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Cryptic multicolored lizards in the Polychrus marmoratus Group (Squamata: Sauria: Polychrotidae) and the status of *Leiolepis auduboni* Hallowell

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Cryptic multicolored lizards in the *Polychrus marmoratus* Group (Squamata: Sauria: Polychrotidae) and the status of *Leiolepis auduboni* Hallowell

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Abstract.—The Neotropical genus *Polychrus* contains seven species of arboreal lizards. The type species for the genus is the widespread *Polychrus marmoratus*. We compared a few populations of *P. marmoratus* using 16S and COI mitochondrial gene sequences (1,035 bp total) and found several lineages existing under the name *Polychrus marmoratus*. Working backwards, using morphology we identify *Polychrus marmoratus* from the Guiana Shield and resurrect the name *Leiolepis auduboni* Hallowell for the species present in Trinidad, Tobago, and northern Venezuela. The number of species in the genus *Polychrus* is raised to eight. However, we also discuss evidence for the existence of other cryptic species within *P. marmoratus*, and the likelihood that both *P. virescens* Schniz and *P. neovidanus* Wagler are valid names.

Keywords. Guyana Shield, Venezuelan Coastal Ranges, Trinidad, Tobago, Atlantic Forest, reptiles

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Introduction

The multi-colored lizards of the genus *Polychrus* have traditionally been treated as part of the Iguanidae since Gray (1845) organized lizards into 24 families. Townsend et al. (2011) note that, while *Polychrus* and *Anolis* have been considered sister taxa (Frost and Etheridge 1989), all published analyses of molecular data contradict this finding (Frost et al. 2001; Schulte et al. 2003; Schulte and Cartwright 2009). Frost et al. (2001) defined Polychrotidae based on morphology-only in a combined molecular and morphological analysis. Using conventional alignment methods and a much larger molecular data set Schulte et al. (2003) failed to recover the Polychrotidae clade. More recently, Pyron et al. (2013) suggested *Polychrus* is more closely related to hoplocerids. Hoploceridae contains four genera and about 24 species of medium

sized Neotropical endemic saurians with spiny tails, pleurodont teeth, diurnal activity, arboreal life styles, and an omnivorous diet. Members of the genus *Hoplocercus* are dry forests lizards, while *Enyaliooides* and *Morunasaurus* inhabit rain forests. *Polychrus*, on the other hand, spans a range of habitats, has an exceptionally long, non-spiny tail, and is diurnal, omnivorous and arboreal. The slow moving, arboreal *Polychrus* range from Honduras southward into continental South America on both sides of the Andes (Avila-Pires 1995; this study), extending as far as 25.63°S on the east side of the Andes.

Polychrus is composed of seven recognized species: *P. marmoratus* Linnaeus 1758, *P. acutirostris* Spix 1825, *P. gutturosus* Berthold 1846, *P. liogaster* Boulenger 1908, *P. femoralis* Werner 1910, *P. peruvianus* Noble 1924, and the most recently described *P. jacquelinae* Koch et al. 2011. Boulenger's (1914) *P. spurrelli* was considered a

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subspecies of *P. gutturosus* by Peters and Donoso-Barros (1970), however Koch et al. (2011) considers the name a junior synonym of *P. gutturosus*.

Much of the distribution of *Polychrus* is occupied by the type species for the genus, *Polychrus marmoratus*. It occurs in South America east of the Andes, including Guyana, French Guyana, Suriname, Venezuela, Colombia, Ecuador, Peru, Brazil, and Paraguay (Hoogmoed 1973; Avila-Pires 1995). Vanzolini (1983) noted *P. marmoratus*' distribution was disjunct with a large gap in northeastern Brazil separating the Caribbean and northern Amazonian populations from the Atlantic Forest populations. A museum specimen (MCZ R-25135) documents Breder's (1946) report of its presence in southern Panama. Other museum specimens suggest its presence in Valparaiso, Chile (MCZ R-3369) and elsewhere on the west side of the Andes. The species also occurs on the Isla de Margarita (Ugueto and Rivas 2010), Trinidad (Court 1858), Tobago (Barbour, 1916), and on the Bocas Islands of Gaspar Grande, Monos, and Chacachacare (Boos 1984a, b, 1990). This distribution covers about 37° of latitude and 45° of longitude with populations ranging in elevation from sea level to at least 2,500 m above sea level (asl) in Venezuela. Rivas et al. (2012) reported *Polychrus marmoratus* occurs in all of the biogeographic divisions of Venezuela except the marine, coastal, and Pantepui divisions. Molina et al. (2004) suggests it is present in the gallery forests and swamp forests of the llanos. It is not likely to be present in open grasslands. Figure 1 illustrates specimens from six different portions of the range.

Lacerta marmorata Linnaeus (1758:208) was based upon specimens documented in the Museum Principis and the Amphibia Gyllenborgiana. Specimens from the later collection were missing when Lönnberg (1896) examined the collections. However, Holm (1957) later found four specimens in the Amphibia Gyllenborgiana apparently overlooked by Lönnberg (1896). Cuvier (1817) established the genus *Polychrus* for *Lacerta marmorata*, citing Lacépède's (1788) illustration which he considered accurate enough for identification. Hoogmoed (1973) restricted the type locality for *Lacerta marmorata* to Paramaribo, Suriname. A specimen collected by Wied-Neuwied at the Villa Viçosa, Bahia, Brazil was the basis for the description of *Polychrus virescens* Schniz (1822). However, when Wied-Neuwied (1822–1831) published on this specimen, he referred to it as *P. marmoratus*.

Fitzinger (1826) listed the name *Polychrus geometricus* as *patria ignota* (locality unknown) and Vanzolini (1983) considered it *nomen nudum*. Delaporte (1826) described *Polychrus fasciatus* based upon a mounted specimen in the Muséum National d'Histoire Naturelle (Paris) and reported its type locality as the Philippines or Moluccas. This specimen was not discussed by Duméril and Bibron (1837) nor Guibé (1954) and remains *nomen dubia*.

Wagler (1828) described *Polychrus strigiventris* in a single sentence in the same account he discusses *Poly-*

chrus virescens. He states that the femoral pores and coloration distinguish it from the other species but, provides no type locality. Wagler's *Polychrus strigiventris* is also a *nomen dubia*.

Wagler (1833a) described *Polychrus neovidanus* (based on Seba's (1734–1765) plate 76, figure 4 and a Spix specimen from Rio de Janeiro) on the basis that the specimen lacked obvious femoral pores (it was a female). Vanzolini (1983) proposed the name *P. neovidanus* Wagler which should be associated with Spix's specimen from Rio de Janeiro.

Hallowell (1845) described *Leiolepis auduboni* collected by Samuel Ashmead at a location within 200 miles of Caracas, Venezuela. Hallowell's specimen was identified as *Polychrus marmoratus* by Roze (1958), however its status as a junior synonym of *Polychrus marmoratus* has been overlooked in more recent works (Peters and Donoso-Barros 1970; Avila-Pires 1995).

Numerous taxonomic changes due to underestimated diversity in other Neotropical lizards (Giugliano et al. 2013; Domingos et al. 2014; Werneck et al. 2015) suggests *Polychrus marmoratus* may also be a good candidate for holding undescribed, cryptic species. *Polychrus marmoratus* has not been examined in detail since Hoogmoed (1973) and Avila-Pires (1995) provided species accounts in their catalogues for Suriname and Brazil. Here, we focus on northeastern South America, define *Polychrus marmoratus*, and discuss possible cryptic species within the species.

