

A New Collared Lizard (Tropidurus: Tropiduridae) Endemic to the Western Bolivian Andes and Its Implications for Seasonally Dry Tropical Forests

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A new collared lizard (*Tropidurus*: Tropiduridae) endemic to the Western Bolivian Andes and its implications for seasonally dry tropical forests

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ABSTRACT

In this study we describe *Tropidurus azurduyae*, a new species of lizard endemic to the Andes. This species is restricted to inter-Andean dry valleys of central and southern Bolivia, within the ecoregion known as Bolivian Montane Dry Forests. It is currently known from the departments of Chuquisaca, Cochabamba, Potosí, and Santa Cruz, where it ranges in elevation from about 1000 to 2800 m. In addition, our analyses of closely related populations of *Tropidurus* from Argentina, Bolivia, Brazil, and Paraguay revealed undescribed species in central and northeastern Brazil and eastern Bolivia that render *T. etheridgei* Cei, 1982, paraphyletic. These results underscore the need for a comprehensive revision of peripheral and disjunct populations currently assigned to widely distributed species of *Tropidurus*. The phylogenetic relationships and distribution patterns of these new taxa concur with recent findings supporting seasonally dry tropical forests and open formations of dry vegetation from South America as distinct biotic units. Furthermore, they offer no support for seasonally dry tropical forests as closely related areas. In line with these discoveries, we refute biogeographic scenarios based exclusively on vicariance to explain the biogeographic history of *Tropidurus*.

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INTRODUCTION

Bolivia is among the most neglected areas of the globe in terms of biodiversity research, and our knowledge of its lizard fauna is nothing but incomplete (Dirksen and De La Riva, 1999; Langstroth, 2005). In an attempt to remedy this situation, organizations such as Conservation International (CI) have funded rapid assessment programs (RAPs; Larsen, 2016), sending multidisciplinary teams to evaluate the state of biodiversity in some of Bolivia's most remote areas (Alonso et al., 2011). For instance, between 1991 and 1995, CI carried out a RAP⁶ in the lowlands and isolated mesa of the Noel Kempff Mercado National Park and surroundings (Killeen and Schulenberg, 1998). This inventory revealed the occurrence of 1094 vertebrates, 97 scarab beetles, and 2705 plants species within an area no larger than 750,000 hectares (7500 km²), and among those taxa, 29 were considered new. As part of that RAP, Harvey (1998) reported three new species of the lizard genus *Tropidurus* Wied, 1825, that were described shortly thereafter as *Tropidurus callathelys*, *T. chromatops*, and *T. xanthochilus* by Harvey and Gutberlet (1998). Nevertheless, even though that single genus (*Tropidurus*) was already known to occur in at least six of the nine Bolivian departments (Dirksen and De La Riva, 1999), ranging from isolated rock outcrops and savanna enclaves in the Amazon to seasonally dry tropical forests along the Andes, a comprehensive taxonomic assessment of highland populations remained undone.

In 2013, we visited the Torotoro National Park, Potosí Department, located in the heart of the Bolivian Montane Dry Forests (Olson et al., 2001; Crispieri et al., 2009). There, we found a new form of *Tropidurus* endemic to high-altitude formations of seasonally dry tropical forests known as "inter-Andean dry valleys" (López, 2003a, 2003b). This new species had been previously overlooked as *T. etheridgei* Cei, 1982, whose distribution range has been long assumed to comprise besides the inter-Andean dry valleys of central and southern Bolivia also the Chaco of northwestern Argentina, southeastern Bolivia, and western Paraguay, rock outcrops in eastern Bolivia and central Brazil, and disjunct patches of sandy habitats in central and northeastern Brazil (Cei, 1982; Rodrigues, 1987; Dirksen and De La Riva, 1999; Carvalho, 2013). In this paper, we describe this new form as the first species of the *T. torquatus* species group (per Frost et al., 2001) endemic to the Andes. Our morphological and molecular analyses of populations historically assigned to nominal *T. etheridgei* also revealed other undescribed species of *Tropidurus* in disjunct seasonally dry tropical forests and in open formations of dry vegetation in South America. The examination of the phylogenetic relationships and distribution of those taxa gave us the opportunity to critically examine the biogeographic history of these areas. In addition to the taxonomic description of our new Andean *Tropidurus* and notes on the systematic advances achieved based on the novel phylogeny produced, a summary of relevant biogeographic results is provided.

⁶ In addition to the RAP carried out in the Noel Kempff Mercado National Park and surroundings (Killeen and Schulenberg, 1998), CI supported five other RAPs in Bolivia between 1990 and 1997, sampling aquatic environments of the Río Orthon Basin in Pando (Chernoff and Willink, 1999) and terrestrial sites of the Alto Madidi region (Parker and Bailey, 1991), Lowland Dry Forests of Santa Cruz (Parker et al., 1993), South Central Chuquisaca (Schulenberg and Awbrey, 1997), and Pando and Alto Madidi (Montambault, 2002). During these studies, species of the lizard genus *Tropidurus* were only registered in localities visited in the departments of Santa Cruz (see main text) and Chuquisaca (*T. melanopleurus*).

MATERIAL AND METHODS

FIELDWORK AND STUDY AREA: Between 13–15 November 2013, two of us (A.L.G.C. and L.R.R.) visited the Torotoro National Park, Bolivia, for collection of specimens of the lizard genus *Tropidurus*. An illustration of the main habitats visited in Torotoro, prepuna and inter-Andean dry valleys, is shown in figure 1. The park, located in the homonymous municipality of Torotoro, Potosí Department, Charcas Province, ~85 km southeast of the municipality of Cochabamba (straight-line path), is the smallest protected area of Bolivia (Crispieri et al., 2009; fig. 2). Its area of 166 km² encompasses semiarid landscapes from 1900 m to 3600 m in elevation, with numerous canyons and valleys, lying altogether within the domains of the Bolivian Montane Dry Forests (locally known as *bosques secos montanos bolivianos* or *valles secos interandinos*). This xeric ecoregion is restricted to central and southern Bolivia and comprises seasonal dry forests, wetland forests along rivers, and dry, sparsely vegetated slopes with contorted trees and shrubs, columnar cacti, and patches of bromeliads over bare or stony soils (Olson et al., 2001). The Bolivian Montane Dry Forests lie between the Andean Yungas and Chaco to the east, and the Puna to the west, at higher elevations, ranging from ~1000 to 3300 m, but it is predominantly found between ~1500 and 3000 m. Precipitation in this zone ranges from 200 to 650 mm (defining a marked, dry winter) and mean temperatures from 14°–19° C (López, 2003a).

SAMPLES: Specimens were collected with the aid of rubber bands, euthanized with an overdose of 2% lidocaine, preserved with 10% unbuffered formalin, and then transferred to 70% ethyl alcohol solution. Before fixation, tissue samples (muscle) from the thigh of all individuals were collected and stored in absolute ethyl alcohol for subsequent molecular analyses. All specimens and tissue samples collected in Torotoro were deposited at the Museo de Historia Natural Alcide d'Orbigny (MHNC), Cochabamba, Bolivia. Collection permits were granted to us by the Bolivian Ministerio de Medio Ambiente y Agua (MMAyA permit #2298/2013). All specimens collected were assigned to the type series of the new species described herein; refer to Species Accounts for details on collections sites and catalog numbers.

Additional material employed in morphological comparisons and ethanol-preserved tissue samples (muscle, liver, finger, and tail tips) analyzed molecularly were obtained from the American Museum of Natural History, New York (AMNH and Ambrose Monell Cryo Collection–AMCC); Museo Nacional de Ciencias Naturales, Madrid (MNCN); Museo de Historia Natural Alcide d'Orbigny, Cochabamba, Bolivia (MHNC); Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay (MNHNP); Museo de Historia Natural Noel Kempff Mercado, Santa Cruz de la Sierra, Bolivia (MNK); Miguel Trefaut Rodrigues Tissue Collection, Instituto de Biociências, Universidade de São Paulo, Brazil (MTR and nonstandardized acronyms); Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP); Universidade Federal do Mato Grosso, Cuiabá, Brazil (UFMT). Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil (UFRGS). In total, we analyzed 85 tissue samples, representing three out of the four *Tropidurus* species groups defined by Frost et al. (2001) (*T. semitaeniatus* group, *T. spinulosus* group, and *T. torquatus* group) plus outgroups. A list of the 109 specimens examined

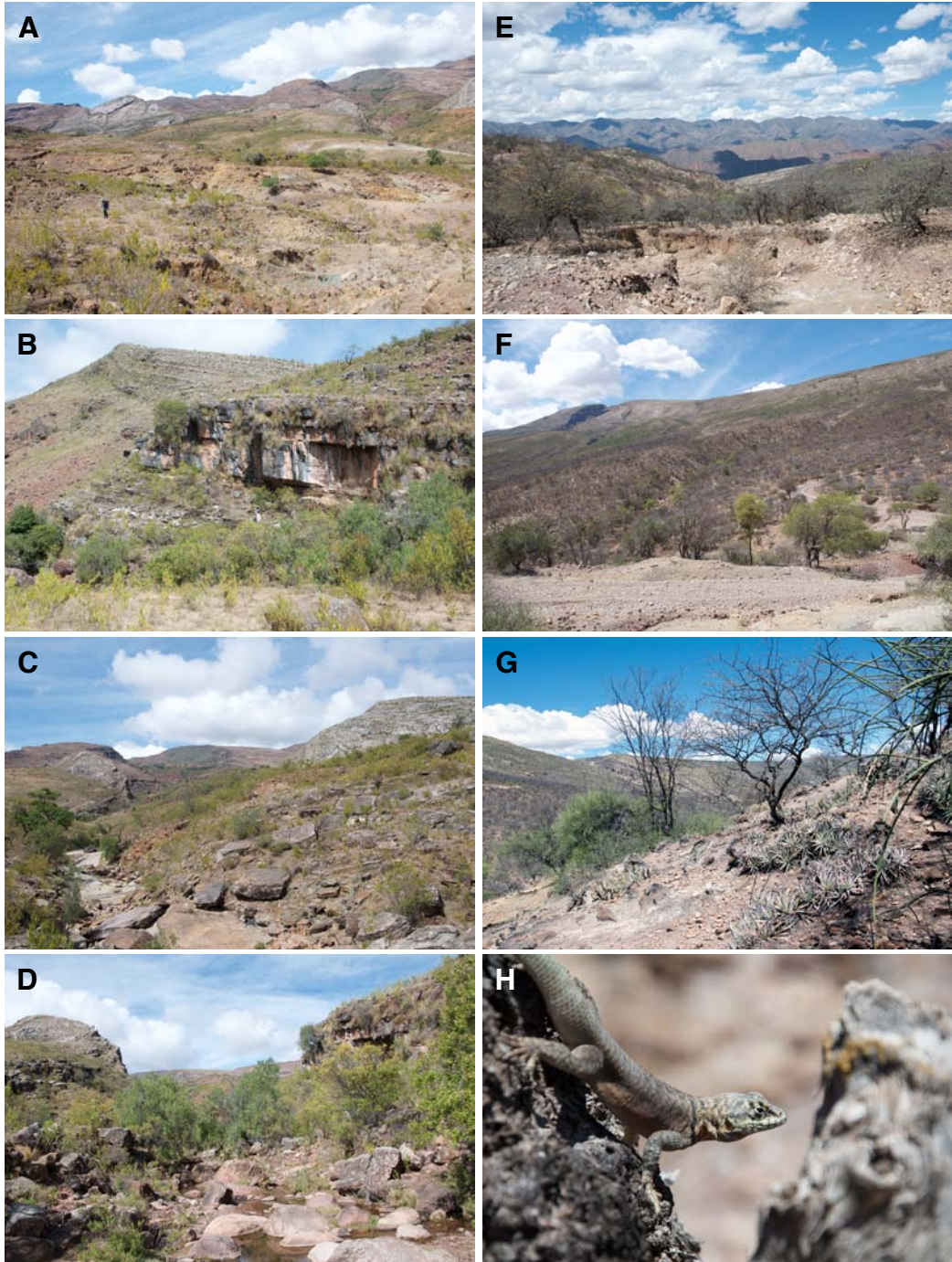


FIGURE 1. Habitats visited in the Torotoro National Park, Potosí, Bolivia. A–D, Prepuna ($18^{\circ} 7' 10.92''$ S, $65^{\circ} 48' 30.24''$ W — WGS84 system; ~ 2798 m). E–G, Inter-Andean dry valleys at the type locality of *Tropidurus azurduyae* ($18^{\circ} 5' 54.24''$ S, $65^{\circ} 44' 57.48''$ W — WGS84 system; ~ 2264 m). H, Adult male of *T. azurduyae*, sighted (not collected) at the type locality of the species.

morphologically (and corresponding collection/field information) and a list of tissue samples, respective voucher specimens, and GenBank accession numbers is provided in appendices 1–4.

MORPHOLOGICAL DESCRIPTIONS, SEX DETERMINATION, AND INTERSPECIFIC VARIATION: We adopted the terminology revised by Carvalho et al. (2016) for description of external morphological structures. Adult male specimens were identified based on the presence of colored patches of scales varying from yellow to black on the ventral side of thighs and preloacal flap. Males also have wider heads and thinner bodies than females of the same body size (Pinto et al., 2005; Ribeiro et al., 2012). Sex determination of juveniles is not as obvious, and required the examination of gonadal condition.

We collected morphometric data from the right side of 45 adult male and 49 adult female specimens of *Tropidurus* with the aid of a digital caliper (to the nearest 0.01 mm). We modified Carvalho et al.'s (2016) morphometric protocol by adding two variables: head length (HL), measured from the tip of the snout to the posterior end of the occipital region; and armpit to groin distance (AGD). In total, we analyzed 13 morphometric variables: **SVL**, snout-vent length; **HH**, head height; **HL**, head length; **HW**, head width; **EOS**, ear opening–snout distance; **AL**, arm length; **FAL**, forearm length; **HDL**, manus length; **THL**, thigh length; **SL**, shank length; **FOL**, foot length; **AGD**, armpit to groin distance; and **TL**, tail length. We calculated basic statistical descriptors (mean, standard deviation, and minimum and maximum values) for all variables and tested the assumptions of normality and variance homoscedasticity using Shapiro-Wilk and Bartlett test, respectively (Sokal and Rohlf, 1995). We log₁₀-transformed all morphometric variables and performed a principal component analysis (PCA; covariance matrix) to investigate morphometric variation. Linear discriminant analysis (LDA) was then used to test for morphometric differences among species (non-log-transformed data). We employed the leave-one-out cross-validation procedure to assess the accuracy of species reclassifications resulting from LDA. We did not incorporate variable TL into the multivariate analyses because a large portion of the specimens measured had broken, regrown, or missing tails. Size differences (SVL) among species were tested with analysis of variance (ANOVA) and post hoc Tukey-Kramer test.

We analyzed 51 male and 57 female specimens to investigate variation in scale counts among species. Meristic variables were tested for normality and variance homoscedasticity using Shapiro-Wilk and Bartlett test, respectively (Sokal and Rohlf, 1995). Following the same procedures adopted for morphometric data analyses, we employed PCA plus LDA to investigate meristic variation and test for differences in scale counts among species, avoiding multiple pairwise comparisons. All statistical analyses were carried out for each sex separately using R version 3.3.2 (R Core Team, 2017).

PHYLOGENETIC INFERENCE: All laboratory procedures employed for generation and manipulation of sequence data followed Carvalho et al. (2016). To infer the phylogenetic relationships of *Tropidurus* and determine the proper allocation of the new species under description within this genus, we analyzed four mitochondrial (12S, 16S, CO1, Cyt *b*) and six nuclear loci (BACH1, kif24, NTF3, PRLR, PTPN, SNCAIP). We initially sampled as ingroups one representative of each species previously sequenced and morphologically analyzed by Carvalho et al. (2016). In addition,

TABLE 1. Primers and PCR profiles for DNA amplification. Sequences encoding the mitochondrial genes 12S rDNA, 16S rDNA, COI, and Cyt *b*, and nuclear genes BACH1, kif24, NTF3, PRLR, PTPN, and SNCAIP, were employed for phylogenetic analyses.

| Gene | Source | Primer | Direction | Sequence (5'–3') | PCR Profile ¹ |
|--------------|------------------------------|-------------------------|-----------|---------------------------------|---|
| mtDNA | | | | | |
| 12S | Benavides et al. (2007) | 12S.tPhe-22 | Forward | AAAGCACRGCCTGAA-GATGC | 95°(30'')/50°(60'')/72°(60'') [35x] |
| 12S | Benavides et al. (2007) | 12S.12e-987 | Reverse | GTRCGCTTACCWTGTTAC-GACT | |
| 16S | Geurgas et al. (2008) | 16S F | Forward | CTGTTTACCAAAAACATM-RCCTYTAGC | 95°(30'')/45°(30'')/72°(60'') [35x] |
| 16S | Whiting et al. (2003) | 16S R | Reverse | TAGATAGAAACCGACCTG-GATT | |
| COI | Folmer et al. (1994) | COI LCO1490 | Forward | GGTCAACAAATCATAAA-GATATTGG | 94°(60'')/45°(60'')/72°(75'') [10x] + 94°(60'')/50°(60'')/72°(75'') [35x] |
| COI | Folmer et al. (1994) | COI HCO2198 | Reverse | TAAACTTCAGGGAC-CAAAAAATCA | |
| Cyt <i>b</i> | Geurgas (unpubl.) | Cyt <i>b</i> Citi-Tropi | Forward | TGAAAAACCCAYCGT-TATTC AAC | 95°(30'')/51°(30'')/72°(60'') [35x] |
| Cyt <i>b</i> | Palumbi (1996) | Cyt <i>b</i> V | Reverse | GGCGAATAGGAAGTAT-CATTC | |
| Cyt <i>b</i> | Geurgas and Rodrigues (2010) | H15149 | Reverse | TGCAGCCCCTCAGAAT-GATATTTGTCCTCA | |
| nucDNA | | | | | |
| BACH1 | Portik et al. (2012) | BACH1_f1 | Forward | GATTTGAHCCYT-TRCTTCAGTTTGC | 95°(15'')/60°(30'')/72°(60'') [2x] + Touchdown –2° [2x] + 95°(15'')/50°(30'')/72°(60'') [30x] |
| BACH1 | Portik et al. (2012) | BACH1_r1 | Reverse | ACCTCACATTCYTGTTCYC-TRGC | |
| kif24 | Portik et al. (2012) | KIF24_f1 | Forward | SAAACGTRTCRCCMAAAC-GCATCC | 95°(30'')/63°(30'')/72°(60'') [10x] + 95°(30'')/60°(30'')/72°(60'') [30x] |
| kif24 | Portik et al. (2012) | KIF24_r2 | Reverse | WGGCGTCTGRAAYTGCTG-GTG | |
| NTF3 | Portik et al. (2012) | NTF3_f1 | Forward | ATGTCCATCTTGTTTTAT-GTGATATTT | 95°(15'')/60°(30'')/72°(60'') [2x] + Touchdown –2° [2x] + 95°(15'')/50°(30'')/72°(60'') [30x] |
| NTF3 | Portik et al. (2012) | NTF3_r1 | Reverse | ACRAGTTTRTTGTTYTCT-GAAGTC | |
| PRLR | Portik et al. (2012) | PRLR_f1 | Forward | GACARYGARGACCAG-CAACTRATGCC | 95°(30'')/45°(30'')/72°(60'') [35x] |
| PRLR | Portik et al. (2012) | PRLR_r3 | Reverse | GACYTTGTGRACTTCY-ACRTAATCCAT | |

| Gene | Source | Primer | Direction | Sequence (5'–3') | PCR Profile ¹ |
|--------|----------------------|------------|-----------|---------------------------------|--|
| PTPN | Portik et al. (2012) | PTPN12_f1 | Forward | AGTTGCCTGTWGA- AGGRGATGC | 95°(30'')/55°(30'')/72°(60'') [10x] + 95°(30'')/52°(30'')/72°(60'') [30x] |
| PTPN | Portik et al. (2012) | PTPN12_r6 | Reverse | CTRGCAATKGACATYGG- YAATAC | |
| SNCAIP | Portik et al. (2012) | SNCAIP_f10 | Forward | CGCCAGYTG YGGGRAAR- GAWAT | 95°(15'')/60°(30'')/72°(60'') [2x] + Touchdown –2° [2x] + 95°(15'')/50°(30'')/72°(60'') [30x] |
| SNCAIP | Portik et al. (2012) | SNCAIP_r13 | Reverse | GGWGAYTTGAGDG- CACTCTTRGGRCT | |

¹ Conditions for denaturation, annealing, and extension steps for each cycle, followed by the number of cycles. All reactions included a 4 minute initial denaturation at 94° C and a 6 minute final extension at 72° C.

because Andean populations assignable to the *T. torquatus* species group (per Frost et al., 2001) have been referred to in the literature as *T. etheridgei* (see Carvalho, 2013, for a review) and preliminary results by our team have indicated that that name might represent a species complex comprising, among others, our new Andean taxon, we broadened our molecular sampling to include individuals from multiple populations of *T. etheridgei* (sensu lato) throughout its distribution range in northern Argentina, central and southeastern Bolivia, central and northeastern Brazil, and western Paraguay. Because *T. chromatops* was recovered in our previous study (Carvalho et al., 2016) as sister of *T. etheridgei* (sensu stricto), we made the decision of including all samples of this species we had in hand in our analyses. We selected the tropidurines *Microlophus quadrivittatus* Tschudi, 1845, *Plica plica* (Linnaeus, 1758), *T. semitaeniatus* (Spix, 1825), *T. spinulosus* (Cope, 1862), and *Uranoscodon superciliosus* (Linnaeus, 1758), and the stenocercine *Stenocercus quinarius* Nogueira and Rodrigues (2006) as outgroups; the latter was chosen to root the phylogenetic trees produced.

