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Distribution and status of *Turdus* thrushes in white-sand areas of eastern Colombia, with a new subspecies of *T. leucomelas*

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Abstract

White-sand areas in the Colombian Amazon harbor many endemic and specialist species that are relatively little studied with respect to their ecology, distribution and zoogeographic affinities, for example *Turdus* thrushes. A recent expedition to the Serranía de Chiribiquete, a mountain range of Guianan origin in the Colombian Amazon, resulted in the discovery of an enigmatic *Turdus* thrush restricted to white-sand vegetation. Molecular phylogenetic analyses of the ND2 gene revealed that this population is genetically similar to *T. leucomelas albiventer*, from which it differs in its smaller size and darker, duller plumage. Therefore, we here describe this population as a new subspecies of *T. leucomelas.* Furthermore, our inspection of specimens of *Turdus* taxa from eastern Colombia revealed the existence of sympatry between *T. ignobilis debilis* and *T. i. arthuri* at two sites. Based on this evidence and previously documented genetic and phenotypic differences, we recognize *T. arthuri* as a distinct biological species. We analyze distributions and measurements of functional traits among four thrush taxa of eastern Colombia.

Key words: endemism, Guiana shield, habitat specialization, species delimitation

Introduction

The Pale-breasted Thrush *Turdus leucomelas* (Vieillot, 1818) has a wide distribution in South America, inhabiting a variety of semiopen habitats from the borders of humid forest, brushy savannas and scrublands to suburban and urban parks. Over most of its distribution, it has been divided into two rather weakly defined subspecies: *T. l. albiventer*, Spix, 1824 of Colombia, Venezuela and the Guianas to northeastern Brazil, and nominate *leucomelas* from southeastern Brazil to eastern Bolivia, Paraguay, Uruguay and northern Argentina; in addition, an isolated population at the humid tip of the otherwise desertic Guajira Peninsula (ca. 12ºN) constitutes a third subspecies, *T. l. cautor* Wetmore, 1946 (Collar 2004) (Fig. 1A). Therefore, the discovery of a population of *T. leucomelas* in the Serranía de Chiribiquete, over 100 km south of previous Colombian records, is interesting and worthy of further study.

The Serranía de Chiribiquete represents the most prominent outcropping of ancient rocks of the Guiana Shield in Colombia, with its spectacular landscape of table-top mesas and buttes recalling the tepuis of southern Venezuela. The tallest of these mountains reach 700–800m, erosion of which has produced white-sand soils supporting savannas, brushlands and forests floristically akin to those of the Venezuelan tepuis (Estrada & Fuertes 1983). The tallest forests, along the major rivers draining this area, include many species of Amazonian affinities among both the flora and the avifauna. However, the brushlands or matorrales and lower forests of the middle levels and the tops of the broader mesas support a biota of predominantly Guianan elements (Estrada & Fuertes 1983; Stiles *et al.* 1995; Alvarez *et al.* 2003; Stiles & Naranjo 2018). The striking landscape and topography of the Serranía stimulated its declaration as Chiribiquete National Park in 1989, although knowledge of its flora was based only upon the explorations and collections of R. E. Schultes in the 1940s (cf. Estrada & Fuertes 1983), and its fauna was virtually unknown.

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The Serranía was previously accessible only via laborious river journeys, such as that by Schultes (see Davis 2001); its avifauna only began to receive study half a century later. In 1990 the Fundación Puerto Rastrojo established a field station at Puerto Abejas (0º24'N, 72º27'W) on the Río Mesay, at the southern extreme of the Serranía, and in 1992 began an inventory of the avifauna with a program of bird collecting. The first specimen of *T. leucomelas* from the Serranía was collected in March 1993 and was notable for its dark coloration overall and small size. Concurrently, the advent of helicopter travel made it possible to visit the mesas of the northern Serranía, and three Spanish-Colombian expeditions between 1990 and 1992 made more extensive studies of the flora (Estrada & Fuertes 1993). The third expedition in late November 1992 produced the first inventory and collection of the birds of these formations (Stiles *et al.* 1995) from a tepui at 0º56'N, 72º40'W, including descriptions of three new taxa (Stiles 1995, 1996). River expeditions by personnel of the Fundación Puerto Rastrojo and the Instituto Alexander von Humboldt between 1998 and 2000 (Álvarez *et al.* 2003) produced three more specimens of *Turdus leucomelas* from the southern sector of Chiribiquete between 0º30' and 1º11'N, all similar in coloration and size to the first. Finally, the last of three expeditions in 2015–2017, using helicopter transport to reach previously unexplored areas of the central and northern sectors of the Serranía, permitted further observations of *T. leucomelas,* definition of its preferred habitat and the collection of two more specimens.

Here we describe this new subspecies as *T. l. upichiarum* and discuss the distributions and taxonomic status of the *Turdus* thrushes of white-sand vegetation in Colombia. We also present morphological data for these thrushes and describe how these data might bear on habitat associations and sympatry among them.

Methods and materials

Field and museum methods.—Observations of *T. leucomelas* during the recent expeditions (November 2015, June 2016 and February 2017) were made by FGS and L. G. Naranjo (Stiles & Naranjo 2018), and on the third of these, FGS collected two *T. leucomelas* in the northern sector of the Serranía (1º21'N,72º54'W; Fig. 1). Later, FGS surveyed all sexed specimens of this species from eastern Colombia in the collections of the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia and the Instituto Alexander von Humboldt to evaluate possible morphological differences between the Chiribiquete birds and those of other Colombian populations. Measurements of total culmen, commissure width, height of bill at nostril, length of closed unflattened wing, tail and tarsus were taken on museum specimens to 0.1 mm with dial calipers; data on body masses were taken when available from the labels of specimens. We also measured specimens of two other *Turdus* taxa found with *T. leucomelas* in some sites in eastern Colombia. We first compared males and females of all taxa with *t*-tests (not shown) to determine whether sexual differences exist in any measured variable. In all taxa, males averaged significantly larger than females in wing and tail lengths but not in measurements of bills or tarsi; on the other hand, females averaged heavier than males (Table 1; see also Supplementary Material Tables S1–3). We used one-way ANOVA to analyze data for measurements of bill and tarsus for both sexes combined, and for each sex separately for wing and tail lengths; because of the wide variation between individuals and the smaller sample sizes, the ANOVA did not detect any significant differences between taxa in body mass. We also conducted a Principal Components Analysis (PCA) for a view of the morphometric differences between species in multivariate space. All tests were made with the PAST 3.0 package (Hammer *et al.* 2001). Color comparisons were made with the color standards of Smithe (1975).