Methods and Materials

We examined 118 alcohol preserved specimens and 17 skeletal and cleared and stained museum specimens labeled *Polychrus marmoratus*, as well as five specimens labeled *Polychrus liogaster* (listed in species accounts, Appendix 1 lists other material examined). Localities with precise information were plotted using ArcView. We also used localities from VertNet and the literature to provide an overall view of the distribution of the *Polychrus marmoratus* group. Preserved specimens were fixed in formalin and stored in 70% ethanol. Morphological data was collected (JCM, SPC, DW, TA) and morphological nomenclature used follows Hoogmoed (1973) and Avila-Pires (1995). Body and tail lengths were taken to the nearest one mm with a metric ruler, and head and scale measurements were taken with dial and digital calipers. Values for paired head scales are given in left/right order. Univariate analyses of morphological data were conducted with Excel in combination with QI Macros. Abbreviations used include: n: number of specimens, X: mean value, SD: standard deviation, SVL: snout vent length, and asl: above sea level.

Two tissue samples were collected by RML in Tobago while the remaining tissue samples were obtained via loan from various museums (see Table 1 for list of localities). Total genomic DNA was extracted from tis-



Fig. 1. A–B: *Polychrus auduboni* from the Arima Valley, Trinidad (JCM). C–D: *Polychrus marmoratus*, probably from Suriname, (Twan Leenders). E: *Polychrus* sp. from 4.5 km S of Cumanacoa, Venezuela at 300–400 m asl (Walter E. Schargel). F: *Polychrus* sp. from Vitória do Xingu, Pará, Brazil (Pedro Peloso). G: *Polychrus* sp. Camamu, Bahia, Brazil. H: *Polychrus* sp. from Guarapari, Espírito Santo, Brazil (bottom) (Pedro Peloso).

sues using a DNeasy blood and tissue kit (Qiagen, Inc., Valencia, California, USA) following the manufacturer's instructions. Using a Qiagen TopTaq PCR Master Mix kit, we amplified a fragment of the cytochrome oxidase I (hereafter, COI) mitochondrial gene (~ 650 bp) using the primers LCO1490 and HCO2198 from Castañeda and de Queiroz (2011). We also amplified a ~ 430 bp fragment of the 16S mitochondrial gene using primers from Haas et al. (1993). Thermocycler conditions for PCR followed Castañeda and de Queiroz (2011).

Amplicons were purified using a Qiagen Min-Elute column purification kit and sequenced on an ABI PRISM 3100xl automated sequencer at the Molecular and Cellular Imaging Center at the Ohio Agricultural Research and Development Center, Ohio State University using the PCR primers. Bases were called in Codon Code Aligner (version 4.0.1). Sequences for each gene were aligned in MEGA 6.06 (Tamura et al. 2013) using the Clustal W

module with the default gap opening and gap extension penalties. Alignments were unambiguous.

We used both parsimony and maximum likelihood analyses in MEGA to analyze the combined aligned sequences of 16S and COI (1,035 bp total). For our maximum likelihood analysis, we used the Hasegawa-Kishino-Yano model of molecular evolution as it was supported by the Bayesian Information Criterion as the closest fit to our data using MEGA. Initial tree(s) for the heuristic search were obtained by applying Neighbor-Joining algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with the best log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites (five categories [+G, parameter = 0.1811]). One thousand bootstrap pseudoreplicates were used to assess topological support. In the parsimony analysis,

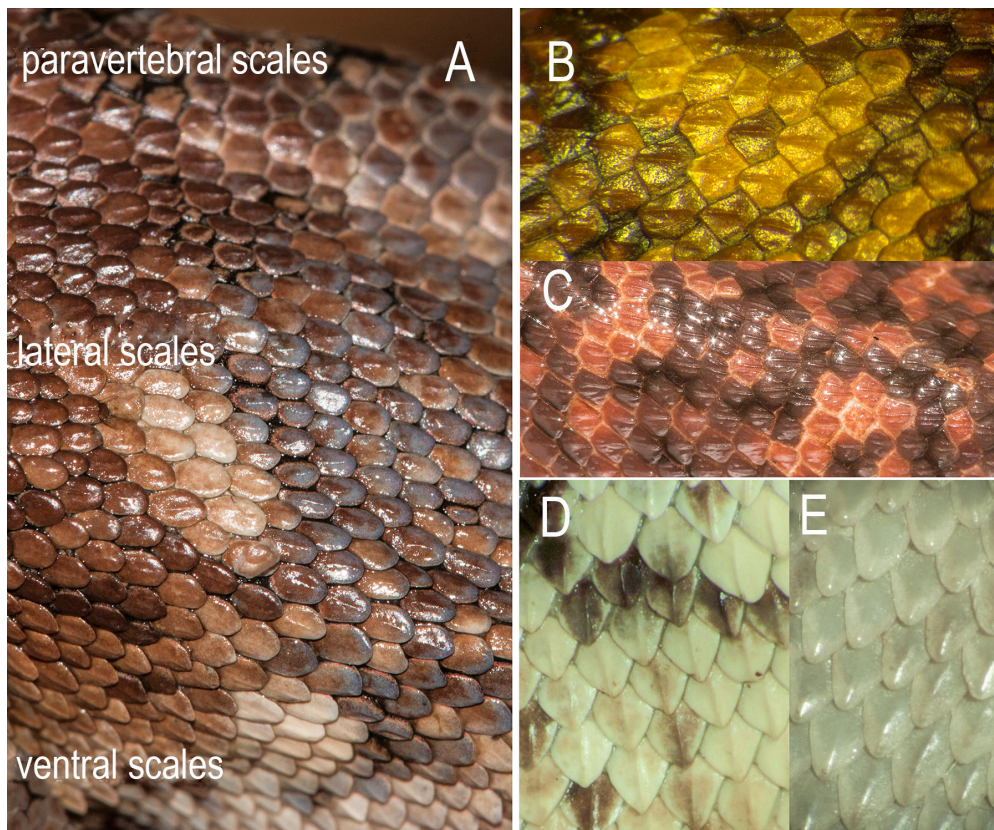


Fig. 2. **A:** the paravertebral, lateral and ventral scales of *Polychrus marmoratus*. **B:** paravertebral scales of *Polychrus auduboni*, a single keel per scale. **C:** paravertebral scales of *Polychrus marmoratus* with multiple keels per scale (multicariniate). **D:** ventral scales of *Polychrus auduboni* with keel extending the length of the scale. **E:** ventral scales of *Polychrus marmoratus* showing short keels, with some terminating in a small swollen gland at the apex of some scales (FMNH 3294, Demerara, Guyana).

all characters were unweighted and we used the subtree pruning-regrafting search method to identify the most parsimonious tree(s). Five thousand bootstrap pseudo-replicates were used to assess topological support. In all analyses, all codon positions were used, positions with less than 90% site coverage were eliminated, and sequences obtained from *P. acutirostris* were used as an outgroup (Table 1). Uncorrected p-distances were calculated for all pairs of sequences for each gene separately, using default settings in MEGA.

Collected specimens were covered by Trinidad and Tobago Forestry Division Special Game Licenses issued to JCM and RML on June 18, 2013 and June 5, 2014.

Results

The *Polychrus marmoratus* Group members share: 85–119 vertebral scales counted between the occiput to the posterior margin of the hind legs with a single keel or multiple keels; nasal scale contacts upper labials 1–2 or 2–3; first pair of chin shields may be in contact, or not; vertebral crest is absent; parietal eye absent; gular crest greatly reduced; 62–93 scales around mid-body; 23–35 lamellae on the fourth finger; 30–44 lamellae on the fourth toe; 10–18 semicircle scales; 5–8 rows of supra-oculars; 8–28 total pores; weak to strongly keeled ventral scales. Scales on the snout (those anterior to semicircle

scales) differ in ornamentation and organization within species, making it difficult to obtain consistent characters. The canthals (scales between the preorbitals and the supranasal) numbered two or three. The loreal is bordered by the canthals, the preorbitals, the upper labials, the nasal, and sometimes the suborbitals. The loreal can be single, divided into two parts, or fragmented into multiple parts and is variable within species. *Polychrus marmoratus* group members lack a gular crest but does have conical shaped scales on the mid line of the gular region. Paravertebrals (scales on the vertebral line and similarly shaped scales on either side of it) are in 8 to 14 transverse rows. These scales differ from lateral scales in ornamentation and size. They are often flat and may be ovate or polygonal with a single keel or two or three keels (multicariniate scales). The ornamentation of these is relatively consistent within species. Paravertebrals may be similar in size to lateral scales, or larger or smaller. Lateral scales are usually convex with a keel. They may be oval or quadrangular, and the interstitial skin contains numerous tiny granules. Ventral scales are triangular, larger than laterals, imbricate, and keeled. The keels may extend the entirety of the scale or only part of its length, and keels may end in a swollen bulb. The transition zone between laterals and ventrals make ventral counts ambiguous. See Figure 2 for the scale shapes and transition zones and other scale characters. *Polychrus marmoratus* has been

Cryptic multicolored lizards in the *Polychrus marmoratus* Group

Table 1. Specimens examined for molecular work, their geographic origins and Genbank accession numbers.