ALIGNMENT, MODEL SELECTION, AND PHYLOGENETIC ANALYSES: To infer the relationships of *Tropidurus* our phylogenetic analyses followed the framework adopted by Carvalho et al. (2016, which see for details on data manipulation and analytical methods and table 1 for PCR protocols). In summary, alignments were performed in MAFFT version 7 (Kato and Toh, 2008; Kato and Standley, 2013) and concatenated in Sequence Matrix version 1.8 (Vaidya et al., 2011). We employed PartitionFinder version 2.1.1 (Lanfear et al., 2012, 2016) to determine the best-fit nucleotide substitution models and data partition schemes. All available models were compared, and the “greedy search” algorithm and linked branch lengths were selected for calculations of likelihood scores; Bayesian information criterion (BIC) was adopted for selecting among alternative partitioning strategies. For maximum-likelihood analyses (hereafter, ML), tree searches were performed in Garli version 2.1 (Zwickl, 2006). Starting tree topologies were generated using the stepwise-addition algorithm and the number of attachment points evaluated for each taxon to be added was set to 171. Our best-tree search was based on 100 replicates and the relative support of the clades recovered was assessed through 1000 nonparametric bootstrap replicates (Felsenstein 1985, 2004). We summarized bootstrap results using SumTrees (Sukumaran and Holder, 2010). All phylogenetic analyses were performed on a Mac

OS X Yosemite 10.10.5, 3.4 GHz Intel core i7 processor, 16GB 1333 MHz DDR3. All alignments and trees produced in this study were made available for download from the AMNH Library Digital Repository (<https://doi.org/10.5531/sd.sp.29>).

GENETIC DISTANCE: We calculated uncorrected genetic distances (p -distances) within and among species using MEGA version 7.0 (Kumar et al., 2016). Genetic distances were computed for partial fragments of Cyt *b* and 12S using the complete deletion method. Of the original 756 and 881 aligned sites of Cyt *b* and 12S, respectively, 330 bp and 878 bp were used for calculation of genetic distances after exclusion of sites containing missing data from sequence tips. We excluded samples [MTR] PNP 189–6207 and AMCC 204493 from genetic distance calculations of Cyt *b* and samples [MTR] 916015, [MTR] 916016, and [MTR] PNP187 from genetic distance calculations of 12S because the fragments sequenced for these samples were much shorter than the longest set of (aligned) overlapping fragments obtained for all other individuals. Cyt-*b* alignment contained no internal gap sites and 12S fragments contained 53 internal gap sites.

SPECIES ACCOUNTS

Tropiduridae Bell, 1843

Tropidurus Wied, 1825

***Tropidurus azurduyae*, n. sp.**

Figures 1H, 3E–H, 4A–F

HOLOTYPE: MHNC-R 3011, adult male from Parque Nacional Torotoro, Potosí, Bolivia (18° 5' 54.24" S, 65° 44' 57.48" W — WGS84 system; ~2264 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, G. Juchazara, E. Lujo, and F. Mamani in 13 November 2013.

ALLOTYPE: MHNC-R 3009, adult female, same locality as holotype (18° 5' 53.88" S, 65° 44' 57.12" W — WGS84 system; ~2262 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, G. Juchazara, E. Lujo, and F. Mamani in 13 November 2013.

PARATYPES: MHNC-R 3007, adult female, same locality as holotype (18° 6' 15.48" S, 65° 45' 36.00" W — WGS84 system; ~2569), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, J. Choque, J. Kamaqui, and E. Lujo in 14 November 2013. MHNC-R 3008, adult female, same locality (18° 6' 25.56" S, 65° 45' 27.36" W — WGS84 system; ~2579 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, J. Choque, J. Kamaqui, and E. Lujo in 14 November 2013. MHNC-R 3010, adult male, same locality (18° 5' 52.32" S, 65° 44' 57.48" W — WGS84 system; ~2269 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, G. Juchazara, E. Lujo, and F. Mamani in 13 November 2013. MHNC-R 3012, adult male, same locality (18° 6' 25.56" S, 65° 45' 25.92" W — WGS84 system; ~2566 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, J. Choque, J. Kamaqui, and E. Lujo in 14 November 2013. MHNC-R 3015, adult male, same locality (18° 6' 25.92" S, 65° 45' 25.92" W — WGS84 system; ~2562 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, J. Choque, J. Kamaqui, and E. Lujo in 14 November 2013. MHNC-R 3016, adult male, same locality (18° 5' 54.24" S, 65° 44' 55.32" W — WGS84

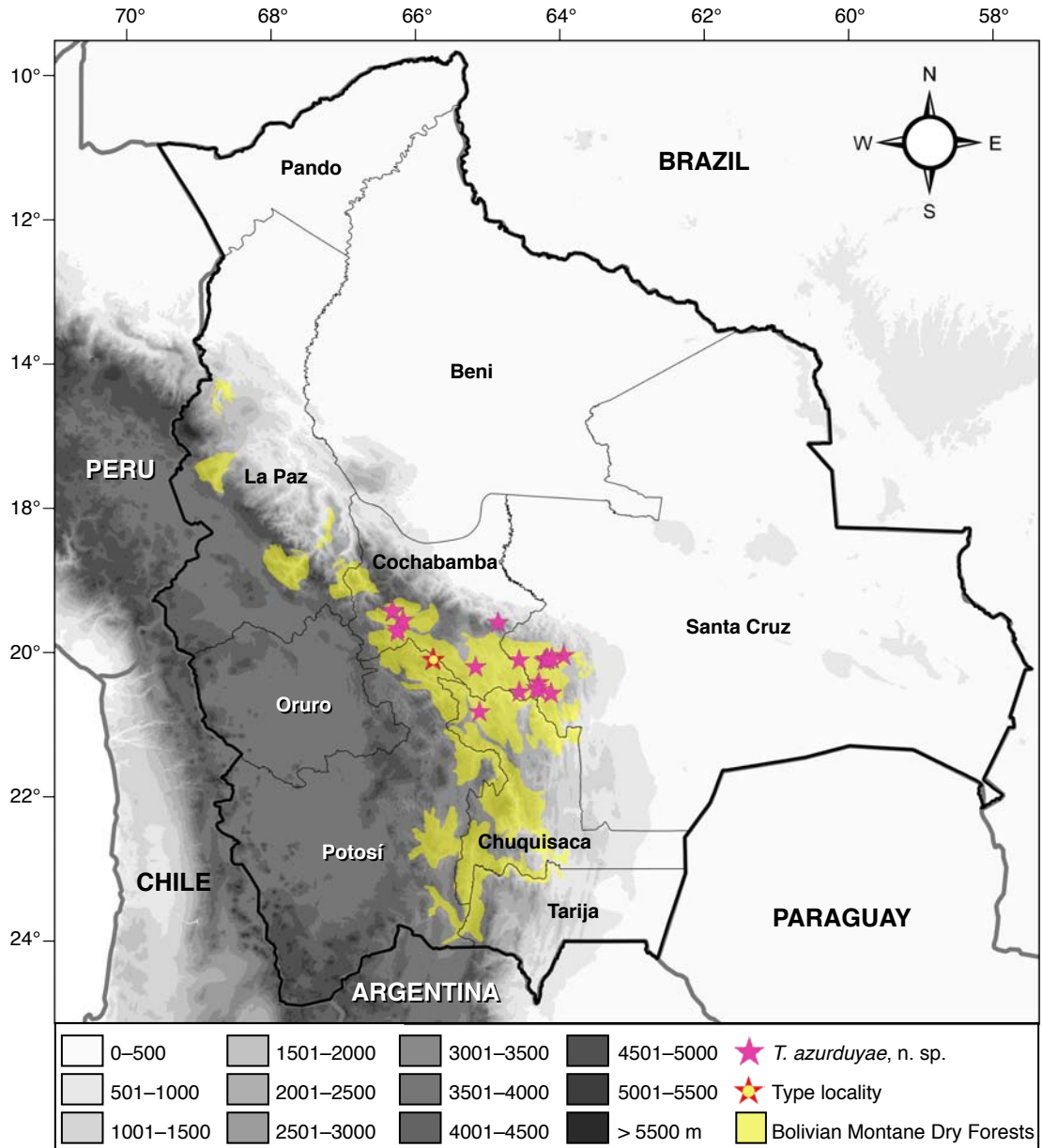


FIGURE 2. Geographic distribution of *Tropidurus azurduyae*. Map shows the altimetric profile of Bolivia and its neighboring countries to illustrate the association of the new species with high-altitude habitats (inter-Andean dry valleys) that compose the Bolivian Montane Dry Forests ecoregion. Type locality (Toro Toro National Park, Potosí, Bolivia; 18° 5' 54.24" S, 65° 44' 57.48" W — WGS84 system; ~2264 m) is highlighted.

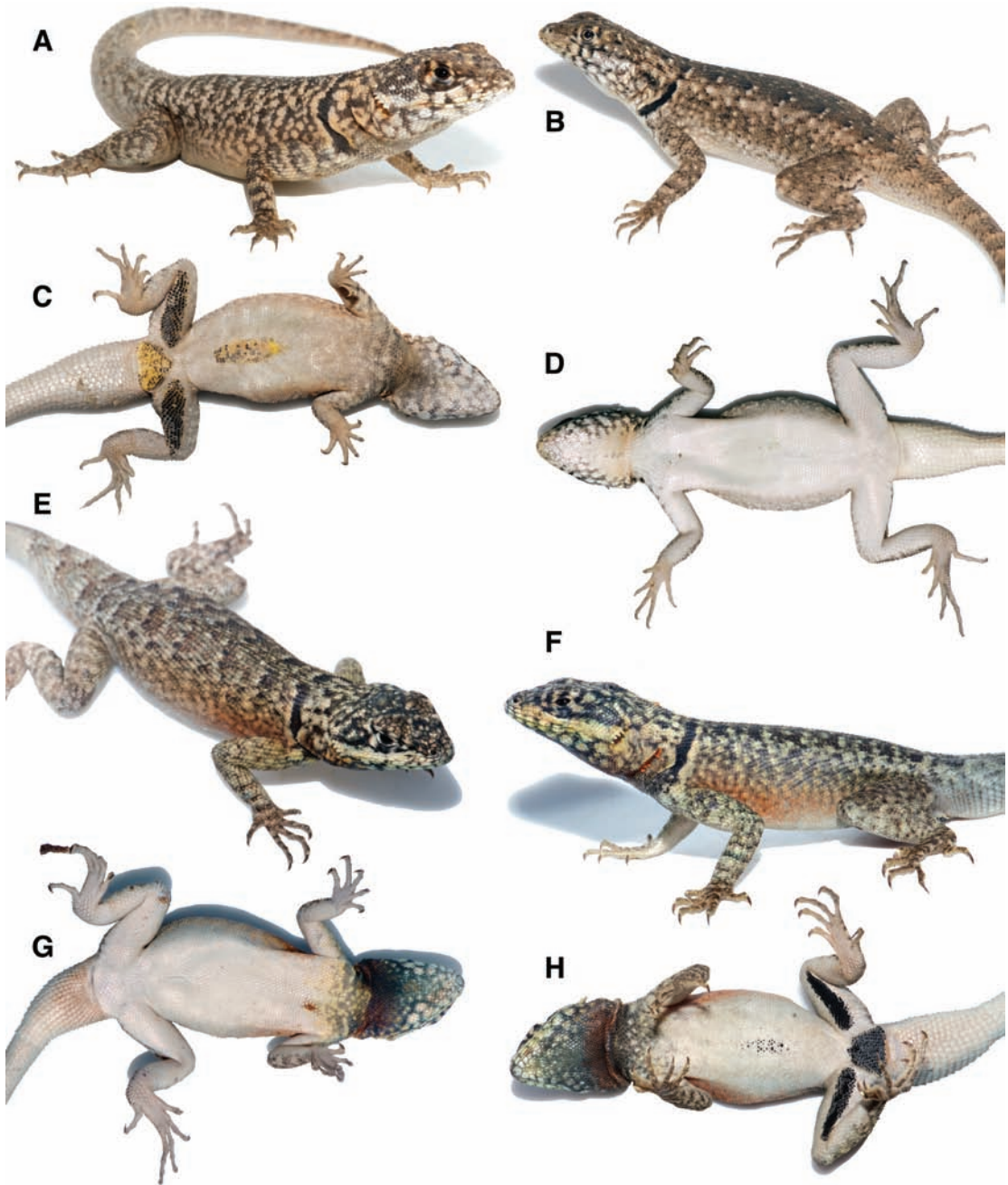


FIGURE 3. Live specimens of *Tropidurus etheridgei* Cei, 1982 and *T. azurduyae*. **A, C**, Adult male of *T. etheridgei* (AMNH-R 176273) from Orloff, Colonia 15, Filadelfia, Boquerón, Paraguay (22° 19' 58.42" S, 59° 55' 00.02" W — WGS84 system; ~136 m). **B, D**, Adult female of *T. etheridgei* (AMNH-R 176277) from Estancia Esmeraldas, Boquerón, Paraguay (20° 59' 15.81" S 61° 59' 27.90" W — WGS84 system; ~329 m). **E, G**, Adult female (allotype MHNC-R 3009) of *T. azurduyae*. **F, H**, Adult male (holotype MHNC-R 3011) of *T. azurduyae*.

system; ~2556 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, G. Juchazara, E. Lujo, and F. Mamani in 13 November 2013. MHNC-R 3017, adult male, same locality (18° 5' 55.32" S, 65° 44' 58.56" W — WGS84 system; ~2274 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, G. Juchazara, E. Lujo, and F. Mamani in 13 November 2013. MHNC-R 3020, adult male, same locality (18° 5' 11.88" S, 65° 45' 44.28" W — WGS84 system; ~2596 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, J. Choque, J. Kamaqui, and E. Lujo in 14 November 2013. MHNC-R 3024, juvenile female, same locality (18° 5' 55.32" S, 65° 44' 57.48" W — WGS84 system; ~2269 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, G. Juchazara, E. Lujo, and F. Mamani in 13 November 2013. MHNC-R 3026, juvenile female, same locality (18° 5' 54.24" S, 65° 44' 55.32" W — WGS84 system; ~2256 m), collected by A.L.G. Carvalho, M.A. Sena, L.R. Rivas, G. Juchazara, E. Lujo, and F. Mamani in 13 November 2013.

MORPHOLOGICAL DIAGNOSIS: *Tropidurus azurduyae* is here morphologically diagnosed as a *Tropidurus* based on the observation of a set of characters suggested by Frost et al. (2001) as exclusive to the genus: skull not highly elevated at the level of the orbits; “flash” marks on underside of thighs present; circumorbitals distinct from other small supraorbital scales; lateral fringe not developed on both sides of fourth toes; enlarged middorsal scale row absent; tail terete; and hemipenis attenuate without apical disks. The presence of a maxilla not broad, nutritive foramina of maxilla strikingly enlarged, lingual process of dentary extending over lingual dentary process of coronoid, angular strongly reduced, and absence of medial centrale could not be examined without dissecting or clearing and staining specimens. These characters should be revised whenever larger series of individuals become available.

Tropidurus azurduyae is a member of the *T. torquatus* group per Frost et al. (2001). It differs from other species groups by lacking an enlarged middorsal scale row (well marked in species of the *T. spinulosus* group, especially in males), by exhibiting black “flash” marks on the underside of thighs and cloacal flap of adult males (yellow, cream, or orangey “flash” marks are present in males of the *T. spinulosus* group), and also by lacking a dorsoventrally flattened body (as observed in species of the *T. semitaeniatus* group and, more moderately, in *T. bogerti*).

Tropidurus azurduyae is the only species in the genus with lower flanks pigmented orange, a condition consistently observed in both sexes (fig. 3E–H). Its ventral head is darkly pigmented and offers contrast to the light circular blotches present on chin and also laterally (fig. 3G, H). The ground color of its throat is charcoal gray impregnated with strong orange coloration (fig. 3G, H). A pair of mite pockets is present on the lateral neck, with the posterior one larger; the anterior pocket originates lower than the posterior, but both usually end ventrally at the same level (fig. 3F). No pockets are found in the armpit and inguinal region of the new species. An elliptical or subrhomboidal black mark is present on the mid venter of adult males of *T. azurduyae* in addition to black “flash” marks on the underside of thighs and preloacal flap (fig. 3H). *Tropidurus azurduyae* is saxicolous, but may climb tree trunks and fallen logs occasionally (fig. 1H). In combination, this set of characters provides a safe diagnosis, distinguishing *T. azurduyae* from all other congeners.

COMPARISON WITH OTHER SPECIES: *Tropidurus azurduyae*, *T. cocorobensis*, *T. chromatops*, *T. etheridgei*, *T. hygomi*, and *T. psammonastes* are the only species of the *T. torquatus* group that have

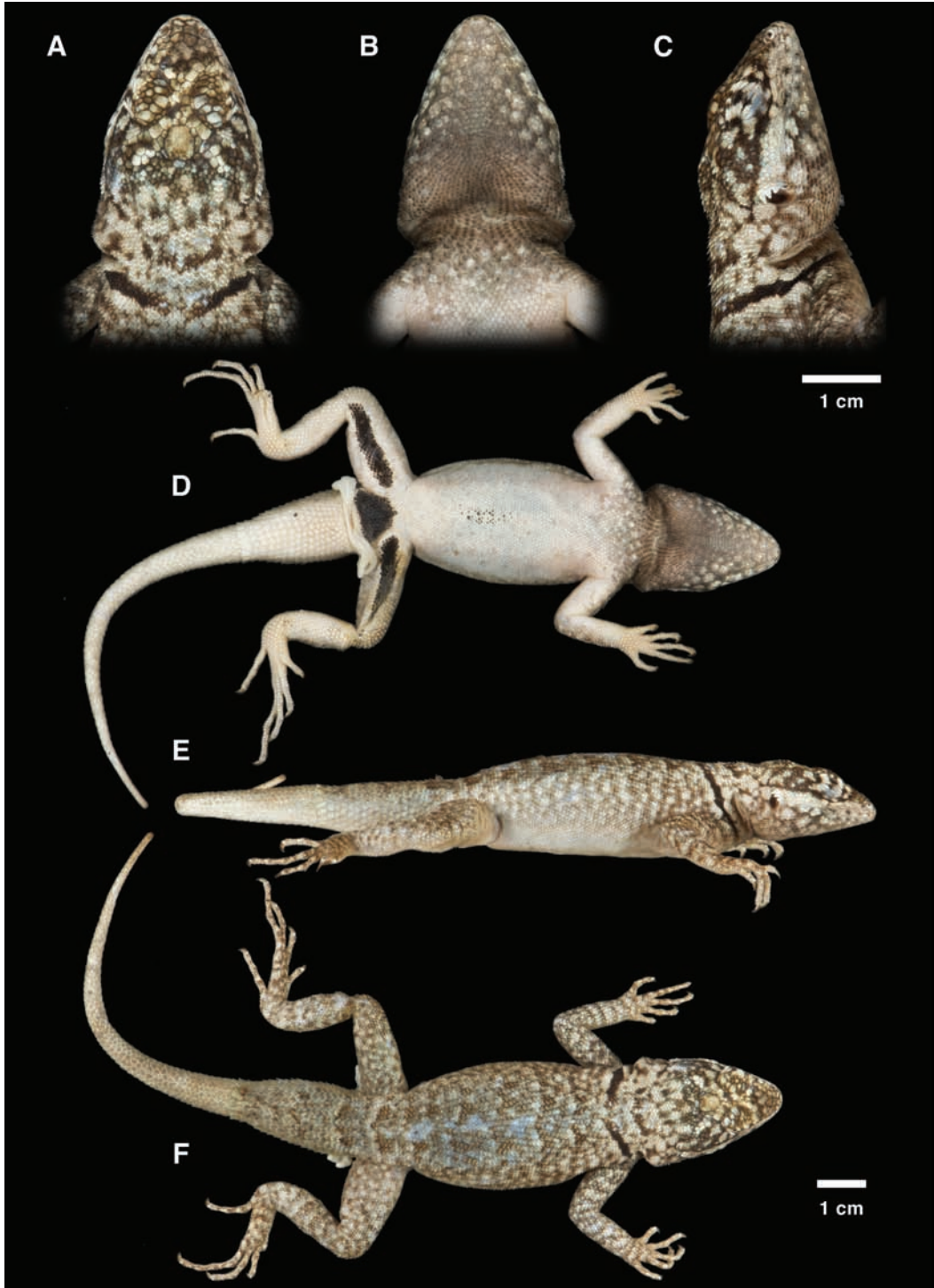


FIGURE 4. Preserved holotype of *Tropidurus azurduyae* (adult male, MHNC-R 3011). A, Dorsal head. B, Ventral head. C, Lateral head. D, Ventral body. E, Lateral body. F, Dorsal body.

two mite pockets on the lateral neck and lack differentiated skin folds or pockets in the axillary and inguinal regions. Although *T. catalanensis*, *T. imbituba*, and *T. torquatus* also have two mite pockets on the lateral neck, all three species exhibit 2–3 shallow granular areas in the axillary region and a fully developed granular inguinal pocket. The two pockets on the lateral neck of *T. azurduyae* are not exceptionally broadened nor deep, and they differ from the extremely enlarged lateral neck pockets of *T. chromatops* (fig. 5). They are also slightly distinct from the pockets of *T. hygomi*, which are oblique and deep, with the anterior one positioned more ventrally than the posterior one in both species. *Tropidurus hygomi* and *T. azurduyae* can be further distinguished by the presence of expanded scales covering the supraocular area of the former species. The anterior lateral neck pocket of *T. azurduyae* is coated with granular scales, while this same structure in *T. psammonastes* is coated with regular scales (only the posterior one is granular). For a more comprehensive summary of mite-pocket morphologies and their taxonomic distribution in the *T. torquatus* group, refer to Rodrigues (1987: figs. 1–13) and Carvalho et al. (2016: table 2, fig. 8).

Tropidurus azurduyae is saxicolous, and its ecology contrasts markedly with the psammophilous habit of three other species of the *T. torquatus* group with two lateral neck mite pockets, *T. cocorobensis*, *T. hygomi*, and *T. psammonastes*. It can also be distinguished from *T. cocorobensis* and *T. hygomi* based on its larger body size (SVL: 66.06–104.85 mm in males and 62.83–89.58 mm in females of *T. azurduyae*, 61.39–74.59 mm in males and 60.27–65.37 mm in females of *T. cocorobensis*, and 54.15–67.30 mm in males and 48.08–60.38 mm in females of *T. hygomi*). The new species also lacks the 2–4 well-marked black ocellar spots that decorate the upper flanks of *T. cocorobensis* anteriorly, from nuchal collar, just above the humerus, reaching to the middle of the body. *Tropidurus azurduyae* differs from *T. chromatops* in terms of coloration by lacking an intense burnt-red dorsal head and a facial mask with touches of blue and cream (figs. 5, 6A–D). The new species exhibits a champagne background, mottled with dark grayish-brown and lead pigmentation, and dark ventral head. This coloration is fairly distinct from the dirty-yellow dorsal background decorated with a brown reticulated pattern, and light ventral head ornate with a loose reticulum or semireticulum, found in *T. etheridgei* (pattern better marked in males than females; fig. 3A–D). Moreover, with regard to coloration, the lower flanks and gular region pigmented in orange in both sexes is, to our knowledge, exclusive to *T. azurduyae*.

