata*, triangles = *D. striaticeps*. Study groups for the vocal analysis (see text) are encircled, and lines connect labels to type localities of available taxon names. Geographic coordinates are expressed in degrees to hundredths of a degree, longitude followed by latitude, positive value for north latitude. 1, *klagesi* (Los Palmales, Sucre, Venezuela, –63.75, 10.28); 2, *aristeguietana* (Cerro Pejochaina, Sierra de Perijá, Venezuela, –72.97, 9.95); 3, Norte de Santander; 4. *hellmayri* (Cincinati, Sierra Nevada de Santa Marta, Colombia, –74.17, 11.17); 5, Santander; 6, upper Magdalena; 7, *striaticeps* (Salento, Quindío, Colombia, –75.57, 4.63); 8, *occidentalis* (Suropata, Chimborazo, Ecuador, –79.03,.–2.27); 9, *peruviana* (Garita del Sol, Junín, Peru, –75.35, –11.28); 10, *boliviana* (Sandillani, La Paz, Bolivia, –67.90, –16.20). The type locality of *caudata* is "Bogota" with no specific locality information (Sclater 1854).

METHODS

PHYLOGENETIC ANALYSIS

To identify independently evolving lineages in *D. caudata* and provide a phylogenetic hypothesis, we sequenced 31 specimens from locations scattered across its distribution (Fig. 1), representing the four currently recognized subspecies (Appendix 1, available at http://dx.doi.org/10.1525/

cond.2012.120012). We included as outgroups *D. devillei*, *D. malura*, *D. genei*, and *D. ferruginea* (type species of the genus), *Hypocnemis hypoxantha*, as well as the more distantly related *Cercomacra parkeri* (Brumfield et al. 2007; Bravo and Brumfield, unpubl. data).

We extracted genomic DNA from ~20 mg of pectoral muscle with a DNeasy kit (Qiagen, Valencia, CA) and sequenced three mitochondrial genes: cytochrome *b* (cyt-*b*, 1029 bp), NADH-dehydrogenase subunit 2 (ND2, 1041 bp), and NADH-dehydrogenase subunit 3 (ND3, 351 bp). We used the primers L14990 and H16065 (Helm-Bychowski and Cracraft 1993) for cyt-*b*, L5215 (Hackett 1996), H6313 (Johnson and Sorenson 1998), and internal sequencing primers L5758 and H5766 (Brumfield et al. 2007) for ND2, and L10755 and H11151 (Chesser 1999) for ND3. Protocols for PCR reactions and sequencing are described in Brumfield et al. (2007). Sequences generated in this study have been deposited in GenBank (accession numbers JQ913056–JQ913140).

We inferred phylogeny on a partition by gene scheme and by maximum likelihood in RAxML 7.0.4 (Stamatakis 2006) and Bayesian inference methods in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) via the Cipres Portal (Miller et al. 2010). RAxML implemented the GTR + Γ model for each partition and a thorough search by maximum likelihood with 1000 bootstrap pseudoreplicates to assess nodal support. Four independent MrBayes runs consisted of four Metropolis-coupled Markov chain Monte Carlo chains of 20 million steps, sampling parameters and trees every 1000 steps, and discarding the first 50% as burn-in. We used default priors except for the exponential prior mean of branch lengths, which we set to 100 to avoid inflated branch lengths (Brown et al. 2010). We inspected convergence diagnostics from MrBayes and the graphical output of Tracer 1.5 (Rambaut and Drummond 2007) to assess consistency in estimated parameters and posterior probabilities of clades among Markov chain Monte Carlo runs. We selected the best-fit substitution model for each partition by MrModelTest 2.3 (Nylander 2004) in conjunction with PAUP* 4.0b10 (Swofford 2002) under the Akaike information criterion.

PLUMAGE CONSIDERATIONS AND STUDY-GROUP DELINEATION

We defined principal lineages with the phylogenetic results. We sought to identify plumage differences among lineages and attempted to evaluate plumage differences in subspecies descriptions by visual comparisons of specimens at IAvH, ICN, USNM, and LSUMZ (for acronyms, see Acknowledgments), supplemented by photographs of specimens at ANSP, IRSN, MCZ, and BMNH, including the syntypes at BMNH and other "Bogota" trade skins. We did not measure specimens because of the lack of mensural differences among populations (Cory and Hellmayr 1924, pers. obs.). Plumage differences primarily involve pattern (e.g., streaking or lack thereof). Consequently, color differences possibly produced by differences in photography were of little consequence. However, given the paucity of specimens, even if we could not verify plumage differences among described subspecies, for the analysis of voice we accepted as study groups all described subspecies augmented by subdivisions of principal lineages found in the phylogeny.

VOCALIZATIONS AND TAXONOMIC EVALUATION

We compiled recordings of vocalizations from our personal inventories, from unarchived contributions of others, from the Xeno-Canto database (XC, www.xeno-canto.org), from the Banco de Sonidos Animales, (BSA, Instituto Alexander von Humboldt, Bogota, Colombia), and from the Macaulay Library (ML, Cornell Laboratory of Ornithology, Ithaca, NY). We examined 224 recordings (Appendix 2 online). Using Raven Pro 1.4 (Cornell Laboratory of Ornithology), we made a spectrogram of every vocalization type delivered by each individual on every recording. We reviewed the documentation of recordings to identify, whenever possible, the number and sex of individuals vocalizing.

We compared all spectrograms visually across and within the principal lineages to assess variation in (1) number of notes, (2) duration, (3) pace, (4) change of pace, (5) note shape, (6) change in note shape, (7) note length, (8) change in note length, (9) interval length, (10) change in interval length, (11) frequency, and (12) change in frequency. On the basis of this assessment, we measured selected characteristics (e.g., duration of initial note) of every clearly delineated spectrogram. These were obtained from spectrograms projected on a 43-cm screen with the default settings of Raven Pro 1.4 (Charif et al. 2010), except the display was set to smooth, overlap was adjusted from 50 to 93.7% depending on the recording's quality, and contrast was adjusted according to the recording's intensity with care taken to retain all elements of the vocalization. Cursor measurements were typically at scales of 0.3 sec cm^{-1} and 0.5 kHz cm^{-1}. Except as noted, sample sizes reflect number of individuals, not number of vocalizations measured.