Specimen	Locality	COI	16S
YPM H-013040	none (pet trade specimen)	KY458391	KY458408
YPM H-014659	none (pet trade specimen)	KY458392	KY458409
KU 212631	Peru, San Martin, 14 km ESE of Shapaja	KY458396	KY458413
MVZ 163071	Peru, Amazonas, vicinity of Sua (Aguaruna village), Rio Cenepa (4°34'12.00"S, 78°13'18.01"W)	KY458406	KY458423
MVZ 230130	none (pet trade specimen, <i>P. acutirostris</i>)	KY458407	KY458424
LSUMZ 14270	Brazil, Para, Agropecuaria Treviso, LTDA, ca 101 km south, 18 km east Santarem (3°09'2.4"S, 54°50'32.9"W)	KY458398	KY458415
LSUMZ 14271	Brazil, Para, Agropecuaria Treviso, LTDA, ca 101 km south, 18 km east Santarem (3°09'2.4"S, 54°50'32.9"W)	KY458395	KY458412
LSUMZ 14392	Brazil, Para, Agropecuaria Treviso, LTDA, ca 101 km south, 18 km east Santarem (3°09'10.2"S, 54°50'28.4"W)	KY458397	KY458414
LSUMZ 4458	Trinidad and Tobago: Trinidad, San Fernando	KY458399	KY458416
AMNH 138080	Guyana: Northern Rupununi Savanna, Yupukari (on Rupununi River), 7 mi (airline) SSW Karanambo, 370 ft	KY458393	KY458410
AMNH 139787	Guyana: Southern Rupununi Savanna, Aishalton (on Kubanawau Creek), 150 m, (2°28'31"N 59°19'16"W)	KY458404	KY458421
CAS 231770	Trinidad and Tobago: Trinidad, Nariva Road, Manzanilla Beach. (10°29'25.6"N, 61° 03'16.8"W)	KY458402	KY458419
CAS 231781	Trinidad and Tobago: Trinidad, 5 km E of Laguna Mar Beach Resort, Blanchisseuse. (10°47'39.9"N, 61°17' 46.4" W)	KY458403	KY458420
UWIZM.2012.27.61	Trinidad and Tobago: Trinidad, Arima Valley, (10° 41' 5.57"N, 61°16'54.12"W)	KY458401	KY458418
UWIZM.2012.27.47	Trinidad and Tobago: Tobago, Arnos Valle Bridge Courtland River (~11°12'21.59"N, 60°45'35.99"W)	KY458400	KY458417
UWIZM.2012.42.12	Trinidad and Tobago: Tobago, 1.5 km upstream from Bloody Bay river bridge	KY458394	KY458411
RML Charlotteville	Trinidad and Tobago: Tobago, west side of Charlotteville (tissue collected, specimen discarded)	KY458405	KY458422

described as having three dark eye stripes: one extending posteriorly over the supratemporals, one extending to the rictus, and one extending ventrally to the upper labials. All specimens examined for this study have these markings, but in some specimens the pigment has faded from light and chemicals. Coloration in *Polychrus marmoratus* is highly variable and we have not emphasized coloration descriptions in alcohol or life for this reason.

The maximum likelihood tree of our 16S and COI sequence data provide evidence for a clade in Trinidad and Tobago but with little inter-island differentiation (Fig. 3). Both sequences from Guyana group together with high support, but are strongly divergent from all other sequences. There is also modest support for a grouping of the three Brazilian sequences, but the position of the Peruvian sequences is not well resolved. The parsimony analysis resulted in a highly similar tree with similar support (not shown).

The molecular phylogenetic results are supported by the p-distance data (Tables 2 and 3). There is little variation within sequences from Trinidad and Tobago (mean 16S p-distance 0.3% mean COI p-distance 0.1%) but

a moderate amount when compared to sequences from elsewhere (mean 16S p-distance 1.5% mean COI p-distance 1.6%). While the two Guyana sequences are nearly identical (16S p-distance 0.5%, COI p-distance 0.3%), they are well differentiated from all the other sequences (mean 16S p-distance 2.1% mean COI p-distance 3.1%). The three samples from Pará, Brazil are identical in their 16S sequence (mean 16S p-distance 0.0%) but somewhat different for COI (mean COI p-distance 1.1%). Compared to all the other sequences, the Brazil samples are moderately differentiated (mean 16S p-distance 1.1% mean COI p-distance 2.1%).

Polychrus head scale arrangements and counts are quite variable and working backwards from the molecular data we found a single species present on Trinidad and Tobago that morphologically appears conspecific with some Venezuelan Caribbean Coastal Range populations. Guyana and Suriname populations are molecularly and morphologically distinct from the Trinidad-Tobago-Venezuela species. The molecular results also suggest a third lineage is present in Para, Brazil.

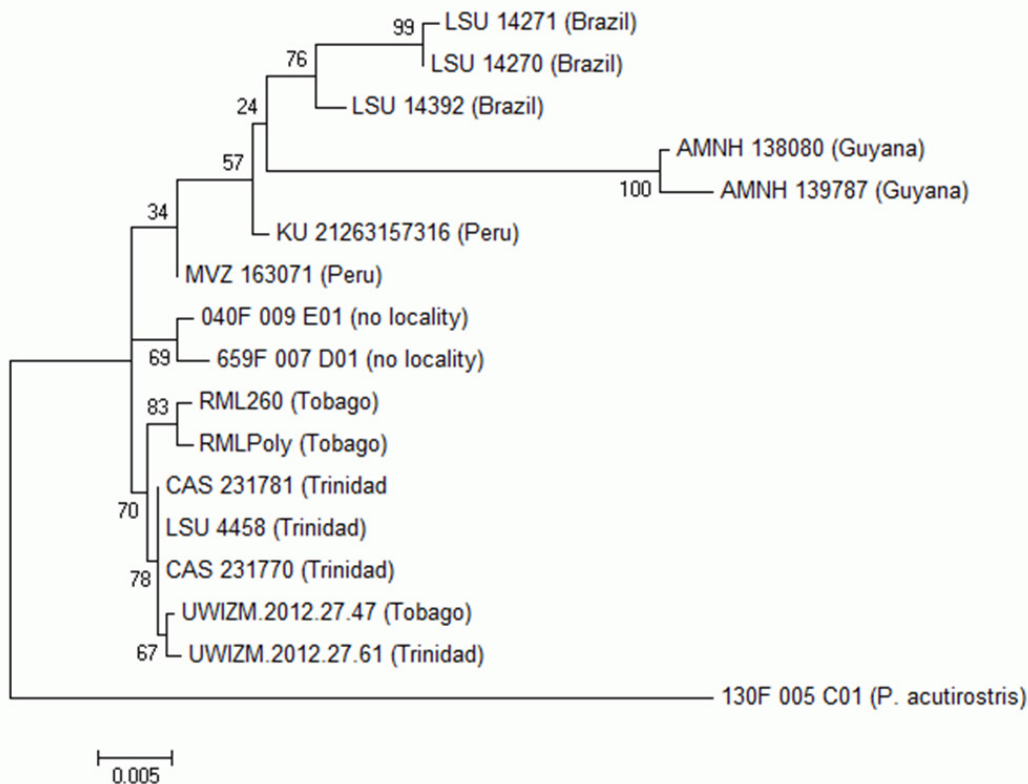


Fig. 3. Consensus maximum likelihood tree for combined 16S and COI sequence data from seventeen *Polychrus* tissue samples (1,035 bp total). Bootstrap support values are indicated at each node, if greater than 50%. Samples are indicated by their museum accession number and country of origin, if known. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. For details of analysis, see text.

