

A CRYPTIC NEW SPECIES OF THRUSH (TURDIDAE: *TURDUS*) FROM WESTERN AMAZONIA

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Abstract. The taxonomy of Hauxwell's Thrush (*Turdus hauxwelli*) with respect to its relationship to the Cocoa Thrush (*Turdus fumigatus*) has been complicated. A confounding factor has been the morphological variation reported within *T. hauxwelli* and the apparent geographic overlap of the two taxa. Recent evidence shows that some of these factors may be explained by the existence of a cryptic, syntopic species, very similar in plumage to *T. hauxwelli*. The new species differs in minor plumage characters, in soft-part colors, and (especially) in voice. On the basis of vocal and molecular data, we propose that the new thrush is not particularly closely related to the *T. fumigatus/hauxwelli* complex but rather is the western Amazonian member of the Spectacled Thrush (*T. nudigenis*) complex. Our molecular phylogeny suggests that the new species is sister to the Unicolored Thrush (*T. haplochrous*) and also that the Ecuadorian Thrush (*T. maculirostris*) should be considered a species separate from the Spectacled Thrush. In the absence of modern, data-rich specimens, the new thrush might well have remained unknown. This hidden taxon provides yet another case that argues strongly for continuing the tradition of general specimen collection. Having removed the new species as a source of confusion, we suggest that a reevaluation of the species status of *T. hauxwelli* with respect to *T. fumigatus* is in order.

Key words: *Turdidae*, *Turdus sanchezorum*, *Turdus hauxwelli*, *Turdus fumigatus*, *Turdus nudigenis*, *Turdus maculirostris*, Amazonian avifauna, cryptic species, modern specimen collection.

Una Especie Nueva y Críptica de Zorzal (*Turdidae: Turdus*) del Oeste de la Cuenca Amazonica

Resumen. La taxonomía de *Turdus hauxwelli* es poco clara con respecto a su relación con *T. fumigatus*. Un factor que ciertamente ha contribuido con la confusión es la variación morfológica descrita en *T. hauxwelli*, así como la aparente sobreposición geográfica de ambos taxones. Nuevas evidencias muestran que algunos de estos factores pueden ser explicados a través de la existencia de una especie simpátrica y críptica muy semejante en plumaje a *T. hauxwelli*. Esta nueva especie difiere en pequeñas características del plumaje, en las partes desnudas, y (especialmente) en la voz. Basados en datos moleculares y vocales, proponemos que la nueva especie no está particularmente relacionada al complejo *T. fumigatus/hauxwelli*, sino que representa el representante occidental en Amazonía del complejo de *T. nudigenis*. La filogenia molecular sugiere que la nueva especie es hermana de *T. haplochrous*, y además que *T. maculirostris* debe ser considerada una especie separada de *T. nudigenis*. Sin la existencia de especímenes modernos, ricos en informaciones, esta nueva especie podría haber pasado desapercibida para la ciencia. El descubrimiento de este taxón críptico demuestra la necesidad de continuar colectando aves con fines científicos. Una vez retirada la nueva especie como factor de confusión, creemos que es necesaria una re-evaluación de la taxonomía de *T. hauxwelli* con respecto a *T. fumigatus*.

INTRODUCTION

On 29 July 1961, while on his first visit to Peru, JPO collected a *Turdus* thrush in seasonally flooded “whitewater” river-edge forest (*várzea*) at Pucallpa, Ucayali (then still Loreto) department. This specimen was deposited at the Louisiana State University Museum of Natural Science (LSUMZ) and identified as Hauxwell's Thrush (*Turdus hauxwelli*). As LSUMZ acquired more specimens of *Turdus* through further field work at nearby sites in the Peruvian Amazon, however, JPO noticed that some specimens of *T. hauxwelli*, including the one he had collected in 1961, had a distinctly grayish-brown

tail, olive bill, and yellow or orange orbital skin, whereas most had a more rufous-brown tail, blackish bill, and a feathered orbital ring. JPO set aside the gray-tailed birds as a curious “color morph” until more information could be uncovered. Indeed, this form has been illustrated in Schulenberg et al. (2007) as the “gray-tailed morph” of *T. hauxwelli*.

In 2003, during field work in San Martín department, northern Peru, B. J. O'Shea and B. Walker made DFL aware of the presence of a “mewing” *Turdus*, making a vocalization they associated with the Spectacled Thrush (*Turdus nudigenis*) from northeastern South America. Shortly thereafter, DFL and G. H. Rosenberg found two silent thrushes

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nearby that fit JPO's "gray-tailed morph" of *T. hauxwelli*. It seemed likely the "mewing" calls and the "gray-tailed morph" were connected. Discovering recordings of a mewing thrush identified as "*T. hauxwelli*" on Moore (1997), DFL contacted J. H. Moore and B. M. Whitney, who made the recordings in *várzea* forest on the lower Río Napo, Loreto department, Peru. In 2005, Whitney finally observed that birds with "mewing" voices matched the morphology of the "gray-tailed" *T. hauxwelli*. Further confirmation came from recordings made in the 1980s by T. A. Parker III, also in *várzea* along the lower Río Napo, in which Parker also provided a description matching the "gray-tailed" *T. hauxwelli*. Therefore, we are confident that the mewing calls are the characteristic call of this *Turdus*.

We searched several museums for "gray-tailed" birds among series of *Turdus hauxwelli*, and found them to be rather widespread in western Amazonia (see below). Further, we inspected the type specimen of *Turdus hauxwelli* (deposited at the American Museum of Natural History), confirming that the name indeed applies to the rufous-tailed bird. The type locality for *T. hauxwelli* is Pebas, Peru, on the north bank of the Río Amazonas downstream from the Río Napo (Loreto department). The distinct morphology and the difference in voice between the "gray-tailed morph" and true *T. hauxwelli*, the occurrence of the two in syntopy at several sites, and a molecular phylogeny we provide here clearly indicate that the gray-tailed birds are a cryptic species distinct from, and not closely related to, *T. hauxwelli*. We can find no indication that this form has already received a name (synonymized or otherwise). Therefore, we here name this new thrush:

***Turdus sanchezorum*, sp. nov.**

Varzea Thrush

Zorzal de várzea (Spanish) / *Sabiá-da-várzea* (Portuguese)

Holotype. LSUMZ 116119; Peru: depto. Loreto, south of Río Amazonas, about 10 km south-southwest of the mouth of Río Napo on the east bank of Quebrada Vainilla, elevation about 100 m. 8 August 1983. Male. Tissue sample: LSUMZ B-5106. Collected and prepared by Tristan J. Davis, field catalog number 2018.

Diagnosis. A large thrush assignable by general morphology and vocal characters to genus *Turdus* (sensu Voelker et al. 2007) (Fig. 1). Contour plumage overall dull brown with paler throat showing contrasting darker longitudinal streaks; center of belly and vent whitish, usually with dark centers to undertail coverts. Underwing coverts rich rufescent, the color bleeding onto the outer web of primaries at their very bases. Bill olive with yellowish tomentum; orbital skin bare and yellow-orange. Similar to several sympatric species of *Turdus* in western Amazonia, particularly *T. hauxwelli*, the Black-billed Thrush (*T. ignobilis*), Pale-breasted Thrush (*T. leucomelas*), and Lawrence's Thrush (*T. lawrencei*); most easily distinguished (even in the field) from the first two by

