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Original Article

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A highly polymorphic South American collared lizard (Tropiduridae: *Tropidurus*) reveals that open–dry refugia from South-western Amazonia staged allopatric speciation

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ABSTRACT

Research on Pleistocene Amazonian refugia has predominantly targeted forest-dwelling taxa, although evidence suggests that endemic species have also evolved in peripheral Amazonian enclaves of open–dry habitats. In Rondônia, Brazil, *Tropidurus* lizards are restricted to savannah relicts that were once connected to the core Cerrado biome. These populations are currently allocated under *Tropidurus oreadicus* but hypothesized to comprise allopatric species that evolved in response to landscape changes induced by Pleistocene climatic fluctuations. Phylogenetic analyses support the monophyly of populations from savannah enclaves from Rondônia but place them as distantly related to *T. oreadicus*. We describe these populations as a new species with unprecedented levels of chromatic polymorphism. A pre-Pleistocene origin is inferred for this new taxon, and dating analysis indicates that *Tropidurus* species endemic to savannah enclaves diverged from relatives distributed in core open–dry biomes in a non-temporally overlapping fashion. Species distribution models estimate vast climatically suitable areas for the new species during the Last Interglacial, followed by significant contraction during the Last Glacial Maximum, and subsequent expansion and northward displacement towards the Holocene and the present. We conclude that landscape transformations played an important role in the evolution of lizards from enclaves, but their speciation history is temporally deeper than previously thought.

Keywords: Cerrado; chromatic polymorphism; endemism; lizards; new species; Pleistocene glaciations; Rondônia; savannah enclaves; *Tropidurus torquatus* species group

INTRODUCTION

Past climatic fluctuations have dramatically altered South American landscapes (Carnaval and Moritz 2008, Werneck *et al.* 2011, 2012, Collevatti *et al.* 2012, Cheng *et al.* 2013, Cohen *et al.* 2014, Leite *et al.* 2016, Bueno *et al.* 2017, Baker *et al.* 2020), with clear reflections on geographical patterns of biodiversity (Antonelli *et al.* 2009, Carnaval *et al.* 2009, Werneck 2011, Leite and Rogers 2013, Leite *et al.* 2016, Baker *et al.* 2020). The highly diverse and geographically heterogeneous Amazonian biota has long attracted the attention of those interested in examining historical and ecological processes underlying speciation (e.g., riverine barriers: Wallace 1852, 1853, Pirani *et al.* 2019; area refugia: Haffer 1969, Bush and Oliveira 2006; river refugia: Haffer 1997, Noonan and Wray 2006; vanishing refugia: Vanzolini

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and Williams 1981, Damasceno *et al.* 2014; gradients: Endler 1977, 1982; disturbance–vicariance: Colinvaux 1993, 1998, Bush 1994; marine incursions: Frailey *et al.* 1988, Hoorn and Vonhof 2006, Hoorn *et al.* 2010; paleoarches and paleobasins: Patton and da Silva 1998, Hoorn *et al.* 2010; taxon pulses: Erwin 1979, Antonelli *et al.* 2009). Nowadays, it is widely agreed upon that only a combination of multiple mechanisms can explain the high biodiversity levels and complex biogeographical patterns of the present-day Amazonia (Haffer 2008, Bonvicino and Weksler 2012, Leite and Rogers 2013). Alpha and beta diversities throughout the biome vary at different rates (Tuomisto *et al.* 2003, Stropp *et al.* 2009, Guedes *et al.* 2018, Fluck *et al.* 2020), and phylogenetic patterns are broadly incongruent among groups (Antonelli *et al.* 2009). Consequently, disentangling the contribution of each particular process that shaped modern Amazonian biodiversity poses a truly daunting challenge (Smith *et al.* 2014).

Quaternary refugia (Haffer 1969), as a model for explaining the impacts of glaciation-driven climatic changes, assumes a classical vicariance-based framework to explain local patterns of high species richness and endemism (Haffer and Prance 2001, Bush and Oliveira 2006, Bonvicino and Weksler 2012, Rocha and Kaefer 2019). Pleistocene climate fluctuations are suggested to have promoted cyclic episodes of retraction and expansion of forested habitats in South America. More specifically, prolonged dry seasons during glacial maxima would have shaped mosaic landscapes composed of forest fragments surrounded by the open-savannah (cerrado) vegetation that invaded and subsumed the once continuous Amazon forest (Haffer 1969, Prance 1973, Bigarella *et al.* 1975, Brown and Ab'Saber 1979, Vanzolini and Williams 1981, Knapp and Mallet 2003, Mayle *et al.* 2004). Nonetheless, despite more recent use of phylogenetic patterns as indices that reflect isolation and speciation associated with forest refugia, some authors argue that geological and palynological data cannot be explained by the fragmentation of Pleistocene forest landscapes. Instead, evidence suggests either continuous occupation by forest habitats (Colinvaux and Oliveira 2000, Colinvaux *et al.* 2000, 2001, Bush and Oliveira 2006) or some uniform retraction as a massive, unfragmented block of humid rainforest (Hooghiemstra and van der Hammen 1998).