Localities for the sources of *Polychrus* DNA, localities from which collected morphological data, type localities, and localities from which *P. marmoratus* has been reported are shown in Figure 4.

In a comparison of Trinidad ($n = 3$) and Guyana ($n = 1$) *Polychrus* skulls, one of us (DW) found the following. The parietal in Trinidad specimens had a slight constriction where the lateral borders give way to the posterior processes. The dorsal crests of the posterior processes angled medially so that, from the dorsal perspective, the lateral surfaces are visible and the medially surfaces are obscured. The lateral edges of the parietal table form slight bony lips that do not overhang the lateral surfaces of the parietal, which are supramedially sloped and un-depressed. Braincase: on the supraoccipital process, from the posterior perspective, there is a median seam running the length of the process, which extends to the rim of the foramen magnum (Fig. 5).

The parietal in Guyana specimens had the lateral edges of the parietal table project laterally, each forming a shelf that overhangs a depression in the adjacent lateral surface of the parietal bone. From the dorsal view, the shape of the parietal table is square and is un-constricted where the lateral borders give way to the posterior processes. The dorsal crests of the posterior processes angle laterally so that, from the dorsal perspective, the medial surfaces are visible and the lateral surfaces are obscured.

The braincase of Guyana specimens lacked a hairline median crest on the supraoccipital process.

The combined molecular and morphological data suggests *Polychrus marmoratus* is composed of multiple lineages. The morphology of the lineage present on Trinidad, Tobago, and the Coastal Ranges of Venezuela agrees well with the morphology of the holotype of *Leiolepis auduboni* Hallowell, including the morphology of the specimens we sequenced from Trinidad (UWIZM 2012.27.61) and Tobago (UWIZM 2012.27.47).

***Polychrus auduboni* (Hallowell) new combination**

Figure 6 (holotype), 1a, b

Leiolepis auduboni Hallowell 1845: ANSP 8138, Type locality: “Colombia within 200 miles of Caracas.” Collected by Samuel Ashmead. Restricted here to La Cumbre, Maracay, Aragua, Venezuela (~10.233333 -67.333336).

Polychrus marmoratus marmoratus – Burt and Burt 1933: 41. [in part]

Polychrus marmoratus – Roze 1958:2.

Referred specimens: Skeletal and cleared and stained specimens examined: Trinidad. AMNH 148543 female; FMNH 49840, FMNH 49845, FMNH 49848, UF 18395, males, UF 18922. Venezuela. FMNH

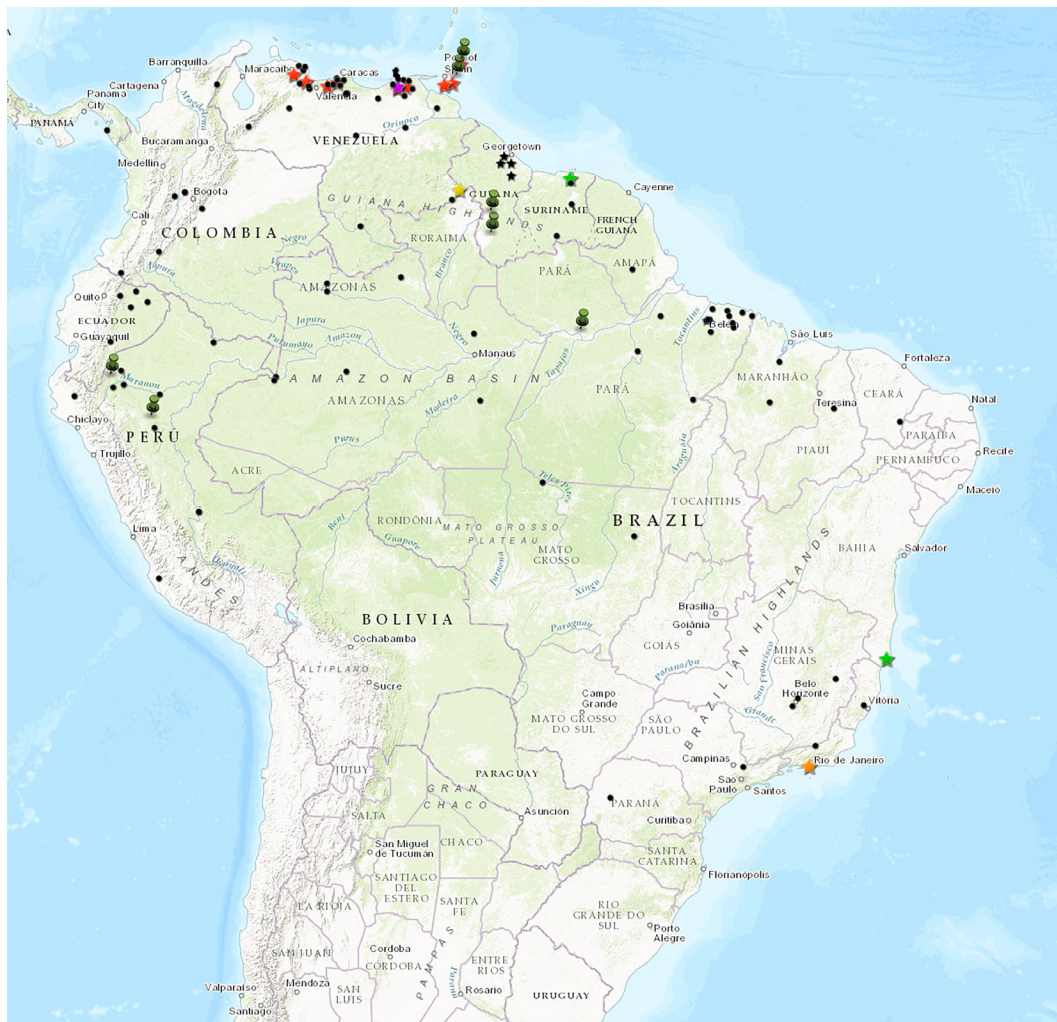


Fig. 4. Localities of members of the *Polychrus marmoratus* Group. Green pushpins denote localities from which DNA was sampled. Red stars denote locations for *Polychrus auduboni*, black stars denote locations for *P. marmoratus*. Black circular markers represent unconfirmed locations for members of the *P. marmoratus* group based upon the literature and specimens reported in VertNet. The blue star is the type locality for *P. marmoratus* (Linnaeus). The purple star is the type locality of *P. auduboni* Hallowell. The green star is the type locality for *Polychrus virescens* Schniz, the orange star is the type locality for *P. neovidanus* Wagler.

