

## **A New *Tropidurus* (Tropiduridae) from the Semiarid Brazilian Caatinga: Evidence for Conflicting Signal between Mitochondrial and Nuclear Loci Affecting the Phylogenetic Reconstruction of South American Collared Lizards**

Authors: Carvalho, André L.G., Sena, Marco A., Peloso, Pedro L.V., Machado, Fabio A., Montesinos, Rachel, et al.

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## A new *Tropidurus* (Tropiduridae) from the semiarid Brazilian Caatinga: evidence for conflicting signal between mitochondrial and nuclear loci affecting the phylogenetic reconstruction of South American collared lizards

ANDRÉ L.G. CARVALHO,<sup>1,2</sup> MARCO A. SENA,<sup>3</sup> PEDRO L.V. PELOSO,<sup>2,4</sup>  
FABIO A. MACHADO,<sup>5</sup> RACHEL MONTESINOS,<sup>3</sup> HÉLIO R. SILVA,<sup>6</sup>  
GWYNETH CAMPBELL,<sup>2</sup> AND MIGUEL T. RODRIGUES<sup>3</sup>

### ABSTRACT

*Tropidurus* Wied, 1825, is one of the most ubiquitous lizard genera distributed in open habitats of tropical and subtropical South America. Nevertheless, the broad representation of specimens of this group in scientific collections is hardly reflected in our knowledge of its taxonomic diversity. Most species currently assigned to *Tropidurus* began to be uncovered in the early 1980's and additional populations in need of formal taxonomic treatment have been cataloged ever since. Herein, we name *Tropidurus sertanejo*, n. sp., a new species of the *T. torquatus* group endemic to the semiarid Brazilian Caatinga. *Tropidurus sertanejo*, n. sp., is currently known from two isolated populations in the municipalities of Caetité and Ibotirama, State of

<sup>1</sup> Richard Gilder Graduate School, American Museum of Natural History.

<sup>2</sup> Division of Vertebrate Zoology (Herpetology), American Museum of Natural History.

<sup>3</sup> Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brasil.

<sup>4</sup> Museu Paraense Emílio Goeldi, Coordenação de Zoologia, Belém, Brasil.

<sup>5</sup> Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brasil.

<sup>6</sup> Departamento de Biologia Animal, Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro, Brasil.

Bahia, Brazil. This is the only species of the *T. torquatus* group lacking granular mite pockets on the lateral neck, and it is also diagnosable by having a conspicuous bronze-colored head, a light-brown dorsal body with small pale salmon spots, and small body size in comparison with most congeners. Phylogenetic analyses recovered a paraphyletic *Tropidurus*, but firmly supported *T. sertanejo*, n. sp., as member of a monophyletic *T. torquatus* species group. Trees generated by independent analyses of nuclear and mitochondrial sequence data conflicted with our total evidence phylogenetic hypotheses. Since topological disagreements were detected among phylogenetic trees resulting from maximum parsimony (MP) and maximum likelihood (ML) reconstructions, and MP analyses do not require distinct evolutionary models or partition schemes to be defined prior to conduction of phylogenetic reconstruction, these factors were considered unlikely to explain all the variation in the observed results, favoring the interpretation of conflicting phylogenetic signal. Because detailed information on the distribution, population size, and ecological requirements of *T. sertanejo*, n. sp., are currently unavailable, we recommend the species to be listed as “data deficient” following the rules proposed by IUCN.

## INTRODUCTION

*Tropidurus* Wied, 1825, is one of the most ubiquitous lizard genera occupying open landscapes in tropical and subtropical South America (Carvalho, 2013). However, the numerous field observations and large number of specimens in scientific collections hardly translate into a complete understanding of its phylogenetic relationships, taxonomic diversity, biogeography, and evolutionary history (Carvalho, 2013; Carvalho et al., 2013). The monophyly and internal relationships in *Tropidurus* were not rigorously established until Frost et al. (2001) employed molecular (mtDNA) and morphological characters—combining novel data with those from Frost (1992) and Harvey and Gutberlet (2000)—to build a comprehensive phylogeny. That study placed *Uranoscodon* as the sister taxon of all other tropidurines; recovered *Plica*, *Uracentron*, and *Strobilurus* as the sister clade of *Tropidurus*; erected a new genus *Eurolophosaurus* for the former *Tropidurus nanuzae* group; and restricted *Tropidurus* to a monophyletic group that predominantly occupies the open-dry South American diagonal, Amazonian savanna enclaves, and large area of the Brazilian Atlantic coast (Rodrigues, 1987, 1988; Frost et al., 2001; Ávila-Pires, 1995; Harvey and Gutberlet, 1998; Carvalho, 2013; Carvalho et al., 2013).

Currently, the genus comprises 25 nominal species in four species groups as per Frost et al. (2001): (1) *Tropidurus bogerti* group, monotypic: *T. bogerti* Roze, 1958; (2) *Tropidurus spinulosus* group: *T. callathelys* Harvey and Gutberlet, 1998, *T. guarani* Alvarez et al., 1994, *T. melanopleurus* Boulenger, 1902, *T. spinulosus* (Cope, 1862), and *T. xanthochilus* Harvey and Gutberlet, 1998; (3) *Tropidurus semitaeniatus* group: *T. helenae* (Manzani and Abe, 1990), *T. jaguaribanus* Passos et al., 2011, *T. pinima* (Rodrigues, 1984), and *T. semitaeniatus* (Spix, 1825); (4) *Tropidurus torquatus* group: *T. catalanensis* Gudynas and Skuk, 1983, *T. chromatops* Harvey and Gutberlet, 1998, *T. cocorobensis* Rodrigues, 1987, *T. erythrocephalus* Rodrigues, 1987, *T. etheridgei* Cei, 1982, *T. hispidus* (Spix, 1825), *T. hygomi* Reinhardt and Lütken, 1861, *T. imbituba* Kunz and Borges-Martins, 2013, *T. insulanus* Rodrigues, 1987, *T. itambere* Rodrigues, 1987, *T. montanus* Rodrigues, 1987, *T. mucujensis* Rodrigues, 1987, *T. oreadicus* Rodrigues, 1987, *T. psammonastes* Rodrigues et al., 1988, and *T. torquatus* (Wied,

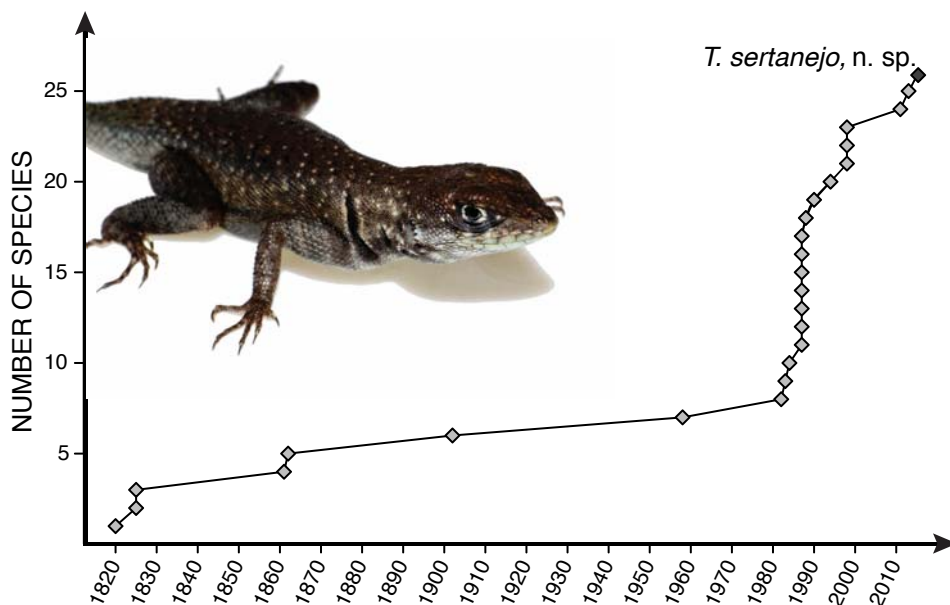


FIGURE 1. Taxonomic curve showing a steep, nonasymptotic increment in the number of species of the lizard genus *Tropidurus* described since 1820. Specimen of *T. sertanejo*, n. sp., MZUSP 104274 (allotype).

1820). Over 70% of these taxa were named in the last 35 years, and this ascending, nonasymptotic taxonomic curve suggests a promising future with respect to the number of *Tropidurus* species still to be uncovered (fig. 1). Morphological variation indicates the existence of species complexes under several nominal species in the genus (e.g., Vanzolini and Gomes, 1979; Vanzolini et al., 1980; Vanzolini, 1986; Rodrigues, 1987; Vitt and Caldwell, 1993; Vitt et al., 1996; Vitt et al., 1997; Frost et al., 1998; Gainsbury and Colli, 2003; Valdujo et al., 2009; Werneck and Colli, 2006; Werneck et al., 2015), although species delimitation based solely on morphology has been proven insufficient to elucidate diversity in several cases (Rodrigues, 1987; Frost et al., 1998; Werneck et al., 2015).

During an expedition undertaken in July 2009 for collection of amphibians and reptiles in several sites in the State of Bahia, Brazil, some of us (A.L.G.C., H.R.S., and R.M.) collected a few juvenile *Tropidurus* at Reserva Particular do Patrimônio Natural (RPPN) Fazenda Pé da Serra, Serra do Arame, Municipality of Ibotirama. These specimens possessed characters unusual among *Tropidurus* such as the absence of mite pockets on the lateral neck, leading us to suspect that they represented an unnamed species. We conducted a second expedition to RPPN Fazenda Pé da Serra, which was focused on sampling additional specimens of the suspected new taxon. This second expedition was carried out in July 2013 by A.L.G.C., P.L.V.P., and R.M., and resulted in the collection of mature individuals of three sympatric *Tropidurus* species (fig. 2). *Tropidurus hispidus* (Spix, 1825) was found around the margins of an artificial dam inside the reserve. *Tropidurus pinima* (Rodrigues, 1984) was collected from rock crevices and while basking on large rock outcrops. The third species corresponded to the morphotype sampled in 2009. Specimens were found using small rocks along trails that cut through the sandy caatingas and dry forests of Serra do Arame. After observing that adults shared the same





FIGURE 2. Syntopic species of *Tropidurus* found at the Reserva Particular do Patrimônio Natural Fazenda Pé da Serra, Serra do Arame, Ibotirama, Bahia, Brazil, and their respective habitats: (A, B) *T. sertanejo*, n. sp. (MZUSP 104274, allotype); (C, D) *T. hispidus* (MZUSP 104276); (E, F) *T. pinima* (MZUSP 104271).

unique combination of characters previously found in the juveniles, we confirmed the occurrence of an unnamed *Tropidurus* for that locality.

The new taxon is most similar to species of the *T. torquatus* species group, with a robust body that is not flattened dorsoventrally and the absence of a vertebral crest. It is easily diagnosable from other members of this group, however, by having a unique dorsal coloration pattern and by lacking mite pockets laterally on the neck. During the investigation of its phylogenetic relationships we were able to identify samples with similar molecular profile, which were originally collected by M.T.R. in the Municipality of Caetité, Bahia, in 1991. Morphological analysis of the specimens from Caetité confirmed the presence of the diagnostic characters and allowed the identification of this second population ~150 km to the south of Ibotirama. Herein, we provide a detailed description of the species based on specimens from both locali-

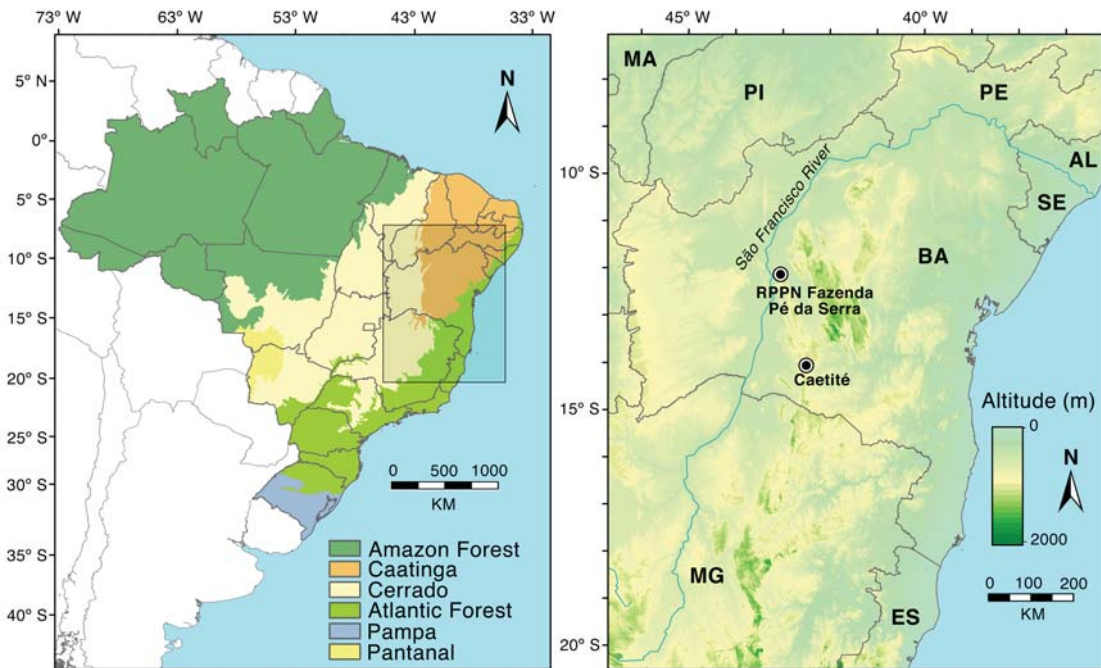


FIGURE 3. Map on left shows the distribution of the Brazilian biomes and highlights the State of Bahia, predominantly covered by the semiarid Caatinga. Map on right (altimetric profile) shows the distribution of *Tropidurus sertanejo*, n. sp.: northernmost dot indicates the type locality (RPPN Fazenda Pé da Serra, Serra do Arame, Ibotirama, Bahia: 12° 08' 45.21 S, 43° 03' 20.83 W) and southernmost dot indicates the only known additional locality of occurrence of the new species (Caetité, Bahia: 14° 04' 17.82 S, 42° 29' 48.33" W).

ties and analyze its phylogenetic position, external morphology, morphometric profile, and distribution. We conclude with a discussion of the impacts of our discoveries to the phylogenetic reconstruction of tropidurine lizards.

#### MATERIAL AND METHODS

**SAMPLES:** Adult and juvenile specimens of *Tropidurus* were collected at the Reserva Particular do Patrimônio Natural (RPPN) Fazenda Pé da Serra, Serra do Arame, Municipality of Ibotirama, State of Bahia, Brazil (12° 08' 45.21 S, 43° 03' 20.83 W, WGS84 system; fig. 3). Some of us visited the area in two nonconsecutive years, the first time between 22–23 July 2009 (A.L.G.C., H.R.S., and R.M.) and a second time in 28 July 2013 (A.L.G.C., P.L.V.P., and R.M.). The specimens collected during the first expedition were originally housed at the herpetological collection of the Universidade Federal Rural do Rio de Janeiro (RU) and recently donated to the Museu de Zoologia da Universidade de São Paulo (MZUSP). Those collected in 2013 were directly deposited at MZUSP. All individuals were collected under permits 39914-3 and 10689-1, granted by the Brazilian Ministério do Meio Ambiente (ICMBio–SISBIO).

Lizards were observed during the day along trails that cut through the caatingas of the Serra do Arame. In total, 13 specimens were collected with the aid of rubber bands or nooses. All specimens were euthanized with an overdose of 2% lidocaine, preserved with 10% unbuffered formalin, then transferred to 70% ethyl alcohol solution. Before fixation, we collected

tissue samples (muscle) from the left thigh of four individuals and stored them in Eppendorf® tubes containing absolute ethyl alcohol for subsequent molecular analyses. Additional ethanol-preserved tissue samples (muscle, liver, or tail tips) of other species selected for phylogenetic analyses were obtained from the Ambrose Monell Cryo Collection, American Museum of Natural History (AMCC-AMNH), and Miguel Trefaut Rodrigues Tissue Collection, Instituto de Biociências, Universidade de São Paulo (MTR-USP). Thirteen specimens originally collected by M.T.R. in the municipality of Caetité, Bahia, in 1991, and housed at MZUSP, were also examined for morphological descriptions and were incorporated in the type series. Tissue samples associated to three of them were included in our phylogenetic analyses. See appendix 1 for a list of tissue samples, voucher specimens, and collection localities.

We determined the sex of the specimens based on the observation of colored patches of glandular scales varying from yellow to black on the ventral side of thighs and precloacal flap in males. Females lack ventral colored patches. Adult males have wider heads and thinner bodies than females of the same body size. This is a common sexually dimorphic pattern observed in *Tropidurus* that facilitates sex identification of adults (Pinto et al., 2005; Ribeiro et al., 2012). Sex determination of juveniles is not as easy based on external morphology alone because young individuals lack the attributes listed above. To avoid dissecting specimens included in type series, we chose to forgo the sex determination of juveniles.

**TAXONOMIC FRAMEWORK AND MORPHOLOGICAL ANALYSIS:** We performed morphological and morphometric comparisons based on the primary analysis of 373 *Tropidurus* representing all 15 valid species currently assigned to the *T. torquatus* group (Frost et al., 2001) plus 25 specimens of the new taxon. We also analyzed data compiled from the literature for scale counts, morphometric measurements, and coloration (see below). Because several nominal species represent unresolved cryptic species complexes, we opted for comparing exclusively specimens from type localities and/or closely related populations. Although the number of individuals considered for comparative analyses was reduced, this conservative approach allowed us to assess morphological differences among populations that unequivocally represent valid nominal taxa, excluding those of uncertain taxonomic status.

Species comparisons and taxonomic placement followed the general framework proposed by Frost et al. (2001), in addition to our own phylogenetic results. Morphological comparisons among clades and species within clades followed Rodrigues (1987), Rodrigues et al. (1988), and Harvey and Gutberlet (1998) for the *T. torquatus* species group; Rodrigues (1984), Manzani and Abe (1990), and Passos et al. (2011) for the *T. semitaeniatus* (Spix, 1825) species group; Roze (1958) and Myers and Donnelly (2008) for *T. bogerti* Roze, 1958; and Alvarez et al. (1994) (accepting the species rank proposed by Frost et al. [1998] for *T. spinulosus* (Cope, 1862) and *T. guarani* Alvarez et al., 1994) and Harvey and Gutberlet (1998) for the *T. spinulosus* species group. All specimens used for comparisons are housed at the herpetological collections of the American Museum of Natural History, New York (AMNH); Museo de Historia Natural Alcide d'Orbigny, Cochabamba, Bolivia (MHNC); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil, (MZUSP); Universidade Federal do Mato Grosso, Mato Grosso, Brazil (UFMT); and Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil (UFRGS). A list of catalog numbers and collection localities of examined



specimens is available for download from the AMNH Digital Library Repository (<http://dx.doi.org/10.5531/sd.sp.16>).

**EXTERNAL MORPHOLOGY:** We adopted the general terminology of Frost (1992) for description of morphological structures, but also adapted and extended protocols for scale counts and scale nomenclature following Harvey and Gutberlet (1998) and others, as noted. The rostral is conserved among *Tropidurus*, however, there is variation in the pattern of contact between rostral and adjacent scales, i.e., postrostrals, supralabials, lorilabials, loreals, and nasal. Postrostrals correspond to the series of scales bordering the rostral posteriorly and are divided or undivided. The canthal ridge is covered with one or two (occasionally three or four) enlarged canthals that contact anteriorly the nasal (or tiny scales surrounding the nasal) and grade posteriorly into superciliaries. Counts of superciliaries included exclusively the row of elongate-laminate overlapping scales beginning with the first scale to flank the supraoculars. On the side of the head, we distinguish loreals and lorilabials. The former corresponds to the scales on the side of the head between nasal and preocular, below the canthals. The latter consists of scales below loreals and subocular, and between these and supralabials. In contrast to the loreals lorilabials are not adherent to the underlying periosteum and are easily lifted by forceps or dissecting needles (Etheridge and Williams, 1991). Supra- and infralabials were counted as the sum of the enlarged scales that give shape to the superior and inferior lips, respectively. Reduced (sometimes nearly granular) scales that follow the enlarged labials posteriorly to reach the end of the *rictus oris* were considered separately.

Scales on the dorsal surface of the orbit are referred to as supraoculars. Two or three (occasionally four) series of supraoculars are found, one row of enlarged scales positioned internally and one or two rows of smaller scales closer to the border of the orbit. *Tropidurus* have supraoculars bordered by one or two rows of small angulate circumorbitals separating the former from the median head shields. In between supraoculars and superciliaries one can find a row of short semilaminate scales. Temporals are located on the temporal region, in between the orbit and anterior border of external ear, below the parietals and occipitals in lateral view. We distinguish infra- and supratemporals (generally slightly enlarged in relation to infratemporals), separated by a line drawn horizontally at the level of the center of the pupil. Parietals are positioned behind supraoculars, separated by a considerably enlarged interparietal bearing a visible pineal eye. One or a few rows of irregular angulate scales referred to as occipitals separate interparietal from dorsals.

The general shape of the mental scale, positioned at the medial edge of the lower lip, is nearly invariable in *Tropidurus*, but the length of its posterior end in relation to adjacent scales was considered. Chinshields (postmentals sensu Etheridge 1968, 1970) consist of paired series of enlarged scales extending posteriorly from mental and contacting one more infralabials anterior to the first sublabial. Sublabials form a row of scales contacting the infralabials (Harvey and Gutberlet, 1998).

Species of the *T. torquatus* group as per Frost et al. (2001) lack a vertebral crest, resulting in vertebrae and paravertebrae indistinguishable from other dorsals. Therefore, scales covering the dorsal surface of the body were considered altogether as dorsals and counted from the posterior head scales (occipitals) in a straight line to the posterior edge of the hind limb where dorsals grade into enlarged caudals. Ventrals were counted midway from a line corresponding to the margin of the antegular fold to the anterior margin of hind legs. Following the same



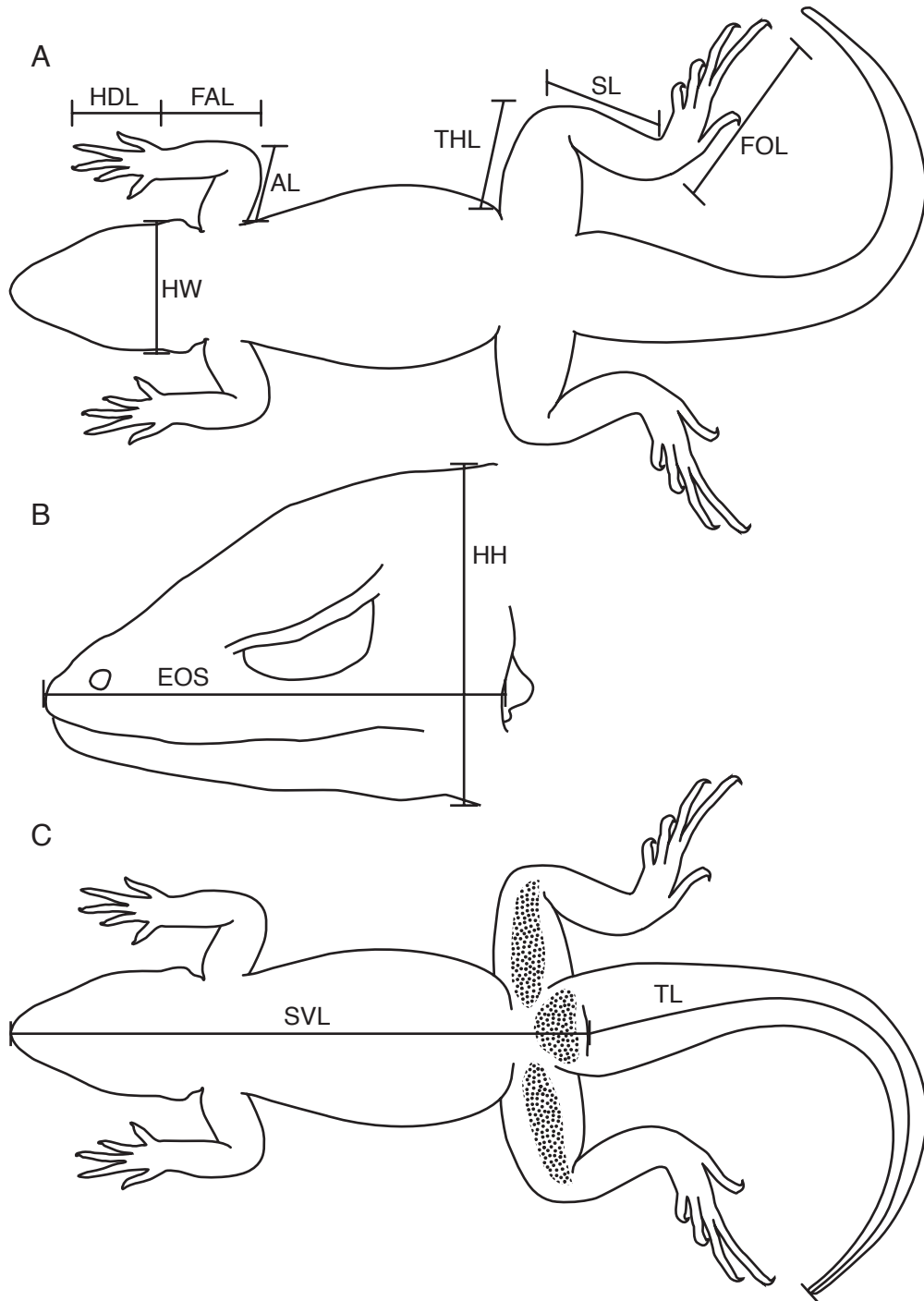


FIGURE 4. Measurements used for morphometric analyses of *Tropidurus*. Abbreviations: AL, arm length; EOS, ear opening–snout distance; FAL, forearm length; FOL, foot length; HDL, hand length; HH, head height; HW, head width; SL, shank length; SVL, snout-vent length; THL, thigh length; TL, tail length.

midline, we counted as cloacals the scales located in between the anterior margin of the hind legs and the anterior margin of the cloaca. Scales were also counted around midbody, halfway between the forelegs and hind legs. Supracarpals/tarsals and infracarpals/tarsals refer to scales on the dorsum and palm of hands and feet, respectively. Subdigital lamellae were counted from the digital articulation to, but not including, the unguis scale (noncarinate or lightly carinate scale just proximal to the claw) in both fingers and toes. Scales covering the dorsum of the fingers and toes are referred as supradigitals.

Harvey and Gutberlet (1998) explained that the “flash” coloration on the ventral surface of the thighs and precloacal region of tropidurids results from pigment in the glandular scales. Rows of glandular scales on the ventral side of the thigh were counted along the short axis of the limb. Continuous rows of both fully and partially pigmented scales were counted. The same applied to rows of glandular precloacal scales, counted along the midline of the cloacal flap. We referred as caudal scales to those covering the dorsal, lateral, and ventral sides of the tail, from the posterior edge of hind limbs to the tip of the tail. Differences in shape and size of caudal scales are noted accordingly.

**MORPHOMETRICS:** Eleven morphometric measurements from the right side of 239 adult specimens (133 males and 106 females) were taken with aid of digital calipers (to the nearest 0.1 mm; fig. 4): **SVL** (snout-vent length), from the tip of snout to the anterior margin of the cloaca; **HH** (head height), from interparietal scale to gular region, measured with caliper positioned frontally; **HW** (head width), distance between temporal regions, measured below the level of the dorsal limit of ear opening; **EOS** (ear opening–snout distance) from tip of snout to the anterior margin of ear opening; **AL** (arm length), from insertion of the arm to tip of humerus; **FAL** (forearm length), from tip of proximal end of brachium to carpals; **HDL** (hand length) from carpals to tip of longest digit (fourth), including the claw; **THL** (thigh length), from insertion of the leg to distal end of thigh; **SL** (shank length), from proximal end crus to heel; **FOL** (foot length), from heel to tip of longest digit (fourth), including the claw; **TL** (tail length), from anterior margin of the cloaca to tip of the tail—taken exclusively from specimens with fully grown tails.

The mean, standard deviation, minimum, and maximum values were calculated for all morphometric variables of each species. To identify outliers, we conducted a visual inspection of the dispersion graphs constructed for each variable, plotted against SVL. The assumptions of normality and variance homoscedasticity were tested using Shapiro-Wilk and Bartlett tests (Sokal and Rohlf, 1995). Because some variables did not show normal distribution and homoscedastic variance, all morphometric measurements were log-transformed to meet these assumptions. Log-transformed variables were double-checked and confirmed for normality and homoscedasticity.

To estimate TL for individuals with broken, regrown, or missing tails, we adopted a three-step approach. First, we centered all variables by subtracting the group mean from each individual morphometric measurement. Second, we performed a multiple linear regression (MLR) between TL and all other mean-centered variables, employing the morphometric measurements of all individuals with fully grown tails. We finally employed the MLR function calculated to estimate missing TL values, and group means were then added back to individual values to obtain the final TL estimates.

We performed an exploratory analysis of morphometric variation employing a principal-component analysis (PCA; covariance matrix), and tested for morphometric differences among species using multivariate analysis of variance (MANOVA) and linear discriminant analysis (LDA). Because size accounted for a large portion of the variation summarized in the first principal component, we performed the Burnaby's size-correction procedure (Burnaby, 1966) by back-projecting the original log-transformed observations into a plane orthogonal to an isometric vector (Somers, 1986) prior to recalculation of MANOVA and LDA. To assess accuracy of species reclassification, we repeated LDA employing a leave-one-out cross-validation procedure and compared correct reclassification rates.

We used scores associated with PC1 as a proxy for size variation and tested for differences in size among species with analysis of variance (ANOVA) and a post hoc Tukey-Kramer test. All morphometric analyses were carried out for adult males and females separately using the packages "nortest" (Gross, 2012), "car" (Fox and Weisberg, 2011), DTK (Lau, 2013), MASS (Venables and Ripley, 2002), and Lattice (Sarkar, 2008) in "R" (version 3.0.2; R Core Team, 2013).

**MERISTICS:** Species description and taxonomic comparisons were based on a large number of meristic characters. Statistical analyses were performed on six scale counts for all species of the *T. torquatus* group: dorsal scales, gular scales, ventral scales, scales around midbody, tibial scales, and subdigital lamellae on fourth toe. The distribution of these scale counts among species was investigated to detect characters potentially useful to distinguish the new taxon from other species and/or identify major species groups based on meristic characters. Because we failed to identify any consistent correlation between SVL (as a proxy for age) and scales counts (results not shown), we pooled juveniles, subadults, and adults of each species for subsequent analyses. In total, we analyzed 337 specimens, including individuals of both sexes and all ages (120 males, 141 females, and 76 undetermined).

The assumptions of normality and homoscedasticity of scale-count distributions were tested using Shapiro-Wilk and Bartlett tests (Sokal and Rohlf, 1995). About 20% of the tests rejected the null hypothesis of normality, yet no consistent pattern was identified with respect to specific variables or taxa. In addition, the Bartlett test rejected homoscedasticity of variances among species for all variables analyzed. Because basic assumptions of parametric methods were violated, we opted for a nonparametric multivariate analysis of variance to test for differences between species, sexes, and potential interaction between these factors (Anderson, 2001). The significance of the nonparametric MANOVA was based on 10,000 permutations. Because LDA is robust to violation of assumptions of normality and homoscedasticity (Krzanowski, 1977), we employed this multivariate technique to investigate differences in scale counts among species, avoiding multiple pairwise comparisons. We repeated LDA employing a leave-one-out cross-validation procedure and compared correct reclassification rates.

All statistical procedures were performed in "R" (version 3.0.2; R Core Team, 2013), as described above, and with aid of the package "vegan" (Oksanen et al., 2015).

**PHYLOGENETIC INFERENCE:** To infer the phylogenetic relationships of the new species within the *T. torquatus* group, we constructed a matrix composed of four mitochondrial (12S, 16S, CO1, Cyt b) and six nuclear loci (BACH1, kif24, NTF3, PRLR, PTPN, SNCAIP). In addition to seven samples corresponding to the new taxon, we included as ingroup all 15 valid

species currently assigned to the *T. torquatus* group as per Frost et al. (2001): *T. catalanensis*, *T. chromatops*, *T. cocorobensis*, *T. erythrocephalus*, *T. etheridgei*, *T. hispidus*, *T. hygomi*, *T. imbituba*, *T. insulanus*, *T. itambere*, *T. montanus*, *T. mucujensis*, *T. oreadicus*, *T. psammonastes*, and *T. torquatus*. We selected the stenocercine *Stenocercus quinarius* Nogueira and Rodrigues, 2006, to root the tree, and the tropidurines *Microlophus quadrivittatus* (Tschudi, 1845), *Plica plica* (Linnaeus, 1758), *T. semitaeniatus* (Spix, 1825), *T. spinulosus* (Cope, 1862), and *Uranoscodon superciliosus* (Linnaeus, 1758) as additional outgroups.