Most investigations of Pleistocene Amazonian refugia have explored differences among populations isolated in forested habitats, whereas research addressing the effects of isolation in open–dry habitats surrounded by forest has received far less attention (e.g. Vanzolini 1986, Vitt 1993, Gainsbury and Colli 2003, de Carvalho and Mustin 2017, Ritter *et al.* 2021). Despite that, under the refugial model, the same processes that operate on the biota of forest habitats are expected to have affected the biota of open formations, producing inverse allopatric scenarios driven by landscape modifications. The long-held assumption is that during more humid and hot periods [e.g. Last Interglacial (LIG), between 130 000 and 115 000 years before present (BP)], savannah habitats were reduced to isolated patches surrounded by the ingrown rainforest. These large-scale landscape modifications were thought to be responsible for the origination of numerous savannah relicts (i.e. cerrado enclaves) along the margins of the forested domains of South America (Vanzolini 1992). Nevertheless, recent landscape distribution models produced for South America disagree with classical refugial theory, suggesting that, instead, the Last Glacial Maximum (LGM, between 31 000 and 16 000 years BP) and the LIG were, respectively, the periods of narrowest and widest distribution of the Cerrado savannahs (Werneck *et al.* 2012). We therefore hypothesize that, after the LIG, expansion of the Amazon forest produced a large number of peripheral savannah enclaves that split ancestral populations of heliophilous species, isolating them from their relatives currently found in the core Cerrado biome. Taxa with pronounced territorial behaviour and low dispersal capacity must have been particularly affected, thereby originating independent evolutionary lineages allopatrically. Populations of the lizard genus *Tropidurus* Wied, 1825 found in savannah enclaves of the state of Rondônia, Brazil (Rodrigues 1987, Vitt 1993, Vitt and Caldwell 1993) are among the candidates that experienced effects of historical isolation following the LIG.

Entirely restricted to open–dry habitats of tropical and subtropical Cis-Andean South America, *Tropidurus* comprises 30 species commonly found in the biomes Caatinga, Cerrado, Chaco, Llanos, and Pantanal, and in open environments of the Atlantic Forest, including rocky outcrops, inselbergs, restingas, and sand dunes (Carvalho 2013, Carvalho *et al.* 2018). Frost *et al.* (2001) divided the genus into four monophyletic species groups, which differ from one another in conspicuous morphological features (Table 1). The *Tropidurus torquatus* species group is widely spread across South America, representing the most diverse radiation in the genus (Carvalho *et al.* 2013). Although recent systematic efforts have shed light on the phylogenetic relationships within this clade, the placement of several nominal species remains controversial (Frost 1992, Harvey and Gutberlet 2000, Frost *et al.* 2001, Carvalho *et al.* 2016, 2018), and genetic data suggest that the current taxonomy greatly underestimates its species diversity (Carvalho *et al.* 2016, 2018, Domingos *et al.* 2017). In Amazonia, populations of the *T. torquatus* species group occur isolated in enclaves of cerrado vegetation and occasionally occupy anthropic environments (e.g. peripheral urban sites and rural areas; Rodrigues 1987, Ávila-Pires 1995, Carvalho 2013). Ecophysiological requirements such as high thermoregulatory demands (heliophilia) and strict association with rocky substrates hamper their dispersal through the encircling closed-canopy environments (Carvalho 2013). Thus, investigators interested in determining the identity of such demes might elucidate the role of cerrado enclaves as potential allopatric speciation sites.

The Brazilian State of Rondônia contains fragments of open savannah that are separated from the core Cerrado biome by the surrounding Amazon forest. The first indication that the savannah enclaves from Rondônia could harbour endemic *Tropidurus* lineages came from Vanzolini (1986), who recognized two potentially distinct forms and discussed their possible relationships with other species of the *T. torquatus* species group. Nonetheless, the author refrained from providing formal descriptions, and used vernacular names (*Tropidurus* 'ariquemes' and *Tropidurus* 'santacruz') to refer to his candidate species (Vanzolini 1992). In the most comprehensive taxonomic revision of the *T. torquatus* species group thus far, Rodrigues (1987) did not examine the samples collected by Vanzolini (1986), but assumed that specimens from Ariquemes, Itapuã do Oeste, and Jaru should be conspecific with those from the region of Porto Velho, located ≥ 100 km north-west. Based on external morphological similarities

Table 1. Taxonomic composition, geographical distribution, and list of external morphological characters used to diagnose the four unranked species groups of *Tropidurus* Wied, 1825 defined by Frost *et al.* (2001). Passos *et al.* (2011), Kunz and Borges-Martins (2013), Carvalho (2016), Carvalho *et al.* (2016), and Carvalho *et al.* (2018) expanded three of these species groups to accommodate newly described species and the revalidation of *Tropidurus catalanensis* Gudynas & Skuk, 1983.