the parietal region are irregular polygonal, juxtaposed, flat, smooth, intermediate in size between those on snout and on supraocular region. Scales in interparietal region polygonal, juxtaposed, rugose, some somewhat swollen. Parietal eye absent. Loreal region with two scales. Nostril directed laterally, in upper anterior of a single nasal, nasal pentagonal and in contact with first and second supralabial. Orbit length 0.29 times head length. Eyelids partially fused, covered by granules of almost same size throughout the eyelids. A continuous series of two preoculars and two suboculars, in direct contact with supralabials and four postoculars. Upper labials seven on both sides, followed to rictus by a few relatively small scales. Temporal region with seven vertical rows of polygonal or rounded, juxtaposed, flat, and smooth scales, followed by two or three rows of granular scales near the ear, delimited dorsally by a single row of five or six enlarged supratemporal scales. Ear opening vertically oval with smooth margin, tympanum superficial. Mental bell-shaped, almost 2.5 times wide as long. Lower labials taller than

upper labials, six on each side, followed by several small scales to rictus. Lateral scales on chin slightly larger than median scales. Gular crest reduced but present, composed of about 10 enlarged, conical scales between mental and dewlap (anterior most obscured by thread holding tag). Dewlap has scales the same size and structure as chin scales, which are separated from each other by an extensible skin covered with granules, reaches level of forelimbs. Scales on anterior nape relatively small, granular, and almost rounded, juxtaposed, convex, in about 17 rows, posteriorly grading into dorsals. Scales on the sides of the neck about the same size as those on the nape but more elongated, merging ventrally with the gulars. Paravertebrals polygonal to rounded, juxtaposed, to some extent convex but mostly flat and keeled, 110 paravertebral scales in a mid-dorsal line between the occiput and the posterior margin of the hind limbs. Lateral scales are of a similar size and same shape as those of dorsum, convex, smooth, in poorly defined, oblique rows. Ventrals larger than dorsals, flat, keeled, lanceo-

sitioning into sharply keeled, pointed, imbricate ventrals; scales similar to the ventrals in size and shape extend onto the anal plate. Scales on tail pentagonal, heavily keeled, and imbricate. Scales on limbs keeled, imbricate, and slightly more ovate proximally than distally.

Coloration: In alcohol the specimen is a uniform brown, see Fig. 5. In life, highly variable, may change quickly from bright green with white lateral blotches bordered in black to almost a uniform brown. See Figure 1a, b.

Distribution: *Polychrus auduboni* occurs in the Cordillera de Costa of Venezuela, Trinidad and Tobago. It is also likely present on the Isla de Margarita, in the forested areas of the llanos, and Orinoco Delta. However, it may be replaced by another species in Bolivar, Venezuela.

Natural History: Beebe (1944) discussed the natural history of this lizard. Unfortunately, he combines information from both Caripito Venezuela and Kartabo, Guyana and it is not possible to unravel the comments he makes about *P. marmoratus* from Guyana, and from this species from Venezuela. However, Test et al. (1966) observed *P. auduboni* in the Botanical Garden at Caracas and above Turiamo Pass, Aragua, Venezuela. The latter individual was kept alive and is described as moving slowly and deliberately, unless grasshoppers were placed in its cage, at which time it jumps or runs towards the insects. The authors also describe tail waving as a human approached the cage, and interpret this as defensive behavior. During the day, the lizard was green in color but changed to gray-green at night while it slept on a branch. Its prey may also include humming birds. We have observed this lizard on Trinidad and Tobago, active during the day in secondary forests, climbing through branches and drinking water from the surface of leaves. Several times we have observed pairs together in the same or adjacent trees. Known predators include the hawk *Leucopternis albicollis*, house cats, and the parrot snake *Lep-*

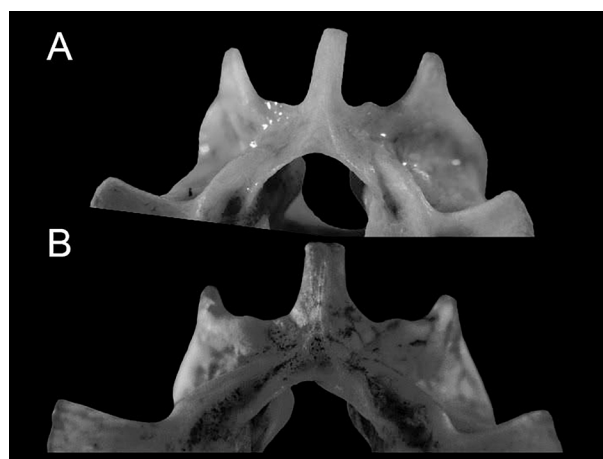


Fig. 5. On the supraoccipital process, from the posterior perspective, the presence of a median seam that runs the length of the process, down to the rim of the foramen magnum (DW).

tophis coeruleodorsus (Murphy 1997; Renoir Auguste, pers. comm.).

Comparisons: Distinguished from *Polychrus marmoratus* by few or no multicarinate paravertebral scales on the dorsum (many in *P. marmoratus*); paravertebrals consistently larger than laterals; loreal is one or two scales (3–4 in *P. marmoratus*); 17–28 femoral pores (8–19 in *P. marmoratus*).

***Polychrus marmoratus* (Linnaeus)**

Figures 1c, d.

Lacerta marmorata Linnaeus 1758: 208. Type locality “Hispania.” Restricted to the vicinity of Paramaribo, Suriname by Hoogmoed (1973).

Polychrus marmoratus – Cuvier 1817: 41.

Psilocercus marmoratus – Wagler 1821: 341.

Agama marmorata – Daudin 1802: 433.

Polychrus marmoratus marmoratus – Burt and Burt, 1933: 41.

Table 4. A comparison of *Polychrus marmoratus* and *P. auduboni* morphology.

Character	<i>P. auduboni</i>	<i>P. marmoratus</i>
<i>n</i> =	66	32
loreal scales (usual number)	1–2	2–3
vertebral rows, range	93–112100.34	95–113108.2
mean = SD =	(6.15)	(5.17)
scales around mid–body, range mean = SD =	62–8071.52 (6.15)	63–9378.5 (8.17)
nasal contacts upper labials	2 or 2–3	1–2
total semicircle scales	10–16	12–18
total pores, range mean = SD =	17–2821.41 (2.91)	8–1914.31 (3.31)
canthals	2	2 or 3
multicarinate paravertebrals	few or none	many
first labial contacts the nasal	rarely	usually



Fig. 6. ANSP 8138. The holotype for *Leiolepis auduboni* Hallowell. Photo credit: Ned Gilmore.

Referred specimens: Skeletal material: Suriname AMNH 141130, AMNH 148544 male, AMNH 141084, UF 56618 (Guyana or Suriname), UF 60914 female, UF 68102. Alcohol material: ($n = 32$). Guyana, Demerara, (6.733 -57.983) FMNH 3294, Dunoon Demerara River UMMZ 47632, 53965, 47630, 47751, 47752, 47753, 47754; Cabacalli Island Moruco River (6.78915 -58.182949) UMMZ 56467, 56468; Wismar (5.9999 -58.30001) UMMZ 76685; Kartabo (6.377459 -58.706761) UMMZ 47631, CM S4244, S4245, S5361; no specific locality; MCZ R-24391, UMMZ 47633, 55839, 55856; Suriname, Paramaribo (5.442523 -55.09896); MCZ R-8255, CM 44369, 52384, 52385, 44362-44368, 49531-32.

Diagnosis: Loreal usually fragmented into three or four scales; supranasal scale frequently (about 0.50) makes contact with loreal. One to three internasals. Vertebral rows 95-117; scales around mid-body 66-90. Snout length is 0.58 of orbit length. Lamellae on fourth toe 35-44. Usually three scales between first canthals, and five between the second; nasal contacts first two upper labials. Total femoral pores 8-19. Many multicarinate paravertebral scales; paravertebrals not much larger than laterals. The number of supraocular rows usually six (rarely 5 or 7). Scales on snout and supraoculars finely striated to smooth with tiny tubercles. Scales on anterior surface of humerus keeled; a reduced gular crest starts at the level of the first or second lower labial.

Variation: Females are significantly larger than males. Females SVL $X = 114.5$ ($n = 29$), males SVL $X = 102.9$ ($n = 11$) ($p < 0.05$, 29 df). Tail length: females $X = 292.3$ ($n = 16$), males $X = 272$ ($n = 10$). Forelegs $X =$

0.40 of SVL; $r = 0.35-0.47$; hind legs $X = 0.52$ of SVL, $r = 0.45-0.57$.