Molecular genetic analysis.—Preliminary phylogenetic analyses (not shown) of sequences of the ND2 mitochondrial gene (1041 pb) from tissue samples of the two specimens of *T. l. upichiarum*, together with 182 published sequences of 26 South American *Turdus* species (Klicka *et al.* 2005; Voelker *et al.* 2007; Nylander *et al.* 2008; O'Neill *et al.* 2011; Cerqueira *et al.* 2016; Núñez-Zapata *et al.* 2016; Avendaño *et al.* 2017) revealed that Chiribiquete birds were closely related to *T. leucomelas* samples from Bolivia (n=2), Brazil (n=3) and Guyana (n=1). Based on these data, we restricted our phylogenetic analyses here to *T. leucomelas* and expanded our geographic sampling by including seven *albiventer* specimens from the Orinoco basin plus an additional sample of *T. l. upichiarum* (Table 2). We estimated ND2 gene trees using Maximum likelihood and Bayesian inference using HKI+G (1st codon) and TrN (2ndand 3rd codons) as the best-fit models of molecular substitution in a three-partition scheme according to the Bayesian Information Criterion implemented in Partition Finder v.1.10 (Lanfear *et al.* 2012). The most likely tree was inferred in RAxML-HPC2 on XSEDE v8.2.10 (Stamatakis 2014), assessing nodal

support through 1000 bootstrap pseudoreplicates. Bayesian inference was implemented in MrBayes on XSEDE v3.2.6 (Ronquist & Huelsenbeck 2003). The analysis included one cold chain and three heated chains with a temperature of 0.175, and four runs, which were run for 30 million generations, sampling trees each 1000 generations. MCMC chain convergence of parameters were assessed in Tracer v1.6 (Rambaut *et al.* 2003), by checking effective sample sizes ≥ 200. The first 7500 trees were discarded as burn in, whereas the remaining 22501 trees were used to reconstruct a single 50% majority rule consensus tree. We selected as outgroups *T. fumigatus* Lichtenstein,1823 and *T. hauxwelli* Lawrence, 1870 which are part of the same clade with *T. leucomelas* (Voelker *et al.* 2007; Nylander *et al.* 2008), plus *T. arthuri* (Chubb, 1914), *T. ignobilis debilis* Hellmayr, 1902 and *T. albicollis phaeopygus* Cabanis, 1848, which are sympatric with the new taxon (see below). This last species had been found to be paraphyletic with respect to Amazonian populations of *T. leucomelas* (Tavares *et al.* 2011). Genetic relationships between the new form and other populations of *T. leucomelas* were analyzed using a median-joining haplotype network in the software PopArt (Leigh & Bryant 2015), and calculated uncorrected-*p* distances among taxa in MEGA6 (Tamura *et al.* 2013) using a partial deletion option.

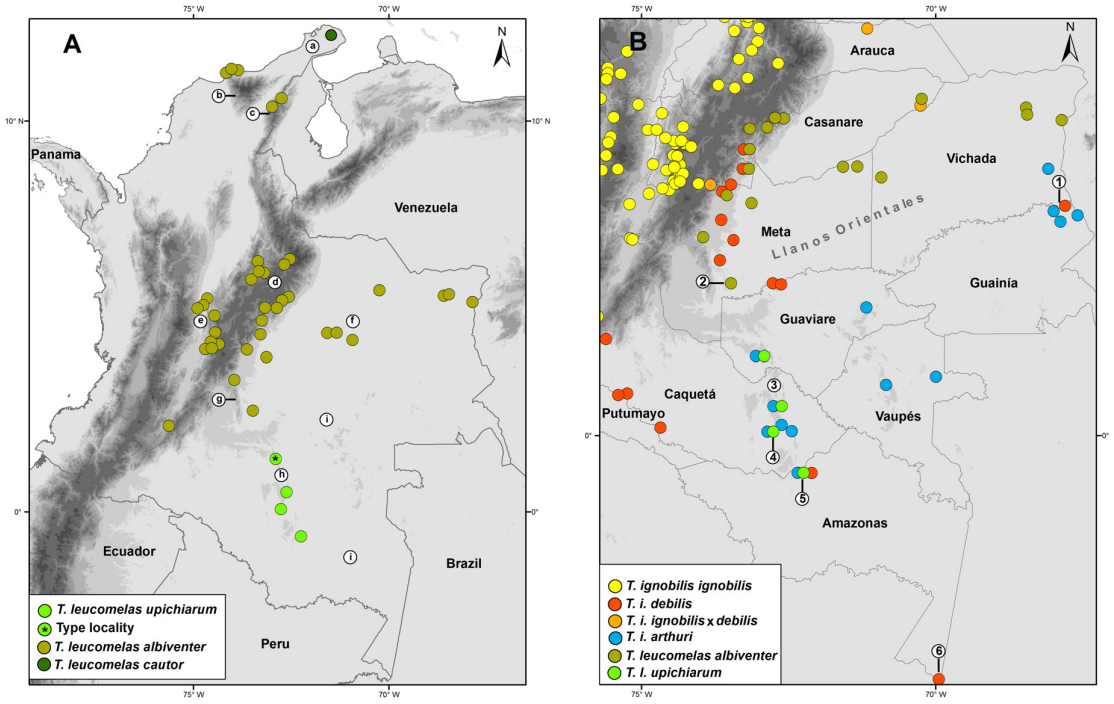

FIGURE 1. Map of Colombia, showing the geographic origin of specimens and tissue samples of *Turdus* thrushes analyzed in this study. **A.** Distribution of *Turdus leucomelas* in Colombia. *T. l. upichiarum* is restricted to the Serranía de Chiribiquete and Araracuara, whereas *T. l. albiventer* is found across the Orinoco basin and trans-Andes and *T. l. cautor* is limited to the humid tip of the Guajira Peninsula. The regions mentioned in this study are listed from north to south as follows: a. the Guajira Peninsula; b. the Santa Marta region; c. Serranía de Perijá; d. Eastern Andes; e. Magdalena River valley; f. Llanos Orientales; g. Serranía de la Macarena; h. Serranía de Chiribiquete (the star denotes the type locality of *T. upichiarum*); i. forested Amazonian lowlands. **B.** Distribution of four *Turdus* thrushes in eastern Colombia. Localities specifically mentioned are numbered north to south as follows; 1. Inírida; 2. Guayabero River; 3. Chiribiquete; d. Puerto Abejas and vicinity; g. Araracuara; h. Leticia. Nominate *T. ignobilis* occurs on the western slope of the Eastern Andes and usually at somewhat higher elevations than *T. i. debilis*, but we note several sites where possible intergrades between them exist. *T. arthuri* occurs rather widely in eastern Colombia, and is sympatric with *T. i. debilis* at Araracuara and Inírida, and with *T. l. upichiarum* in Chiribiquete and Araracuara.