Species group	Geographical distribution	Diagnostic external morphological traits
Tropidurus bogerti group *T. bogerti* Roze, 1958	Endemic to the Auyantepui, Department of Bolivar, Southern Venezuela	1. Body cylindrical, moderately compressed dorsoventrally 2. One well-defined row of circumorbitals distinct from other small supraorbital scales 3. Postmental scale series well defined 4. Antegular fold absent 5. Projecting tufts of elongate, spiny scales on the neck present 6. Enlarged middorsal scale row absent 7. Black flash marks delineating α-gland patches on the ventral side of the body
Tropidurus semitaeniatus group *T. helenae* (Manzani & Abe, 1990) *T. jaguaribanus* Passos, Lima & Borges-Nojosa, 2011 *T. pinima* (Rodrigues, 1984) *T. semitaeniatus* (Spix, 1825)	Widespread in the semi-arid Brazilian Caatinga, in the states of Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, and Sergipe	1. Body flat, extremely compressed dorsoventrally 2. One well-defined row of circumorbitals distinct from other small supraorbital scales 3. Postmental scale series well defined 4. Antegular fold absent 5. Projecting tufts of elongate, spiny scales on the neck absent 6. Enlarged middorsal scale row absent 7. Black flash marks delineating α-gland patches on the ventral side of the body, except in *T. helenae* (yellow sulphur)
Tropidurus spinulosus group *T. callathelys* Harvey & Gutberlet, 1998 *T. guarani* Alvarez, Cei & Scolaro, 1994 *T. lagunablanca* Carvalho, 2016 *T. melanopleurus* Boulenger, 1902 *T. spinulosus* (Cope, 1862) *T. tarara* Carvalho, 2016 *T. teyumirim* Carvalho, 2016 *T. xanthochilus* Harvey & Gutberlet, 1998	Open environments of the Cis-Andean Tropical and Sub-tropical South America between parallels 12° and 32°S, including the domains of the Yungas in southern Peru, eastern Bolivia, and northern Argentina, the Chaco in central and southern Bolivia, western Paraguay and north-western Argentina, the southern part of the Cerrado and areas of Pantanal in Central Brazil, northern Paraguay, and south-eastern Bolivia, and exposed sedimentary mountain tops surrounded by semi-deciduous Atlantic Forest in eastern Paraguay	1. Body cylindrical, not particularly compressed 2. Usually, two rows of circumorbitals distinct from other small supraorbital scales, except in *T. callathelys* and *T. melanopleurus* (one row) 3. Postmental scale series relatively poorly defined 4. Antegular fold present, well marked 5. Projecting tufts of elongate, spiny scales on the neck present 6. Enlarged middorsal scale row forming a dorsal crest from nape to tail, taller anteriorly 7. Yellow, orange, or pale flash marks delineating α-gland patches on the ventral side of the body

Table 1. Continued

Species group	Geographical distribution	Diagnostic external morphological traits
Tropidurus torquatus group *T. azurduyae* Carvalho, Rivas, Céspedes & Rodrigues, 2018 *T. catalanensis* Gudynas & Skuk, 1983 *T. chromatops* Harvey & Gutberlet, 1998 *T. cocorobensis* Rodrigues, 1987 *T. erythrocephalus* Rodrigues, 1987 *T. etheridgei* Cei, 1982 *T. hispidus* (Spix, 1825) *T. hygomi* Reinhardt & Lütken, 1862 *T. imbituba* Kunz & 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, Kasahara & Yonenaga-Yassuda, 1988 *T. sertanejo* Carvalho, Sena, Peloso, Machado, Montesinos, Silva, Campbell & Rodrigues, 2016 *T. torquatus* (Wied, 1820)	Open–dry South American diagonal, Amazonian savannah enclaves, and large area of the Brazilian Atlantic coast. From southern Venezuela east through the Guianas to north-eastern Brazil, from there west south of the Amazon region to eastern Bolivia, Paraguay, northern Argentina, and northern Uruguay	1. Body cylindrical, not particularly compressed 2. One well-defined row of circumorbitals distinct from other small supraorbital scales 3. Postmental scale series well defined 4. Antegular fold absent 5. Projecting tufts of elongate, spiny scales on the neck absent; aculeate spines on the lateral neck may be present in *T. mucujensis* 6. Enlarged middorsal scale row absent 7. Black flash marks delineating α-gland patches on the ventral side of the body

(e.g. mite pocket patterns), Rodrigues (1987) adopted the name *Tropidurus oreadicus* Rodrigues, 1987, known to represent a species widespread in the Cerrado biome (Rodrigues 1987, Ávila-Pires 1995, Carvalho 2013), to accommodate all *Tropidurus* populations from savannah enclaves distributed along the edges of Brazilian Amazonia. However, in noting some apparent variation in scale counts, Rodrigues (1987) acknowledged that such populations could represent distinct taxonomic entities.

Six years later, Vitt (1993) and Vitt and Caldwell (1993) analysed colour patterns of the *Tropidurus* from Rondonian savannah enclaves and recognized an additional morphotype among the populations studied by Vanzolini (1986). Nonetheless, Vitt (1993) and Vitt and Caldwell (1993) followed Vanzolini (1986) in using vernacular names to distinguish those populations. These studies by Vitt (1993) and Vitt and Caldwell (1993) provide the first objective summary of the geographical variation of the *Tropidurus* populations from Rondônia. The authors adopted the names *Tropidurus* 'ariquemes', *Tropidurus* 'santacruz', and *Tropidurus* 'santabarbara' to refer to specimens respectively exhibiting the flanks marked by an interrupted white line, a continuous white line, or no line at all. Such variation, however, has never been explored in detail, in part owing to insufficient geographical sampling, but also because an accurate systematic assessment of the polymorphism detected would require a more integrative approach.