the color of the bill and orbital ring. In the hand, *T. sanchezorum* can be further distinguished from *T. hauxwelli* by its gray-brown tail (rufous-brown in *hauxwelli*), less extensively rufescent undersides of the primaries (this rufescence averages more extensive on *T. hauxwelli*), and more contrastingly dark throat streaks on a whiter background (on average). *Turdus leucomelas* is easily distinguished from *T. sanchezorum* by its grayer head contrasting with more rufescent back. *Turdus lawrencei* has a yellower bill (in male) and orbital ring and deeper chocolate-brown plumage than does *T. sanchezorum*. The voices of these four species differ strongly from that of *T. sanchezorum* (see Schulenberg et al. 2007 for distinctions). *Turdus sanchezorum* is also similar (in voice, as well as plumage) to several allopatric species such as the Spectacled Thrush (formerly Bare-eyed Robin, *T. nudigenis*), Unicolored Thrush (*T. haplochrous*), Clay-colored Thrush (*T. grayi*), and Ecuadorian Thrush (*T. maculirostris*, often considered a subspecies of *T. nudigenis*). *Turdus haplochrous* is colder brown overall than others of this latter group of species, with the throat less boldly streaked, and no pale feathering below at all; instead, *T. haplochrous* has a uniform brown belly and undertail coverts, less saturated warm buff underwing coverts, and a darker tail, contrasting more with the uppertail coverts. *Turdus nudigenis* has a larger exposed patch of face skin and is paler overall. *Turdus grayi* has a uniformly colored belly and undertail coverts (contrastingly whitish in *T. sanchezorum*), the plumage is brighter warm tan, and it does not have so noticeably colored an orbital ring. *Turdus maculirostris* is a paler grayish-brown, lacks rufescent underwings, and is more weakly streaked on the throat. We cannot find any morphological measurements that reliably distinguish *T. sanchezorum* from *T. hauxwelli*, *T. fumigatus*, *T. nudigenis*, but the primary-extension ratio of *T. sanchezorum* averages longer than that of the other species (Table 1, Fig. 2).

Description of the holotype. Crown, lores, ear coverts, nape, dorsum, wing coverts, rump, and upper tail coverts uniform rich rufous brown, nearest Warm Sepia (capitalized colors from Ridgway 1912). Rectrices grayish brown, nearest Light Seal Brown, narrowly edged, especially basally, with Warm Sepia, and sharply contrasting with upper tail coverts. Chin and throat warm buffy white (whitest near center), streaked with dusky brown, fading into warm brown of breast (nearest Verona Brown). Upper breast and flanks slightly darker than lower breast; belly and under tail coverts warm white, the outer edge of the outer vanes of the latter marked with the same warm brown as the breast. Upper surface of primaries and secondaries Light Seal Brown, edged on the outer web with Warm Sepia. Underwing coverts bright orange rufous, nearest Cinnamon, the same color strongly edging the basal inner edges of the primaries, forming an obvious patch under the folded wing. Soft part colors, as noted on label: bill dull yellow at tip, darkening to black at base; eyering dull orange; iris brown; tarsi and feet olive-gray. Weight 58 g. Light body molt noted on label.



FIGURE 1. The newly described Varzea Thrush (*Turdus sanchezorum*: lower bird, LSUMZ 52344) and Hauxwell's Thrush (*T. hauxwelli*; upper bird, LSUMZ 27740). Painted in acrylic by J. P. O'Neill.

Etymology. We take great pleasure in honoring our long-time field companions and friends Manuel Sánchez S. and Marta Chávez de Sánchez. The Sánchezes have worked with JPO, and many other LSU (and non-LSU) researchers, in Peru, Bolivia, and Venezuela since the 1960s and were present for many of the bird discoveries that resulted from those field expeditions. Without Manuel and Marta's tireless work, good company, and logistical know-how, the LSUMZ

South American field program would not have been the success it is. The English name refers to the preferred habitat of the species. There are other species of *Turdus* that are largely restricted to *várzea* habitats in Amazonia, including *T. hauxwelli* and *T. ignobilis*, but these latter species are also frequently found in non-*várzea* habitats elsewhere in their ranges. Thus, *T. sanchezorum* appears to be the *Turdus* most confined to *várzea* habitat.

TABLE 1. Mean measurements (in mm) of females (♀) and males (♂) of *Turdus sanchezorum* and other selected species of *Turdus*^a.

Taxon	Sex	Wing chord	Primary extension ratio ^b	Tail	Culmen length	Tarsus
<i>T. sanchezorum</i>	♀ (8) ^c	109.1 ± 1.67 (106.7–111.2) ^d	5.9 ± 0.72 (4.8–6.8)	83.8 ± 2.74 (78.5–87.3)	13.5 ± 1.07 (12.5–15.7)	29.3 ± 2.15 (26.9–33.8)
	♂ (25)	109.9 ± 3.03 (103.98–116.4)	6.3 ± 1.03 (4.5–8.7)	87.08 ± 3.74 (78.8–96.8)	13.5 ± 0.77 (11.9–15.2)	30.3 ± 1.96 (26.2–33.6)
<i>T. hauxwelli</i>	♀ (30)	108.9 ± 3.66 (102.7–113.9)	5.3 ± 0.58 (4.44–6.51)	80.4 ± 4.13 (73.1–90.7)	13.1 ± 0.79 (11.4–14.9)	27.7 ± 1.39 (23.4–30.2)
	♂ (37)	112.9 ± 3.59 (104.6–121.4)	5.3 ± 0.78 (4.3–7.8)	83.6 ± 4.78 (76.1–95.0)	13.3 ± 0.73 (12.3–15.3)	28.7 ± 1.37 (25.7–30.8)
<i>T. fumigatus</i>	♀ (10)	109.1 ± 1.67 (106.7–111.2)	5.5 ± 0.41 (4.9–6.2)	83.5 ± 1.72 (80.6–85.6)	14.0 ± 0.78 (12.6–13.3)	29.7 ± 1.22 (27.9–31.8)
	♂ (8)	111.0 ± 2.84 (107.9–115.2)	5.6 ± 0.71 (4.2–6.5)	85.6 ± 3.75 (80.1–90.4)	13.4 ± 0.76 (12.5–14.6)	31 ± 1.73 (27.5–32.6)
<i>T. nudigenis</i>	♀ (5)	108.0 ± 3.11 (105.0–111.6)	5.3 ± 1.22 (3.8–7.2)	84.2 ± 2.73 (80.3–86.6)	13.2 ± 0.55 (12.6–13.6)	29.5 ± 0.59 (28.6–30)
	♂ (7)	114.7 ± 4.16 (109.2–121.3)	5.1 ± 0.68 (4.3–5.8)	88 ± 4.49 (83.1–93.1)	13.2 ± 0.43 (12.7–13.8)	30 ± 1.64 (27.8–32.1)
<i>T. maculirostris</i>	♀ (3)	113.1 ± 1.25 (112.0–114.5)	5.1 ± 0.3 (4.9–5.5)	85.3 ± 4.4 (82.1–90.3)	14.2 ± 0.76 (13.7–15.1)	30.6 ± 0.51 (30.0–31.0)
	♂ (6)	116.93 ± 2.44 (113.3–120.0)	5.01 ± 0.42 (4.7–5.8)	90.7 ± 2.62 (87.6–93.7)	13.7 ± 0.55 (13.3–14.7)	32.2 ± 2.02 (30.0–34.4)
<i>T. haplochrous</i>	♀ (1)	117.9	6.21	95.1	13.9	31.6
	♂ (2)	108.0, 119.6	5.2, 5.4	90.0, 100.2	13.0, 13.2	29.9, 30.6
<i>T. grayi</i>	♀ (7)	117.7 ± 2.76 (112.0–119.8)	4.8 ± 0.34 (4.3–5.2)	91.3 ± 1.47 (89.6–93.5)	14.5 ± 0.74 (13.1–15.5)	30.3 ± 1.17 (28.1–31.8)
	♂ (5)	119.2 ± 5.67 (110.8–126.1)	5.2 ± 0.27 (5.0–5.6)	94.9 ± 3.38 (90.6–99.4)	14.4 ± 0.44 (14.0–15.0)	31.7 ± 1.71 (29.7–33.8)

^aNo juvenile specimens included. Specimen information available upon request.