Taxonomic recommendations are based on diagnostic differences in vocal characters. We defined diagnostic differences as discrete, non-overlapping character states that have the potential for unambiguous recognition of a signal (Isler et al. 1998, 2007). Ranges of samples of continuous variables could not overlap, and we estimated the likelihood that ranges would not overlap with larger sample sizes by requiring the means ($\bar{x}$) and standard deviations (SD) of the population with the smaller set of measurements (*a*) and the population with the larger set of measurements (*b*) to meet the test

$$\bar{x}_a + t_a \mathrm{SD}_a \leq \bar{x}_b - t_b \mathrm{SD}_b$$

where t_i = the *t*-score at the 97.5 percentile of the *t* distribution for $n - 1$ degrees of freedom.

ECOLOGICAL DIVERGENCE

To assess whether principal clades differ in the macroecological conditions that they experience, we integrated information on precipitation and temperature across the species' distribution with 192 points of record from museum specimens, literature, and sound recordings contained in an updated version of a distributional database of the Thamnophilidae (Isler 1997). We extracted and log-transformed precipitation and temperature information for each locality from 19 climatic variables from the WorldClim database with a spatial resolution of 1 km^2 (Hijmans et al. 2005). When available, a unique elevation value was obtained directly from the primary source of the record. For other localities, we extracted unique elevation values from the digital elevation model available from WorldClim with a spatial resolution of 1 km^2 (Hijmans et al. 2005).

We assessed elevation differences among the principal clades with one-way ANOVAs and post-hoc Tukey HSD tests. To assess whether localities of different populations occupy diagnosable units in environmental space, we ran a discriminant function analysis (DFA) on the 19 WorldClim climatic variables by using the entire dataset for both training and evaluation because of low sample sizes for *hellmayri* and *caudata*. To evaluate possible effects of multicollinearity, we also ran DFA on a reduced subset of seven uncorrelated climatic variables (mean temperature diurnal range, temperature seasonality, maximum temperature of the warmest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter) that also included altitude. Because results did not differ from those based on the complete set of variables, we provide results from the complete set only.

RESULTS

PHYLOGENETIC ANALYSIS

All genetic samples of *Drymophila caudata* formed a monophyletic group that was sister to *D. devillei* (Fig. 2). The Bayesian and maximum-likelihood results consistently showed deep phylogeographic differentiation in *D. caudata*, recovering four major lineages: (A) A highly divergent northern clade included the subspecies *klagesi*, a sample from Norte de Santander allegedly of *klagesi*, and subspecies *aristeguietana*; this clade was sister to the other three clades. (B) Subspecies *hellmayri* from the Sierra Nevada de Santa Marta represented a highly differentiated lineage and was recovered as sister, with moderate support, to clade C. (C) A strongly supported clade of the Eastern Andes of Colombia was formed by one sample from Santander and two from the upper Magdalena valley. (D) A widespread Andean clade having some geographic structure included the formerly recognized subspecies *striaticeps*, *occidentalis*, *peruviana*, and *boliviana*. Pairwise divergence in mitochondrial sequences among the four major clades ranged from ~5% between clades A and D and 2.1% between clades B and C (Table 1).

PLUMAGE CONSIDERATIONS AND STUDY-GROUP DELINEATION

Three of the four major clades recovered in the phylogenetic analysis (clades A, B, and D) could be clearly distinguished visually by plumage characters in examination of museum specimens. Specimens of clade C are insufficient for firm conclusions of its phenotypic diagnosability, yet they most likely represent the nominate subspecies (see below). We confirmed three diagnostic plumage characters.

Forecrown, crown, and nape of male. The extent of white streaking on the black forecrown, crown, and nape was a source of confusion throughout the early 20th century. The syntypes at the BMNH have streaking restricted from the forecrown to the center of the crown approximately to behind the eye, beyond which the black centers of the crown and nape are unstreaked (*contra* Hellmayr as cited in Chapman 1917 and Todd and Carriker 1922). The northern subspecies *klagesi* (including samples from Norte de Santander and subspecies *aristeguietana*; clade A) and *hellmayri* (clade B) also have the white streaking typically restricted to the forecrown; less often the forecrown is unstreaked or the streaking ends before the eye. Conversely, the entire forecrown, crown, and nape are streaked in the western and southern populations formerly ascribed to subspecies *striaticeps*, *occidentalis*, *peruviana*, and *boliviana* (clade D). Male specimens of the geographically intermediate populations of Santander and upper Magdalena (clade C) were unavailable.

Tail color of male and female. In subspecies *hellmayri* (clade B), the rectrices are reddish brown dorsally and clearly distinct from those of all other populations, whose tails are primarily gray.

Underpart streaking of male. Blackish streaking of the underparts is greatly reduced in subspecies *klagesi* and *aristeguietana* and specimens from Norte de Santander (clade A). Their throat streaking is absent or reduced to a few dots or fine hairlines in the center and to light streaks on the malar; their breast streaks are nearly or completely obsolete centrally or limited to a narrow band on the upper breast, to the extent that the underparts appear extensively white.

Although we found these plumage differences among principal lineages, we could not verify further plumage distinctions among subspecies, discussed in Appendix 3 (online), with available materials.

VOCALIZATIONS

For analysis of voice, we defined 10 study groups (Fig. 2):

1. *klagesi* (kla): Coastal mountains and Andes of Venezuela except for the Serranía de Perijá. Previously described subspecies (Hellmayr and Seilern 1912). Clade A.
2. *aristeguietana* (aris): Serranía de Perijá, Venezuela and Colombia. Previously described subspecies (Aveledo and Pérez 1994). Clade A.
3. Norte de Santander (Nort): Both slopes of the northern Eastern Andes, Norte de Santander, Colombia.