DESCRIPTION OF HOLOTYPE (figs. 3F, H, 4A–F): Medium-sized specimen of *Tropidurus*, SVL 87.31 mm; head triangular, length 30% of SVL and width 71% of head length; skull not compressed, not strongly elevated at level of orbits; rostrum not noticeably shortened relative to most other species in the genus; scales of frontonasal region not imbricating posteriorly, lenticulate scale organs distributed on the head, more abundant on the frontonasal and supraocular areas; rostral tall, about 3× (in lateral view) as high as first supralabial, contacting first supralabials, first lorilabials, nasals, and two postrostrals; 1/1 postrostrals; nasal single, slightly protruding, pentagonal, elongated anteroposteriorly with the tip of the pentagon directed anteriorly, in contact with rostral; 6/7 enlarged supralabials followed by 3/6 smaller scales reaching the rictus oris, never contacting subocular; nostril elliptical, occupying about 1/3 of nasal, positioned posteriorly, directed posterolaterally; 3/3 canthals; anteriormost canthal separated from supralabials by 1/1 rows of lorilabials; 8/8 laminate superciliary

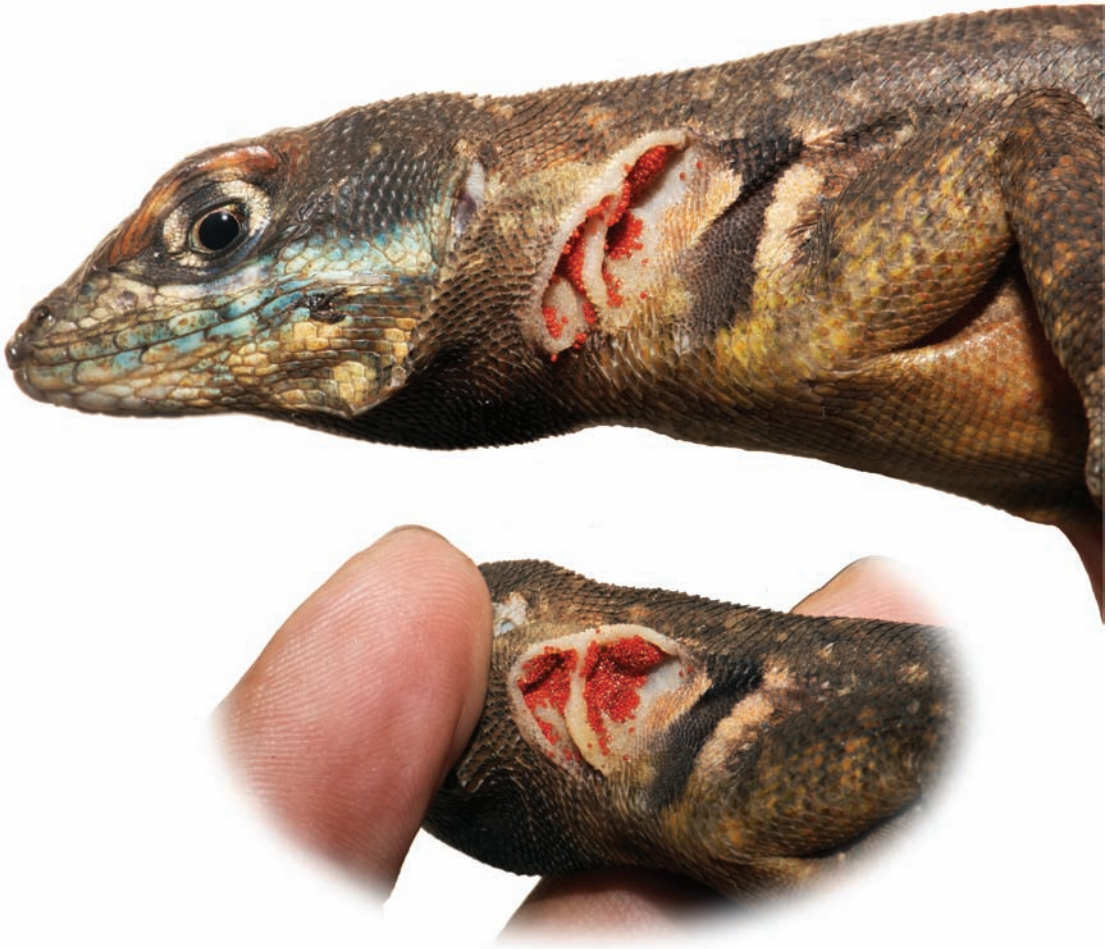


FIGURE 5. Adult male of *Tropidurus chromatops* Harvey and Gutberlet, 1998 (MHNC-R 3018), illustrating the expanded lateral neck mite pockets and the colorful facial mask with touches of blue and cream, characteristic of the species.

scales weakly produced vertically; 1/1 dorsally keeled preoculars contacting third canthal and 3/3 loreals; 2/1 suboculars dorsally keeled, elongate, separated from supralabials by one row of lorilabials posteriorly; palpebrals granular; second row of palpebrals larger, with scale organ on tip, central palpebrals unpigmented, nearly translucent; pupil circular; 3/3 main rows of supraoculars, oblique internal row with 8/8, medial row with 8/8, external row with 7/7 scales, the enlarged internal ones occupying up to half the width of the supraocular area; 1/1 rows of small, angulate circumorbitals; 1/1 rows of short semilaminate scales separating circumorbitals from superciliaries; interparietal enlarged, about 1.2× longer than wide; parietal eye visible, positioned medially on the posterior limit of the first third of the interparietal scale; temporals slightly imbricate, keeled, at least 3× larger than lateral neck scales and smaller than dorsals and parietals; ear shaped like inverted keyhole, canal deep, largest diameter (~5.5 mm) of ear opening 25% of ear opening to snout distance; tympanum translucent;

preauricular fringe consisting of row of 6/6 smooth, lanceolate scales; width of mental 60% of the width of rostral; mental extending posteriorly to the level of half of the first adjacent infralabials; 7/7 enlarged infralabials followed by 3/3 smaller scales reaching the rictus oris; 4/4 angulate, enlarged postmentals; 1/1 postmentals in contact with first infralabial; first postmentals not in contact; 11/11 sublabials; 46 gulars, imbricating posteriorly.

Vertebral crest absent; 85 dorsals; 82 scale rows around midbody; 79 ventrals; dorsals large, strongly keeled and mucronate, particularly on the dorsal neck; keels on dorsal and caudal scales align forming continuous, longitudinal, slightly oblique lines observable macroscopically; postmeral region with small, nearly granular, smooth, nonmucronate scales, increasing in size, intensity of keels and mucronation toward the flanks; ventrals smooth, nonmucronate, imbricate, about half the size of dorsals; midventral, dark-pigmented “flash” mark present, not intensely marked, subrhomboidal; “flash” marks on underside of thighs formed by 6/6 rows of dark glandular scales; 13 cloacal scales, cloacal flap with 12 rows of dark precloacal glandular scales; supracarpal scales smooth near finger I and slightly keeled toward finger V, rhomboidal or subrhomboidal; supratarsal scales smooth toward finger I and keeled and mucronate toward finger V, rhomboidal; both supracarpals and supratarsals with very rare scale organ positioned on the distal end of the scale, when present; infracarpal and infratarsal scales carinate, tricarinate toward fingers and toes; fingers and toes thin, cylindrical, slightly compressed laterally; supradigital lamellae keeled, rhomboidal, scale organ positioned on the distal end of the scales, when present; infradigital lamellae tricarinate and mucronate, 17/17 under fourth finger + ungual, 26/24 under fourth toe + ungual, medial careen larger and more projected than laterals; claws long, curved; preaxial scales of forearm strongly keeled and mucronate grading to smooth scales with no or short mucrons and smaller size on ventral and postaxial surfaces; 28/28 tibial scales, keeled and mucronate; dorsal body scales large, keeled, mucronate; lateral neck scales several times smaller than dorsals; rictal, nuchal, postauricular, supraauricular, dorsolateral, and antegular fold absent; shallow postauricular depression present; oblique neck fold well marked defining two lateral neck mite pockets on each side of the neck; anteriormost mite pocket half the size and originating lower than the posteriormost, both ending ventrally at the same level; antehumeral fold present and well marked, coated with imbricate scales similar to those on lateral neck; gular fold incomplete medially; axillary and inguinal mite pockets absent; tail slightly compressed laterally, regrown, tapering from the end of the first third to a point; caudal verticils absent; scales of tail imbricate, keeled, mucronate, up to 3× larger than dorsals.

COLORATION IN LIFE (fig. 3F, H): Dorsal head with champagne background, mottled with brownish and lead pigmentation. A champagne facial stripe decorates the lateral head, covering labials, lorilabials, loreals, inferior portion of preocular and suboculars, lower temporals, and preauricular fringe. Keeled portion of preocular and suboculars, palpebrals, superciliaries, and upper temporals dark pigmented, similar in coloration to dorsal head. Iris golden brown. Mental region champagne grading into a lead ventral head with touches of champagne. Sublabial and posterolateral region of the head decorated with champagne blotches, 1–7 scales in size, that reach the area behind ear opening. Throat charcoal gray with intense orange pigmentation permeating its dark background until the antegular fold. Area between antegular fold and

TABLE 2. Mean \pm standard deviation and (in parentheses) minimum and maximum values of morphometric measurements (in mm) of the species analyzed. Abbreviations: **SVL**, snout-vent length; **TL**, tail length; **HH**, head height; **HL**, head length; **HW**, head width; **EOS**, ear opening-snout distance; **AL**, arm length; **FAL**, forearm length; **HDL**, manus length; **THL**, thigh length; **SL**, shank length; **FOL**, foot length; **AGD**, armpit to groin distance. Number of measured individuals is followed (between parentheses) by the number of individuals with fully grown tails. See Material and Methods for details on treatment of individuals with broken, regrown, or missing tails.

| | MALES | | | FEMALES | | |
|-----|------------------------------------|--------------------------------------|---------------------------------------|-----------------------------------|------------------------------------|--------------------------------------|
| | <i>T. chromatops</i> N = 4 (1) | <i>T. etheridgei</i> N = 14 (10) | <i>T. azurduyae</i> N = 27 (12) | <i>T. chromatops</i> N = 7 (4) | <i>T. etheridgei</i> N = 13 (7) | <i>T. azurduyae</i> N = 29 (12) |
| SVL | 92.52 \pm 6.55 (86.22–101.59) | 79.61 \pm 9.65 (66.78–96.48) | 85.16 \pm 9.22 (66.06–104.85) | 72.03 \pm 3.68 (67.17–77.79) | 68.92 \pm 7.76 (57.59–86.28) | 72.84 \pm 6.96 (62.83–89.58) |
| TL | 140.97 | 111.75 \pm 11.11 (94.60–126.31) | 123.78 \pm 15.96 (101.19–153.92) | 85.20 \pm 5.12 (80.19–91.94) | 87.04 \pm 6.80 (76.80–95.49) | 106.36 \pm 13.87 (91.13–131.89) |
| HH | 14.08 \pm 1.74 (12.15–16.33) | 12.55 \pm 1.66 (9.58–14.44) | 12.73 \pm 1.52 (9.75–16.10) | 10.05 \pm 0.84 (8.95–11.26) | 10.03 \pm 0.76 (8.82–11.41) | 10.41 \pm 1.38 (8.02–13.71) |
| HL | 26.85 \pm 2.42 (24.95–30.22) | 23.45 \pm 2.30 (19.99–27.33) | 24.24 \pm 2.64 (18.70–29.38) | 19.49 \pm 1.15 (18.44–21.60) | 19.52 \pm 1.69 (16.16–21.98) | 19.61 \pm 1.83 (16.46–23.76) |
| HW | 19.60 \pm 1.57 (18.18–21.69) | 17.28 \pm 2.26 (13.71–20.23) | 17.51 \pm 2.26 (13.68–22.92) | 13.73 \pm 0.88 (12.51–14.87) | 14.01 \pm 1.40 (11.95–17.40) | 14.03 \pm 1.28 (11.97–16.71) |
| EOS | 22.70 \pm 2.41 (20.63–26.09) | 19.99 \pm 2.16 (16.81–23.71) | 20.81 \pm 2.19 (16.29–25.26) | 16.54 \pm 0.90 (15.34–18.26) | 16.33 \pm 1.38 (14.16–19.22) | 16.87 \pm 1.57 (13.91–20.74) |
| AL | 15.57 \pm 1.79 (13.82–17.56) | 12.97 \pm 1.43 (10.68–15.89) | 14.12 \pm 1.61 (11.28–16.87) | 11.95 \pm 1.39 (10.51–14.42) | 11.23 \pm 0.84 (9.94–12.53) | 11.79 \pm 1.36 (9.22–14.35) |
| FAL | 13.21 \pm 1.06 (12.28–14.46) | 11.51 \pm 1.37 (8.91–13.32) | 12.15 \pm 1.44 (8.91–14.73) | 9.88 \pm 0.61 (9.17–10.97) | 9.96 \pm 0.71 (8.50–10.73) | 10.03 \pm 1.22 (8.14–13.06) |
| HDL | 15.80 \pm 0.72 (15.11–16.63) | 14.53 \pm 1.24 (12.49–16.80) | 16.07 \pm 1.56 (13.17–19.99) | 13.07 \pm 0.63 (11.92–13.88) | 12.87 \pm 0.80 (11.68–14.19) | 13.77 \pm 1.54 (11.17–17.10) |
| THL | 21.80 \pm 1.71 (20.52–24.32) | 17.85 \pm 2.40 (13.65–22.27) | 19.29 \pm 2.19 (15.00–23.21) | 15.85 \pm 1.06 (14.72–17.11) | 14.85 \pm 1.17 (12.96–16.26) | 15.89 \pm 1.99 (12.84–20.51) |
| SL | 18.63 \pm 0.70 (17.69–19.35) | 16.12 \pm 1.74 (13.47–18.52) | 17.08 \pm 1.66 (13.67–19.97) | 13.73 \pm 0.53 (13.28–14.80) | 13.42 \pm 0.90 (11.39–14.57) | 14.02 \pm 1.43 (11.79–17.87) |
| FOL | 28.37 \pm 1.19 (26.92–29.84) | 25.10 \pm 2.12 (22.39–28.85) | 28.31 \pm 2.30 (23.87–33.54) | 22.24 \pm 0.57 (21.53–22.84) | 22.08 \pm 1.06 (20.32–23.45) | 23.45 \pm 2.33 (19.41–29.56) |
| AGD | 41.23 \pm 4.68 (36.31–47.53) | 34.47 \pm 4.66 (28.06–41.01) | 36.95 \pm 4.85 (27.17–47.37) | 32.81 \pm 3.04 (27.91–37.21) | 31.82 \pm 5.31 (23.34–42.56) | 32.88 \pm 4.21 (23.93–43.03) |

beginning of chest mottled with lead pigmentation and touches of yellow. Neck and dorsal body champagne, mottled with brownish and lead pigmentation; dark coloration more concentrated along the vertebral area. Nuchal collar black, well marked, nearly complete dorsally, formed by 4–5 rows of dark scales extending from humeral attachment to the vertebral area, outlined by 2–4 rows of champagne scales. Uppermost limits of flanks similar to dorsum, lower flanks pigmented in orange from axillary to inguinal region. Chest cream, anteriorly sprinkled with lead pigmentation. Ventral ground coloration cream; black spotted subrhomboidal mark oriented anteroposteriorly present on the mid venter. Limbs with champagne background and lead pigmentation forming a pattern similar to dorsum anteriorly (arms and thighs), and a

TABLE 3. Tukey-Kramer pairwise comparisons of mean snouth-vent length among *Tropidurus* species. Abbreviations: *Tchr*, *T. chromatops*; *Teth*, *T. etheridgei*; *Tazu*, *T. azurduyae*

| Species | Males | | | | Species | Females | | | |
|---------------------------|------------|--------|--------|----------|---------------------------|------------|--------|-------|----------|
| | Difference | Lower | Upper | <i>p</i> | | Difference | Lower | Upper | <i>p</i> |
| <i>Tchr</i> – <i>Teth</i> | -0.067 | -0.134 | -0.001 | 0.046 | <i>Tchr</i> – <i>Teth</i> | -0.021 | -0.068 | 0.025 | 0.514 |
| <i>Tchr</i> – <i>Tazu</i> | -0.038 | -0.100 | 0.025 | 0.321 | <i>Tchr</i> – <i>Tazu</i> | 0.003 | -0.038 | 0.045 | 0.978 |
| <i>Teth</i> – <i>Tazu</i> | 0.030 | -0.009 | 0.068 | 0.157 | <i>Teth</i> – <i>Tazu</i> | 0.025 | -0.008 | 0.058 | 0.178 |

slightly diffuse, stripelike ornamentation perpendicular to limb axis posteriorly, including forearms and legs and supracarpal and supratarsal regions, and digits. Femoral and preloacal “flash” marks well marked, black in color, 31/33 and 12 scales long, respectively. Tail greenish champagne, mottled with lead pigmentation anteriorly; regenerated section greenish champagne; ventral side of the whole tail pale cream.

COLORATION IN PRESERVATIVE (fig. 4A–F): Overall coloration pattern of head and body preserved. Champagne background partially faded into pale cream and lead pigmentation became lighter, gaining a brownish tone. Facial stripe decorating the lateral head preserved. Same is true for the light blotches distributed over sublabial and posterolateral area of the head, and area behind ear opening. Originally lead-pigmented area of ventral head became brownish. Intense orange pigmentation of gular region faded almost completely, remaining a merely elusive orangey tone over brownish scales. Nuchal collar remained well marked. Orange coloration on the lower flanks was completely washed out, increasing the contrast between the now paler background and brownish mottled pigmentation that decorates the lateral body. Loss of orange pigmentation revealed irregular light blotches composing the mottled pattern on the flanks. Lead pigmentation sprinkled anteriorly on the chest became brownish. Venter preserved its cream aspect. Dark “flash” marks fully preserved underneath the thighs, cloacal flap, and mid venter. Limbs gained a slightly lighter background and brownish pigmentation in the place of original lead tones. Tail coloration nearly unaltered.

MEASUREMENTS OF HOLOTYPE (in mm): SVL 87.31, TL 96.08 (regrown), HH 13.02, EOS 22.11, HL 25.99, HW 18.58, AL 15.80, FAL 13.36, HDL 15.94, THL 21.16, SL 17.72, FOL 29.72, AGD 36.78.

MORPHOMETRICS: *Tropidurus azurduyae* is a middle-sized species of the *T. torquatus* group, with adult males ranging from 66.06 to 104.85 mm SVL and females from 62.83 to 89.58 mm SVL. This species is statistically indistinct in body size from its closest, formally described relatives, *T. chromatops* and *T. etheridgei*, but males of *T. chromatops* were found to be (marginally) larger than those of *T. etheridgei* (ANOVA SVL: males: *df* (degrees of freedom) = 2, sum of squares = 0.017, mean square = 0.008, *F* value = 3.563, *p* = 0.037; females: *df* = 2, sum of squares = 0.006, mean square = 0.003, *F* value = 1.668, *p* = 0.200; tables 2–3). In terms of shape, PCA captured extensive overlap among species and showed relatively similar contribution of most variables for morphometric groupings, while LDA showed better success discriminating groups (fig. 7; table 4). For males, LDA indicated FAL and EOS as important variables separating species in LD1, and EOS, FAL, and THL in LD2. For females, FAL and AL contributed more for species

TABLE 4. Summary of the principal component analyses and linear discriminant analyses performed on morphometric variables. PC, component loadings; LD, discriminant coefficients; EVL, eigenvalues; SD, standard deviations; % Variance, explained variances.

| | PCA Males | | LDA Males | | PCA Females | | LDA Females | |
|------------|-----------|---------|-----------|---------|-------------|---------|-------------|---------|
| | PC 1 | PC 2 | LD 1 | LD 2 | PC 1 | PC 2 | LD 1 | LD 2 |
| SVL | 0.0496 | 0.0032 | 0.0795 | -0.0639 | 0.0383 | 0.0110 | -0.4313 | -0.1710 |
| HH | 0.0474 | -0.0204 | -0.2892 | 0.1002 | 0.0424 | 0.0011 | -0.3308 | 0.1037 |
| HL | 0.0454 | -0.0089 | 0.3426 | 0.6099 | 0.0345 | 0.0062 | 0.5292 | -0.9443 |
| HW | 0.0526 | -0.0159 | -0.3245 | -0.0721 | 0.0355 | 0.0071 | 2.0200 | 1.0696 |
| EOS | 0.0467 | -0.0045 | -1.0115 | -1.0339 | 0.0352 | 0.0008 | -0.1832 | 0.8335 |
| AL | 0.0494 | 0.0047 | 0.6660 | 0.0990 | 0.0403 | -0.0086 | -0.6139 | -0.4587 |
| FAL | 0.0505 | 0.0040 | -1.1760 | -0.8719 | 0.0398 | -0.0062 | 1.9788 | -0.6883 |
| HDL | 0.0324 | 0.0192 | 0.0887 | -0.3145 | 0.0326 | -0.0116 | 0.1768 | -0.4581 |
| THL | 0.0545 | 0.0030 | 0.5132 | 0.8595 | 0.0402 | -0.0179 | -0.4382 | -0.6633 |
| SL | 0.0430 | 0.0011 | -0.1112 | 0.6239 | 0.0347 | -0.0075 | -0.3089 | 0.5873 |
| FOL | 0.0352 | 0.0129 | 0.8172 | -0.2330 | 0.0306 | -0.0120 | -0.3677 | 1.1359 |
| AGD | 0.0559 | 0.0096 | -0.0204 | 0.1834 | 0.0486 | 0.0280 | 0.0362 | 0.0755 |
| EVL | 0.0269 | 0.0015 | 6.7050 | 3.1490 | 0.0173 | 0.0018 | 6.5513 | 2.6032 |
| SD | 0.1641 | 0.0382 | 2.5894 | 1.7745 | 0.1317 | 0.0419 | 2.5596 | 1.6135 |
| % Variance | 85.19 | 4.61 | 68.04 | 31.96 | 77.69 | 7.88 | 71.56 | 28.44 |

discrimination in LD1, and FOL, HW, and HL in LD2. LDA functions reached >85% correct reclassifications, distinguishing male individuals of all three species and female individuals of *T. etheridgei* and *T. azurduyae* (table 5). However, correct reclassifications dropped considerably with the implementation of the leave-one-out cross-validation procedure, indicating that morphometric parameters alone may not safely distinguish all species analyzed (table 5).