Rostral broader than tall, contacts two or three postrostrals. Scales on snout juxtaposed. Nasal with large nare, one or two supranasal above nasal on the snout, separated by 3-5 scales. Supranasal frequently makes contact with loreal. First pair of canthals (most anterior pair) separated by three (rarely two) scales; second pair of canthals separated by 4-5 scales (usually five). Semicircle scales 5-9, the total bilateral average 14.4; usually separated by a single scale (or scale row) anteriorly, and a double row posteriorly. Ciliaries 10-13, usually with two keels. Supraocular scales polygonal to round in five or six rows between ciliaries and semicircle scales, first row or first two rows of supraoculars with keels (first row sometimes appears to be a second row of ciliaries); supraoculars highly variable in number (31-44) and in five or six rows (rarely seven). A prenasal scale usually separates the postrostral from the nasal. The nasal is usually square and in contact with the first two upper labials, sometimes in narrow contact with the third upper labial. Loreal usually in two or three parts, anterior scale quadrangular and posterior triangular scale. Loreal usually contacts upper labials 2-3-4, sometimes 2-3 or 3-4; first canthal usually makes contact with loreal. Upper labials numbered 5-9 per side, usually six; bilateral average for total upper labials 14.7; upper labial under middle of eye usually fifth, or 4-5, or 5-6. Lower labials 6-9, usually 7; total bilateral average for lower labials 14.1 scales. Orbital scales: preorbitals two; suborbitals 2-4, usually 2-3; postorbitals usually two, sometimes 3 or 4. Tem-

Table 5. A comparison of eight species currently recognized in the genus *Polychrus*. K = keeled, r = reduced, nd = no data, both means smooth and keeled in same species. Based on the literature for species not examined in this study.

	<i>acutirostris</i>	<i>auduboni</i>	<i>femorialis</i>	<i>gutturosus</i>	<i>jacquelineae</i>	<i>liogaster</i>	<i>marmoratus</i>	<i>peruvianus</i>
vertebrals	111–126	93–112	nd	75–105	198–215	103–125	95–113	56–70
SAB	57–73	62–80	53–73	63–82	131–186	66–95	63–93	52–74
ventral ornamentation	none	k	no	k	no	both	k	k
parietal eye	yes	no	no	no	no	no	no	no
vertebral crest	no	no	no	no	no	no	no	yes
gular crest obvious	no	r	no	no	no	yes	r	yes
4 th finger	23–32	23–34	nd	25–36	33–36	29–37	23–35	25–33
4 th toe	19–32	30–43	nd	35–45	42–48	38–47	34–44	32–43
femoral pores	23–24	17–28	30–34	18–42	13–15	15–24	8–19	12–26

poral scales usually in eight vertical rows between post orbitals and tympanum, separated from parietal scales by a row of 4–5 enlarged supratemporals. Gulars (counted between tympani 42–55 ($X = 47.0$)), rows of gulars separated by numerous micro-scales that vary in size. Dorsal scales around mid-body $X = 78.5$ ($r = 66–90$, $SD = 8.71$). Vertebrals and paravertebrals in 10–14 rows; slightly enlarged, pentagonal, and keeled; radially become elongate and ovate laterally often losing the keels; and transition into sharply keeled, pointed, imbricate ventrals. Scales similar to the ventrals in size and shape extend onto the anal plate. Vertebral scales rows $X = 108.2$ ($r = 95–113$, $SD = 5.17$) between the occiput and posterior edge of hind legs. Lamellae on fourth finger 25–35 ($X = 30.5$, $SD = 3.18$), lamellae on fourth toe 30–43 ($X = 38.69$, $SD = 3.01$). Total pores 8–19 ($X = 14.3$, $SD = 3.31$). Scales on tail pentagonal, heavily keeled, and imbricate. Scales on limbs keeled, imbricate, and slightly more ovate near the body, than distally.

Coloration: In preservative most specimens are a uniform brown-tan with black pigmented eye stripes and labial seams. In life, coloration is highly variable and can change in less than a minute from green to brown. See Figures 1c,d.

Distribution: We have only documented this species from Guyana and Suriname, but it may be expected to occur in French Guyana and northern Brazil.

Natural history: Hoogmoed (1973) described it as being diurnal, arboreal, and omnivorous; females lay 4–6 eggs in July and August. It is capable of rapid color change from bright green to brown. Comments on its natural history in the literature are deeply entangled with other members of the species group.

Comparisons: Distinguished from *Polychrus auduboni* by numerous multicarinate paravertebral scales (few or none in *P. auduboni*); paravertebrals not much larger than laterals; a loreal fragmented in two or more parts (as opposed to one or two in *P. auduboni*); a nasal that is pentagonal and usually contacts the first upper labial (it usually does not in *auduboni*); 8–19 ($X = 14.32$, $SD = 3.31$) femoral pores (*auduboni* has 17–28, $X = 21.4$, $SD = 2.91$); the supranasal often makes contact with the loreal (in *auduboni* it rarely does so).

Discussion

We have been unable to examine specimens from the west side of the Andes and Panama. However, we suspect the localities are in error, or the lizards have been misidentified. It is likely that members of the *Polychrus marmoratus* group are restricted to the east side of the Andes.

Given the high degree of morphological variation within the *P. marmoratus* complex, there are likely other cryptic species present. The *P. marmoratus* group will likely also include populations currently considered *Polychrus liogaster*. The two species are supposedly separated by keeled ventrals in *P. marmoratus* and smooth or weakly keeled scales in *P. liogaster* (Peters and Donoso-Barrio 1970). Additionally, the latter species has a post-ocular stripe that extends onto the neck and body. However, preliminary examination of museum specimens labeled *P. liogaster* revealed that all had keeled ventrals, as well as slightly higher upper labial counts than those reported in the literature.

We cannot rule out the possibility that other taxa remain to be found within *Polychrus auduboni* in fact, we think it likely. Ugueto and Rivas (2010) note that the Isla de Margarita population has a red dewlap and a white vertebral stripe. A mainland Venezuelan specimen (CM 22797) that we have tentatively included in *auduboni*, also has a red dewlap. Only recently have we observed a red dewlap in a Trinidad *Polychrus auduboni*. Additionally, we have observed *P. auduboni* often have a broad vertebral stripe that frequently contains white pigment. This may be normal variation in a species capable of significant changes in coloration, or it may signal a cryptic species within *P. auduboni*. Two specimens from Cocolar, Sucre (FMNH 17792–93) also appear to be distinct from *P. auduboni*, with the lowest number of vertebral scale counts (85) we observed in *Polychrus* and an exceptionally well defined canthal ridge. A single specimen from Bolivar, Venezuela (UMMZ 85232) does not appear to be *P. auduboni* or *P. marmoratus*. It has three postrostrals, exceptionally small nape scales that are tuberculate, and other traits that are uncommon or unobserved in our sample. Barrio-Amorós and Ortiz (2015)

suggest an undescribed *Polychrus* exists in eastern Venezuela. It is unclear if they are referring to *P. auduboni* or another species. Unraveling the natural history of *P. auduboni* from *P. marmoratus* from the extant literature will be difficult because locality data is often missing. Further collections with tissues for DNA work are necessary to fully document the diversity of these lizards.

Our examination of the morphology of three specimens from Pará, Brazil (MCZ 2889, 5549, 92644) agrees with the molecular results which suggest populations in Pará are neither *P. auduboni* nor *P. marmoratus*. These specimens have a higher vertebral count, more lamellae on the fourth finger and toe, and a loreal which contacts upper labials 3-4-5.

Additional taxa are likely present in Brazil's Atlantic Forest. *Polychrus virescens* Schniz (1822: 65) is likely a valid species. The type locality was not given by Schniz, but Wied-Neuwied (1825) considered the specimens to be *Polychrus marmoratus* when he published and reported the specimens as being from "Villa Viçosa am Flusse Peruhype." Vanzolini (1983: 119) noted this is now Nova Vicosá, Bahia, Brazil (-17.900872 -39.371644). Myers et al. (2011: 8) examined the history of this name and found Wagler (1828: pl 12) contained an illustration labeled *Polychrus virescens* and attributed the name to Wied-Neuwied in Schinz, but suggest it should be attributed to Schinz alone. They reason that Wied-Neuwied used *Polychrus virescens* as a manuscript name only and when he published referred the specimens to *Polychrus marmoratus*. We examined photographs of two specimens collected by Wied-Neuwied. An adult female has about 99 vertebrae which are keeled and some are multicarinate. Indicated femoral pores total 22, and the canthal contacts the loreal. The loreal is in three parts; it has one large scale between the supranasals (the largest scale on the snout); three scales separate the first canthals and four or five separate the second canthals; and the loreal contacts the supranasal. The semicircle scales are completely separated by a single row of scales.