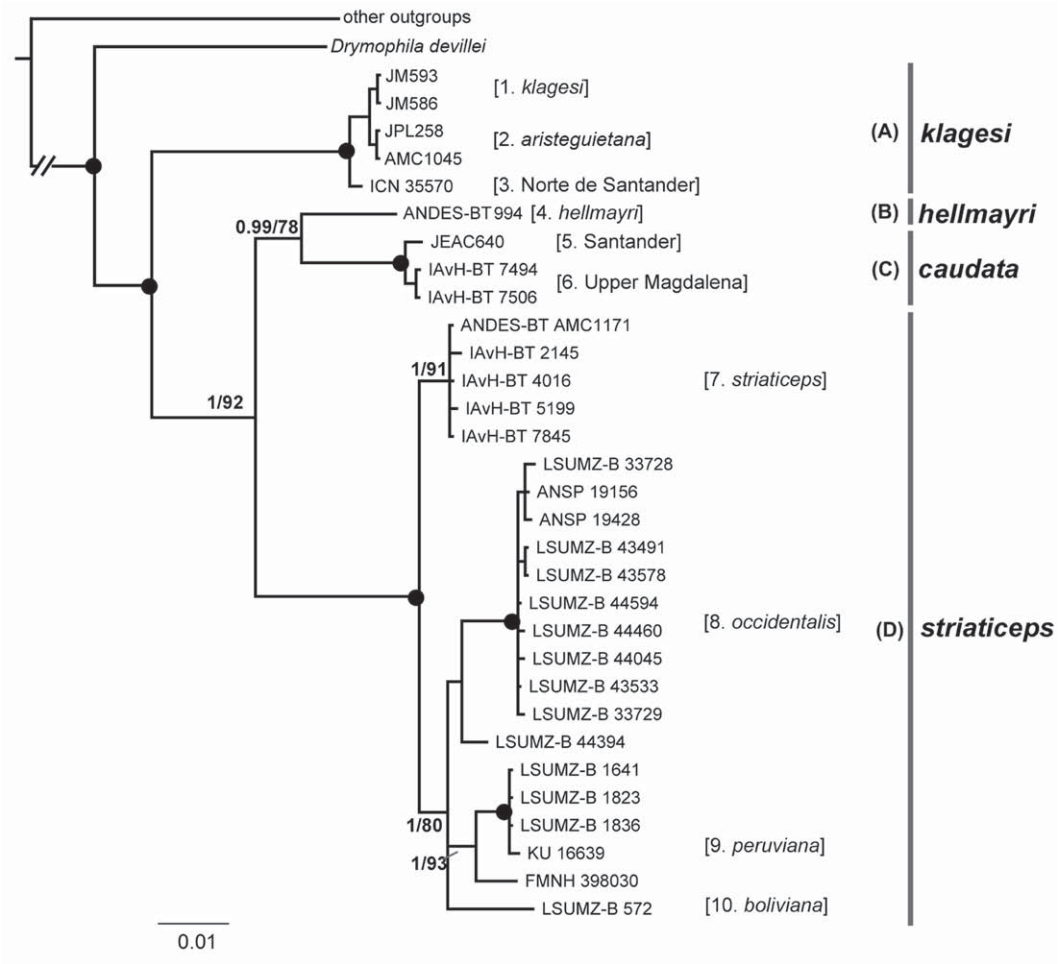

FIGURE 2. Phylogram showing the relationships among mitochondrial sequences of *Drymophila caudata*. The gene tree is a 50% majority-rule consensus tree from the Bayesian estimation of the genealogy of cyt-*b*, ND2, and ND3. Black dots on nodes represent high posterior probability (>0.97) and high maximum-likelihood bootstrap support (>95%); nodal supports below any of these thresholds are indicated numerically on nodes, unless below (0.8/70%). In brackets, study groups for the vocal analysis (see text and Fig. 1); in parentheses, the four resulting clades (A–D). The recommended species ranks indicated on the right.

Phylogenetic analysis; previously identified as *hellmayri* or *klagesi* (Meyer de Schauensee 1950, 1952). Clade A.

4. *hellmayri* (hel): Sierra Nevada de Santa Marta, Colombia. Previously described subspecies (Todd 1915). Clade B.
5. Santander (San): Western slope of Eastern Andes, south of the Chicamocha River Valley, Santander, Colombia. Phylogenetic analysis and plumage. Clade C.
6. Upper Magdalena (UpM): Head of the Magdalena River Valley in Huila and adjacent Caquetá, Colombia. Phylogenetic analysis. Clade C.
7. *striaticeps* (stri): Western and Central Andes south to Cauca, Colombia. Previously described subspecies (Chapman 1912). Clade D.
8. *occidentalis* (occ). Nariño, Colombia, through Ecuador to San Martín, northern Peru. Previously described subspecies (Domaniewski and Sztolcman 1922). Clade D.
9. *peruviana* (per): Eastern Andean slope from Huánuco to Cusco, Peru. Previously described subspecies (Domaniewski and Sztolcman 1922). Clade D.
10. *boliviana* (bol): Puno, Peru, and La Paz, Bolivia. Previously described subspecies (Carriker 1935). Clade D.

We identified four distinct types of vocalizations: male loudsongs, female loudsongs, short-note calls, and long-note calls. Typically, females begin their loudsongs during the terminal notes of the male's loudsong, less often after the male's loudsong is completed. The short-note call consists of a brief series of abrupt notes; the long-note call includes one or more notes of longer duration. Calls have been recorded much less frequently than have loudsongs and not at all for some study groups for which samples of recordings are small. For all vocal characters, we examined data geographically, and no instances of clinality along the range of *D. caudata* were

TABLE 1. Genetic divergence among the four principal lineages of *Drymophila caudata* (clades A–D) and its closest relative (*D. devillei*). Below diagonal: average uncorrected pairwise distances in mtDNA sequences; diagonal: average genetic distances among individuals within clades; above diagonal: net average distances between clades (d_A). Nomenclature follows recommendations of this paper.

	(A) *D. klagesi*	(B) *D. hellmayri*	(C) *D. caudata*	(D) *D. striaticeps*	(outgroup) *D. devillei*
(A) *D. klagesi*	0.001	0.040	0.042	0.045	0.066
(B) *D. hellmayri*	0.040	—	0.021	0.030	0.068
(C) *D. caudata*	0.043	0.021	0.001	0.030	0.067
(D) *D. striaticeps*	0.050	0.035	0.036	0.010	0.063
(outgroup) *D. devillei*	0.066	0.068	0.067	0.068	—

apparent. Additional descriptions and supporting data are provided in Appendix 3 (online).