^bCalculated by dividing total wing chord by the distance that primaries protruded beyond longest tertial (“primary extension”).

^cSample size in parentheses.

^dRange in parentheses.

Distribution. *Turdus sanchezorum* has been documented from several localities in western Amazonia (Fig. 3). Specimens, photographs, or voice recordings provide the documentation for the sites listed below, progressing from northwest to southeast. We here list only those specimens or recordings that we have been able to verify ourselves, with the sole exception of specimens in the Naturhistoriska Riksmuseet, Stockholm. Asterisks (*) denote sites where *T. hauxwelli* is confirmed to be sympatric, daggers (†) where *T. fumigatus* is confirmed to be sympatric. Institutional abbreviations: American Museum of Natural History, New York (AMNH), Carnegie Museum of Natural History, Pittsburgh (CM), LSUMZ, Museo Nacional de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MUSM), Museu de Zoologia da Universidade de São Paulo (MZUSP), Naturhistoriska Riksmuseet (NRM). Additionally, our colleagues Gustavo Bravo and Alexandre Aleixo searched for specimens of the new species in Colombia [Instituto de Ciencias Naturales, Bogotá (ICN), and Instituto Alexander von Humboldt, Bogotá (IAvH)], and Brazil [Museo Paraense Emilio Goeldi, Belém (MPEG)], respectively, without success. We provide the coordinates for any localities that are not covered by the ornithological gazetteers (Stephens and Traylor 1983, Paynter and Traylor 1991a, b, Vanzolini 1992, Paynter 1997):

Peru: San Martín department: Aguas Verdes (5° 41' S, 77° 38' W, elevation 1100 m; photograph, G. H. Rosenberg); Posic (6° 00' S, 77° 11' W, elevation 850 m; voice recording, DFL, Xeno-Canto 41072). Loreto department: Boca de Río Curaray on Río Napo* (AMNH 232549); island in Río Napo at mouth of Río Yanayacu* (LSUMZ 116117); Isla Yarina, Río Napo (voice recordings, B. M. Whitney); ExplorNapo Lodge, Río Sucuari (3° 15' S, 72° 55' W, elevation 100 m; voice recordings, Hardy and Parker 1985, Moore 1997, Macaulay Library 29133); Quebrada Yanamono, Río Amazonas (3° 26' S, 72° 46' W, elevation 80 m; CM 170043, 170148; voice recordings, B. M. Whitney, T. A. Parker III, Macaulay Library 34152, 34153, 34154, 34155, 34164, 34165, 34406); S bank Río Amazonas, E side Quebrada Vainilla (3° 30' S, 72° 49' W, elevation 80 m; LSUMZ 116119); Orosa, Río Amazonas* (AMNH 232542, 232543, 232544); Santa Isabel (MUSM 18637), Pampa Hermosa, Río Ucayali (7° 14' S, 75° 19' W, elevation 150 m; voice recording, DFL, Xeno-Canto 41071). Ucayali department: Yarinacochoa* (LSUMZ 52343, 62439, 64472, 62438); Pucallpa (LSUMZ 27740, MUSM 18638). Cuzco department: Nuevo Mundo, Río Urubamba (11° 33' S, 73° 08' W, elevation 450 m; MUSM 27020).

Colombia: Amazonas department: Isla Ronda, Río Amazonas (voice recordings, A. M. Cuervo, Xeno-Canto 41114).

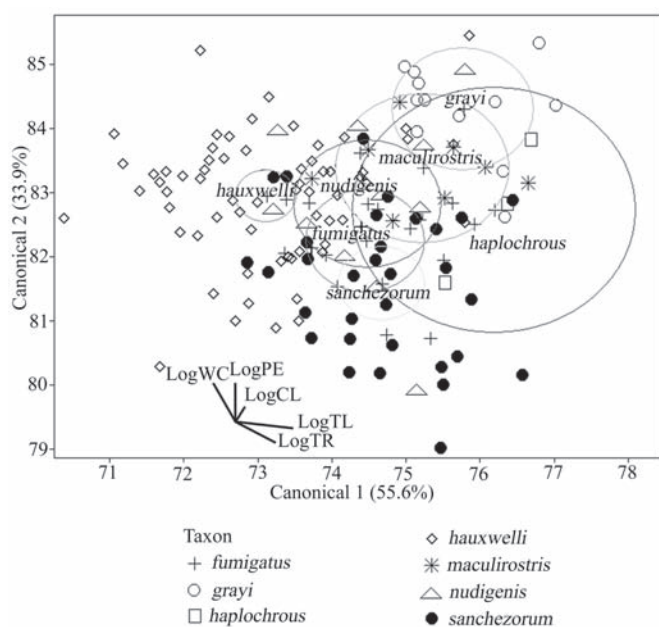


FIGURE 2. Morphometric variation of *Turdus sanchezorum* and other selected species of *Turdus* illustrated in a discriminant function analysis using log-transformed measurements of culmen length (CL), primary extension (PE), tarsus length (TR), tail length (TL), and wing chord (WC). Sexes were combined, as independent analysis by sex showed no difference from the present plot. Larger circles with taxon names on the plot represent the 95% confidence intervals. Lengths of log vectors (at lower left of plot) show weighting for those measurements. Angles of log vectors show their influences on point distribution along the x (canonical 1) and y (canonical 2) axes.

Brazil: Amazonas state: Tefe, Rio Solimões (AMNH 503320); Villa Bella Imperatriz (= Parintins), Rio Amazonas† (AMNH 278256, 278257, 278258, 278259, 278260, 278261, 278262, 278263, 278821); Lago Beruri (MZUSP 61917); Rio Purús, Igarape da Castanha* (NRM 557364, 557366, 557367); Huitanaa (= Hyutanahan), right bank of Rio Purús* (CM 86469, 88060); Rio Purús, Itaboca (NRM uncatalogued); Rosarinho, Rio Madeira† (AMNH 282752, 282753, 282755); Borba, Rio Madeira*† (AMNH 280098, 280099, 280105, 280106, 280108, 280109); Auare Igarapé, Rio Madeira*† (AMNH 280104, 280111); Santa Isabel, Rio Preto (AMNH 503323).

Variation within paratype series. Eleven specimens were available for direct comparison with the holotype, the seven additional LSUMZ specimens (LSUMZ 27740, 52343, 62435, 62438, 62439, 64472, 116117) and four specimens on loan from CM (CM 86469, 88060, 170043, 170148). Of these, only two (LSUMZ 27740 and CM 86469) are females, but neither shows any obvious morphological difference from the holotype (or any other male) that might suggest sexual dimorphism. The remaining males appear relatively uniform, although most show less white on the undertail coverts than the holotype. The throat streaking on LSUMZ 62435, 62439, 64472, and CM 170043 is weaker, with a buffier (not whitish) background. LSUMZ 52343 (6 June 1966) and 116117 (3 July 1983) are molting remiges, and the latter is molting contour

feathers; no other specimens in the type series show overt molt (although the label of the holotype mentions “light body molt”) and were collected between late July and February.