In this study, we revisit the taxonomy of the *Tropidurus* populations from savannah enclaves of the State of Rondônia, analysing their external morphology and molecular data (mitochondrial and nuclear markers) and modelling their distribution. To test the putative relationship of such populations to *T. oreadicus* from Central Brazil, we compared specimens from Rondônia with the type series of the latter and performed phylogenetic analyses including samples of all valid nominal species currently assigned to the *T. torquatus* species group. Our results confirmed that the *Tropidurus* populations isolated in Rondônia differ both genetically and morphologically from all other congeners, and we describe them as a single, highly polymorphic species, with broad but largely fragmented distribution in savannah enclaves. Finally, we discuss the processes that might underlie the differentiation the new *Tropidurus* from Rondônia, proposing that the same historical scenario inferred for that species might also explain the evolution of other species that make up the Amazonian peripheral biota.

MATERIALS AND METHODS

Fieldwork and sampling

Fieldwork took place between 14 and 27 November 2017, and during this period A.L.G.C. and R.C.B.P. sampled 133 *Tropidurus* lizards in 9 of 12 localities visited in the State of Rondônia, Brazil, including three sites sampled by Vanzolini (1986) and Vitt (1993) (Fig. 1). The areas were originally covered with savannah (Cerrado) physiognomies, characterized by the presence of sparse trees and a Gramineae matrix interspaced by granitic outcrops. Sampling localities inside or near conservation units were surrounded by dense Amazon rainforest (e.g. Floresta Nacional Jamari), whereas some localities close to urban areas in Porto Velho and Guajará-Mirim had masonry constructions and rubble piles. Anthropic activities such as large-scale plantations and cattle ranching suppressed the forest encircling most cerrado enclaves (Fig. 1).

We euthanized the specimens with an overdose of 2% lidocaine, then extracted tissue samples (muscle or liver) and preserved them in absolute ethyl alcohol for molecular analyses. All specimens were preserved in 10% unbuffered formalin, then transferred to 70% ethyl alcohol solution for permanent deposit in the herpetological collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. Besides our newly collected specimens, we analysed the morphology of 61 museum individuals sampled by P. E. Vanzolini and L. J. Vitt (also housed at MZUSP), for a total sample of 194 *Tropidurus* specimens from Rondônia. Finally, we examined 16 specimens of the type series of *T. oreadicus* Rodrigues, 1987 to assess differences between this nominal species and the *Tropidurus* populations from Rondônia, provisionally allocated under the same name by Rodrigues (1987). Collection permits were granted to us by the Brazilian Ministério do Meio Ambiente through the Sistema de Autorização e Informação em Biodiversidade (SISBIO permits #9005-1, #10126-1, and #60633-1). A full list of specimens examined morphologically is provided in the Supporting Information (File S1). Geographical coordinates associated with all specimens treated in this study have standard datum WGS84.

Molecular analyses

Molecular laboratory procedures

DNA extractions were performed with Promega Wizard Genomic DNA® Kit, following the protocol recommended by the manufacturer, and quantified using a Nanodrop™. Partial fragments of two mitochondrial loci (12S and 16S) and one nuclear locus (*kif24*) were amplified through PCRs, using the sequencing protocol and PCR primers outlined by Carvalho *et al.* (2016). The only modification to their protocol involved the DNA purification step, which was performed via ExoSap reactions (GE Healthcare). Sequencing was performed on an ABI 3100 platform (Applied Biosystems) at the Instituto de Química da Universidade de São Paulo (IQ-USP); DNA fragments were sequenced in the forward and reverse directions. Chromatograms were checked for sequencing errors, and sequence contigs were paired and assembled in GENEIOUS v.9.1.8 (Biomatters, www.geneious.com).

Molecular sampling and outgroups

In addition to the 12S, 16S, and *kif24* fragments sequenced for the samples collected by A.L.G.C. and R.C.B.P., we included data from four mitochondrial (12S, 16S, *Cyt-b*, and *COI*) and six nuclear (*BACH1*, *kif24*, *NTF3*, *PRLR*, *PTPN*, and *SNCAIP*) loci produced by Carvalho (2015) for four specimens of *Tropidurus* previously sampled in Rondônia (two of them from the Parque Nacional da Serra da Cutia, municipality of Guajará-Mirim, and two from the municipality of Porto Velho). Additional sequences corresponding to those same 10 loci, produced by Carvalho *et al.* (2016, 2018) for other tropidurid species treated herein as outgroup taxa, were obtained from GenBank. A full list of samples used in this study is provided in the Supporting Information (File S2).