Male loudsongs. Male loudsongs (Fig. 3) are short (typically ~2 sec or less) and include a burst of clear whistles followed by raspy notes accompanied by clear introductory and/or terminal elements. The following characters distinguish the study groups. (1) Number of whistled notes. Upper Magdalena loudsongs ($n = 9$; Fig. 3A) have four to six; other groups have two. (2) Peak frequencies of whistled notes. Those of five northern groups (*klagesi*, *aristeguietana*, Norte de Santander, *hellmayri*, and Upper Magdalena; example *klagesi* Fig. 3B) are significantly lower pitched than those of the remaining groups (example *striaticeps* Fig. 3C). (3) Change in peak frequency of whistled notes. Only those in Upper Magdalena loudsongs increase. (4) Clear element preceding raspy notes. Lacking in *klagesi*, *aristeguietana*, and Norte de Santander loudsongs, present elsewhere. (5) Duration of whistled notes. Those of four northern groups (*klagesi*, *aristeguietana*, Norte de Santander, *hellmayri*) are significantly longer than those of four other groups (Upper Magdalena, *occidentalis*, *peruviana*, and *boliviana*), whereas *striaticeps* is intermediate. We consider an additional characteristic provisional and awaiting verification: the clear element following initial raspy notes is absent from loudsongs of *occidentalis* (Fig. 3D) except for two examples from San Martín, Peru, at the southern end of the distribution. Table 2 provides the total number of characters distinguishing male loudsongs of different study groups.

Female loudsongs. Female loudsongs (Fig. 3) consist of a short (~2 sec) series of whistles typically dropping in pitch and ending with a single raspy note (sometimes none or two). The following characters distinguish groups. (1) Peak frequencies of whistled notes. Notes of *klagesi*, *aristeguietana*, and Norte de Santander (example *klagesi* Fig. 3E) are significantly lower than those of other groups (example *striaticeps* Fig. 3F) except *hellmayri*. (2) Change in peak frequency of whistled notes. Unlike those in other groups, peaks in upper Magdalena loudsongs (Fig. 3G) initially rise in frequency. (3) Presence of clear introductory element preceding initial raspy notes. Differences are consistent with those in male loudsongs. An additional characteristic is not diagnostic but provides supporting evidence that groups are evolving independently: the number of whistled notes is typically greater in the five northern groups. Table 2 provides the total number of characters distinguishing female loudsongs of different groups.

Short-note calls. Short-note calls recorded for *occidentalis*, *peruviana*, and *boliviana* (example *peruviana* Fig. 4A) include abrupt notes of <0.05 sec delivered rapidly (intervals between notes <0.10 sec) in groups of two or three (rarely four); note peaks typically decline in frequency (rarely flat in *occidentalis*). Short-note calls of *striaticeps* (Fig. 4B) are similar but we provisionally consider them distinct from those of the foregoing groups on the basis of the longer duration of the first note and the common reduction to a single note (Fig. 4C). Also probably distinct are the short-note calls of *hellmayri* (Fig. 4D) and *klagesi* (Fig. 4E). In a single recording of *hellmayri* this call differed from that in one of *klagesi* in its lower frequency and longer interval between notes. Table 3 identifies the number of characters distinguishing short-note calls.

Long-note calls (sample sizes are examples, not individuals). The inverted U-shaped long calls of *striaticeps*, *occidentalis*, *peruviana*, and *boliviana* are given singly (Fig. 4F) or in a pair with the second note shorter than the first (Fig. 4G). Only 3 of 29 examples are 3-noted. Calls of *klagesi* (Fig. 4H) are all single-noted, down-slurred, and based on a low-frequency fundamental; a single recording from Norte de Santander is similar. The shape of the note and the frequency of the fundamental of *klagesi* calls are distinct from calls of the foregoing groups. We provisionally consider the single recording of a call of *hellmayri* containing a long note (Fig. 4I) distinct from calls of all other study groups on the basis of its multi-note structure and from all but *klagesi* in note frequency. Table 3 identifies the number of characters distinguishing long-note calls.

The number of characters of all vocal types that differ among study groups are summed up in Table 4. Diagnostic differences in multiple vocal characters distinguish the four major lineages uncovered in the phylogeny: *klagesi* (populations 1–3), *hellmayri* (population 4), *caudata* (populations 5–6), and *striaticeps* (populations 7–10). Within these lineages, however, vocal differences among study groups are