**LABORATORY PROCEDURES:** We extracted and isolated DNA from frozen ethanol-preserved tissues (muscle, liver, or tail tips) using the Qiagen DNeasy kit following the manufacturer's guidelines. Polymerase chain reactions (PCR) for amplification of DNA fragments were carried out in 25  $\mu$ l reactions using Illustra PuRe Taq Ready-To-Go PCR Beads (GE Healthcare Life Sciences). Primers and PCR parameters adopted for amplification and sequencing are listed in table 1. PCR products were cleaned and desalted in an AMPure (Agencourt Biosciences Corporation) reaction in a Beckman Coulter Biomek 2000 robot ("Becky") or by hand. Cycle sequencing using BigDye Terminators, v. 3.0 (Applied Biosystems) was run in 8  $\mu$ l reactions, adapting the protocol of Platt et al. (2007), and products were cleaned and desalted using cleanSEQ (Agencourt Biosciences Corporation) in "Becky." Sequencing was performed in a Roche ABI 3730 XL automated sequencer. Samples were sequenced in both directions to check for sequencing errors and ambiguities. Sequence contigs were assembled and edited in Geneious 6.1.8 (Biomatters, [www.geneious.com](http://www.geneious.com)). Genbank accession numbers are given in appendix 2.

**ALIGNMENT, MODEL SELECTION, AND OPTIMALITY CRITERIA:** Alignments were conducted separately for each locus using the MAFFT (Kato and Toh, 2008) plugin in Geneious 6.1.8 (Biomatters, [www.geneious.com](http://www.geneious.com)); we employed the 200 PAM ( $k = 2$ ) scoring matrix, gap open penalty 1.53, offset value 0.123 and used the "auto" function to select the best algorithm according to data size. Subsequently, we concatenated the alignments in Sequence Matrix 1.8 (Vaidya et al., 2011). All alignments produced in this study were made available for download from the AMNH Digital Library Repository (<http://dx.doi.org/10.5531/sd.sp.16>).

To investigate the contribution/conflict of mitochondrial and nuclear loci determining/affecting phylogenetic reconstruction, we performed partial and total evidence analyses based on different data sets: (1) mitochondrial loci concatenated, (2) nuclear loci concatenated, and (3) mitochondrial plus nuclear loci concatenated; hereafter referred as mitochondrial, nuclear, and total evidence data sets, respectively. Each dataset was phylogenetically analyzed under maximum parsimony (MP) and maximum likelihood (ML). Analyses were based on the same alignments and under the same treatment of gap characters (as missing data). Although we are well aware that gap characters can be informative in a phylogenetic context—hypothesized to represent natural length variation, i.e., insertion/deletion events (Giribet and Wheeler, 1999; Simmons and Ochoterena, 2000)—we made a practical decision not to treat gap characters as an additional state, to make the parsimony and maximum likelihood results more comparable to each other, at least with respect of use of evidence. The issue of comparability among optimality criteria and its implications are discussed thoroughly in Peloso et al. (2015).

Parsimony tree searches were carried out in TNT version 1.1 (Goloboff et al., 2000). Heuristic searches were based on a combination of the random addition of sequences algorithm



TABLE 1. Primers and PCR profiles for DNA amplification. Conditions for denaturation, annealing, and extension steps for each cycle, followed by the number of cycles. All reactions included a 4 min initial denaturation at 94° C and a 6 min final extension at 72° C. Mitochondrial sequences encoding the mitochondrial genes 12S rDNA, 16S rDNA, COI and Cyt b, and nuclear genes BACH1, BNDF, kif24, MKL1, NTF3, PRLR, PTPN, RAG1, and SNCAIP, were employed for phylogenetic analyses.

| Gene          | Source                     | Primer          | Direction | Sequence (5' -3')              | PCR Profile   |
|---------------|----------------------------|-----------------|-----------|--------------------------------|---|
| <b>mtDNA</b>  |                            |                 |           |                                |   |
| 12S           | Benavides et al. (2007)    | 12S.tPhe-22     | Forward   | AAAGCACRGCACCTGAAGATGC         | 95°(30'')/50°(60'')/72°(60'') [35x]   |
| 12S           | Benavides et al. (2007)    | 12S.12e-987     | Reverse   | GTRCGCTTACCWCWTGTACGACT        |   |
| 16S           | Geurgas et al. (2008)      | 16S F           | Forward   | CTGTTTACCAAAAACATMRCCCTYTAGC   | 95°(30'')/45°(30'')/72°(60'') [35x]   |
| 16S           | Whiting et al. (2003)      | 16S R           | Reverse   | TAGATAGAAAACCGACCTGGATT        |   |
| COI           | Folmer et al. (1994)       | COI LCO1490     | Forward   | GGTCAACAATAATCAATAAGATATTGG    | 94°(60'')/45°(60'')/72°(75'') [10x] +<br>94°(60'')/50°(60'')/72°(75'') [35x]                        |
|               | Folmer et al. (1994)       | COI HCO2198     | Reverse   | TAAACTTCAGGGAGCAAAAATCA        |   |
| Cyt b         | Geurgas (unpubl.)          | Cyt b CitiTropi | Forward   | TGAAAAACCAAYCGTTATTCAAC        | 95°(30'')/51°(30'')/72°(1') [35x]   |
| Cyt b         | Palumbi (1996)             | Cyt b V         | Reverse   | GGGGAATAGGAAGTATCATTC          |   |
| Cyt b         | Geurgas (unpubl.)          | Cyt B LGL       | Forward   | GA AAA ACCAYCGTTGTWATCAACT     | 95°(30'')/45°(30'')/72°(60'') [35x]   |
| Cyt b         | Geurgas & Rodrigues (2010) | H15149          | Reverse   | TGCAGCCCTCAGAAATGATATTTGTCCTCA |   |
| <b>nucDNA</b> |                            |                 |           |                                |   |
| BACH1         | Portik et al. (2012)       | BACH1_f1        | Forward   | GATTTGAHCCYTTTRCTTCAGTTTGC     | 95°(15'')/60°(30'')/72°(60'') [2x] +<br>Touchdown -2° [2x] +<br>95°(15'')/50°(30'')/72°(60'') [30x] |
| BACH1         | Portik et al. (2012)       | BACH1_r1        | Reverse   | ACCTCACATTCTYTGTTCTCYCTRGC     | 95°(30'')/63°(30'')/72°(60'') [10x]   |
| kif24         | Portik et al. (2012)       | KIF24_f1        | Forward   | SAAACGTRTRCMAAACGCATCC         | + 95°(30'')/60°(30'')/72°(60'') [30x]   |
| kif24         | Portik et al. (2012)       | KIF24_r2        | Reverse   | WGGCGTCTGRAAYTGCTGGTIG         | 95°(15'')/60°(30'')/72°(60'') [2x] +<br>Touchdown -2° [2x] +<br>95°(15'')/50°(30'')/72°(60'') [30x] |
| NTF3          | Portik et al. (2012)       | NTF3_f1         | Forward   | ATGTCCATCTTGTTTTATGTGATATTT    |   |
| NTF3          | Portik et al. (2012)       | NTF3_r1         | Reverse   | ACRAGTTTRITTGTTYTCTGAAGTC      | 95°(30'')/45°(30'')/72°(60'') [35x]   |
| PRLR          | Portik et al. (2012)       | PRLR_f1         | Forward   | GACARYGARGACCAGCAACTRATGCC     |   |
| PRLR          | Portik et al. (2012)       | PRLR_r3         | Reverse   | GACYTTGTGRACITCYACRTAATCCAT    | 95°(30'')/55°(30'')/72°(60'') [10x] +<br>95°(30'')/52°(30'')/72°(60'') [30x]                        |
| PTPN          | Portik et al. (2012)       | PTPN12_f1       | Forward   | AGTTGCCTTGTWGAAGGRGATGC        |   |
| PTPN          | Portik et al. (2012)       | PTPN12_r6       | Reverse   | CTRCAAATKGACATYGGYAATAC        | 95°(15'')/60°(30'')/72°(60'') [2x] +<br>Touchdown -2° [2x] +<br>95°(15'')/50°(30'')/72°(60'') [30x] |
| SNCAIP        | Portik et al. (2012)       | SNCAIP_f10      | Forward   | CGCCAGYTGTYGGGRAARGAWAT        |   |
| SNCAIP        | Portik et al. (2012)       | SNCAIP_r13      | Reverse   | GGWGAYTTGAGDGCACCTCTTRGGRCT    |   |

(RAS) and subsequent rearrangement of branches through tree bisection-reconnection (TBR), parsimony ratchet (Nixon, 1999), tree fusing (Goloboff, 1999), and sectorial searches (Goloboff, 1999) under driven searches. For each search the best solution was reached 500 times before the search was stopped (command *hits 500*). In cases where more than one equally parsimonious MP tree was found, support values were plotted over a strict consensus tree summarizing competing hypotheses.

We used PartitionFinder (version 1.1.1; Lanfear et al., 2012) to identify the optimal partition schemes for our data, and the best-fit nucleotide substitution model for each partition. We ran PartitionFinder allowing all available models of molecular evolution to be compared, and used the “greedy search” algorithm and linked branch lengths in calculations of likelihood scores. Bayesian information criterion (BIC) was adopted for selecting among alternative partitioning strategies. ML tree searches were performed in Garli (version 2.1) using the molecular-evolution.org web platform (Zwickl, 2006; Bazinet et al., 2014). Starting tree topologies were generated using the stepwise-addition algorithm and the number of attachment points evaluated for each taxon to be added (attachmentspertaxon) was set to 57 (= two times the number of taxa + 1), meaning that all attachment points were evaluated for each taxon. We performed an adaptive best-tree search using a minimum of 10 replicates and determined the necessary number of search replicates to perform by calculating the number of replicates needed to recover the best topology with 0.95 probability. The relative support for each clade was assessed through 1000 nonparametric bootstrap replicates (Felsenstein, 2004). We summarized bootstrap results by plotting support values over the best tree using the Python package SumTrees of the DendroPy phylogenetic computing library (Sukumaran and Holder, 2010).

## SPECIES ACCOUNTS

### TROPIDURIDAE BELL, 1843

#### *TROPIDURUS* WIED, 1825

#### *Tropidurus sertanejo*, n. sp.

Figures 1, 2, 5–8

**HOLOTYPE:** MZUSP 104273, adult male from Reserva Particular do Patrimônio Natural Fazenda Pé da Serra, Serra do Arame, Municipality of Ibotirama, State of Bahia, Brazil, (12° 08' 45.21 S, 43° 03' 20.83 W, WGS84 system; ~507 m above sea level), collected by A.L.G.C., P.L.V.P., and R.M. in 28 July 2013.

**ALLOTYPE:** MZUSP 104274, adult female, collected with the holotype (12° 08' 41.99 S, 43° 03' 08.32 W, WGS84 system, ~516 m above sea level).

**PARATYPES:** MZUSP 104272, juvenile, collected with the holotype (12° 08' 41.99 S, 43° 03' 08.32 W, WGS84 system; ~516 m above sea level) by A.L.G.C., P.L.V.P., and R.M. on 28 July 2013. MZUSP 105262 (= RU 6311), adult male, MZUSP 105263 (= RU 6312), adult female, MZUSP 105261 (= RU 6310) and MZUSP 105264–65 (= RU 6313–14), three juveniles, collected in the type locality (12° 08' 40.06 S, 43° 03' 23.40 W, WGS84 system; ~490 m above sea level) by

A.L.G.C., H.R.S., and R.M. on 22 July 2009. MZUSP 105266–69 (= RU 6353–6356): four juveniles, collected in the type locality (12° 08' 40.06 S, 43° 03' 23.40" W, WGS84 system; ~490 m above sea level) by A.L.G.C., H.R.S., and R.M. on 22 July 2009. MZUSP 76048–49, 76055, three adult males, MZUSP 76050–52, three adult females, MZUSP 76046–47, 76053–54, 76056–58, seven juveniles collected in the municipality of Caetité, State of Bahia, Brazil (14° 04' 17.82 S, 42° 29' 48.33" W, WGS84 system; ~940 m above sea level), by M.T.R. on 19 September 1991.

**MORPHOLOGICAL DIAGNOSIS:** *Tropidurus sertanejo*, n. sp., is diagnosed based on a combination of macrostructural characters<sup>7</sup> suggested by Frost et al. (2001) as exclusive to *Tropidurus*: skull not highly elevated at the level of the orbits; premaxilla not broad; nutritive foramina of maxilla strikingly enlarged; lingual process of dentary present, extending over lingual dentary process of coronoid; angular strongly reduced; medial centrale absent; “flash” marks on undersides 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; and tail terete. Frost et al. (2001) also listed the hemipenis attenuate without apical disks as characteristic of *Tropidurus*, however the hemipenial morphology of *T. sertanejo*, n. sp., was not examined.

*Tropidurus sertanejo*, n. sp., is diagnosed as a member of the *T. torquatus* group by lacking the enlarged middorsal scale row (well marked in species of the *T. spinulosus* group, especially in males), by having black thigh flash marks (males of *T. spinulosus* group have yellow, pale, or white flash marks), and by not being extremely flattened dorsoventrally (as observed in species of the *T. semitaeniatus* group and, more moderately, in *T. bogerti*).

*Tropidurus sertanejo*, n. sp., lacks granular mite pockets on the lateral neck. The oblique neck fold of the species is covered with imbricate, smooth, mucronate scales, similar to but smaller than temporals and dorsals (fig. 8). The new species has deep, oblique axillary and wide inguinal mite pockets, both coated with unpigmented diminutive granular scales. The bronze head and light brown dorsal body decorated with small pale salmon spots constitute a unique coloration pattern (figs. 2, 4–5). This exclusive combination of macroscopic attributes makes *T. sertanejo*, n. sp., a rare example of easily diagnosable species within the *T. torquatus* group.

**COMPARISON WITH OTHER SPECIES:** *Tropidurus sertanejo*, n. sp., is the only species of the *T. torquatus* group lacking mite pockets on the lateral neck and could not be classified according to the eight mite pockets patterns described by Rodrigues (1987). We amended that classification scheme by adding two patterns (I and J) to accommodate *T. sertanejo*, n. sp., and *T. psammonastes* (fig. 8; table 2). *Tropidurus sertanejo*, n. sp., is known to occur in sympatry with only two other forms of the *T. torquatus* group: *T. hispidus* and *T. aff. etheridgei*. However, those species differ considerably with respect to number and morphology of their mite pockets. *Tropidurus hispidus* has one mite pocket on the lateral neck, one deep and oblique granular axillary mite pocket, and lacks an inguinal pocket. *Tropidurus aff. etheridgei* has two mite pockets on the lateral neck, and lacks both axillary or inguinal mite pockets, while *T. sertanejo*, n. sp., lacks a mite pocket on the lateral neck and has both axillary and inguinal pockets well developed and coated with granular scales.

<sup>7</sup> Osteological characters were analyzed through digital inspection of the skeleton of the holotype via computed tomography.

The state of conservation of old specimens sometimes precludes accurate identification of the type and number of mite pockets on the lateral neck of specimens. Therefore, checking for the presence of axillary and inguinal granular pockets is an easy way to narrow down the number of species for comparison. *Tropidurus sertanejo*, n. sp., shares both axillary and inguinal mite pockets exclusively with *T. erythrocephalus*, *T. montanus*, and *T. mucujensis*. These three forms are allopatric with respect to *T. sertanejo*, n. sp., and have distributions nearly restricted to rocky fields known as *campos rupestres*, spread over the Espinhaço mountain range, in the states of Minas Gerais and Bahia, Brazil (Rodrigues, 1987, 1988; Carvalho, 2013). In terms of coloration, *T. sertanejo*, n. sp., has a bronze dorsal head, distinct from the intense brick-reddish head coloration of *T. erythrocephalus*. The ventral side of its head is pale salmon, and grades into a dark bronze throat, differing from the orange pigmentation covering the throat and chest of *T. erythrocephalus*. *Tropidurus sertanejo*, n. sp., has a dotted dorsal pattern somewhat similar to *T. mucujensis*, but the former is decorated with pale salmon spots on the dorsum, while the dorsal color pattern in the latter is scattered with sky-blue spots against the dark background of its dorsum and tail. *Tropidurus sertanejo*, n. sp., also lacks aculeate spines on the lateral neck, a morphological attribute exclusive to *T. mucujensis*.

**DESCRIPTION OF HOLOTYPE:** Small species of *Tropidurus*, SVL 79.92 mm; head subtriangular, length 29% of SVL and width 66% of head length; skull not compressed, not strongly elevated at level of orbits; rostrum not noticeably shortened relative to most other species of *Tropidurus*; scales of frontonasal region not imbricating posteriorly, several lenticulate scale organs present (scale organs randomly distributed on other areas of the head); rostral tall, about three times as high as first supralabial, slightly tumescent, contacting first supralabials, first lorilabials, and three postrostrals; 1/2 postrostrals (i.e., right postrostral entire, left divided); nasal single, higher than adjacent scales, separated from rostral by postrostral-lorilabial contact; 5/6 enlarged supralabials followed by 3/3 smaller scales reaching the *riktus oris*, never contacting subocular; nostril elliptical, occupying about one third of nasal, positioned posteriorly, directed dorsolaterally; 2/2 canthals between nasal and first superciliary; anteriormost canthal separated from supralabials by 1/1 rows of lorilabials and 1/1 rows of loreals; 8/9 laminate superciliary scales weakly produced vertically; 1/1 dorsally keeled preoculars contacting second canthal and 6/5 loreals; 1/1 dorsally keeled elongate suboculars separated from supralabials by one row of lorilabials; palpebrals granular; second row of palpebrals larger, with developed scale organs; 3 rows of supraoculars, oblique internal row with 8/9, medial row with 6/4, external row with 8/8 small scales, the enlarged ones occupying up to two thirds, and two posteriormost internal scales occupying the whole width of the supraocular area; 1/1 rows of small, angulate circumorbitals; 1/1 rows of short semilaminate scales with lenticulate scale organs linearly distributed along their dorsal face separating circumorbitals and superciliaries; interparietal enlarged, about 1.2 times longer than wide; parietal eye visible, positioned medially on the posterior limit of the first third of the interparietal scale; temporals imbricate, keeled, larger than lateral neck scales and smaller than dorsals and parietals, scale organ positioned on the posterior end of the keel or next to the base of a slight mucron, keels more pronounced on upper than lower temporals; ear shaped as inverted keyhole, canal deep, largest



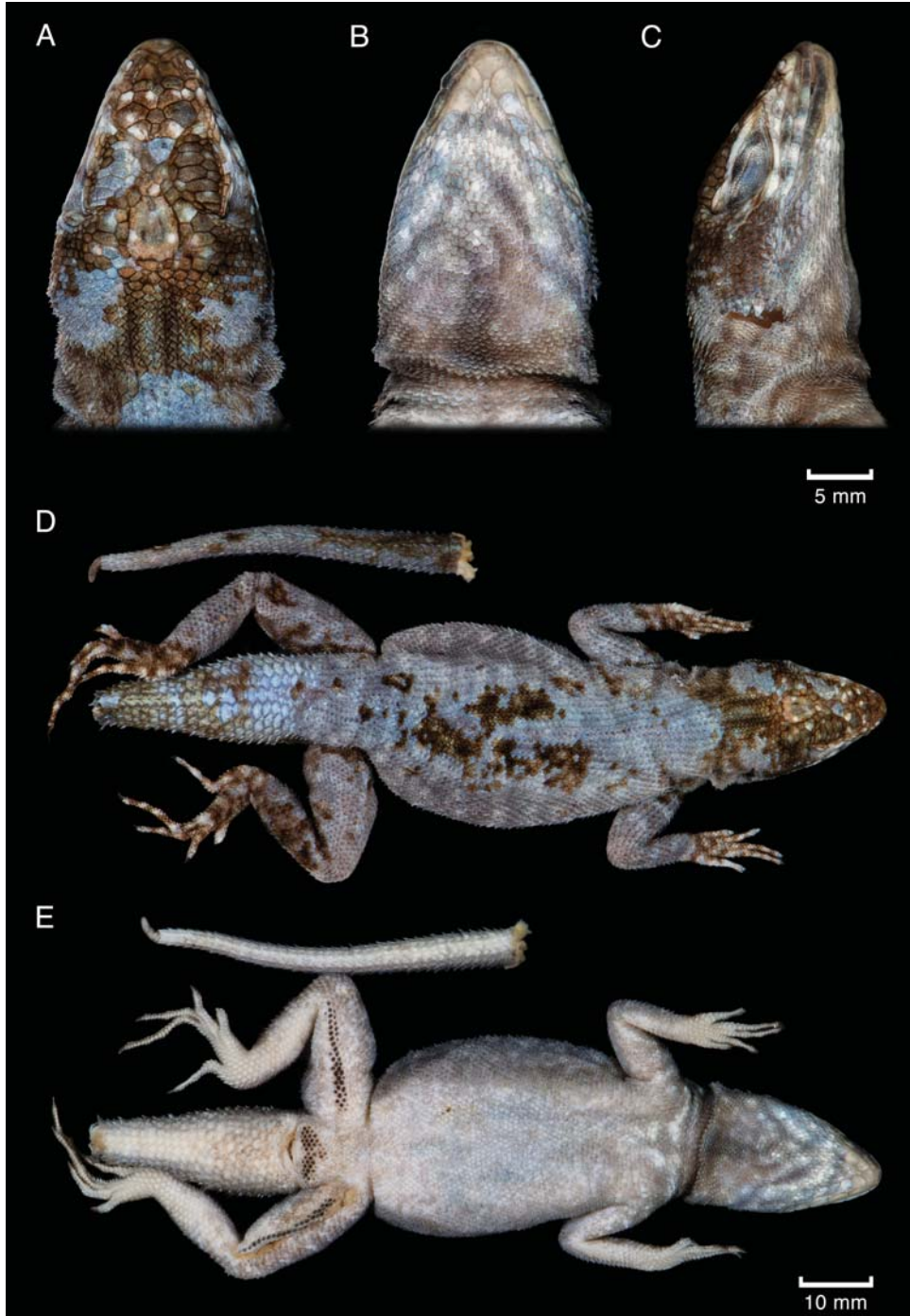


FIGURE 5. Holotype of *Tropidurus sertanejo*, n. sp. (MZUSP 104273): (A) head in dorsal view; (B) head in ventral view showing intense pigmentation toward gular region; (C) head in lateral view; (D) dorsal body; (E) ventral body showing the typical dark flash marks on the underside of the thighs and cloacal flap of adult males.

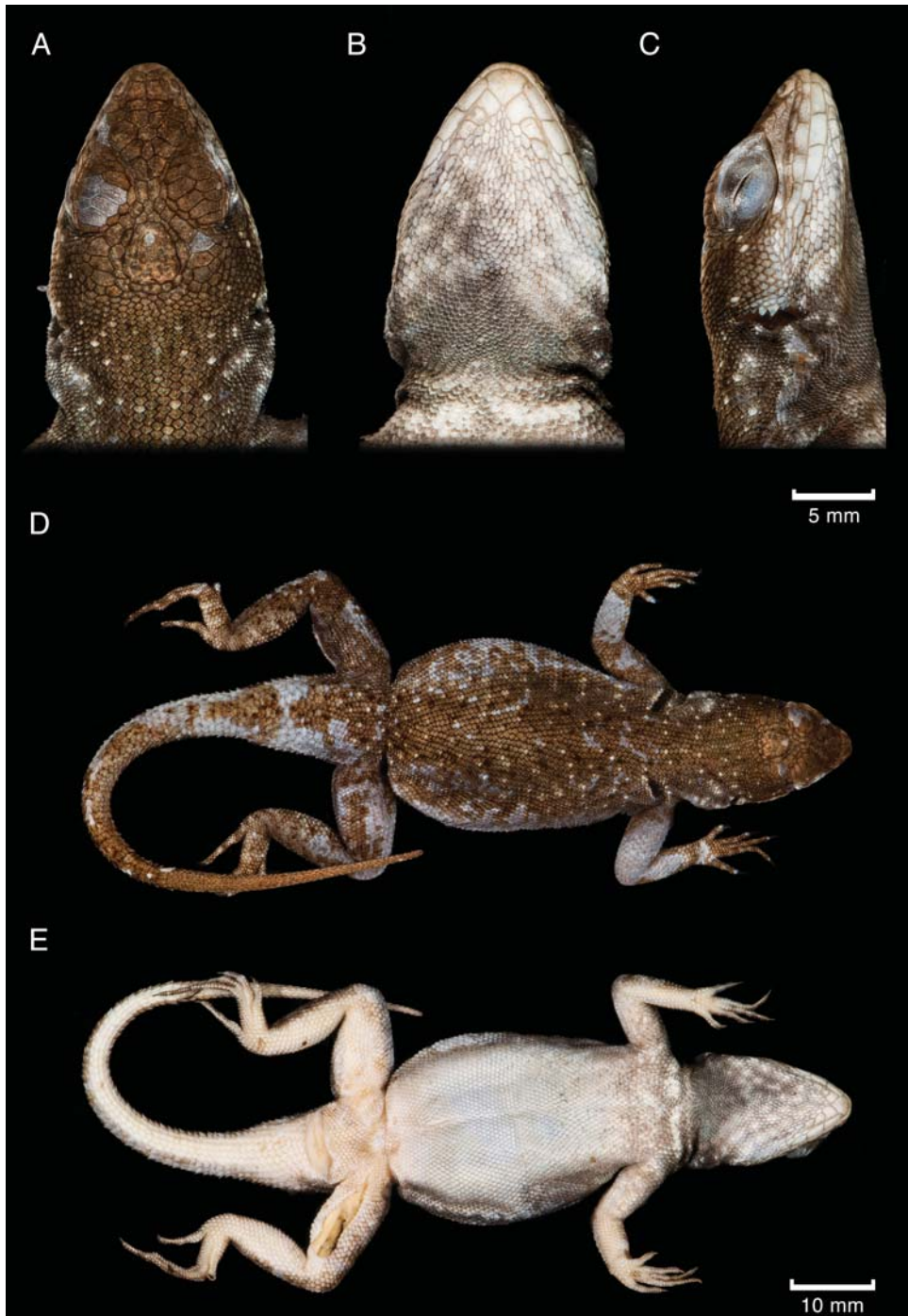


FIGURE 6. Allotype of *Tropidurus sertanejo*, n. sp. (MZUSP 104274): (A) head in dorsal view; (B) head in ventral view; (C) head in lateral view; (D) dorsal body illustrating the spotted pattern typical of the new species; (E) ventral body showing the unpigmented underside of the thighs and cloacal flap characteristic of females.



FIGURE 7. (A) Dorsal, (B) ventral, and (C) lateral views of the head of the holotype (MZUSP 104273), illustrating in detail the scutellation of *Tropidurus sertanejo*, n. sp.

diameter of ear opening 20% of ear opening to snout distance; tympanum semitranslucent, discretely iridescent zones visible when exposed to direct light; preauricular fringe consisting of row of 6/6 smooth, lanceolate scales; width of mental 70% of the width of rostral; mental extending posteriorly to the level of half of the adjacent infralabials; 5/5 enlarged infralabials followed by 2/2 smaller scales reaching the *rictus oris*; 4/4 angulate, enlarged postmentals; 1/1 postmentals in contact with first infralabial; first postmentals not in contact; 9/9 sublabials; 46 gulars, imbricating posteriorly.

Vertebral crest absent; 84 dorsals; 76 scale rows around midbody; 72 ventrals; dorsals large, strongly keeled and mucronate, particularly on the anterior portion of the dorsum, after the head; keels on dorsal and caudal scales align forming continuous longitudinal, slightly oblique lines observable macroscopically; posthumeral region with small, smooth, nonmucronate scales, increasing in size, intensity of keels and mucronation toward the flanks; ventrals smooth, nonmucronate, imbricate, about two thirds the size of dorsals; flash marks on underside of thighs formed by 3/3 rows of dark glandular scales; 17 cloacal scales, cloacal flap with 8 rows of dark precloacal glandular scales; supracarpal scales smooth, rhomboidal; supratarsal scales smooth toward finger V and keeled and mucronate toward finger I, rhomboidal; both supracarpals and supratarsals with scale organ positioned on the distal end of the scale or next to the base of the mucron, when present; infracarpal and



infratarsal scales carinate, tricarinate toward fingers and toes; fingers and toes thin, cylindrical, slightly compressed laterally; supradigital lamellae smooth, rhomboidal, scale organ positioned on the distal end of the scales; infradigital lamellae tricarinate and mucronate, 14/14 under fourth finger, 20/20 under fourth toe, medial caren 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 on ventral and postaxial surfaces; scales on hind limb decreasing in size toward ventral surface, 24/24 tibial scales, heavily keeled and mucronate; dorsal body scales large, keeled, mucronate, grading to scales up to 80% smaller at the level of ear opening and neck; rictal, nuchal, postauricular, supraauricular, dorsolateral, longitudinal neck, and antegular fold absent; shallow postauricular depression present; oblique neck fold well marked and covered with smooth, slightly mucronate, imbricate scales, similar in shape, but smaller than dorsals and temporals, not forming a mite pocket (i.e., lateral neck fold not forming a pocket coated with granular scales; see fig. 8); antehumeral fold present and well marked, coated with imbricate scales similar to those on lateral neck; gular fold incomplete medially; axillary pocket deep and oblique, coated with diminutive granular scales; inguinal pocket wide, with granular scales similar to those in the axillary pocket; tail compressed, tapering from the end of the first third to become pointed; second half of tail broken, separated from the first half, tip regrown; caudal verticils absent; scales of tail imbricate, keeled, mucronate, up to three times larger than dorsals; middorsal row of caudal scales expanded, laterally deflected, with strong and highly projected keels, forming a caudal crest after the first third of the tail.

**COLORATION IN LIFE:** Bronze coloration on the dorsal head encompassing the frontonasal, supraocular, and parietal regions. Loreals and lorilabials transition from bronze to irregularly brown-pigmented scales, with pale salmon or cream background toward labials. Labials cream; infralabials slightly lighter than supralabials. Coloration of labials extends posteriorly forming a light facial stripe that crosses the lower temporal region and reaches the preauricular fringe. Inferior portion of preocular and subocular similar in coloration to lorilabials; uppermost, keeled portion of both scales darker. Spot formed by 3–4 pale salmon angulate scales located above the posterior limit of preocular, internally to preocular corner. First and second rows of

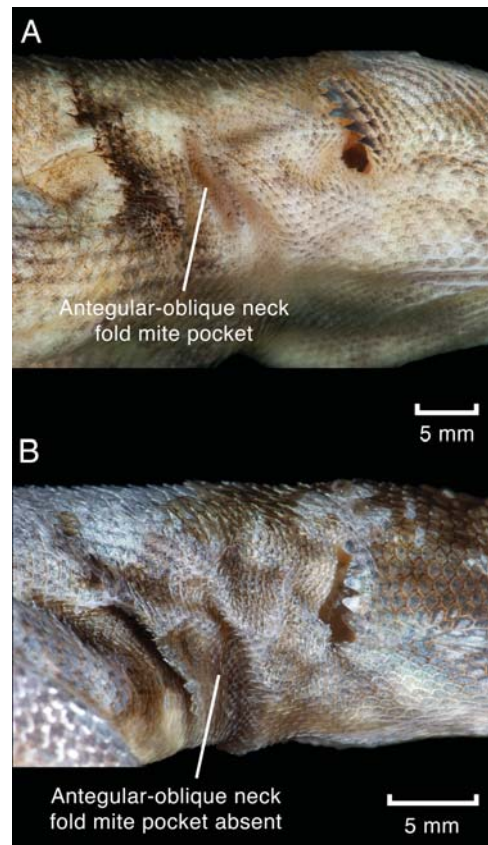


FIGURE 8. Lateral view of the neck of (A) *Tropidurus psammonastes* (AMNH 138852) and (B) *T. sertanejo*, n. sp. (holotype MZUSP 104273), illustrating the lateral mite pockets associated with types I and J, respectively. See table 2 for details on mite pocket patterns in *Tropidurus*.



