

Article



https://doi.org/10.11646/zootaxa.4320.2.11 http://zoobank.org/urn:lsid:zoobank.org:pub:0D3991A1-E8F2-4FB9-8261-36AF7DDD99D3

A new species of manakin (Aves: Pipridae; *Machaeropterus*) from Peru with a taxonomic reassessment of the Striped Manakin (*M. regulus*) complex

DANIEL F. LANE^{1,3}, ANDREW W. KRATTER^{1,2} & JOHN P. O'NEILL¹

¹LSU Museum of Natural Science, 119 Foster Hall, Baton Rouge, Louisiana, USA, 70803-3216.

Abstract

We describe a new taxon of manakin in the *Machaeropterus regulus* complex, from the foothills of southwestern Loreto and northern San Martín departments, Peru. This new form appears to be almost identical morphologically to the Tepui form *M. regulus aureopectus* but differs strongly from that and all other members of the *M. regulus* complex in voice. Therefore, we conclude that this population represents a new biological species that we here name *Machaeropterus eckelberryi*. Based on voice and some morphological characters, we concur with several previous authors (e.g., Whittaker & Oren 1999; Snow 2004; Ridgely & Tudor 2009) that nominate *M. regulus* (Eastern Striped Manakin), of the Atlantic Forest of Brazil, should be separated as a biological species from the polytypic *Machaeropterus striolatus* of western South America (Western Striped Manakin), including *M. s. striolatus* of Amazonia, *M. r. obscurostriatus* and *M. r. zulianus* of the Venezuelan Andes, *M. r. antioquiae* of the Colombian Andes, and *M. r. aureopectus* of the tepuis region.

Key words: Vocal differentiation, San Martín, Cordillera Azul, suboscine, Neotropical, Aves

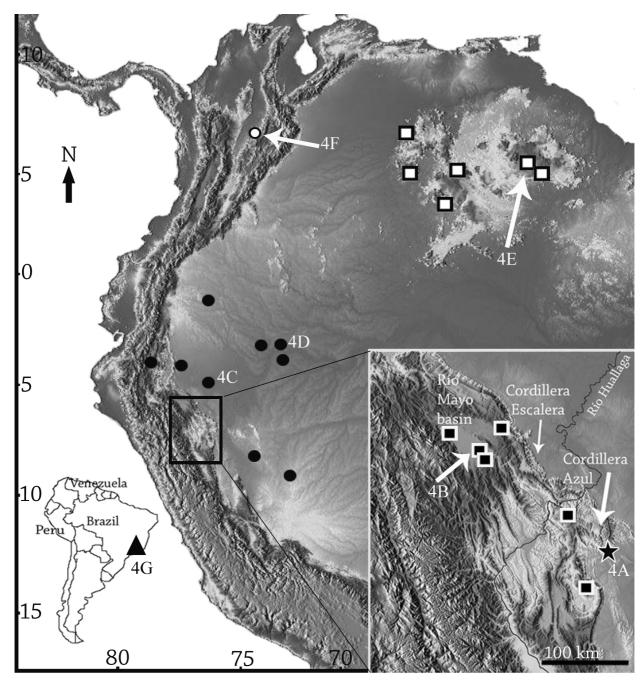
Introduction

The Striped Manakin *Machaeropterus regulus* (Hahn, 1818) is a complex of six named taxa found in humid lowland and foothill forests: *M. r. regulus* in eastern Brazil; *M. r. striolatus* (Bonaparte, 1837) in western Amazonia; *M. r. antioquiae* Chapman, 1924 in valleys of the western and central Andes of Colombia; *M. r. obscurostriatus* Phelps, Sr. & Gilliard, 1941 and *M. r. zulianus* Phelps, Sr. & Phelps, Jr., 1952 in the Andean slopes of western Venezuela; and *M. r. aureopectus* Phelps, Sr. & Gilliard, 1941 locally in the tepuis of southeastern Venezuela and nearby Brazil. Some authorities (e.g., Snow 2004; Ridgely & Tudor 2009; Gill & Donsker 2017) have suggested that the nominate form be separated from the remainder of the taxa, the latter then being called *M. striolatus*, based on differences in voice and plumage (Whittaker & Oren 1999; Snow 2004; Kirwan & Green 2012), but a lack of published data and rationale has prevented the AOS-SACC (Remsen *et al.* 2017) from changing the classification of these two groups.

In 1996, JPO led an avifaunal inventory in the Cordillera Azul of western Loreto dept., Peru (O'Neill *et al.* 2000; Schulenberg *et al.* 2001). The expedition's field party comprised personnel from Louisiana State University Museum of Natural Science (LSUMZ), including DFL and AWK, and the Museo de Historia Natural de la Universidad Mayor de San Marcos (MUSM), Lima, Peru. We encountered a unique, previously undescribed population of *Machaeropterus* that was clearly part of the *M. regulus* complex (Schulenberg *et al.* 2001). The highly distinctive advertising song of this population immediately distinguished it from the nearby Amazonian form *M. r. striolatus*. Four years later, on another LSUMZ/MUSM expedition that included JPO and DFL, we found this form in another section of the Cordillera Azul about 40 km to the southwest of the 1996 locality (Schulenberg *et al.* 2001). Subsequently, on 6 August 2003, DFL detected the same form on the flanks of Morro de Calzada, an isolated peak jutting from the floor of the Mayo valley of northern San Martín dept., about 180 km northwest of the Cordillera Azul sites, leading us to conclude that female specimens housed at LSUMZ and collected nearby in the Mayo valley area in 1977 and 1983 likely also represented this unnamed taxon.