Other specimens. In addition to LSUMZ and CM, DFL visited several museums—AMNH, MUSM, and MZUSP—to view their holdings of Amazonian species of *Turdus*, and contacted others for their assistance (NRM, MPEG, ICN, and IAvH). Species series searched were *T. hauxwelli*, *T. nudigenis*, *T. lawrencei*, and *T. fumigatus*. This research revealed an additional twenty-four specimens of *T. sanchezorum* that DFL confirmed by personal inspection (listed above under Distribution), another seven that are likely *T. sanchezorum*, and four more that were reported (by P. Ericson of NRM) to have definitive characters of *T. sanchezorum*. All these specimens were found among the series of *T. hauxwelli*, save the single MZUSP specimen, which had been identified as *T. nudigenis*. Among this series are two juvenile birds (AMNH 280108 and 280109) that are very likely *T. sanchezorum*, collected in February, a third molting from juvenile into first basic plumage (AMNH 282755), and an additional bird showing “definitive plumage” characters of the species but retaining juvenile wing coverts (thus probably representing first basic plumage), collected in late October (AMNH 278262). The former three specimens, and several additional adults (AMNH 280111, 280098, 280099, and 280106) are identified as “likely” *T. sanchezorum*, because of the lack of recorded soft-part colors, indeterminate tail color (which may be due to foxing), or weak throat streaks, but otherwise appeared more similar to *T. sanchezorum* than to *T. hauxwelli* in other characters (e.g., bills appeared to have retained “olive” color, or reduced rufescent wash to the underwing). If soft-part colors are not noted by the collector, the color of the orbital ring cannot be determined on a dried specimen. Specimens with the bill “olive” in life (according to the tag) often do appear paler-billed than birds with the bill blackish in life, but this character must be used with great caution (preferably in conjunction with tail color) for identification of specimens.

PHYLOGENETIC RELATIONSHIPS

METHODS

LNN obtained DNA sequences from the NADH dehydrogenase subunit 2 (ND2) mitochondrial gene of *T. sanchezorum* and all other known members of the *T. nudigenis* clade (including *T. grayi*, *T. maculirostris*, *T. haplochrous*, and *T. rufiventris*). We also included several individuals of *T. hauxwelli* and a few samples of *T. leucomelas*, *T. obsoletus*, and *T. albicollis*, used as outgroups. For the phylogenetic analyses, we used 10 samples already available from Klicka et al. (2005) and Voelker et al. (2007) in GenBank and sequenced another 13 to complement the sampling, including the only known tissue sample of the new species (Table 2).

We extracted DNA from frozen tissues with a DNeasy Kit, following the manufacturer’s instructions (Qiagen Inc., Valencia, CA). Following standard PCR protocols, we amplified the complete ND2 gene (1041 base pairs) by using the primer L5215 for the light strand (Hackett 1996) and H6313 for the heavy strand

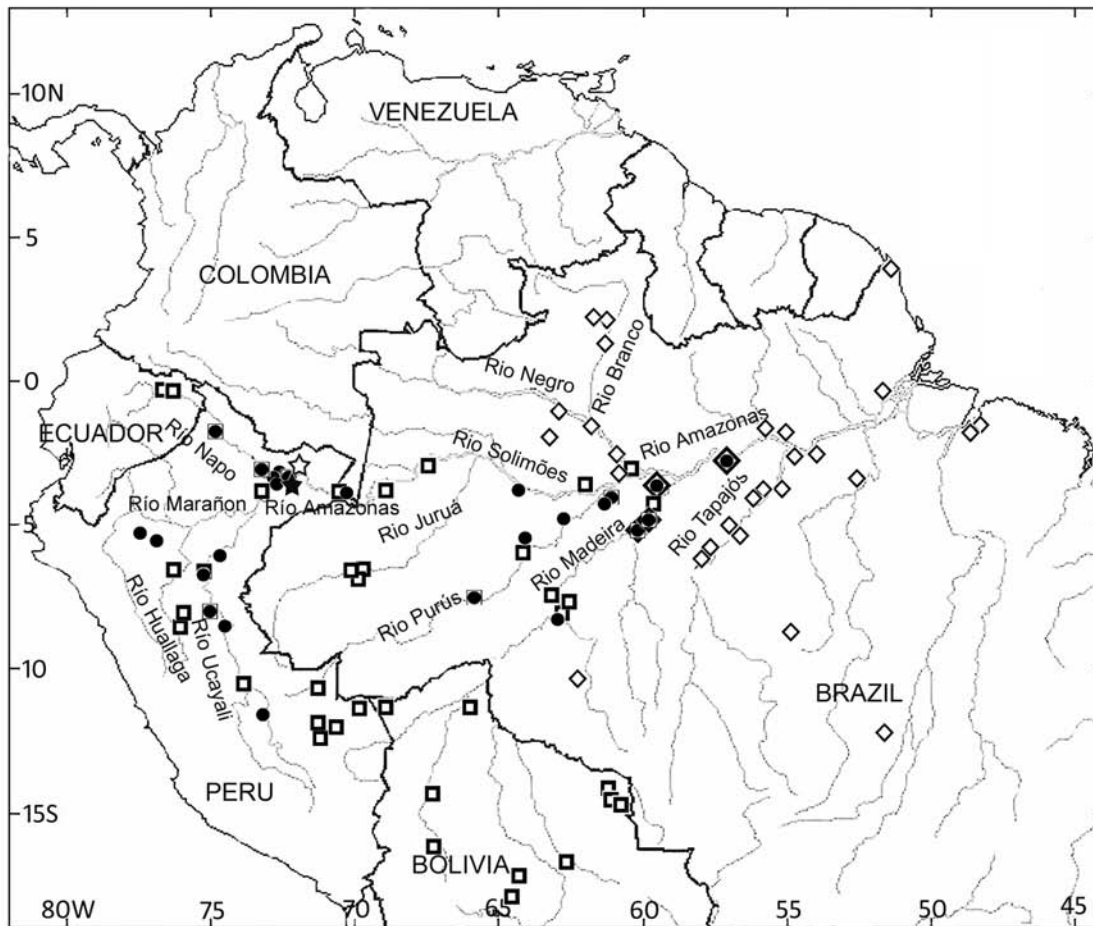


FIGURE 3. The distribution of *Turdus sanchezorum* (black star, type locality; black circles, other localities where occurrence documented by specimen, voice recording, or photograph), *T. hauxwelli* (open star, type locality; open squares, other localities where occurrence documented by specimen or voice recording), and selected records of *T. fumigatus* (open diamonds, localities documented by specimens). Where more than one species occurs in syntopy, symbols are stacked. For example, sites where *T. sanchezorum* overlaps with *T. hauxwelli* are marked with a black circle within an open square. All three species are known from several sites on the lower Rio Madeira in Brazil, designated with the three symbols stacked (see Distribution).

(Sorenson et al. 1999). PCR products were purified with 20% polyethylene glycol, and cycle sequence reactions were completed with a Big Dye terminator Cycle Sequencing Kit, version 3.1 (ABI). Reactions were cleaned with Sephadex (G-50 fine) columns and analyzed on an ABI 3100 Genetic Analyzer at the Museum of Natural Science at Louisiana State University. Complementary strands were aligned unambiguously and edited with Sequencher version 4.6 (GeneCodes Corporation, Madison, WI). No gaps, insertions or deletions were apparent in the data, and all sequences translated amino acids, without stop codons.

To assess the phylogenetic relationships of *T. sanchezorum*, we conducted both maximum likelihood and Bayesian inference analyses. We used PAUP* (Swofford 2002) to implement the maximum likelihood analysis, employing ModelTest 3.7 (Posada and Crandall 1998) to select the model that best fitted our data. The most likely model of evolution under Akaike's information criterion (AIC) was TrN + I, which is basically a Tamura and Nei (1993) model, plus a proportion of invariant

sites, representing a submodel of the GTR + I model. We obtained support for individual nodes of the most likely tree by running a maximum likelihood bootstrap analysis with heuristic search and 500 replicates. Bayesian analysis was executed in MRBAYES 3.2 (Huelsenbeck and Ronquist 2001) with a general time-reversible model with six nucleotide-substitution rates and a proportion of invariant sites (GTR + I). Parameter values (including base composition) were estimated during the analysis. Four heated chains of the Metropolis-coupled Monte Carlo simulations were run for 2 000 000 generations, sampling trees every 100 generations. The first 2500 trees were discarded as burn-in. We carried out two independent runs to check for convergence. A total of 15 000 trees were then combined to reconstruct a single 50% majority rule consensus tree, which depicts the posterior Bayesian probabilities of each clade (Fig. 4). We considered a value equal to or greater than 95% statistically significant. The topologies of the tree with the best maximum likelihood score ($-\ln L = 3131.51$; tree not presented) and the

TABLE 2. Species, tissue samples, locality, and GenBank accession number of the birds used in the phylogenetic analyses.