TABLE 2. Expanded classification of mite pockets of the *Tropidurus torquatus* species group. Types A–H are treated in detail by Rodrigues (1987). We classify the mite pockets of *T. psammonastes* (originally described by Rodrigues et al., 1988) as Type I, and describe for the first time Type J as exclusive to *T. sertanejo*, n. sp. Internal surfaces of antegular-oblique neck, axillary, and inguinal mite pockets are coated with diminutive granular scales, unless noted.

| Species                      | Lateral neck  | Axillary                             | Inguinal | Type |
|------------------------------|---|--------------------------------------|----------|------|
| <i>T. catalanensis</i>       | Two pockets, lower one poorly developed   | 2–3 shallow granular areas           | Present  | A    |
| <i>T. imbituba</i>           | Two pockets   | 2–3 shallow granular areas           | Present  | A    |
| <i>T. torquatus</i>          | Two pockets, posterior deeper   | 2–3 shallow granular areas           | Present  | A    |
| <i>T. cocorobensis</i>       | Two shallow pockets   | Absent                               | Absent   | B    |
| <i>T. etheridgei</i>         | Two shallow pockets   | Absent                               | Absent   | B    |
| <i>T. itambere</i>           | One oblique, deep pocket  | Absent                               | Present  | C    |
| <i>T. oreadicus</i>          | One oblique, deep pocket  | Absent                               | Absent   | D    |
| <i>T. hispidus</i>           | One pocket  | Present                              | Absent   | E    |
| <i>T. erythrocephalus</i>    | One oblique, deep pocket  | Present                              | Present  | F    |
| <i>T. montanus</i>           | One oblique, deep pocket  | Present                              | Present  | F    |
| <i>T. mucujensis</i>         | One oblique, pocket   | Present                              | Present  | F    |
| <i>T. chromatops</i>         | Two enlarged subequal pockets   | Absent                               | Absent   | G    |
| <i>T. hygomi</i>             | Two oblique, deep pockets; anterior positioned more ventrally   | Absent                               | Absent   | G    |
| <i>T. insulanus</i>          | One oblique, deep pocket  | Postaxillar, oblique, extremely deep | Absent   | H    |
| <i>T. psammonastes</i>       | Two pockets; the one anterior (positioned more ventrally) with regular scales, the posterior with granular scales | Absent                               | Absent   | I    |
| <i>T. sertanejo</i> , n. sp. | Absent  | Present                              | Present  | J    |

pale salmon palpebrals form a light ring around the eye, contrasting with the surrounding dark brown granular scales. Upper temporal region light brown, grading into bronze coloration toward the top of the head. Pupil circular. Iris turquoise green. Mental region cream to the level of second pair of postmentals grading into salmon, decorated with 1–2 scales thick oblique irregular dark-pigmented stripes directed posterolaterally. Throat dark bronze with touches of salmon, dark pigmentation coming from mental region forms a semireticulate pattern posteriorly, grading into a dark gular background that retains a bronze brightness in preservative.

Neck, dorsal body, and flanks light brown with discrete bronze brightness, decorated with pale salmon spots 1–3 scales in size, and sparser, randomly distributed smaller dark spots, creating a side-to-side coarsely aligned light dotted pattern. Nuchal collar positioned at the level of gular fold, complete ventrally, incomplete dorsally, formed by 3–4 rows of dark scales extending dorsally to the uppermost limit of the flank, outlined by one row of cream scales anteriorly and two rows posteriorly. Uppermost limits of flanks with artichoke green brightness along the second half of the body, toward the tail. Chest pigmented; irregular discontinuous dark stripe positioned before the insertion of forearms, separated from nuchal collar by cream stripe that outlines it posteriorly. Ventral ground coloration grayish cream with sparse light brown pigmentation that faints toward the belly. Forearms light brown; small irregular dark

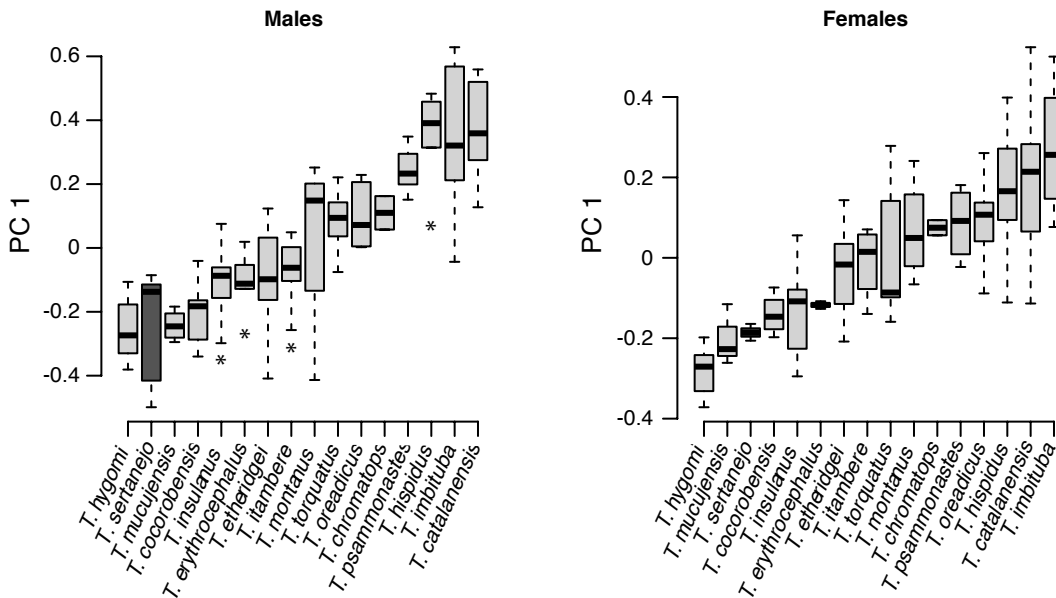


FIGURE 9. Boxplot of PC1 generated by principal component analysis of log-transformed morphometric variables as proxy for body size variation among *Tropidurus* species. *Tropidurus sertanejo*, n. sp., highlighted in dark gray.

spots randomly spread over. Anterior plane of thighs light brown, posterior plane and shanks artichoke green; small irregular dark spots randomly distributed. Supracarpal and supratarsal regions light brownish bronze; digits light brown with touches of cream. Black femoral and preloacal patches 22/21 and 16 scales long, respectively. Tail artichoke green grading into light brown toward the tip, ventral side pale cream.

**COLORATION IN PRESERVATIVE:** Intense bronze coloration on the dorsal head faded. Head and dorsal body brown. Oberhautchen on most dorsal and lateral scales lost, and with it the dotted pattern of the holotype (dorsal pattern was preserved in the allotype, with pale cream spots contrasting against the darker background; see fig. 6). Pale longitudinal stripe below the eyes extends from labials to preauricular fringe, and narrow dark interruptions formed by pigmented vertical bars are more evident against the cream background. Mental region cream. Postmental salmon background absent, dark pigmentation toward the throat preserved, without the original bronze brightness. Nuchal collar well marked, but the row of pale salmon scales outlining it became pale cream. Chest coloration persisted nearly unchanged. Ventral coloration preserved the grayish cream coloration, but ventral surfaces of forelimbs, hind limbs and tail became slightly more pale cream. Artichoke green coloration of the posterior plane of thighs and on shanks became brown, similar to dorsum. Artichoke green brightness along the second half of the body toward the tail absent.

**MORPHOMETRICS:** *Tropidurus sertanejo*, n. sp., is one of the four smallest species in the *T. torquatus* group, with adult males ranging from 60.09–79.92 mm SVL and females from 61.98–72.46 mm SVL. Reduced mean body size is also observed in *T. hygomi*, *T. mucujensis*, and *T. cocorobensis* (fig. 9; tables 3–4). Because PC1 held the majority of the explained variance and

TABLE 3. Mean  $\pm$  standard deviation, minimum and maximum values of morphometric measurements (in millimeters) of adult males of the *Tropidurus torquatus* species group. SVL, snout-vent length; HH, head height; HW, head width; EOS, ear opening–snout distance; AL, arm length; FAL, forearm length; HDL, hand length; THL, thigh length; SL, shank length; FOL, foot length; TL, tail length. The number of individuals measured followed by the number of individuals with fully grown tails. See Morphometrics in Material and Methods for details on statistical treatment of individuals with broken or missing tails.

| Males                        | N      | SVL                   | TL                    | HH                  | EOS                 | HW                  | AL                  | FAL                 | HDL                 | THL                 | SL                  | FOL                 |
|------------------------------|--------|-----------------------|-----------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| <i>T. catalanensis</i>       | 9 (5)  | 105.71 $\pm$<br>11.91 | 156.90 $\pm$<br>16.69 | 15.39 $\pm$<br>2.04 | 26.21 $\pm$<br>2.86 | 21.75 $\pm$<br>2.72 | 18.51 $\pm$<br>2.37 | 16.34 $\pm$<br>2.43 | 19.92 $\pm$<br>2.59 | 23.22 $\pm$<br>2.95 | 26.12 $\pm$<br>3.64 | 34.58 $\pm$<br>3.07 |
|                              |        | (85.53–<br>121.79)    | (138.00–<br>183.00)   | (12.22–<br>17.72)   | (21.93–<br>30.17)   | (17.27–<br>25.07)   | (14.37–<br>21.31)   | (12.76–<br>21.48)   | (14.37–<br>22.67)   | (15.11–<br>15.28)   | (18.21–<br>26.71)   | (22.05–<br>31.48)   |
| <i>T. chromatops</i>         | 2 (1)  | 91.14 $\pm$<br>1.73   | 140.97<br>140.97      | 12.87 $\pm$<br>1.02 | 21.63 $\pm$<br>1.41 | 19.04 $\pm$<br>1.21 | 15.21 $\pm$<br>1.96 | 13.04 $\pm$<br>0.93 | 15.20 $\pm$<br>0.12 | 20.87 $\pm$<br>0.49 | 18.29 $\pm$<br>0.84 | 27.65 $\pm$<br>1.03 |
|                              |        | (89.91–<br>92.36)     |                       | (12.15–<br>13.59)   | (20.63–<br>22.63)   | (18.18–<br>19.89)   | (13.82–<br>16.59)   | (12.38–<br>13.70)   | (15.11–<br>15.28)   | (20.52–<br>21.21)   | (17.69–<br>18.88)   | (17.69–<br>18.88)   |
| <i>T. cocorobensis</i>       | 11 (7) | 69.83 $\pm$<br>4.75   | 102.65 $\pm$<br>6.91  | 9.96 $\pm$<br>1.20  | 17.05 $\pm$<br>1.33 | 13.51 $\pm$<br>1.20 | 12.42 $\pm$<br>1.27 | 10.53 $\pm$<br>0.74 | 13.21 $\pm$<br>1.16 | 15.09 $\pm$<br>1.15 | 18.04 $\pm$<br>2.46 | 25.01 $\pm$<br>1.14 |
|                              |        | (61.39–<br>74.59)     | (94.44–<br>113.00)    | (8.26–<br>12.14)    | (15.37–<br>19.46)   | (11.69–<br>15.84)   | (10.77–<br>14.74)   | (9.31–<br>11.91)    | (10.99–<br>14.59)   | (13.46–<br>17.45)   | (13.46–<br>17.45)   | (13.56–<br>22.44)   |
| <i>T. sertanejo</i> , n. sp. | 5 (3)  | 70.24 $\pm$<br>9.03   | 112.83 $\pm$<br>6.54  | 9.99 $\pm$<br>1.28  | 17.83 $\pm$<br>2.63 | 14.30 $\pm$<br>2.47 | 12.08 $\pm$<br>1.98 | 10.72 $\pm$<br>1.96 | 11.68 $\pm$<br>1.08 | 14.81 $\pm$<br>2.35 | 15.95 $\pm$<br>4.08 | 20.70 $\pm$<br>2.38 |
|                              |        | (60.09–<br>79.92)     | (105.48–<br>118.00)   | (8.44–<br>11.19)    | (14.54–<br>20.03)   | (11.00–<br>16.55)   | (9.85–<br>14.17)    | (8.61–<br>12.72)    | (10.70–<br>13.45)   | (12.86–<br>18.47)   | (12.86–<br>18.47)   | (10.91–<br>19.94)   |
| <i>T. erythrocephalus</i>    | 6 (3)  | 76.22 $\pm$<br>5.97   | 120.25 $\pm$<br>19.23 | 10.52 $\pm$<br>0.67 | 19.10 $\pm$<br>0.80 | 15.64 $\pm$<br>1.33 | 12.52 $\pm$<br>1.05 | 11.44 $\pm$<br>0.66 | 13.66 $\pm$<br>1.57 | 16.60 $\pm$<br>1.26 | 18.42 $\pm$<br>1.08 | 24.17 $\pm$<br>2.18 |
|                              |        | (67.90–<br>84.20)     | (99.00–<br>136.46)    | (9.20–<br>10.99)    | (18.07–<br>20.15)   | (13.34–<br>17.46)   | (10.95–<br>13.66)   | (10.55–<br>12.48)   | (11.94–<br>16.04)   | (11.94–<br>16.04)   | (15.05–<br>18.49)   | (17.23–<br>19.55)   |
| <i>T. etheridgei</i>         | 17 (8) | 76.98 $\pm$<br>9.18   | 117.91 $\pm$<br>8.00  | 11.36 $\pm$<br>1.57 | 19.46 $\pm$<br>2.18 | 16.02 $\pm$<br>2.37 | 12.86 $\pm$<br>1.68 | 11.45 $\pm$<br>1.17 | 13.78 $\pm$<br>1.17 | 16.91 $\pm$<br>2.24 | 18.16 $\pm$<br>1.96 | 24.02 $\pm$<br>1.80 |
|                              |        | (59.23–<br>96.48)     | (103.79–<br>126.31)   | (8.58–<br>14.37)    | (15.31–<br>23.71)   | (12.00–<br>20.23)   | (9.00–<br>15.89)    | (9.48–<br>13.32)    | (10.50–<br>15.37)   | (10.50–<br>15.37)   | (13.77–<br>22.27)   | (14.46–<br>21.18)   |
| <i>T. hispidus</i>           | 6 (2)  | 103.30 $\pm$<br>10.58 | 159.00 $\pm$<br>28.28 | 14.52 $\pm$<br>1.70 | 25.91 $\pm$<br>2.83 | 21.51 $\pm$<br>2.53 | 17.86 $\pm$<br>1.62 | 16.65 $\pm$<br>1.92 | 18.58 $\pm$<br>1.84 | 22.34 $\pm$<br>2.16 | 26.84 $\pm$<br>3.61 | 30.98 $\pm$<br>2.67 |
|                              |        | (84.82–<br>104.82)    | (139.00–<br>179.00)   | (12.01–<br>16.96)   | (20.85–<br>28.47)   | (16.78–<br>23.71)   | (14.94–<br>19.31)   | (13.45–<br>18.88)   | (15.27–<br>20.77)   | (15.27–<br>20.77)   | (18.65–<br>24.74)   | (20.55–<br>30.09)   |
| <i>T. hygomi</i>             | 14 (5) | 62.36 $\pm$<br>4.02   | 101.72 $\pm$<br>8.48  | 10.49 $\pm$<br>1.19 | 16.85 $\pm$<br>1.11 | 13.45 $\pm$<br>1.06 | 10.73 $\pm$<br>1.41 | 9.93 $\pm$<br>0.81  | 13.18 $\pm$<br>0.97 | 14.47 $\pm$<br>1.48 | 18.09 $\pm$<br>2.61 | 25.86 $\pm$<br>1.99 |
|                              |        |                       |                       |                     |                     |                     |                     |                     |                     |                     |                     |                     |

| Males                  | N         | SVL                | TL                  | HH                | EOS               | HW                | AL                | FAL               | HDL               | THL               | SL                | FOL               |
|------------------------|-----------|--------------------|---------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| <i>T. imbituba</i>     | 10<br>(5) | (54.15–<br>67.30)  | (94.00–<br>116.00)  | (8.61–<br>13.28)  | (15.13–<br>18.97) | (11.74–<br>14.97) | (8.41–<br>13.06)  | (8.62–<br>11.51)  | (12.00–<br>14.96) | (12.09–<br>16.69) | (13.31–<br>21.67) | (21.91–<br>28.44) |
|                        |           | 102.87 ±<br>14.66  | 175.80 ±<br>14.46   | 14.54 ±<br>3.53   | 25.67 ±<br>4.54   | 20.78 ±<br>3.92   | 18.30 ±<br>2.59   | 15.66 ±<br>2.23   | 20.18 ±<br>2.30   | 23.31 ±<br>3.83   | 26.48 ±<br>4.41   | 34.70 ±<br>4.28   |
|                        |           | (76.00–<br>120.93) | (157.00–<br>191.00) | (9.39–<br>20.02)  | (17.83–<br>32.82) | (14.97–<br>26.56) | (13.60–<br>21.36) | (11.87–<br>19.21) | (16.08–<br>23.36) | (17.70–<br>28.66) | (19.60–<br>32.30) | (26.61–<br>40.31) |
|                        |           | 75.73 ±<br>6.92    | 104.57 ±<br>8.94    | 11.52 ±<br>1.22   | 19.01 ±<br>1.73   | 15.67 ±<br>1.41   | 13.21 ±<br>1.15   | 11.57 ±<br>1.13   | 13.30 ±<br>0.99   | 17.03 ±<br>2.12   | 19.04 ±<br>2.12   | 22.53 ±<br>1.49   |
|                        |           | (61.49–<br>86.18)  | (93.00–<br>118.00)  | (9.46–<br>13.26)  | (15.92–<br>21.67) | (12.94–<br>13.43) | (11.52–<br>15.13) | (9.83–<br>13.74)  | (11.38–<br>14.58) | (13.91–<br>20.14) | (15.18–<br>22.40) | (18.95–<br>24.29) |
| <i>T. itambere</i>     | 9 (2)     | 77.04 ±<br>7.35    | 105.73 ±<br>6.04    | 11.66 ±<br>1.48   | 19.88 ±<br>2.03   | 17.00 ±<br>1.58   | 13.39 ±<br>1.42   | 11.52 ±<br>1.22   | 14.47 ±<br>1.21   | 16.44 ±<br>1.47   | 18.14 ±<br>2.41   | 22.90 ±<br>1.75   |
|                        |           | (62.28–<br>84.77)  | (101.46–<br>110.00) | (9.15–<br>14.05)  | (16.37–<br>22.01) | (14.16–<br>19.05) | (11.23–<br>15.35) | (9.44–<br>13.19)  | (12.64–<br>16.39) | (13.72–<br>18.12) | (12.72–<br>20.04) | (20.25–<br>25.56) |
| <i>T. montanus</i>     | 4 (2)     | 86.20 ±<br>16.26   | 125.00 ±<br>31.11   | 11.93 ±<br>3.13   | 21.29 ±<br>4.49   | 17.95 ±<br>4.44   | 14.63 ±<br>2.57   | 12.18 ±<br>2.08   | 15.96 ±<br>2.58   | 19.17 ±<br>4.24   | 19.99 ±<br>4.28   | 25.79 ±<br>3.70   |
|                        |           | (62.34–<br>98.72)  | (103.00–<br>147.00) | (7.53–<br>14.25)  | (14.73–<br>24.78) | (11.55–<br>21.34) | (10.91–<br>16.68) | (9.43–<br>13.97)  | (12.45–<br>18.47) | (12.90–<br>22.05) | (12.90–<br>22.05) | (14.18–<br>23.78) |
| <i>T. mucujensis</i>   | 5 (2)     | 71.04 ±<br>3.44    | 107.50 ±<br>4.95    | 9.72 ±<br>0.32    | 17.15 ±<br>0.58   | 13.80 ±<br>1.09   | 11.24 ±<br>0.89   | 10.34 ±<br>0.56   | 12.65 ±<br>0.40   | 15.65 ±<br>0.76   | 16.78 ±<br>0.57   | 21.57 ±<br>0.68   |
|                        |           | (67.67–<br>75.32)  | (104.00–<br>111.00) | (9.30–<br>10.17)  | (16.25–<br>17.73) | (12.82–<br>15.57) | (10.04–<br>12.24) | (9.47–<br>10.79)  | (12.16–<br>13.21) | (14.78–<br>16.80) | (16.06–<br>17.35) | (20.87–<br>22.43) |
| <i>T. oreadictus</i>   | 6 (4)     | 85.80 ±<br>4.79    | 141.25 ±<br>11.09   | 12.44 ±<br>1.14   | 20.90 ±<br>1.98   | 17.79 ±<br>1.48   | 14.84 ±<br>0.88   | 12.96 ±<br>1.30   | 16.75 ±<br>1.23   | 19.37 ±<br>1.88   | 21.33 ±<br>2.34   | 26.46 ±<br>1.85   |
|                        |           | (79.02–<br>91.63)  | (127.00–<br>151.00) | (11.47–<br>14.42) | (18.83–<br>23.64) | (16.35–<br>19.86) | (13.90–<br>15.89) | (11.78–<br>14.96) | (15.48–<br>18.90) | (17.38–<br>22.14) | (17.06–<br>23.87) | (24.36–<br>29.25) |
| <i>T. psammonastes</i> | 8 (2)     | 93.34 ±<br>4.60    | 142.50 ±<br>0.71    | 14.60 ±<br>1.15   | 23.47 ±<br>0.95   | 19.51 ±<br>0.75   | 16.23 ±<br>1.57   | 14.94 ±<br>1.23   | 17.89 ±<br>0.93   | 19.56 ±<br>2.54   | 24.87 ±<br>2.72   | 32.83 ±<br>2.19   |
|                        |           | (86.57–<br>99.06)  | (142.00–<br>143.00) | (13.37–<br>16.15) | (22.10–<br>24.50) | (18.32–<br>20.47) | (13.34–<br>17.97) | (12.54–<br>16.58) | (16.74–<br>19.11) | (13.90–<br>21.76) | (19.43–<br>28.22) | (29.12–<br>35.81) |
| <i>T. torquatus</i>    | 8 (3)     | 85.65 ±<br>6.14    | 129.00 ±<br>10.00   | 13.14 ±<br>1.36   | 21.41 ±<br>1.86   | 17.11 ±<br>1.66   | 14.67 ±<br>1.43   | 13.27 ±<br>1.00   | 15.64 ±<br>1.10   | 18.39 ±<br>1.52   | 22.13 ±<br>1.54   | 27.87 ±<br>1.62   |
|                        |           | (74.40–<br>93.01)  | (119.00–<br>139.00) | (10.58–<br>14.45) | (17.60–<br>23.38) | (14.14–<br>19.02) | (13.30–<br>17.22) | (11.77–<br>14.84) | (14.08–<br>17.77) | (16.49–<br>21.33) | (19.91–<br>24.04) | (25.65–<br>30.54) |



TABLE 4. Mean  $\pm$  standard deviation, minimum and maximum values of morphometric measurements (in mm) of adult females of the *Tropidurus torquatus* species group. SVL, snout-vent length; BH, body height; HH, head height; HW, head width; EOS, ear opening-snout distance; AL, arm length; FAL, forearm length; HDL, hand length; THL, thigh length; SL, shank length; FOL, foot length; TL, tail length. The number of individuals measured followed by the number of individuals with fully grown tails. See Morphometrics in Material and Methods for details on statistical treatment of individuals with broken, regrown or missing tails.

| Females                      | N      | SVL         | TL           | HH          | EOS         | HW          | AL          | FAL         | HDL         | THL         | SL          | FOL         |
|------------------------------|--------|-------------|--------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| <i>T. catalanensis</i>       | 16 (8) | 80.04 $\pm$ | 116.76 $\pm$ | 9.88 $\pm$  | 18.62 $\pm$ | 14.95 $\pm$ | 13.27 $\pm$ | 11.27 $\pm$ | 15.45 $\pm$ | 16.75 $\pm$ | 18.45 $\pm$ | 26.15 $\pm$ |
|                              |        | 10.91       | 16.37        | 1.47        | 2.45        | 2.21        | 1.99        | 1.43        | 1.89        | 2.39        | 2.88        | 2.68        |
| <i>T. chromatops</i>         | 2 (1)  | 75.20 $\pm$ | 80.19        | 11.07 $\pm$ | 18.37 $\pm$ | 14.82 $\pm$ | 12.71 $\pm$ | 10.87 $\pm$ | 12.68 $\pm$ | 16.45 $\pm$ | 16.85 $\pm$ | 22.20 $\pm$ |
|                              |        | 3.66        |              | 0.21        | 0.16        | 0.07        | 2.42        | 0.74        | 0.47        | 0.93        | 2.90        | 0.91        |
| <i>T. cocorobensis</i>       | 4 (4)  | 62.66 $\pm$ | 85.25 $\pm$  | 7.97 $\pm$  | 14.57 $\pm$ | 11.32 $\pm$ | 11.21 $\pm$ | 9.09 $\pm$  | 12.13 $\pm$ | 12.40 $\pm$ | 15.84 $\pm$ | 21.34 $\pm$ |
|                              |        | 2.33        | 4.99         | 0.50        | 0.70        | 0.69        | 1.10        | 0.64        | 1.19        | 1.05        | 0.64        | 0.78        |
| <i>T. sertanejo</i> , n. sp. | 3 (2)  | 63.37 $\pm$ | 79.74 $\pm$  | 8.88 $\pm$  | 15.69 $\pm$ | 12.49 $\pm$ | 10.20 $\pm$ | 8.64 $\pm$  | 10.61 $\pm$ | 12.97 $\pm$ | 13.13 $\pm$ | 17.76 $\pm$ |
|                              |        | 1.72        | 4.00         | 0.12        | 0.83        | 0.41        | 0.43        | 0.32        | 0.45        | 1.32        | 2.21        | 0.43        |
| <i>T. erythrocephalus</i>    | 3 (2)  | 64.95 $\pm$ | 88.50 $\pm$  | 8.38 $\pm$  | 15.56 $\pm$ | 12.24 $\pm$ | 10.36 $\pm$ | 9.31 $\pm$  | 11.59 $\pm$ | 13.99 $\pm$ | 15.43 $\pm$ | 19.25 $\pm$ |
|                              |        | 0.91        | 3.54         | 0.30        | 0.25        | 0.27        | 0.37        | 0.24        | 0.58        | 0.53        | 0.52        | 0.40        |
| <i>T. etheridgei</i>         | 13 (6) | 67.66 $\pm$ | 92.19 $\pm$  | 9.42 $\pm$  | 16.26 $\pm$ | 13.15 $\pm$ | 11.35 $\pm$ | 10.14 $\pm$ | 12.52 $\pm$ | 13.99 $\pm$ | 15.75 $\pm$ | 21.47 $\pm$ |
|                              |        | 7.57        | 6.27         | 1.07        | 1.45        | 1.95        | 1.07        | 0.75        | 1.30        | 1.64        | 1.60        | 1.33        |
| <i>T. hispidus</i>           | 9 (5)  | 76.10 $\pm$ | 113.00 $\pm$ | 9.73 $\pm$  | 18.20 $\pm$ | 14.92 $\pm$ | 12.67 $\pm$ | 12.05 $\pm$ | 14.22 $\pm$ | 16.13 $\pm$ | 18.80 $\pm$ | 23.76 $\pm$ |
|                              |        | 11.18       | 10.05        | 1.15        | 2.16        | 1.77        | 1.92        | 1.81        | 1.74        | 2.38        | 2.46        | 2.54        |
| <i>T. hygomi</i>             | 10 (6) | 52.85 $\pm$ | 81.11 $\pm$  | 7.77 $\pm$  | 13.64 $\pm$ | 10.43 $\pm$ | 8.73 $\pm$  | 8.06 $\pm$  | 10.53 $\pm$ | 12.19 $\pm$ | 15.35 $\pm$ | 21.11 $\pm$ |
|                              |        | 4.08        | 13.72        | 0.65        | 0.79        | 0.72        | 0.68        | 0.52        | 0.61        | 0.88        | 2.65        | 0.84        |

| Females                | N     | SVL           | TL              | HH           | EOS           | HW            | AL            | FAL           | HDL           | THL           | SL            | FOL           |
|------------------------|-------|---------------|-----------------|--------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| <i>T. imbituba</i>     | 4 (3) | (48.08–60.38) | (64.00–95.46)   | (6.66–8.74)  | (12.59–14.73) | (9.45–11.50)  | (7.84–9.65)   | (7.17–8.91)   | (9.50–11.33)  | (11.06–14.13) | (12.64–22.05) | (19.57–22.11) |
|                        |       | 83.12 ± 12.07 | 113.33 ± 10.02  | 10.21 ± 1.04 | 19.31 ± 2.59  | 14.92 ± 1.60  | 14.27 ± 2.08  | 12.48 ± 1.74  | 16.72 ± 2.80  | 18.40 ± 2.47  | 20.51 ± 2.66  | 27.92 ± 2.92  |
|                        |       | (70.16–99.05) | (102.00–121.00) | (9.38–11.65) | (16.83–22.95) | (13.90–17.28) | (11.82–16.89) | (11.16–15.04) | (13.37–19.58) | (15.63–21.26) | (17.74–23.82) | (25.19–32.06) |
|                        |       | 63.82 ± 6.33  | 93.58 ± 8.77    | 8.50 ± 0.90  | 15.24 ± 1.27  | 12.49 ± 1.28  | 10.45 ± 1.45  | 9.79 ± 0.99   | 11.09 ± 1.12  | 13.19 ± 1.32  | 15.55 ± 1.76  | 18.51 ± 1.15  |
| <i>T. itambere</i>     | 4 (2) | (52.65–77.12) | (83.00–103.00)  | (6.94–9.50)  | (13.52–17.64) | (10.76–15.40) | (8.04–12.99)  | (8.01–11.23)  | (8.60–12.85)  | (11.20–14.76) | (12.26–18.07) | (16.35–20.54) |
|                        |       | 71.39 ± 8.47  | 86.50 ± 9.19    | 9.45 ± 1.64  | 17.09 ± 1.32  | 14.50 ± 0.58  | 11.36 ± 0.67  | 10.73 ± 0.54  | 12.20 ± 1.06  | 14.70 ± 1.13  | 16.42 ± 1.55  | 19.26 ± 1.58  |
|                        |       | (58.88–77.43) | (80.00–93.00)   | (7.39–10.85) | (15.14–18.07) | (13.89–15.26) | (10.77–12.29) | (9.99–11.23)  | (11.10–13.28) | (13.10–15.57) | (14.77–18.19) | (17.30–20.64) |
|                        |       | 74.71 ± 8.97  | 93.63 ± 13.26   | 9.23 ± 1.31  | 17.29 ± 1.77  | 14.40 ± 1.62  | 12.33 ± 1.26  | 10.87 ± 1.23  | 13.97 ± 1.59  | 16.23 ± 1.32  | 17.27 ± 2.23  | 22.04 ± 1.77  |
| <i>T. mucujensis</i>   | 3 (1) | (63.43–83.40) | (84.25–103.00)  | (7.84–10.71) | (15.42–19.14) | (12.32–15.80) | (11.41–14.18) | (9.58–12.54)  | (12.38–16.08) | (14.71–17.50) | (15.56–20.51) | (20.59–24.60) |
|                        |       | 60.81 ± 1.71  | 76.00           | 7.88 ± 0.36  | 14.72 ± 0.39  | 12.05 ± 0.72  | 9.84 ± 1.19   | 9.22 ± 1.07   | 10.95 ± 0.47  | 13.23 ± 1.10  | 14.22 ± 0.46  | 18.80 ± 1.21  |
|                        |       | (59.17–62.59) | (80.00–93.00)   | (7.59–8.29)  | (14.42–15.16) | (11.58–12.88) | (8.91–11.19)  | (8.36–10.41)  | (10.45–11.37) | (12.21–14.39) | (13.71–14.60) | (18.06–20.20) |
|                        |       | 71.83 ± 6.71  | 113.17 ± 12.01  | 10.07 ± 0.54 | 17.23 ± 1.30  | 14.46 ± 0.95  | 12.19 ± 1.46  | 11.61 ± 1.37  | 13.05 ± 1.62  | 15.41 ± 1.43  | 17.60 ± 1.41  | 21.91 ± 1.50  |
| <i>T. psammonastes</i> | 4 (1) | (62.28–81.75) | (97.00–127.00)  | (9.37–10.72) | (15.24–19.43) | (13.09–16.26) | (10.27–14.19) | (9.94–14.04)  | (10.38–14.85) | (13.90–17.94) | (15.65–19.39) | (19.73–24.51) |
|                        |       | 71.06 ± 7.41  | 107.00          | 8.93 ± 1.10  | 17.42 ± 1.48  | 14.17 ± 1.45  | 11.74 ± 1.39  | 11.37 ± 0.63  | 14.46 ± 1.03  | 14.85 ± 1.25  | 17.67 ± 1.81  | 25.28 ± 1.38  |
|                        |       | (61.67–79.52) | (97.00–127.00)  | (7.98–10.51) | (15.44–18.83) | (12.35–15.75) | (9.77–12.90)  | (10.60–12.04) | (12.93–15.13) | (13.20–15.98) | (15.75–20.04) | (23.54–26.91) |
|                        |       | 68.70 ± 8.65  | 91.33 ± 2.52    | 8.92 ± 1.32  | 16.51 ± 1.91  | 12.97 ± 1.39  | 11.96 ± 1.66  | 10.10 ± 1.21  | 14.16 ± 2.66  | 14.68 ± 2.22  | 17.56 ± 3.07  | 24.07 ± 3.21  |
| <i>T. torquatus</i>    | 7 (3) | (60.16–80.39) | (89.00–94.00)   | (7.69–11.00) | (14.61–19.59) | (11.50–14.97) | (10.14–14.28) | (8.73–11.76)  | (10.28–18.09) | (12.11–17.88) | (14.79–22.70) | (19.42–28.38) |
|                        |       | 60.16 ± 80.39 | 89.00 ± 94.00   | 7.69 ± 11.00 | 14.61 ± 19.59 | 11.50 ± 14.97 | 10.14 ± 14.28 | 8.73 ± 11.76  | 10.28 ± 18.09 | 12.11 ± 17.88 | 14.79 ± 22.70 | 19.42 ± 28.38 |

showed positive weights on all variables, it was interpreted as a general measure of size. Although size variation is nearly continuous among *Tropidurus* species (fig. 9), ANOVA showed a significant difference in mean body size (males:  $df = 15$ , sum sq = 6.45, mean sq = 0.43,  $F$  value = 23.31,  $p < 0.001$ ; females:  $df = 15$ , sum sq = 2.52, mean sq = 0.17,  $F$  value = 10.05,  $p < 0.001$ ). *Tropidurus sertanejo*, n. sp., differed statistically from larger species; pairwise comparisons indicated that males of the new species differ from *T. catalanensis*, *T. hispidus*, *T. imbituba*, *T. oreadicus*, *T. psammonastes*, and *T. torquatus*, while females differ from *T. catalanensis*, *T. hispidus*, and *T. imbituba* (mean body size comparisons for all species pairs shown in appendix 3).