MERISTICS: *Tropidurus chromatops*, *T. etheridgei*, and *T. azurduyae* overlap at least partially in most scale counts (figs. 8–10; table 6). *Tropidurus etheridgei* has, in general, lower scale counts in comparison to the other species analyzed; exceptions were observed only in the number of subdigital lamellae (fig. 9). Number of gulars and scales around midbody differ between *T. chromatops* and *T. etheridgei* (males only), but cannot be used to fully distinguish any of these species from *T. azurduyae* (fig. 8; table 6). Although a few individuals overlap (fig. 9), *T. azurduyae* has in average a higher number of tibials than *T. chromatops* and *T. etheridgei* (table 6). PCA based on meristic variables showed complete separation between *T. azurduyae* and *T. etheridgei*, but not in relation to *T. chromatops* (fig. 10; table 7). Number of tibials provided the strongest contribution for species groupings in both PCA and LDA, followed by the number of gulars, ventrals, and subdigital lamellae (table 7). LDA effectively discriminated species, showing correct reclassification >90% in all cases but one (female *T. chromatops*). Even with the implementation of the leave-one-out cross-validation procedure, correct reclassifications remained high; *T. chromatops* was the only poorly discriminated species (table 7). In general, scale counts can be used to distinguish *T. azurduyae* from *T. etheridgei*, and this latter species from *T. chromatops*, but they may

TABLE 5. Species reclassification rates based on the linear discriminant functions generated with morphometric and meristic data. Cross-validation results (leave-one-out method) shown within parentheses and correct classifications highlighted in boldface.

| Species | Morphometric | | | | | | Meristic | | | | | |
|-------------------------|--------------|---------------|---------------|-------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| | Male | | | Female | | | Male | | | Female | | |
| | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| 1. <i>T. chromatops</i> | 1.00 | – | – | 0.43 | 0.14 | 0.43 | 1.00 | – | – | 0.88 | 0.13 | – |
| | – | (0.25) | (0.75) | – | (0.14) | (0.86) | (1.00) | – | – | (0.50) | (0.38) | (0.12) |
| 2. <i>T. etheridgei</i> | – | 0.86 | 0.14 | – | 1.00 | – | – | 1.00 | – | 0.06 | 0.94 | – |
| | (0.07) | (0.64) | (0.29) | – | (0.69) | (0.31) | – | (1.00) | – | (0.06) | (0.94) | – |
| 3. <i>T. azurduyae</i> | – | (0.04) | (0.96) | 0.04 | 0.03 | 0.93 | 0.03 | 0.03 | 0.94 | 0.06 | 0.03 | 0.91 |
| | (0.07) | (0.11) | (0.81) | (0.14) | (0.10) | (0.76) | (0.03) | (0.10) | (0.87) | (0.06) | (0.03) | (0.91) |

be insufficient to separate *T. azurduyae* from *T. chromatops* (though the number of tibials is informative in most cases). For specimens with overlapping scale counts, additional diagnostic characters treated in Comparisons with Other Species should be considered.

ETYMOLOGY: The species name *azurduyae* is a noun in the feminine genitive case honoring Juana Azurduy de Padilla (Chuquisaca, Bolivia: July 12, 1780–May 25, 1862), one of the most distinguished Latin American leaders who bravely fought for the independence of the Spanish territory of Upper Peru, which comprised part of today’s Bolivia and Peru, and formed along with Argentina, Uruguay, and Paraguay the Viceroyalty of the Río de La Plata during colonial times. Her memory remained nearly forgotten for more than a century, until President Cristina Kirchner conferred on her the title of General of the Argentinian Army in 2009, and in that same year, the Bolivian Senate promoted Juana Azurduy posthumously to the rank of Marshal of the Republic, declaring her “Liberator of Bolivia.” Although the biography of Juana Azurduy assuredly places her as one of the most important women of Latin America, the history of her fight for freedom and equality has not received enough attention outside history classes and political events. Naming *Tropidurus azurduyae* we do not aim to merely reverence her as a historical personage and revolutionary soldier, but to genuinely honor her intelligence, courage, and heroic actions against a male-dominated colonialist world whose roots remain alive at the present time. This is an affirmative action to remind all Latin American women and men of our female heritage of strength and combativeness.

For a more comprehensive biography of Juana Azurduy, refer to the work of the Argentinian writer Mario “Pacho” O’Donnell (1994), available online (<http://www.portaldesalta.gov.ar/juana%20azurduy.htm>). Those interested may follow the YouTube link (<https://youtu.be/SERg-8GKCNeA>) to hear the song “Juana Azurduy” in the voice of the Argentinian singer Mercedes Sosa, honoring the valiant spirit of Juana Azurduy.

DISTRIBUTION, ENDEMISM, NATURAL HISTORY, AND CONSERVATION: *Tropidurus azurduyae* was discovered from its type locality, Torotoro National Park, Department of Potosí, Bolivia (figs. 1–2). There, it is abundant in the xerophytic inter-Andean valleys, not being found in adjacent habitats such as the prepuna, located at altitudes above ~2800 m. Specimens deposited

TABLE 6. Mean \pm standard deviation and (in parentheses) minimum and maximum scale counts of the species analyzed.

| | MALES | | | FEMALES | | |
|-----------------|-------------------------------|--------------------------------|-------------------------------|-------------------------------|--------------------------------|-------------------------------|
| | <i>T. chromatops</i> N = 4 | <i>T. etheridgei</i> N = 16 | <i>T. azurduyae</i> N = 31 | <i>T. chromatops</i> N = 8 | <i>T. etheridgei</i> N = 16 | <i>T. azurduyae</i> N = 33 |
| Dorsals | 99.25 \pm 6.65 (91–107) | 83.19 \pm 4.61 (75–93) | 92.00 \pm 4.86 (82–102) | 97.50 \pm 9.24 (87–108) | 90.75 \pm 5.42 (79–98) | 97.67 \pm 4.81 (87–108) |
| Gulars | 47.50 \pm 4.04 (44–53) | 38.75 \pm 2.08 (36–43) | 44.06 \pm 2.80 (39–51) | 43.25 \pm 3.20 (39–48) | 38.69 \pm 2.75 (34–43) | 43.21 \pm 2.77 (36–47) |
| Ventrals | 73.75 \pm 4.50 (68–79) | 70.56 \pm 4.32 (60–77) | 78.39 \pm 4.98 (67–93) | 74.25 \pm 4.68 (68–80) | 71.50 \pm 4.84 (64–83) | 79.45 \pm 4.85 (70–93) |
| Midbody | 88.75 \pm 4.86 (84–95) | 73.06 \pm 3.60 (68–78) | 80.84 \pm 5.27 (69–94) | 90.25 \pm 7.29 (78–102) | 80.88 \pm 3.76 (73–88) | 89.09 \pm 6.25 (78–104) |
| Tibials | 22.75 \pm 2.06 (20–25) | 20.75 \pm 1.13 (19–23) | 26.94 \pm 2.21 (23–31) | 21.00 \pm 1.69 (19–24) | 20.19 \pm 1.05 (19–23) | 26.27 \pm 2.11 (21–30) |
| Lamellae Finger | 16.00 \pm 1.41 (15–18) | 15.81 \pm 1.52 (14–20) | 15.84 \pm 1.27 (13–18) | 14.25 \pm 1.75 (12–17) | 15.06 \pm 1.12 (13–17) | 15.06 \pm 1.09 (12–17) |
| Lamellae Toe | 22.75 \pm 1.71 (21–25) | 22.44 \pm 1.26 (20–25) | 23.06 \pm 1.39 (21–26) | 21.62 \pm 1.60 (20–24) | 22.31 \pm 0.95 (21–24) | 22.73 \pm 1.21 (21–25) |

at the Museo de Historia Natural Noel Kempff Mercado (Santa Cruz) and Museo de Historia Natural Alcide d'Orbigny (Cochabamba) revealed the occurrence of *T. azurduyae* in several other localities to the north, south, and east of Torotoro. Currently, the species is known from the Bolivian departments of Chuquisaca, Cochabamba, Potosí, and Santa Cruz, ranging from approximately 1040 to 2764 m. (fig. 2).

Tropidurus azurduyae is endemic to the Bolivian Montane Dry Forests (Olson et al., 2001), restricted to inter-Andean dry valleys from central and southern Bolivia (López, 2003a, 2003b; fig. 2). This is the first species of the *T. torquatus* species group (per Frost et al., 2001) endemic to the Andes, and it reaches the highest altitudes among all *Tropidurus*. *Tropidurus melanopleurus* Boulenger, 1902, member of the *T. spinulosus* species group (per Frost et al., 2001), is the only other species in the genus recognized as an Andean endemic. However, it is found in more mesic habitats along the eastern Andean slopes, from river margins and foothills of 400–500 m to altitudes near 2000 m (Laurent, 1982; Schumacher and Barts, 2003). *Tropidurus melanopleurus* ranges from southeastern Peru to northwestern Argentina, crossing the Bolivian territory from north to south predominantly along the Yungas and the Tucuman-Bolivian forests (Meier, 1982; Cei, 1993; Dirksen and De La Riva, 1999; Rivadeneira, 2008; Carvalho, 2013). The species is known to be sympatric (but never syntopic) with *T. azurduyae* in just a few areas of inter-Andean dry valleys in the Department of Santa Cruz (e.g., La Angostura; E. Cortez, personal commun.). However, as in most of its distribution, it is restricted to *quebradas* (river margins), and thus it is absent in the harsh dry environments dominated by *T. azurduyae*.

The type locality and a few dry valley sites visited in Cochabamba are the only areas for which information on the natural history of *T. azurduyae* is available currently. The new species is heliophilous and basks over small to large rock blocks (40 cm to >150 cm in diameter), either

TABLE 7. Summary of the principal component analyses and linear discriminant analyses performed on meristic variables. PC, component loadings; LD, discriminant coefficients; EVL, eigenvalues; SD, standard deviations; % Variance: explained variances.

| | PCA Males | | LDA Males | | PCA Females | | LDA Females | |
|-----------------|-----------|---------|-----------|---------|-------------|---------|-------------|---------|
| | PC 1 | PC 2 | LD 1 | LD 2 | PC 1 | PC 2 | LD 1 | LD 2 |
| Dorsals | 0.0249 | 0.0013 | 0.0373 | 0.0592 | 0.0213 | -0.0077 | -0.0372 | 0.0249 |
| Gulars | 0.0329 | 0.0043 | 0.0601 | 0.3092 | 0.0248 | -0.0042 | 0.1088 | 0.1739 |
| Ventrals | 0.0268 | -0.0005 | -0.0260 | -0.1068 | 0.0278 | -0.0094 | 0.0694 | -0.0366 |
| Midbody | 0.0228 | 0.0053 | 0.0970 | 0.1073 | 0.0234 | -0.0060 | 0.0032 | 0.1137 |
| Tibials | 0.0570 | -0.0123 | 0.3987 | -0.3997 | 0.0574 | 0.0199 | 0.5036 | -0.1639 |
| Lamellae Finger | 0.0083 | 0.0326 | -0.2427 | 0.0187 | 0.0116 | -0.0278 | -0.1485 | -0.1737 |
| Lamellae Toe | 0.0087 | 0.0171 | 0.0870 | -0.0999 | 0.0114 | -0.0133 | -0.1184 | -0.3393 |
| EVL | 0.0063 | 0.0016 | 8.6150 | 6.0560 | 0.0059 | 0.0015 | 9.3135 | 3.6048 |
| SD | 0.0796 | 0.0394 | 2.9351 | 2.4609 | 0.0771 | 0.0393 | 3.0518 | 1.8986 |
| % Variance | 58.29 | 14.32 | 58.72 | 41.28 | 57.58 | 14.97 | 72.10 | 27.90 |

isolated or forming large rock aggregations throughout the dry valleys. *Tropidurus azurduyae* occasionally uses the trunk of the contorted trees that dominate the landscape. The dry valleys of Torotoro have reddish, stony soil similar in color to the flanks and gular region of the new species. *Tropidurus azurduyae* is territorial and reacts to invasion of its home range with aggressive head movements and body push-ups, but rapidly flees to holes underneath boulders, hides in crevices between rock blocks, or climbs up tree trunks if truly threatened. Our short visit to the type locality did not allow us to determine the exact period and pattern of activity of *T. azurduyae*; however, lizards were seen active even during the hottest periods of the day. Specimens were collected in Torotoro from the second half of the morning (around 11 AM) to the second half of the afternoon (around 4 PM). In dry valleys sites from Cochabamba, *T. azurduyae* has been observed active throughout the whole year (including the winter), basking over rocks after approximately 8 AM. Nothing is known about the diet of *T. azurduyae*, but a few lizards were observed feeding on ants at the type locality. Most specimens collected by us had their mite pockets filled with a large number of bright orange chigger-mite larvae (fig. 3F), likely trombiculids, but the specific identity of these ectoparasites has not been investigated.

The conservation status of the Bolivian Montane Dry Forests has been defined as critical (WWF, 2017), with habitat loss one of the most severe threats to this region (Ibisch and Mérida, 2003; Aguirre et al., 2009; Navarro, 2011) and other seasonally dry tropical forests around the globe (Janzen, 1988; Miles et al., 2006). Records of *T. azurduyae* (and other endemic taxa) obtained from museum specimens collected years or decades ago are, therefore, no guarantee that previously sampled populations persist to date. Although the local abundance of *T. azurduyae* in the protected Torotoro National Park and its broader distribution in the inter-Andean dry valleys from central and southern Bolivia indicate that the species is unlikely to be threatened, the lack of information about the size, connectivity, genetic parameters, and ecological requirements of local populations compels us to recommend its classification as “data deficient,” following the rules proposed by IUCN (2001).

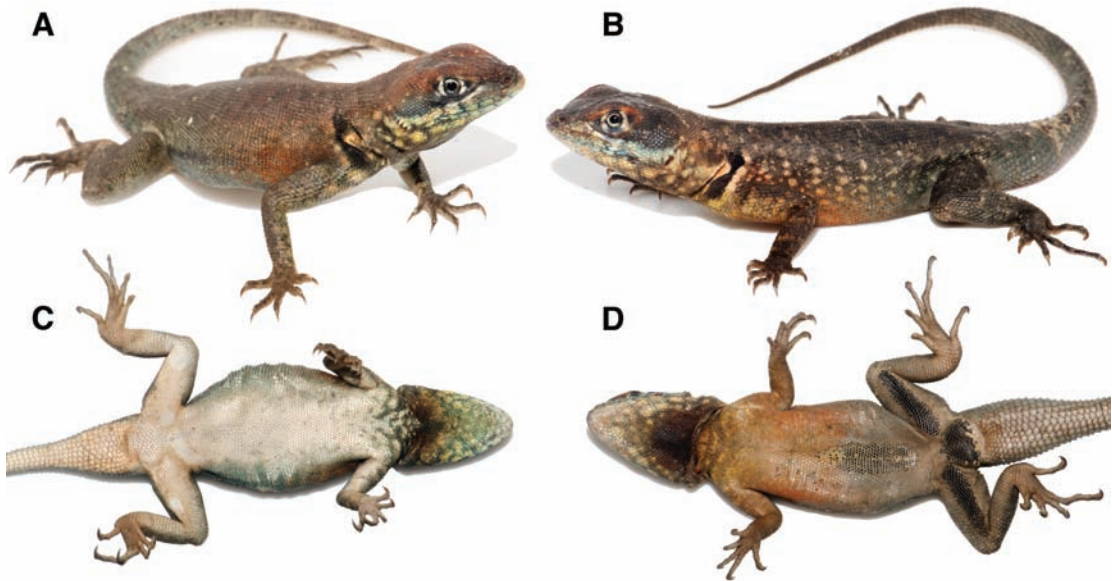


FIGURE 6. Live specimens of *Tropidurus chromatops* Harvey and Gutberlet, 1998 from isolated granitic outcrops ~30 km W Florida, Santa Cruz, Bolivia ($14^{\circ} 36' 17.28''$ S, $61^{\circ} 29' 32.64''$ W — WGS84 system; ~309 m). **A, C**, Adult female (MHNC-R 3003). **B, D**, Adult male (MHNC-R 3018).

MOLECULES

ALIGNMENT AND PARTITIONING: We compiled and aligned sequence data for 79 ingroup and six outgroup species, summing up 85 samples. For mitochondrial and nuclear genes, molecular coverage varied from 29 to 84 samples per fragment (34%–99%), with average coverage of 72 terminals (85%) regarding all 10 genes. Our molecular data set summed up to 7001 aligned sites, varying from 477–1211 per locus. A summary of taxon coverage, number of variable, conserved, parsimony informative sites, and singletons is shown in table 8. Details on selected nucleotide evolution models and partition schemes employed in ML analyses are shown in table 9.

PHYLOGENETIC RESULTS (fig. 11): In agreement with previous results (Carvalho et al., 2016), our analysis recovered *Tropidurus* as paraphyletic, yet confirmed the monophyly of the *T. torquatus* species group. *Uranoscodon superciliosus* was recovered as sister of all other tropidurines and *M. quadrivittatus* as sister of a large clade formed by *T. spinulosus*, *P. plica*, *T. semitaeniatus*, and the *T. torquatus* species group. Nested within this large tropidurine clade, *T. spinulosus* was recovered as sister of *P. plica*, while *T. semitaeniatus* was placed as sister of the *T. torquatus* species group. Relationships among species in the *T. torquatus* group differed only slightly in relation to our previous phylogenetic hypothesis (Carvalho et al., 2016). *Tropidurus hygomi* was again supported as sister of all other species in this group. *Tropidurus itambere* and *T. psammonastes* were confirmed as closely related taxa and formed the sister group of all species but *T. hygomi*. *Tropidurus sertanejo* is now placed as sister of the remaining species, including the closely related *Tropidurus* species endemic to the Espinhaço Mountain

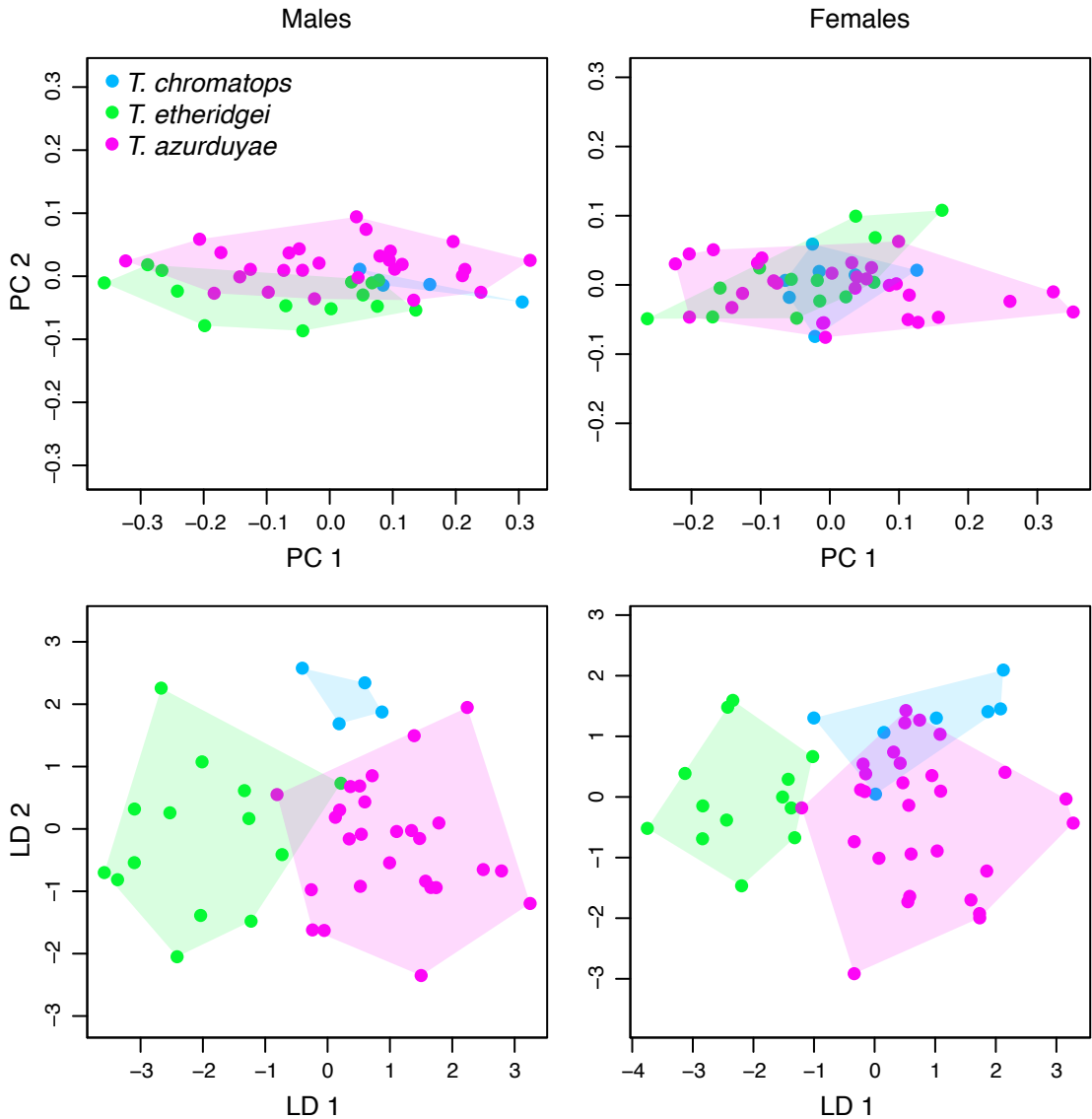


FIGURE 7. Scatterplots of PC1 and PC2 generated by the principal component analyses and LD1 and LD2 generated by the linear discriminant analyses performed on morphometric variables. See table 4 for corresponding summary statistics. Figure color-coded following species labels in figure 11.