²Current address: Florida Museum of Natural History, Box 117800, Gainesville, Florida, USA, 32611.

³Corresponding author. E-mail: dlane@lsu.edu



- Machaeropterus eckelberryi (★ type locality)
- M. r. striolatus
- M. r. aureopectus
- o M. r. antioquiae
- ▲ M. r. regulus

FIGURE 1. Map of distribution of *Machaeropterus eckelberryi* (inset map at lower right: black squares, star representing type locality, see "Distribution" for localities) with selected localities of *M. r. striolatus* from western Amazonia (black circles, LSUMZ specimens and XC170139), and *M. r. aureopectus* (white squares, from Phelps Collection and FMNH specimens, Hilty 2002, and XC66415) from the tepuis. Single localities are provided for *M. r. antioquiae* (white circle, XC16781), and *M. r. regulus* (continental map in lower left: black triangle, XC82253). Localities labeled with a number-letter code coincide with the letters of the recordings featured in Figure 4. Base map adapted from relief layer available at www.maps-for-free.com.

DFL reviewed material at the American Museum of Natural History, New York (AMNH; which also houses Phelps Collection types), and Field Museum of Natural History, Chicago (FMNH), made comparisons to named forms, and compiled documented localities of occurrence from both specimens and archived recordings (Fig.1). The undescribed population of *Machaeropterus* appears, based on present knowledge, to be restricted to poor-soil humid woodlands, particularly on ridges, that are present around the Mayo valley, thence southeast along the Cordillera Azul (and presumably on the intervening Cordillera Escalera) at elevations of ca. 400–1400 m. The new taxon phenotypically resembles the tepui form *M. r. aureopectus*, with males sharing the yellow chest patch, but differs subtly in coloration (Fig. 2) and morphology (Table 1, Fig. 3). Remarkable distinctions in the advertising song of the two forms indicate, however, that the Peruvian form is best recognized as a species separate from *M. r. aureopectus* (Fig 4). In this last character, the lack of undertones, in combination with a one-noted rising vocalization in the Peruvian form, rather than two-noted falling vocalization with undertones as with all other Amazonian forms, or a rather different falling monosyllabic vocalization with undertones, as in the eastern Brazilian nominate form, strongly suggest that the Peruvian form is far down a unique evolutionary trajectory, and should be considered a separate species. We therefore propose to name this new species:

Machaeropterus eckelberryi, species novum

Painted Manakin

Holotype. MUSM 17725, male, netted and prepared on 12 July 1996 by John P. O'Neill, personal catalog number 7795. PERU: dept. Loreto; ca. 77 km WNW Contamana, 7°5'S, 75°39'W, ca. 1000m. Tissue B-27712 (deposited at LSUMZ).

Description of holotype. Specimen neither worn nor showing molt. Crown from culmen to occiput deep crimson red closest to 7.5R 3/12 (color standards from Munsell n.d.) with whiter bases to feathers showing where the feathers are disheveled. Lores, malar, and auriculars olive closest to 7.5Y 4/4, with rear supercilium grayer olive (7.5Y 5/2). Nape to uppertail coverts, wing coverts, and outer margins of secondaries olive closest to 10Y 4/6. Dorsal surface of remiges dull olive gray (10Y 3/4) with whitish inner edges, particularly pronounced on inner secondaries (often visible even when wing closed), but lacking on tertials. Shafts of secondaries 6–8 thickened, slightly twisted outward about 3–4mm from tip, and notably stunted, exposing the white inner, ventral webs of the (more distal) secondaries on the closed wing. Underwing coverts whitish. Rectrices dull grayish olive (7.5Y 4/2) dorsally, with white on underside of inner webs and on ventral surface of shafts (which seem stiffened). Feathers from chin to upper breast dingy whitish with pale gray tips (10YR 5/2). A narrow whitish collar separates the throat from the chest, which is pale lemon-yellow closest to 7.5Y 8.5/12. Feathers of belly and undertail coverts elongated and lanceolate with a whitish streak along the shaft and broad chestnut (2.5YR 3/6) margins. Label data: weight 10g. Iris red-brown; bill black, base of mandible grayish-pink; tarsi and toes medium brown; netted in humid montane forest; testes 3x2 mm; skull 100% ossified; trace fat; no molt; no bursa; stomach empty.

Diagnosis. A tiny manakin (Pipridae) clearly assignable to the *Machaeropterus regulus* complex by a combination of male plumage characters including red crown, olive upperparts becoming grayish on face, whitish throat, and white and chestnut streaking below. Additionally, the rachises of secondaries 6–8 are thickened but attenuating distally and bending slightly outward about 3 mm before tip, and the rectrices have stiffened rachises. The new form is most similar to *M. r. aureopectus* in having a bold yellow chest patch, but differs in having upperparts greenish-olive (less golden-olive than *M. aureopectus*), similar to 7.5Y 4/6 on the back and slightly more golden, similar to 7.5Y 5/8, on rump (Fig. 2), in morphometrics (see below; Table 1; Fig. 3), and voice (see below; Fig. 4). Females are very similar to females of *M. r. aureopectus*, differing, like males, in being slightly deeper greenish-olive (rather than golden-olive); they appear to be indistinguishable from female *M. r. striolatus*.