Species	Tissue source	Tissue number	Locality	GenBank accession no.
<i>Turdus albicollis</i> ^a	LSUMNS	B22690	Bolivia: Dept. La Paz	DQ911063
<i>T. fumigatus</i> ^a	STRI	SV-TFU1	St. Vincent	DQ911076
<i>T. grayi</i> 1	LSUMNS	B28608	Panama: Prov. Panama	JN049520
<i>T. grayi</i> 2	LSUMNS	B26416	Panama: Prov. Chiriquí	JN049519
<i>T. grayi</i> 3 ^b	MBM	6620	Honduras: Dept. Copan	AY752346
<i>T. haplochrous</i> ^a	LSUMNS	B7620	Bolivia: Dept. Beni	DQ911077
<i>T. hauxwelli</i> 1	LSUMNS	B18143	Bolivia: Dept. Santa Cruz	JN049513
<i>T. hauxwelli</i> 2	LSUMNS	B1004	Bolivia: Dept. La Paz	JN049515
<i>T. hauxwelli</i> 3	LSUMNS	B15030	Bolivia: Dept. Santa Cruz	JN049516
<i>T. hauxwelli</i> 4 ^a	LSUMNS	B18551	Bolivia: Dept. Santa Cruz	DQ911078
<i>T. hauxwelli</i> 5	LSUMNS	B18252	Bolivia: Dept. Santa Cruz	JN049512
<i>T. hauxwelli</i> 6	LSUMNS	B9445	Bolivia: Dept. Pando	JN049514
<i>T. leucomelas</i> 1	LSUMNS	B48579	Guyana	JN049524
<i>T. leucomelas</i> 2 ^a	LSUMNS	B14719	Bolivia: Dept. Santa Cruz	DQ911086
<i>T. maculirostris</i> 1	LSUMNS	B7869	Ecuador: Prov. El Oro	JN049518
<i>T. maculirostris</i> 2	LSUMNS	B7873	Ecuador: Prov. El Oro	JN049517
<i>T. maculirostris</i> 3 ^a	LSUMNS	B7740	Ecuador: Prov. Bolivar	DQ911087
<i>T. nudigenis</i> 1	LSUMNS	B48549	Guyana: Ireng River	JN049521
<i>T. nudigenis</i> 2 ^a	STRI	MA-TNU1	Martinique: Vendredi	DQ911093
<i>T. obsoletusa</i>	LSUMNS	B12002	Ecuador: Prov. Esmeraldas	DQ911095
<i>T. rufiventris</i> 1	LSUMNS	B38327	Bolivia: Dept. Santa Cruz	JN049522
<i>T. rufiventris</i> 2 ^b	LSUMNS	B25910	Paraguay: Dept. Caaguazú	AY752351
<i>T. sanchezorum</i>	LSUMNS	B5106	Peru: Dept. Loreto	JN049523

^aSequence from Voelker et al. 2007.

^bSequence from Klicka et al. 2005.

consensus tree of the Bayesian inference were fully congruent; none resolved the polytomy in the *T. nudigenis* clade.

RESULTS

Recent studies have placed most New World thrushes into strongly supported clades (Voelker et al. 2007, Nylander et al. 2008); some clades were novel associations, but others confirmed the suspicions of systematists who had been working largely with morphological characters (e.g., Hellmayr 1934, Ripley 1964, Ridgely and Tudor 1989). One example is the clade consisting of *T. nudigenis*, *T. grayi*, *T. maculirostris*, *T. haplochrous*, and *T. rufiventris*, a relationship first suggested by Ridgely and Tudor (1989). It remains unclear which species or clade represents this group's closest relative (Voelker et al. 2007, Nylander et al. 2008),

We recognize *T. sanchezorum* as a member of the *T. nudigenis* clade, as suggested by the results of our phylogenetic analysis (Fig. 4). Most taxonomists consider the five taxa listed as members of this clade as separate species, with the exception of *T. maculirostris*, which is often considered a subspecies of *T. nudigenis* (e.g., Hellmayr 1934, Ripley 1964). Our molecular phylogeny suggests that *T. sanchezorum* is sister to *T. haplochrous*, but this is only a preliminary conclusion based on one sample of each taxon. The branching patterns of our tree specify clear

sister relationships of only two taxa: *T. rufiventris* is sister to the rest of the clade (and, indeed, it is the most divergent in voice and morphology, pers. obs.), and *T. sanchezorum* and *T. haplochrous* are sisters. The other taxa (including the *T. sanchezorum*/*haplochrous* branch) form a polytomy with respect to one another (we present a distance matrix in Table 3).

Delimiting species within the *T. nudigenis* clade is not straightforward. The members of this group of thrushes are highly constrained in morphology and voice and are entirely allopatric (Fig. 5). Nevertheless, taxonomists have never considered *T. nudigenis*, *T. grayi*, *T. rufiventris*, and *T. haplochrous* as conspecific even in the "age of lumping" of the early 20th century (e.g., Hellmayr 1934, Ripley 1964). Given the limited characters and knowledge of natural history available to us, we cannot ascertain the degree of reproductive isolation that has been reached by the members of the *T. nudigenis* clade with respect to one another. Instead, we choose to maintain the status quo with regard to assigning species status to the members of the group, including the raising of *T. maculirostris* to species status (an action also sanctioned by Remsen et al. 2010). Using plumage characters, we conclude that *T. sanchezorum* is as divergent from *T. haplochrous* as any other taxon in the complex currently considered a species (see Diagnosis above for plumage differences).

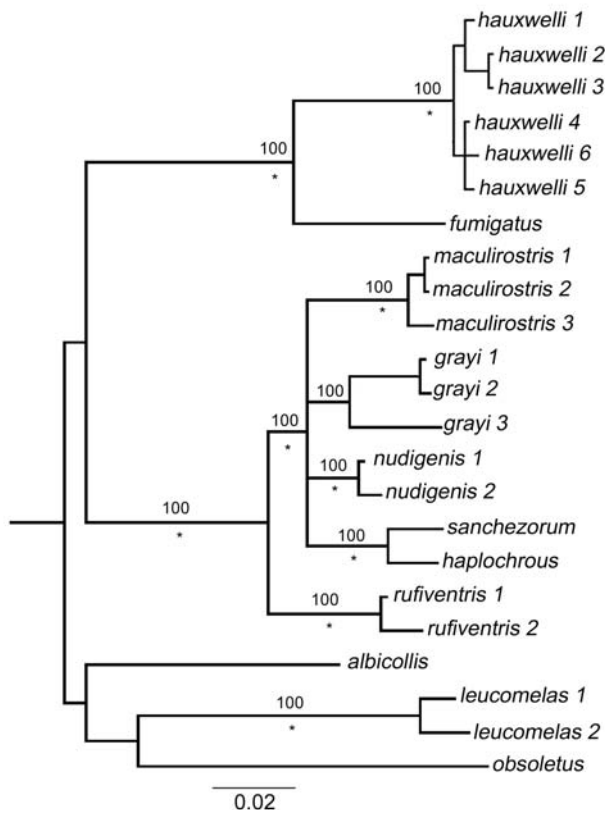


FIGURE 4. Bayesian phylogenetic hypothesis including *T. sanchezorum* and its closest relatives, based 1035 base pairs of the ND2 gene. This phylogeny represents a consensus of 15 000 Bayesian trees (from an original run of 1 000 000 generations sampled every 100 trees, with the first 2500 discarded as burn-in) under the GTR + I model of molecular evolution. Values above the nodes represent posterior Bayesian probabilities, and the asterisks represent bootstrap support higher than 95% in a maximum likelihood tree (not presented). Specimen information is presented in Table 2.