Although MANOVA has identified statistical differences among species centroids (males:  $df = 15$ , Wilks'  $\lambda = 0.0022$ , approx.  $F = 5.7780$ ,  $df_{\text{num}} = 165$ ,  $df_{\text{den}} = 977.2494$ ,  $p < 0.001$ ; females:  $df = 15$ , Wilks'  $\lambda = 0.0031$ , approx.  $F = 4.0070$ ,  $df_{\text{num}} = 165$ ,  $df_{\text{den}} = 727.0808$ ,  $p < 0.001$ ), PCA plots showed large morphometric overlap for all species analyzed (fig. 10; table 5). The high morphological similarity was statistically confirmed by the low discrimination power of the LDA. The assignment of individuals to species using the LDA function showed 77.44% and 86.67% success rate based on males and females, respectively. These values dropped to 57.14% and 51.43% when the leave-one-out cross-validation procedure was implemented (appendices 4–5). Size-free LDA showed even lower reclassification rates, with 64.6% and 76.19% correct assignment of individuals. The cross-validation procedure resulted in 42.11% and 46.67% correct reclassifications (appendices 6–7).

These results indicate that the morphometric profile of the *T. torquatus* species group is highly conserved, and body size is an important variable promoting discrimination among species (table 5). For *T. sertanejo*, n. sp., elimination of isometric size resulted in significant decrease in reclassification success from 60% to 20% in the cross-validation LDA for males and 33% to 0% for females. Males of *T. sertanejo*, n. sp., were frequently misclassified as *T. etheridgei*, *T. hispidus*, or *T. imbituba*, and females as *T. etheridgei*, *T. erythrocephalus*, or *T. insulanus* (appendices 6–7). The size-free LDA for both sexes indicated that FOL is the most important attribute explaining differences in shape among species. However, the plots of FOL against SVL (not shown) suggest a common allometric trend for all *Tropidurus* species, except for *T. hygomi* and, to lesser degree, *T. cocorobensis*, which have feet proportionally larger with respect to body size (tables 3–4). Therefore, differences in the proportions of FOL in relation to SVL can only be used to discriminate *T. sertanejo*, n. sp., from two of the four smallest species of the *T. torquatus* group. Foot length in *T. sertanejo*, n. sp., corresponded to 26.41%–32.18% of snout-vent length in males and 26.53%–29.32% in females, while values between 32.51%–40.82% and 32.49%–34.56%, and 35.11%–48.42% and 36.01%–44.30%, were observed for males and females of *T. cocorobensis* and *T. hygomi*, respectively. Body size and foot length were useful variables distinguishing *T. sertanejo*, n. sp., from the largest and smallest species of the *T. torquatus* group, respectively, but morphometric attributes alone were insufficient to separate it from middle-sized forms of the group. Additional morphological attributes are needed to unambiguously distinguish *T. sertanejo*, n. sp., from most congeners; see “Comparison with other species.”

**MERISTICS:** All meristic variables showed continuous variation and large overlap among species (fig. 11; table 6). *Tropidurus sertanejo*, n. sp., had intermediate scale counts and overlapped all other species considerably in number of dorsals, ventrals, gulars, and midbody scales. The

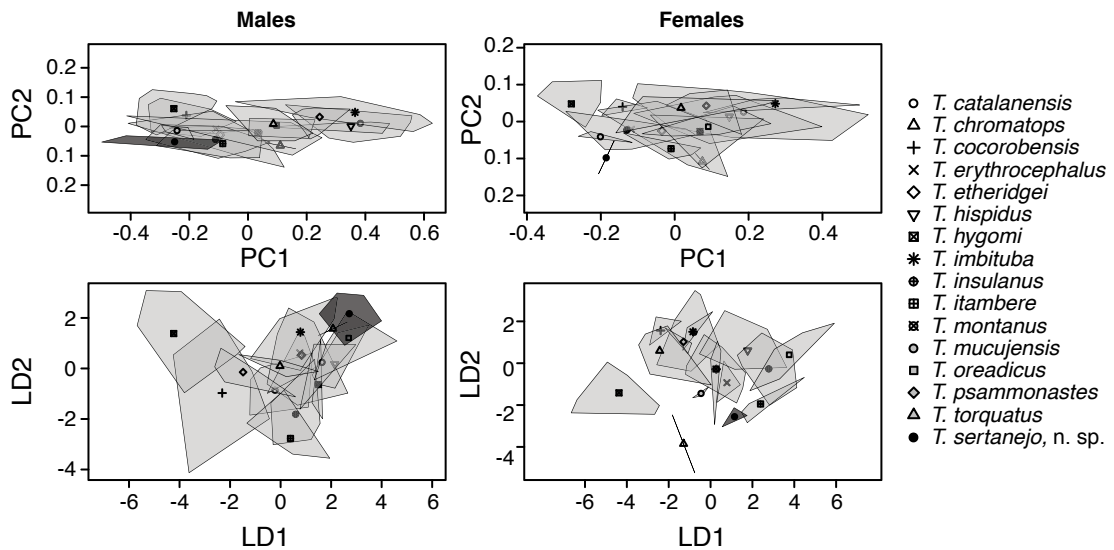


FIGURE 10. Scatterplot of PC1 and PC2 generated by the principal component analyses and LD1 and LD2 generated by the size-free discriminant analyses performed on the log-transformed morphometric variables of *Tropidurus*. *Tropidurus sertanejo*, n. sp., highlighted in dark gray. See table 5 for corresponding summary statistics.

number of tibials and subdigital lamellae on fourth toe were the only variables useful for separating *T. sertanejo*, n. sp., from other congeners. However, *T. cocorobensis*, *T. imbituba*, and *T. psammonastes* were the only species whose number of tibials or subdigital lamellae was nearly or totally nonoverlapping with *T. sertanejo*, n. sp. (fig. 11; table 6). Nonparametric MANOVA detected statistical differences in scale counts among species and between sexes, but most of the variance was explained by the former factor (table 7). The absence of interaction between species and sex allowed us to pool individuals of both sexes for the subsequent LDA. LDA confirmed that scale counts are highly similar within the *T. torquatus* group and meristic variables are not effective in separating most species. The overall reclassification success of the LDA function was 68.84%, and this value dropped to 62.61% when applying the leave-one-out cross-validation procedure. LD1 and LD2 showed large overlap among *T. sertanejo*, n. sp., and most other species, except for *T. catalanensis*, *T. cocorobensis*, *T. hygomi*, *T. imbituba*, *T. psammonastes*, and *T. torquatus* (fig. 12; table 8). The LDA function had an overall reclassification success of 42.86% for specimens of *T. sertanejo*, n. sp., and this value dropped to 38.10% when adopting the leave-one-out cross-validation procedure (appendix 8).

The number of subdigital lamellae on fourth toe had the strongest contribution on both LD1 and LD2, yet not allowing complete separation of any species in both axes. By plotting LD1 against LD2 we were able to identify two species groups that differed in number of scales. The first group included the psammophilous species *T. cocorobensis*, *T. hygomi*, and *T. psammonastes*, characterized by a higher number of subdigital lamellae in relation to the number of dorsals and ventrals. The second included all other species with a relatively lower number of subdigital lamellae. We observed that species with proportionally larger feet had higher numbers of subdigital lamellae on the fourth toe (Pearson correlation: males:  $r = 0.634$ ,  $p = 0.008$ ;



TABLE 5. Summary of the principal component analyses and size free linear discriminant analyses performed with 11 morphometric measurements of male and female *Tropidurus*. **PC**, component loadings; **LD**, discriminant coefficients, **EVL**, eigenvalues; **SD**, standard deviations; % **Variance**, percentage of explained variances.

|            | PCA males |         |         | LDA males |          |          | PC females |         |         | LDA females |          |          |
|------------|-----------|---------|---------|-----------|----------|----------|------------|---------|---------|-------------|----------|----------|
|            | PC 1      | PC 2    | PC 3    | LD 1      | LD 2     | LD 3     | PC 1       | PC 2    | PC 3    | LD 1        | LD 2     | LD 3     |
| SVL        | 0.0776    | -0.0133 | 0.0069  | 25.1473   | -24.2023 | -57.2868 | 0.0654     | -0.0140 | 0.0009  | -10.4295    | 30.8564  | 32.6393  |
| TL         | 0.0769    | 0.0114  | 0.0202  | 32.2194   | 57.2225  | 2.2264   | 0.0578     | 0.0175  | 0.0032  | 21.4519     | 13.5833  | -19.6751 |
| HH         | 0.0761    | -0.0140 | -0.0179 | 4.4342    | 15.8745  | 2.3209   | 0.0492     | -0.0248 | -0.0012 | 11.2080     | -10.7702 | -19.0909 |
| EOS        | 0.0751    | -0.0115 | -0.0002 | -16.3122  | -3.5051  | 2.4427   | 0.0556     | -0.0088 | -0.0018 | -29.2811    | -62.6398 | 15.4347  |
| HW         | 0.0805    | -0.0219 | 0.0002  | -3.7256   | -3.1726  | 29.2168  | 0.0603     | -0.0197 | -0.0024 | -0.9361     | -2.4714  | 12.6218  |
| AL         | 0.0829    | -0.0043 | 0.0019  | -3.1297   | -9.6830  | -11.4690 | 0.0680     | 0.0002  | -0.0048 | -3.0283     | 5.6695   | 9.7620   |
| FAL        | 0.0792    | -0.0021 | -0.0129 | 7.3692    | -16.3779 | 4.1252   | 0.0598     | -0.0021 | -0.0212 | 25.2093     | 5.3082   | 0.5515   |
| HDL        | 0.0738    | 0.0165  | 0.0156  | 4.5895    | -31.2816 | 19.5853  | 0.0680     | 0.0135  | 0.0194  | 7.2029      | 8.7570   | 11.4582  |
| THL        | 0.0781    | -0.0095 | 0.0104  | 6.0288    | 3.8402   | 2.2947   | 0.0620     | -0.0095 | 0.0094  | 1.7758      | -15.2921 | -5.7569  |
| SL         | 0.0797    | 0.0263  | -0.0285 | -3.6199   | 0.6071   | -5.5096  | 0.0490     | 0.0300  | -0.0266 | -11.8232    | -6.7053  | 0.9865   |
| FOL        | 0.0656    | 0.0274  | 0.0068  | -48.7706  | 6.7943   | -17.9010 | 0.0512     | 0.0217  | 0.0206  | -60.7071    | 6.3094   | 1.4817   |
| EVL        | 0.0652    | 0.0029  | 0.0022  | 5.7391    | 3.8563   | 2.3697   | 0.0381     | 0.0032  | 0.0021  | 5.9391      | 3.2744   | 2.6569   |
| SD         | 0.2553    | 0.0543  | 0.0465  | 2.3956    | 1.9638   | 1.5394   | 0.1951     | 0.0569  | 0.0456  | 2.4370      | 1.8095   | 1.6300   |
| % Variance | 86.84     | 3.93    | 2.87    | 29.63     | 19.91    | 12.24    | 78.18      | 6.64    | 4.26    | 32.75       | 18.05    | 14.65    |

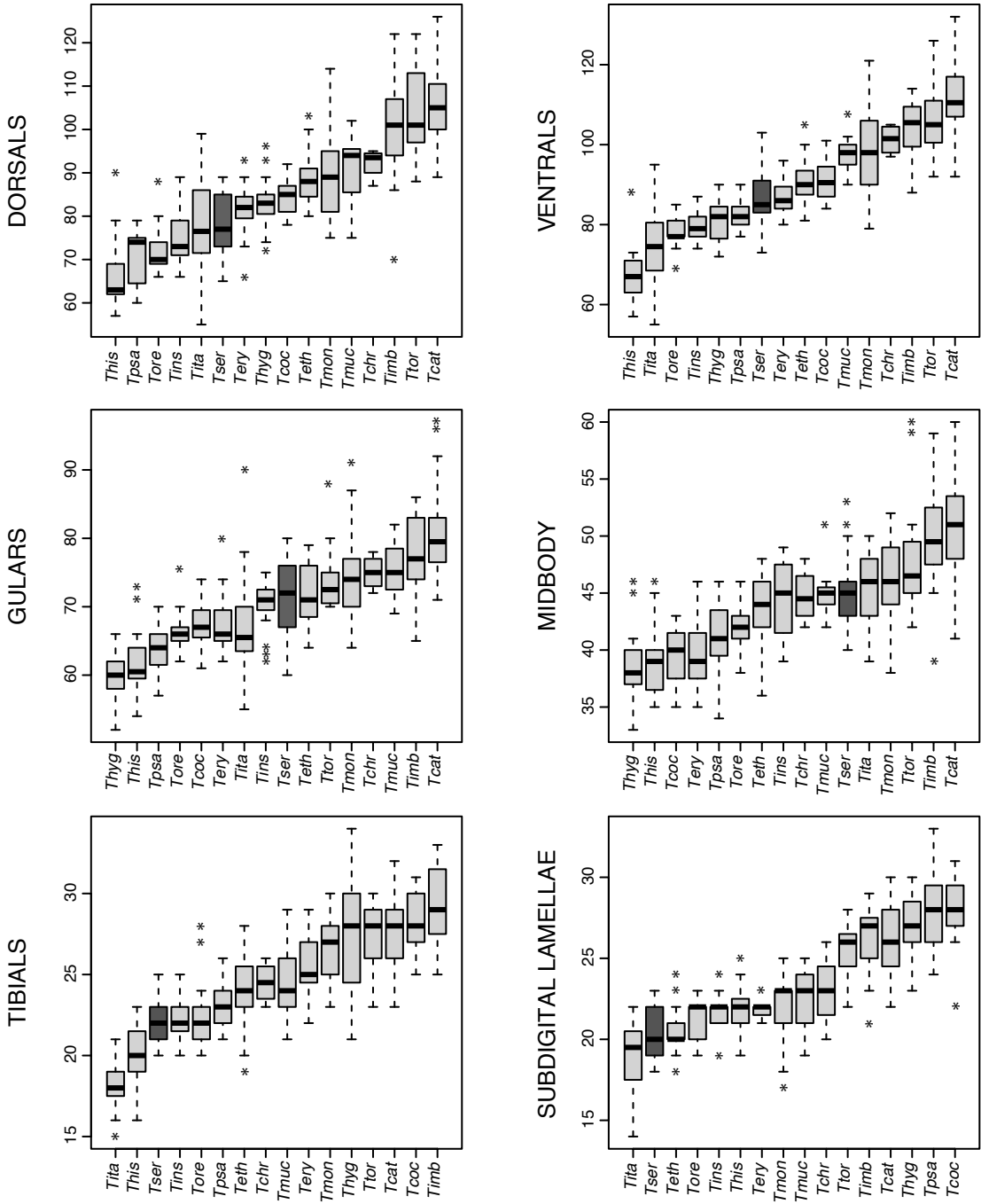


FIGURE 11. Boxplot showing variation in scale counts among *Tropidurus* species (ordinated by mean): (*Tcat*) *T. catalanensis*, (*Tchr*) *T. chromatops*, (*Tcoc*) *T. cocorobensis*, (*Tery*) *T. erythrocephalus*, (*Teth*) *T. etheridgei*, (*This*) *T. hispidus*, (*Thyg*) *T. hygomi*, (*Timb*) *T. imbituba*, (*Tins*) *T. insulanus*, (*Tita*) *T. itambere*, (*Tmon*) *T. montanus*, (*Tmuc*) *T. mucujensis*, (*Tore*) *T. oreadicus*, (*Tpsa*) *T. psammonastes*, (*Tser*) *T. sertanejo*, n. sp. (high-lighted in dark gray.), (*Ttor*) *T. torquatus*.

TABLE 6. Mean  $\pm$  standard deviation, minimum and maximum values of scale counts of males (M), females (F), and juveniles, subadults and adults whose sex could not be determined based on external morphology plus males and females (All) of the *Tropidurus torquatus* species group.

| Species                      | Sex | N  | Dorsals                       | Ventrals                     | Gulars                      | Midbody                       | Tibials                     | Subdigital lamellae         |
|------------------------------|-----|----|-------------------------------|------------------------------|-----------------------------|-------------------------------|-----------------------------|-----------------------------|
| <i>T. catalanensis</i>       | All | 80 | 111.99 $\pm$ 8.59<br>(92–132) | 80.04 $\pm$ 5.36<br>(71–97)  | 50.90 $\pm$ 4.01<br>(41–60) | 105.44 $\pm$ 8.33<br>(89–126) | 27.50 $\pm$ 1.81<br>(23–32) | 26.15 $\pm$ 1.88<br>(22–30) |
|                              | M   | 13 | 105.38 $\pm$ 4.96<br>(94–110) | 78.62 $\pm$ 3.91<br>(71–87)  | 51.15 $\pm$ 3.21<br>(46–59) | 97.38 $\pm$ 6.53<br>(89–106)  | 27.62 $\pm$ 2.14<br>(24–32) | 26.38 $\pm$ 2.10<br>(22–30) |
|                              | F   | 47 | 113.21 $\pm$ 8.48<br>(96–132) | 80.91 $\pm$ 5.91<br>(71–97)  | 50.91 $\pm$ 4.56<br>(41–60) | 107.34 $\pm$ 7.14<br>(97–126) | 27.43 $\pm$ 1.92<br>(23–31) | 25.89 $\pm$ 1.91<br>(22–30) |
| <i>T. chromatops</i>         | All | 4  | 101.25 $\pm$ 3.86<br>(97–105) | 75.00 $\pm$ 2.58<br>(72–78)  | 44.75 $\pm$ 2.50<br>(42–48) | 92.25 $\pm$ 3.59<br>(87–95)   | 24.50 $\pm$ 1.29<br>(23–26) | 23.00 $\pm$ 2.45<br>(20–26) |
|                              | M   | 2  | 101 $\pm$ 5.66<br>(97–105)    | 75.00 $\pm$ 4.24<br>(72–78)  | 45.00 $\pm$ 4.24<br>(42–48) | 91.00 $\pm$ 5.66<br>(87–95)   | 24.50 $\pm$ 2.12<br>(23–26) | 24.50 $\pm$ 2.12<br>(23–26) |
|                              | F   | 2  | 101.5 $\pm$ 3.54<br>(99–104)  | 75.00 $\pm$ 1.41<br>(74–76)  | 44.50 $\pm$ 0.71<br>(44–45) | 93.50 $\pm$ 0.71<br>(93–94)   | 24.50 $\pm$ 0.71<br>(24–25) | 21.50 $\pm$ 2.12<br>(20–23) |
| <i>T. cocorobensis</i>       | All | 16 | 91.06 $\pm$ 5.48<br>(84–101)  | 67.31 $\pm$ 3.77<br>(61–74)  | 39.50 $\pm$ 2.42<br>(35–43) | 84.50 $\pm$ 4.23<br>(78–92)   | 28.56 $\pm$ 1.90<br>(25–31) | 27.88 $\pm$ 2.13<br>(22–31) |
|                              | M   | 10 | 88.3 $\pm$ 3.47<br>(84–95)    | 66.70 $\pm$ 2.95<br>(61–71)  | 39.20 $\pm$ 2.3<br>(36–43)  | 82.20 $\pm$ 3.01<br>(78–86)   | 28.60 $\pm$ 1.78<br>(26–31) | 28.40 $\pm$ 1.26<br>(27–30) |
|                              | F   | 6  | 95.67 $\pm$ 5.28<br>(87–101)  | 68.33 $\pm$ 5.01<br>(61–74)  | 40.00 $\pm$ 2.76<br>(35–42) | 88.33 $\pm$ 3.01<br>(84–92)   | 28.5 $\pm$ 2.26<br>(25–31)  | 27.00 $\pm$ 3.03<br>(22–31) |
| <i>T. sertanejo</i> , n. sp. | All | 21 | 86.48 $\pm$ 7.78<br>(73–103)  | 71.10 $\pm$ 5.81<br>(60–80)  | 45.33 $\pm$ 3.4<br>(40–53)  | 78.38 $\pm$ 6.82<br>(65–89)   | 21.90 $\pm$ 1.37<br>(20–25) | 20.48 $\pm$ 1.72<br>(18–23) |
|                              | M   | 5  | 80.60 $\pm$ 4.28<br>(75–84)   | 68.60 $\pm$ 6.31<br>(62–76)  | 43.20 $\pm$ 2.59<br>(40–46) | 76.00 $\pm$ 3.94<br>(72–82)   | 22.00 $\pm$ 1.41<br>(21–24) | 20.00 $\pm$ 1.22<br>(19–22) |
|                              | F   | 3  | 93.33 $\pm$ 7.37<br>(85–99)   | 73.00 $\pm$ 11.27<br>(60–80) | 46.67 $\pm$ 3.06<br>(44–50) | 84.67 $\pm$ 6.66<br>(77–89)   | 23.33 $\pm$ 1.53<br>(22–25) | 21.67 $\pm$ 2.31<br>(19–23) |
| <i>T. erythrocephalus</i>    | All | 15 | 87.07 $\pm$ 4.64<br>(80–96)   | 67.67 $\pm$ 4.92<br>(62–80)  | 39.80 $\pm$ 3.14<br>(35–46) | 81.47 $\pm$ 6.32<br>(66–93)   | 25.60 $\pm$ 1.96<br>(22–29) | 21.80 $\pm$ 0.56<br>(21–23) |
|                              | M   | 6  | 83.67 $\pm$ 2.42<br>(80–86)   | 67.67 $\pm$ 3.93<br>(62–73)  | 39.33 $\pm$ 3.83<br>(35–46) | 76.17 $\pm$ 5.64<br>(66–80)   | 25.67 $\pm$ 2.16<br>(23–29) | 22.00 $\pm$ 0.63<br>(21–23) |
|                              | F   | 6  | 90.00 $\pm$ 2.97<br>(86–95)   | 66.33 $\pm$ 4.23<br>(62–74)  | 40.50 $\pm$ 2.81<br>(37–45) | 85.50 $\pm$ 3.94<br>(82–93)   | 25.83 $\pm$ 1.72<br>(24–28) | 21.67 $\pm$ 0.52<br>(21–22) |
| <i>T. etheridgei</i>         | All | 19 | 90.84 $\pm$ 5.70<br>(81–105)  | 71.63 $\pm$ 4.78<br>(64–79)  | 43.47 $\pm$ 3.81<br>(36–48) | 88.58 $\pm$ 6.28<br>(80–103)  | 24.05 $\pm$ 2.27<br>(19–28) | 20.53 $\pm$ 1.43<br>(18–24) |
|                              | M   | 8  | 90.12 $\pm$ 4.85<br>(85–100)  | 73.62 $\pm$ 5.07<br>(67–79)  | 44.62 $\pm$ 3.38<br>(38–48) | 87.88 $\pm$ 5.57<br>(81–100)  | 24.00 $\pm$ 1.07<br>(23–26) | 20.88 $\pm$ 1.36<br>(19–23) |
|                              | F   | 7  | 92.71 $\pm$ 7.78<br>(81–105)  | 71.57 $\pm$ 3.60<br>(67–77)  | 43.14 $\pm$ 5.11<br>(36–48) | 89.86 $\pm$ 8.47<br>(80–103)  | 24.86 $\pm$ 2.79<br>(20–28) | 20.57 $\pm$ 1.62<br>(19–24) |
| <i>T. hispidus</i>           | All | 20 | 67.95 $\pm$ 6.61<br>(57–88)   | 61.85 $\pm$ 4.70<br>(54–73)  | 38.85 $\pm$ 2.85<br>(35–46) | 65.80 $\pm$ 7.68<br>(57–90)   | 20.30 $\pm$ 1.81<br>(16–23) | 21.75 $\pm$ 1.48<br>(19–25) |
|                              | M   | 7  | 66.57 $\pm$ 5.38<br>(57–72)   | 60.71 $\pm$ 2.81<br>(57–66)  | 37.29 $\pm$ 1.80<br>(35–40) | 61.86 $\pm$ 3.34<br>(57–66)   | 20.14 $\pm$ 1.77<br>(18–23) | 22.00 $\pm$ 1.91<br>(19–25) |
|                              | F   | 10 | 69.20 $\pm$ 7.90<br>(60–88)   | 62.60 $\pm$ 6.19<br>(54–73)  | 40.30 $\pm$ 3.13<br>(36–46) | 70.10 $\pm$ 8.63<br>(62–90)   | 20.30 $\pm$ 1.95<br>(16–23) | 21.50 $\pm$ 1.18<br>(19–23) |
| <i>T. hygomi</i>             | All | 23 | 80.78 $\pm$ 4.88<br>(72–90)   | 59.74 $\pm$ 3.60<br>(52–66)  | 38.39 $\pm$ 3.07<br>(33–46) | 83.00 $\pm$ 5.61<br>(72–96)   | 27.35 $\pm$ 3.32<br>(21–34) | 27.17 $\pm$ 1.77<br>(23–30) |
|                              | M   | 11 | 81.27 $\pm$ 4.71<br>(72–88)   | 60.91 $\pm$ 3.21<br>(54–66)  | 38.73 $\pm$ 3.20<br>(34–46) | 79.00 $\pm$ 3.77<br>(72–84)   | 28.55 $\pm$ 3.42<br>(23–34) | 27.64 $\pm$ 2.06<br>(23–30) |
|                              | F   | 8  | 81.38 $\pm$ 5.63<br>(75–90)   | 58.75 $\pm$ 3.81<br>(52–63)  | 38.00 $\pm$ 3.78<br>(33–45) | 88.00 $\pm$ 4.84<br>(81–96)   | 26.88 $\pm$ 3.31<br>(21–30) | 27.25 $\pm$ 1.39<br>(26–30) |

| Species                | Sex | N  | Dorsals                    | Ventrals                | Gulars                  | Midbody                    | Tibials                 | Subdigital lamellae     |
|------------------------|-----|----|----------------------------|-------------------------|-------------------------|----------------------------|-------------------------|-------------------------|
| <i>T. imbituba</i>     | All | 16 | 103.81 ± 7.12<br>(88–114)  | 77.75 ± 6.17<br>(65–86) | 50.06 ± 4.93<br>(39–59) | 99.19 ± 11.60<br>(70–122)  | 29.31 ± 2.57<br>(25–33) | 26.12 ± 2.13<br>(21–29) |
|                        | M   | 10 | 103.40 ± 5.66<br>(93–110)  | 78.90 ± 5.22<br>(69–86) | 50.00 ± 3.43<br>(45–57) | 96.80 ± 6.05<br>(86–106)   | 29.30 ± 2.67<br>(25–33) | 26.60 ± 1.65<br>(24–29) |
|                        | F   | 4  | 107.75 ± 6.85<br>(98–114)  | 79.5 ± 5.92<br>(73–85)  | 50.75 ± 4.27<br>(46–56) | 110.25 ± 8.42<br>(102–122) | 29.25 ± 2.75<br>(26–32) | 26.00 ± 2.16<br>(23–28) |
| <i>T. insulanus</i>    | All | 23 | 79.74 ± 3.76<br>(74–87)    | 70.30 ± 3.47<br>(62–75) | 44.43 ± 3.20<br>(39–49) | 74.96 ± 5.79<br>(66–89)    | 22.00 ± 1.28<br>(20–25) | 21.65 ± 1.34<br>(19–24) |
|                        | M   | 11 | 78.27 ± 2.49<br>(74–82)    | 70.45 ± 3.30<br>(63–75) | 45.55 ± 3.47<br>(40–49) | 71.09 ± 2.70<br>(66–76)    | 21.55 ± 0.93<br>(20–23) | 21.64 ± 1.29<br>(19–24) |
|                        | F   | 9  | 81.44 ± 3.88<br>(75–87)    | 71.11 ± 3.18<br>(64–75) | 44.33 ± 2.35<br>(41–48) | 79.00 ± 6.14<br>(71–89)    | 23.00 ± 1.00<br>(22–25) | 22.33 ± 0.71<br>(22–24) |
| <i>T. itambere</i>     | All | 16 | 74.62 ± 9.51<br>(55–95)    | 67.69 ± 7.88<br>(55–90) | 45.38 ± 3.24<br>(39–50) | 78.00 ± 10.34<br>(55–99)   | 18.25 ± 1.57<br>(15–21) | 19.00 ± 2.13<br>(14–22) |
|                        | M   | 9  | 70.56 ± 7.37<br>(55–80)    | 65.11 ± 4.43<br>(55–70) | 45.11 ± 3.82<br>(39–50) | 75.56 ± 10.24<br>(55–89)   | 18.22 ± 1.64<br>(15–21) | 19.11 ± 1.54<br>(17–21) |
|                        | F   | 4  | 86.00 ± 6.38<br>(81–95)    | 77.50 ± 9.00<br>(70–90) | 47.00 ± 1.83<br>(45–49) | 88.25 ± 7.46<br>(82–99)    | 19.00 ± 1.41<br>(18–21) | 20.50 ± 1.29<br>(19–22) |
| <i>T. montanus</i>     | All | 29 | 98.28 ± 10.70<br>(79–121)  | 74.10 ± 6.45<br>(64–91) | 46.24 ± 3.75<br>(38–52) | 89.28 ± 9.27<br>(75–114)   | 26.59 ± 1.80<br>(23–30) | 22.14 ± 1.87<br>(17–25) |
|                        | M   | 5  | 94.40 ± 8.41<br>(89–109)   | 72.00 ± 4.85<br>(64–76) | 46.40 ± 2.07<br>(44–49) | 83.40 ± 3.78<br>(80–89)    | 27.80 ± 1.92<br>(25–30) | 23.00 ± 1.22<br>(22–25) |
|                        | F   | 16 | 99.44 ± 11.34<br>(79–119)  | 75.75 ± 7.43<br>(66–91) | 46.25 ± 4.36<br>(38–52) | 92.06 ± 10.32<br>(77–114)  | 26.69 ± 1.66<br>(23–30) | 21.81 ± 1.72<br>(18–25) |
| <i>T. mucujensis</i>   | All | 15 | 97.6 ± 4.72<br>(90–108)    | 75.53 ± 3.83<br>(69–82) | 45.00 ± 2.04<br>(42–51) | 90.33 ± 7.76<br>(75–102)   | 24.80 ± 2.37<br>(21–29) | 22.53 ± 1.88<br>(19–25) |
|                        | M   | 5  | 96.80 ± 4.55<br>(90–102)   | 75.40 ± 5.22<br>(69–82) | 45.60 ± 3.29<br>(43–51) | 84.20 ± 7.19<br>(75–94)    | 25.80 ± 2.95<br>(21–29) | 22.20 ± 2.77<br>(19–25) |
|                        | F   | 3  | 99.33 ± 2.08<br>(97–101)   | 75.67 ± 2.08<br>(74–78) | 43.67 ± 1.53<br>(42–45) | 92.00 ± 9.17<br>(82–100)   | 22.67 ± 0.58<br>(22–23) | 22.33 ± 2.31<br>(21–25) |
| <i>T. oreadicus</i>    | All | 13 | 78.15 ± 4.02<br>(69–85)    | 66.46 ± 3.60<br>(62–76) | 42.00 ± 2.04<br>(38–46) | 72.38 ± 6.09<br>(66–88)    | 22.62 ± 2.53<br>(20–28) | 21.31 ± 1.18<br>(19–23) |
|                        | M   | 5  | 75.80 ± 4.76<br>(69–82)    | 65.20 ± 2.17<br>(62–68) | 42.00 ± 1.58<br>(40–44) | 69.40 ± 2.19<br>(66–72)    | 23.20 ± 2.28<br>(21–27) | 21.00 ± 1.41<br>(19–22) |
|                        | F   | 6  | 79.17 ± 2.04<br>(77–82)    | 67.83 ± 4.79<br>(62–76) | 42.50 ± 2.59<br>(38–46) | 74.33 ± 7.50<br>(68–88)    | 21.83 ± 3.13<br>(20–28) | 21.33 ± 1.21<br>(20–23) |
| <i>T. psammonastes</i> | All | 11 | 82.55 ± 3.78<br>(77–90)    | 63.73 ± 40<br>(57–70)   | 41.18 ± 3.43<br>(34–46) | 70.27 ± 6.57<br>(60–79)    | 23.36 ± 1.63<br>(21–26) | 27.73 ± 2.80<br>(24–33) |
|                        | M   | 6  | 82.50 ± 1.87<br>(80–85)    | 63.50 ± 3.33<br>(58–68) | 40.17 ± 3.66<br>(34–45) | 65.50 ± 4.76<br>(60–74)    | 23.67 ± 2.07<br>(21–26) | 29.50 ± 2.26<br>(26–33) |
|                        | F   | 3  | 85.33 ± 5.69<br>(79–90)    | 64.00 ± 6.56<br>(57–70) | 42.00 ± 3.00<br>(39–45) | 76.67 ± 2.52<br>(74–79)    | 23.33 ± 1.15<br>(22–24) | 24.67 ± 1.15<br>(24–26) |
| <i>T. torquatus</i>    | All | 16 | 106.19 ± 8.77<br>(92–126)  | 73.94 ± 4.81<br>(70–88) | 47.88 ± 5.18<br>(42–60) | 104.00 ± 9.99<br>(88–122)  | 27.38 ± 1.86<br>(23–30) | 25.50 ± 1.59<br>(22–28) |
|                        | M   | 7  | 99.57 ± 4.86<br>(92–108)   | 71.71 ± 2.06<br>(70–75) | 44.86 ± 2.27<br>(42–48) | 95.86 ± 4.95<br>(88–101)   | 27.00 ± 1.29<br>(26–29) | 25.00 ± 1.15<br>(23–26) |
|                        | F   | 7  | 112.71 ± 7.83<br>(104–126) | 77.14 ± 5.64<br>(71–88) | 51.57 ± 5.77<br>(45–60) | 110.71 ± 8.08<br>(97–122)  | 28.57 ± 1.27<br>(26–30) | 26.00 ± 1.91<br>(22–28) |



females:  $r = 0.509$ ,  $p = 0.044$ ). Positive associations between body size and other meristic variables were similarly expected, but we failed to find significant correlations between SVL and number of dorsal, ventral, gular, and midbody scales. These results are in agreement with our previous observations that SVL and scales counts lack consistent correlation within species (results not shown), suggesting that the number of scales is determined from birth and shows no significant ontogenetic, static, or interspecific allometric trends. Although meristic variables are commonly used to distinguish lizard species, our results showed that we cannot rely on scale counts to separate *T. sertanejo*, n. sp., from most species of the *T. torquatus* group.