Etymology. We are pleased to name this colorful manakin after one of the greatest American bird artists of the twentieth century, Donald R. Eckelberry. Not only did Eckelberry's artwork increase the world's awareness of the beauty of the birds of the Americas, particularly the Neotropics, but he also was a great force in the establishment of the Asa Wright Nature Center in Trinidad, and a wonderful mentor to young bird artists (Angell 2001; Gilbert & Amadon 2001). Both JPO and DFL personally benefitted from Eckelberry's generous advice and coaching in artistic matters. Don Eckelberry passed away on 14 January 2000, and we are sorry he did not live to see this paper published. We are, however, pleased to say that he was aware of our intention to grace this bird with his name and



FIGURE 2. Comparison of ventral and dorsal plumage of some taxa in the *Machaeropterus regulus* complex. Males are on left, females on right, except in the case of *M. regulus*, in which the male is above and the female below. Specimens exhibited (male, female): *M. eckelberryi* (MUSM 17725 [holotype], LSUMZ 161896); *M. regulus aureopectus* (FMNH 344155, 344154); *M. r. striolatus* (LSUMZ 115836, 110617); *M. r. regulus* (AMNH 43053, 493115).

excited by the prospect. May his influence continue to inspire other nature artists in the future! The suggested English name refers to the colorful plumage of the male, and also serves as a nod to Eckelberry's forte. If taxonomic committees that follow our recommendation of splitting up the *M. regulus* complex (see below) would prefer all sibling species retain "Striped" in the English name, a fine alternative name for *M. eckelberryi* would be "Peruvian Striped Manakin."

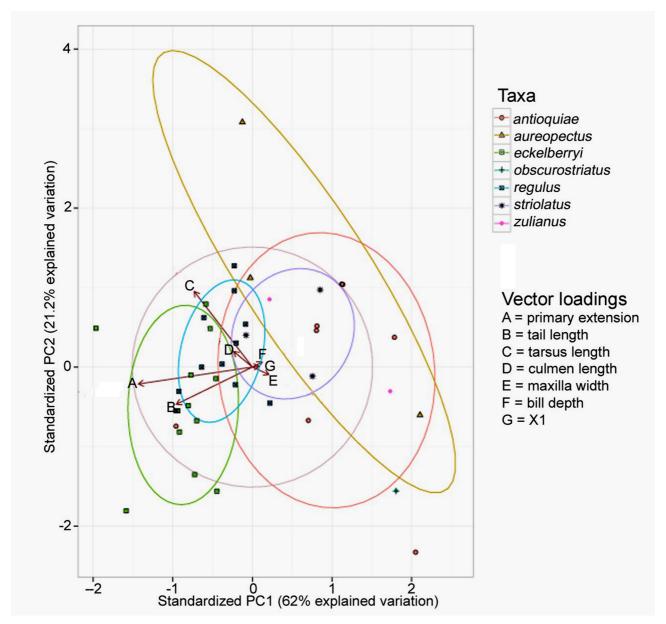


FIGURE 3. Principal components analysis (PCA) of morphometrics of specimens of the *Machaeropterus regulus* complex (see also Table 1). See "Specimens examined" for list of specimens measured. Vector loadings show which measurements had the strongest effect on the plot analysis.

Distribution. Based on localities vouchered by specimens and recordings ("XC###"" refers to recordings available at www.xeno-canto.org/####), it appears that *M. eckelberryi* is restricted to a fairly small region in northern Peru in the departments of San Martín and Loreto (Fig. 1). Localities in San Martín dept. are: ca. 50 km (by road) west of Rioja, ca. 775m (LSUMZ 85047) and ca. 825m (LSUMZ 85046); Morro de Calzada, 6°01'S, 77°03'W, 1000m (XC17041–17043); Quebrada Mishquiyacu, 6°06'S, 77°00'W, 1000m (XC23488), 1300m (XC83479), 1600m (XC161229); ca. 15 km by trail NE Jirillo on trail to Balsapuerto, 1350m (LSUMZ 117122–117124), ca. 5 km S Sianbal, 6°41'S, 76°05'W, 575-950m (Merkord et al. 2009). Loreto dept.: ca. 85 km SE Juanjui 7°34'S, 75°55'W, 1100m (LSUMZ 171009, 171010, MUSM 22661, 22693); ca 77 km WNW Contamana 7°5'S,

75°39'W, 1000m (LSUMZ 16893–16899, MUSM 17721–17726). A female specimen (AMNH 822267), taken 2 November 1971 from "59 km W of Pucallpa [Ucayali department]", could potentially also represent *M. eckelberryi*, but its identity should be confirmed by genetic analysis or by visiting the locality and documenting male plumage and voice there. The taxon is probably truly restricted to this foothills region of the north-central Peruvian Andes, particularly where there are short-stature woodlands on poor, sandy-soil ridges.