Results

Phylogenetic analyses confirmed the identity of the Chiribiquete birds as *T. leucomelas* because they formed a well-supported clade with other *T. leucomelas* samples (PP=1.0; 100% bootstrap support; Fig. 2). Chiribiquete birds were found to have a single haplotype, which is shared with one *albiventer* individual from Guyana and three

albiventer individuals from Casanare and Meta departments in the Llanos Orientales of Colombia. Samples of *T. albicollis* from Colombia formed a well-supported clade that was more closely related to *T. albicollis* samples from Bolivia and Argentina than to *T. leucomelas* (Fig. 2).

Measurements of 41 specimens from throughout the eastern Colombian range of *T. leucomelas* showed that the Chiribiquete birds averaged smaller in nearly all parameters, these differences being significant for wing (males only) and tarsus lengths and bill height (Table 3, Figs. 3 and 4); a larger sample of *upichiarum* would be desirable to confirm these differences. In the course of examination of these specimens, an additional specimen of *T. leucomelas* similar to those of Chiribiquete was discovered, included in a series of specimens labeled as *T. ignobilis debilis* (Hellmayr, 1902) collected by H. Romero in September 1978 at Araracuara (0°34'S, 73°24'W), still further south from other known populations of this species (Fig. 1B). Color comparisons also demonstrated differences of these southern populations, justifying their recognition as a new subspecies, which we name

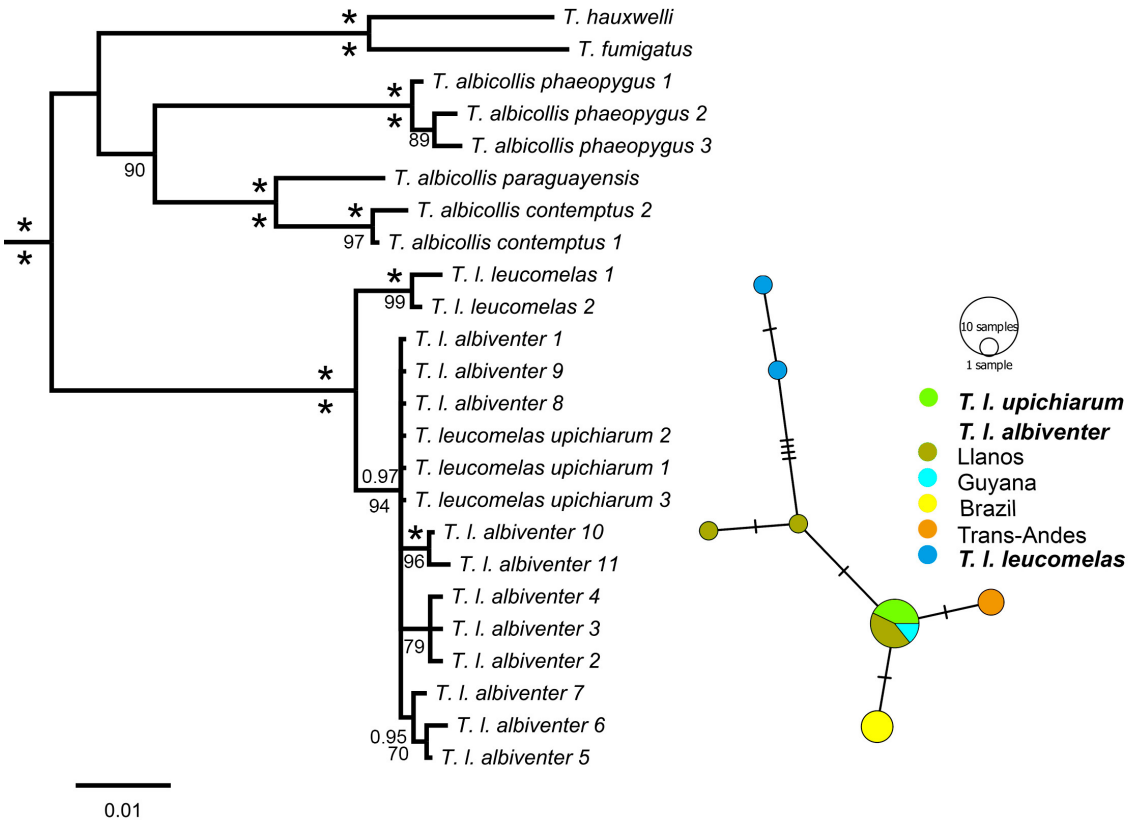

FIGURE 2. Bayesian tree based on ND2 sequences showing phylogenetic relationships between *T. l. upichiarum* and other *T. leucomelas* from South America. Bayesian posterior probabilities (PP) and maximum likelihood bootstrap values are indicated above and below nodes, respectively, with asterisks indicating maximum values (PP=1.0; bootstrap support= 100). Numbers in front of taxon names refer to sample data in Table 1. The median-joining haplotype network depicts shallow genetic divergence and haplotypes (circles) shared among *T. leucomelas* from several regions (colors). The size of each circle denotes the number of samples per haplotype. Vertical bars represent the number of substitutions among haplotypes. Note that three *T. l. upichiarum* share the same haplotype with samples from the Llanos Orientales and Guyana.

***Turdus leucomelas upichiarum*, ssp. nov.**

Holotype. ICN no. 39668 (Fig. 3), adult male, collected by F. G. Stiles on 21 February 2017 (original number FGS 4652). Skull 100% ossified, trace of fat. Left testis 15x9, right 9x7 mm; large cloacal protuberance; plumage fresh, no molt. Stomach contents: 3 brown, round seeds ca. 8 mm diameter, green fruit pulp (Lauraceae). A tissue sample (breast muscle) was saved (now in Uniandes: Andes-T 2662); no voice recordings were made.