Range, in Brazil, *T. montantus* (*T. mucujensis* + *T. erythrocephalus*). However, low-support values retrieved for nodes supporting several interspecific relationships around this section of the tree indicate topological instabilities resulting from conflicting phylogenetic signal recovered from mitochondrial and nuclear loci (see Carvalho et al., 2016, for details). Consequently, we expect future changes in the phylogenetic placement of *T. sertanejo* and related species. The same is true for the internal relationships in the clade comprising *T. cororobensis* (*T. imbituba* + *T. torquatus*) (*T. catalanensis* + *T. etheridgei* complex).

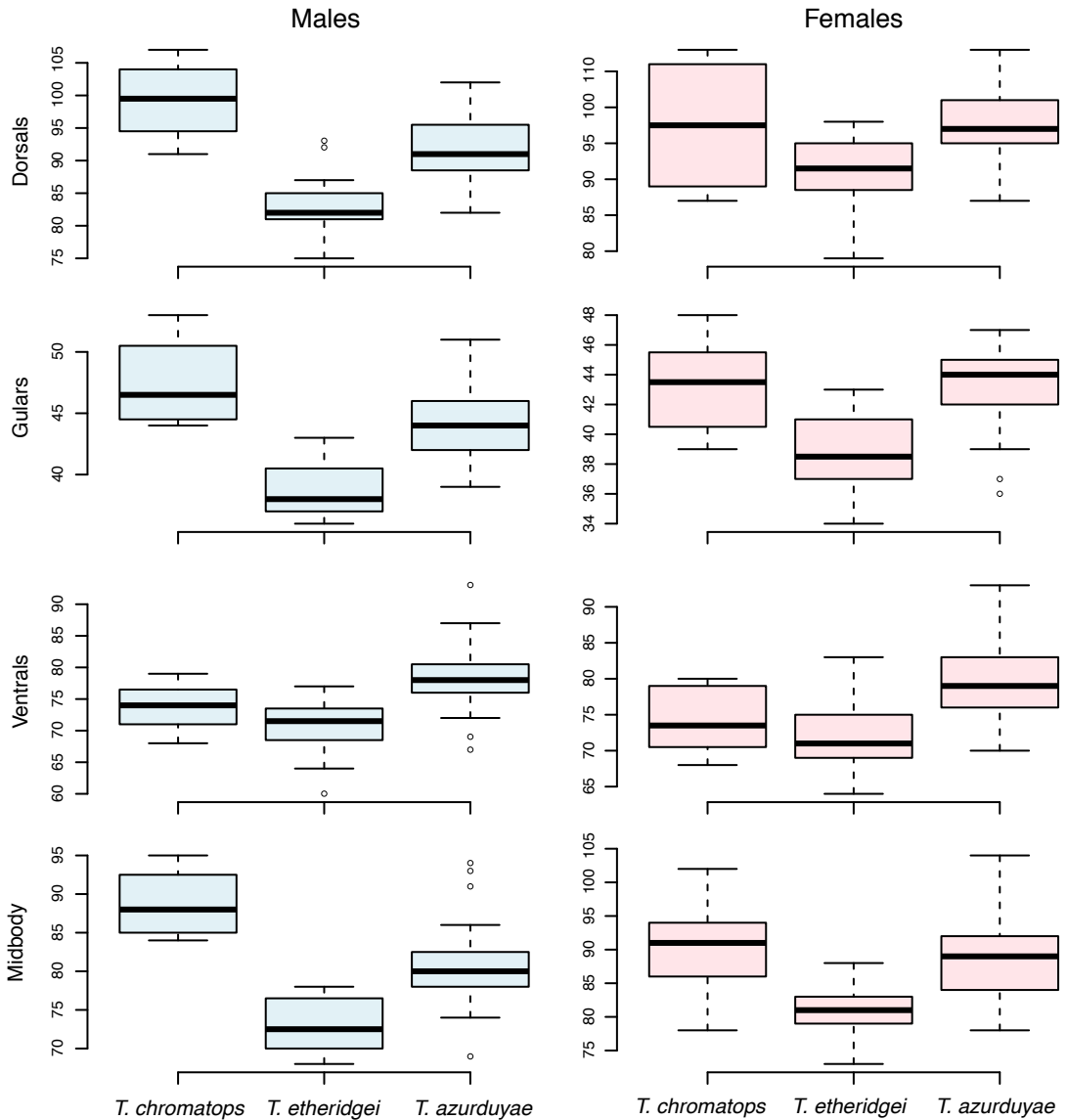


FIGURE 8. Boxplots showing variation in scale counts among *Tropidurus chromatops*, *T. etheridgei*, and *T. azurduyae*.

Our current analysis recovered *Tropidurus etheridgei* as paraphyletic and confirmed our suspicion that this name represents a species complex. This clade, referred to as the *T. etheridgei* species complex or simply *T. etheridgei* complex, is well supported and deeply nested within the *T. torquatus* species group, in turn, sister of *T. catalanensis*. Within the *T. etheridgei* species complex, an undescribed species sampled from disjunct patches of sandy habitats located in the domains of the Atlantic Dry Forests, in the states of Minas Gerais and Bahia, Brazil, was recovered as sister of all remaining species. *Tropidurus azurduyae* is sister of a clade formed by an undescribed species associated to limestone outcrops found in the Chiquitano Dry Forests/Pantanal/

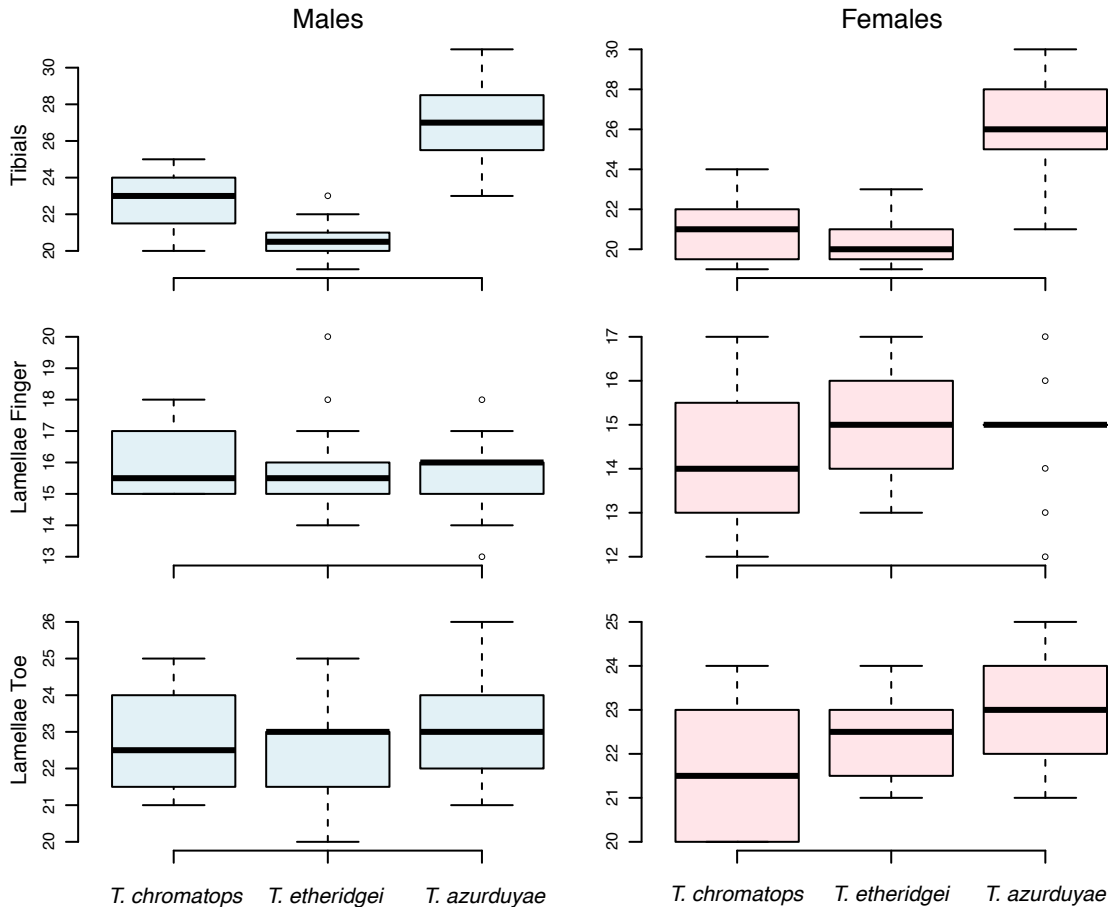


FIGURE 9. Boxplots showing variation in scale counts among *Tropidurus chromatops*, *T. etheridgei*, and *T. azurduyae*.

Cerrado contact, in the states of Mato Grosso and Mato Grosso do Sul (Brazil), and Department of Santa Cruz (Bolivia), plus the closely related *T. chromatops*, known from isolated granitic outcrops and from the Serranía de Huanchaca/Serra Ricardo Franco and surroundings, on the Bolivia-Brazil border, and *T. etheridgei* (sensu stricto), restricted (though widely distributed) to the Chaco of northern Argentina, western Paraguay, and southeastern Bolivia.

GENETIC DISTANCES: Pairwise genetic distances estimated using *Cyt-b* fragments were, on average, approximately two times as high as those of 12S. However, a clear trend of increase in genetic differences correlated with phylogenetic distance was observed in both cases. The average pairwise genetic distances registered among species in the *Tropidurus torquatus* group were 11.04% (*Cyt b*) and 5.07% (12S), and ranged from 4.30% to 16.20% (*Cyt b*) and 1.60% to 7.60% (12S) (refer to table 10 for details). Average intraspecific genetic distances calculated for species composing the *T. etheridgei* species complex varied from 0% to 3.7% (*Cyt b*) and from 0% to 0.8% (12S), while average interspecific distances were up to five times higher, ranging from 6% to 9% (*Cyt b*) and 3% to 4% (12S). Similar values were observed between most species pairs

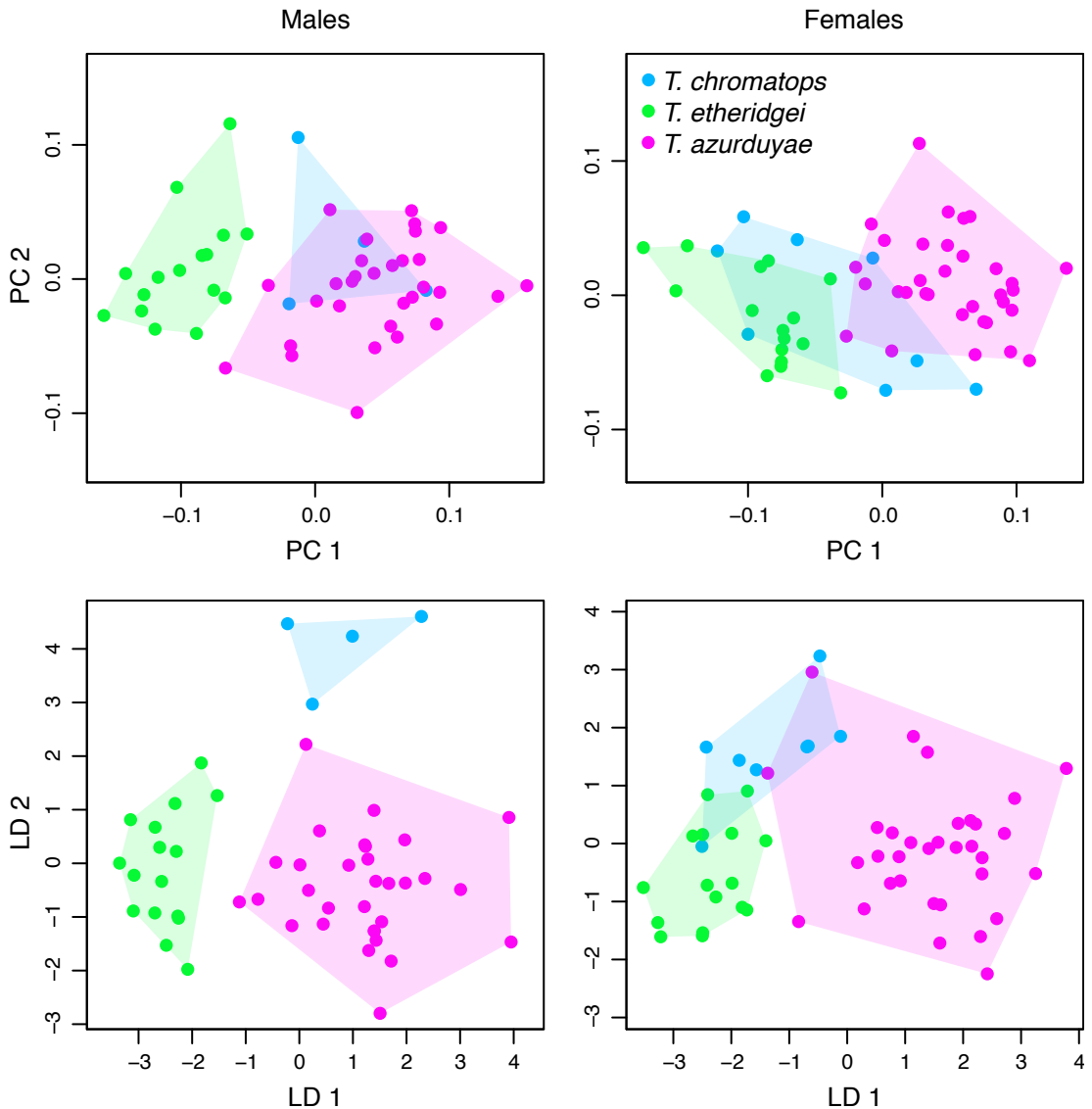


FIGURE 10. Scatterplots of PC1 and PC2 generated by the principal component analyses and LD1 and LD2 generated by the linear discriminant analyses performed on meristic variables (scale counts). See table 7 for corresponding summary statistics. Figure color-coded following species labels in figure 11.

within the *T. torquatus* group (see table 10). Although we agree that arbitrary genetic-distance cutoffs alone are by no means justifiable as criteria to define species limits (DeSalle et al., 2005; Padial et al., 2010), p -distance values can be informative to establish a molecular profile of populations and species. Indeed, p -distances calculated for *Cyt-b* and 12S fragments of *Tropidurus* corroborate the morphological and phylogenetic evidence we gathered. Overall, our results support a novel taxonomic framework that recognizes at least four distinct species under nominal *T. etheridgei* (see Taxonomic Advances).

TABLE 8. Taxon coverage, number of aligned, conserved, variable, parsimony-informative sites, and singletons present in the alignments of mitochondrial and nuclear loci.

| Loci | Genome | Coverage | Sites | Conserved | Variable | PI | Singletons |
|--------|---------------|----------|-------|-----------|----------|------|------------|
| 12S | Mitochondrial | 80 (94%) | 881 | 511 | 339 | 224 | 113 |
| 16S | Mitochondrial | 84 (99%) | 553 | 383 | 163 | 111 | 52 |
| CO1 | Mitochondrial | 79 (93%) | 662 | 408 | 254 | 222 | 32 |
| Cyt b | Mitochondrial | 72 (85%) | 756 | 415 | 341 | 243 | 98 |
| BACH1 | Nuclear | 68 (80%) | 1211 | 938 | 273 | 102 | 171 |
| kif24 | Nuclear | 80 (94%) | 545 | 328 | 217 | 120 | 97 |
| NTF3 | Nuclear | 29 (34%) | 670 | 572 | 98 | 36 | 62 |
| PRLR | Nuclear | 81 (95%) | 525 | 348 | 174 | 70 | 104 |
| PTPN | Nuclear | 78 (92%) | 821 | 661 | 157 | 53 | 104 |
| SNCAIP | Nuclear | 70 (82%) | 477 | 377 | 100 | 35 | 65 |
| TOTAL | | | 7101 | 4941 | 2116 | 1216 | 898 |

TAXONOMIC ADVANCES: Although morphological and morphometric conservatism and convergence in traits are known to be a common occurrence within tropidurine clades (Frost, 1992; Harvey and Gutberlet, 2000; Frost et al., 2001; Carvalho et al., 2016), a number of species with different levels of cryptic await description (Carvalho et al., 2016; Domingos et al., 2017). Adding up to recent findings (Carvalho, 2016; Carvalho et al., 2016), *Tropidurus azurduyae* represents one more example of a conspicuous but previously overlooked taxon. The description of this new species raises to 30 the number of valid names assigned to *Tropidurus*; however, revealing its existence and phylogenetic relationships is only the first step toward resolving *T. etheridgei*'s paraphyly. The evidence gathered so far supports the recognition of *T. etheridgei* as a Chacoan endemic, restricted to western Paraguay, northern Argentina, and southeastern Bolivia (figs. 11–12A). Hereafter, we recommend populations of *T. etheridgei* (sensu lato) found outside the Chaco, within the limits of the Atlantic Dry Forests, Chiquitano Dry Forests, Pantanal, and Cerrado, be referred as candidate species assignable to clades “*Tropidurus* n. sp. 1 Atlantic Dry Forests” and “*Tropidurus* n. sp. 2 Chiquitano/Pantanal/Cerrado” (figs. 11–12A). These populations are being treated taxonomically elsewhere and formal names will be available soon.

The discovery of *Tropidurus azurduyae* and two undescribed species underscores the need for a comprehensive revision of peripheral and disjunct populations assigned to *Tropidurus* species with wide distributions. Unfortunately, samples housed in herpetological collections are in great part restricted to specimens in alcohol, and lack tissue samples, photographs, and field notes describing morphological, ecological, and behavioral traits. For example, potentially useful traits for species discrimination, such as eye color, dorsal pattern, condition of mite pockets and skin folds, ecological habit, and substrate preferences are rarely described. Thus, we take the opportunity to make a call of attention to other taxonomists and professional collectors dealing with tropidurines to include fine details and photographs in their field notes, reports, and catalog records—information that preferably be incorporated into the database of the zoological collections chosen to house the specimens. This simple initiative is expected to

TABLE 9. Data partitions and respective models of nucleotide evolution selected for maximum likelihood analysis.

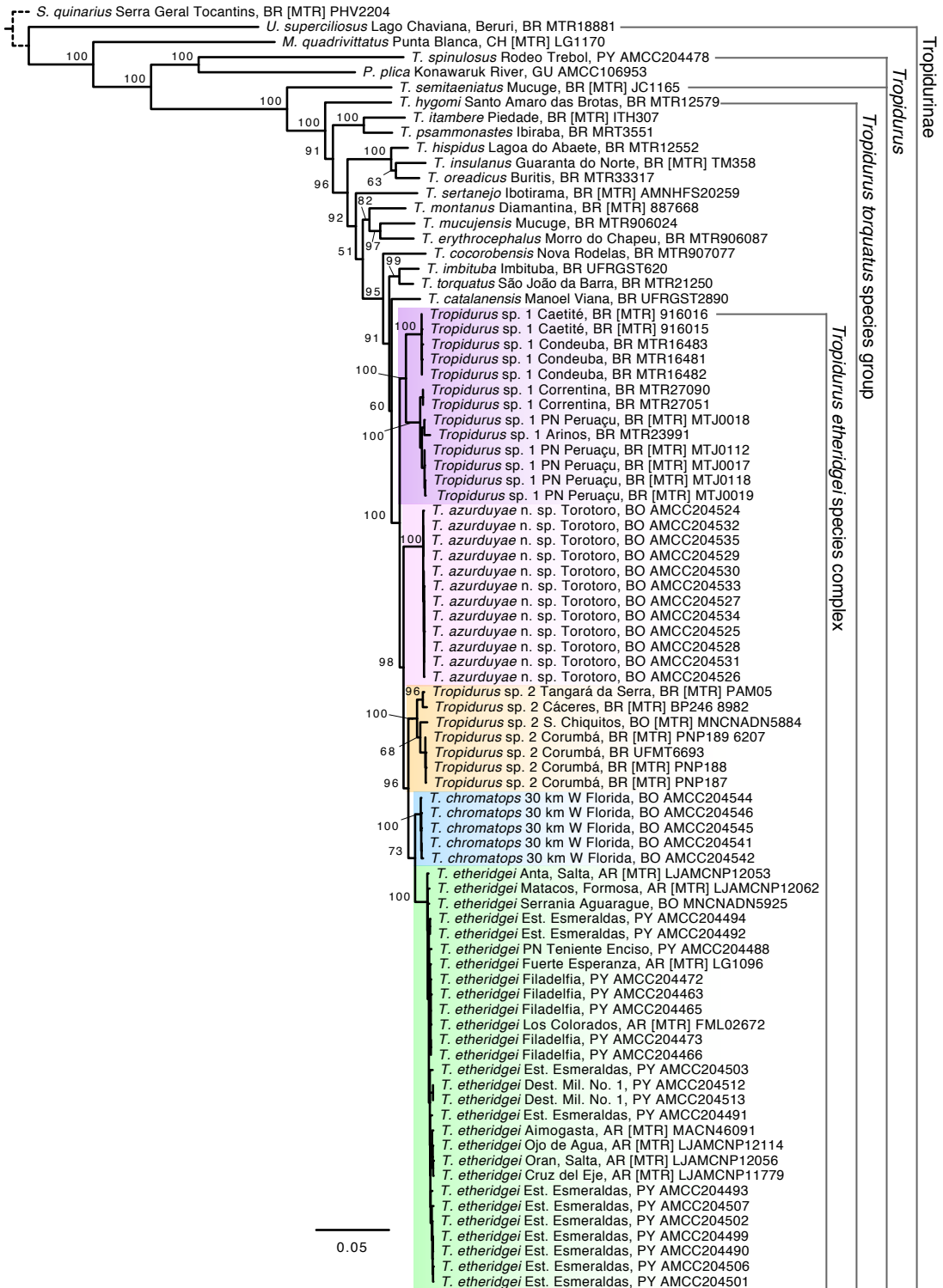
| Data set | Subset | Best model | # Sites | Subset Partitions | Subset Sites |
|-------------------------|--------|------------|---------|---|---|
| Mitochondrial + nuclear | 1 | GTR+I+G | 1434 | 12S, 16S | 1–881, 882–1434 |
| Scheme lnL -33915.47 | 2 | HKY+G | 1075 | PRLR_2, NTF3_1, PTPN_3, BACH1_2 | 5279–5803, 4610–5278, 5806– 6624, 1435–2645 |
| Scheme BIC 69835.10 | 3 | HKY+G | 2120 | PTPN_2, BACH1_1, SNCAIP_1, NTF3_3, NTF3_2, PTPN_1, BACH1_3, SNCAIP_3 | 5805–6624, 1437–2645, 6627– 7101, 4609–5278, 4611–5278, 5804–6624, 1436–2645, 6626– 7101 |
| | 4 | TRNEF+I+G | 473 | Cyt_B_1, COI_1 | 3308–4063, 2646–3307 |
| | 5 | HKY+I | 473 | COI_2, Cyt_B_2 | 2647–3307, 3309–4063 |
| | 6 | TRN+I+G | 220 | COI_3 | 2648–3307 |
| | 7 | TRN+I+G | 252 | Cyt_B_3 | 3310–4063 |
| | 8 | K80+G | 873 | Kif24_1, PRLR_1, PRLR_3, Kif24_2, SNCAIP_2 | 4064–4608, 5281–5803, 5280– 5803, 4065–4608, 6625–7101 |
| | 9 | K81UF+G | 181 | Kif24_3 | 4066–4608 |

facilitate the taxonomic revision of morphologically conservative clades in the future, including complexes of cryptic species within the *T. torquatus* group.