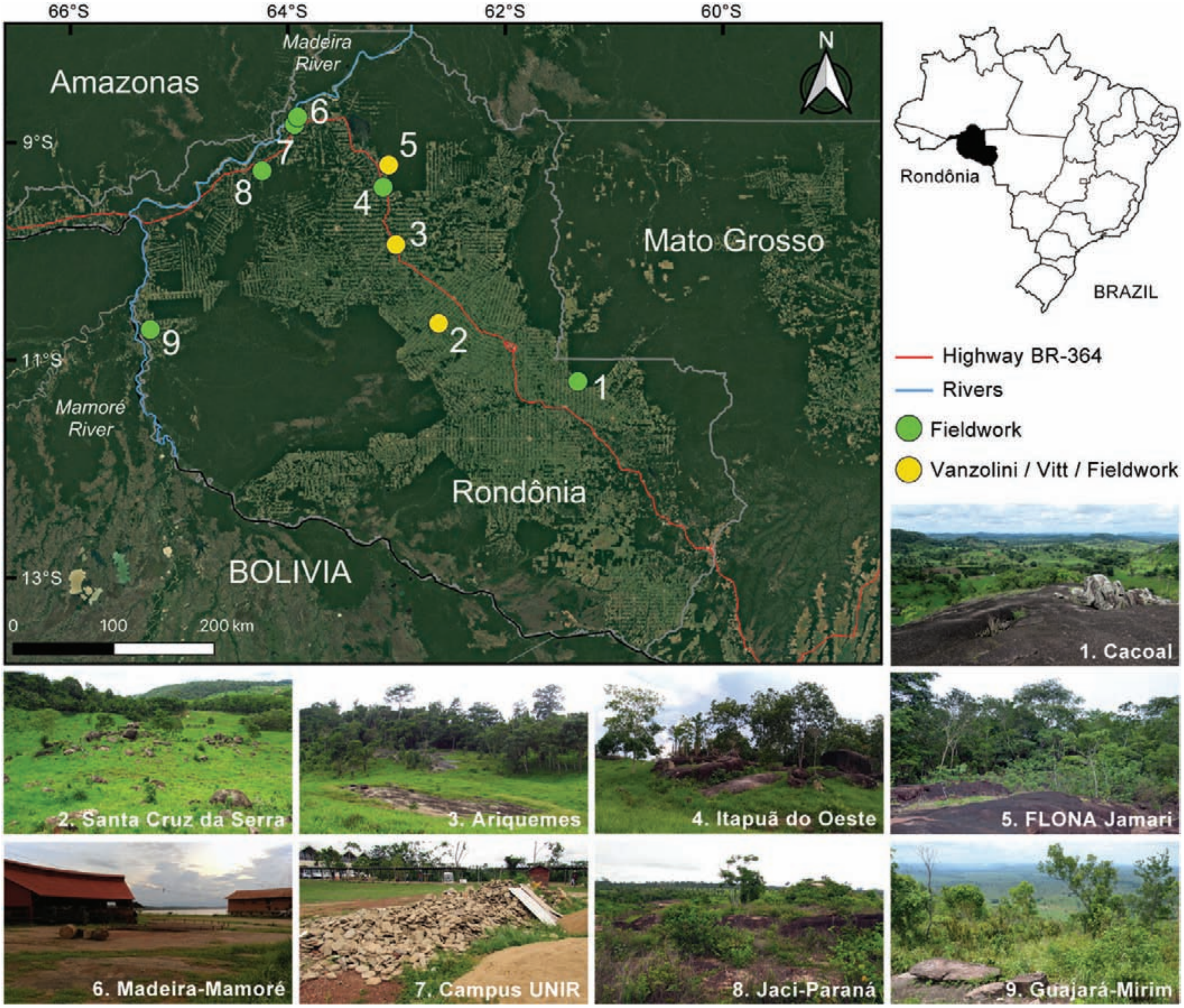

Figure 1. Localities sampled by A.L.G.C. and R.C.B.P. during fieldwork in the State of Rondônia, Brazil, between 14 and 27 November 2017, for collection of *Tropidurus* Wied, 1845. P. E. Vanzolini and L. J. Vitt originally sampled sites 2, 3, and 5 during their studies of the herpetofauna of the state of Rondônia in the early 1980s (for details, see Vanzolini 1986, Vitt 1993). Full locality names: (1) inselberg 'Pedrona da [linha] 10', Cacoal; (2) rock outcrops ~3.5 km west of Santa Cruz da Serra, Jaru; (3) rock outcrops on the southern outskirts of Ariquemes; (4) rock outcrops on the margin of highway BR-364, Itapuã do Oeste; (5) Floresta Nacional (FLONA) Jamari, Itapuã do Oeste (= Vila de Santa Bárbara); (6) margin of the Madeira River near the Museu da Estrada de Ferro Madeira-Mamoré (EFMM), Porto Velho; (7) Universidade Federal de Rondônia (UNIR), Porto Velho; (8) rock outcrops in Jaci-Paraná, Porto Velho; (9) top of Serra dos Parecis, Guajará-Mirim. Refer to the Supporting Information (File S1) for the geographical coordinates of the specimens sampled in each locality.