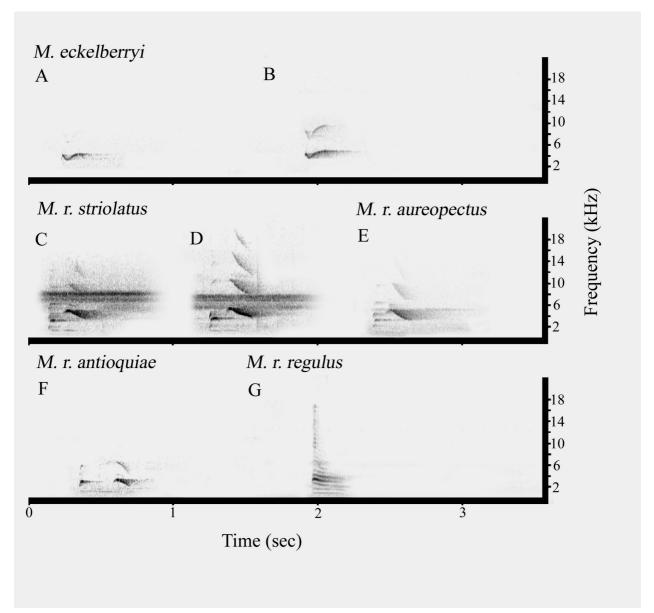


FIGURE 4. A comparison of "advertising songs" of some taxa in the *Machaeropterus regulus* complex. A) *M. eckelberryi* (PERU: Loreto dept.; ca 77 km WNW Contamana, ca. 1000m. 12 July 1996. D. F. Lane, XC170145). B) *M. eckelberryi* (PERU: San Martín dept.; Morro de Calzada, ca. 1000m. 29 July 2005. D. F. Lane, XC170143). C) *M. regulus striolatus* (PERU: Loreto dept.; Jeberos, ca. 350m. 15 June 2001. D. F. Lane, XC170138). D) *M. r. striolatus* (PERU: Loreto dept.; Oran, ca 200m. 24 July 2013. D. F. Lane, XC170139). E) *M. r. aureopectus* (VENEZUELA: Bolivar state; El Pauji. 4 December 2010. A. Renaudier, XC66415). F) *M. r. antioquiae* (COLOMBIA: Santander dept.; Serranía de la Quinchas, RNA El Paujil. F. Lambert, XC16781). G) *M. r. regulus* (BRAZIL: Rio de Janeiro; Reserva Ecológica de Guapiaçu. J. Minns, XC82253). Notice the light flat lines (around 1kHz and 3 kHz) "underscoring" the notes of the songs in figures C-G, but lacking in A and B. Also note that the song of *M. r. antioquiae* (F) is very similar in structure to those of *M. r. striolatus* (C, D), but the spacing between the two main notes is longer. The dark band running above the loudest fundamental frequencies of the notes in C and D is insect noise. "XC####" refers to recordings available at www.xeno-canto.org/####.

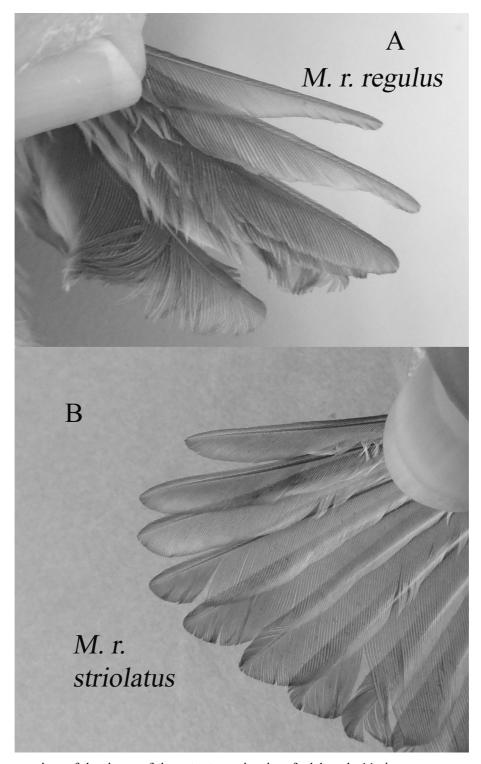


FIGURE 5. A comparison of the shapes of the outer two primaries of adult male *Machaeropterus r. regulus* (A, AMNH 493126) and *M. r. striolatus* (B, LSUMZ uncataloged, GFS 465). The attenuated shape of these remiges in *M. r. regulus* is unique within the Striped Manakin complex; all other members share the wing shape exhibited here by *M. r. striolatus*.

Specimens examined. *Machaeropterus eckelberryi*: MUSM 17721 (female); 17725 (male, holotype); 17722–17724, 17726, 22661, 22693 (males); LSUMZ 85046, 85047, 117122–117124, 161896, 161898 (females); 161893–161895, 161897, 161899, 171009, 171010 (males). *M. r. aureopectus*: Phelps 12847 (male, holotype); FMNH 344154 (female); 344155 (male). *M. r. striolatus*: AMNH 6792, 6793 (males); 822267 (female, taxon not certain). LSUMZ 110587, 173118, 173120 (females); 110585, 110586, 110593, 110594, 110596, 115845, 156714–156716, 173119, 173121 (males). *M. r. antioquiae*: AMNH 133839 (male, holotype); AMNH 94973, 133838,

493128, 493129, 824685 (males); 133840, 133841 (females); LSUMZ 38712, 61663 (males). *M. r. zulianus*: Phelps 998 (male, holotype); 468596 (male). *M. r. obscurostriatus*: Phelps 9816 (male, holotype). *M. r. regulus*: AMNH 6792, 6793, 43053, 43055, 493117, 493119–493124, 493126, 131037 (males); AMNH 493115 (female?).