ECOLOGY AND BEHAVIOR

Turdus sanchezorum apparently is primarily a várzea forest species found along the larger tributaries of the upper Amazon/Solimões river system. To date, the species is found away from large Amazonian rivers only along the upper Río Mayo valley in

the Peruvian department of San Martín, where it occupies open white sand forest/savanna and disturbed edge at an elevation of about 800–1100 m. However, those sites are close to a fairly large patch of intermittently (?) flooded forest along the Río Mayo itself, thus a habitat similar to that of other populations of *T. sanchezorum*. One interesting difference, however, is that the Río Mayo is a blackwater, rather than a whitewater, river, unlike the habitat in the remainder of the new thrush’s distribution.

T. A. Parker III noted the new species (although he identified it at the time as *T. hauxwelli*, his description of the voice specifies *T. sanchezorum*) in his field notes from the ExplorNapo Lodge on the Río Sucusari (left bank of the Río Napo in northern Loreto department, Peru). In his field notes labeled “18, 19 May 1982” (deposited at LSUMZ), Parker stated “common in flooded forest at lodge. Several always about in lower branches of partly submerged trees or hopping on damp leaf litter at edge of swamp.” In the Río Mayo valley in San Martín, DFL has noted the species at the edge of open campo (scrub and grassland with scattered trees) by forest with relatively low canopy (~15 m). On 7 August 2003, DFL and G. H. Rosenberg encountered two birds of the new species (one in definitive plumage and one in first basic plumage) foraging on small palm fruits at the edge of medium-stature (~20 m) white-sand forest.

Turdus sanchezorum, like most species of *Turdus*, is likely to be omnivorous. Only one specimen, LSUMZ 116117, has data on stomach contents: blackish fruit pulp with a few seeds (7 × 5 × 4 mm). DFL’s sighting of two individuals eating small palm fruit (probably of genus *Euterpe*, *vide* R. Foster, pers. comm.) is the only other documented diet information available.

Two male specimens (collected in December and January) from near the type locality in northeastern Loreto department, Peru (CM 170043, 170148), had enlarged testes, but no other specimens (most collected July–August) with explicit gonad data indicate breeding condition. The tentative identification of juveniles of *T. sanchezorum* along the Rio Madeira in February and May, coupled with the presence of molting birds from May through July, suggests that breeding begins around December or January, young fledge in February, and the adults begin their post-breeding molt thereafter, completing it by late July/August. These dates coincide with the rainy season in southern Amazonia (December–May), when many

TABLE 3. Average genetic uncorrected distances (above the diagonal line) and TrN + G model-corrected distances (below the diagonal) between samples of *Turdus sanchezorum* and closely related species (see Table 2).

	<i>T. sanchezorum</i>	<i>T. haplochrous</i>	<i>T. nudigenis</i>	<i>T. grayi</i>	<i>T. maculirostris</i>	<i>T. rufiventris</i>	<i>T. fumigatus</i>	<i>T. hauxwelli</i>
<i>T. sanchezorum</i>	—	1.45	2.75 (.48)	3.18 (.09)	3.40 (.07)	3.91 (.36)	7.36	7.98 (.11)
<i>T. haplochrous</i>	1.58	—	2.66 (.06)	3.09 (.10)	3.32 (.05)	3.82 (.34)	7.44	8.52 (.13)
<i>T. nudigenis</i>	3.28 (.11)	3.13 (.09)	0.30	2.49 (.19)	2.40 (.17)	3.19 (.33)	6.72 (.48)	7.38 (.21)
<i>T. grayi</i>	3.89 (.13)	3.74 (.14)	2.90 (.25)	1.85 (1.52)	3.22 (.10)	3.78 (.33)	7.61 (.32)	8.19 (.15)
<i>T. maculirostris</i>	4.23 (.10)	3.13 (.09)	2.78 (.22)	3.89 (.57)	0.33 (.29)	3.66 (.18)	7.07 (.38)	7.97 (.11)
<i>T. rufiventris</i>	5.06 (.61)	4.48 (.57)	3.91 (.50)	4.79 (.53)	4.59 (.31)	0.60	6.92 (.06)	7.53 (.22)
<i>T. fumigatus</i>	11.52	11.63	9.97 (.16)	11.87 (.67)	10.77 (.35)	10.51 (.30)	—	0.45 (.24)
<i>T. hauxwelli</i>	12.99 (.26)	14.10 (.28)	11.42 (.45)	13.23 (.34)	12.83 (.25)	11.93 (.59)	5.37 (.12)	0.46 (.25)

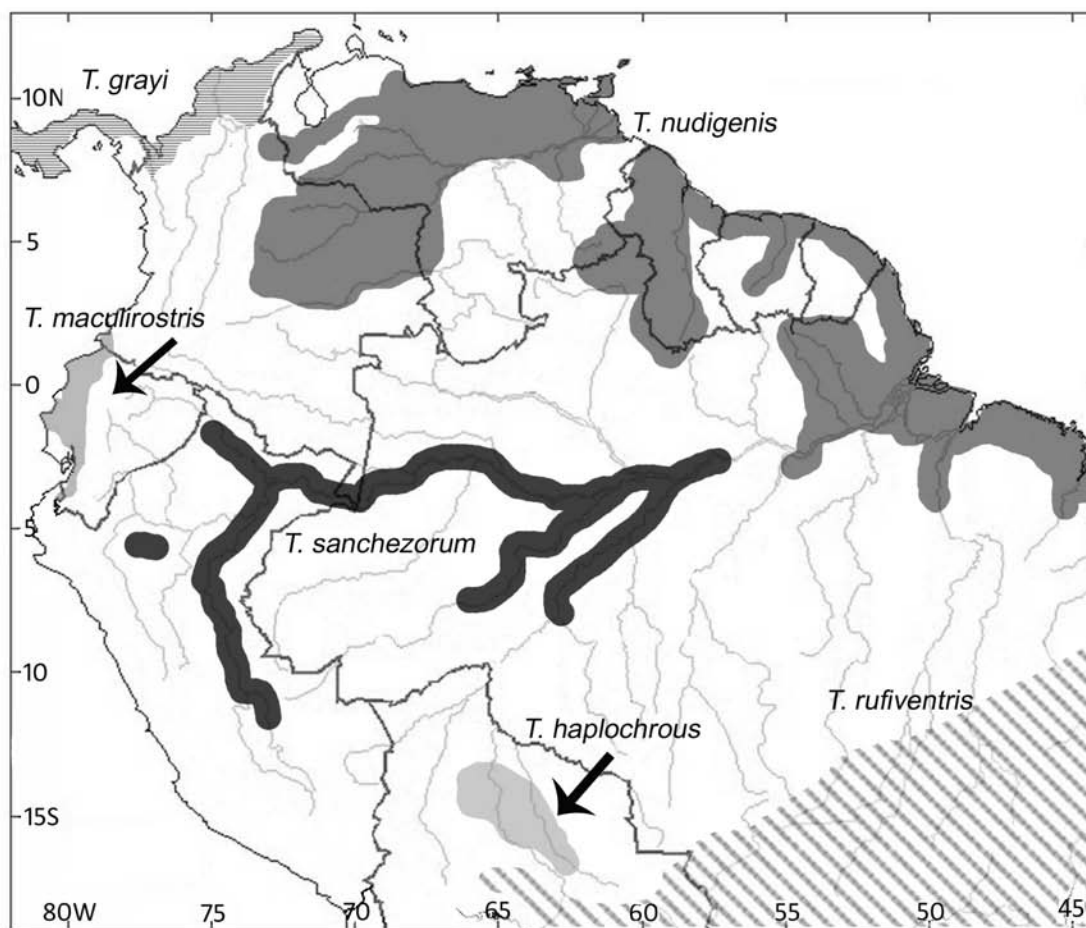


FIGURE 5. General distributions of the members of the *Turdus nudigenis* complex in northern South America. 1, *T. sanchezorum* (west-central Amazonia); 2, *T. nudigenis* (northeast South America); 3, *T. rufiventris* (southeast South America); 4, *T. grayi* (Central America and northern Colombia); 5, *T. maculirostris* (western Ecuador); 6, *T. haplochrous* (northern Bolivia).

bird species breed. However, we have no information about the nesting of the species.