The selection of outgroups for the present study followed Carvalho *et al.* (2016, 2018). We chose *Stenocercus quinarius* Nogueira & Rodrigues, 2006, a member of the subfamily Stenocercinae, sister to Tropidurinae (Frost *et al.* 2001), for rooting the phylogenetic trees. From Tropidurinae, we sampled *Eurolophosaurus nanuzae* (Rodrigues, 1981), *Microlophus quadrivittatus* (Tschudi, 1845), *Plica plica* (Linnaeus, 1758), *Strobilurus torquatus* Wiegmann, 1834, *Tropidurus bogerti* Roze (1958), *Tropidurus semitaeniatus* (Spix, 1825), *Tropidurus spinulosus* (Cope, 1862), *Uracentron azureum* (Linnaeus, 1758), *Uranoscodon superciliosus* (Linnaeus, 1758), and representatives from all 17 nominal species currently assigned to the *T. torquatus* species group.

Alignment, model selection, and multi-locus phylogenetics

Each locus was aligned separately using the MAFFT v.7 plugin (Katoh and Standley 2013) in GENEIOUS v.9.1.8 (Biomatters, www.geneious.com). We adopted 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. Alignments were concatenated with the aid of SEQUENCEMATRIX v.1.8 (Vaidya *et al.* 2011). The concatenated data set contained 7094 characters, with 4725 conserved sites, 2330 variable sites, 1349 parsimony-informative sites, and 973 singletons. The individual profile of mitochondrial and nuclear loci is shown in Table 2.

To search for the best nucleotide substitution models and determine the most appropriate partitioning scheme, we used PartitionFinder v.2.1.1 (Lanfear *et al.* 2017), which compared all available models using the 'greedy search' algorithm and linked branch lengths. Partitioning schemes were compared statistically using the Bayesian information criterion. In addition to the analysis of the concatenated molecular data, phylogenetic analyses were performed separately for mitochondrial and nuclear loci to inspect potentially contrasting phylogenetic signals between the genomes, affecting tree topology. Tables S1–S3 in the Supporting Information (File S3) provide a summary of the parameters relative to partition schemes and models of nucleotide evolution favoured by PartitionFinder2.

Searches for the best maximum likelihood (ML) trees were carried out in Garli v.2.1 (Zwickl 2006), using the parameters outlined by Carvalho *et al.* (2016). In brief, the initial topologies were generated with the stepwise-addition algorithm, and the search for the best ML tree was based on 100 independent replicates. Clade support was evaluated through 1000 non-parametric bootstrap replicates (Felsenstein 1985). The results of the bootstrap analyses were summarized using the Python package SumTrees v.4.0.0 of the DendroPy phylogenetic computing library (Sukumaran and Holder 2010). All alignments used for phylogenetic analyses and the resulting trees are provided as Supporting Information (Files S4–S9).

Divergence dating

We estimated divergence times in a Bayesian framework using sequence data from the 12S, 16S, and *kif24* loci in BEAST v.2.6.6 (Bouckaert *et al.* 2014). Given that tropidurid fossils are unknown to date, we used the evolution rate of 12S estimated for *Liolaemus* Wiegmann, 1843 by Olave *et al.* (2015) to set a strict molecular clock. We assigned a molecular rate of 0.6339×10^{-2} substitutions/site/Myr to the mitochondrial partition (12S + 16S) and let the *kif24* rate be estimated in relationship to the rate of the mitochondrial DNA. Given that the molecular rate of the nuclear locus is expected to be lower than the mitochondrial rate, we set an exponential prior for *kif24* with a mean of 0.6339×10^{-2} substitutions/site/Myr in order to have a large proportion of the prior distribution density, covering rate values between zero and the informed mean rate. We selected GTR+Γ as the nucleotide evolution model and chose the birth–death speciation model as the tree prior, given that our sampling of terminals is unbalanced. No topological constraints were enforced. Three independent tree search replicates were implemented, adopting random starting seeds and a chain length equal to 900 million generations, sampling every 90 000 steps. We inspected Markov chain Monte Carlo trace files in Tracer v.1.7.1 (Rambaut *et al.* 2018) for chain convergence, adequate effective sample size (≥ 200), and to determine the proportion of burn-in samples. We discarded the first 10% of trees of each run as burn-in and combined samples from independent runs in LogCombiner v.1.10.4 (Drummond and Rambaut 2007). We selected the median heights option to summarize node heights and computed the maximum clade credibility tree with TreeAnnotator v.1.10.4 (Drummond and Rambaut 2007). The .xml file used for divergence dating analysis and the maximum clade credibility tree produced are provided as Supporting Information (Files S10 and S11).

Molecular distances

We calculated molecular distances (*p*-distances) within and between groups of 12S and 16S fragments in MEGA v.11 (Tamura *et al.* 2021), using the complete deletion method. Given that sequence length varied considerably in the original alignments used for the multi-locus phylogenetic analyses, we reduced our molecular matrices and re-aligned the data considering the maximization of sample coverage and sequence length. After eliminating short sequences and trimming sequence tips, a total of 110 and 133 samples were represented in the 12S (423 aligned sites) and 16S (449 aligned sites) matrices, respectively. Alignments used for calculation of *p*-distances are provided as Supporting Information (Files S12 and S13).