Variation in the type series. We designate all specimens of M. eckelberryi that we examined (listed above) as paratypes, and all were compared alongside the holotype. Among adult males of M. eckelberryi, there is little plumage variation, but most are whiter-throated than the holotype, with only a few (e.g., LSUMZ 161894, 161899, MUSM 17726) approaching it in its dingy grayness. On some female M. eckelberryi (LSUMZ 85046, 161896, 161898, MUSM 17721), there is an indistinct whitish inner edge to rectrices (visible from underneath), but this is not apparent in all specimens (and is lacking in M. r. striolatus and the only M. r. aureopectus female available to us, FMNH 344154). Females lack the modified, thickened shafts on the inner secondaries and stiffened shafts of the rectrices. The plumage of immature males (skull 100% ossified in MUSM 22693; 99% ossified and bursa of Fabricius 4x2 mm in LSUMZ 171009) is female-like overall, but there is already a suggestion of a pure yellow breast band, and LSUMZ 171009 has one crimson crown feather. Males in immature plumage also lack the modified inner secondaries of adult males. The feather modifications exhibited by adult male M. eckelberryi are shared by M. r. striolatus, M. r. zulianus, M. r. antioquiae, M. r. aureopectus, and M. r. regulus. By comparison, the holotype of M. r. obscurostriatus seems to have secondaries 5–8 modified. Furthermore, it is noteworthy that the outer two primaries of M. r. regulus are distally attenuated and slightly curved (Fig. 5). Based on label data, irides tend to be chestnut or brick red on adult male M. eckelberryi, but dark brown on most females and immature males. Tarsi and toes vary from dark brown to pinkish-gray and have yellow soles. Specimen preparators described maxilla color as blackish, often with grayish-black tomia, and mandibles as pinkish-gray or gray.

Morphometrics. DFL made standard measurements of the museum skins listed in the "specimens examined" section (above): culmen (measured from distal edge of nares to maxilla tip); bill depth (at nares); maxilla width (at nares); flat wing; primary extension (measured from tip of longest secondary to tip of longest primary); tail length (from insertion point to tip of longest rectrices); and tarsus length (measured from joint of tarsometatarsus to the underside of the hallux at its base). Bret Whitney took measurements (not including primary extension) of the larger series of *M. r. regulus* available at the Museo Zoologia da Universidade de Sao Paulo (MZUSP) to augment our sample size of that taxon. Whitney measured the following MZUSP specimens: MZUSP 33495, 33497, 91013, 91472, 91473 (females); 33494, 91011, 91474, 91475, 94423, 94425–94427 (males). The means and standard deviations of these measurements were calculated and are presented in Table 1. We present a PCA of the measurements (minus those from MZUSP due to the missing primary extension measurement) in Fig. 3 to illustrate the overlap in morphospace among the various taxa in the *M. regulus* complex. In this PCA, we see no overlap in the plotting of *M. eckelberryi* and *M. r. aureopectus*, indicative of apparent morphological distinctiveness, particularly in primary extension and tail length, but note that sample size for *M. r. aureopectus* is very small.

Vocalizations. Members of *Machaeropterus* are generally quiet and unobtrusive unless a male is giving an advertising song from a perch. This song can be vocally produced, as by *M. eckelberryi*, *M. r. regulus*, *M. r. striolatus*, *M. r. aureopectus*, *M. r. antioquiae*, and the Fiery-capped Manakin *M. pyrocephalus* (Sclater), or mechanically produced using modified secondaries, as by the Club-winged Manakin *M. deliciosus* (Sclater). In all members of the genus, the advertising song is short, fairly simple in structure, and strongly stereotyped. When a female is present, the singing male may become more active and perform a courtship display (e.g., as described for *M. r. regulus* in Sick 1993: 500), but these displays have not been fully described for several members of *Machaeropterus* (Bostwick 2000; Schulenberg *et al.* 2010; Kirwan & Green 2012), and we have not observed any such display by *M. eckelberryi* (although the thickened secondary shafts and stiffened rectrices suggest it must have a display involving mechanical sound production), so we will not consider the courtship display further.

The advertising song of *M. eckelberryi* is noticeable and persistent, and often is the best means of detecting the bird; it may be delivered as rapidly as 30 songs/min, at shorter intervals than is typical of any other taxon in the *M. regulus* complex on average. It is a simple, unmodulated, rising "chiWEE?" (Fig. 4A, B), which is quite distinct from the homologous monosyllabic "DJEW!" of *M. r. regulus* (Fig. 4G), and the two-noted "cli-CHEW!" vocalizations of *M. r. striolatus* (Fig. 4C, D), *M. r. aureopectus* (Fig. 4E), and *M. r. antioquiae* (Fig. 4F). In addition, the advertising song of these latter three taxa also has a lower-frequency hollow, whistled component. After considering that this undertone may be produced by mechanical means, much in the same way as Bostwick (2000) described for *M. deliciosus*, DFL discovered that this undertone is also given by *M. r. striolatus* when vocalizing in the hand (when their wings are immobilized), and thus we can discard this hypothesis. There is no such audible undertone associated with the advertising song of *M. eckelberryi*.

TABLE 1. Selected measurements (in mm) of specimens of *Machaeropterus eckelberryi* and other taxa in the *M. regulus* complex. Specimens measured are listed in "Specimens examined" in the text. Measurements are given as means followed by standard deviation (when applicable). *= damage to a specimen precluded taking this measurement. †=MZUSP specimens excluded from this measurement.