BIOGEOGRAPHY

The discovery of *Tropidurus azurduyae* and two other closely related undescribed species gives us the opportunity to critically review the historical association among dry areas in South America (Carvalho et al., 2013). This time, instead of investigating patterns of area relationships based on major biogeographic provinces (Morrone, 2004, 2006), we employed a scheme of areas that distinguishes seasonally dry tropical forests from savannas and dry spinose woodlands (following definitions in Werneck, 2011). The Atlantic Dry Forests, Bolivian Montane Dry Forests, and Chiquitano Dry Forests represented seasonally dry tropical forests in our analysis, and the Cerrado, Pantanal, and Chaco corresponded to additional open biogeographic units. Besides mapping species ranges and endemism, we summarized the biogeographic information contained in our taxon cladogram (fig. 11) by replacing species names with the names of their respective areas of occurrence. The area cladogram produced (fig. 12B) revealed two aspects of the biotic identity and historical relationships between seasonally dry tropical forests and open dry areas that carry important biogeographic implications. First, most areas analyzed⁷

⁷ The Chiquitano Dry Forests and Pantanal are exceptions, sharing an undescribed species of the *Tropidurus etheridgei* complex (figs. 11–12A). It is likely, however, that the distribution of “*Tropidurus* n. sp. 2 Chiquitano/Pantanal/Cerrado,” and also “*Tropidurus* n. sp. 1 Atlantic Dry Forests,” actually follows the occurrence of dry forests associated to limestone formations found in central and northeastern South America (e.g., some geomorphological formations of the “Bambuí group”). The ecological and biogeographic associations of both species must be revisited after analysis of additional populations and field observations.



were found to harbor an endemic species of the *T. etheridgei* species complex. Second, we did not find support for seasonally dry tropical forests as closely related biogeographic units.

Indeed, the distribution of endemism observed herein is consistent with studies that recognize the unique biotic identity of open dry areas (Silva, 1995; Nogueira et al., 2011; Gutiérrez and Marinho-Filho, 2017) versus seasonally dry tropical forests in South America (Prado and Gibbs, 1993; Silva et al., 2004; López et al., 2006; Queiroz, 2006; Werneck and Colli, 2006). Interestingly, endemics and codistributed taxa with disjunct distributions in seasonally dry tropical forests were for a long time assumed as evidence of the fragmentation of a formerly more extensive and contiguous biome that covered areas currently dominated by the Cerrado and the Amazon. More specifically, the “Pleistocene Arc hypothesis” states that seasonally dry tropical forests reached their maximum range during the Last Glacial Maximum (~21,000 years bp), in the late Pleistocene, and formed an arc of dry vegetation that once crossed the heart of South America (Prado and Gibbs, 1993) and perhaps even Amazonian lowlands (Pennington et al., 2000). Nevertheless, contrary to empirical evidence gathered from raw distribution data and molecular evidence of plant and animal groups associated to seasonally dry tropical forests (Prado, 2000; Werneck and Colli, 2006; Caetano et al., 2008), recent studies based on palaeodistribution modeling and reexamination of palynological records have failed to predict continuous dry forests in South America even during the Last Glacial Maximum (Mayle, 2004, 2006; Werneck et al., 2011; but see Collevatti et al., 2013). In consonance with these studies, we found no support for seasonally dry tropical forests as closely related areas (fig. 12B); therefore, we refute the strict vicariance scenario implied by the Pleistocene Arc hypothesis.

In contrast, the inferred area-relationship patterns support area breakups resulting from vicariance as well as dispersals from core areas as relevant processes responsible for shaping the biogeographic history of *Tropidurus*. Our interpretation recognizes the close association between areas with markedly distinct ages and geological histories as evidence in favor of dispersal. For instance, the occurrence of endemic *T. azurduyae* in the dry valleys of central and southern Bolivia is hypothesized to reflect a dispersal event from open dry areas of central South America, followed by speciation in the xerophytic Andean slopes. The origin of high-altitude formations such as the dry valleys is contingent on the last phase of the Andean orogenesis, and consequently, the evolution of these areas is unlikely to be historically linked to ancient regions from central South America. López (2003b) pointed out that the Andes apparently reached half their present altitude only 10 Ma bp, and suggested that the intense speciation leading to the present flora found in the dry valleys of Bolivia likely took place in the Pliocene and extended even to the Pleistocene. In his phylogeographic analysis, Lopez (2003b) interprets the occurrence of very few genera and absence of endemic plant families in the inter-Andean dry valleys as evidence of a relatively recent origin of its

←
FIGURE 11. Maximum likelihood tree based on four mitochondrial (12S, 16S, CO1, Cyt *b*) and six nuclear loci (BACH1, kif24, NTF3, PRLR, PTPN, SNCAIP). Nonparametric bootstrap values (1000 replicates) shown above or associated to branches. Dashed lines correspond to branches shortened for graphical purposes.

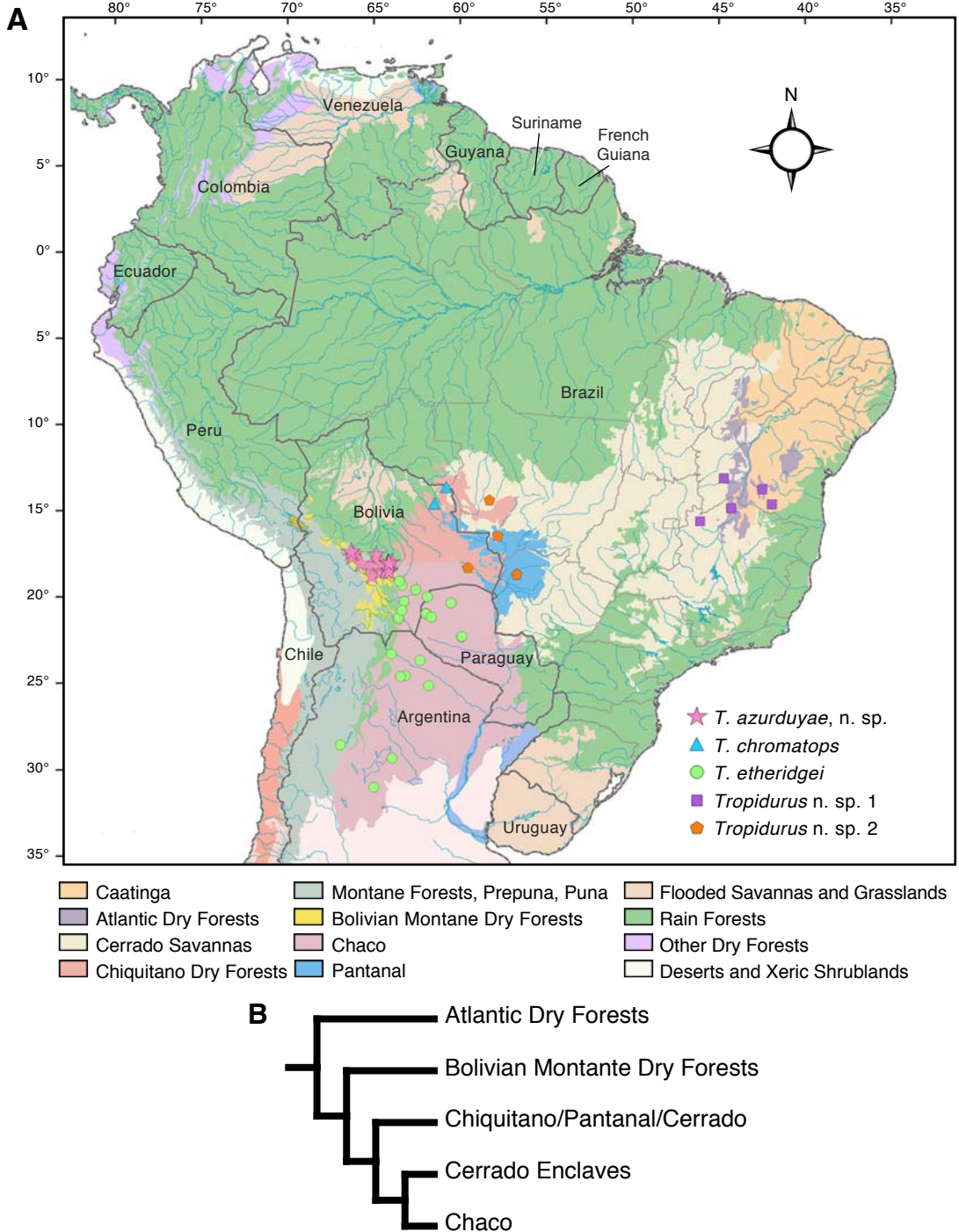


FIGURE 12. **A**, Geographic distribution of sampled populations of the *Tropicidurus etheridgei* species complex. Symbols on the map are color coded as species labels on the ML tree shown in figure 11. **B**, Area cladogram summarizing area relationships patterns supported by the phylogeny of the *Tropicidurus etheridgei* species complex.

flora. In the same manner, the evolution of the endemic fauna associated to the inter-Andean dry valleys must have taken place in a relatively recent period, regardless if it is derived from adjacent proto-Andean elements, lineages dispersed from central South America, or both.

The position of the Atlantic Dry Forests in our area cladogram, indicating its early segregation in relation to all other seasonally dry tropical forests and open dry areas (fig. 12B), adds more complexity to the vicariance scenario proposed by Carvalho et al. (2013), where the uplift of the Brazilian Central Plateau in the Late Pliocene–Early Pleistocene (4–2 Ma) was hypothesized to have promoted geographic isolation and subsequent differentiation of distinct biotas in areas covered by the Caatinga, Cerrado, and Chaco. This earlier hypothesis disregarded the limits and independent history of the Atlantic Dry Forests and other seasonally dry tropical forests, and, consequently, failed to effectively address the biogeographic history of dry areas of South America. Interestingly, dynamic vegetation simulations and palaeodistribution models have supported long-term historical stability for disjunct seasonally dry tropical forest areas in South America during the Last Glacial Maximum, including the Chiquitano Dry Forests from eastern Bolivia (and the Caatinga, Misiones, and Piedmont nuclei of seasonally dry tropical forests; see Werneck, 2011, for a review). However, these models sustain the occurrence of the Chiquitano only from the Pleistocene (Werneck et al., 2011) or even the Holocene (Mayle, 2004), when it is predicted to have advanced southward from areas that are now covered by the Amazon in eastern Bolivia (Burbridge et al., 2004; Mayle, 2004; Mayle et al., 2007). A recent origin of the Chiquitano Dry Forests contrasts with the position occupied by this area in our area cladogram, where it appears closely related to the more ancient Cerrado and Chaco. We interpret this conflict as evidence that the broad distribution of *Tropidurus* n. sp. 2 Chiquitano/Pantanal/Cerrado results from past dispersal and speciation in the Chiquitano, followed by recent distribution expansion toward adjacent areas. Thus, we predict recent range-expansion signatures in future phylogeographic analyses of this species.

The close association between Cerrado and Chaco observed in our area cladogram (fig. 12B) is in disagreement with palaeodistribution models that recognize the Venezuelan Llanos as the biogeographical counterpart of the Cerrado in South America (Werneck et al., 2012). Further, floristic evidence associates the Chaco with more meridional biogeographic regions, including temperate dry formations such as the Monte (Pennington et al., 2004; Roig-Junent et al., 2006; Roig et al., 2009). Werneck (2011) appropriately noted that the Chaco fauna has been often described as widely distributed over other South American regions, and show only moderate diversity and endemism levels, possibly as a consequence of its central location and accessibility. Despite our current data sustain that the open corridor of dry vegetation formed by the Caatinga, Cerrado, and Chaco does not stand as a historical biogeographic unit, understanding the close association between Cerrado and Chaco will require further empirical studies. Future tests of historical links between their biotas, if any, will certainly benefit from comparative phylogenetic and phylogeographic frameworks involving multiple taxonomic groups.

CONCLUDING REMARKS

The taxonomic description and reconstruction of the phylogenetic relationships of *Tropidurus azurduyae* reflect on our efforts to advance the systematics of widely distributed complexes of cryptic species of *Tropidurus*. Because tropidurine fossils have not been discovered to date, we were unable to perform a safe chronological analysis to determine minimum ages for clades and species. However, the identification of endemic species restricted to the inter-Andean dry valleys from central and southern Bolivia and other seasonally dry tropical forests and open dry areas from South America allow us to expand the body of evidence supporting these areas as distinct biotic units. Furthermore, our results provide evidence against the Pleistocene Arc hypothesis, and call our attention to revisiting the biogeographic history of the dry areas of South America based on improved data sets and comparative analyses of a larger number of clades. For the first time, our results show with clarity that scenarios based exclusively on vicariance are unlikely to explain the complex biogeographic history of *Tropidurus*. Nevertheless, even if the distribution data and phylogenetic patterns recovered thus far allow us to rule out certain hypotheses in favor of others, determining the timeframe of the events involved in the diversification and biogeographic history of *Tropidurus* is crucial. Certainly, the incorporation of the time component (Donoghue and Moore, 2003) remains as a major challenge for us to fully understand the evolutionary history of this lizard clade (Carvalho et al., 2013).

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APPENDIX 1

LIST OF SAMPLES ANALYZED MORPHOLOGICALLY AND MOLECULARLY

| Species | Tissue Number ^{1,2} | Voucher | Meristic | Morpho- metric | DNA | Locality ³ |
|---------------------------|------------------------------|---------------|----------|-------------------|-----|------------------------------------|
| <i>M. quadrivittatus</i> | [MTR] LG 1170 | — | — | — | X | Chile, Antofagasta (83) |
| <i>P. plica</i> | AMCC 106953 | — | — | — | X | Guyana, Potaro-Siparuni (84) |
| <i>S. quinarius</i> | [MTR] PHV 2204 | — | — | — | X | Brazil, Bahia (60) |
| <i>T. catalanensis</i> | UFRGS-T 2890 | UFRGS 6181 | — | — | X | Brazil, Rio Grande do Sul (79) |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20463 | MHNC-R 3003 | X | X | X | Bolivia, Santa Cruz (46) |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20461 | MHNC-R 3004 | X | X | X | Bolivia, Santa Cruz (45) |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20458 | MHNC-R 3005 | X | X | X | Bolivia, Santa Cruz (44) |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20462 | MHNC-R 3018 | X | X | X | Bolivia, Santa Cruz (44) |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20459 | MHNC-R 3050 | X | X | X | Bolivia, Santa Cruz (46) |
| <i>T. chromatops</i> | — | MNK-R 1082 | X | X | — | Bolivia, Santa Cruz (31) |
| <i>T. chromatops</i> | — | MNK-R 1083 | X | X | — | Bolivia, Santa Cruz (31) |
| <i>T. chromatops</i> | — | MNK-R 1084 | X | X | — | Bolivia, Santa Cruz (31) |
| <i>T. chromatops</i> | — | MNK-R 1085 | X | X | — | Bolivia, Santa Cruz (31) |
| <i>T. chromatops</i> | — | MNK-R 5321 | X | — | — | Bolivia, Santa Cruz (46) |
| <i>T. chromatops</i> | — | MNK-R 5323 | X | X | — | Bolivia, Santa Cruz (46) |
| <i>T. chromatops</i> | — | MNK-R 5324 | X | X | — | Bolivia, Santa Cruz (46) |
| <i>T. cocorobensis</i> | MTR 907077 | MZUSP 78450 | — | — | X | Brazil, Bahia (66) |
| <i>T. erythrocephalus</i> | MTR 906087 | — | — | — | X | Brazil, Bahia (64) |
| <i>T. etheridgei</i> | [MTR] FML 2672 | — | — | — | X | Argentina, Salta (6) |
| <i>T. etheridgei</i> | [MTR] LG 1096 | — | — | — | X | Argentina, Chaco (1) |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 11779 | — | — | — | X | Argentina, Córdoba (2) |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 12053 | — | — | — | X | Argentina, Salta (7) |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 12056 | — | — | — | X | Argentina, Salta (5) |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 12062 | — | — | — | X | Argentina, Formosa (3) |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 12114 | — | — | — | X | Argentina, Santiago del Estero (8) |
| <i>T. etheridgei</i> | [MTR] MACN 46091 | — | — | — | X | Argentina, La Rioja (4) |
| <i>T. etheridgei</i> | MNCN-ADN 5925 | — | — | — | X | Bolivia, Tarija (55) |
| <i>T. etheridgei</i> | AMCC 204465 | AMNH-R 176271 | X | X | X | Paraguay, Boquerón (97) |
| <i>T. etheridgei</i> | AMCC 204466 | AMNH-R 176272 | X | X | X | Paraguay, Boquerón (98) |
| <i>T. etheridgei</i> | AMCC 204472 | AMNH-R 176273 | X | X | X | Paraguay, Boquerón (98) |
| <i>T. etheridgei</i> | AMCC 204491 | AMNH-R 176274 | X | X | X | Paraguay, Boquerón (93) |
| <i>T. etheridgei</i> | AMCC 204493 | AMNH-R 176275 | X | X | X | Paraguay, Boquerón (87) |

| Species | Tissue Number ^{1,2} | Voucher | Meristic | Morpho- metric | DNA | Locality ³ |
|----------------------|------------------------------|---------------|----------|-------------------|-----|-----------------------------|
| <i>T. etheridgei</i> | AMCC 204501 | AMNH-R 176276 | X | X | X | Paraguay, Boquerón (93) |
| <i>T. etheridgei</i> | AMCC 204502 | AMNH-R 176277 | X | X | X | Paraguay, Boquerón (87) |
| <i>T. etheridgei</i> | AMCC 204506 | AMNH-R 176278 | X | X | X | Paraguay, Boquerón (91) |
| <i>T. etheridgei</i> | AMCC 204507 | AMNH-R 176279 | X | X | X | Paraguay, Boquerón (88) |
| <i>T. etheridgei</i> | AMCC 204512 | AMNH-R 176280 | X | X | X | Paraguay, Boquerón (85) |
| <i>T. etheridgei</i> | — | MHNC-R 224 | X | — | — | Bolivia, Santa Cruz (42) |
| <i>T. etheridgei</i> | — | MHNC-R 225 | X | — | — | Bolivia, Santa Cruz (42) |
| <i>T. etheridgei</i> | — | MHNC-R 226 | X | — | — | Bolivia, Santa Cruz (42) |
| <i>T. etheridgei</i> | — | MHNC-R 373 | X | — | — | Bolivia, Santa Cruz (35) |
| <i>T. etheridgei</i> | AMCC 204473 | MNHNP 11738 | X | X | X | Paraguay, Boquerón (96) |
| <i>T. etheridgei</i> | AMCC 204463 | MNHNP 11739 | X | X | X | Paraguay, Boquerón (99) |
| <i>T. etheridgei</i> | AMCC 204513 | MNHNP 11740 | X | X | X | Paraguay, Boquerón (86) |
| <i>T. etheridgei</i> | AMCC 204490 | MNHNP 11741 | X | X | X | Paraguay, Boquerón (95) |
| <i>T. etheridgei</i> | AMCC 204492 | MNHNP 11742 | X | X | X | Paraguay, Boquerón (92) |
| <i>T. etheridgei</i> | AMCC 204494 | MNHNP 11743 | X | X | X | Paraguay, Boquerón (89) |
| <i>T. etheridgei</i> | AMCC 204499 | MNHNP 11744 | X | X | X | Paraguay, Boquerón (94) |
| <i>T. etheridgei</i> | AMCC 204503 | MNHNP 11745 | X | X | X | Paraguay, Boquerón (90) |
| <i>T. etheridgei</i> | AMCC 204488 | MNHNP 11746 | X | X | X | Paraguay, Boquerón (100) |
| <i>T. etheridgei</i> | — | MNK-R 2775 | X | X | — | Bolivia, Santa Cruz (43) |
| <i>T. etheridgei</i> | — | MNK-R 2777 | X | X | — | Bolivia, Santa Cruz (43) |
| <i>T. etheridgei</i> | — | MNK-R 2796 | X | X | — | Bolivia, Santa Cruz (53) |
| <i>T. etheridgei</i> | — | MNK-R 2798 | X | X | — | Bolivia, Santa Cruz (53) |
| <i>T. etheridgei</i> | — | MNK-R 2799 | X | X | — | Bolivia, Santa Cruz (53) |
| <i>T. etheridgei</i> | — | MNK-R 2802 | X | — | — | Bolivia, Santa Cruz (53) |
| <i>T. etheridgei</i> | — | MNK-R 4772 | X | X | — | Bolivia, Santa Cruz (49) |
| <i>T. etheridgei</i> | — | MNK-R 4773 | — | X | — | Bolivia, Santa Cruz (49) |
| <i>T. etheridgei</i> | — | MNK-R 5237 | X | X | — | Bolivia, Tarija (54) |
| <i>T. etheridgei</i> | — | MNK-R 5242 | X | X | — | Bolivia, Chuquisaca (10) |
| <i>T. hispidus</i> | MTR 12552 | — | — | — | X | Brazil, Bahia (63) |
| <i>T. hygomi</i> | MTR 12579 | — | — | — | X | Brazil, Sergipe (82) |
| <i>T. imbituba</i> | UFRGS-T 620 | UFRGS 5092 | — | — | X | Brazil, Santa Catarina (80) |
| <i>T. insulanus</i> | [MTR] TM 358 | UFMT 7691 | — | — | X | Brazil, Mato Grosso (69) |
| <i>T. itambere</i> | [MTR] ITH 307 | — | — | — | X | Brazil, São Paulo (81) |
| <i>T. azurduyae</i> | — | MHNC-R 147 | X | X | — | Bolivia, Cochabamba (15) |
| <i>T. azurduyae</i> | — | MHNC-R 148 | X | X | — | Bolivia, Cochabamba (15) |
| <i>T. azurduyae</i> | — | MHNC-R 149 | X | X | — | Bolivia, Cochabamba (17) |
| <i>T. azurduyae</i> | — | MHNC-R 150 | X | — | — | Bolivia, Cochabamba (18) |
| <i>T. azurduyae</i> | — | MHNC-R 151 | X | — | — | Bolivia, Cochabamba (19) |
| <i>T. azurduyae</i> | — | MHNC-R 152 | X | X | — | Bolivia, Cochabamba (17) |
| <i>T. azurduyae</i> | — | MHNC-R 153 | X | X | — | Bolivia, Cochabamba (17) |
| <i>T. azurduyae</i> | — | MHNC-R 164 | X | X | — | Bolivia, Chuquisaca (9) |