Morphological analyses

Determination of sex and age

Using a well-known parameter of sexual dimorphism in the *T. torquatus* species group, adult males were identified as having dark-coloured patches of α-gland scales on the ventral surface of the thighs and the precloacal flap (Carvalho *et al.* 2021). They were differentiated further from females by the larger snout–vent

Table 2. Taxon coverage, number of aligned, conserved, variable, parsimony-informative (Pi) sites, and singletons present in the alignments of mitochondrial and nuclear loci.

Loci	Genome	Coverage	Sites	Conserved	Variable	Pi	Singletons
12S	Mitochondrial	123 (85.4%)	885	481	376	253	115
16S	Mitochondrial	135 (93.8%)	551	357	189	138	51
COI	Mitochondrial	26 (18.1%)	662	404	258	230	28
Cyt-b	Mitochondrial	30 (20.8%)	747	398	349	274	75
BACH1	Nuclear	27 (18.8%)	1211	892	319	103	216
kif24	Nuclear	111 (77.1%)	545	299	246	138	108
NTF3	Nuclear	23 (16.0%)	670	562	108	43	65
PRLR	Nuclear	31 (21.5%)	525	324	198	74	124
PTPN	Nuclear	30 (20.8%)	821	639	179	62	117
SNCAIP	Nuclear	29 (20.1%)	477	369	108	34	74
Total			**7094**	**4725**	**2330**	**1349**	**973**

length (SVL), wider head, and thinner body (Pinto *et al.* 2005). When external secondary sexual characters were not evident or fully developed, gonadal inspection under a stereomicroscope allowed us to determine the sex and developmental stage (juvenile or adult), with adults being identified by the presence of vitellogenic follicles, eggs, or corpora lutea (females) or by enlarged testes and epididymides (males).

Collection of morphological data

Terminology for external morphological features followed Carvalho *et al.* (2016, 2018) . The first step of our morphological approach involved qualitative comparisons of mite pockets (Rodrigues 1987) and coloration patterns. Earlier indications of variation in the presence and composition of stripes on the flanks of specimens by Vitt (1993) and Vitt and Caldwell (1993) helped to guide our assessment of the geographical segregation of chromatic morphotypes. In turn, quantitative analyses were used to compare populations statistically for variation in morphometric and meristic (scale counts) traits that proved informative to distinguish species in the *T. torquatus* group (Rodrigues 1987, Carvalho 2016, 2018). Males and females were treated separately in all statistical analyses. Morphometric measurements and scale counts were taken from the right side of the specimens, with the exception of those whose limbs were partly or fully amputated.

To avoid biases associated with ontogenetic allometry, we measured only adult specimens. We used digital callipers (to the nearest 0.01 mm) to measure snout–vent length (SVL; from rostral tip to the anterior margin of the vent), tail length (TL; from anterior margin of the vent to the tail tip, measured only in specimens with intact tails), body height (BH; halfway between arm and thigh insertion on the trunk), midbody width (MB; at the widest body width between arm and thigh insertion on the trunk), snout–ear opening distance (EOS; from the rostral tip to the anterior margin of the ear), head width (HW; at the widest point), head height (HH; from interparietal to gular region), arm length (AL; from arm insertion on the trunk to humerus tip), forearm length (FAL; from proximal tip of brachium to carpals), thigh length (THL; from thigh insertion on the trunk to knee level), shank length (SL; from knee to heel), foot length (FOL; from heel to tip of toe IV), and armpit to groin distance (AGD; from arm to thigh insertion on the trunk).

For meristic data collection, we counted the number of postrostrals, postmentals, postmentals contacting first infralabials, horizontal rows of loreals and lorilabials, canthals, preoculars, superciliaries, supralabials, infralabials, dorsals, gulars, scales around the midbody, ventrals, cloacals, tibials, lamellae under finger IV, and lamellae under toe IV. Additional meristic features compared among specimens were the presence/absence of contact between the rostral and nasal, and between the posteriormost canthal and preocular.

Statistical comparisons

Morphological comparisons were aimed to test the taxonomic hypotheses erected by Vanzolini (1986), Vitt (1993), and Vitt and Caldwell (1993), in addition to potential novel groupings of populations from areas recently sampled by our team. Qualitative parameters served as our first yardsticks in recognizing candidate species. However, in the absence of qualitative markers consistently supporting assignment of groups to specific localities as suggested by Vanzolini (1986), Vitt (1993), and Vitt and Caldwell (1993), we compared quantitative traits, considering each sampled population as a distinct group. Our statistical analyses involved morphometric and meristic features of 197 (94 males and 103 females) and 163 (75 males and 88 females) specimens, respectively. For all morphological characters, we provide descriptive statistics as: minimum–maximum (mean ± SD), considering specimens from all 12 localities included in our sample (11 in the case of meristic data).

Statistical comparisons followed the protocol outlined by Carvalho *et al.* (2016, 2018). Principal component analyses (PCAs) were applied to the morphometric data sets scaling all traits. We tested for morphometric differences among groups using multivariate analyses of variance (MANOVAs) and linear discriminant analyses (LDAs). To verify the accuracy of group reclassifications, we repeated LDAs using a leave-one-out cross-validation procedure and compared correct reclassification rates. To investigate variation in scale counts, we followed similar procedures to those adopted for morphometric analyses. We centred all meristic traits and performed principal component analyses (PCAs, covariance matrix) with scaled variables. We proceeded with MANOVAs and LDAs based on the original data set, without scaling variables beforehand. All statistical analyses were performed in R v.3.5.1 (R Core Team 2021) using RStudio v.1.1.456 (RStudio Team 2020).