FIGURE 3. Plumage variation among populations of *T. leucomelas* from eastern Colombia. From left to right: *T. l. albiventer*, male ICN 38400, Meta, Villavicencio, vereda La Llanerita, finca Villa Oria; male ICN 30851, Cundinamarca, Medina, San Francisco de Gazaduje, finca Serranía los Alpes; *T. l. upichiarum*, male ICN 39668 (Holotype) and female ICN 39667, Guaviare, Calamar, PNN Serranía de Chiribiquete, caño Negro; *T. l. upichiarum*, female ICN 24696 (Paratype), Amazonas, Araracuara, río Caquetá. Note the overall darker coloration of *T. l. upichiarum* compared with the contrasting gray and brown upperparts and brighter brown to rufescent wing coverts and primaries in *T. l. albiventer*.

Type locality. Colombia: department of Guaviare: municipality of Calamar: beside the caño Negro (1º21'N, 72º54'W; Fig. 1), a large creek at an elevation of 470 m, in rolling terrain in the northern sector of the Serranía in Chiribiquete National Park, in dense shrubby matorral dominated by the shrubs *Bonnetia sessilis, Senfelderopsis chiribiquetensis* and *Clusia columnaris* of heights between 2 and 3 m: this is the most extensive habitat of the Serranía at middle and upper elevations (Cárdenas *et al* 2018).

Diagnosis. Distinguished from *T. a. albiventer* by the following characteristics: overall size smaller with significantly shorter tarsi, lesser bill height and (males only) wing length (Table 3, Fig. 2); these parameters, and also culmen and tail length, showed little overlap (Table 1, Figs. 3–4); overall darker and more uniform coloration, with less contrast between the gray of the crown and the back, which in *albiventer* is brighter brown; little or no difference between the color of the back and the shoulders, wing coverts and margins of the outer primaries, which are brighter brown to rufescent in *albiventer;* the dark streaks of the throat browner, less blackish and averaging less heavy; anterior wing linings darker rufous; underparts averaging darker gray, especially on the chest and flanks. Distinguished from other sympatric *Turdus* species (*T. arthuri, T. ignobilis debilis*) by the rufous wing linings and bill color (not black, but dark horn color with yellowish tomia); additionally, from the latter by the grayer, less brownish chest, much less extensive white on the abdomen and with the white of the throat not extending beyond the dark streaks onto the upper chest, and by its longer wing and tail.

Description of the holotype. Iris chestnut; bill dark horn color, shading to blackish at base of culmen and dull yellowish on tomia; tarsi and feet dark horn color. Throat white, streaked with dark Brown (near 119B, Dark Drab); chest brownish gray (between 79 and 80, Glaucous), tinged brownish (27, Drab); passing to paler brownish gray (near 27, Drab but grayer) over the lower breast and abdomen; lower medial abdomen and crissum whitish, washed brownish (119D, Drab Gray). Upperparts and tail dark brown, tinged gray (near 119a, Hair Brown); feathers of hindcrown and nape slightly grayer. Outer webs of middle primaries slightly paler (near 27, Drab); wing linings rufous (near 340, Robin Rufous, or slightly darker anteriorly, slightly paler posteriorly); inner webs of secondaries edged pale dull rufous. Total culmen 21.6, commissure width 12.5, bill height 6.0, wing length 115.4, tail length 86.3, tarsus length 30.3 (all measurements in mm), body mass 59.6 g.

Variation among the type series. Seven specimens comprise this series: ICN 39667, adult female, collected in the same net as the type and probably its mate; ICN 33202 and IAVH-A 10770, adult females, both from Puerto Abejas, IAVH-A 11452 and 11562, adult males, from the Cuñare-Amú River on the southeastern edge of the Park; and ICN 24696, adult female, from Araracuara, some 89 km southeast of the Serranía. These specimens present an aggregate distribution between 1º21'N and 0º34'S, and 72º27'and 72º57'W. Most of the seven specimens agree closely with the holotype in coloration; the most divergent is ICN 39667 (Fig. 3), which is decidedly paler on the chest (between Drab 27 and Light Drab 119c), although it agrees in its dorsal coloration and measurements with the rest of the type series (Table S1).

Etymology. The name for the new taxon commemorates the indigenous Upichía tribe, who were possibly the first to inhabit the Chiribiquete area. This tribe, already reduced by disease during the colonial period, was further decimated and dispersed by the slave-labor practices of the rubber trade of the late 19th and early 20th centuries and is presently being absorbed into the more numerous Yukuna peoples. Their language, Matapí, is now all but extinct; some of their lore and worldview was expressed by Matapí-Yukuna (2018), who noted that their name for Chiribiquete, *mejeime meme*, translates to "echoes of silence", evocative of its impressive and remote landscape.

Discussion

An overview of Turdus leucomelas in Colombia.—Nearly the entire range of the species in Colombia is occupied by *T. l. albiventer,* from the northeastern Caribbean lowlands and the foothills of the Sierra Nevada de Santa Marta (ca. 11ºN), south through the lowlands and adjacent foothills of the Magdalena Valley to central Huila (2º18'N). East of the Andes, *albiventer* occurs from Norte de Santander (ca. 8ºN), Arauca (ca. 7ºN) and Vichada (ca. 6º30'N) south and west through the Llanos Orientales to the vicinity of the Serranía de la Macarena (ca. 2º10'N) along the río Guayabero (Olivares 1962); (Fig. 1A). Locally this race extends upwards in the adjacent foothills of the Andes to ca. 1000–1600m. Throughout its extensive range, *albiventer* shows little geographic and local variation in measurements and plumage. In plumage, occasional individuals with darker gray breasts occur throughout this distribution, approaching the color of *upichiarum,* although differing from the latter consistently in the brighter, more contrasting colors of the wings and the gray of the crown and nape, as well as being larger in most parameters (Table 1, Fig. 2).