Taxon	Sex (n)	Flat wing	Primary extension	Tail	Tarsus	Culmen
M. eckelberryi	F (7)	52.8 (<u>+</u> 1.6)	12.5 (<u>+</u> 1.4)	19.8 (<u>+</u> 1.6)	14.3 (<u>+</u> 0.5)	6.4 (<u>+</u> 0.3)
M. eckelberryi	M (12)	54.7 (<u>+</u> 1.1) 52.9	13.8 (±1.1)	19.5 (±1.4) 23.7	14.8 (±0.8) 15.3	6.2 (±0.3)
M. r. aureopectus M. r. aureopectus	F (1) M (2)	48, 52	9.3 10, 12	16, 21	15.3	6.6 6.4*
M. r. striolatus	F (3)	49.5 (<u>+</u> 0.9)	11 (<u>+</u> 1.2)	20.5 (<u>+</u> 2.4)	14.4 (<u>+</u> 0.5)	6.9 (<u>+</u> 0.1)
M. r. striolatus	M(11)	50.7 (<u>+</u> 1.1)	12.2 (<u>+</u> 1.1)	20.1 (<u>+</u> 1.2)	14.3 (<u>+</u> 0.5)	$6.3 (\pm 0.4)$
M. r. antioquiae	F (2)	48, 49	8.4, 9.6	17.1, 20.7	13.9, 14	6.4, 7
M. r. antioquiae	M(8)	50.2 (<u>+</u> 2.0)	11.3 (<u>+</u> 01.9)	18.2 (<u>+</u> 1.9)	14.1 (<u>+</u> 0.5)	$6.3 (\pm 0.4)$
M. r. obscurostriatus	M(1)	50	10	15	13	*
M. r. zulianus	M (2)	50, 53	9, 10	17, 19.8	13, 15.3	8.5, 6.6
M. r. regulus	F (6)	51.9 (<u>+</u> 1.9)	11.7†	19.9 (<u>+</u> 1.5)	14.6 (<u>+</u> 0.6)	$6.0 (\pm 0.5)$
M. r. regulus	M (21)	53.5 (<u>+</u> 1.0)	12.8 (<u>+</u> 0.9)†	20.7 (<u>+</u> 1.8)	14.4 (<u>+</u> 1.2)	6.1 (<u>+</u> 0.7)

The single-noted, rising inflection, in addition to the missing low frequency band, of the advertising song of M. eckelberryi immediately distinguishes it from all other taxa in the complex. The songs from two populations within M. r. striolatus, one from only about 100 km from the nearest population of M. eckelberryi (Fig. 4C) and another from near the type locality (Fig. 4D), but on the opposite bank of the Amazon River, show no difference in structure from one another, supporting the widely held suspicion that voice is innate in most suboscine passerines, including piprids. The advertising song of M. r. antioquiae from the Colombian Andes is very similar to M. r. striolatus, differing only in having a longer pause between the two syllables. The song of M. r. aureopectus is poorly known, but appears to be identical to that of M. r. striolatus based on two recordings (XC66401, XC66415) from El Pauji, eastern Bolivar state, Venezuela (Fig. 4E), and recordings of six individuals kindly supplied by Kevin Zimmer from the Pacaraima Mountains, west of Santa Elena, Venezuela. Hilty (2002) mentioned another record from 15 km west of Santa Elena de Uairén (a locality near El Pauji) and implied that the voices of birds from the Venezuelan Andes and the tepui region of Amazonas state are similar. Two recordings from the Venezuelan Andes, thus presumably of M. r. obscurostriatus (XC42943, 42944), also sound identical to vocalizations of M. r. striolatus and M. r. aureopectus. Nominate M. r. regulus sounds very different from M. eckelberryi as well as from M. r. striolatus, M. r. aureopectus, M. r. obscurostriatus, and M. r. antioquiae (we call these last four taxa, and also zulianus, the "striolatus group" hereafter) as has been previously mentioned (Whittaker & Oren 1999; Snow 2004; Ridgely & Tudor 2009; Kirwan & Green 2012; Fig. 4).

Remarks. DFL's observations of *Machaeropterus eckelberryi* suggest that its behavior is very similar to that of *M. r. striolatus*. Males and females of *M. eckelberryi* both tend to remain in the mid-story and canopy of shorter-stature (5–20m canopy height) woodland, particularly around trees in the family Melastomaceae, the fruits of which are an important part of their diet (pers. obs.). A male's persistent advertising song is given from one of several perches on a small territory in a dispersed or exploded lek (Prum 1994; Kirwan & Green 2012), just below the canopy. The small size and relatively inactive behavior of these manakins can make them difficult to spot, even when their general position is revealed by persistent vocalization. Both sexes can also be observed as they forage at fruiting trees, from which they pluck small, berry-sized fruits while performing brief hovering maneuvers typical of most small piprids. Presumably, these manakins also eat some arthropods to supplement their largely frugivorous diet (Snow 2004). We have no information on nesting habits of *M. eckelberryi*, but specimens collected in early July and early August appeared to be entering breeding condition (males with testes over 4x2mm, females with ova over 1mm diameter), suggesting that breeding begins near the end of the dry season (August–October). Gonad data from female specimens which we suspect to be *M. eckelberryi* (from NE of Jirillo, San Martín dept.) from November did not indicate breeding condition.