**ETYMOLOGY:** The species name, *sertanejo*, is to be treated as an indeclinable word. In Portuguese, *sertanejo* is an adjective that alludes to interior or rural areas. It is also used as a noun to refer to the people born in the *sertão*. In current times, the term *sertão* is mostly used to refer to the dry areas of northeastern Brazil dominated by the Caatinga biome, where *T. sertanejo*, n. sp., occurs. Naming *T. sertanejo*, n. sp., we aim to honor all men and women who bravely thrive in the historically neglected semiarid Brazilian Caatinga.

**GEOGRAPHIC DISTRIBUTION AND CONSERVATION STATUS:** *Tropidurus sertanejo*, n. sp., is endemic to the semiarid Brazilian Caatinga and known exclusively from two localities in the State of Bahia, northeastern Brazil. The first is the RPPN Fazenda Pé da Serra, Serra do Arame, Municipality of Ibotirama, a private natural reserve located in the western portion of the state. The second is the Municipality of Caetité, approximately 150 km south of Ibotirama (fig. 3). Although *Tropidurus sertanejo*, n. sp., has part of its distribution covered by a small protected area (total area of the RPPN Fazenda Pé da Serra: 12.59 km<sup>2</sup>; Portaria IBAMA 60-92/N), the fact that only one additional (disjunct) population is known from Caetité represents a critical conservation issue. However, since actual distribution limits, population size, and local abundance of *T. sertanejo*, n. sp., are unknown, the data currently available allow us to recommend its classification only as “data deficient” according to the criteria proposed by IUCN (2001). In addition to confirming the unique identity of the Caatinga herpetofauna (Rodrigues, 2003; Rodrigues et al., 2003; Carvalho et al., 2013; Guedes et al., 2014), the discovery of *T. sertanejo*, n. sp., calls attention to the need of extensive mapping of lizard populations within the biome. It also corroborates the existence of higher taxonomic diversity in *Tropidurus* (Carvalho, 2013), and makes clear that besides cryptic species even easily diagnosable taxa still remain to be described in this group (A.L.G. Carvalho, unpublished data; M.A. Sena, unpublished data).

**ECOLOGICAL REMARKS:** At the RPPN Fazenda Pé da Serra, Municipality of Ibotirama, *T. sertanejo*, n. sp., occurs in syntopy with *T. pinima* and *T. hispidus*, although these species exhibit distinct spatial niches and have not been observed using the same microhabitats. With a common behavior found among species of the *T. semitaeniatus* group, *T. pinima* was observed using rock crevices in large rock outcrops. Several individuals, including up to five juveniles, were seen basking on the same rock surfaces. *Tropidurus hispidus* was observed exclusively around an artificial dam inside the RPPN Fazenda Pé da Serra, and seemed limited to rocks and concrete structures in the area. The distribution of this species in the region is apparently limited to human-modified areas, and it remains unclear whether its occurrence is opportunistic or

TABLE 7. Summary of the results of the nonparametric MANOVA performed on six meristic variables of *Tropidurus*.

|               | <i>df</i> | SSq         | MS        | $F_{\text{model}}$ | $R^2$  | <i>p</i> |
|---------------|-----------|-------------|-----------|--------------------|--------|----------|
| Species       | 15        | 147408.3479 | 9827.2232 | 69.9178            | 0.7395 | < 0.001  |
| Sex           | 2         | 6376.6231   | 3188.3115 | 22.6839            | 0.0320 | < 0.001  |
| Species : Sex | 28        | 4638.2541   | 165.6519  | 1.1786             | 0.0233 | 0.2197   |
| Residuals     | 291       | 40901.1725  | 140.5539  |                    | 0.2052 |          |
| Total         | 336       | 199324.3976 |           |                    | 1      |          |

the species is established in localities apart from those sampled during our visits to the reserve. Several adult males and females were observed basking on the walls of the dam, and hiding in cracks or underneath concrete structures during the hottest periods of the day. A few meters south of the main river that crosses the RPPN Fazenda Pé da Serra, we observed *T. sertanejo*, n. sp., using small to middle-sized rocks (~40–120 cm) on trails that cut through sandy areas covered with dry forests and caatingas (fig. 2). The local distribution of the new species seems to be determined by the presence of both rocks on sandy soils, rather than each of these elements individually. *Tropidurus sertanejo*, n. sp., was never observed using branches or tree trunks, but we confirmed it uses holes underneath rocks as shelters. As we approached the lizards, they fled to the surrounding bushes and remained motionless on the leaf litter where their coloration served as camouflage. When threatened, they also fled to their shelters and hid for a few minutes until returning to their original location on the rocks. In general, the lizards returned to the very same rocks even after being approached several times, which suggests that they defend their territories and have small home ranges of a few square meters. *Tropidurus sertanejo*, n. sp., is diurnal and active individuals were observed until sunset (approximately 6 P.M.). Nothing is known about its diet. The large extension of the natural landscapes suggests that *T. sertanejo*, n. sp., occurs in contiguous areas along the Serra do Arame. However, additional fieldwork is needed to determine its actual distribution limits and ecological requirements at the type locality. Specimens of *T. sertanejo*, n. sp., from Caetité were active on rocky outcrops emerging from a wide plateau of white sands covered by dense thickets of low vegetation. Cactaceae, Bromeliaceae, Velloziaceae, and Euphorbiaceae compose the dominant plant cover at the rocky areas. When approached, lizards took refuge in rock crevices among the vegetation. The species is sympatric but never syntopic with a still undescribed species of *Eurolophosaurus* (see Passoni et al., 2008) and with another relative of the *T. torquatus* group preliminarily identified as *T. aff. etheridgei*. The latter two species were never observed on rocks. They occupy exclusively the adjacent sandy soil areas, moving among thickets of vegetation separated by variable extensions of bare sand.

## PHYLOGENETICS

**ALIGNMENT AND PARTITIONING:** Alignments of four mitochondrial and six nuclear loci included 19–28 species (69%–100%), with average taxon coverage of 25.9 terminals (92.5%).

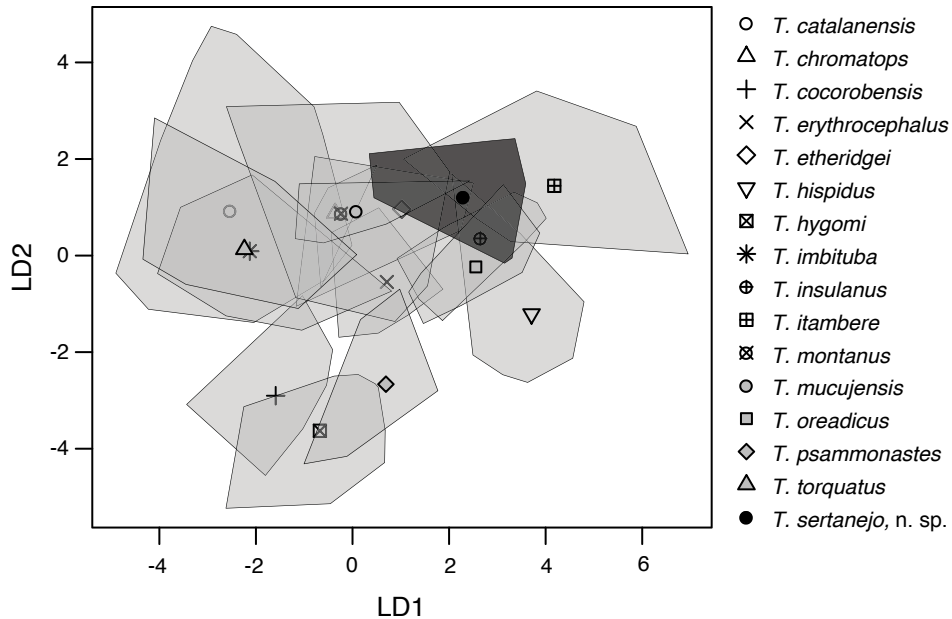


FIGURE 12. Scatterplot of LD1 and LD2 generated by the discriminant analysis performed on the scale counts of *Tropidurus*. See table 8 for corresponding summary statistics. *Tropidurus sertanejo*, n. sp., highlighted in dark gray.

Number of aligned sites varied from 477–1211 per locus, summing up to 7098 characters. Of those, 4977 were conserved among all species, 2078 were variable, and 1159 were parsimony informative; singletons totaled 917 sites (table 9). The proportion of parsimony-informative sites over the total number of aligned sites varied from 19.78%–32.32% to 4.93%–21.10% among mitochondrial and nuclear loci, respectively. Numbers of parsimony-informative characters were up to 6.5 times higher in mitochondrial loci when compared with nuclear fragments.

BIC analyses favored five distinct partitions of the mitochondrial and nuclear data sets, and 10 partitions of the total evidence data set. The number of models of nucleotide evolution selected varied from three to seven depending on the data set. In total, the models summed up 80, 90, and 118 parameters employed in subsequent ML analyses of the nuclear, mitochondrial, and total evidence data sets. Parameters relative to partition schemes and models of nucleotide evolution selected are shown in table 10.

**PHYLOGENETIC RESULTS:** MP and ML phylogenetic analyses consistently placed *Uranoscodon superciliosus* as sister taxon of all tropidurines, and more internally the trans-Andean *Microlophus quadrivattatus* was recovered as the sister taxon of the remaining cis-Andean tropidurine species. *Plica plica* was placed as closely related to *Tropidurus spinulosus* in all MP and ML trees, rendering a paraphyletic *Tropidurus* (figs. 13–15).

*Tropidurus semitaeniatus* was highly supported as sister taxon of a monophyletic *T. torquatus* species group. Within this group, *T. hygomi* formed the sister clade of all other species in nuclear and total evidence trees. Mitochondrial analyses placed this species either as closely

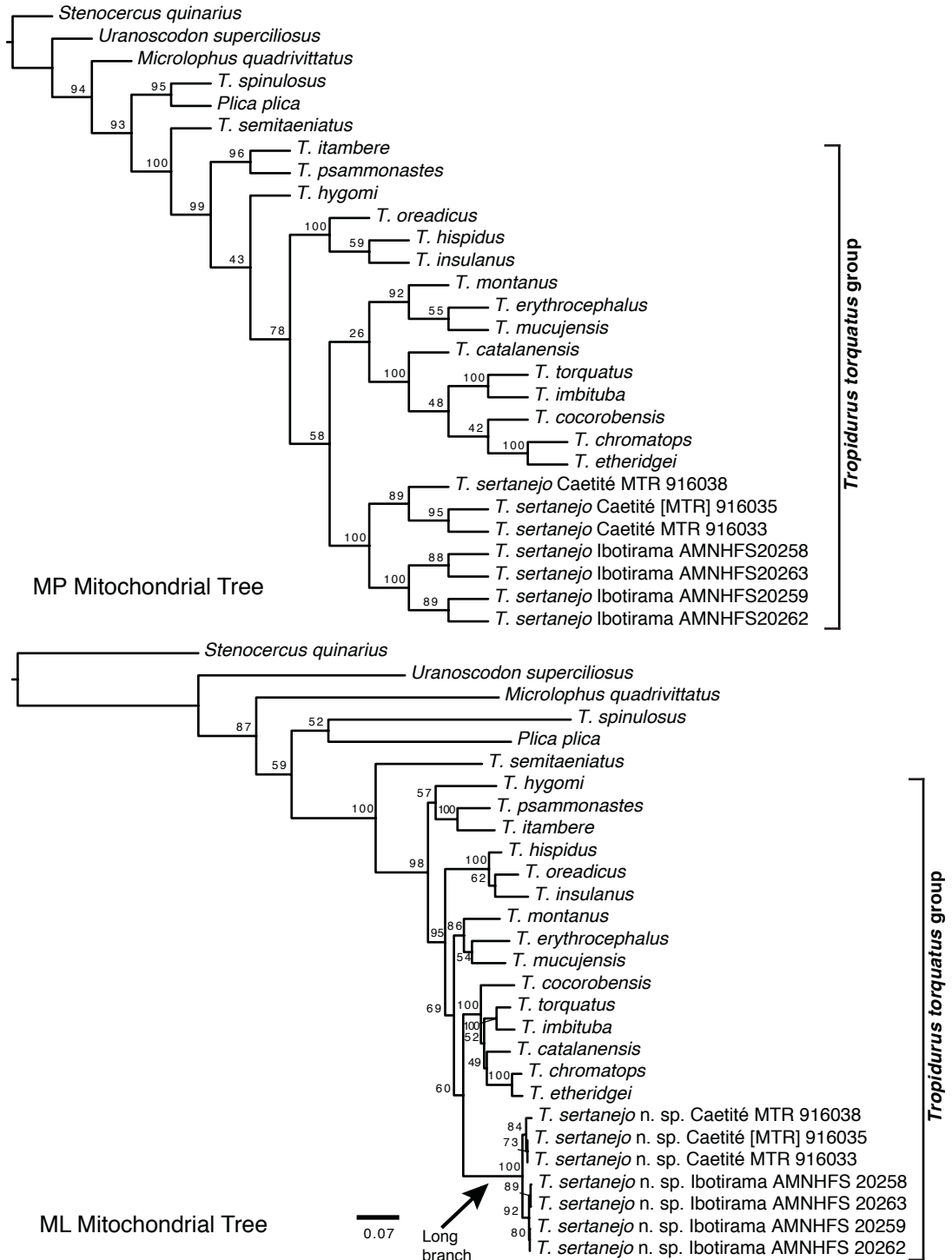


FIGURE 13. Maximum parsimony (upper) and maximum likelihood trees (lower) of *Tropidurus* based on four mitochondrial (12S, 16S, CO1, Cyt b) loci. Numbers associated to nodes refer to bootstrap values.

TABLE 8. Summary of the LDA performed on six meristic variables of *Tropidurus*. **LD**, discriminant coefficients; **EVL**, eigenvalues; **SD**, standard deviations; % **Variance**, percentage of explained variances.

|                     | LD1     | LD2     | LD3     | LD4     | LD5     | LD6     |
|---------------------|---------|---------|---------|---------|---------|---------|
| Dorsals             | -0.0813 | 0.0400  | 0.0264  | 0.1242  | 0.1074  | 0.0961  |
| Ventrals            | 0.0430  | 0.0778  | 0.0036  | 0.0786  | -0.0601 | -0.2210 |
| Gular               | 0.0417  | 0.1068  | -0.1780 | -0.0650 | -0.1857 | 0.1839  |
| Midbody             | -0.0397 | 0.0026  | 0.0031  | -0.1602 | 0.0189  | -0.0521 |
| Tibial              | -0.2078 | -0.1278 | 0.3413  | -0.0139 | -0.3213 | 0.0384  |
| Subdigital lamellae | -0.1996 | -0.3432 | -0.4017 | 0.0757  | 0.0279  | -0.1206 |
| EVL                 | 10.5316 | 7.0268  | 3.7192  | 2.7338  | 1.7817  | 1.1451  |
| SD                  | 3.2453  | 2.6508  | 1.9285  | 1.6534  | 1.3348  | 1.0701  |
| % Variance          | 39.10   | 26.08   | 13.81   | 10.15   | 6.61    | 4.25    |

related to *T. itambere* + *T. psammonastes* (ML tree) or as sister of all species of the *T. torquatus* group but *T. itambere* + *T. psammonastes* (MP tree).

Mitochondrial, nuclear, and total evidence trees conflicted with respect to the relationships of several taxa, including *T. sertanejo*, n. sp. The first incongruence concerns the placement of *T. hispidus*, *T. insulanus*, and *T. oreadicus*. Although these species have always formed a well-supported monophyletic group, *T. hispidus* + *T. insulanus* were recovered in a more derived position (in relation to *T. oreadicus*) in MP mitochondrial and total evidence analyses, whereas *T. oreadicus* + *T. insulanus* occupied that same position (in relation to *T. hispidus*) in ML mitochondrial and total evidence topologies. Nuclear trees either placed the three species in a polytomy (MP tree) or supported *T. insulanus* as the sister taxon of *T. hispidus* + *T. oreadicus* (ML tree) (figs. 13–15).

The second incongruence in topological arrangement involves the placement of *T. montanus* as sister species of *T. mucujensis* + *T. erythrocephalus* in all mitochondrial and total evidence trees, but recovered as closely related to (*T. torquatus*, (*T. chromatops* + *T. etheridgei*), (*T. catalanensis* + *T. imbituba*)) in MP and ML nuclear trees (figs. 13–15). Labile phylogenetic placement was also observed for *T. cocorobensis*. This species was recovered as closely related to *T. chromatops* + *T. etheridgei* in the MP mitochondrial tree ((*T. torquatus* + *T. imbituba*) (*T. catalanensis* (*T. chromatops* + *T. etheridgei*))) in ML mitochondrial and total evidence trees, as sister species of *T. sertanejo*, n. sp., in MP and ML nuclear trees, and, finally, as the sister of the clade (*T. catalanensis* ((*T. chromatops* + *T. etheridgei*) (*T. imbituba* + *T. torquatus*))) in the MP total evidence tree (figs. 13–15).

In all analyses, individuals of *T. sertanejo*, n. sp., clustered together forming a highly supported monophyletic group, however, the phylogenetic affinities of the species itself were conflicting. The new species was recovered in MP and ML nuclear trees as the sister taxon of *T. cocorobensis*, but placed as sister of the clade formed by (*T. cocorobensis* (*T. catalanensis* ((*T. chromatops* + *T. etheridgei*) (*T. torquatus* + *T. imbituba*)))) and (*T. cocorobensis* ((*T. torquatus* + *T. imbituba*) ((*T. catalanensis* (*T. chromatops* + *T. etheridgei*)))))) in MP and ML total evidence analysis, respectively; and by ((*T. montanus* (*T. erythrocephalus* + *T. mucujensis*)) ((*T. catalanensis* (*T. torquatus* + *T. imbituba*) (*T. cocorobensis* (*T. chromatops* + *T. etheridgei*)))))) and (*T.*



TABLE 9. Taxon coverage, number of aligned, conserved, variable, parsimony informative sites and singletons present in the alignment of mitochondrial and nuclear loci.

| Loci         | Genome        | Taxon coverage (%) | Sites       | Conserved   | Variable    | PI          | Singletons |
|--------------|---------------|--------------------|-------------|-------------|-------------|-------------|------------|
| 12S          | Mitochondrial | 28 (100)           | 880         | 509         | 339         | 212         | 125        |
| 16S          | Mitochondrial | 28 (100)           | 551         | 385         | 161         | 109         | 52         |
| CO1          | Mitochondrial | 21 (75)            | 662         | 415         | 247         | 214         | 33         |
| Cyt b        | Mitochondrial | 27 (96)            | 756         | 418         | 338         | 237         | 101        |
| BACH1        | Nuclear       | 25 (89)            | 1211        | 941         | 270         | 98          | 172        |
| kif24        | Nuclear       | 28 (100)           | 545         | 331         | 214         | 115         | 99         |
| NTF3         | Nuclear       | 19 (69)            | 670         | 578         | 92          | 33          | 59         |
| PRLR         | Nuclear       | 28 (100)           | 525         | 355         | 167         | 62          | 105        |
| PTPN         | Nuclear       | 27 (96)            | 821         | 664         | 154         | 49          | 105        |
| SNCAIP       | Nuclear       | 28 (100)           | 477         | 381         | 96          | 30          | 66         |
| <b>TOTAL</b> |               |                    | <b>7098</b> | <b>4977</b> | <b>2078</b> | <b>1159</b> | <b>917</b> |

*cocorobensis* ((*T. torquatus* + *T. imbituba*) (*T. catalanensis* (*T. chromatops* + *T. etheridgei*))) in MP and ML mitochondrial analyses.

**TOTAL EVIDENCE AND TOPOLOGICAL CONFLICT:** Inasmuch as separate analyses were useful for understanding differences and inferring the sources of topological conflict (Nixon and Carpenter, 1996; Peloso et al., 2015; but see Grant and Kluge, 2003, and Fitzhugh, 2006, for a critique on this kind of data exploration), we favored the phylogenetic hypotheses based on the analyses of our concatenated data set following the principle of character congruence or total evidence (Carnap, 1950, who credited much earlier workers; subsequently championed by others including Kluge, 1989; Rieppel, 2005, and Fitzhugh, 2006). The ML total evidence tree was preferred as the best hypothesis representing the phylogenetic relationships of tropidurines (fig. 15).<sup>8</sup> This decision was based on the fact that ML analyses incorporate models of nucleotide evolution that account for heterogeneous rates of nucleotide substitution within and among loci, and also alleviate the detrimental effects of multiple substitutions affecting phylogenetic reconstruction and branch-length estimation (Felsenstein, 2004; Gadagkar and Kumar, 2005; but see Padial et al., 2014, and Peloso et al., 2015, for alternative views).

The observation that trees generated by independent analyses of nuclear and mitochondrial sequence data conflicted with our total evidence hypotheses caught our attention. In a model-based framework, the topological incongruities noted in the previous section of this study might result from at least one of the following factors: misspecification of models of nucleotide evolution (Lemmon and Moriarty, 2004), inadequate determination of partition schemes (Brown and Lemmon, 2007; Lanfear et al., 2012), or conflicting phylogenetic signal in mitochondrial versus nuclear loci (Leaché and McGuire, 2006; Leaché, 2010; Leaché et al. 2013, 2014). However, since topological disagreements were detected among phylogenetic trees

<sup>8</sup> The choice of a preferred optimality criteria is very much dependent on the investigators theoretical and philosophical backgrounds, but is also based on a few practical assumptions. Inasmuch as there is some divergence of opinion among authors regarding what should be the *preferred* method of inference, we came down to a decision to endorse this view even if not in complete accordance with it.

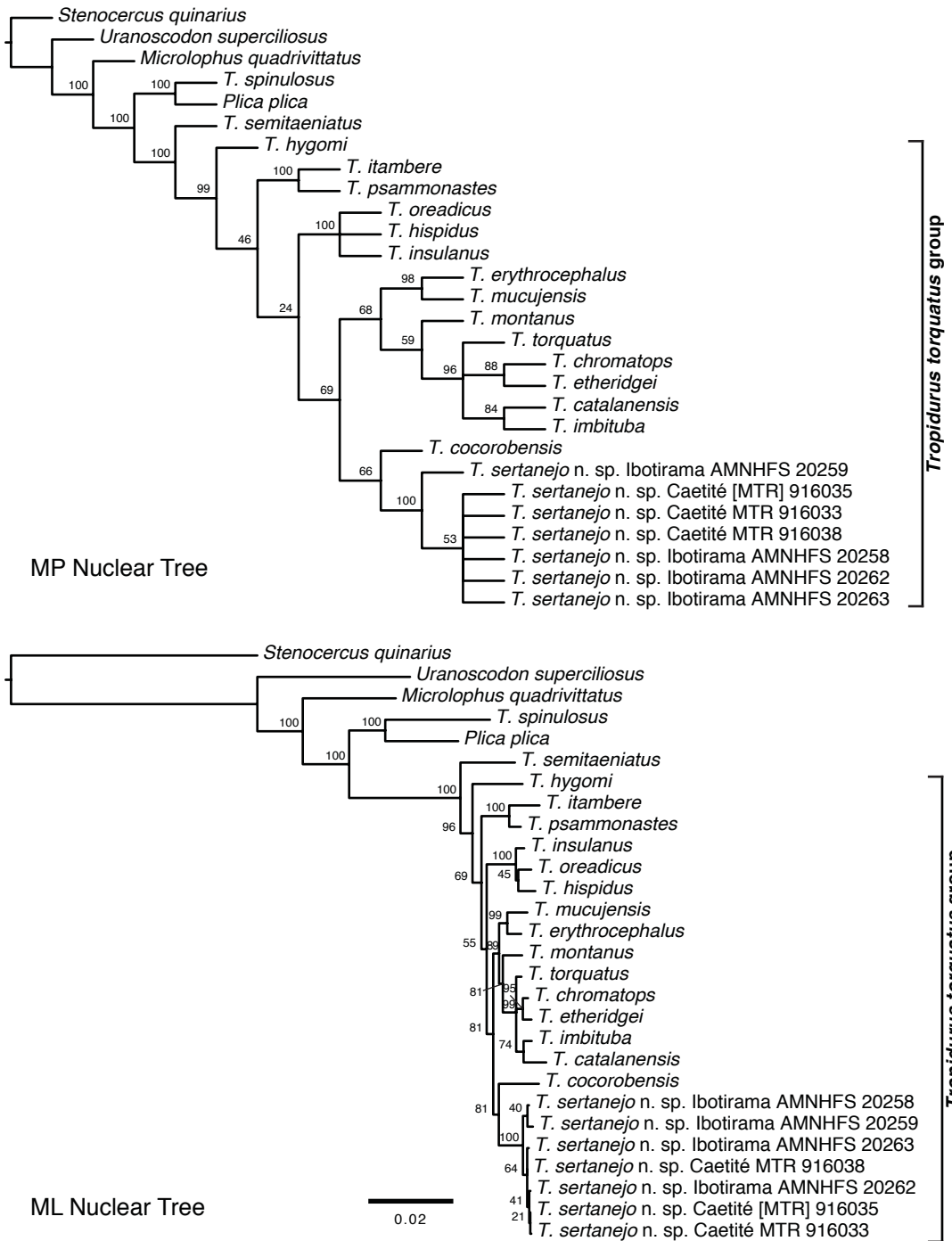


FIGURE 14. Maximum parsimony (upper) and maximum likelihood trees (lower) of *Tropidurus* based on four nuclear (BACH1, kif24, NTF3, PRLR, PTPN, SNCAIP) loci. Numbers associated to nodes refer to bootstrap values.

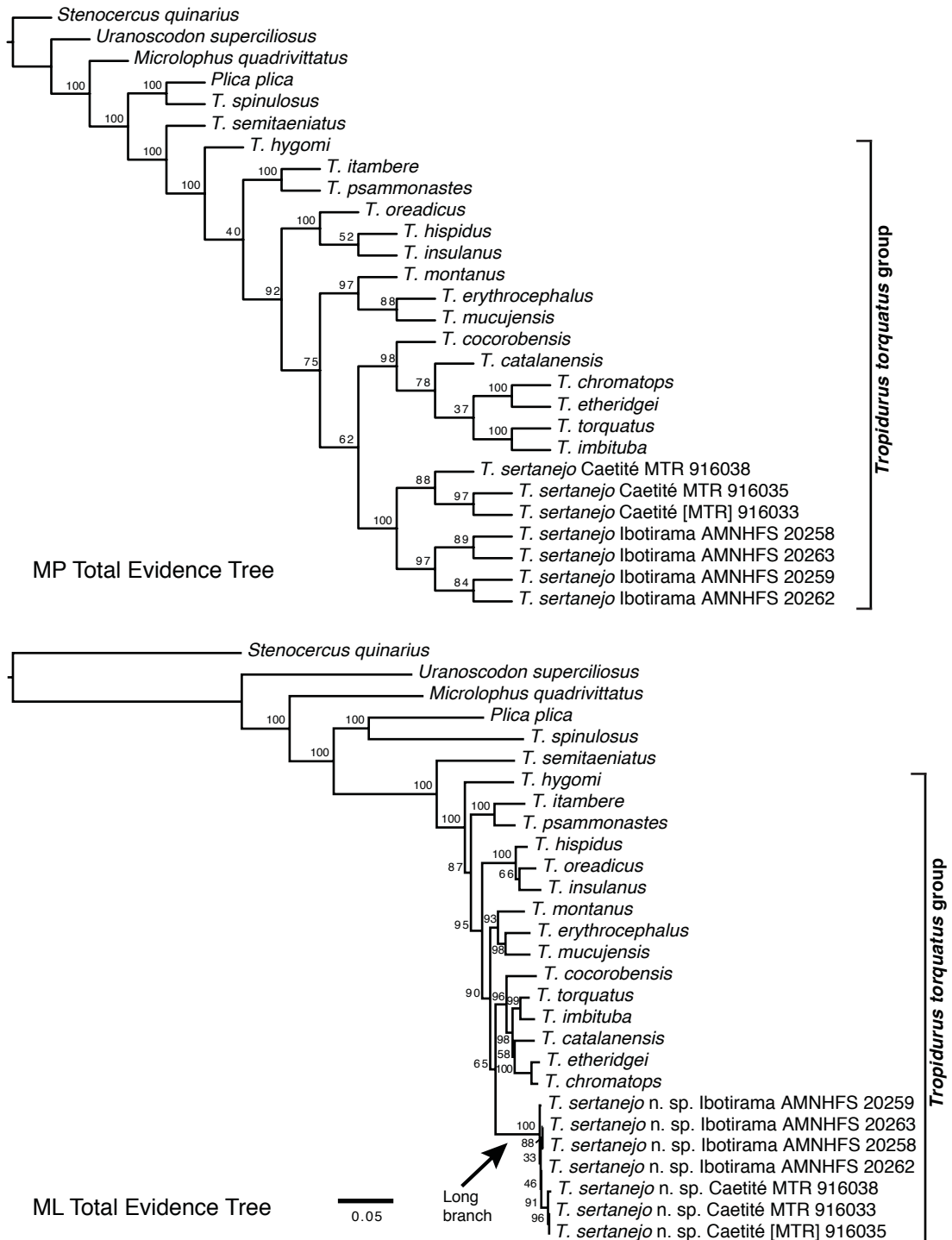


FIGURE 15. Maximum parsimony (upper) and maximum likelihood trees (lower) of *Tropidurus* on four mitochondrial (12S, 16S, CO1, Cyt b) and six nuclear loci (BACH1, kif24, NTF3, PRLR, PTPN, SNCAIP). Numbers associated to nodes refer to bootstrap values.