| Species | Tissue Number ^{1,2} | Voucher | Meristic | Morpho- metric | DNA | Locality ³ |
|---------------------|------------------------------|-------------|----------|-------------------|-----|--------------------------|
| <i>T. azurduyae</i> | — | MHNC-R 250 | X | X | — | Bolivia, Cochabamba (12) |
| <i>T. azurduyae</i> | — | MHNC-R 262 | X | X | — | Bolivia, Cochabamba (14) |
| <i>T. azurduyae</i> | — | MHNC-R 274 | X | X | — | Bolivia, Cochabamba (16) |
| <i>T. azurduyae</i> | — | MHNC-R 275 | X | X | — | Bolivia, Cochabamba (16) |
| <i>T. azurduyae</i> | — | MHNC-R 276 | X | X | — | Bolivia, Cochabamba (16) |
| <i>T. azurduyae</i> | — | MHNC-R 502 | X | X | — | Bolivia, Potosí (20) |
| <i>T. azurduyae</i> | — | MHNC-R 514 | X | X | — | Bolivia, Cochabamba (13) |
| <i>T. azurduyae</i> | — | MHNC-R 527 | X | X | — | Bolivia, Cochabamba (13) |
| <i>T. azurduyae</i> | — | MHNC-R 531 | X | X | — | Bolivia, Potosí (20) |
| <i>T. azurduyae</i> | AMCC 204533 | MHNC-R 3007 | X | X | X | Bolivia, Potosí (24) |
| <i>T. azurduyae</i> | AMCC 204525 | MHNC-R 3008 | X | X | X | Bolivia, Potosí (22) |
| <i>T. azurduyae</i> | AMCC 204535 | MHNC-R 3009 | X | X | X | Bolivia, Potosí (30) |
| <i>T. azurduyae</i> | AMCC 204527 | MHNC-R 3010 | X | X | X | Bolivia, Potosí (26) |
| <i>T. azurduyae</i> | AMCC 204534 | MHNC-R 3011 | X | X | X | Bolivia, Potosí (28) |
| <i>T. azurduyae</i> | AMCC 204532 | MHNC-R 3012 | X | X | X | Bolivia, Potosí (23) |
| <i>T. azurduyae</i> | AMCC 204531 | MHNC-R 3015 | X | X | X | Bolivia, Potosí (21) |
| <i>T. azurduyae</i> | AMCC 204528 | MHNC-R 3016 | X | X | X | Bolivia, Potosí (29) |
| <i>T. azurduyae</i> | AMCC 204529 | MHNC-R 3017 | X | X | X | Bolivia, Potosí (27) |
| <i>T. azurduyae</i> | AMCC 204530 | MHNC-R 3020 | X | X | X | Bolivia, Potosí (25) |
| <i>T. azurduyae</i> | AMCC 204526 | MHNC-R 3024 | X | X | X | Bolivia, Potosí (26) |
| <i>T. azurduyae</i> | AMCC 204524 | MHNC-R 3026 | X | X | X | Bolivia, Potosí (29) |
| <i>T. azurduyae</i> | — | MNK-R 1097 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 1251 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 1252 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 1989 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 2217 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 2310 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 2628 | X | — | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 2725 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 2726 | X | — | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 413 | X | X | — | Bolivia, Santa Cruz (38) |
| <i>T. azurduyae</i> | — | MNK-R 4326 | X | X | — | Bolivia, Santa Cruz (34) |
| <i>T. azurduyae</i> | — | MNK-R 4327 | X | X | — | Bolivia, Santa Cruz (34) |
| <i>T. azurduyae</i> | — | MNK-R 4328 | X | X | — | Bolivia, Santa Cruz (34) |
| <i>T. azurduyae</i> | — | MNK-R 4751 | X | X | — | Bolivia, Santa Cruz (33) |
| <i>T. azurduyae</i> | — | MNK-R 5271 | X | X | — | Bolivia, Santa Cruz (52) |
| <i>T. azurduyae</i> | — | MNK-R 530 | X | X | — | Bolivia, Cochabamba (11) |
| <i>T. azurduyae</i> | — | MNK-R 531 | X | X | — | Bolivia, Cochabamba (11) |
| <i>T. azurduyae</i> | — | MNK-R 5494 | X | X | — | Bolivia, Santa Cruz (50) |
| <i>T. azurduyae</i> | — | MNK-R 5504 | X | X | — | Bolivia, Santa Cruz (39) |
| <i>T. azurduyae</i> | — | MNK-R 5542 | X | X | — | Bolivia, Santa Cruz (47) |

| Species | Tissue Number ^{1,2} | Voucher | Meristic | Morpho- metric | DNA | Locality ³ |
|----------------------------|------------------------------|--------------|----------|-------------------|-----|---------------------------------|
| <i>T. azurduyae</i> | — | MNK-R 5543 | X | X | — | Bolivia, Santa Cruz (51) |
| <i>T. azurduyae</i> | — | MNK-R 5544 | X | X | — | Bolivia, Santa Cruz (51) |
| <i>T. azurduyae</i> | — | MNK-R 5545 | X | X | — | Bolivia, Santa Cruz (51) |
| <i>T. azurduyae</i> | — | MNK-R 5547 | X | X | — | Bolivia, Santa Cruz (32) |
| <i>T. azurduyae</i> | — | MNK-R 5548 | X | X | — | Bolivia, Santa Cruz (51) |
| <i>T. azurduyae</i> | — | MNK-R 681 | X | — | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 715 | X | X | — | Bolivia, Santa Cruz (41) |
| <i>T. azurduyae</i> | — | MNK-R 733 | X | X | — | Bolivia, Santa Cruz (36) |
| <i>T. azurduyae</i> | — | MNK-R 735 | X | X | — | Bolivia, Santa Cruz (36) |
| <i>T. azurduyae</i> | — | MNK-R 737 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 743 | X | X | — | Bolivia, Santa Cruz (36) |
| <i>T. azurduyae</i> | — | MNK-R 744 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 749 | X | X | — | Bolivia, Santa Cruz (37) |
| <i>T. azurduyae</i> | — | MNK-R 750 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. azurduyae</i> | — | MNK-R 964 | X | X | — | Bolivia, Santa Cruz (40) |
| <i>T. montanus</i> | [MTR] 887668 | — | — | — | X | Brazil, Minas Gerais (73) |
| <i>T. mucujensis</i> | MTR 906024 | — | — | — | X | Brazil, Bahia (65) |
| <i>T. oreadicus</i> | MTR 33317 | — | — | — | X | Brazil, Minas Gerais (77) |
| <i>T. psammonastes</i> | MRT 3551 | — | — | — | X | Brazil, Bahia (62) |
| <i>T. semitaeniatus</i> | [MTR] JC1165 | — | — | — | X | Brazil, Bahia (65) |
| <i>T. sertanejo</i> | [MTR] AMNH-FS 20259 | MZUSP 104272 | — | — | X | Brazil, Bahia (67) |
| <i>Tropidurus</i> n. sp. 1 | [MTR] 916015 | — | — | — | X | Brazil, Bahia (57) |
| <i>Tropidurus</i> n. sp. 1 | [MTR] 916016 | — | — | — | X | Brazil, Bahia (57) |
| <i>Tropidurus</i> n. sp. 1 | MTR 16481 | — | — | — | X | Brazil, Bahia (61) |
| <i>Tropidurus</i> n. sp. 1 | MTR 16482 | — | — | — | X | Brazil, Bahia (61) |
| <i>Tropidurus</i> n. sp. 1 | MTR 16483 | — | — | — | X | Brazil, Bahia (61) |
| <i>Tropidurus</i> n. sp. 1 | MTR 23991 | — | — | — | X | Brazil, Minas Gerais (72) |
| <i>Tropidurus</i> n. sp. 1 | MTR 27051 | — | — | — | X | Brazil, Bahia (59) |
| <i>Tropidurus</i> n. sp. 1 | MTR 27090 | — | — | — | X | Brazil, Bahia (58) |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0017 | MZUSP 99708 | — | — | X | Brazil, Minas Gerais (74) |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0018 | MZUSP 99709 | — | — | X | Brazil, Minas Gerais (75) |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0019 | MZUSP 99710 | — | — | X | Brazil, Minas Gerais (75) |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0112 | MZUSP 99713 | — | — | X | Brazil, Minas Gerais (75) |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0118 | MZUSP 99714 | — | — | X | Brazil, Minas Gerais (76) |
| <i>Tropidurus</i> n. sp. 2 | [MTR] BP246/8982 | — | — | — | X | Brazil, Mato Grosso (68) |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PAM 05 | — | — | — | X | Brazil, Mato Grosso (70) |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP 187 | — | — | — | X | Brazil, Mato Grosso do Sul (71) |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP 188 | — | — | — | X | Brazil, Mato Grosso do Sul (71) |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP189/6207 | — | — | — | X | Brazil, Mato Grosso do Sul (71) |

| Species | Tissue Number ^{1,2} | Voucher | Meristic | Morpho- metric | DNA | Locality ³ |
|----------------------------|------------------------------|---------------|----------|-------------------|-----|---------------------------------|
| <i>Tropidurus</i> n. sp. 2 | MNCN-ADN 5884 | — | — | — | X | Bolivia, Santa Cruz (48) |
| <i>Tropidurus</i> n. sp. 2 | UFMT 6693 | — | — | — | X | Brazil, Mato Grosso do Sul (71) |
| <i>T. spinulosus</i> | AMCC 204478 | AMNH-R 176295 | — | — | X | Paraguay, Boquerón (101) |
| <i>T. torquatus</i> | MTR 21250 | — | — | — | X | Brazil, Rio de Janeiro (78) |
| <i>U. superciliosus</i> | MTR 18881 | — | — | — | X | Brazil, Amazonas (56) |

¹ AMCC–AMNH, Ambrose Monell Cryo Collection at the American Museum of Natural History, New York, United States of America; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MHNC, Museo de Historia Natural Alcide d'Orbigny, Cochabamba, Bolivia; MNHNP, Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay; MNK, Museo de Historia Natural Noel Kempff Mercado, Santa Cruz de la Sierra, Bolivia; MTR, Miguel Trefaut Rodrigues Tissue Collection, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; UFMT, Universidade Federal do Mato Grosso, Cuiabá, Brazil; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

² Missing numbers indicate specimens in process of being cataloged or cases where tissue samples could not be linked to whole specimens.

³ Numbers in parentheses refer to entries in the Gazetteer (appendix 2).

APPENDIX 2

GAZETTEER OF SAMPLES ANALYZED

Italicized names are those of the largest political units (states, departments, or provinces) within each country. Geographic coordinates marked with asterisks (*) were obtained directly in the field by the authors (or research team members). Other geographic coordinates were either obtained from collection's labels or georeferenced online using Google Earth Pro, version 7.3.1.4507.

ARGENTINA

1. *Chaco*, Fuerte Esperanza (25.1607° S, 61.8390° W)
2. *Córdoba*, road between La Higuera and Estancia Jesuitica La Candelaria, 1.8 km E Piedra Blanca, Cruz del Eje (31.0442° S, 64.9983° W)
3. *Formosa*, Ruta Nacional 81, Puesto Policia de Formosa, Salta-Formosa limit, 3 km E Capitan Page, Matacos (23.6939° S, 62.3383° W)
4. *La Rioja*, Aimogasta, 2 km entrance of "Finca Ascha," Arauco (28.5855° S, 66.9446° W)
5. *Salta*, Bermejo River margin, 10 km W El Carmen, Oran (23.3318° S, 63.9870° W)
6. *Salta*, Los Colorados, Anta (24.5833° S, 63.1833° W)
7. *Salta*, Ruta Provincial 41, 8.6 km S split Ruta Provincial 52, 92 km NE Joaquin V., Anta (24.6341° S, 63.4518° W)
8. *Santiago del Estero*, Route between Villa Ojo de Agua and Lomitas Blancas, Sierra de Ambargasta, 34.8 km W Villa Ojo de Agua, 14.8 km W Amiman, Ojo de Agua (29.3582° S, 63.9498° W)

BOLIVIA

9. *Chuquisaca*, El valle carretera Sucre-Cochabamba (before Mojtulo), Oropesa (18.8253° S, 65.1122° W)
10. *Chuquisaca*, Machareti, Tati, Machareti, Luis Calvo (20.8025° S, 63.3763° W)
11. *Cochabamba*, 1/2 Km from Río Julpe, Pojo, Carrasco (17.5893° S, 64.8549° W)
12. *Cochabamba*, Aiquile (18.2020° S, 65.1667° W)
13. *Cochabamba*, Buena Vista, Pasorapa (18.5500° S, 64.5610° W)
14. *Cochabamba*, Capinota (17.7167° S, 66.2500° W)
15. *Cochabamba*, Caramarca, Quillacollo (17.4318° S, 66.3105° W)
16. *Cochabamba*, Cerro Cota, Quillacollo (17.4208° S, 66.3126° W)
17. *Cochabamba*, Huañacota, Capinota (17.5568° S, 66.1716° W)
18. *Cochabamba*, Playa Ancha, Capinota (17.6693° S, 66.2445° W)
19. *Cochabamba*, Vinto Chico, Quillacollo (17.4327° S, 66.3186° W)
20. *Potosí*, Toro Toro, Charcas (18.1016° S, 65.7672° W)
21. *Potosí*, Torotoro National Park (18.1072° S, 65.7572° W)*
22. *Potosí*, Torotoro National Park (18.1071° S, 65.7576° W)*
23. *Potosí*, Torotoro National Park (18.1071° S, 65.7572° W)*
24. *Potosí*, Torotoro National Park (18.1043° S, 65.7600° W)*
25. *Potosí*, Torotoro National Park (18.1033° S, 65.7626° W)*
26. *Potosí*, Torotoro National Park (18.0987° S, 65.7493° W)*
27. *Potosí*, Torotoro National Park (18.0987° S, 65.7496° W)*
28. *Potosí*, Torotoro National Park (18.0984° S, 65.7493° W)*

29. *Potosí*, Torotoro National Park (18.0984° S, 65.7487° W)*
30. *Potosí*, Torotoro National Park (18.0983° S, 65.7492° W)*
31. *Santa Cruz*, Campamento Las Torrez, San Ignacio de Velasco, Velasco (13.6551° S, 60.8123° W)
32. *Santa Cruz*, Cueva de Anamal, Vallegrande (18.0896° S, 64.1125° W)
33. *Santa Cruz*, El Tholar, Moro Moro, Vallegrande (18.4201° S, 64.2928° W)
34. *Santa Cruz*, Estancia Valparaiso, Mairana, Florida (18.0445° S, 63.9455° W)
35. *Santa Cruz*, Itembeguazú, Cordillera (19.3500° S, 63.3833° W)
36. *Santa Cruz*, Margin of Matara River, Pampagrande, Florida (18.0989° S, 64.1696° W)
37. *Santa Cruz*, Mataral 5 km E, Pampagrande, Florida (18.0932° S, 64.1730° W)
38. *Santa Cruz*, Mataral, Pampagrande, Florida (18.1153° S, 64.2157° W)
39. *Santa Cruz*, Pampa Negra, Moro Moro, Vallegrande (18.5253° S, 64.2937° W)
40. *Santa Cruz*, Pampagrande, Florida (18.0896° S, 64.1125° W)
41. *Santa Cruz*, Pampagrande, Florida (18.0868° S, 64.1125° W)
42. *Santa Cruz*, Pozo del Monte, Cordillera (20.2850° S, 63.2541° W)
43. *Santa Cruz*, Puesto Militar 27 de Noviembre, Charagua, Cordillera (20.0131° S, 61.9042° W)
44. *Santa Cruz*, Rock outcrops 30 km W Florida (14.6064° S, 61.4924° W)*
45. *Santa Cruz*, Rock outcrops 30 km W Florida (14.6054° S, 61.4922° W)*
46. *Santa Cruz*, Rock outcrops 30 km W Florida (14.6048° S, 61.4924° W)*
47. *Santa Cruz*, Saipina, San Rafael, Manuel Maria Caballero (18.1077° S, 64.5641° W)
48. *Santa Cruz*, Santiago de Chiquitos, Cerro del Arco, Roboré, Chiquitos (18.3460° S, 59.5532° W)
49. *Santa Cruz*, Tatarenda, Camiri, Cordillera (19.1064° S, 63.5141° W)
50. *Santa Cruz*, Torrecillas, Moro Moro, Vallegrande (18.4903° S, 64.3230° W)
51. *Santa Cruz*, Vallegrande, Chañara, Vallegrande (18.5679° S, 64.1216° W)
52. *Santa Cruz*, Villa Merced, Pampagrande, Florida (18.0937° S, 64.1883° W)
53. *Santa Cruz*, Yapiroa, Charagua, Cordillera (19.6056° S, 62.5750° W)
54. *Tarija*, La Central, Villamontes, Gran Chaco (21.2273° S, 63.5744° W)
55. *Tarija*, Serranía Aguargue, 17 km from Villa Montes toward Entre Ríos (21.3039° S, 63.5646° W)

BRAZIL

56. *Amazonas*, Lago Chaviana, Itapurú, right margin of Purus River, Beruri (4.3104° S, 61.8160° W)*
57. *Bahia*, Caetité (14.0633° S, 42.5121° W)*
58. *Bahia*, Correntina (13.4259° S, 44.7337° W)*
59. *Bahia*, Correntina (13.4253° S, 44.7334° W)*
60. *Bahia*, Estação Ecológica Serra Geral do Tocantins, Formoso do Rio Preto (10.6800° S, 46.1508° W)*
61. *Bahia*, Fazenda Santo Antônio, Condeúba (14.9336° S, 41.9496° W)*
62. *Bahia*, Ibiraba, Barra (10.8000° S, 42.8333° W)*
63. *Bahia*, Lagoa do Abaeté, Salvador (12.9442° S, 38.3578° W)*
64. *Bahia*, Morro do Chapéu (11.4893° S, 41.3344° W)*
65. *Bahia*, Mucugê (13.0117° S, 41.3889° W)
66. *Bahia*, Nova Rodelas (8.9833° S, 38.8000° W)*
67. *Bahia*, RPPN Pé da Serra, Ibotirama (12.1450° S, 43.0523° W)*
68. *Mato Grosso*, Cáceres (16.5165° S, 57.8369° W)
69. *Mato Grosso*, Guarantã do Norte (9.6831° S, 54.9628° W)*
70. *Mato Grosso*, Tangará da Serra (14.4346° S, 58.3104° W)
71. *Mato Grosso do Sul*, Corumbá (18.7310° S, 56.7233° W)

72. *Minas Gerais*, Arinos (15.9107° S, 46.1132° W)*
73. *Minas Gerais*, Diamantina (18.2373° S, 43.6036° W)
74. *Minas Gerais*, Parque Nacional Cavernas do Peruaçu, Januária (15.1551° S, 44.3094° W)*
75. *Minas Gerais*, Parque Nacional Cavernas do Peruaçu, Januária (15.1547° S, 44.3051° W)*
76. *Minas Gerais*, Parque Nacional Cavernas do Peruaçu, Januária (15.1544° S, 44.3030° W)*
77. *Minas Gerais*, Primeira cachoeira do Rio Urucuia, Buritis (15.5953° S, 46.2494° W)*
78. *Rio de Janeiro*, Restinga de Grussaí, São João da Barra (21.6812° S, 41.0305° W)*
79. *Rio Grande do Sul*, Manoel Viana (29.5859° S, 55.4840° W)
80. *Santa Catarina*, Imbituba (28.2389° S, 48.6528° W)
81. *São Paulo*, Piedade (23.7196° S, 47.4153° W)
82. *Sergipe*, Santo Amaro das Brotas (10.7858° S, 36.9781° W)

CHILE

83. *Antofagasta*, Punta Blanca (24.5211° S, 69.7114° W)*

GUYANA

84. *Potaro-Siparuni*, Magdalen's Creek Camp, near (\pm 300 yds) NW bank of the Konawaruk River [\sim 25 mi (linear) WSW Mabura Hill] (5.2186° N, 59.0453° W)

PARAGUAY

85. *Boquerón*, Destacamento Militar Número 1, III Cuerpo de Ejército, 5ª Division de Infanteria, Mayor Pablo Lagerenza (20.3766° S, 60.5340° W)*
86. *Boquerón*, Destacamento Militar Número 1, III Cuerpo de Ejército, 5ª Division de Infanteria, Mayor Pablo Lagerenza (20.3755° S, 60.5335° W)*
87. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9877° S, 61.9911° W)*
88. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9855° S, 61.9867° W)*
89. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9853° S, 61.9870° W)*
90. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9851° S, 61.9865° W)*
91. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9846° S, 61.9861° W)*
92. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9798° S, 61.9763° W)*
93. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9797° S, 61.9762° W)*
94. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9788° S, 61.9737° W)*
95. *Boquerón*, Estancia Esmeraldas, General Eugenio A. Garay (20.9787° S, 61.9754° W)*
96. *Boquerón*, Orloff, Colonia 15, Mariscal José Félix Estigarribia (22.3332° S, 59.9242° W)*
97. *Boquerón*, Orloff, Colonia 15, Mariscal José Félix Estigarribia (22.3331° S, 59.9160° W)*
98. *Boquerón*, Orloff, Colonia 15, Mariscal José Félix Estigarribia (22.3329° S, 59.9167° W)*
99. *Boquerón*, Orloff, Colonia 15, Mariscal José Félix Estigarribia (22.3176° S, 59.9081° W)*
100. *Boquerón*, Parque Nacional Teniente Agripino Enciso (21.1891° S, 61.6707° W)*
101. *Boquerón*, Rodeo Trebol, Loma Plata (22.3439° S, 59.8619° W)*