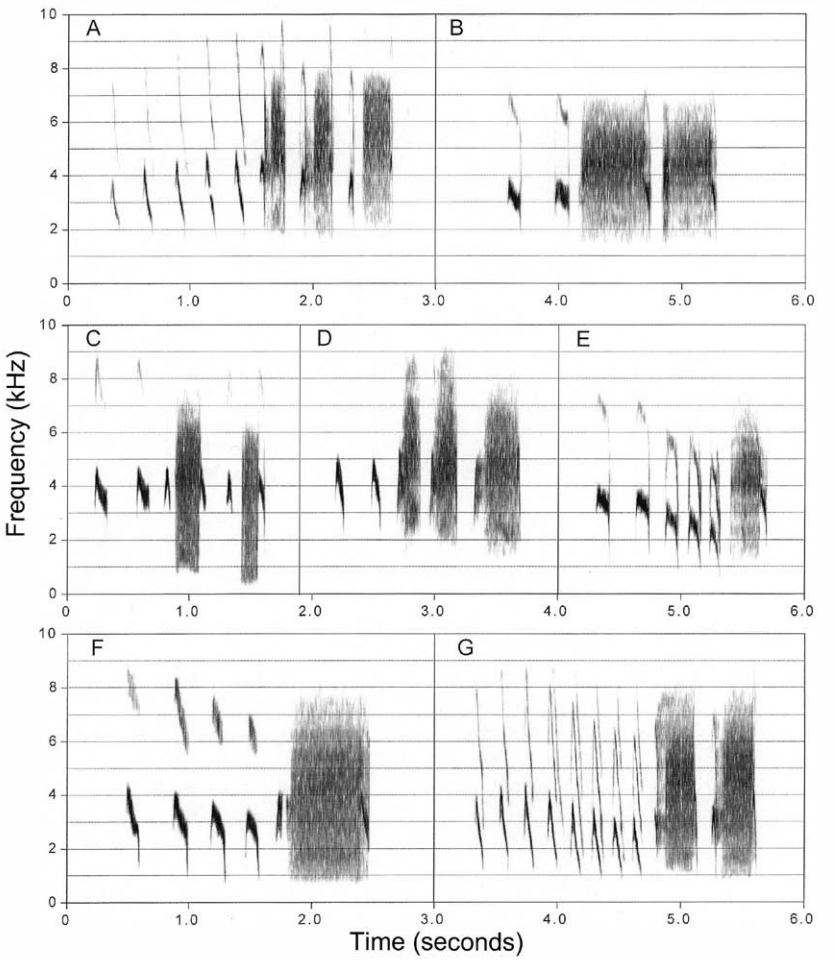

FIGURE 3. Loudsongs of study groups in the *Drymophila caudata* complex. Acronyms for archives of recordings are translated in Appendix 2. (A) Upper Magdalena (clade C), male, Parque Nacional Natural Cordillera de los Picachos, Caquetá, Colombia (BSA 298), (B) *klagesi*, male (clade A), Rancho Grande, Aragua, Venezuela (ML 61989); (C) *striaticeps*, male, (clade D), Jardín, Antioquia, Colombia (ISL AMC C 029), (D) *occidentalis*, male (clade D), Reserva Natural La Planada, Nariño, Colombia (BSA 10942); (E) *klagesi*, female (clade A), Rancho Grande, Aragua, Venezuela (ML 61988); (F) *striaticeps*, female (clade D), Alto El Silencio, Antioquia, Colombia (ISL MISC C 071); (G) upper Magdalena (clade C), female, Parque Nacional Natural Cordillera de los Picachos, Caquetá, Colombia (BSA 297).

TABLE 2. Number of vocal characters distinguishing loudsongs of males (above the diagonal) and females (below the diagonal).[a]

	1 kla	2 aris	3 Nort	4 hel	5 San[b]	6 UpM	7 stri	8 occ	9 per	10 bol
1 kla		0	0	1	X	4	2	4	3	3
2 aris	0		0	1	X	4	2	4	3	3
3 Nort	0	0		1	X	4	2	4	3	3
4 hel	1	1	1		X	3	1	3	2	2
5 San[b]	X	X	X	X		X	X	X	X	X
6 UpM	3	3	3	1	X		3	4	3	3
7 stri	2	2	2	0	X	1		1[c]	0	0
8 occ	2	2	2	0	X	1	0		1[c]	1[c]
9 per	2	2	2	0	X	1	0	0		0
10 bol	2	2	2	0	X	1	0	0	0	

[a]Population acronyms: 1 kla, *klagesi*; 2 aris, *aristeguietana*; 3 Nort, Norte de Santander; 4 hel, *hellmayri*; 5 San, Santander; 6 UpM, upper Magdalena; 7 stri, *striaticeps*; 8 occ, *occidentalis*; 9 per, *peruviana*; 10 bol, *boliviana*. See Fig. 1 for ranges.
[b]No recordings available.
[c]Provisional because of inconsistent data.

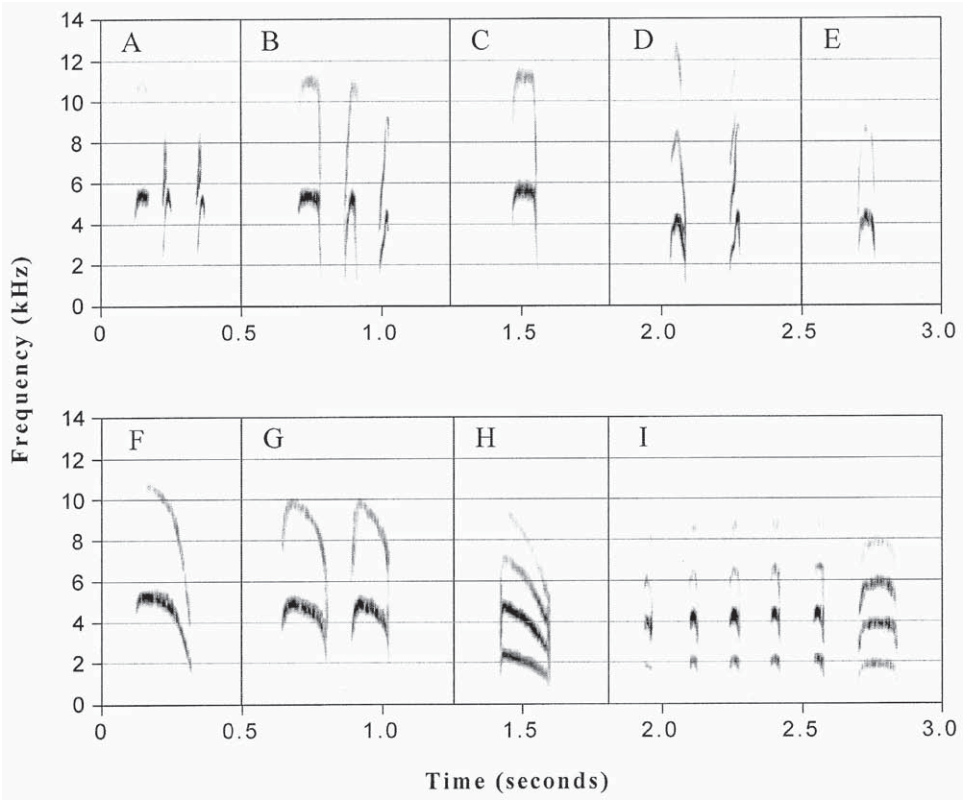

FIGURE 4. Calls of study groups in the *Drymophila caudata* complex. Acronyms for archives of recordings are translated in Appendix 2. (A) *peruviana* (clade D) short-note call. Paty Trail, Huánuco, Peru (ISL NK 007 035). (B) *striaticeps* (clade D) three-note short-note call. Reserva Natural Río Blanco, Caldas, Colombia (ISL AMC C 032). (C) *striaticeps* (clade D) one-note short-note call. Reserva Natural Río Blanco, Caldas, Colombia (ISL AMC C 032). (D) *hellmayri* (clade B) short-note call. Cuchilla San Lorenzo, Magdalena, Colombia (ISL NK C 017). (E) *klagesi* (clade A) short-note call. Rancho Grande, Aragua, Venezuela (ML 61995). (F) *striaticeps* (clade D) long-note call. El Viao, Antioquia, Colombia (ISL AMC C 021). (G) *occidentalis* (clade D) long-note call. Reserva Natural La Planada, Nariño, Colombia (BSA 10762). (H) *klagesi* (clade A) long-note call. Rancho Grande, Aragua, Venezuela (ML 61995). (I) *hellmayri* (clade B) long-note call. Reserva Natural El Congo, Magdalena, Colombia (BSA 12377).