Polychrus neovidanus Wagler (1833b: 897) is also a candidate for being a valid species. Vanzolini (1983) noted the description was based upon a figure in Seba (1734–1765, Volume 2, Plate 76, Figure 4) and on Spix's *P. marmoratus*. He states the name should be attached to Spix's specimen from Rio de Janeiro. We examined three specimens from Rio de Janeiro. They had 103–107 multicarinate paravertebrals and 70–88 scales around the mid-body. The canthal does not contact the loreal and the loreal contacts the supranasal. These specimens also differed from all other *Polychrus marmoratus* group members by having five scales between the first pair of canthals and seven scales between the second pair of canthals.

Hoogmoed (1973) Vanzolini (1983) and Avila-Pires (1995) suggest the *Polychrus marmoratus* group is disjunct with a population present in north and western South America, as well as with a second population in

the Atlantic Forest. However, Kawashita-Ribeiro and Ávila (2008) reported a specimen from Aripuanã in Mato Grosso which narrows the gap, suggesting the *P. marmoratus* group may be found throughout the area, and the disjunct distribution simply reflects a lack of collecting and knowledge.

Much remains to be learned about the *Polychrus marmoratus* group and how it reflects the historic landscapes of the South American continent. It seems likely that additional, unrecognized species remain to be discovered and we encourage further work on these remarkable and poorly studied lizards.

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Literature Cited

- Avila-Pires TCS. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandelingen* 299: 1–706.
- Barbour T. 1916. Amphibians and reptiles from Tobago. *Proceedings of the Biological Society of Washington* 29: 221–224.
- Barrio-Amorós CL, Ortiz JC. 2015. Material herpetológico colectado por Roberto Donoso Barros en Venezuela (excepto geckos) en el Museo de Zoología de la Universidad de Concepción, Chile. *Gayana (Concepción)* 79(1): 68–93.
- Beebe W. 1944. Field notes on the lizards of Kartabo, British Guiana and Caripito, Venezuela. Part 2. Iguanidae. *Zoologica* 29: 195–216.
- Berthold AA. 1846. Ueber verschiedene neue oder seltene reptilien aus neu-Granada und crustaceen aus China. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen* 3: 1–16.
- Boos HEA. 1984a. The terrestrial reptiles of Monas Island. *Living World, Journal of the Trinidad and Tobago Field Naturalist's Club* 1983–1984: 14–18.

- Boos HEA. 1984b. A consideration of the terrestrial reptile fauna on some offshore islands northwest of Trinidad. *Living World, Journal of the Trinidad and Tobago Field Naturalist's Club* 1983–1984: 19–26.
- Boos HEA. 1990. Additions to the terrestrial fauna of the offshore islands northwest of Trinidad. *Living World, Journal of the Trinidad and Tobago Field Naturalist's Club* 1989–1990: 9.
- Boulenger GA. 1908. Descriptions of new South-American reptiles. *Annals and Magazine of Natural History* (8)1: 111–115.
- Boulenger GA. 1914. On a second collection of batrachians and reptiles made by Dr. H.G. F. Spurrell, F.Z.S., in the Choco, Colombia. *Proceedings of the Zoological Society of London* 1914: 813–817.
- Breder CM. 1946. Amphibians and reptiles of the Rio Chucunaque drainage, Darien, Panama, with notes on their life histories. *Bulletin of the American Museum Natural History* 86: 375–436.
- Burt CE, Burt MD. 1933. A preliminary check list of the lizards of South America. *Transactions of the Academy of Science, St. Louis* 28: 1–104.
- Castañeda M del R, de Queiroz K. 2011. Phylogenetic Relationships of the Dactyloa Clade of Anolis Lizards Based on Nuclear and Mitochondrial DNA Sequence Data. *Molecular Phylogenetics and Evolution* 61: 784–800.
- Court J. 1858. Catalogue of Reptiles. Pp. 440–441 In: *Trinidad: Its Geography, Natural Resources, Administration, Present Condition, and Prospects*. Editor, De Verteuil LAA. Ward and Lock, London, United Kingdom. 508 p
- Cuvier G. 1817. *Le regne Animal, Distribute d'apres son Organisation*. Volume ii. Deterville, Paris, France. 532 p.
- Daudin FM. 1802. *Histoire Naturelle Generale et Particuliere des Reptiles*. Volume 3. F. Dufart, Paris, France. 452 p.
- Delaporte F. 1826. Description d'une nouvelle espece de reptile du genre marbre (*Polychrus*). *Annales des Sciences Naturelles* 9: 110–111.
- Domingos FM, Bosque RJ, Cassimiro J, Colli GR, Rodrigues MT, Santos MG, Beheregaray LG. 2014. Out of the deep: Cryptic speciation in a Neotropical gecko (Squamata, Phyllodactylidae) revealed by species delimitation methods. *Molecular Phylogenetics and Evolution* 80: 113–124.
- Duméril AMC, Bibron G. 1837. *Erpétologie Générale ou Histoire Naturelle Complete des Reptiles*. Volume 4. Librairie encyclopédique, Paris, France. 570 p.
- Fitzinger L. 1826. *Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften*. J. G. Heubner, Wien, Austria. 92 p.
- Frost DR, Etheridge R. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *University of Kansas Museum of Natural History Miscellaneous Publications* 81: 1–65.
- Frost DR, Etheridge R, Janies D, Titus T. 2001. Total evidence, sequence alignment, the evolution of poly-chrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). *American Museum Novitates* 3343: 1–38.
- Giugliano LG, de Campos Nogueira G, Valdujo PH, Collevatti RG, Colli GR. 2013. Cryptic diversity in South American Teiinae (Squamata, Teiidae) lizards. *Zoologica Scripta* 42: 473–487.
- Gray JE. 1845. *Catalogue of the Specimens of Lizards in the Collection of the British Museum*. Trustees of the British Museum/Edward Newman, London, United Kingdom. 289 p.
- Guibé J. 1954. *Catalogue des Types de Lézards du Muséum National d'Histoire Naturelle*. Colas, Bayeux. 119 p.
- Hallowell E. 1845. Description of reptiles from South America, supposed to be new. *Proceedings of the Academy of Natural Sciences* 2: 241–247.
- Haas WH, Butler WR, Woodley CLT, Crawford JT. 1993. Mixed-linker polymerase chain reaction: A new method for rapid fingerprinting of isolates of the Mycobacterium tuberculosis complex. *Journal of Clinical Microbiology* 31(5): 1,293.
- Holm Å. 1957. Specimina Linnæana i Uppsala bevarade zoologiska samlingar från Linnés tid. *Uppsala Universitets Årsskrift* 6:1–68.
- Hoogmoed MS 1973. *Notes on the Herpetofauna of Surinam IV. The Lizards and Amphisbaenians of Surinam*. W. Junk, The Hague, Netherlands. ix+ 419 p.
- Kawashita-Ribeiro RA, Ávila RW. 2008. Reptilia, Squamata, *Polychrus* spp.: New record, range extensions, and distribution map in the state of Mato Grosso, Brazil. *Check List* 4: 362–365.
- Koch C, Venegas PJ, Garcia-Bravo A, Böhme W. 2011. A new bush anole (Iguanidae, Polychrotinae, *Polychrus*) from the upper Marañon basin, Peru, with a redescription of *Polychrus peruvianus* (Noble, 1924) and additional information on *Polychrus gutturosus* Berthold, 1845. *ZooKeys* 141: 79–107.
- de Lacépède BGÉ. 1788. *Histoire Naturelle des Quadrupèdes Ovipares et des Serpens*. Volume 1. Imprimerie du roi. Chez Saugrain, Paris, France. xviii + 651 p.
- Linnaeus C. 1758. *Systema Naturæ per regna tria Naturæ, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. 10th Edition. Tomus I. Laurentii Salvii, Stockholm, Södermanland, Sweden. 824 p.
- Lönnberg E. 1896. Linnean type-specimens of birds, reptiles, batrachians, and fishes in the Zoological Museum of the R. University in Uppsala. *Bihang Till Koeniger Svenska Vetenskaps-Akademiens Handlingar* 22: 1–45.
- Murphy JC. 1997. *Amphibians and Reptiles of Trinidad and Tobago*. Krieger Publishing, Malabar, Florida, USA. 243 p.
- Molina C, Señaris C, Rivas G. 2004. Los reptiles del Del-