Within its range, M. eckelberryi does not appear to come into contact with any other member of the M. regulus group, although there is a population of M. r. striolatus only about 100 km to the northeast of the Mayo valley localities, where specimens (e.g., LSUMZ 173121) document M. r. striolatus in white-sand forest at Jeberos, Loreto dept., at 165m elevation (Fig. 1). Machaeopterus r. striolatus is typically a species of lowland terra firme forest, where there are fruiting melastomes (pers. obs.), however, it reaches elevations of about 1100m locally in southern Ecuador (Ridgely & Greenfield 2001). We suspect that the geologic formations of the Cordillera Azul/ Escalera and the Mayo valley act as a barrier separating M. eckelberryi from the nearby, lower-lying habitat of M. r. striolatus. Available records of M. r. aureopectus indicate that it is largely a species of ridges and higher elevations—the holotype of the taxon is from about 550m, and the two FMNH specimens are from 900m. Kevin Zimmer (in litt., Feb. 2016) noted that he had encountered M. r. aureopectus west of Santa Elena, Bolivar, Venezuela, at about 940m elevation. Hilty (2002) noted that Striped Manakin (referring to aureopectus, obscuriostriatus, and zulianus) occurs in Venezuela at elevations from 100-1200m, with most records above 300m. In short-stature woodlands of the Mayo Valley, M. eckelberryi does occur in syntopy with the slightly smaller, congeneric Fiery-capped Manakin M. pyrocephalus, although the latter tends to be found in disturbed habitats and flatter terrain (DFL, pers. obs.). To date, fieldwork in the Cordillera Azul has only detected M. pyrocephalus at low elevations (below 400m) on the Río Huallaga side, below the elevations preferred by M. eckelberryi there (Schulenberg et al. 2001; Merkord et al. 2009).

Despite the fairly limited distribution of *M. eckelberryi*, its presence within one of Peru's largest national parks (Parque Nacional Cordillera Azul), and its preference for poor-soil environments unlikely to be converted to agriculture suggests that the taxon is probably not in any serious conservation danger. A review of satellite imagery of the region suggests that there has been minimal anthropogenic damage to the ridges that we suspect hold its preferred habitat on the eastern flanks of the cordilleras Escalera and Azul.

Taxonomy within the Machaeropterus regulus complex. At present, there is some taxonomic turmoil regarding the Machaeropterus regulus complex, with some authorities considering it two species (e.g., Snow 2004; Ridgely & Tudor 2009; Gill & Donsker 2014), and others retaining all taxa as one species (e.g., Kirwan & Green 2012; Remsen et al. 2014). Our initial reluctance to describe M. eckelberryi, despite recognizing that it was likely a new taxon, was because of the lack of crucial information about the morphologically very similar M. r. aureopectus. Their similarity suggested a sister relationship to us, but convergence in plumage characters could not be ruled out without genetic analyses. Further, the presence of an isolated population of several "Guianan" or "Tepui" taxa in the Cordillera Azul and nearby San Martín region of Peru provided a pattern to which Machaeropterus could conceivably conform. These include Cnemotriccus fuscatus duidae Zimmer; Cotinga cotinga (Linnaeus); Tachyphonus phoenicius Swainson; Tangara cayana (Linnaeus); Tangara varia (Statius Müller); and Euphonia plumbea Du Bus de Gisignies. Unfortunately, M. r. aureopectus remains a poorly known and understudied taxon; even its distribution is poorly known, as exemplified by the fact that the first probable specimen (a female) of this taxon from Guyana was not published until 1998 (Agro & Ridgely 1998). More information on the life history and voice, and additional specimens, including tissue samples, of M. r. aureopectus would be very useful for a more in-depth study of the taxonomic and systematics of the M. regulus complex. In lieu of genetic data, however, we use voice as a proxy to indicate genetic similarity, as differing vocalizations among most suboscine passerines have been shown to correlate strongly with genetic differentiation (e.g., Kirwan and Green 2011:26). The strong distinction in note structure in the advertising songs between M. eckelberryi and the striolatus group has led us to the conclusion that M. eckelberryi is most appropriately considered a biological species apart from the rest of the *striolatus* group.

In addition to the remarkable vocal differentiation of advertising songs of the *striolatus* group and nominate *M. regulus* (Fig. 4) cited above, their differences are further augmented by the distinctive, attenuated outer two primaries of *M. r. regulus* (Fig. 5). This character is unique within the *M. regulus* complex, and noteworthy in not having been mentioned in the literature previously. Taken together, these characters point to the presence of two biological species within the existing *M. regulus* (*sensu lato*), in addition to the new *M. eckelberryi*. Thus, we suggest a systematic reorganization to recognize a monotypic *M. regulus* (Eastern Striped Manakin), a polytypic *M. striolatus* (including *M. s. antioquiae*, *M. s. aureopectus*, *M. s. obscurostriatus*, *and M. s. zulianus*; Western Striped Manakin), and a monotypic *M. eckelberryi* (Painted Manakin).

Acknowledgments

We gratefully recognize our esteemed colleagues of the 1996 and 2000 expeditions of the LSUMZ who worked so hard and provided great companionship: Letty Alamia, Christian Albujar, Jim Armacost, Louise Augustine, Angelo Capparella, Cecilia Fox, Tom Hurd, Manuel Sanchez, Marta Chavez de Sanchez, Abraham Urbay, and Thomas Valqui. Bret Whitney kindly measured specimens at the MZUSP collection. We thank the curators and collection managers of MUSM (Irma Franke and Letty Salinas) and FMNH (David Willard, John Bates, and Ben Marks) for permitting loans of specimen material to us, the MZUSP (Luis Fabio Silveira) for allowing Bret Whitney access to specimens, and the AMNH (George Barrowclough, Peter Capaniolo, and Paul Sweet) for allowing us access to the collection there. Fieldwork that resulted in additional observations by DFL was partially financed by WINGS and Field Guides tour companies. Jeremy Minns and Frank Lambert kindly permitted us use of their recordings posted to the website www.xeno-canto.org for the sonogram figure; Alexandre Renaudier had passed away before we were able to request permission. Kevin J. Zimmer sent much-appreciated recordings and field notes of *M. s. aureopectus* from Venezuela. Ryan Terrill helped with statistical analyses. Collecting permits were issued by the Instituto Nacional de Recursos Naturales (INRENA) in Lima, Peru. This paper was improved by comments by Mike Harvey, Guy Kirwan, Pamela Rasmussen, Van Remsen, Glenn Seeholzer, Bret Whitney, and Kevin Zimmer.