TABLE 3. Number of vocal characters distinguishing short-note (above the diagonal) and long-note calls (below the diagonal).[a]

	1 kla	2 aris	3 Nort	4 hel	5 San	6 UpM	7 stri	8 occ	9 per	10 bol
1 kla		X[b]	X	1[c]	X	X	1[c]	1[c]	1[c]	1[c]
2 aris	X		X	X	X	X	X	X	X	X
3 Nort	0	X		X	X	X	X	X	X	X
4 hel	2[c]	X	2[c]		X	X	1[c]	1[c]	1[c]	1[c]
5 San	X	X	X	X		X	X	X	X	X
6 UpM	X	X	X	X	X		X	X	X	X
7 stri	2	X	2[c]	2[c]	X	X		1[c]	1[c]	1[c]
8 occ	2	X	2[c]	2[c]	X	X	0		0	0
9 per	2[c]	X	2[c]	2[c]	X	X	0	0		0
10 bol	2[c]	X	2[c]	2[c]	X	X	0	0	0	

[a]Population acronyms: 1 kla, *klagesi*; 2 aris, *aristeguietana*; 3 Nort, Norte de Santander; 4 hel, *hellmayri*; 5 San, Santander; 6 UpM, upper Magdalena; 7 stri, *striaticeps*; 8 occ, *occidentalis*; 9 per, *peruviana*; 10 bol, *boliviana*. See Fig. 1 for ranges.
[b]No recordings available for at least one population.
[c]Provisional because of inadequate sample size.

TABLE 4. Total number of vocal characters distinguishing populations.[a]

	1 kla	2 aris	3 Nort	4 hel	5 San	6 UpM	7 stri	8 occ	9 per	10 bol
1 kla		0	0	2 + 3[c]	X[b]	7	6 + 1[c]	8 + 1[c]	5 + 3[c]	5 + 3[c]
2 aris			0	2	X	7	4	6	5	5
3 Nort				2 + 2[c]	X	7	4 + 2[c]	6 + 2[c]	5 + 2[c]	5 + 2[c]
4 hel					X	4	4 + 3[c]	3 + 3[c]	2 + 3[c]	2 + 3[c]
5 San						X	X	X	X	X
6 UpM							4	5	4	4
7 stri								2[c]	1[c]	1[c]
8 occ									1[c]	1[c]
9 per										0

[a]Population acronyms: 1 kla, *klagesi*; 2 aris, *aristeguietana*; 3 Nort, Norte de Santander; 4 hel, *hellmayri*; 5 San, Santander; 6 UpM, upper Magdalena; 7 stri, *striaticeps*; 8 occ, *occidentalis*; 9 per, *peruviana*; 10 bol, *boliviana*. See Fig. 1 for ranges.
[b]No recordings available for at least one population.
[c]Provisional because of inadequate sample size or inconsistent data.

only found within *striaticeps*, and we considered them provisional pending further data and analysis.

ECOLOGICAL DIVERGENCE

The four principal clades identified by the phylogenetic analysis (Fig. 2) differed significantly ($F_{3,161} = 64.56$, $P < 0.001$) in the elevations at which they occur. These can be categorized into a lower-elevation group formed by the northern clades *klagesi* and *hellmayri* that occurs primarily between 500 and 1500 m (range 300–2150 m) and a higher-elevation group formed by the core Andean clades *striaticeps* and *caudata* that is distributed primarily between 1800 and 2300 m (range 1000–3150 m) (Fig. 5).

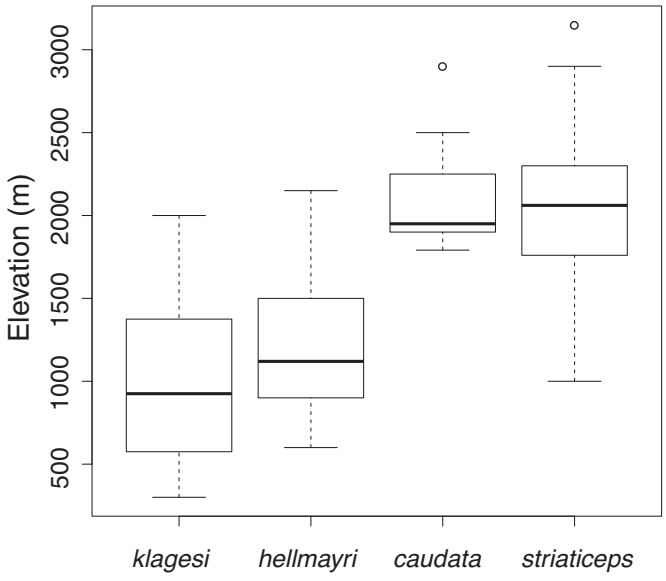

FIGURE 5. Elevational ranges of the four principal lineages in the *Drymophila caudata* complex. Nomenclature follows recommendations of this paper. Medial line denotes the median, and 2nd and 3rd quartiles delimit the box.