VOICE

Turdus sanchezorum has a varied repertoire. The species' most distinctive vocalization is a rising, querulous, mewling call note (Fig. 6A), unique among western Amazonian species of *Turdus*. Several other call notes have been recorded, including two rapid series of "cuk" notes (Fig. 6B, C), and a rather unusual call that begins with "cuk" notes and ends with one (Fig. 6D) or several musical, reedy notes (Fig. 6E). Finally, the song of *T. sanchezorum* (Fig. 6F) is a slow, mellow caroling in which individual phrases are slurred. Typically, song phrases are short (only four to ten notes) and follow frequent breaks over 2 sec in length.

The calls of *T. sanchezorum* so far recorded are very similar to those known from the species in the *T. nudigenis* clade. In Figure 6, we show examples of the "mewling" calls of *T. haplochrous* (Fig. 6G), *T. grayi* (Fig. 6H), *T. nudigenis* (Fig. 6I), *T. maculirostris* (Fig. 6J), and *T. rufiventris*

(Fig. 6K) for comparison with the mewling call of *T. sanchezorum* (Fig. 6A). This call seems to be a clear unifying character for the members of this clade. By comparison, *T. hauxwelli* lacks the mewling call. We believe that the inclusion of a mewling call as part of the repertoire of *T. hauxwelli* in various publications such as Ridgely and Greenfield (2001) and Collar (2005) is based on misidentified recordings of *T. sanchezorum* (see below). Instead, *T. hauxwelli* gives a series of falling or rising nasal "rhee?" notes (Fig. 6L, 5M).

The songs of the members of the *T. nudigenis* clade are uniformly leisurely, rich, slurred caroling phrases with frequent pauses. In these characters, *T. sanchezorum* fits in very well. *Turdus hauxwelli* and *T. fumigatus* differ in having longer, more rapidly delivered, unbroken songs with fewer rich, slurred phrases. As an example, we present an unsolicited song of *T. hauxwelli* (Fig. 6N). In addition, at least *T. hauxwelli* is known to respond to playback with a different song—one that includes shorter, choppy note-phrases, many "hisselly" notes (term from Kroodsma 2005:30), and mimicry (Fig. 6O, from the same individual as Fig. 6N). This song type is missing from the known repertoires

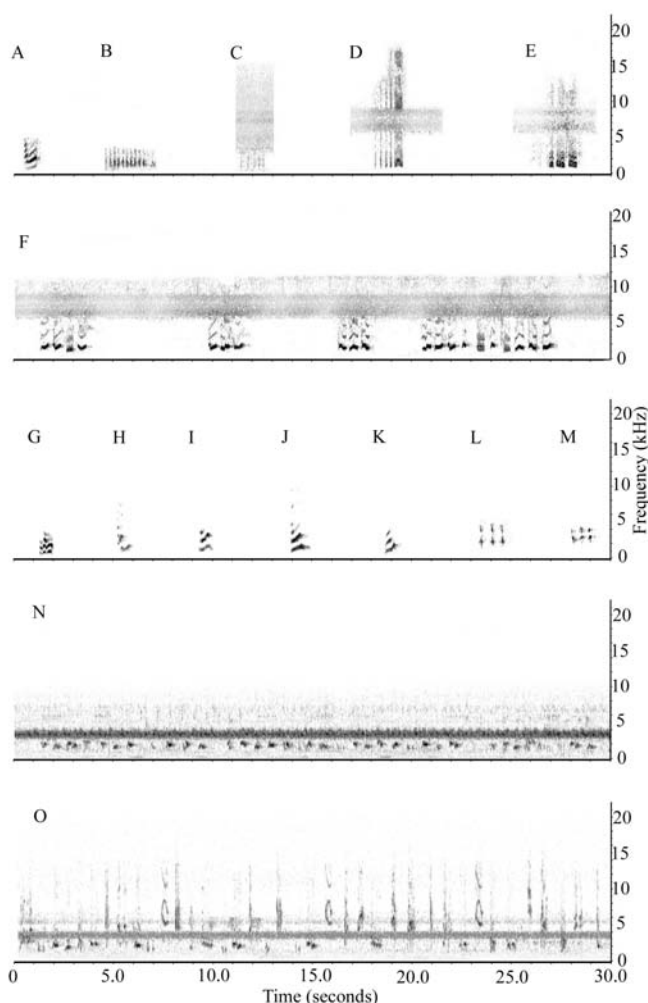


FIGURE 6. Vocalizations of *Turdus sanchezorum* with some comparative material of other species of *Turdus*. Vocalizations of *T. sanchezorum*: A, “mewing” call (T. A. Parker III, ML 34165; Peru: Loreto, Quebrada Yanamono, junction of ríos Napo and Amazonas, 12 January 1985). B, C, various “cuk” notes (B. M. Whitney; Peru: Loreto, Quebrada Yanamono, junction of ríos Napo and Amazonas, 6 August 2005). D, E, nasal call series (T. A. Parker III, ML 34155, 34165; Peru: Loreto, Quebrada Yanamono, junction of ríos Napo and Amazonas, 12 January 1985). F, song (T. A. Parker III, ML 34165; Peru: Loreto, Quebrada Yanamono, junction of ríos Napo and Amazonas, 12 January 1985). “Mewing” calls of other species of *Turdus*: G, *T. haplochrous* (DFL; Bolivia: Beni; north of Trinidad, 11 September 2010). H, *T. grayi* (DFL; Mexico: Oaxaca, Oaxaca City, 1 March 2007). I, *T. nudigenis* (DFL; Venezuela: Aragua, Cumboto, 31 January 2008). J, *T. maculirostris* (DFL; Peru: Tumbes, near Pozo del Pato, 11 June 2009). K, *T. rufiventris* (DFL; Bolivia: Santa Cruz, Chuchial, 16 August 1999). Vocalizations of *T. hauxwelli*: L, nasal rising call (DFL; Peru: San Martín, Quebrada Upaquiuhua, 13 August 2002). M, nasal rising call (T. A. Parker III, ML 29815; Peru: Madre de Dios, Cocha Cashu, 3 September 1982). N, “typical” song, unsolicited (DFL; Peru: San Martín, Quebrada Upaquiuhua, 20 July 2003). O, mimicry song, after playback (DFL; Peru: San Martín, Quebrada Upaquiuhua, 20 July 2003).

of the members of the *T. nudigenis* clade. A deeper comparison of the vocalizations of the members of the *T. nudigenis* clade is precluded at present because of the small sample sizes available to us.