South of the southern limits of *albiventer* is a zone of ca. 80–100+ km of humid Amazonian forest from which *T. leucomelas* has not been recorded. Beyond this, the subspecies *upichiarum* occurs throughout the Serranía de Chiribiquete (from ca. 1º26'N to 0º24'S), the northern extreme of which is ca. 120 km SE of the southern limit of *albiventer*, as well as at Araracuara along the Río Caquetá, some 80 km further SE of Chiribiquete (0º34'S) (Fig.1B). Vegetation data from Araracuara (Arbeláez & Callejas 1999; Duque Montoya 2004) indicate the existence there of matorral with a flora of Guianan affinities, similar in composition and stature to that of Chiribiquete. Moreover, another species of *Turdus* of Guianan affinities, *T. arthuri*, occurs sympatrically with *T. l. upichiarum* both in Chiribiquete and at Araracuara. The discovery of several individuals of *arthuri* among the series of thrushes collected by H. Romero at Araracuara in 1978 stimulated us to compile the records of *arthuri* as well as those of *T. ignobilis debilis* from Colombia.

Distributions of Turdus thrushes in "white-sand" areas of eastern Colombia.—Turdus arthuri was described by Chubb from the slopes of Mt. Roraima in southeastern Venezuela and evidently occurs rather widely in this region (Hilty 2002; Cerqueira *et al.* 2016) as well as in Brazil (Borgia *et al.* 2016), but its occurrence in Colombia appears to have been entirely overlooked by nearly all previous authors (Hellmayr 1934; Deignan *et al.* 1964; Hilty & Brown 1986; Cerqueira *et al.* 2016) although Stiles (unpubl. data) had tentatively identified specimens from eastern Guainía and eastern Vaupés as this taxon based upon an examination of the series of *arthuri* in the American Museum of Natural History. *Turdus arthuri* was widely considered to represent a subspecies of *T. ignobilis* Sclater, 1857 until Cerqueira *et al.* (2016) recognized it as a separate species. These authors also separated *T. i. debilis* from *T. ignobilis* based on color differences (browner overall, especially below, with a different throat pattern), but they also were unaware of the Colombian distribution of *debilis*, and did not include genetic data from nominate *ignobilis*! Because both *debilis* and *arthuri* are lowland birds, Cerqueira *et al.* (2016) considered them to be more closely related to each other than either was to the more montane *ignobilis.* A more thorough genetic analysis with better sampling of these forms by Avendaño *et al.* (2017) demonstrated that *ignobilis, goodfellowi* (a transandean subspecies of *ignobilis*) and *debilis* formed a compact clade, and there exist several specimens possibly showing intergradation between the nominate and *debilis* (Fig. 1B), such that the separation of the latter from *ignobilis* by Cerqueira *et al.* (2016) was unjustified. Moreover, *Turdus murinus* Salvin, 1885 of the tepuis of Venezuela, included in *ignobilis* as a subspecies based on plumage similarities and its more montane distribution, was shown to be genetically distant and clearly a distinct species. The long-standing but erroneous inclusion of *murinus* as a subspecies *of T. ignobilis* explained the supposedly parapatric nature of *ignobilis.* Avendaño *et al.* (2017) included *arthuri* as a subspecies of *ignobilis*, but confirmed considerable genetic differences between *arthuri* and *debilis*; they declined to separate them at the species level because evidence for sympatry was lacking.

Our analysis has clarified this situation. First, *T. i. debilis* occupies a wide range in eastern Colombia, inhabiting open and semiopen areas of the foothills of the Eastern Andes from Arauca south to Putumayo as well as Leticia on the Amazon River, and into the adjacent lowlands of the Llanos east to the Orinoco River and along major rivers further south, possibly following the opening of the forests by human settlements (Fig. 1B). *Turdus arthuri* also occurs widely in eastern Colombia, but always in savannas and brushland and along forest edges over white sand soils originating from the erosion of Guianan Shield rocks. Localities from which specimens or field observations of *T. arthuri* come include several sites in Vichada, Guainía (the area of Inírida), Vaupés (vicinity of Mitú), Chiribiquete (several sites in Caquetá and Guaviare), Guaviare (Reserva Indígena Nukak-Maku, east of Chiribiquete), and Araracuara (on the border between Guaviare and Caquetá) (Fig. 1B). In an inventory of the birds of Araracuara, the only thrush listed by Cuadros (1993) was *T. i. debilis*, perhaps because the thrushes collected there by Romero in 1978 were all originally labeled as this taxon. However, upon detailed examination this series was found to include four *arthuri,* seven *debilis* and one *T. l. upichiarum*. This definitively proves the sympatry of *arthuri* and *debilis* (Fig. 6), thus justifying the separation of the former as a distinct species: moreover, sympatry of these two was also detected in specimens from Inírida in Guainía (Fig. 1B). It also substantiates the association of *arthuri* and *upichiarum* with the matorral habitat on white-sand soils in Chiribiquete and Araracuara. Given its wide distribution, *arthuri* apparently has a longer history of association with this habitat, whereas that of *T. l. upichiarum* appears to be more recent given its more restricted distribution and genetic affinities with *T. l. albiventer*, and probably represents a late Pleistocene colonization. In any case, the apparent coexistence of two or three species of *Turdus* at some Amazonian sites is of particular interest, and merits detailed study of the ecology and habitat use of these birds.

TABLE 1. Summary of measurements in mm of four *Turdus* thrushes of eastern Colombia; body mass in g.