TABLE 10. Data partitions and respective models of nucleotide evolution selected for ML analyses of mitochondrial and nuclear loci.

| Data Set                       | Subset | Best Model | Subset Partitions                                   | Subset sites  |
|--------------------------------|--------|------------|---|---|
| <b>Mitochondrial</b>           | 1      | GTR+I+G    | 12S, 16S  | 1–880, 881–1431   |
| Scheme lnL -17236.72           | 2      | TrNef+I+G  | COI_1, Cytb_1                                       | 1432–2093, 2094–2849  |
| Scheme BIC 35189.36            | 3      | HKY+I      | COI_2, Cytb_2                                       | 1433–2093, 2095–2849  |
|                                | 4      | TrN+I+G    | COI_3   | 1434–2093   |
|                                | 5      | TrN+I+G    | Cytb_3  | 2096–2849   |
| <b>Nuclear</b>                 | 1      | HKY+G      | BACH1_2, NTF3_1, PRLR_2, PTPN_3                     | 1–1211, 1213–1881, 1882–2406, 2409–3227                       |
| Scheme lnL -13392.63           | 2      | HKY+I      | BACH1_3, PTPN_1                                     | 2–1211, 2407–3227   |
| Scheme BIC 27453.62            | 3      | HKY+G      | BACH1_1, NTF3_2, NTF3_3, PTPN_2, SNCAIP_1, SNCAIP_3 | 3–1211, 1212–1881, 1214–1881, 2408–3227, 3229–3704, 3230–3704 |
|                                | 4      | K81+G      | PRLR_1, PRLR_3, SNCAIP_2, KIF24_1, KIF24_2          | 1883–2406, 1884–2406, 3228–3704, 3705–4249, 3706–4249         |
|                                | 5      | HKY+G      | KIF24_3   | 3707–4249   |
| <b>Mitochondrial + Nuclear</b> | 1      | GTR+I+G    | 12S, 16S, Cytb_1                                    | 1–880, 881–1431, 3305–4060                                    |
| Scheme lnL -30849.40           | 2      | HKY+G      | BACH1_2, NTF3_1, PRLR_2, PTPN_3                     | 1432–2642, 4062–4730, 4731–5255, 5258–6076                    |
| Scheme BIC 62745.17            | 3      | HKY+G      | BACH1_3, PTPN_1, SNCAIP_3                           | 1433–2642, 5256–6076, 6078–6553                               |
|                                | 4      | HKY+G      | BACH1_1, NTF3_2, NTF3_3, PTPN_2, SNCAIP_1           | 1434–2642, 4061–4730, 4063–4730, 5257–6076, 6079–6553         |
|                                | 5      | TrNef+G    | COI_1   | 2643–3304   |
|                                | 6      | HKY+I      | COI_2, Cytb_2                                       | 2644–3304, 3306–4060  |
|                                | 7      | TrN+I+G    | COI_3   | 2645–3304   |
|                                | 8      | TrN+I+G    | Cytb_3  | 3307–4060   |
|                                | 9      | K81+G      | PRLR_1, PRLR_3, SNCAIP_2, KIF24_1, KIF24_2          | 4732–5255, 4733–5255, 6077–6553, 6554–7098, 6555–7098         |
|                                | 10     | K81uf+G    | KIF24_3   | 6556–7098   |

resulting from ML and MP reconstructions, and MP analyses do not require distinct evolutionary models or partition schemes to be defined prior to conduction of phylogenetic reconstruction, these factors were considered unlikely to explain all the variation in the observed results, favoring the interpretation of conflicting phylogenetic signal. Furthermore, phylogenetic analyses of the genus *Microlophus* performed by Benavides et al. (2007, 2009) revealed that conflicting phylogenetic signals promoted by mtDNA introgression might be more frequent among tropidurines than previously thought. mtDNA introgression and other processes that prevent complete fixation of alleles (e.g., incomplete lineage sorting, rapid speciation events) should not be

ruled out as potential factors generating conflict between mitochondrial and nuclear genes, and ultimately influencing the phylogenetic reconstruction of *Tropidurus*.

**COMPARISON WITH PREVIOUS PHYLOGENETIC HYPOTHESES:** Inasmuch as our taxon sampling was originally designed with the sole objective of inferring the phylogenetic placement of *T. sertanejo*, n. sp., within the *T. torquatus* group, the results produced revealed a paraphyletic *Tropidurus*. Prior analyses that recovered *Tropidurus* as nonmonophyletic were affected by significant amounts of homoplasy resulting from morphological convergence among some tropidurine genera (Frost, 1992; Harvey and Gutberlet, 2000). The combined analysis of morphological characters and mtDNA sequence data performed by Frost et al. (2001) was the first to successfully support a restricted, but monophyletic arrangement of *Tropidurus*. This phylogenetic hypothesis remained unrevised until Pyron et al. (2013) identified a sister-taxon relationship between *T. bogerti* and *Uracentron*; although a monophyletic clade including *T. bogerti*, *Uracentron*, *Plica*, and *Strobilurus* had been previously found by the mtDNA-only analysis of Frost et al. (2001). However, Pyron et al.'s results suffered from poor character sampling (12S was the only locus shared by all tropidurine taxa in their analysis). Thus, it remains unclear whether their hypothesis accurately reflects the tropidurine relationships or is a byproduct of insufficient data. Our total evidence analysis benefited from complete or nearly complete taxon coverage for most mitochondrial and nuclear loci, surpassing all previous studies. Herein, for the first time, an analysis with high nodal support recovered a paraphyletic *Tropidurus*, resulting from a close relationship between *T. spinulosus* and *Plica*, which formed the sister clade of the remaining *Tropidurus* (fig. 15).

We corroborate *T. semitaeniatus* as the sister species of the *T. torquatus* species group, as previously suggested by Frost et al. (2001). However, better progress in understanding the phylogeny of *Tropidurus* came with the identification of *T. hygomi* as sister clade to the remaining species of the *T. torquatus* group. *Tropidurus chromatops* had been previously placed at the base of this group by Frost et al. (2001), but those authors made clear that this result was suggestive—observing the weak nodal support resulting from the absence of molecular data for *T. chromatops*. In our total evidence tree, *T. chromatops* was recovered in a highly derived position, in close association with *T. etheridgei*. This arrangement is not surprising if we take into account the overall morphological similarity they exhibit. However, the position of this species pair is clearly unstable, and the same can be noted about the relationships of *T. catalanensis*, *T. cocorobensis*, *T. imbituba*, and *T. torquatus*.

Our larger, multilocus data set supported greater resolution in the weakly supported clade associated with stem 11 of Frost et al.'s (2001: fig. 6) total evidence tree. We found greater support for a clade including *T. hispidus*, *T. insulanus*, and *T. oreadicus*, and also the sister taxon relationship between *T. montanus* and the species pair formed by *T. erythrocephalus* and *T. mucujensis*. However, the sister-group relationships between *T. torquatus* and *T. hispidus*, and between *T. insulanus* and *T. oreadicus*, hypothesized by Frost et al. (2001), are contradicted by our results. We argue for the first time that *T. torquatus* is actually more closely related to the recently described *T. imbituba*, with both placed in a larger clade that includes (*T. cocorobensis*



TABLE 11. Uncorrected genetic distance among pairs of tropidurine species calculated for 12S sequences.

| Species                               | 1     | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16 | 17 | 18 | 19 | 20 | 21 |  |
|---------------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|----|----|----|----|----|----|--|
| 1. <i>Stenocercus quinarius</i>       | —     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 2. <i>Uranoscodon superciliosus</i>   | 0.167 | —     |       |       |       |       |       |       |       |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 3. <i>Microlophus quadrivittatus</i>  | 0.174 | 0.158 | —     |       |       |       |       |       |       |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 4. <i>Plica plica</i>                 | 0.179 | 0.167 | 0.140 | —     |       |       |       |       |       |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 5. <i>Tropidurus spinulosus</i>       | 0.213 | 0.177 | 0.170 | 0.152 | —     |       |       |       |       |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 6. <i>Tropidurus semitaeniatus</i>    | 0.187 | 0.164 | 0.145 | 0.127 | 0.149 | —     |       |       |       |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 7. <i>Tropidurus hygomi</i>           | 0.179 | 0.163 | 0.148 | 0.140 | 0.152 | 0.078 | —     |       |       |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 8. <i>Tropidurus psammomastes</i>     | 0.178 | 0.154 | 0.138 | 0.132 | 0.147 | 0.076 | 0.056 | —     |       |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 9. <i>Tropidurus itambere</i>         | 0.173 | 0.148 | 0.143 | 0.135 | 0.150 | 0.081 | 0.068 | 0.041 | —     |       |       |       |       |       |       |    |    |    |    |    |    |  |
| 10. <i>Tropidurus erythrocephalus</i> | 0.168 | 0.155 | 0.140 | 0.137 | 0.152 | 0.084 | 0.071 | 0.054 | 0.059 | —     |       |       |       |       |       |    |    |    |    |    |    |  |
| 11. <i>Tropidurus montanus</i>        | 0.167 | 0.152 | 0.143 | 0.138 | 0.144 | 0.074 | 0.056 | 0.053 | 0.045 | —     |       |       |       |       |       |    |    |    |    |    |    |  |
| 12. <i>Tropidurus mucujensis</i>      | 0.168 | 0.153 | 0.139 | 0.137 | 0.140 | 0.073 | 0.061 | 0.055 | 0.054 | 0.038 | 0.034 | —     |       |       |       |    |    |    |    |    |    |  |
| 13. <i>Tropidurus cocorobensis</i>    | 0.172 | 0.155 | 0.145 | 0.140 | 0.148 | 0.078 | 0.061 | 0.051 | 0.061 | 0.056 | 0.049 | 0.046 | —     |       |       |    |    |    |    |    |    |  |
| 14. <i>Tropidurus imbituba</i>        | 0.173 | 0.159 | 0.143 | 0.142 | 0.160 | 0.084 | 0.071 | 0.061 | 0.066 | 0.058 | 0.049 | 0.050 | 0.041 | —     |       |    |    |    |    |    |    |  |
| 15. <i>Tropidurus torquatus</i>       | 0.170 | 0.154 | 0.145 | 0.142 | 0.159 | 0.083 | 0.070 | 0.061 | 0.064 | 0.054 | 0.045 | 0.048 | 0.035 | 0.019 | —     |    |    |    |    |    |    |  |
| 16. <i>Tropidurus catalanensis</i>    | 0.164 | 0.150 | 0.140 | 0.135 | 0.149 | 0.074 | 0.055 | 0.055 | 0.060 | 0.048 | 0.031 | 0.035 | 0.030 | 0.038 | 0.031 | —  |    |    |    |    |    |  |

| Species                                  | 1     | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16    | 17    | 18    | 19    | 20    | 21    |
|--|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 17. <i>Tropidurus chromatops</i>         | 0.178 | 0.158 | 0.145 | 0.147 | 0.148 | 0.083 | 0.063 | 0.061 | 0.070 | 0.051 | 0.043 | 0.049 | 0.040 | 0.045 | 0.044 | 0.031 | —     | —     | —     | —     | —     |
| 18. <i>Tropidurus etheridgei</i>         | 0.179 | 0.157 | 0.155 | 0.138 | 0.149 | 0.081 | 0.066 | 0.063 | 0.070 | 0.053 | 0.049 | 0.055 | 0.044 | 0.046 | 0.045 | 0.035 | 0.020 | —     | —     | —     | —     |
| 19. <i>Tropidurus oreadicus</i>          | 0.177 | 0.159 | 0.139 | 0.134 | 0.154 | 0.080 | 0.060 | 0.046 | 0.054 | 0.058 | 0.049 | 0.048 | 0.054 | 0.060 | 0.059 | 0.051 | 0.058 | 0.061 | —     | —     | —     |
| 20. <i>Tropidurus hispidus</i>           | 0.173 | 0.159 | 0.137 | 0.129 | 0.157 | 0.075 | 0.056 | 0.039 | 0.049 | 0.058 | 0.044 | 0.049 | 0.048 | 0.056 | 0.055 | 0.046 | 0.055 | 0.056 | 0.019 | —     | —     |
| 21. <i>Tropidurus insulanus</i>          | 0.184 | 0.160 | 0.143 | 0.144 | 0.162 | 0.088 | 0.069 | 0.054 | 0.063 | 0.069 | 0.065 | 0.064 | 0.063 | 0.065 | 0.066 | 0.059 | 0.071 | 0.073 | 0.029 | 0.025 | —     |
| 22. <i>Tropidurus sertanejo</i> , n. sp. | 0.175 | 0.163 | 0.149 | 0.135 | 0.154 | 0.079 | 0.066 | 0.060 | 0.066 | 0.052 | 0.047 | 0.048 | 0.054 | 0.069 | 0.060 | 0.052 | 0.059 | 0.059 | 0.060 | 0.054 | 0.074 |

((*T. torquatus* + *T. imbituba*) (*T. catalanensis* (*T. chromatops* + *T. etheridgei*))), although part of the relationships in this clade remain poorly supported.

PHYLOGENETIC PLACEMENT OF *T. sertanejo*, n. sp.: Most mitochondrial and total evidence trees showed that samples of *T. sertanejo*, n. sp., from Ibotirama and Caetité, Bahia, formed reciprocally monophyletic groups, but our nuclear trees did not recover the same result. Because mitochondrial loci sort at a faster rate than nuclear loci (Avice, 1994; Funk and Omland, 2003; Zink and Barrowclough, 2008), these results are not surprising and probably imply maintenance of ancestral polymorphism.

We were successful in firmly placing *T. sertanejo*, n. sp., within the *T. torquatus* species group. However, the phylogenetic relationships of the new species in relation to other representatives of this group remain unclear. Our trees resulting from the analyses of the mitochondrial, nuclear, and total evidence data sets conflicted considerably, and support values of nodes linking *T. sertanejo*, n. sp., to other taxa were as low as 58% in our MP mitochondrial tree. In addition to the previously discussed disagreement between mitochondrial and nuclear loci affecting the phylogenetic reconstruction of the *T. torquatus* species group, the extensive topological conflict was also consistent with the observation of a relatively longer branch supporting the clade formed by samples of *T. sertanejo*, n. sp. The exclusion of multiple representatives of *T. sertanejo*, n. sp., from our analyses in an attempt to eliminate that long branch resulted in only slightly increased nodal support in most analyses (see appendices 9–12).

Our preferred tree (fig. 15; ML total evidence tree) placed *T. sertanejo*, n. sp., as the sister lineage of the clade (*T. cocorobensis* ((*T. imbituba* + *T. torquatus*) (*T. catalanensis* (*T. chromatops*, *T. etheridgei*)))) with poor nodal support. Uncorrected pairwise genetic distances calculated for 12S indicated that *T. sertanejo*, n. sp., is more similar genetically to *T. montanus* and *T. mucujensis* (table 11). Indeed, our morphological analyses also showed that the latter species share both axillary and inguinal mite pockets with *T. sertanejo*, n. sp., which might indicate their close relationship. Nevertheless, we failed to determine with confidence the closest relative of *T. sertanejo*, n. sp., because of the conflict between molecular data and also with respect to morphological characters. The putative association between the new species and other Caatinga endemics distributed along the Espinhaço mountain range should be carefully investigated in future analyses including additional data.

CLASSIFICATION OF TROPIDURINES AND FUTURE STEPS: Although the phylogenetic hypothesis presented herein represents the best-supported phylogenetic tree currently available for tropidurines, and recovers a surprisingly new arrangement of several species and genera in this group, we refrain from proposing a new taxonomic classification. This decision is founded on the fact that a solid phylogenetic classification of tropidurines would require broader taxonomic sampling than currently represented in our analyses. Nomenclatural changes resulting from a taxonomically incomplete phylogenetic assessment of the group might result in taxonomic instability and is, thus, unjustified. Nevertheless, our study achieved the major goals of confirming the placement of *T. sertanejo*, n. sp., within the *T. torquatus* species group and testing the monophyly of the group itself. Since Frost (1992), the relationships within the *T. torquatus* group have been proven extremely hard to solve either employing morphological

(Frost, 1992; Harvey and Gutberlet, 2000), molecular (Pyron et al., 2013; this study) or combined evidence (Frost et al., 2001). Future studies might benefit from the inclusion of additional molecular loci, additional morphological characters, and greater coverage of terminals.

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## APPENDIX 1

LIST OF TISSUE SAMPLES, RESPECTIVE VOUCHER SPECIMENS, AND  
GEOGRAPHIC LOCALITIES OF THE SPECIES EMPLOYED IN THE PHYLOGENETIC  
RECONSTRUCTION OF *TROPIDURUS*

| Species                            | Tissue Number <sup>a</sup> | Voucher <sup>a,b</sup> | Locality   |
|------------------------------------|----------------------------|------------------------|--|
| <i>Microlophus quadrivittatus</i>  | [MTR] LG 1170              | —                      | Punta Blanca, Antofagasta, Chile   |
| <i>Plica plica</i>                 | AMCC 106953                | —                      | Magdalen's Creek Camp, near ( $\pm$ 300 yds) NW bank of the Konawaruk River (ca. 25 mi (linear) WSW Mabura Hill), Guyana |
| <i>Stenocercus quinarius</i>       | [MTR] PHV-2204             | —                      | Estação Ecológica Serra Geral do Tocantins, Formoso do Rio Preto, Bahia, Brazil  |
| <i>Tropidurus catalanensis</i>     | UFRGS-T 2890               | UFRGS 6181             | Manoel Viana, Rio Grande do Sul, Brazil  |
| <i>Tropidurus chromatops</i>       | [MHNC] AMNHFS 20458        | —                      | Rock outcrops 30 km W Florida, Santa Cruz, Bolivia   |
| <i>Tropidurus cocorobensis</i>     | MTR 907077                 | MZUSP 78450            | Nova Rodelas, Bahia, Brazil  |
| <i>Tropidurus erythrocephalus</i>  | MTR 906087                 | —                      | Morro do Chapéu, Bahia, Brazil   |
| <i>Tropidurus etheridgei</i>       | [MTR] LG 1096              | —                      | Fuerte Esperanza, Chaco, Argentina   |
| <i>Tropidurus hispidus</i>         | MTR 12552                  | —                      | Lagoa do Abaeté, Salvador, Bahia, Brazil   |
| <i>Tropidurus hygomi</i>           | MTR 12579                  | —                      | Santo Amaro das Brotas, Sergipe, Brazil  |
| <i>Tropidurus imbituba</i>         | UFRGS-T 620                | UFRGS 5092             | Imbituba, Santa Catarina, Brazil   |
| <i>Tropidurus insulanus</i>        | [MTR] TM 358               | UFMT 7691              | Guarantã do Norte, Mato Grosso, Brazil   |
| <i>Tropidurus itambere</i>         | [MTR] IT H307              | —                      | Piedade, São Paulo, Brazil   |
| <i>Tropidurus montanus</i>         | [MTR] 887668               | —                      | Diamantina, Minas Gerais, Brazil   |
| <i>Tropidurus mucujensis</i>       | MTR 906024                 | —                      | Mucugê, Bahia, Brazil  |
| <i>Tropidurus oreadicus</i>        | MTR 33317                  | —                      | Primeira cachoeira do rio Urucuia, Butiris, Minas Gerais, Brazil   |
| <i>Tropidurus psammonastes</i>     | MRT 3551                   | —                      | Ibiraba, Barra, Bahia, Brazil  |
| <i>Tropidurus semitaeniatus</i>    | [MTR] JC 1165              | —                      | Mucugê, Bahia, Brazil  |
| <i>Tropidurus sertanejo n. sp.</i> | MTR 916033                 | MZUSP 76047            | Caetitê, Bahia, Brazil   |
| <i>Tropidurus sertanejo n. sp.</i> | MTR 916035                 | MZUSP 76049            | Caetitê, Bahia, Brazil   |
| <i>Tropidurus sertanejo n. sp.</i> | MTR 916038                 | MZUSP 76052            | Caetitê, Bahia, Brazil   |
| <i>Tropidurus sertanejo n. sp.</i> | AMNH-FS 20258              | No voucher             | RPPN Pé da Serra, Ibotirama, Bahia, Brazil   |
| <i>Tropidurus sertanejo n. sp.</i> | AMNH-FS 20259              | MZUSP 104272           | RPPN Pé da Serra, Ibotirama, Bahia, Brazil   |
| <i>Tropidurus sertanejo n. sp.</i> | AMNH-FS 20262              | MZUSP 104273           | RPPN Pé da Serra, Ibotirama, Bahia, Brazil   |
| <i>Tropidurus sertanejo n. sp.</i> | AMNH-FS 20263              | MZUSP 104274           | RPPN Pé da Serra, Ibotirama, Bahia, Brazil   |
| <i>Tropidurus spinulosus</i>       | AMCC 204478                | AMNH 176295            | Rodeo Trebol, Loma Plata, Boquerón, Paraguay   |
| <i>Tropidurus torquatus</i>        | MTR 21250                  | —                      | Restinga de Grussaí, São João da Barra, Rio de Janeiro   |
| <i>Uranoscodon superciliosus</i>   | MTR 18881                  | —                      | Lago Chaviana, Itapuru, margem direita do Rio Purus, Beruri, Amazonas, Brazil  |

<sup>a</sup>AMCC: Ambrose Monell Cryo Collection at the American Museum of Natural History, New York, United States. MTR: Coleção de Tecidos Miguel Trefaut Rodrigues, Instituto de Biociências, Universidade de São Paulo. MZUSP: Museo de Zoologia da Universidade de São Paulo, São Paulo, Brazil. UFRGS: Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. .

<sup>b</sup>Missing numbers indicate specimens in process of being catalogued or cases where tissue samples could not be linked to whole specimens.



## APPENDIX 2

GENBANK ACCESSION NUMBERS OF MITOCHONDRIAL AND NUCLEAR SEQUENCES USED IN THE PHYLOGENETIC  
RECONSTRUCTION OF *TROPIDURUS*

| Species                   | Tissue Number       | Mitochondrial |          |          |          |          |          |          |          |          |        | Nuclear |     |       |     |       |       |      |      |      |        |  |
|---------------------------|---------------------|---------------|----------|----------|----------|----------|----------|----------|----------|----------|--------|---------|-----|-------|-----|-------|-------|------|------|------|--------|--|
|                           |                     | 12S           | 16S      | Cyt b    | COI      | BACHI    | KIF24    | NTF3     | PRLR     | PTPN     | SNCAIP | 12S     | 16S | Cyt b | COI | BACHI | KIF24 | NTF3 | PRLR | PTPN | SNCAIP |  |
| <i>M. quadrivittatus</i>  | [MTR] LG 1170       | KU245285      | KU245316 | KU245083 | KU245176 | KU245130 | KU245149 | KU245202 | KU245231 | KU245257 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>P. plica</i>           | AMCC 106953         | KU245286      | KU245313 | KU245084 | KU245104 | KU245131 | KU245152 | KU245203 | KU245229 | KU245259 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>S. quinarius</i>       | [MTR] PHV 2204      | KU245289      | KU245317 | KU245081 | KU245106 | KU245134 | KU245153 | KU245206 | KU245233 | KU245261 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. catalanensis</i>    | UPRGST 2890         | KU245277      | KU245311 | KU245060 | KU245091 | KU245113 | KU245136 | KU245190 | KU245220 | KU245250 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. chromatops</i>      | [MHNC] AMNHFS 20458 | KU245275      | KU245297 |          | KU245087 | KU245112 |          |          | KU245214 | KU245252 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. cocorobensis</i>    | MTR 907077          | KU245274      | KU245301 | KU245067 | KU245092 | KU245127 |          |          | KU245224 | KU245256 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. erythrocephalus</i> | MTR 906087          | KU245269      | KU245306 | KU245075 | KU245095 | KU245116 |          |          | KU245223 | KU245247 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. etheridgei</i>      | [MTR] LG 1096       | KU245276      | KU245298 | KU245063 | KU245088 | KU245111 |          |          | KU245216 | KU245251 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. hispidus</i>        | MTR 12552           | KU245279      | KU245305 | KU245065 | KU245099 | KU245107 |          |          | KU245218 | KU245253 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. hygomi</i>          | MTR 12579           | KU245283      | KU245308 | KU245078 | KU245101 | KU245128 |          |          | KU245225 | KU245255 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. imbituba</i>        | UPRGST 620          | KU245272      | KU245299 | KU245061 | KU245089 | KU245114 |          |          | KU245213 | KU245244 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. insularis</i>       | [MTR] TM 358        | KU245280      | KU245307 | KU245066 | KU245098 | KU245109 |          |          | KU245219 | KU245248 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. itambere</i>        | [MTR] ITH 307       | KU245282      | KU245310 | KU245080 | KU245097 | KU245125 |          |          | KU245226 | KU245235 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. montanus</i>        | [MTR] 887668        | KU245270      | KU245303 | KU245077 | KU245093 | KU245124 |          |          | KU245221 | KU245245 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. mucujensis</i>      | MTR 906024          | KU245271      | KU245302 | KU245076 | KU245094 | KU245115 |          |          | KU245222 | KU245246 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. oreadicus</i>       | MTR 33317           | KU245278      | KU245304 | KU245064 | KU245100 | KU245108 |          |          | KU245217 | KU245249 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. psammomastis</i>    | MRT 3551            | KU245281      | KU245309 | KU245079 | KU245096 | KU245126 |          |          | KU245227 | KU245234 |        |         |     |       |     |       |       |      |      |      |        |  |
| <i>T. semitaeniatus</i>   | [MTR] JC1165        | KU245284      | KU245312 | KU245059 | KU245102 | KU245129 |          |          | KU245228 | KU245254 |        |         |     |       |     |       |       |      |      |      |        |  |

| Species                    | Tissue Number        | Mitochondrial |          |          |          |          | Nuclear  |          |          |          |          |
|----------------------------|----------------------|---------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
|                            |                      | 12S           | 16S      | Cyt b    | COI      | BACH1    | KIF24    | NTF3     | PRLR     | PTPN     | SNCAIP   |
| <i>T. sertanejo</i> n. sp. | [MTR] 916035         | KU245262      | KU245291 | KU245073 |          |          | KU245119 |          | KU245196 |          | KU245237 |
| <i>T. sertanejo</i> n. sp. | MTR 916033           | KU245263      | KU245292 | KU245072 |          | KU245163 | KU245117 | KU245145 | KU245198 | KU245211 | KU245238 |
| <i>T. sertanejo</i> n. sp. | MTR 916038           | KU245264      | KU245290 | KU245074 | KU245086 | KU245165 | KU245118 | KU245146 | KU245195 | KU245212 | KU245239 |
| <i>T. sertanejo</i> n. sp. | [MTR] AMIN-HFS 20258 | KU245266      | KU245293 | KU245070 |          | KU245167 | KU245122 |          | KU245193 | KU245207 | KU245242 |
| <i>T. sertanejo</i> n. sp. | [MTR] AMIN-HFS 20259 | KU245267      | KU245295 | KU245068 |          | KU245164 | KU245123 | KU245147 | KU245194 | KU245209 | KU245236 |
| <i>T. sertanejo</i> n. sp. | [MTR] AMIN-HFS 20262 | KU245268      | KU245296 | KU245069 |          | KU245166 | KU245120 |          | KU245197 | KU245210 | KU245241 |
| <i>T. sertanejo</i> n. sp. | [MTR] AMIN-HFS 20263 | KU245265      | KU245294 | KU245071 |          |          | KU245121 |          | KU245192 | KU245208 | KU245240 |
| <i>T. spinulosus</i>       | AMCC 204478          | KU245287      | KU245314 | KU245085 | KU245103 | KU245175 | KU245132 | KU245151 | KU245204 | KU245230 | KU245258 |
| <i>T. torquatus</i>        | MTR 21250            | KU245273      | KU245300 | KU245062 | KU245090 | KU245157 | KU245110 | KU245135 | KU245186 | KU245215 | KU245243 |
| <i>U. superciliosus</i>    | MTR 18881            | KU245288      | KU245315 | KU245082 | KU245105 | KU245177 | KU245133 | KU245150 | KU245205 | KU245232 | KU245260 |

## APPENDIX 3

TUKEY-KRAMER PAIRWISE COMPARISONS OF MEAN PC1 SCORES, ADOPTED AS  
A PROXY FOR SIZE VARIATION AMONG *TROPIDURUS* SPECIES (SIGNIFICANT  
VALUES HIGHLIGHTED IN BOLD)

(*Tcat*) *T. catalanensis*, (*Tchr*) *T. chromatops*, (*Tcoc*) *T. cocorobensis*, (*Tery*) *T. erythrocephalus*, (*Teth*)  
*T. etheridgei*, (*This*) *T. hispidus*, (*Thyg*) *T. hygomi*, (*Timb*) *T. imbituba*, (*Tins*) *T. insulanus*, (*Tita*) *T.*  
*itambere*, (*Tmon*) *T. montanus*, (*Tmuc*) *T. mucujensis*, (*Tore*) *T. oreadicus*, (*Tpsa*) *T. psammonastes*,  
(*Tser*) *T. sertanejo*, n. sp., (*Ttor*) *T. torquatus*.