Within the complex based on the environmental space occupied, we found three diagnosable ecological groups, based primarily on temperature-related variables: *klagesi*, *hellmayri,* and *caudata–striaticeps* (Fig. 6). Annual mean temperature and mean temperature of the warmest quarter were the variables with highest discriminant ability. Highest values of the first discriminant function reflected localities with highest annual mean temperatures, and lowest values

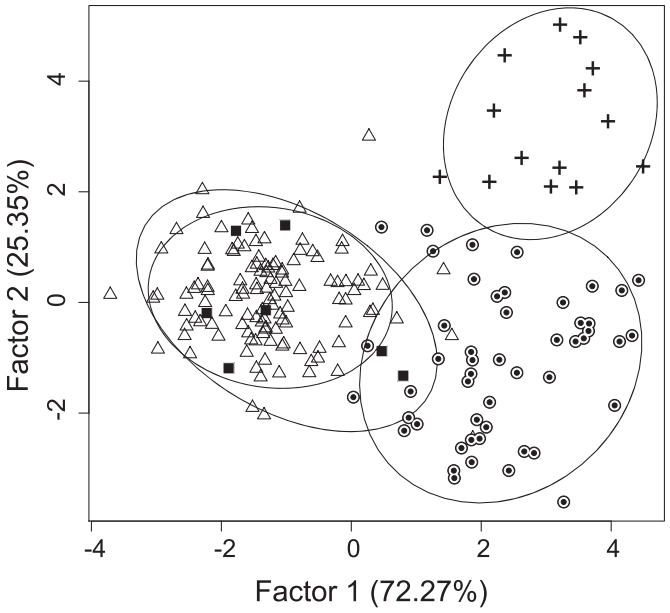

FIGURE 6. Discriminant factors for environmental variables associated with principal lineages in the *Drymophila caudata* complex. Nomenclature follows recommendations of this paper. Symbols as in Fig. 1: circles = *D. klagesi*, crosses = *D. hellmayri*, squares = *D. caudata*, triangles = *D. striaticeps*. Ellipses represent 95% confidence intervals. Both factors 1 and 2 were correlated with two variables associated with temperature (mean annual temperature and temperature of the warmest quarter of the year).

represented lowest values of the mean temperature of the warmest quarter. The second discriminant function showed the opposite pattern. No precipitation variable discriminated strongly, and precipitation of the wettest month was weakly reflected only in the second discriminant function. That the two principal discriminant functions are based only on temperature-related variables is explained by the low variability of precipitation relative to that of temperature along the Andes. Although discriminant functions are statistically independent, they can be explained by the same predictor variables if they provide variation sufficient to discriminate records among groups. Ninety-two percent of *klagesi* records (n = 50) were predicted as *klagesi,* with the remaining 8% assigned to *striaticeps*; all *hellmayri* locations (n = 14) were predicted correctly as *hellmayri*; 97% of *striaticeps* records (n = 121) were predicted as *striaticeps*, 3% as *klagesi*. Only 1 of 7 records of *caudata* was correctly predicted as *caudata*; 5 were predicted as *striaticeps*. The high predictability of assignment of samples among ecological groups (*klagesi*, *hellmayri*, *caudata–klagesi*) suggests that this procedure is likely not biased by using the same points for training and evaluation.

DISCUSSION

The vocal characters and genetic structure of *Drymophila caudata* were congruent in revealing four main populations. Examination of plumage patterns with museum specimens further confirmed the phenotypic and biogeographic correspondence of that structure. The extent of vocal differences and congruent phylogeographic and morphological distinctions calls for a taxonomic revision of *Drymophila caudata*. Some of these lineages are diverging in environmentally dissimilar forests.

SPECIES LIMITS IN *DRYMOPHILA CAUDATA*

The two syntypes of *caudata* are "Bogota" skins from Colombia purchased in Paris with no further geographic information (Sclater 1854). Therefore, taxonomic considerations must begin by deducing the geographic provenance in Colombia of the types and assigning them to one of the populations based on available vocal, genetic, and morphological samples. No male specimens of any population resemble the syntypes closely, not even other "Bogota" male specimens that were assumed to correspond to the same taxon as the syntypes of *D. caudata* (Hellmayr and Seilern 1912, Todd and Carriker 1922). Unstreaked posterior crowns and napes eliminate *striaticeps, occidentalis, peruviana,* and *boliviana* altogether (clade D), placing the types of *caudata* among northern populations, but plumages of *klagesi* (clade A) and *hellmayri* (clade B) are decidedly distinct in other respects. Museum collections lack male specimens from the Eastern Andes from Santander to the upper Magdalena valley (clade C), and it appears likely that the types of *caudata* came from somewhere in this area, probably Santander. The single dark female specimen from Santander seems like a good match for the dark, heavily streaked syntype males, given the correspondence in darkness of males and females of other populations, whereas specimens of the upper Magdalena female (n = 3) are lighter. We lack vocal recordings of the Santander population, but those of the upper Magdalena population are sufficiently distinct to warrant species status. In addition, one of the four major mitochondrial clades is constituted by the Santander and the upper Magdalena specimens, which differ by 2.1% (ND2 uncorrected p-distance) from *hellmayri* and 3.3% from *striaticeps* of the nearby Central Andes (Table 1). Mitochondrial differentiation between two specimens from the upper Magdalena and one from Santander was negligible (<0.2 %). Given current knowledge, we recommend that the Eastern Andes populations from Santander to the upper Magdalena be maintained as a single taxon, that this taxon be considered specifically distinct from all other populations in the complex on the basis of vocal and genetic differentiation, and that this taxon should retain the name *caudata*. Further specimen collections and voice recordings, especially along the Eastern Andes, a detailed study of the syntypes (see Whitney et al. 2000), and complementary molecular analysis are needed to confirm these findings.

We recommend that *klagesi* and *hellmayri* each be considered specifically distinct on the basis of differences in their vocalizations, supported by molecular and morphological distinctions. The only uncertainty regarding vocal differences stems from our having only two recordings of calls of *hellmayri*. Each recording contains a different type of call, both of which are distinct from the corresponding calls of all other populations. It seems reasonable to assume that at least one of these represents a distinct call, in which case *hellmayri* vocalizations would meet our vocal "yardstick" for species status. We found no differences in vocalizations, genetic variation, and plumage pattern between *klagesi*, *aristeguietana*, and the population in Norte de Santander. According to Aveledo H. and Pérez C. (1994), *aristeguietana* differs from *klagesi* in having a more streaked breast, duller rufous flanks, and upperparts not as dark on average. The few specimens from Norte de Santander have been ambiguously identified in the past as *hellmayri* (Meyer de Schauensee 1950) or *klagesi* (Meyer de Schauensee 1952). We recommend that *aristeguietana* Aveledo H. and Pérez C., 1994, be considered a junior synonym of *klagesi* Hellmayr and Seilern, 1912.