At least two published compilations of sounds have included *T. sanchezorum* among recordings of *T. hauxwelli*. Hardy and Parker (1985) included the voice of true *T. hauxwelli* as cuts 1, 2, and 4 under that species name, but *T. sanchezorum* as cuts 3, 5, and 6. Moore (1997) included voice of true *T. hauxwelli* in his cuts 1, 3, and (presumably) 5, but *T. sanchezorum* as cuts 2 and 4. We located the following archived recordings we have identified as *T. sanchezorum*: Macaulay Library 29133, 34152, 34153, 34154, 34155, 34164, 34165, 34406; Xeno-canto 28115, 41071, 41072, 41114, 48046.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS OF *TURDUS SANCHEZORUM*

The *T. nudigenis* clade is widespread within the neotropics; its members are distributed allopatrically, occupying humid forest and edge, gallery forest, and semi-deciduous forest from Mexico to northern Argentina. Until now, it seemed to lack a member in Amazonia, but this gap has been filled by *T. sanchezorum* (Fig. 5). Most of the members of the *T. nudigenis* clade (with the notable exception of the almost unknown *T. haplochrous*) are normally fairly conspicuous, if not particularly brightly colored, and usually are first detected by their characteristic mewing call note (see Voice above). By comparison, the *T. fumigatus* complex (including *T. hauxwelli*), although similar to the *T. nudigenis* clade in its dull coloration and, for some members, choice of habitat, is more retiring and lacks the mewing call.

Turdus sanchezorum appears to be entirely allopatric from other members of the *T. nudigenis* clade (Fig. 5). It is separated from *T. grayi* and *T. maculirostris* to the north and west by the Andes, and from *T. rufiventris* by the Brazilian Shield to the southeast. *Turdus haplochrous* appears to be separated from *T. sanchezorum* by more than about 600 km to the south along the Rio Madeira drainage. The nearest site where we can find evidence for *T. nudigenis* is at Santarem, Pará state, Brazil, at the mouth of the Rio Tapajos and the type locality of *T. n. extimus*. Santarem is less than 150 km downriver on the south (right) bank of the Rio Amazonas from Parintins, the easternmost confirmed locality for *T. sanchezorum*. On the north (left) bank of the Rio Amazonas, *T. nudigenis* is known from Monte Alegre, Pará state, Brazil, where specimens (MPEG) and recordings (Xeno-Canto 7687) were taken by S. de Melo Dantas in a semi-deciduous forest-savanna habitat (pers. comm.). Whether the gaps between the distributions of *T. sanchezorum* and *T. haplochrous* and *T. nudigenis* are real or an artifact of sampling remains to be determined.

The distribution pattern exemplified by the sister taxa *T. sanchezorum* and *T. haplochrous* is not a novel one. Some other groups contain obviously closely related taxa that share a similar

distribution, with one member in *várzea* forest of Amazonia, another in the gallery forest of the Beni region of Bolivia. For example, *Ara ararauna* (Blue-and-yellow Macaw) is a widespread species of the humid neotropics whereas the rare and local *A. glaucogularis* (Blue-throated Macaw) is (presumably) a sister form that evolved in the Beni, where the two are syntopic. Highly distinctive forms—almost certainly best considered biological species—within the Plain Softtail, *Thripophaga fusciceps* (with *dimorpha* in western Amazonia and *fusciceps* in the Beni), and Velvet-fronted Grackle, *Lampropsar tanagrinus* (with *tanagrinus* in western Amazonia and *bolivianus* in the Beni) mirror even better the distributions of these two species of *Turdus* (B. Whitney, J. V. Remsen Jr., pers. comm.).

TURDUS SANCHEZORUM AND THE TAXONOMY OF THE *T. FUMIGATUS*/HAUXWELLI COMPLEX

During the 20th century, various ornithologists attempted to understand the complex biogeography of the members of the Cocoa Thrush (*Turdus fumigatus*) complex in Central and South America. Depending on the authority, this complex contains from one (*T. fumigatus*) to three (*T. fumigatus*, *T. obsoletus*, and *T. hauxwelli*) species, and several additional subspecies, most of which are allopatric, that have been variably shuffled from one species to another. In central Amazonia, however, two of these taxa (*T. fumigatus* and *T. hauxwelli*) appear to occur parapatrically, with perhaps a narrow zone of sympatry (Fig. 3). Morphological variation in this zone of apparent overlap caused some authors to suggest that the apparent clinal variation indicates introgression between the two forms (Snow 1985) or, alternatively, that the overlap of “parent morphotypes” at the same sites requires the two taxa to be considered separate species (e.g., Hellmayr 1934, Gyldenstolpe 1945a, b, 1951, Ripley 1964). Certainly, the two forms are similar in behavior, voice, and many plumage traits; the main difference is the degree of saturation of warm rufescent color of the plumage (especially ventrally), with *T. fumigatus* more saturated than *T. hauxwelli*. We note that some of the characters (e.g., upper surface of tail with “blue-purple sheen,” which when combined with brown would make the tail appear gray) used by Snow (1985) to define birds at the far “*T. hauxwelli*” end of the spectrum actually are characters of *T. sanchezorum*.

While examining specimens freshly received from the Olalla brothers, Hellmayr (1934) and Gyldenstolpe (1945a) both complained in their accounts of *T. hauxwelli* that the species was variable in some plumage and soft-part colors: both authors mentioned individuals with yellowish or olive bills as well as individuals with blackish bills. These comments were again repeated by Snow (1985), who studied the same specimens decades later. Clearly, the olive-billed specimens represent the then-unrecognized *T. sanchezorum*, and we are quite certain that those same specimens are among the specimens we list above for that species.

Now that we can remove the specimens of *Turdus sanchezorum* as a source of confusion regarding the distributions and

taxonomic status of *T. hauxwelli* with relation to *T. fumigatus* in Amazonia, it appears that the picture is still muddled in two areas: the north bank of the lower Rio Solimões and the lower Rio Madeira (Fig. 3). To settle the question of the evolutionary relationships within the *Turdus fumigatus* complex, we recommend more complete population sampling (with vouchered tissues) with the aim of producing a phylogenetic tree of the various populations within the complex. These data, as well as research into the habitat preferences, vocal repertoires, and breeding behaviors (and the presence/absence of interbreeding) within Brazil should finally put to rest the nagging question of the species-level relationships among the various members of the *T. fumigatus* complex.

IMPORTANCE OF CONTINUED COLLECTING

Despite there being more than 30 specimens of *Turdus sanchezorum* already deposited in various museums, it was not until modern (post-1960) specimens—complete with data about soft-part colors, molt, reproductive condition, etc.—were available, that this species was detected. Seasoned museum taxonomists such as Hellmayr (1934), Gyldenstolpe (1945a, b, 1951), and Snow (1985) all pondered the variation in *T. hauxwelli*, but none had the information available to recognize the undescribed form before them. In the field, *T. sanchezorum* has repeatedly been misidentified as *T. hauxwelli* or *T. lawrencei* even by the most experienced field ornithologists. Without the modern LSUMZ specimens that allowed JPO to note the correlation of the colors of the bill and orbital ring with the grayish tail, how much longer would *T. sanchezorum* have escaped notice? This case focuses a spotlight on the importance of continued collecting, even at oft-visited sites. We believe that critics of continued collecting, particularly of general collecting (e.g., Bekoff and Elzanowski 1997, Donegan 2000, 2008, American Bird Conservancy 2007), underestimate the importance of such collections in unraveling such complicated and intriguing stories such as that of *T. sanchezorum*, improving our understanding of the true biodiversity of our planet. Additional reasons supporting the continued collection of specimens and the importance of having vouchered tissue specimens have been published elsewhere (e.g., Remsen 1995, Peterson et al 2007). As an even more powerful vouchering technique, we emphasize the importance of recording the voice of a specimen subsequently collected (e.g., Cohn-Haft et al. 1997). As new techniques to study birds (and other organisms) evolve, individual specimens will prove yet more valuable. We cannot foresee a time when legally regulated, responsible specimen collection will not be one of the most powerful tools available for the study of all aspects of bird biology, particularly their phylogenetics, systematics, and taxonomy.

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