Sex	N	Statistic	Total culmen	Commissure width	Height of bill at nostril	Length of folded wing	Length of tail	Length of tarsus	Body mass	N (body mass)
Turdus leucomelas albiventer										
♂♂	17	Mean	21.94	12.11	6.26	116.34	89.86	30.92	58.84	9
		SD	0.70	0.40	0.38	3.63	5.15	1.28	3.90	
		Range	20.8–23.2	12.0–12.3	5.7–7.2	110.3–123.5	81.3–96.3	28.8–33.7	54.3–64.9	
♀♀	17	Mean	21.76	11.98	6.37	112.89	85.15	31.24	66.25	6
		SD	0.93	0.44	0.30	3.14	2.82	0.93	7.62	
		Range	19.9–22.9	11.1–12.8	5.8–6.8	108.9–119.3	80.7–90.0	30.0–33.3	51.8–73.4	
Turdus leucomelas upichiarum										
♂♂	4	Mean	21.20	12.28	6.10	110.08	85.35	29.65	57.15	4
		SD	0.81	0.26	0.37	4.11	5.35	0.74	3.50	
		Range	19.9–21.6	11.9–12.5	5.7–6.6	106.5–115.4	79.1–92.0	19.7–30.3	52.0–59.6	
♀♀	3	Mean	21.13	12.13	6.27	108.30	84.93	29.90	59.05	2
		SD	0.61	0.15	0.25	3.70	2.60	0.26	1.48	
		Range	20.6–21.8	12.0–12.3	6.0–6.5	105.0–112.8	82.4–87.6	29.7–30.2	58.0–60.1	
Turdus arthuri										
♂♂	16	Mean	20.24	11.63	5.99	109.20	79.25	30.49	56.53	10
		SD	0.74	0.32	0.38	2.20	2.32	0.69	3.90	
		Range	19.1–21.9	11.1–12.3	5.2–6.6	104.7–113.0	75.8–84.0	28.8–31.2	51.5–65.0	
♀♀	10	Mean	20.33	11.45	5.96	105.20	76.51	30.63	62.5	4
		SD	0.81	0.53	0.17	3.58	1.56	0.60	5.20	
		Range	18.8–21.4	10.4–12.0	5.8–6.1	100.4–111.9	74.7–79.6	29.8–31.5	55.0–66.0	
Turdus ignobilis debilis										
♂♂	22	Mean	19.93	11.34	5.78	107.84	78.12	28.87	55.73	13
		SD	0.69	0.43	0.34	3.91	2,68	0.90	1.94	
		Range	18.5–21.4	10.8–12.3	5.3–6.3	101.6–114.6	71.2–83.0	27.7–30.8	48.0–65.1	
♀♀	17	Mean	19.69	11.29	5.79	104.44	74.30	28.38	58.03	5
		SD	0.70	0.37	0.36	4.10	3.30	0.92	4.55	
		Range	18.8–21.3	10.8–11.8	5.3–6.2	98.2–110.2	68.9–78.4	27.5–30.2	50.3–62.3	

TABLE 2. Data on taxon, voucher, locality and Genbank accession numbers of *Turdus* thrushes used in phylogenetic analyses. DNA sequence sources: [a]O'Neill *et al.* (2011); [b]Bates *et al.* (2003); [c]Voelker *et al.* (2007); [d]Cerqueira *et al.* (2016); [e]Avendaño *et al.* (2017); [f]Núñez-Zapata *et al.* (2016).

Taxon	Voucher	Locality	GenBankaccession no.
T. leucomelas albiventer 1	LSUMNS B48579	Guyana	JN049524[a]
T. l. albiventer 2	MPEG ch303	Brazil: Amapá, Tartarugalzinho, Fazenda São Bento	AY115445[b]
T. l. albiventer 3	MPEG ch069	Brazil: Amapá, Porto Grande, Fazenda Teimoso	AY115446[b]
T. l. albiventer 4	MPEG ch224	Brazil: Amapá, Tartarugalzinho, Lago Cujubim	AY115447[b]
T. l. albiventer 5	IAvH-A 12873	Colombia: Vichada, Cumaribo, Cgto. Santa Rita, PNN El Tuparro, río Tomo	MG950240
T. l. albiventer 6	IAvH-A 12874	Colombia: Vichada, Cumaribo, Cgto. Santa Rita, PNN El Tuparro, río Tomo	MG950241
T. l. albiventer 7	UMNG-JEA1074	Colombia: Casanare, Aguazul, vereda San Lorenzo, finca San Lorenzo	MG950242
T. l. albiventer 8	ICN 37770	Colombia: Casanare, Trinidad, vereda La Esperanza, finca Canta Claro	MG950243
T. l. albiventer 9	MHNU-O 406	Colombia: Meta, Puerto Gaitán, vereda San Miguel, finca Mitimiti	MG950244
T. l. albiventer 10	ICN 37156	Colombia: Cesar, Manaure, vereda San Antonio, finca Villa Luz	MG950245
T. l. albiventer 11	IAvH-A 13976	Colombia: Cundinamarca, Puerto Salgar, Laguna del Coco	MG950246
T. l. upichiarum 1	ICN 39668	Colombia: Guaviare, Calamar, PNN Serranía de Chiribiquete, caño Negro	MG950247
T. l. upichiarum 2	ICN 39667	Colombia: Guaviare, Calamar, PNN Serranía de Chiribiquete, caño Negro	MG950248
T. l. upichiarum 3	IAvH-A 11452	Colombia: Caquetá, río Cuñare, Chorro del Acuario	MG950249
T. l. leucomelas 1	LSUMNS B14694	Bolivia: Santa Cruz, Serranía de Huanchaca, 21 km SE Catarata Arco Iris	AY115448[b]
T. l. leucomelas 2	LSUMNS B14719	Bolivia: Santa Cruz, Serranía de Huanchaca, 21 km SE Catarata Arco Iris	DQ911086[c]
T. fumigatus	STRI SV-TFU1	St. Vincent	DQ911076[c]
T. hauxwelli	MPEG 70045	Brazil: Acre, Feijó, Rio Jurupari, margen esquerda, Novo Oriente	KU569386[d]
T. arthuri	IAvH-A 11460	Colombia: Caquetá, PNN Serranía de Chiribiquete, río Cuñaré	KY806842[e]
T. ignobilis debilis	ICN 38050	Colombia: Meta, Cumaral, Cuacavía, Reserva Natural Kaliawirinae	KY806836[e]
T. albicollis phaeopygus 1	IAvH-A 11484	Colombia: Caquetá, río Cuñare, Chorro del Acuario	MG950250
T. a. phaeopygus 2	IAvH-A 14340	Colombia: Vichada, Cumaribo, selva de Mataven, Caño Cajaro	MG950251
T. a. phaeopygus 3	IAvH-A 12777	Colombia: Vichada, Cumaribo, Cgto. Santa Rita, PNN El Tuparro, Bosque asociado al cerro Peinilla	MG950252
T. a. contemptus 1	LSU B22690	Bolivia: La Paz	DQ911063[c]
T. a. contemptus 2	AMNH-DOT 2688	Bolivia: La Paz	KX077545[f]
T. a. paraguayensis	AMNH-DOT 2444	Argentina: Misiones	KX077546[f]