Literature cited

Agro, D.J. & Ridgely, R.S. (1998) First record of the Striped Manakin *Machaeropterus regulus* in Guyana. *Bulletin of the British Ornithologists' Club*, 118, 122–123.

Angell, T. (2001) Don Richard Eckelberry (obituary). Ornitologia Neotropical, 12, 357–359.

Bonaparte, C.L. (1837) The Prince of Musignano laid before the meeting the following communication. *Proceedings of the Zoological Society of London*, 5, 108–122.

Bostwick, K.S. (2000) Display behaviors, mechanical sounds, and evolutionary relationships of the Club-winged Manakin (*Machaeropterus deliciosus*). *Auk*, 117, 465–478.

https://doi.org/10.1642/0004-8038(2000)117[0465:DBMSAE]2.0.CO;2

Chapman, F.M. (1924) Descriptions of new birds from Ecuador, Colombia, Peru, and Bolivia. *American Museum Novitates*, 138, 1–16.

Gilbert, A.E. & Amadon, D. (2001) In Memorium: Don Richard Eckelberry 1921–2001. Auk, 118, 736–739.

Gill, F. & Donsker, D. (Eds.) (2017) *IOC World Bird List*. Version 4.1. Available from: http://www.worldbirdnames.org/bow/cotingas/ (accessed 15 February 2014)

https://doi.org/10.14344/IOC.ML.4.1

Hahn, C.W. (1818) Vögel aus Asien, Afrika, Amerika und Neuholland: in Abbildungen nach der Natur. Privately published, Nürnberg, unpaginated.

Hilty, S.L. (2002) Birds of Venezuela. 2nd Edition. Princeton University Press, Princeton, New Jersey, 878 pp.

Kirwan, G.M. & Green, G. (2011) Cotingas and Manakins. Princeton University Press, Princeton, New Jersey, 624 pp.

Merkord, C.L., Mark, T., Susanibar, D., Johnson, A. & Witt, C.C. (2009) Avifaunal survey of the Río Chipaota valley in the Cordillera Azul region, San Martín, Peru. *Ornitologia Neotropical*, 20, 535–552.

 $\label{thm:munsell} \mbox{Munsell [No date]} \ \mbox{\it The Munsell Book of Color.} \mbox{\it Gretag Macbeth, New Britain, New York.}$

O'Neill, J.P., Lane, D.F., Kratter, A.W., Capparella, A.P. & Fox J., C. (2000) A striking new species of barbet (Capitoninae: *Capito*) from the eastern Andes of Peru. *Auk*, 117, 569–577.

https://doi.org/10.1642/0004-8038(2000)117[0569:ASNSOB]2.0.CO;2

Phelps, W.H. Sr. & Gilliard, E.T. (1941) Seventeen new birds from Venezuela. American Museum Novitates, 1153, 1–17.

Phelps, W.H. Sr. & Phelps Jr., W.H. (1952) Nine new birds from the Perijá mountains and eleven extensions of ranges to Venezuela. *Proceedings of the Biological Society of Washington*, 65, 89–108.

Prum, R.O. (1994) Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). *Evolution*, 48, 1657–1675.

https://doi.org/10.2307/2410255

Prum, R.O. (1998) Sexual selection and the evolution of mechanical sound production in manakins (Aves: Pipridae). *Animal Behavior*, 55, 977–994.

https://doi.org/10.1006/anbe.1997.0647

Remsen, J.V., Jr., Areta, J.I., Cadena, C.D., Claramunt, S., Jaramillo, A., Pacheco, J.F., Pérez-Emán, J., Robbins, M.B., Stiles, F.G., Stotz, D.F. & Zimmer, K.J. ((2017) A classification of the bird species of South America. American Ornithologists' Union. Available from: http://www.museum.lsu.edu/~Remsen/SACCBaseline.html (accessed 15 February 2014).

Ridgely, R.S. & Greenfield, P.J. (2001) The Birds of Ecuador: Field Guide. Cornell University Press, Ithaca, New York, 740 pp.

- Ridgely, R.S. & Tudor, G. (2009) Songbirds of South America. University of Texas Press, Austin, Texas, 750 pp.
- Schulenberg, T.S., O'Neill, J.P., Lane, D.F., Valqui, T. & Albujar, C. (2001) Birds. *In:* Alverson, W.S., Rodriguez, L.O. & Moskovitz, D.K. (Eds.), Perú: Biabo Cordillera Azul. *Rapid Biological Inventories*, 2, pp. 146–155.
- Schulenberg, T.S., Stotz, D.F., Lane, D.F., O'Neill, J.P. & Parker III, T.A. (2010) *Birds of Peru. Revised Edition.* Princeton University Press, Princeton, New Jersey, 664 pp.
- Sick, H. (1993) Birds in Brazil. Princeton University Press, Princeton, New Jersey, 703 pp.
- Snow, D.W. (2004) Family Pipridae (Manakins). *In*: del Hoyo, J., Elliott, A. & Christie, D.A. (Eds.), *Handbook of Birds of the World. Vol. 9*. Lynx Edicions, Barcelona, 110–169.
- Whittaker, A. & Oren, D.C. (1999) Important ornithological records from the Rio Juruá, western Amazonia, including twelve additions to the Brazilian avifauna. *Bulletin of the British Ornithologists' Club*, 119, 235–260.