Populations from the Central and Western Andes in Colombia through Ecuador and Peru to Bolivia are vocally, genetically, and morphologically uniform and should be maintained as a single species, *Drymophila striaticeps*, which includes the three formerly recognized subspecies *occidentalis*, *peruviana*, and *boliviana*. Four to seven vocal characters distinguish *D. striaticeps* from *D. klagesi*, *D. hellmayri*, and *D. caudata*, and although some of these are provisional, the

preponderance of provisional characters is between the most geographically distant study groups (*hellmayri* compared to *peruviana* and *boliviana*). Morphologically, crown streaking readily distinguishes *D. striaticeps* from *D. klagesi, D. hellmayri*, and *D. caudata*, except for one male *striaticeps* in a large series from Santa Elena, Antioquia (Zimmer 1931; specimen not located or examined). Other plumage characters seem to be distinct as well but can be better characterized when larger samples are available.

Vocal differences among study groups within *D. striaticeps* were inconclusive. Short-note calls of the *striaticeps* study group differed from those of the three other study groups (*occidentalis*, *peruviana*, and *boliviana*), but the differences did not meet our statistical test of likelihood that they will be maintained with larger samples. Unlike those of other study groups within *striaticeps*, loudsongs of males of *occidentalis* lacked a clear terminal element to most raspy notes except loudsongs with and without this element have been recorded in close proximity in Dpto. San Martín, Peru. Morphologically, it appears that males of *peruviana* may have rufous flanks warmer than those of *occidentalis*, females may differ in the color of their underparts, as might males in the color and extent of the black bar on their tails, but ascertaining differences in plumage color must await careful measurement of larger samples. The pattern of genetic structure within *D. striaticeps* corresponded well to a priori study groups; however, genetic divergence among the four study groups of *D. striaticeps* was small overall (genetic distances ranged from 0.7 to 1.6 %). The shallow differentiation within *D. striaticeps* suggests genetic connectivity and recent population subdivision along the main body of the Andes. Although possible differences among the study groups suggest that some or all may be cohesive evolutionary units worthy of subspecies status (Remsen 2010), no character was unequivocally diagnostic with available material, and final consideration must await future data collection and analysis along the lines suggested by Patten and Unitt (2002).

In summary, we propose the following taxonomic positions and English names for members of the complex. Regarding the English names, we have rejected the inclusion of "long-tailed" in the names, as proposed by Cory and Hellmayr (1924), because the names would become too cumbersome. The sequence reflects the estimated phylogeny:

Drymophila klagesi Hellmayr and Seilern, 1912—Klages's Antbird. Eastern and northern Venezuela, Serranía de Perijá, and northern Eastern Andes in Norte de Santander, Colombia (includes *klagesi*, *aristeguietana*, and Norte de Santander study groups; clade A).

Drymophila hellmayri Todd, 1915—Santa Marta Antbird. Sierra Nevada de Santa Marta, Colombia (includes *hellmayri*; clade B).

Drymophila caudata (Sclater, 1854)—Long-tailed Antbird. Eastern Andes from Santander (west of the Chicamocha Canyon) to Caquetá and Huila, Colombia (includes Santander and Upper Magdalena study groups; clade C).

Drymophila striaticeps Chapman, 1912—Streak-headed Antbird. The Western and Central Andes of Colombia south through Ecuador (both slopes) and Peru (eastern slope) to northwestern Bolivia in La Paz (includes *striaticeps*, *occidentalis*, *peruviana*, and *boliviana*; clade D).

BIOGEOGRAPHY AND ECOLOGY OF ANDEAN *DRYMOPHILA* ANTBIRDS

The phylogenetic results (Fig. 2) revealed four principal lineages whose divergent vocalizations have led to our recommendation that they be elevated to species status. This phylogenetic diversity is concentrated in montane regions of northern South America, especially in Colombia, where the two geographically widespread and the two restricted species all occur (Fig. 1). *Drymophila hellmayri* and *D. klagesi* are not each other's closest relatives despite their geographic proximity; *D. hellmayri* is more closely related to *D. caudata* of the western slope of the southern Eastern Andes. In contrast, differentiation in *D. striaticeps* through the Andes from the northern Western and Central Andes in Antioquia, Colombia, to extreme southern Puno, Peru, is more subtle. We found little genetic differentiation and uncertain vocal and morphological distinctions across some prominent biogeographic barriers for Andean forest birds such as the Marañón river valley (Parker et al. 1985, Gutiérrez-Pinto et al. 2012). Specialization on the patchily distributed thickets of *Chusquea* bamboo and vegetation tangles may be associated with high vagility across putative barriers and may partially explain the low level of differentiation across the extensive region occupied by *D. striaticeps*.

The recommended species have distributions that extend over different elevational ranges and temperature conditions but over similar rainfall regimes. The higher-elevation pair of *D. striaticeps* and *D. caudata* inhabit overlapping portions of environmental space but do not overlap in temperature with the lower-elevation group formed by *D. klagesi* and *D. hellmayri*. The latter pair inhabit the same elevational range but differ in temperature-based conditions (Fig. 6). These elevational and environmental differences among species suggest that although related populations (*D. striaticeps* and *D. caudata*) may experience similar environmental conditions because they are restricted to similar elevational ranges (i.e., niche conservatism; Peterson et al. 1999), elevational range does not comprehensively explain ecological divergence (*D. klagesi* and *D. hellmayri)*.

Our phylogenetic hypothesis (Fig. 2) indicates that the two pairs of species sharing the same elevational range, one of which occupies the same environmental space, do not constitute monophyletic groups. This finding suggests that ecological shifts can take place over short periods of evolutionary time and that ecological divergence may have accompanied

speciation of the four lineages of the *D. caudata* complex, as described in other vertebrate groups (e.g., Raxworthy et al. 2007). The multidimensional results of vocal, morphological, molecular, and environmental analysis concur in revealing evolutionary isolation among these four species of Andean *Drymophila* and suggest that associated ecological, morphological, and vocal divergence may play a role in maintaining differentiation in the possible event of secondary contact.

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