APPENDIX 3

GENBANK ACCESSION NUMBERS OF MITOCHONDRIAL SEQUENCES

| Species | Tissue Number | Mitochondrial | | | |
|---------------------------|----------------------|---------------|----------|----------|----------|
| | | 12S | 16S | Cyt b | COI |
| <i>M. quadrivittatus</i> | [MTR] LG 1170 | KU245285 | KU245316 | KU245083 | — |
| <i>P. plica</i> | AMCC 106953 | KU245286 | KU245313 | KU245084 | KU245104 |
| <i>S. quinarius</i> | [MTR] PHV 2204 | KU245289 | KU245317 | KU245081 | KU245106 |
| <i>T. catalanensis</i> | UFRGS-T 2890 | KU245277 | KU245311 | KU245060 | KU245091 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20458 | KU245275 | KU245297 | — | KU245087 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20459 | MG759790 | MG759850 | — | MG759958 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20461 | MG759791 | MG759851 | — | MG759959 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20462 | MG759792 | MG759852 | — | MG759960 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20463 | MG759793 | MG759853 | — | MG759961 |
| <i>T. cocorobensis</i> | MTR 907077 | KU245274 | KU245301 | KU245067 | KU245092 |
| <i>T. erythrocephalus</i> | MTR 906087 | KU245269 | KU245306 | KU245075 | KU245095 |
| <i>T. etheridgei</i> | [MTR] LG 1096 | KU245276 | KU245298 | KU245063 | KU245088 |
| <i>T. etheridgei</i> | AMCC 204512 | MG759768 | MG759826 | MG760220 | MG759935 |
| <i>T. etheridgei</i> | AMCC 204513 | MG759769 | MG759827 | MG760221 | MG759936 |
| <i>T. etheridgei</i> | AMCC 204490 | MG759757 | MG759815 | MG760212 | MG759924 |
| <i>T. etheridgei</i> | AMCC 204491 | MG759758 | MG759816 | MG760213 | MG759925 |
| <i>T. etheridgei</i> | AMCC 204492 | MG759759 | MG759817 | — | MG759926 |
| <i>T. etheridgei</i> | AMCC 204494 | MG759761 | MG759819 | — | MG759928 |
| <i>T. etheridgei</i> | AMCC 204499 | MG759762 | MG759820 | MG760215 | MG759929 |
| <i>T. etheridgei</i> | AMCC 204501 | MG759763 | MG759821 | — | MG759930 |
| <i>T. etheridgei</i> | AMCC 204503 | MG759765 | MG759823 | MG760217 | MG759932 |
| <i>T. etheridgei</i> | AMCC 204506 | MG759766 | MG759824 | MG760218 | MG759933 |
| <i>T. etheridgei</i> | AMCC 204507 | MG759767 | MG759825 | MG760219 | MG759934 |
| <i>T. etheridgei</i> | AMCC 204493 | MG759760 | MG759818 | MG760214 | MG759927 |
| <i>T. etheridgei</i> | AMCC 204502 | MG759764 | MG759822 | MG760216 | MG759931 |
| <i>T. etheridgei</i> | AMCC 204465 | MG759752 | MG759810 | MG760207 | MG759919 |
| <i>T. etheridgei</i> | AMCC 204466 | MG759753 | MG759811 | MG760208 | MG759920 |
| <i>T. etheridgei</i> | AMCC 204472 | MG759754 | MG759812 | MG760209 | MG759921 |
| <i>T. etheridgei</i> | AMCC 204473 | MG759755 | MG759813 | MG760210 | MG759922 |
| <i>T. etheridgei</i> | AMCC 204463 | MG759751 | MG759809 | MG760206 | MG759918 |
| <i>T. etheridgei</i> | AMCC 204488 | MG759756 | MG759814 | MG760211 | MG759923 |
| <i>T. etheridgei</i> | MNCN-ADN 5925 | MG759746 | MG759804 | — | MG759913 |
| <i>T. etheridgei</i> | [MTR] FML 02672 | — | — | — | MG759903 |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 12053 | MG759742 | MG759800 | MG760200 | MG759910 |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 12062 | MG759740 | MG759798 | MG760198 | MG759908 |

| Species | Tissue Number | Mitochondrial | | | |
|----------------------------|----------------------|---------------|----------|----------|----------|
| | | 12S | 16S | Cyt b | COI |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 12114 | MG759741 | MG759799 | MG760199 | MG759909 |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 12056 | MG759743 | MG759801 | MG760201 | MG759911 |
| <i>T. etheridgei</i> | [MTR] LJAM-CNP 11779 | MG759744 | MG759802 | MG760202 | MG759912 |
| <i>T. etheridgei</i> | [MTR] MACN 46091 | MG759771 | MG759829 | MG760223 | MG759938 |
| <i>T. hispidus</i> | MTR 12552 | KU245279 | KU245305 | KU245065 | KU245099 |
| <i>T. hygomi</i> | MTR 12579 | KU245283 | KU245308 | KU245078 | KU245101 |
| <i>T. imbituba</i> | UFRGS-T 620 | KU245272 | KU245299 | KU245061 | KU245089 |
| <i>T. insulanus</i> | [MTR] TM 358 | KU245280 | KU245307 | KU245066 | KU245098 |
| <i>T. itambere</i> | [MTR] ITH 307 | KU245282 | KU245310 | KU245080 | KU245097 |
| <i>T. azurduyae</i> | AMCC 204524 | MG759778 | MG759838 | MG760232 | MG759946 |
| <i>T. azurduyae</i> | AMCC 204525 | MG759779 | MG759839 | MG760233 | MG759947 |
| <i>T. azurduyae</i> | AMCC 204526 | MG759780 | MG759840 | MG760234 | MG759948 |
| <i>T. azurduyae</i> | AMCC 204527 | MG759781 | MG759841 | MG760235 | MG759949 |
| <i>T. azurduyae</i> | AMCC 204528 | MG759782 | MG759842 | MG760236 | MG759950 |
| <i>T. azurduyae</i> | AMCC 204529 | MG759783 | MG759843 | MG760237 | MG759951 |
| <i>T. azurduyae</i> | AMCC 204530 | MG759784 | MG759844 | MG760238 | MG759952 |
| <i>T. azurduyae</i> | AMCC 204531 | MG759785 | MG759845 | MG760239 | MG759953 |
| <i>T. azurduyae</i> | AMCC 204532 | MG759786 | MG759846 | MG760240 | MG759954 |
| <i>T. azurduyae</i> | AMCC 204533 | MG759787 | MG759847 | MG760241 | MG759955 |
| <i>T. azurduyae</i> | AMCC 204534 | MG759788 | MG759848 | MG760242 | MG759956 |
| <i>T. azurduyae</i> | AMCC 204535 | MG759789 | MG759849 | MG760243 | MG759957 |
| <i>T. montanus</i> | [MTR] 887668 | KU245270 | KU245303 | KU245077 | KU245093 |
| <i>T. mucujensis</i> | MTR 906024 | KU245271 | KU245302 | KU245076 | KU245094 |
| <i>T. oreadicus</i> | MTR 33317 | KU245278 | KU245304 | KU245064 | KU245100 |
| <i>T. psammonastes</i> | MRT 3551 | KU245281 | KU245309 | KU245079 | KU245096 |
| <i>T. semitaeniatus</i> | [MTR] JC1165 | KU245284 | KU245312 | KU245059 | KU245102 |
| <i>T. sertanejo</i> | [MTR] AMNHFS 20259 | KU245267 | KU245295 | KU245068 | — |
| <i>T. spinulosus</i> | AMCC 204478 | KU245287 | KU245314 | KU245085 | KU245103 |
| <i>Tropidurus</i> n. sp. 1 | MTR 16483 | — | MG759854 | MG760244 | — |
| <i>Tropidurus</i> n. sp. 1 | MTR 16481 | MG759770 | MG759828 | MG760222 | MG759937 |
| <i>Tropidurus</i> n. sp. 1 | MTR 16482 | — | MG759830 | MG760224 | — |
| <i>Tropidurus</i> n. sp. 1 | [MTR] 916015 | MG759736 | MG759794 | MG760195 | MG759904 |
| <i>Tropidurus</i> n. sp. 1 | [MTR] 916016 | MG759737 | MG759795 | — | MG759905 |
| <i>Tropidurus</i> n. sp. 1 | MTR 27090 | — | MG759855 | MG760245 | — |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0017 | MG759738 | MG759796 | MG760196 | MG759906 |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0018 | MG759739 | MG759797 | MG760197 | MG759907 |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0019 | MG759747 | MG759805 | MG760203 | MG759914 |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0112 | MG759748 | MG759806 | MG760204 | MG759915 |

| Species | Tissue Number | Mitochondrial | | | |
|----------------------------|-------------------|---------------|----------|----------|----------|
| | | 12S | 16S | Cyt b | COI |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0118 | MG759749 | MG759807 | MG760205 | MG759916 |
| <i>Tropidurus</i> n. sp. 1 | MTR 23991 | MG759750 | MG759808 | — | MG759917 |
| <i>Tropidurus</i> n. sp. 1 | MTR 27051 | MG759775 | MG759835 | MG760229 | MG759943 |
| <i>Tropidurus</i> n. sp. 2 | MNCN-ADN 5884 | MG759745 | MG759803 | — | — |
| <i>Tropidurus</i> n. sp. 2 | UFMT 6693 | MG759772 | MG759831 | MG760225 | MG759939 |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP189/6207 | — | MG759832 | MG760226 | MG759940 |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP 188 | MG759773 | MG759833 | MG760227 | MG759941 |
| <i>Tropidurus</i> n. sp. 2 | [MTR] BP246/8982 | MG759774 | MG759834 | MG760228 | MG759942 |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP 187 | MG759776 | MG759836 | MG760230 | MG759944 |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PAM 05 | MG759777 | MG759837 | MG760231 | MG759945 |
| <i>T. torquatus</i> | MTR 21250 | KU245273 | KU245300 | KU245062 | KU245090 |
| <i>U. superciliosus</i> | MTR 18881 | KU245288 | KU245315 | KU245082 | KU245105 |

APPENDIX 4

GENBANK ACCESSION NUMBERS OF NUCLEAR SEQUENCES

| Species | Tissue Number | Nuclear | | | | | |
|---------------------------|----------------------|----------|----------|----------|----------|----------|----------|
| | | BACH1 | KIF24 | NTF3 | PRLR | PTPN | SNCAIP |
| <i>M. quadrivittatus</i> | [MTR] LG 1170 | KU245176 | KU245130 | KU245149 | KU245202 | KU245231 | KU245257 |
| <i>P. plica</i> | AMCC 106953 | | KU245131 | KU245152 | KU245203 | KU245229 | KU245259 |
| <i>S. quinarius</i> | [MTR] PHV 2204 | KU245178 | KU245134 | KU245153 | KU245206 | KU245233 | KU245261 |
| <i>T. catalanensis</i> | UFRGS-T 2890 | KU245155 | KU245113 | KU245136 | KU245190 | KU245220 | KU245250 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20458 | KU245156 | KU245112 | — | KU245189 | KU245214 | KU245252 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20459 | MG759899 | MG760014 | — | MG760085 | MG760141 | MG760191 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20461 | MG759900 | MG760015 | — | MG760086 | MG760142 | MG760192 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20462 | MG759901 | MG760016 | — | MG760087 | MG760143 | MG760193 |
| <i>T. chromatops</i> | [MHNC] AMNH-FS 20463 | MG759902 | MG760017 | — | MG760088 | MG760144 | MG760194 |
| <i>T. cocorobensis</i> | MTR 907077 | KU245162 | KU245127 | — | KU245199 | KU245224 | KU245256 |
| <i>T. erythrocephalus</i> | MTR 906087 | KU245159 | KU245116 | KU245143 | KU245183 | KU245223 | KU245247 |
| <i>T. etheridgei</i> | [MTR] LG 1096 | KU245161 | KU245111 | KU245137 | KU245187 | KU245216 | KU245251 |
| <i>T. etheridgei</i> | AMCC 204512 | MG759882 | MG759991 | MG760029 | MG760062 | MG760119 | MG760172 |
| <i>T. etheridgei</i> | AMCC 204513 | MG759883 | MG759992 | — | MG760063 | MG760120 | MG760173 |
| <i>T. etheridgei</i> | AMCC 204490 | MG759871 | MG759980 | — | MG760051 | MG760108 | MG760161 |
| <i>T. etheridgei</i> | AMCC 204491 | MG759872 | MG759981 | — | MG760052 | MG760109 | MG760162 |
| <i>T. etheridgei</i> | AMCC 204492 | MG759873 | MG759982 | — | MG760053 | MG760110 | MG760163 |
| <i>T. etheridgei</i> | AMCC 204494 | MG759875 | MG759984 | — | MG760055 | MG760112 | MG760165 |
| <i>T. etheridgei</i> | AMCC 204499 | MG759876 | MG759985 | — | MG760056 | MG760113 | MG760166 |
| <i>T. etheridgei</i> | AMCC 204501 | MG759877 | MG759986 | — | MG760057 | MG760114 | MG760167 |
| <i>T. etheridgei</i> | AMCC 204503 | MG759879 | MG759988 | MG760028 | MG760059 | MG760116 | MG760169 |
| <i>T. etheridgei</i> | AMCC 204506 | MG759880 | MG759989 | — | MG760060 | MG760117 | MG760170 |
| <i>T. etheridgei</i> | AMCC 204507 | MG759881 | MG759990 | — | MG760061 | MG760118 | MG760171 |
| <i>T. etheridgei</i> | AMCC 204493 | MG759874 | MG759983 | — | MG760054 | MG760111 | MG760164 |
| <i>T. etheridgei</i> | AMCC 204502 | MG759878 | MG759987 | MG760027 | MG760058 | MG760115 | MG760168 |
| <i>T. etheridgei</i> | AMCC 204465 | MG759866 | MG759975 | MG760026 | MG760046 | MG760103 | MG760156 |
| <i>T. etheridgei</i> | AMCC 204466 | MG759867 | MG759976 | — | MG760047 | MG760104 | MG760157 |
| <i>T. etheridgei</i> | AMCC 204472 | MG759868 | MG759977 | — | MG760048 | MG760105 | MG760158 |
| <i>T. etheridgei</i> | AMCC 204473 | MG759869 | MG759978 | — | MG760049 | MG760106 | MG760159 |
| <i>T. etheridgei</i> | AMCC 204463 | MG759865 | MG759974 | MG760025 | MG760045 | MG760102 | MG760155 |
| <i>T. etheridgei</i> | AMCC 204488 | MG759870 | MG759979 | — | MG760050 | MG760107 | MG760160 |
| <i>T. etheridgei</i> | MNCN-ADN 5925 | MG759860 | MG759969 | MG760023 | MG760040 | MG760097 | MG760154 |

| Species | Tissue Number | Nuclear | | | | | |
|----------------------------|-------------------------|----------|----------|----------|----------|----------|----------|
| | | BACH1 | KIF24 | NTF3 | PRLR | PTPN | SNCAIP |
| <i>T. etheridgei</i> | [MTR] FML 02672 | — | — | — | — | — | — |
| <i>T. etheridgei</i> | [MTR] LJM— CNP 12053 | — | MG759966 | — | MG760036 | — | MG760151 |
| <i>T. etheridgei</i> | [MTR] LJM— CNP 12062 | — | MG759964 | — | MG760034 | MG760093 | MG760149 |
| <i>T. etheridgei</i> | [MTR] LJM— CNP 12114 | MG759858 | MG759965 | MG760022 | MG760035 | MG760094 | MG760150 |
| <i>T. etheridgei</i> | [MTR] LJM— CNP 12056 | — | MG759967 | — | MG760037 | MG760095 | MG760152 |
| <i>T. etheridgei</i> | [MTR] LJM— CNP 11779 | — | MG759968 | — | MG760038 | — | MG760153 |
| <i>T. etheridgei</i> | [MTR] MACN 46091 | — | MG759994 | — | MG760065 | MG760122 | — |
| <i>T. hispidus</i> | MTR 12552 | KU245171 | KU245107 | KU245142 | KU245179 | KU245218 | KU245253 |
| <i>T. hygomi</i> | MTR 12579 | KU245174 | KU245128 | KU245139 | KU245191 | KU245225 | KU245255 |
| <i>T. imbituba</i> | UFRGS—T 620 | KU245154 | KU245114 | — | KU245185 | KU245213 | KU245244 |
| <i>T. insulanus</i> | [MTR] TM 358 | KU245170 | KU245109 | KU245140 | KU245181 | KU245219 | KU245248 |
| <i>T. itambere</i> | [MTR] ITH 307 | KU245173 | KU245125 | KU245138 | KU245200 | KU245226 | KU245235 |
| <i>T. azurduyae</i> | AMCC 204524 | MG759887 | MG760002 | — | MG760073 | MG760129 | MG760179 |
| <i>T. azurduyae</i> | AMCC 204525 | MG759888 | MG760003 | — | MG760074 | MG760130 | MG760180 |
| <i>T. azurduyae</i> | AMCC 204526 | MG759889 | MG760004 | — | MG760075 | MG760131 | MG760181 |
| <i>T. azurduyae</i> | AMCC 204527 | MG759890 | MG760005 | — | MG760076 | MG760132 | MG760182 |
| <i>T. azurduyae</i> | AMCC 204528 | MG759891 | MG760006 | — | MG760077 | MG760133 | MG760183 |
| <i>T. azurduyae</i> | AMCC 204529 | MG759892 | MG760007 | — | MG760078 | MG760134 | MG760184 |
| <i>T. azurduyae</i> | AMCC 204530 | MG759893 | MG760008 | — | MG760079 | MG760135 | MG760185 |
| <i>T. azurduyae</i> | AMCC 204531 | MG759894 | MG760009 | — | MG760080 | MG760136 | MG760186 |
| <i>T. azurduyae</i> | AMCC 204532 | MG759895 | MG760010 | — | MG760081 | MG760137 | MG760187 |
| <i>T. azurduyae</i> | AMCC 204533 | MG759896 | MG760011 | — | MG760082 | MG760138 | MG760188 |
| <i>T. azurduyae</i> | AMCC 204534 | MG759897 | MG760012 | — | MG760083 | MG760139 | MG760189 |
| <i>T. azurduyae</i> | AMCC 204535 | MG759898 | MG760013 | — | MG760084 | MG760140 | MG760190 |
| <i>T. montanus</i> | [MTR] 887668 | KU245158 | KU245124 | KU245144 | KU245188 | KU245221 | KU245245 |
| <i>T. mucujensis</i> | MTR 906024 | KU245160 | KU245115 | KU245148 | KU245184 | KU245222 | KU245246 |
| <i>T. oreadicus</i> | MTR 33317 | KU245172 | KU245108 | KU245141 | KU245180 | KU245217 | KU245249 |
| <i>T. psammonastes</i> | MRT 3551 | KU245168 | KU245126 | — | KU245182 | KU245227 | KU245234 |
| <i>T. semitaeniatus</i> | [MTR] JC1165 | KU245169 | KU245129 | — | KU245201 | KU245228 | KU245254 |
| <i>T. sertanejo</i> | [MTR] AMNHFS 20259 | KU245164 | KU245123 | KU245147 | KU245194 | KU245209 | KU245236 |
| <i>T. spinulosus</i> | AMCC 204478 | KU245175 | KU245132 | KU245151 | KU245204 | KU245230 | KU245258 |
| <i>Tropidurus</i> n. sp. 1 | MTR 16483 | — | MG760018 | — | MG760089 | MG760145 | — |
| <i>Tropidurus</i> n. sp. 1 | MTR 16481 | — | MG759993 | MG760030 | MG760064 | MG760121 | MG760174 |
| <i>Tropidurus</i> n. sp. 1 | MTR 16482 | — | — | — | — | — | — |

| Species | Tissue Number | Nuclear | | | | | |
|----------------------------|----------------------|----------|----------|----------|----------|----------|----------|
| | | BACH1 | KIF24 | NTF3 | PRLR | PTPN | SNCAIP |
| <i>Tropidurus</i> n. sp. 1 | [MTR] 916015 | — | — | — | — | — | — |
| <i>Tropidurus</i> n. sp. 1 | [MTR] 916016 | — | — | — | — | — | — |
| <i>Tropidurus</i> n. sp. 1 | MTR 27090 | — | MG760019 | — | MG760090 | MG760146 | — |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0017 | MG759856 | MG759962 | MG760020 | MG760032 | MG760091 | MG760147 |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0018 | MG759857 | MG759963 | MG760021 | MG760033 | MG760092 | MG760148 |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0019 | MG759861 | MG759970 | MG760024 | MG760041 | MG760098 | — |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0112 | MG759862 | MG759971 | — | MG760042 | MG760099 | — |
| <i>Tropidurus</i> n. sp. 1 | [MTR] MTJ 0118 | MG759863 | MG759972 | — | MG760043 | MG760100 | — |
| <i>Tropidurus</i> n. sp. 1 | MTR 23991 | MG759864 | MG759973 | — | MG760044 | MG760101 | — |
| <i>Tropidurus</i> n. sp. 1 | MTR 27051 | MG759885 | MG759999 | MG760031 | MG760070 | MG760126 | MG760177 |
| <i>Tropidurus</i> n. sp. 2 | MNCN-ADN 5884 | MG759859 | — | — | MG760039 | MG760096 | — |
| <i>Tropidurus</i> n. sp. 2 | UFMT 6693 | — | MG759995 | — | MG760066 | MG760123 | — |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP189/6207 | — | MG759996 | — | MG760067 | — | — |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP 188 | — | MG759997 | — | MG760068 | MG760124 | MG760175 |
| <i>Tropidurus</i> n. sp. 2 | [MTR] BP246/8982 | MG759884 | MG759998 | — | MG760069 | MG760125 | MG760176 |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PNP 187 | — | MG760000 | — | MG760071 | MG760127 | — |
| <i>Tropidurus</i> n. sp. 2 | [MTR] PAM 05 | MG759886 | MG760001 | — | MG760072 | MG760128 | MG760178 |
| <i>T. torquatus</i> | MTR 21250 | KU245157 | KU245110 | KU245135 | KU245186 | KU245215 | KU245243 |
| <i>U. superciliosus</i> | MTR 18881 | KU245177 | KU245133 | KU245150 | KU245205 | KU245232 | KU245260 |

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