| Males              | Difference | Lower   | Upper  | p             | Females            | Difference | Lower   | Upper  | p             |
|--------------------|------------|---------|--------|---------------|--------------------|------------|---------|--------|---------------|
| <i>Tchr - Tcat</i> | 0.2729     | -0.0989 | 0.6447 | 0.4290        | <i>Tcat - Timb</i> | 0.0860     | -0.1685 | 0.3405 | 0.9980        |
| <i>Tchr - This</i> | 0.2409     | -0.1474 | 0.6293 | 0.7137        | <i>Tchr - Tcat</i> | 0.1115     | -0.2300 | 0.4529 | 0.9986        |
| <i>Tchr - Timb</i> | 0.2550     | -0.1134 | 0.6234 | 0.5339        | <i>Tchr - This</i> | 0.0729     | -0.2830 | 0.4288 | 1.0000        |
| <i>Tchr - Tpsa</i> | 0.1342     | -0.2418 | 0.5102 | 0.9968        | <i>Tchr - Timb</i> | 0.1975     | -0.1968 | 0.5917 | 0.9217        |
| <i>Tcoc - Tcat</i> | 0.5929     | 0.3792  | 0.8067 | <b>0.0000</b> | <i>Tchr - Tore</i> | 0.0160     | -0.3490 | 0.3810 | 1.0000        |
| <i>Tcoc - Tchr</i> | 0.3200     | -0.0456 | 0.6856 | 0.1593        | <i>Tchr - Tpsa</i> | 0.0105     | -0.3838 | 0.4048 | 1.0000        |
| <i>Tcoc - Tery</i> | 0.1008     | -0.1405 | 0.3422 | 0.9845        | <i>Tcoc - Tcat</i> | 0.3274     | 0.0729  | 0.5820 | <b>0.0018</b> |
| <i>Tcoc - Teth</i> | 0.1160     | -0.0680 | 0.3001 | 0.6895        | <i>Tcoc - Tchr</i> | 0.2160     | -0.1783 | 0.6102 | 0.8541        |
| <i>Tcoc - This</i> | 0.5610     | 0.3196  | 0.8023 | <b>0.0000</b> | <i>Tcoc - Tery</i> | 0.0237     | -0.3240 | 0.3715 | 1.0000        |
| <i>Tcoc - Timb</i> | 0.5750     | 0.3672  | 0.7828 | <b>0.0000</b> | <i>Tcoc - Teth</i> | 0.1065     | -0.1538 | 0.3668 | 0.9859        |
| <i>Tcoc - Tins</i> | 0.0991     | -0.0957 | 0.2940 | 0.9180        | <i>Tcoc - This</i> | 0.2889     | 0.0153  | 0.5625 | <b>0.0280</b> |
| <i>Tcoc - Tita</i> | 0.1240     | -0.0897 | 0.3378 | 0.8022        | <i>Tcoc - Timb</i> | 0.4134     | 0.0915  | 0.7354 | <b>0.0019</b> |
| <i>Tcoc - Tmon</i> | 0.2439     | -0.0338 | 0.5216 | 0.1555        | <i>Tcoc - Tins</i> | 0.0112     | -0.2516 | 0.2741 | 1.0000        |
| <i>Tcoc - Tore</i> | 0.3078     | 0.0664  | 0.5491 | <b>0.0019</b> | <i>Tcoc - Tita</i> | 0.1313     | -0.1906 | 0.4532 | 0.9863        |
| <i>Tcoc - Tpsa</i> | 0.4542     | 0.2332  | 0.6752 | <b>0.0000</b> | <i>Tcoc - Tmon</i> | 0.2095     | -0.1124 | 0.5315 | 0.6283        |
| <i>Tcoc - Ttor</i> | 0.2966     | 0.0756  | 0.5176 | <b>0.0008</b> | <i>Tcoc - Tore</i> | 0.2320     | -0.0534 | 0.5173 | 0.2530        |
| <i>Tser - Tcat</i> | 0.6331     | 0.3679  | 0.8984 | <b>0.0000</b> | <i>Tcoc - Tpsa</i> | 0.2265     | -0.0954 | 0.5484 | 0.4948        |
| <i>Tser - Tchr</i> | 0.3602     | -0.0377 | 0.7581 | 0.1234        | <i>Tcoc - Ttor</i> | 0.1582     | -0.1272 | 0.4435 | 0.8427        |
| <i>Tser - Tcoc</i> | 0.0402     | -0.2163 | 0.2967 | 1.0000        | <i>Tser - Tcat</i> | 0.3720     | 0.0855  | 0.6584 | <b>0.0015</b> |
| <i>Tser - Tery</i> | 0.1410     | -0.1469 | 0.4290 | 0.9387        | <i>Tser - Tchr</i> | 0.2605     | -0.1551 | 0.6761 | 0.6879        |
| <i>Tser - Teth</i> | 0.1562     | -0.0857 | 0.3982 | 0.6522        | <i>Tser - Tcoc</i> | 0.0445     | -0.3032 | 0.3922 | 1.0000        |
| <i>Tser - This</i> | 0.6012     | 0.3132  | 0.8891 | <b>0.0000</b> | <i>Tser - Tery</i> | 0.0683     | -0.3035 | 0.4400 | 1.0000        |
| <i>Tser - Timb</i> | 0.6152     | 0.3547  | 0.8757 | <b>0.0000</b> | <i>Tser - Teth</i> | 0.1510     | -0.1406 | 0.4426 | 0.9003        |
| <i>Tser - Tins</i> | 0.1393     | -0.1110 | 0.3896 | 0.8469        | <i>Tser - This</i> | 0.3334     | 0.0299  | 0.6369 | <b>0.0176</b> |
| <i>Tser - Tita</i> | 0.1642     | -0.1010 | 0.4295 | 0.7169        | <i>Tser - Timb</i> | 0.4579     | 0.1102  | 0.8057 | <b>0.0012</b> |
| <i>Tser - Tmon</i> | 0.2841     | -0.0350 | 0.6031 | 0.1403        | <i>Tser - Tins</i> | 0.0558     | -0.2381 | 0.3496 | 1.0000        |
| <i>Tser - Tmuc</i> | 0.0083     | -0.2925 | 0.3091 | 1.0000        | <i>Tser - Tita</i> | 0.1758     | -0.1719 | 0.5235 | 0.9160        |
| <i>Tser - Tore</i> | 0.3480     | 0.0600  | 0.6359 | <b>0.0045</b> | <i>Tser - Tmon</i> | 0.2540     | -0.0937 | 0.6018 | 0.4283        |
| <i>Tser - Tpsa</i> | 0.4944     | 0.2233  | 0.7656 | <b>0.0000</b> | <i>Tser - Tore</i> | 0.2765     | -0.0377 | 0.5906 | 0.1506        |

| Males              | Difference | Lower   | Upper  | p             | Females            | Difference | Lower   | Upper  | p             |
|--------------------|------------|---------|--------|---------------|--------------------|------------|---------|--------|---------------|
| <i>Tser - Ttor</i> | 0.3368     | 0.0657  | 0.6079 | <b>0.0029</b> | <i>Tser - Tpsa</i> | 0.2710     | -0.0767 | 0.6187 | 0.3184        |
| <i>Tery - Tcat</i> | 0.4921     | 0.2414  | 0.7428 | <b>0.0000</b> | <i>Tser - Ttor</i> | 0.2027     | -0.1115 | 0.5168 | 0.6427        |
| <i>Tery - Tchr</i> | 0.2192     | -0.1692 | 0.6075 | 0.8329        | <i>Tery - Tcat</i> | 0.3037     | 0.0173  | 0.5901 | <b>0.0267</b> |
| <i>Tery - Teth</i> | 0.0152     | -0.2106 | 0.2410 | 1.0000        | <i>Tery - Tchr</i> | 0.1922     | -0.2234 | 0.6078 | 0.9581        |
| <i>Tery - This</i> | 0.4601     | 0.1855  | 0.7347 | <b>0.0000</b> | <i>Tery - Teth</i> | 0.0827     | -0.2089 | 0.3743 | 0.9997        |
| <i>Tery - Timb</i> | 0.4742     | 0.2286  | 0.7198 | <b>0.0000</b> | <i>Tery - This</i> | 0.2651     | -0.0384 | 0.5687 | 0.1588        |
| <i>Tery - Tita</i> | 0.0232     | -0.2275 | 0.2739 | 1.0000        | <i>Tery - Timb</i> | 0.3897     | 0.0420  | 0.7374 | <b>0.0137</b> |
| <i>Tery - Tmon</i> | 0.1430     | -0.1640 | 0.4500 | 0.9591        | <i>Tery - Tita</i> | 0.1075     | -0.2402 | 0.4553 | 0.9993        |
| <i>Tery - Tore</i> | 0.2069     | -0.0677 | 0.4815 | 0.3828        | <i>Tery - Tmon</i> | 0.1858     | -0.1619 | 0.5335 | 0.8761        |
| <i>Tery - Tpsa</i> | 0.3534     | 0.0965  | 0.6102 | <b>0.0005</b> | <i>Tery - Tore</i> | 0.2082     | -0.1060 | 0.5224 | 0.5982        |
| <i>Tery - Ttor</i> | 0.1958     | -0.0611 | 0.4526 | 0.3632        | <i>Tery - Tpsa</i> | 0.2027     | -0.1450 | 0.5505 | 0.7868        |
| <i>Teth - Tcat</i> | 0.4769     | 0.2808  | 0.6729 | <b>0.0000</b> | <i>Tery - Ttor</i> | 0.1344     | -0.1798 | 0.4486 | 0.9787        |
| <i>Teth - Tchr</i> | 0.2040     | -0.1516 | 0.5595 | 0.8152        | <i>Teth - Tcat</i> | 0.2210     | 0.0510  | 0.3910 | <b>0.0015</b> |
| <i>Teth - This</i> | 0.4449     | 0.2191  | 0.6708 | <b>0.0000</b> | <i>Teth - Tchr</i> | 0.1095     | -0.2363 | 0.4553 | 0.999         |
| <i>Teth - Timb</i> | 0.4590     | 0.2694  | 0.6485 | <b>0.0000</b> | <i>Teth - This</i> | 0.1824     | -0.0150 | 0.3798 | 0.1031        |
| <i>Teth - Tita</i> | 0.0080     | -0.1881 | 0.2040 | 1.0000        | <i>Teth - Timb</i> | 0.3069     | 0.0466  | 0.5673 | <b>0.0069</b> |
| <i>Teth - Tmon</i> | 0.1278     | -0.1365 | 0.3921 | 0.9445        | <i>Teth - Tita</i> | 0.0248     | -0.2355 | 0.2851 | 1.0000        |
| <i>Teth - Tore</i> | 0.1917     | -0.0341 | 0.4176 | 0.1972        | <i>Teth - Tmon</i> | 0.1031     | -0.1573 | 0.3634 | 0.9897        |
| <i>Teth - Tpsa</i> | 0.3382     | 0.1343  | 0.5421 | <b>0.0000</b> | <i>Teth - Tore</i> | 0.1255     | -0.0880 | 0.3389 | 0.7765        |
| <i>Teth - Ttor</i> | 0.1806     | -0.0233 | 0.3845 | 0.1463        | <i>Teth - Tpsa</i> | 0.1200     | -0.1403 | 0.3803 | 0.9592        |
| <i>This - Tcat</i> | 0.0320     | -0.2187 | 0.2826 | 1.0000        | <i>Teth - Ttor</i> | 0.0517     | -0.1618 | 0.2651 | 1.0000        |
| <i>This - Timb</i> | 0.0141     | -0.2315 | 0.2597 | 1.0000        | <i>This - Tcat</i> | 0.0386     | -0.1511 | 0.2283 | 1.0000        |
| <i>Thyg - Tcat</i> | 0.6357     | 0.4325  | 0.8389 | <b>0.0000</b> | <i>This - Timb</i> | 0.1245     | -0.1490 | 0.3981 | 0.9633        |
| <i>Thyg - Tchr</i> | 0.3628     | 0.0033  | 0.7223 | <b>0.0455</b> | <i>Thyg - Tcat</i> | 0.4661     | 0.2826  | 0.6497 | <b>0.0000</b> |
| <i>Thyg - Tcoc</i> | 0.0428     | -0.1488 | 0.2344 | 1.0000        | <i>Thyg - Tchr</i> | 0.3546     | 0.0020  | 0.7073 | <b>0.0472</b> |
| <i>Thyg - Tser</i> | 0.0026     | -0.2452 | 0.2504 | 1.0000        | <i>Thyg - Tcoc</i> | 0.1387     | -0.1307 | 0.4080 | 0.9042        |
| <i>Thyg - Tery</i> | 0.1436     | -0.0884 | 0.3757 | 0.7173        | <i>Thyg - Tser</i> | 0.0942     | -0.2055 | 0.3939 | 0.9991        |
| <i>Thyg - Teth</i> | 0.1588     | -0.0128 | 0.3305 | 0.1030        | <i>Thyg - Tery</i> | 0.1624     | -0.1373 | 0.4621 | 0.8639        |
| <i>Thyg - This</i> | 0.6038     | 0.3717  | 0.8358 | <b>0.0000</b> | <i>Thyg - Teth</i> | 0.2452     | 0.0537  | 0.4367 | <b>0.0019</b> |
| <i>Thyg - Timb</i> | 0.6178     | 0.4209  | 0.8147 | <b>0.0000</b> | <i>Thyg - This</i> | 0.4276     | 0.2184  | 0.6367 | <b>0.0000</b> |
| <i>Thyg - Tins</i> | 0.1419     | -0.0413 | 0.3251 | 0.3354        | <i>Thyg - Timb</i> | 0.5521     | 0.2828  | 0.8214 | <b>0.0000</b> |
| <i>Thyg - Tita</i> | 0.1668     | -0.0364 | 0.3700 | 0.2436        | <i>Thyg - Tins</i> | 0.1499     | -0.0450 | 0.3449 | 0.3402        |
| <i>Thyg - Tmon</i> | 0.2867     | 0.0170  | 0.5563 | <b>0.0255</b> | <i>Thyg - Tita</i> | 0.2700     | 0.0006  | 0.5393 | <b>0.0488</b> |
| <i>Thyg - Tmuc</i> | 0.0109     | -0.2369 | 0.2586 | 1.0000        | <i>Thyg - Tmon</i> | 0.3482     | 0.0789  | 0.6176 | <b>0.0017</b> |
| <i>Thyg - Tore</i> | 0.3506     | 0.1185  | 0.5826 | <b>0.0001</b> | <i>Thyg - Tmuc</i> | 0.0786     | -0.2211 | 0.3783 | 0.9999        |
| <i>Thyg - Tpsa</i> | 0.4970     | 0.2862  | 0.7078 | <b>0.0000</b> | <i>Thyg - Tore</i> | 0.3706     | 0.1463  | 0.595  | <b>0.0000</b> |
| <i>Thyg - Ttor</i> | 0.3394     | 0.1286  | 0.5502 | <b>0.0000</b> | <i>Thyg - Tpsa</i> | 0.3652     | 0.0958  | 0.6345 | <b>0.0007</b> |
| <i>Timb - Tcat</i> | 0.0179     | -0.2006 | 0.2364 | 1.0000        | <i>Thyg - Ttor</i> | 0.2968     | 0.0725  | 0.5212 | <b>0.0011</b> |
| <i>Tins - Tcat</i> | 0.4938     | 0.2876  | 0.7000 | <b>0.0000</b> | <i>Tins - Tcat</i> | 0.3162     | 0.1423  | 0.4901 | <b>0.0000</b> |

APPENDIX 3 *Continued*

| Males              | Difference | Lower   | Upper  | <i>p</i>      | Females            | Difference | Lower   | Upper  | <i>p</i>      |
|--------------------|------------|---------|--------|---------------|--------------------|------------|---------|--------|---------------|
| <i>Tins - Tchr</i> | 0.2209     | -0.1403 | 0.5821 | 0.7346        | <i>Tins - Tchr</i> | 0.2047     | -0.1430 | 0.5524 | 0.7748        |
| <i>Tins - Tery</i> | 0.0017     | -0.2330 | 0.2365 | 1.0000        | <i>Tins - Tery</i> | 0.0125     | -0.2814 | 0.3064 | 1.0000        |
| <i>Tins - Teth</i> | 0.0169     | -0.1583 | 0.1922 | 1.0000        | <i>Tins - Teth</i> | 0.0952     | -0.0870 | 0.2775 | 0.8936        |
| <i>Tins - This</i> | 0.4618     | 0.2271  | 0.6966 | <b>0.0000</b> | <i>Tins - This</i> | 0.2776     | 0.0769  | 0.4784 | <b>0.0005</b> |
| <i>Tins - Timb</i> | 0.4759     | 0.2759  | 0.6759 | <b>0.0000</b> | <i>Tins - Timb</i> | 0.4022     | 0.1393  | 0.6650 | <b>0.0001</b> |
| <i>Tins - Tita</i> | 0.0249     | -0.1813 | 0.2312 | 1.0000        | <i>Tins - Tita</i> | 0.1201     | -0.1428 | 0.3829 | 0.9623        |
| <i>Tins - Tmon</i> | 0.1447     | -0.1272 | 0.4167 | 0.8864        | <i>Tins - Tmon</i> | 0.1983     | -0.0646 | 0.4611 | 0.3727        |
| <i>Tins - Tore</i> | 0.2086     | -0.0261 | 0.4434 | 0.1421        | <i>Tins - Tore</i> | 0.2207     | 0.0042  | 0.4373 | <b>0.0411</b> |
| <i>Tins - Tpsa</i> | 0.3551     | 0.1414  | 0.5688 | <b>0.0000</b> | <i>Tins - Tpsa</i> | 0.2152     | -0.0476 | 0.4781 | 0.2423        |
| <i>Tins - Ttor</i> | 0.1975     | -0.0162 | 0.4112 | 0.1042        | <i>Tins - Ttor</i> | 0.1469     | -0.0696 | 0.3634 | 0.5581        |
| <i>Tita - Tcat</i> | 0.4689     | 0.2447  | 0.6931 | <b>0.0000</b> | <i>Tita - Tcat</i> | 0.1962     | -0.0584 | 0.4507 | 0.3366        |
| <i>Tita - Tchr</i> | 0.1960     | -0.1758 | 0.5678 | 0.8939        | <i>Tita - Tchr</i> | 0.0847     | -0.3096 | 0.4789 | 1.0000        |
| <i>Tita - This</i> | 0.4369     | 0.1863  | 0.6876 | <b>0.0000</b> | <i>Tita - This</i> | 0.1576     | -0.1160 | 0.4312 | 0.8013        |
| <i>Tita - Timb</i> | 0.4510     | 0.2325  | 0.6695 | <b>0.0000</b> | <i>Tita - Timb</i> | 0.2821     | -0.0398 | 0.6041 | 0.1552        |
| <i>Tita - Tmon</i> | 0.1198     | -0.1660 | 0.4056 | 0.9840        | <i>Tita - Tmon</i> | 0.0782     | -0.2437 | 0.4002 | 1.0000        |
| <i>Tita - Tore</i> | 0.1837     | -0.0669 | 0.4344 | 0.4318        | <i>Tita - Tore</i> | 0.1007     | -0.1847 | 0.3860 | 0.9968        |
| <i>Tita - Tpsa</i> | 0.3302     | 0.0991  | 0.5613 | <b>0.0002</b> | <i>Tita - Tpsa</i> | 0.0952     | -0.2267 | 0.4171 | 0.9996        |
| <i>Tita - Ttor</i> | 0.1726     | -0.0585 | 0.4037 | 0.3988        | <i>Tita - Ttor</i> | 0.0269     | -0.2585 | 0.3122 | 1.0000        |
| <i>Tmon - Tcat</i> | 0.3491     | 0.0633  | 0.6349 | <b>0.0038</b> | <i>Tmon - Tcat</i> | 0.1179     | -0.1366 | 0.3724 | 0.9575        |
| <i>Tmon - Tchr</i> | 0.0761     | -0.3357 | 0.4880 | 1.0000        | <i>Tmon - Tchr</i> | 0.0064     | -0.3878 | 0.4007 | 1.0000        |
| <i>Tmon - This</i> | 0.3171     | 0.0101  | 0.6241 | <b>0.0355</b> | <i>Tmon - This</i> | 0.0793     | -0.1942 | 0.3529 | 0.9997        |
| <i>Tmon - Timb</i> | 0.3312     | 0.0498  | 0.6125 | <b>0.0067</b> | <i>Tmon - Timb</i> | 0.2039     | -0.1180 | 0.5258 | 0.6718        |
| <i>Tmon - Tore</i> | 0.0639     | -0.2431 | 0.3709 | 1.0000        | <i>Tmon - Tore</i> | 0.0224     | -0.2629 | 0.3078 | 1.0000        |
| <i>Tmon - Tpsa</i> | 0.2104     | -0.0809 | 0.5016 | 0.4579        | <i>Tmon - Tpsa</i> | 0.017      | -0.3050 | 0.3389 | 1.0000        |
| <i>Tmon - Ttor</i> | 0.0527     | -0.2385 | 0.3440 | 1.0000        | <i>Tmuc - Tcat</i> | 0.3876     | 0.1011  | 0.6740 | <b>0.0007</b> |
| <i>Tmuc - Tcat</i> | 0.6249     | 0.3596  | 0.8901 | <b>0.0000</b> | <i>Tmuc - Tchr</i> | 0.2761     | -0.1395 | 0.6917 | 0.5943        |
| <i>Tmuc - Tchr</i> | 0.3519     | -0.0460 | 0.7498 | 0.1476        | <i>Tmuc - Tcoc</i> | 0.0601     | -0.2876 | 0.4078 | 1.0000        |
| <i>Tmuc - Tcoc</i> | 0.0319     | -0.2246 | 0.2884 | 1.0000        | <i>Tmuc - Tser</i> | 0.0156     | -0.3561 | 0.3873 | 1.0000        |
| <i>Tmuc - Tery</i> | 0.1328     | -0.1552 | 0.4208 | 0.9625        | <i>Tmuc - Tery</i> | 0.0839     | -0.2879 | 0.4556 | 1.0000        |
| <i>Tmuc - Teth</i> | 0.1480     | -0.0940 | 0.3899 | 0.7344        | <i>Tmuc - Teth</i> | 0.1666     | -0.1250 | 0.4582 | 0.8106        |
| <i>Tmuc - This</i> | 0.5929     | 0.3049  | 0.8809 | <b>0.0000</b> | <i>Tmuc - This</i> | 0.349      | 0.0455  | 0.6525 | <b>0.0097</b> |
| <i>Tmuc - Timb</i> | 0.6070     | 0.3465  | 0.8674 | <b>0.0000</b> | <i>Tmuc - Timb</i> | 0.4735     | 0.1258  | 0.8213 | <b>0.0007</b> |
| <i>Tmuc - Tins</i> | 0.1311     | -0.1192 | 0.3813 | 0.8988        | <i>Tmuc - Tins</i> | 0.0714     | -0.2225 | 0.3652 | 1.0000        |
| <i>Tmuc - Tita</i> | 0.1560     | -0.1093 | 0.4212 | 0.7863        | <i>Tmuc - Tita</i> | 0.1914     | -0.1563 | 0.5391 | 0.8494        |
| <i>Tmuc - Tmon</i> | 0.2758     | -0.0432 | 0.5948 | 0.1741        | <i>Tmuc - Tmon</i> | 0.2697     | -0.0781 | 0.6174 | 0.3265        |
| <i>Tmuc - Tore</i> | 0.3397     | 0.0517  | 0.6277 | <b>0.0065</b> | <i>Tmuc - Tore</i> | 0.2921     | -0.0221 | 0.6063 | 0.0978        |
| <i>Tmuc - Tpsa</i> | 0.4862     | 0.2150  | 0.7573 | <b>0.0000</b> | <i>Tmuc - Tpsa</i> | 0.2866     | -0.0611 | 0.6343 | 0.2330        |
| <i>Tmuc - Ttor</i> | 0.3285     | 0.0574  | 0.5997 | <b>0.0043</b> | <i>Tmuc - Ttor</i> | 0.2183     | -0.0959 | 0.5325 | 0.5168        |

## APPENDIX 3 Continued

| Males              | Difference | Lower   | Upper  | <i>p</i>      | Females            | Difference | Lower   | Upper  | <i>p</i> |
|--------------------|------------|---------|--------|---------------|--------------------|------------|---------|--------|----------|
| <i>Tore - Tcat</i> | 0.2852     | 0.0345  | 0.5358 | <b>0.0108</b> | <i>Tore - Tcat</i> | 0.0955     | -0.1108 | 0.3018 | 0.9579   |
| <i>Tore - Tchr</i> | 0.0122     | -0.3761 | 0.4006 | 1.0000        | <i>Tore - This</i> | 0.0569     | -0.1725 | 0.2864 | 0.9999   |
| <i>Tore - This</i> | 0.2532     | -0.0214 | 0.5278 | 0.1061        | <i>Tore - Timb</i> | 0.1815     | -0.1039 | 0.4668 | 0.6655   |
| <i>Tore - Timb</i> | 0.2673     | 0.0217  | 0.5129 | <b>0.0193</b> | <i>Tpsa - Tcat</i> | 0.1010     | -0.1535 | 0.3555 | 0.9895   |
| <i>Tore - Tpsa</i> | 0.1465     | -0.1104 | 0.4033 | 0.8219        | <i>Tpsa - This</i> | 0.0624     | -0.2112 | 0.3360 | 1.0000   |
| <i>Tpsa - Tcat</i> | 0.1387     | -0.0924 | 0.3698 | 0.7601        | <i>Tpsa - Timb</i> | 0.1869     | -0.1350 | 0.5089 | 0.7917   |
| <i>Tpsa - This</i> | 0.1067     | -0.1501 | 0.3636 | 0.9853        | <i>Tpsa - Tore</i> | 0.0055     | -0.2799 | 0.2908 | 1.0000   |
| <i>Tpsa - Timb</i> | 0.1208     | -0.1048 | 0.3464 | 0.8818        | <i>Ttor - Tcat</i> | 0.1693     | -0.0370 | 0.3756 | 0.2394   |
| <i>Ttor - Tcat</i> | 0.2963     | 0.0652  | 0.5274 | <b>0.0017</b> | <i>Ttor - Tchr</i> | 0.0578     | -0.3072 | 0.4228 | 1.0000   |
| <i>Ttor - Tchr</i> | 0.0234     | -0.3526 | 0.3994 | 1.0000        | <i>Ttor - This</i> | 0.1307     | -0.0987 | 0.3602 | 0.8137   |
| <i>Ttor - This</i> | 0.2644     | 0.0075  | 0.5212 | <b>0.0369</b> | <i>Ttor - Timb</i> | 0.2553     | -0.0301 | 0.5406 | 0.1333   |
| <i>Ttor - Timb</i> | 0.2784     | 0.0528  | 0.5040 | <b>0.0032</b> | <i>Ttor - Tmon</i> | 0.0514     | -0.2340 | 0.3367 | 1.0000   |
| <i>Ttor - Tore</i> | 0.0112     | -0.2457 | 0.2680 | 1.0000        | <i>Ttor - Tore</i> | 0.0738     | -0.1695 | 0.3172 | 0.9994   |
| <i>Ttor - Tpsa</i> | 0.1576     | -0.0802 | 0.3954 | 0.6090        | <i>Ttor - Tpsa</i> | 0.0683     | -0.2170 | 0.3537 | 1.0000   |



## APPENDIX 4

RECLASSIFICATION RATES BASED ON THE LINEAR DISCRIMINANT FUNCTION  
GENERATED WITH MORPHOMETRIC DATA OF MALE *TROPIDURUS*. CROSS-  
VALIDATION RESULTS (LEAVE-ONE-OUT METHOD) SHOWN IN PARENTHESES  
AND CORRECT CLASSIFICATIONS HIGHLIGHTED IN BOLD.

| Species                         | 1                     | 2                     | 3                     | 4                     | 5                     | 6                     | 7                     | 8                     | 9                     | 10                    | 11                    | 12                    | 13                    | 14                    | 15                    | 16                    |
|---------------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| 1. <i>T. catalanensis</i>       | <b>0.56</b><br>(0.33) | -                     | -                     | -                     | -                     | -                     | -                     | -                     | 0.11<br>(0.22)        | -                     | -                     | -                     | -                     | -                     | 0.22<br>(0.33)        | 0.11<br>(0.11)        |
| 2. <i>T. chromatops</i>         | -                     | <b>1.00</b><br>(0.00) | -                     | -                     | -                     | 0.00<br>(0.50)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.50)        | -                     | -                     |
| 3. <i>T. cocorobensis</i>       | -                     | -                     | <b>0.91</b><br>(0.82) | -                     | -                     | -                     | -                     | 0.09<br>(0.09)        | -                     | 0.00<br>(0.09)        | -                     | -                     | -                     | -                     | -                     | -                     |
| 4. <i>T. sertanejo</i> , n. sp. | -                     | -                     | -                     | <b>0.80</b><br>(0.60) | -                     | 0.20<br>(0.40)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     |
| 5. <i>T. erythrocephalus</i>    | -                     | 0.17<br>(0.17)        | -                     | -                     | <b>0.17</b><br>(0.00) | 0.50<br>(0.67)        | -                     | -                     | -                     | 0.17<br>(0.17)        | -                     | -                     | -                     | -                     | -                     | -                     |
| 6. <i>T. etheridgei</i>         | -                     | -                     | -                     | -                     | 0.12<br>(0.18)        | <b>0.76</b><br>(0.59) | -                     | -                     | -                     | -                     | 0.06<br>(0.06)        | 0.00<br>(0.06)        | 0.00<br>(0.06)        | -                     | -                     | 0.06<br>(0.06)        |
| 7. <i>T. hispidus</i>           | 0.00<br>(0.17)        | -                     | -                     | -                     | -                     | -                     | <b>0.83</b><br>(0.67) | -                     | -                     | -                     | -                     | -                     | -                     | -                     | 0.17<br>(0.17)        | -                     |
| 8. <i>T. hygomi</i>             | -                     | -                     | 0.07<br>(0.07)        | -                     | -                     | 0.07<br>(0.14)        | -                     | <b>0.86</b><br>(0.79) | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     |
| 9. <i>T. imbituba</i>           | 0.10<br>(0.40)        | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.10)        | -                     | <b>0.80</b><br>(0.40) | -                     | -                     | -                     | -                     | -                     | 0.10<br>(0.10)        | -                     |
| 10. <i>T. insulanus</i>         | -                     | -                     | -                     | -                     | -                     | 0.08<br>(0.08)        | -                     | -                     | -                     | <b>0.92</b><br>(0.77) | (0.15)                | -                     | -                     | -                     | -                     | -                     |
| 11. <i>T. itambere</i>          | -                     | -                     | -                     | -                     | -                     | 0.11<br>(0.11)        | -                     | -                     | -                     | 0.11<br>(0.11)        | <b>0.78</b><br>(0.78) | -                     | -                     | -                     | -                     | -                     |
| 12. <i>T. montanus</i>          | -                     | -                     | -                     | -                     | -                     | 0.25<br>(0.25)        | -                     | -                     | -                     | -                     | -                     | <b>0.50</b><br>(0.25) | 0.25<br>(0.25)        | 0.00<br>(0.25)        | -                     | -                     |
| 13. <i>T. mucujensis</i>        | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.40)        | -                     | -                     | -                     | 0.20<br>(0.20)        | -                     | -                     | <b>0.80</b><br>(0.40) | -                     | -                     | -                     |
| 14. <i>T. oreadicus</i>         | -                     | 0.00<br>(0.17)        | -                     | -                     | -                     | -                     | 0.00<br>(0.17)        | -                     | -                     | -                     | -                     | 0.17<br>(0.17)        | -                     | <b>0.83</b><br>(0.50) | -                     | -                     |
| 15. <i>T. psammonastes</i>      | 0.13<br>(0.25)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | <b>0.75</b><br>(0.50) | 0.13<br>(0.25)        |
| 16. <i>T. torquatus</i>         | -                     | -                     | -                     | -                     | -                     | 0.13<br>(0.25)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.13)        | <b>0.88</b><br>(0.63) |

## APPENDIX 5

SPECIES RECLASSIFICATION RATES BASED ON THE LINEAR DISCRIMINANT FUNCTION GENERATED WITH MORPHOMETRIC DATA OF FEMALE *TROPIDURUS*.  
CROSS-VALIDATION RESULTS (LEAVE-ONE-OUT METHOD) SHOWN IN PARENTHESES AND CORRECT CLASSIFICATIONS HIGHLIGHTED IN BOLD.

| Species                         | 1                     | 2                     | 3                     | 4                     | 5                     | 6                     | 7                     | 8                     | 9                     | 10                    | 11                    | 12                   | 13                    | 14                    | 15 | 16                    |
|---------------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|----------------------|-----------------------|-----------------------|----|-----------------------|
| 1. <i>T. catalanensis</i>       | <b>0.88</b><br>(0.69) | -                     | -                     | -                     | -                     | 0.06                  | -                     | -                     | 0.00                  | -                     | -                     | -                    | -                     | -                     | -  | 0.06<br>(0.13)        |
| 2. <i>T. chromatops</i>         | -                     | <b>1.00</b><br>(0.00) | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                    | 0.00                  | -                     | -  | -                     |
| 3. <i>T. cocorobensis</i>       | -                     | -                     | <b>0.75</b><br>(0.25) | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                    | -                     | -                     | -  | 0.25<br>(0.75)        |
| 4. <i>T. sertanejo</i> , n. sp. | -                     | -                     | -                     | <b>1.00</b><br>(0.33) | 0.00                  | -                     | -                     | -                     | -                     | -                     | -                     | -                    | -                     | -                     | -  | -                     |
| 5. <i>T. erythrocephalus</i>    | -                     | -                     | -                     | -                     | <b>1.00</b><br>(0.33) | 0.00                  | -                     | -                     | -                     | 0.00                  | -                     | -                    | -                     | -                     | -  | -                     |
| 6. <i>T. etheridgei</i>         | -                     | -                     | 0.00                  | -                     | 0.08                  | <b>0.92</b><br>(0.54) | 0.00                  | -                     | -                     | -                     | 0.00                  | -                    | -                     | -                     | -  | 0.00<br>(0.08)        |
| 7. <i>T. hispidus</i>           | 0.22<br>(0.22)        | -                     | -                     | -                     | -                     | 0.11                  | <b>0.56</b><br>(0.33) | -                     | -                     | 0.00                  | -                     | -                    | -                     | 0.11                  | -  | -                     |
| 8. <i>T. hygomi</i>             | -                     | -                     | -                     | -                     | -                     | -                     | -                     | <b>1.00</b><br>(1.00) | -                     | -                     | -                     | -                    | -                     | -                     | -  | -                     |
| 9. <i>T. imbituba</i>           | 0.50<br>(0.75)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | <b>0.50</b><br>(0.25) | -                     | -                     | -                    | -                     | -                     | -  | -                     |
| 10. <i>T. insulanus</i>         | -                     | -                     | -                     | -                     | -                     | 0.00                  | -                     | -                     | -                     | <b>1.00</b><br>(0.58) | 0.00                  | -                    | -                     | -                     | -  | -                     |
| 11. <i>T. itambere</i>          | -                     | -                     | -                     | -                     | -                     | 0.00                  | -                     | -                     | -                     | 0.00                  | <b>1.00</b><br>(0.25) | -                    | 0.00                  | -                     | -  | -                     |
| 12. <i>T. montanus</i>          | -                     | -                     | -                     | 0.00                  | -                     | 0.00                  | -                     | -                     | -                     | -                     | -                     | <b>1.00</b><br>(0.5) | -                     | -                     | -  | -                     |
| 13. <i>T. mucujensis</i>        | -                     | -                     | -                     | -                     | 0.00                  | -                     | -                     | -                     | -                     | -                     | -                     | 0.00                 | <b>1.00</b><br>(0.33) | -                     | -  | -                     |
| 14. <i>T. oreadicus</i>         | -                     | -                     | -                     | -                     | -                     | 0.00                  | 0.14                  | -                     | -                     | -                     | -                     | -                    | -                     | <b>0.86</b><br>(0.57) | -  | -                     |
| 15. <i>T. psammonastes</i>      | 0.25<br>(0.50)        | -                     | -                     | -                     | -                     | 0.25                  | -                     | -                     | -                     | -                     | -                     | -                    | -                     | -                     | -  | <b>0.50</b><br>(0.25) |
| 16. <i>T. torquatus</i>         | 0.00<br>(0.14)        | -                     | 0.00                  | -                     | -                     | 0.14                  | -                     | -                     | 0.00                  | -                     | -                     | -                    | -                     | -                     | -  | <b>0.86</b><br>(0.43) |