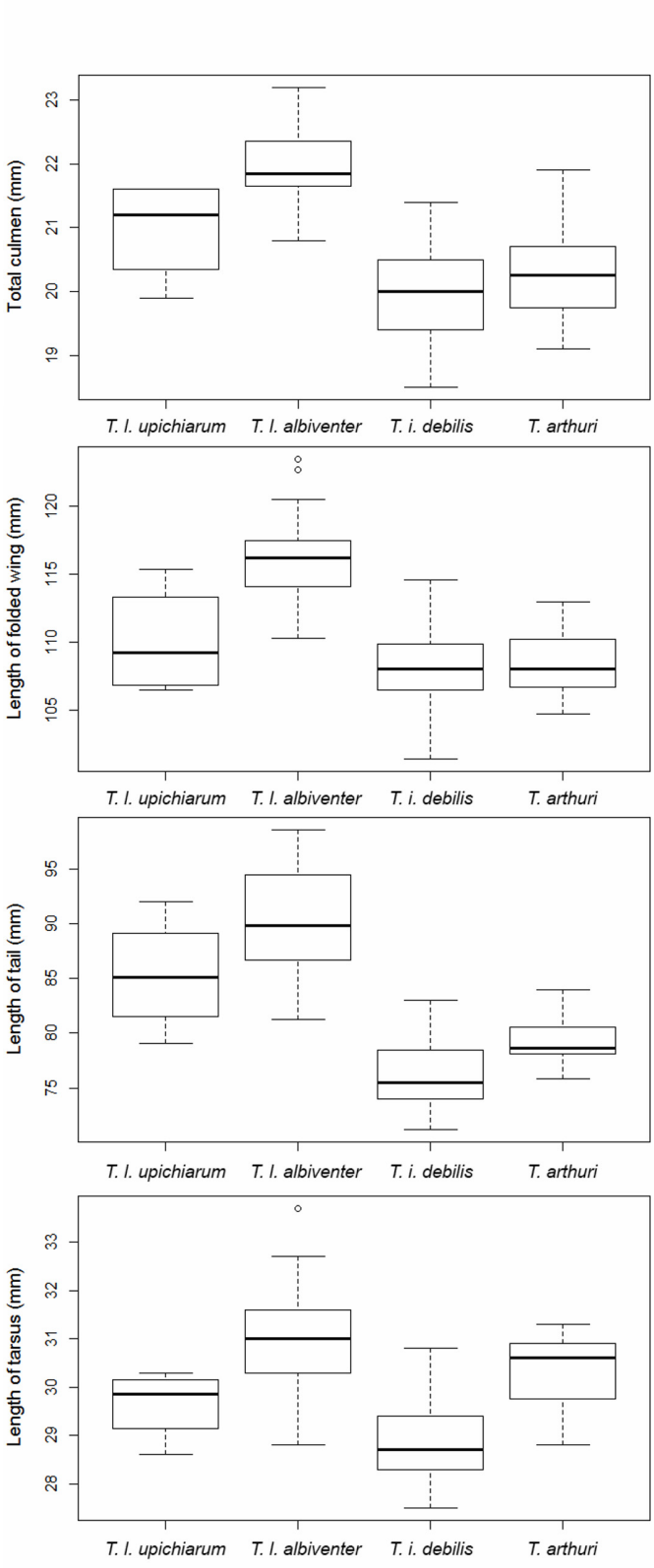

FIGURE 4. Morphological comparisons among four *Turdus* thrushes found in eastern Colombia. Note the smaller size overall of *T. l. upichiarum* with respect to cisandean *T. l. albiventer*. *Turdus i. debilis* and *T. arthuri* show similar morphology, except for the longer tail and tarsi of the latter. Medial line denotes the median, and 2nd and 3rd quartiles delimit the box.

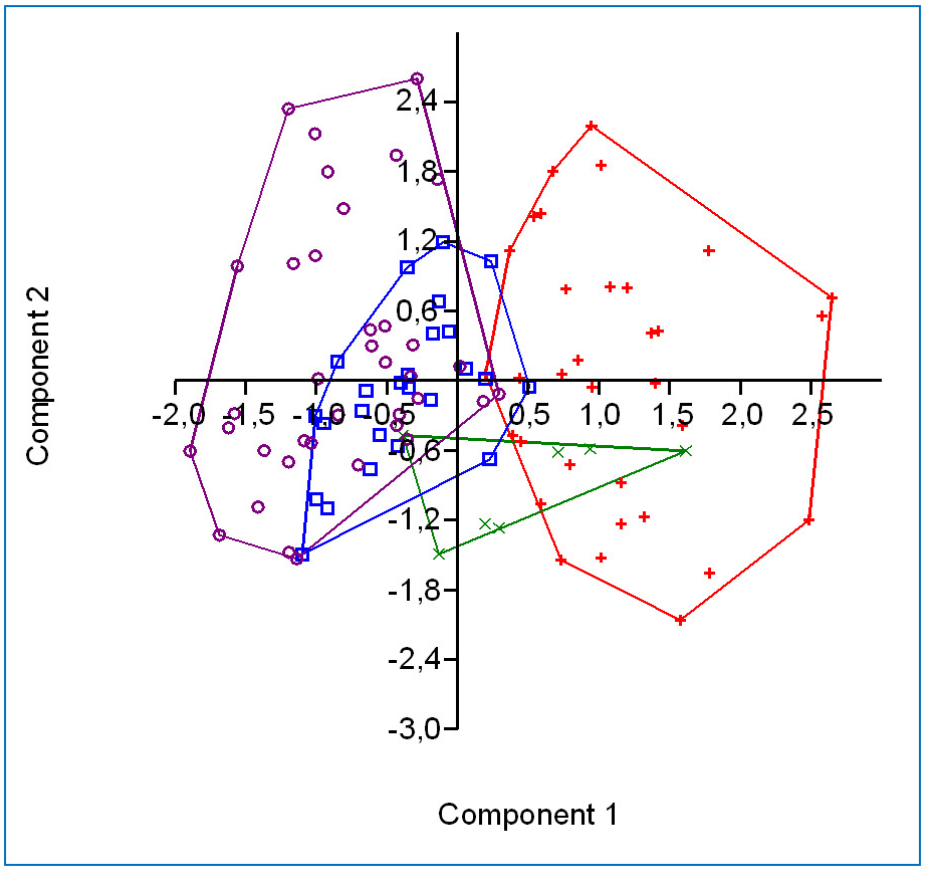

FIGURE 5. Principal Components Analysis of the morphological measurements (Tables S1, S2, S3) of the four *Turdus* thrushes of the present study. red = *T. leucomelas albiventer;* green = *T. l. upichiarum*; blue = *T. arthuri*; purple = *T. ignobilis debilis.* Note the virtually complete separation between *T. l. albiventer* and *T. i. debilis*; *T. l. upichiarum* overlaps most with *T. l. albiventer*, less with *T. arthuri* and still less with *T. i. debilis*; *T. arthuri* shows considerable overlap with *T. i. debilis.* See text for further details.