- ta del Orinoco, Venezuela. *Memoria de la Fundación La Salle de Ciencias Naturales* 2004: 159–60.
- Myers CW, Rodrigues MT, Vanzolini PE. 2011. Status of early 19th-century names authored in parallel by Wied and Schinz for South American reptiles and amphibians, with designations of three Nomina protecta. *American Museum Novitates* 3714: 1–21.
- Noble GK. 1924. New lizards from northwestern Peru. *Occasional Papers of the Boston Society of Natural History* 5: 107–113.
- Peters JA, Donoso-Barros R. 1970. Catalogue of the Neotropical Squamata. Part II. Lizards and amphisbaenians. *Bulletin of the United States National Museum* 297: 1–293.
- Pyron RA, Burbrink FT, Wiens JJ. 2013 A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 93.
- Rivas GA, Molina CR, Ugueto G, Barros TR, Barrio-Amorós CL. 2012. Reptiles of Venezuela: An updated and commented checklist. *Zootaxa* 3211: 1–64.
- Roze JA. 1958. On Hallowell's type specimens of reptiles from Venezuela in the collection of the Academy of Natural Sciences of Philadelphia. *Notulae Naturae* 309: 1–4.
- Schinz HR. 1822. *Das Thierreich Eingetheilt nach dem Bau der Thiere als Grundlage Ihrer Naturgeschichte und der Vergleichende Anatomie van dem Herm Ritter van Cuvier*. Volume 2. J. G. Cotta, Stuttgart, Baden-Württemberg, Germany. 189 p.
- Schulte JA, Cartwright EM. 2009. Phylogenetic relationships among iguanian lizards using alternative partitioning methods and TSHZ1: A new phylogenetic marker for reptiles. *Molecular Phylogenetics and Evolution* 50: 391–396.
- Schulte JA, Valladares JP, Larson A. 2003. Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. *Herpetologica* 59: 399–419.
- Seba A. 1734–1765. *Locupletissimi rerum Naturalium Thesauri Accurata Descriptio, et Iconibus Artificio-sissimis Expressio, per Universam Physiees Historiam*. Apud J. Wetstenium, & Gul. Smith, & Janssonio-Waesbergios, Amsterdam, Netherlands. 582 p.
- Spix JB. 1825. *Animalia Nova sive Species Novae Lacer-tarum quas in itinere per Brasiliam Annis MDCCCX-VII-MDCCCXX jussu et Auspicio Maximiliani Josephi I Bavariae Regis Suscepto Collegit et Descripsit Dr. J. B. de Spix*. T. O. Weigel, F. S. Hybschmanni, Monachii, Lipsiae. 26 p.
- Spix JB. 1826. Berichtigung der bemerkungen des herm Dr. Boie in leyden ueber die van herm dr. Spix abgebildet saurier. *Isis von Oken* 18: 601–604.
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30: 2,725–2,729.
- Test FH, Sexton OJ, Heatwole H. 1966. Reptiles of Rancho Grande and vicinity, Estado Aragua, Venezuela. *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 128: 1–63.
- Townsend TM, Mulcahy DG, Noonan BP, Sites JW, Kuczynski CA, Wiens JJ, Reeder TW. 2011. Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Molecular Phylogenetics and Evolution* 61: 363–380.
- Ugueto G, Rivas GA. 2010. *Amphibians and Reptiles of Margarita, Coche, and Cubagua*. Edition Chimaira, Frankfurt am Main, Germany. 350 p.
- Vanzolini PE. 1983. Guiano-Brasilian *Polychrus*: distribution and speciation (Sauria: Iguanidae). Pp. 118–131 In: *Advances in Herpetology and Evolutionary Biology*. Editors, Rhodin A, Miyata K. Museum of Comparative Zoology, Cambridge, Massachusetts, USA. 725 p.
- Wagler J. 1821. Ankiindigung: Die Amphibien. *Isis von Oken* 8: 337–342.
- Wagler J. 1828. *Descriptiones et icones Amphibiorum*. Volume 1. JG Cotttae, Stuttgart, Baden-Württemberg, Germany. 12 p.
- Wagler J. 1833a. *Descriptiones et Icones Amphibiorum*. Volume 3. JG Cotttae, Stuttgart, Baden-Württemberg, Germany. 15 p.
- Wagler J. 1833b. Deutung die in Sebas's Thesaurio Rerum Naturalium T. 1. et 2. enthaltenen Abbildungen von Lurchen, mit kritische Bemerkungen. *Isis von Oken* 1833: 896–905.
- Werneck FP, Leite RN, Geurgas SR, Rodrigues MT. 2015. Biogeographic history and cryptic diversity of saxicolous Tropiciduridae lizards endemic to the semi-arid Caatinga. *BMC Evolutionary Biology* 15: 94.
- Werner F. 1910. Ueber neue oder seltene reptilien des naturhistorischen museums in hamburg ii. Eidechsen. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg* 27: 1–46.
- Wied-Neuwied MAP. 1832. *Beitrag zur Naturgeschichte von Brasilien*. (4 Volumes). Volume 1. Landes-Industrie-Comptoirs, Weimar, Thuringa, Germany. 614 p.
- Wied-Neuwied MAP. 1822–1831. *Abbildungen zur Naturgeschichte Brasiliens Weimar*. 2 volumes. Landes-Industrie-Comptoirs, Weimar, Thuringa, Germany. 90 p.

Appendix 1. Other specimens examined.

Skeletal and cleared and stained specimens examined: Ecuador: FMNH 42501; Peru: AMNH 71170 (Upper Ucayali), AMNH 71171 (Upper Ucayali); Suriname AMNH 141130, AMNH 148544 male AMNH 141084, UF 56618 (Guyana or Surinam), UF 60914 female, UF 68102. Trinidad: AMNH 148543 female, FMNH 49848, FMNH 49845, FMNH 49840, UF 18395, male, UF 18922. Venezuela FMNH 17791 (Sucre, Venezuela) male.

Polychrus liogaster ($n = 5$). Peru: FMNH 40586, 45499, 59184, 68599, 68600.

Polychrus neovidanus ($n = 3$). Brazil, Rio de Janeiro (-22.9 -43.23333) MCZ R-3390, R-170011, R-170012. *Polychrus virescens* Nova Vicosa, Bahai, Brazil (~17°54'15"S 39°22'W) AMNH R105, R1695. *Polychrus* sp. A ($n = 3$). Sucre Cocollar (10.147126 -63.808614) FMNH 17791–93.

Polychrus sp. B ($n = 3$). Brazil, Para (-1.45 -48.48333) MCZ R-2889, R-5549, R-92644.

Polychrus sp. C ($n = 4$) Bolivia: no specific locality BMNH 61.3.23.1; Buena Vista (-17.459161 -63.659221) FMNH 16163; 21510. Ecuador: FMNH 53890. *Polychrus* sp D. ($n = 1$) Venezuela, Bolivar (1.93965 -64.716248) UMMZ 85232.



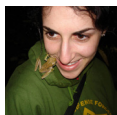
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