## APPENDIX 6

SPECIES RECLASSIFICATION RATES BASED ON THE SIZE-FREE LINEAR DISCRIMINANT FUNCTION GENERATED WITH MORPHOMETRIC DATA OF MALE *TROPIDURUS*. CROSS-VALIDATION RESULTS (LEAVE-ONE-OUT METHOD) SHOWN IN PARENTHESES AND CORRECT CLASSIFICATIONS HIGHLIGHTED IN BOLD.

| Species                         | 1                     | 2                     | 3                     | 4                     | 5                     | 6                     | 7                     | 8                     | 9                     | 10                    | 11                    | 12                    | 13                    | 14                    | 15                    | 16                    |
|---------------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| 1. <i>T. catalanensis</i>       | <b>0.44</b><br>(0.22) | -                     | 0.00<br>(0.11)        | -                     | -                     | 0.11<br>(0.11)        | -                     | -                     | 0.11<br>(0.11)        | 0.11<br>(0.11)        | -                     | -                     | -                     | -                     | 0.22<br>(0.33)        | -                     |
| 2. <i>T. chromatops</i>         | -                     | <b>1.00</b><br>(0.00) | -                     | -                     | -                     | 0.00<br>(0.50)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.50)        | -                     | -                     |
| 3. <i>T. cocorobensis</i>       | 0.09<br>(0.09)        | -                     | <b>0.73</b><br>(0.64) | -                     | -                     | -                     | -                     | 0.09<br>(0.09)        | -                     | -                     | -                     | -                     | -                     | -                     | 0.09<br>(0.18)        | -                     |
| 4. <i>T. sertanejo</i> , n. sp. | -                     | -                     | -                     | <b>1.00</b><br>(0.20) | -                     | 0.00<br>(0.20)        | 0.00<br>(0.40)        | -                     | 0.00<br>(0.20)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     |
| 5. <i>T. erythrocephalus</i>    | -                     | -                     | -                     | -                     | <b>0.17</b><br>(0.00) | 0.67<br>(0.67)        | -                     | -                     | 0.00<br>(0.17)        | 0.17<br>(0.17)        | -                     | -                     | -                     | -                     | -                     | -                     |
| 6. <i>T. etheridgei</i>         | 0.06<br>(0.12)        | -                     | -                     | -                     | 0.06<br>(0.12)        | <b>0.76</b><br>(0.47) | -                     | -                     | 0.06<br>(0.18)        | 0.00<br>(0.06)        | -                     | -                     | -                     | -                     | -                     | 0.06<br>(0.06)        |
| 7. <i>T. hispidus</i>           | -                     | -                     | -                     | -                     | 0.00<br>(0.17)        | 0.17<br>(0.33)        | <b>0.67</b><br>(0.17) | -                     | -                     | -                     | -                     | 0.00<br>(0.17)        | -                     | 0.17<br>(0.17)        | -                     | -                     |
| 8. <i>T. hygomi</i>             | -                     | -                     | 0.07<br>(0.07)        | -                     | -                     | 0.14<br>(0.14)        | -                     | <b>0.79</b><br>(0.71) | -                     | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.07)        | -                     |
| 9. <i>T. imbituba</i>           | -                     | -                     | 0.10<br>(0.10)        | 0.10<br>(0.10)        | -                     | 0.30<br>(0.30)        | -                     | -                     | <b>0.50</b><br>(0.40) | -                     | -                     | -                     | -                     | 0.00<br>(0.10)        | -                     | -                     |
| 10. <i>T. insulanus</i>         | -                     | -                     | -                     | -                     | -                     | 0.08<br>(0.15)        | -                     | -                     | -                     | <b>0.92</b><br>(0.54) | 0.00<br>(0.15)        | -                     | -                     | -                     | -                     | 0.00<br>(0.15)        |
| 11. <i>T. itambere</i>          | -                     | -                     | -                     | -                     | -                     | 0.11<br>(0.11)        | -                     | -                     | -                     | 0.11<br>(0.11)        | <b>0.78</b><br>(0.67) | -                     | -                     | -                     | 0.00<br>(0.11)        | -                     |
| 12. <i>T. montanus</i>          | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | 0.50<br>(0.50)        | 0.25<br>(0.25)        | 0.25<br>(0.25)        | <b>0.00</b><br>(0.00) | -                     | -                     | -                     | -                     |
| 13. <i>T. mucujensis</i>        | 0.20<br>(0.20)        | -                     | -                     | -                     | -                     | 0.40<br>(0.20)        | -                     | -                     | 0.00<br>(0.20)        | -                     | -                     | -                     | <b>0.40</b><br>(0.40) | -                     | -                     | -                     |
| 14. <i>T. oreadicus</i>         | -                     | 0.00<br>(0.17)        | -                     | -                     | -                     | 0.00<br>(0.17)        | -                     | -                     | -                     | -                     | -                     | 0.17<br>(0.17)        | -                     | <b>0.83</b><br>(0.50) | -                     | -                     |
| 15. <i>T. psammonastes</i>      | 0.25<br>(0.25)        | -                     | -                     | -                     | -                     | -                     | -                     | 0.13<br>(0.13)        | -                     | -                     | -                     | -                     | -                     | -                     | <b>0.50</b><br>(0.50) | 0.13<br>(0.13)        |
| 16. <i>T. torquatus</i>         | -                     | -                     | 0.00<br>(0.13)        | -                     | -                     | 0.50<br>(0.50)        | -                     | -                     | 0.13<br>(0.13)        | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.13)        | <b>0.38</b><br>(0.13) |

## APPENDIX 7

SPECIES RECLASSIFICATION RATES BASED ON THE SIZE-FREE LINEAR DISCRIMINANT FUNCTION GENERATED WITH MORPHOMETRIC DATA OF FEMALE *TROPIDURUS*. CROSS-VALIDATION RESULTS (LEAVE-ONE-OUT METHOD) SHOWN IN PARENTHESES AND CORRECT CLASSIFICATION HIGHLIGHTED IN BOLD.

| Species                         | 1                     | 2                     | 3                     | 4                     | 5                     | 6                     | 7                     | 8                     | 9                     | 10                    | 11                    | 12                    | 13                    | 14                    | 15             | 16                    |
|---------------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|----------------|-----------------------|
| 1. <i>T. catalanensis</i>       | <b>0.81</b><br>(0.75) | -                     | -                     | -                     | -                     | 0.13<br>(0.13)        | -                     | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.06)        | -                     | -              | 0.06<br>(0.06)        |
| 2. <i>T. chromatops</i>         | -                     | <b>1.00</b><br>(0.00) | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | 0.00<br>(1.00)        | -                     | -              | -                     |
| 3. <i>T. cocorobensis</i>       | 0.25<br>(0.25)        | -                     | <b>0.50</b><br>(0.00) | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -              | 0.25<br>(0.75)        |
| 4. <i>T. sertanejo</i> , n. sp. | -                     | -                     | -                     | <b>1.00</b><br>(0.00) | 0.00<br>(0.33)        | 0.00<br>(0.33)        | -                     | -                     | -                     | 0.00<br>(0.33)        | -                     | -                     | -                     | -                     | -              | -                     |
| 5. <i>T. erythrocephalus</i>    | 0.33<br>(0.33)        | -                     | -                     | -                     | <b>0.67</b><br>(0.33) | 0.00<br>(0.33)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -              | -                     |
| 6. <i>T. etheridgei</i>         | 0.15<br>(0.31)        | -                     | -                     | 0.08<br>(0.15)        | -                     | <b>0.77</b><br>(0.46) | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.08)        | -                     | -                     | -              | -                     |
| 7. <i>T. hispidus</i>           | 0.22<br>(0.22)        | -                     | -                     | -                     | -                     | 0.00<br>(0.11)        | <b>0.44</b><br>(0.33) | -                     | -                     | 0.22<br>(0.22)        | -                     | -                     | -                     | -                     | 0.11<br>(0.11) | -                     |
| 8. <i>T. hygomi</i>             | -                     | -                     | -                     | -                     | -                     | -                     | -                     | <b>1.00</b><br>(1.00) | -                     | -                     | -                     | -                     | -                     | -                     | -              | -                     |
| 9. <i>T. imbituba</i>           | 0.50<br>(1.00)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | <b>0.50</b><br>(0.00) | -                     | -                     | -                     | -                     | -                     | -              | -                     |
| 10. <i>T. insulanus</i>         | 0.00<br>(0.08)        | -                     | -                     | -                     | -                     | 0.00<br>(0.08)        | 0.25<br>(0.25)        | -                     | -                     | <b>0.75</b><br>(0.42) | 0.00<br>(0.08)        | -                     | -                     | 0.00<br>(0.08)        | -              | -                     |
| 11. <i>T. itambere</i>          | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.25)        | -                     | -                     | -                     | 0.00<br>(0.25)        | <b>1.00</b><br>(0.25) | -                     | 0.00<br>(0.25)        | -                     | -              | -                     |
| 12. <i>T. montanus</i>          | 0.00<br>(0.25)        | -                     | -                     | 0.00<br>(0.25)        | -                     | -                     | -                     | -                     | 0.00<br>(0.25)        | -                     | -                     | <b>1.00</b><br>(0.25) | -                     | -                     | -              | -                     |
| 13. <i>T. mucujensis</i>        | -                     | -                     | -                     | -                     | 0.00<br>(0.33)        | -                     | -                     | -                     | -                     | -                     | -                     | 0.00<br>(0.33)        | <b>1.00</b><br>(0.33) | -                     | -              | -                     |
| 14. <i>T. oreadicus</i>         | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | 0.29<br>(0.43)        | -                     | -                     | -                     | <b>0.71</b><br>(0.57) | -              | -                     |
| 15. <i>T. psammonastes</i>      | 0.25<br>(0.50)        | -                     | -                     | -                     | -                     | 0.25<br>(0.25)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -              | <b>0.50</b><br>(0.25) |
| 16. <i>T. torquatus</i>         | 0.14<br>(0.14)        | -                     | 0.00<br>(0.14)        | -                     | -                     | 0.14<br>(0.14)        | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -                     | -              | <b>0.71</b><br>(0.57) |

## APPENDIX 8

SPECIES RECLASSIFICATION RATES BASED ON THE LINEAR DISCRIMINANT FUNCTION GENERATED WITH MERISTIC DATA OF *TROPIDURUS*. CROSS-VALIDATION RESULTS (LEAVE-ONE-OUT METHOD) SHOWN IN PARENTHESES AND CORRECT CLASSIFICATIONS HIGHLIGHTED IN BOLD.

| Species                         | 1                              | 2                              | 3                              | 4                              | 5                              | 6                              | 7                              | 8                              | 9                              | 10                             | 11                             | 12                             | 13                             | 14                             | 15                             | 16                             |
|---------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|
| 1. <i>T. catalanensis</i>       | <b>0.91</b><br>( <b>0.90</b> ) | -                              | -                              | -                              | -                              | -                              | -                              | -                              | 0.05<br>(0.05)                 | -                              | -                              | 0.01<br>(0.01)                 | 0.01<br>(0.01)                 | -                              | -                              | 0.01<br>(0.03)                 |
| 2. <i>T. chromatops</i>         | 0.25<br>(0.25)                 | <b>0.00</b><br>( <b>0.00</b> ) | -                              | -                              | -                              | 0.25<br>(0.25)                 | -                              | -                              | -                              | -                              | -                              | 0.50<br>(0.50)                 | -                              | -                              | -                              | -                              |
| 3. <i>T. cocorobensis</i>       | -                              | -                              | <b>0.75</b><br>( <b>0.69</b> ) | -                              | 0.06<br>(0.06)                 | -                              | -                              | 0.13<br>(0.19)                 | -                              | -                              | -                              | -                              | 0.06<br>(0.06)                 | -                              | -                              | -                              |
| 4. <i>T. sertanejo</i> , n. sp. | -                              | -                              | -                              | <b>0.43</b><br>( <b>0.38</b> ) | -                              | 0.05<br>(0.05)                 | -                              | -                              | -                              | 0.19<br>(0.19)                 | 0.05<br>(0.05)                 | 0.05<br>(0.05)                 | 0.10<br>(0.14)                 | 0.14<br>(0.14)                 | -                              | -                              |
| 5. <i>T. erythrocephalus</i>    | -                              | -                              | -                              | -                              | <b>0.67</b><br>( <b>0.60</b> ) | -                              | -                              | -                              | -                              | -                              | -                              | 0.27<br>(0.27)                 | -                              | 0.07<br>(0.13)                 | -                              | -                              |
| 6. <i>T. etheridgei</i>         | -                              | -                              | -                              | 0.11<br>(0.11)                 | 0.11<br>(0.16)                 | <b>0.63</b><br>( <b>0.53</b> ) | -                              | -                              | -                              | 0.05<br>(0.05)                 | -                              | 0.11<br>(0.16)                 | -                              | -                              | -                              | -                              |
| 7. <i>T. hispidus</i>           | -                              | -                              | -                              | -                              | -                              | 0.05<br>(0.05)                 | <b>0.80</b><br>( <b>0.80</b> ) | -                              | -                              | -                              | 0.05<br>(0.05)                 | -                              | -                              | 0.05<br>(0.05)                 | 0.05<br>(0.05)                 | -                              |
| 8. <i>T. hygomi</i>             | -                              | -                              | 0.09<br>(0.09)                 | -                              | 0.04<br>(0.04)                 | -                              | -                              | <b>0.87</b><br>( <b>0.87</b> ) | -                              | -                              | -                              | -                              | -                              | -                              | -                              | -                              |
| 9. <i>T. imbituba</i>           | 0.63<br>(0.69)                 | -                              | -                              | -                              | 0.06<br>(0.06)                 | -                              | -                              | -                              | <b>0.31</b><br>( <b>0.25</b> ) | -                              | -                              | -                              | -                              | -                              | -                              | -                              |
| 10. <i>T. insulanus</i>         | -                              | -                              | -                              | 0.09<br>(0.17)                 | -                              | 0.00<br>(0.04)                 | 0.04<br>(0.04)                 | -                              | -                              | <b>0.87</b><br>( <b>0.65</b> ) | -                              | -                              | -                              | 0.00<br>(0.09)                 | -                              | -                              |
| 11. <i>T. itambere</i>          | -                              | -                              | -                              | 0.06<br>(0.06)                 | -                              | 0.06<br>(0.06)                 | -                              | -                              | -                              | 0.00<br>(0.06)                 | <b>0.88</b><br>( <b>0.81</b> ) | -                              | -                              | -                              | -                              | -                              |
| 12. <i>T. montanus</i>          | 0.03<br>(0.07)                 | -                              | -                              | -                              | 0.10<br>(0.17)                 | 0.10<br>(0.10)                 | -                              | -                              | 0.03<br>(0.03)                 | -                              | -                              | <b>0.69</b><br>( <b>0.59</b> ) | 0.03<br>(0.03)                 | -                              | -                              | -                              |
| 13. <i>T. mucujensis</i>        | 0.13<br>(0.13)                 | -                              | -                              | 0.07<br>(0.07)                 | -                              | 0.13<br>(0.13)                 | -                              | -                              | -                              | -                              | -                              | 0.40<br>(0.47)                 | <b>0.20</b><br>( <b>0.13</b> ) | -                              | -                              | 0.07<br>(0.07)                 |
| 14. <i>T. oreadicus</i>         | -                              | -                              | -                              | -                              | 0.15<br>(0.15)                 | -                              | -                              | -                              | -                              | 0.46<br>(0.62)                 | 0.08<br>(0.08)                 | -                              | -                              | <b>0.31</b><br>( <b>0.15</b> ) | -                              | -                              |
| 15. <i>T. psammonastes</i>      | -                              | -                              | -                              | -                              | -                              | -                              | 0.00<br>(0.09)                 | -                              | -                              | -                              | -                              | -                              | -                              | 0.09<br>(0.09)                 | <b>0.91</b><br>( <b>0.82</b> ) | -                              |
| 16. <i>T. torquatus</i>         | 0.56<br>(0.63)                 | -                              | -                              | -                              | -                              | -                              | -                              | -                              | 0.06<br>(0.06)                 | -                              | -                              | 0.13<br>(0.13)                 | -                              | -                              | -                              | <b>0.25</b><br>( <b>0.19</b> ) |

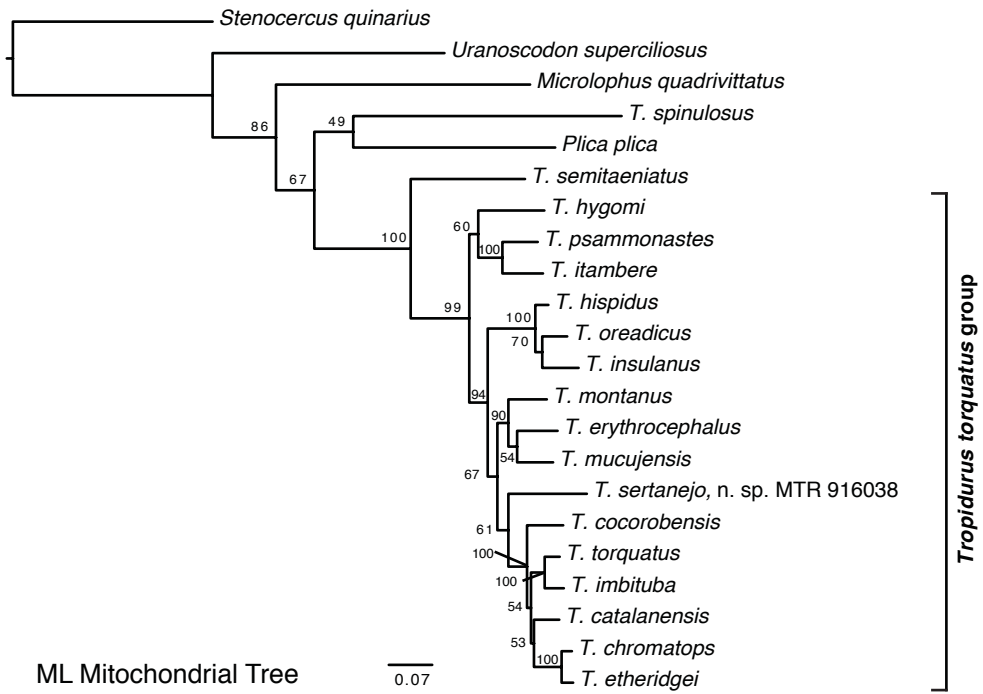
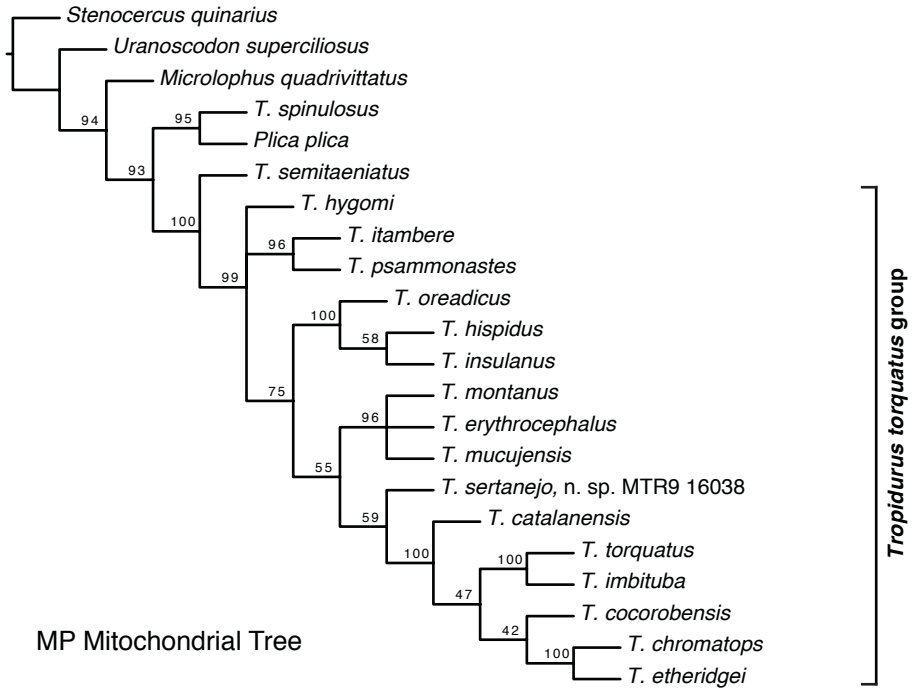
## APPENDIX 9

DATA PARTITIONS AND RESPECTIVE MODELS OF NUCLEOTIDE EVOLUTION  
SELECTED FOR ML ANALYSES OF MITOCHONDRIAL AND NUCLEAR LOCI OF  
*TROPIDURUS*. ALIGNMENTS INCLUDING ONLY ONE SAMPLE OF  
*T. SERTANEJO*, N. SP. (MTR 916038).

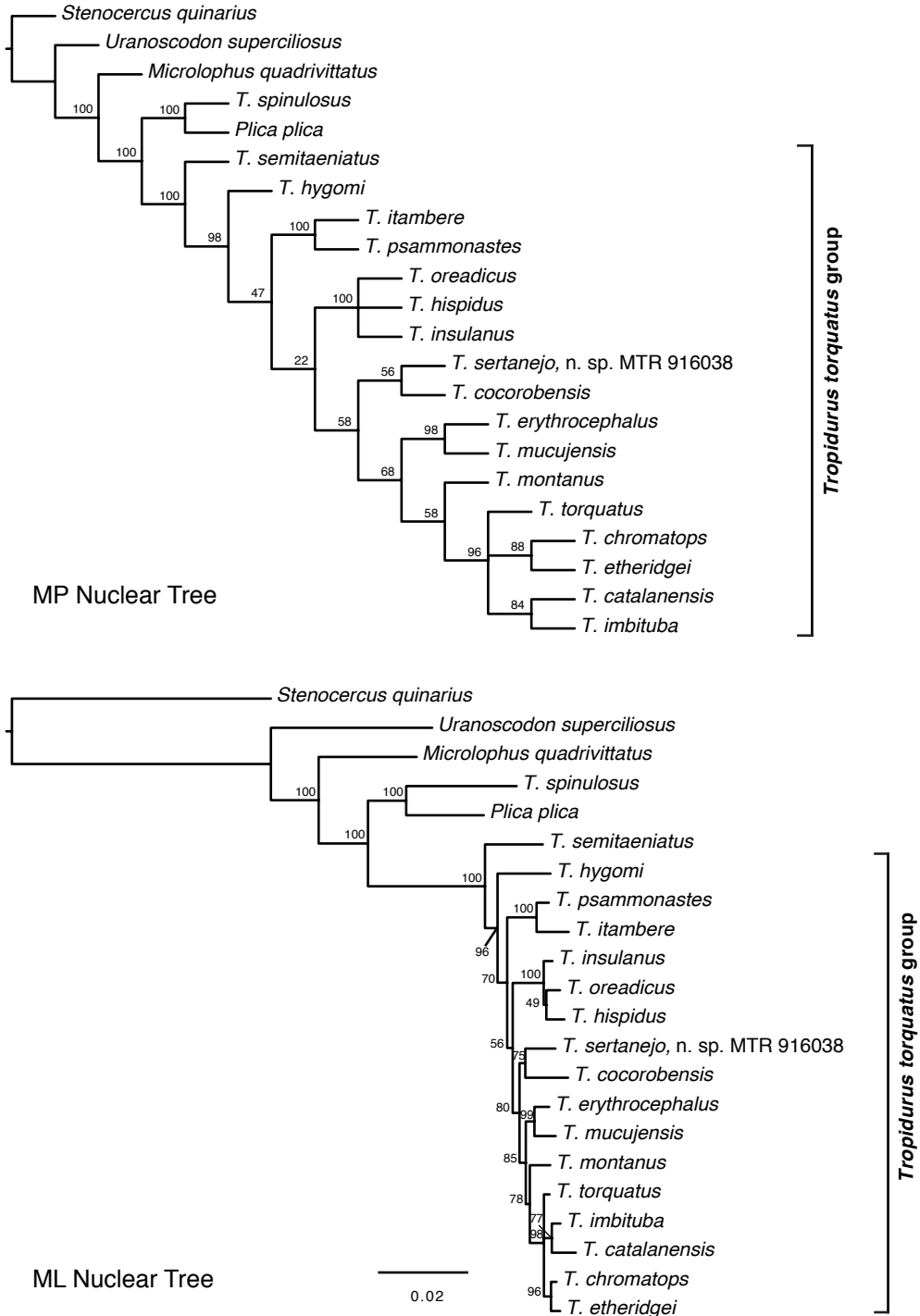
| Data Set                       | Subset | Best Model | Subset Partitions                                   | Subset sites  |
|--------------------------------|--------|------------|---|---|
| <b>Mitochondrial</b>           | 1      | GTR+I+G    | 12S, 16S, Cytb_1                                    | 1-880, 881-1431, 2094-2849                                    |
| Scheme lnL -16956.89           | 2      | TrNef+G    | COL_1   | 1432-2093   |
| Scheme BIC 34526.29            | 3      | HKY+I      | COL_2, Cytb_2                                       | 1433-2093, 2095-2849  |
|                                | 4      | TrN+I+G    | COL_3   | 1434-2093   |
|                                | 5      | TrN+I+G    | Cytb_3  | 2096-2849   |
| <b>Nuclear</b>                 | 1      | HKY+G      | BACH1_2, NTF3_1, PRLR_2, PTPN_3                     | 1-1211, 1213-1881, 1882-2406, 2409-3227                       |
| Scheme lnL -13228.88           | 2      | HKY+I      | BACH1_3, PTPN_1                                     | 2-1211, 2407-3227   |
| Scheme BIC 27050.92            | 3      | HKY+G      | BACH1_1, NTF3_2, NTF3_3, PTPN_2, SNCAIP_1, SNCAIP_3 | 3-1211, 1212-1881, 1214-1881, 2408-3227, 3229-3704, 3230-3704 |
|                                | 4      | K81uf+G    | PRLR_1, PRLR_3, SNCAIP_2, kif24_1, kif24_2          | 1883-2406, 1884-2406, 3228-3704, 3705-4249, 3706-4249         |
|                                | 5      | HKY+G      | kif24_3   | 3707-4249   |
| <b>Mitochondrial + Nuclear</b> | 1      | GTR+I+G    | 12S, 16S, Cytb_1                                    | 1-880, 881-1431, 3305-4060                                    |
| Scheme lnL -30350.96           | 2      | HKY+G      | BACH1_2, NTF3_1, PRLR_2, PTPN_3                     | 1432-2642, 4062-4730, 4731-5255, 5258-6076                    |
| Scheme BIC 61668.48            | 3      | HKY+G      | BACH1_3, PTPN_1, SNCAIP_3                           | 1433-2642, 5256-6076, 6078-6553                               |
|                                | 4      | HKY+G      | BACH1_1, NTF3_2, NTF3_3, PTPN_2, SNCAIP_1           | 1434-2642, 4061-4730, 4063-4730, 5257-6076, 6079-6553         |
|                                | 5      | TrNef+G    | COL_1   | 2643-3304   |
|                                | 6      | HKY+I      | COL_2, Cytb_2                                       | 2644-3304, 3306-4060  |
|                                | 7      | TrN+I+G    | COL_3   | 2645-3304   |
|                                | 8      | TrN+I+G    | Cytb_3  | 3307-4060   |
|                                | 9      | K81uf+G    | PRLR_1, PRLR_3, SNCAIP_2, KIF24_1, KIF24_2          | 4732-5255, 4733-5255, 6077-6553, 6554-7098, 6555-7098         |
|                                | 10     | K81uf+G    | KIF24_3   | 6556-7098   |



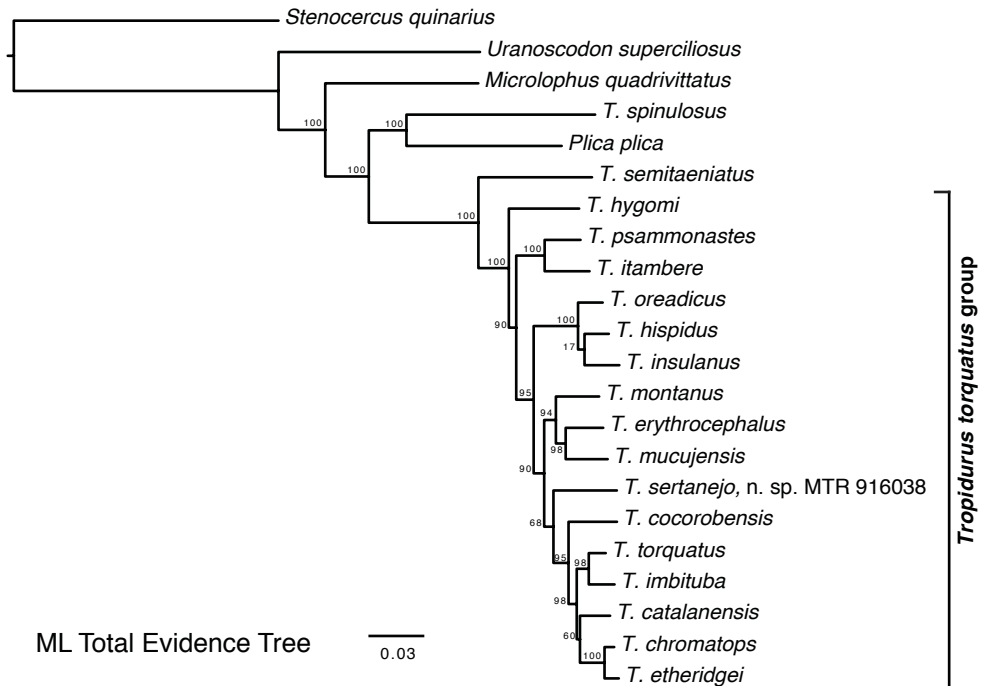
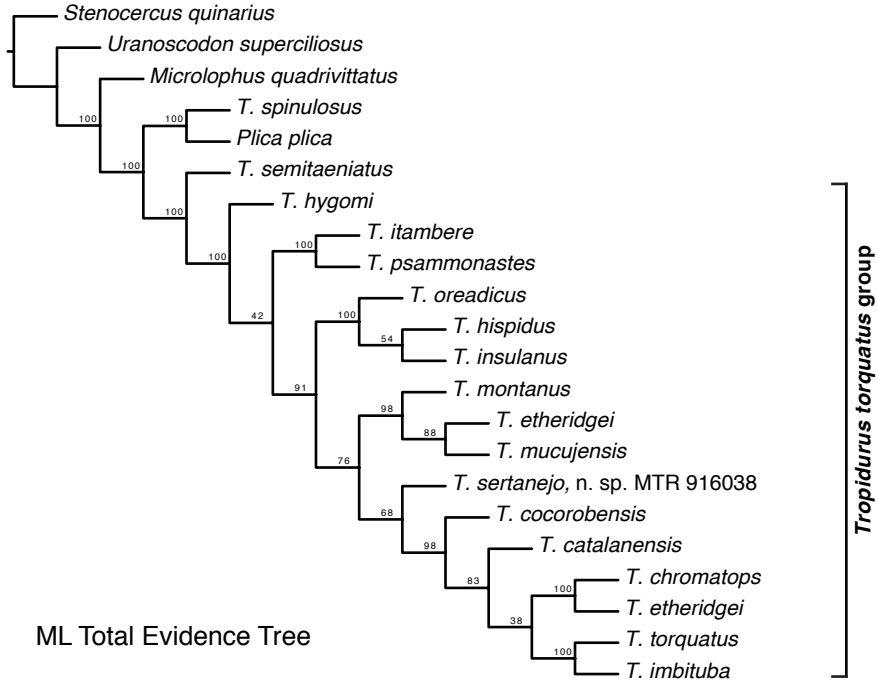
APPENDIX 10. MAXIMUM PARSIMONY (UPPER) AND MAXIMUM LIKELIHOOD (LOWER) TREES OF *TROPIDURUS* BASED ON FOUR MITOCHONDRIAL (12S, 16S, CO1, CYT B) LOCI. NUMBERS ASSOCIATED TO NODES REFER TO BOOTSTRAP VALUES.



APPENDIX 11. MAXIMUM PARSIMONY (UPPER) AND MAXIMUM LIKELIHOOD (LOWER) TREES OF *TROPIDURUS* BASED ON FOUR NUCLEAR (BACH1, KIF24, NTF3, PRLR, PTPN, SNCAIP) LOCI. NUMBERS ASSOCIATED TO NODES REFER TO BOOTSTRAP VALUES.



APPENDIX 12. MAXIMUM PARSIMONY (UPPER) AND MAXIMUM LIKELIHOOD (LOWER) TREES OF *TROPIDURUS* ON 4 MITOCHONDRIAL (12S, 16S, CO1, CYT B) AND 6 NUCLEAR LOCI (BACH1, KIF24, NTF3, PRLR, PTPN, SNCAIP). NODE NUMBERS REFER TO BOOTSTRAP VALUES.





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