As a first step in this direction, we analyzed morphometrics of the four taxa of this study in more detail as suggested by López-O. *et al.* (2016) with respect to possible functional differences (Table 3, Fig. 4, Tables S1, S2 and S3). *T. l. albiventer* is the largest species in all measurements and *T. i. debilis*, the smallest; this size difference might facilitate the coexistence of these habitat generalists in open or semiopen sites in eastern Colombia. However, *T. l. upichiarum* is closer in overall size to *T. arthuri* and *T. i. debilis. T. arthuri* and *T. l. upichiarum* are coexisting habitat specialists; in fact, both were taken in the same mist-nets at the type locality of the latter. Although *upichiarum* averages somewhat larger than *arthuri* in most measurements, the difference is only significant for total culmen in males and tail length in females: clearly a larger sample of *upichiarum* is needed to properly evaluate the differences between them in morphology, and more field observations might shed light on possible differences in resource use. The sympatry of *T. i. debilis* with both species at Araracuara might be the result of habitat disturbance resulting from the longer period of human presence there; this species differs strongly from the similar-sized *T. arthuri* in its shorter tarsi (Table 3; Fig. 3), perhaps reflecting more terrestrial foraging habits by the latter. The PCA (Fig. 4) clearly shows the virtually complete morphometric separation between *T. l. albiventer* and *T. i. debilis* and the considerable overlap between the latter and *T. arthuri. Turdus l. upichiarum* shows partial overlap in measurements with all of the other three taxa, this being most extensive with *T. l. albiventer* and least with *T. i. debilis.* While outside the scope of the present study, the collection and analysis of vocal recordings of calls and songs of these apparently syntopic thrushes, including comparisons with their other, conspecific populations—especially in the case of *T. ignobilis*—would be important in any future reevaluation of their taxonomic status.

FIGURE 6. Plumage variation among populations of *T. ignobilis* and *T. arthuri* from eastern Colombia. From left to right: *T. i. ignobilis*, male ICN 20637, Cundinamarca, Laguna de Pedropalo, and male ICN 21095, Cundinamarca, Planicies de Fusagasugá; *T. i. debilis*, male ICN 37676, Norte de Santander, San Cayetano, vereda Ayacucho, finca El Palmar, and female ICN 24706, Amazonas, Araracuara, río Caquetá; *T. arthuri*, female ICN 24710, Amazonas, Araracuara, río Caquetá, and male ICN 31982, Caquetá, río Mesay. Plumage differences between *ignobilis* and *debilis* are mainly in the extent of white in throat and belly; note also the larger size of *ignobilis*; whereas *arthuri* is distinguished by its grayer underparts and duller upperparts.

TABLE 3. Results of one-way ANOVA tests for measurement data between taxa of *Turdus* thrushes of eastern Colombia; significance levels for *p* values with Bonferroni correction; *p* values: ns= not significantly different; *=significant difference; **= highly significant difference; ***= very highly significant difference ($p<0.001$). TLA=*T. leucomelas albiventer*; TLU=*T. leucomelas upichiarum*; TA= *T. arthuri*; TID=*T. ignobilis debilis.*

Measurement	*F*, *p*, df	Values of p : values of Q from Tukey pairwise tests					
		TLA-TLU	TLA-TA	TLA-TID	TLU-TA	TLU-TID	TA-TID
Total culmen: sexes combined	45.12*** 3, 100	0.059 ns	***	***	0.010*	0.0096*	0.092 ns
Commissure width: sexes combined	23.93*** 3, 102	0.745 ns	***	***	0.016 ns	***	0.052 ns
Bill height: sexes combined	13.67*** 3, 93	0.664 ns	0.0026*	***	0.650 ns	0.603 ns	0,181 ns
Wing length: males	22.75*** 3, 55	0.0081*	***	***	0.815 ns	0.612 ns	0.956 ns
Wing length: females	17.64*** 3, 43	0.198 ns	***	***	0.572 ns	0.339 ns	0.953 ns
Tail length: males	29.77*** 3, 59	0,654 ns	***	***	0.069 ns	0.00014**	0.138 ns
Tail length: females	50.04*** 3, 44	0.995 ns	***	***	0.00033**	***	0.136 ns
Tarsus length: sexes combined	44.78*** 3, 101	0.0048*	0.071 ns	***	0.267 ns	0.0241 ns	***

Patterns of endemism of white-sand species in Colombia.—Three taxa were described by Stiles (1995, 1996) as results of the 1992 expedition, and on present knowledge two of these (the hummingbird *Chlorostilbon olivaresi* Stiles, 1996 and the small tyrannid *Hemitriccus margaritaceiventer chiribiquetensis* Stiles, 1995) have so far not been detected beyond the limits of the Serranía de Chiribiquete. Because their preferred matorral habitat is unsuited for agriculture due to its thin, sandy, infertile soils, neither appears to be at risk from human intervention; in fact, *C. olivaresi* is the most common hummingbird in this habitat. The third taxon, the sparrow *Zonotrichia capensis bonnetiana* Stiles, 1995, is widely distributed in white-sand savannas and brushlands throughout much of northeastern Colombia from Vichada, northern Guainía and the Mitú area south to the southern Macarena region (although this latter population might yet be found to be a distinct subspecies), northern Guaviare (the northern end of the Sierra de la Lindosa), Chiribiquete and Araracuara. By contrast, *Turdus leucomelas upichiarum* has been recorded only from Chiribiquete and Araracuara. A brief summary of the occurrences of white-sand specialist species in Colombia was given by Stiles & Beckers (2015). However, there are several more or less extensive areas of white-sand habitats for which few ornithological data exist, notably the Sabanas del Yarí northwest of Chiribiquete, hence such areas should represent a high priority for future inventories and biogeographic studies.

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