Species model and recognition

Our criterion for species recognition relies on the search for unique character combinations [i.e. diagnosis; see Eldredge and Cracraft (1980) and Cracraft (1983, 1987)] linked with the least-inclusive clades revealed by phylogenetic analysis (Rosen 1978, 1979, Donoghue 1985, Pinna 1999). In this sense, we contrasted our candidate species circumscribed by morphological and geographical parameters with the patterns revealed by the phylogenetic analysis of genetic markers, searching for a potential monophyletic cluster formed exclusively by terminals from Rondonian savannah enclaves. Thus, we assigned species status and formally named a diagnosable monophyletic unit according to the provisions of the International Code of Zoological Nomenclature (ICZN 1999). The new taxonomic entity identified in Rondônia is hypothesized to represent an independent evolutionary lineage (*sensu* de Queiroz 2007) and formed the basis for all subsequent evolutionary inferences about speciation events driven by landscape transformations.

Species distribution modelling

We spatially filtered 80 occurrence records obtained from museum specimens, the literature, and collected directly in the field, with the aid of spThin v.0.2.0 (Supporting Information, File S14; Aiello-Lammens *et al.* 2015). Filtering based on a minimum distance of 5 km between points resulted in 25 unique points used for subsequent spatial distribution modelling. For production of the distributional models, we used bioclimatic variables with a spatial resolution of 2.5′ (~4.5 km) obtained from the WorldClim (v.1.4, http://www.worldclim.org/; Hijmans *et al.* 2005) and PaleoClim (v.1.0, http://www.paleoclim.org/;

Brown *et al.* 2018) databases. From WorldClim, we had access to climatic data from the Present (1960–1990), the Mid-Holocene (~6000 years ago), and the LGM (~22 000 years ago) for the Global Climate Model CCSM4, and from PaleoClim we obtained data from the LIG (~130 000 years ago; Otto-Bliesner *et al.* 2006) for CCSM3.

We used the Maximum Entropy algorithm (MAXENT v.3.4.1; Phillips and Dudík 2008) to build species distribution models in different contexts. Initially, we performed Pearson correlation analyses to detect and ultimately eliminate highly correlated climatic variables ($r \geq .75$). Before that, we discarded the bioclimatic variables bio18 (precipitation of warmest quarter) and bio19 (precipitation of coldest quarter) from our analyses for presenting pixel discontinuity in the study area. Six continuous and biologically relevant variables for squamate reptiles were selected, following recommendations by Clusella-Trullas *et al.* (2011) and Camacho *et al.* (2015): isothermality (bio3), temperature seasonality (bio4), maximum temperature of warmest month (bio5), minimum temperature of coldest month (bio6), precipitation of wettest month (bio13), and precipitation of driest month (bio14). We built a minimal convex polygon with a 1.5° buffer to guarantee the necessary environmental heterogeneity for model calibration (Barve *et al.* 2011) using ENMWIZARD v.0.3.0 (Heming *et al.* 2018).

MAXENT models were adjusted using ENMEVAL v.0.3.1 (Muscarella *et al.* 2014) in the ENMWIZARD package v.0.1.9 (Heming *et al.* 2018). For this, we adopted 10 different values of regularization multiplier (varying from 0.5 to 5, with an interval of 0.5), 15 resource classes [linear (L), product (P), quadratic (Q), hinge (H), LP, LQ, LH, PQ, PH, QH, LPQ, LPH, LQH, PQH, and LPQH], and the 'block' geographical partition method, resulting in a total of 150 preliminary models. The best model was determined using the corrected Akaike information criterion (AICc), which has been proved to outperform the area under the curve (AUC) method, selecting models that are more efficient in estimating environmental suitability (Warren and Seifert 2011, Moreno-Amat *et al.* 2015). We also report on the AUC, 10% training omission rate (OR10), and minimum training presence omission rate (ORmtp) estimated for each selected model. The selected model was applied to the present and the aforementioned palaeoclimatic scenarios using the 10-percentile training presence as threshold. All analyses were performed in R v.4.0.4 (R Core Team 2021) using the ENMWIZARD script by Heming *et al.* (2018), accessible at: https://github.com/HemingNM/ENMwizard.

RESULTS

Phylogenetic analyses and molecular variation

Phylogenetic analysis

Phylogenetic analyses of nuclear, mitochondrial, and combined data sets (Figs. 2, 3) inferred a paraphyletic *Tropidurus*, with *T. spinulosus* and *T. bogerti* separated from *T. semitaeniatus* and the *T. torquatus* species group. The analyses also support *T. semitaeniatus* as sister to a monophyletic *T. torquatus* species group. *Tropidurus hygomi* is recovered as the sister group of all members of *T. torquatus* species group in the nuclear and combined trees, followed by the *Tropidurus* from Rondônia + (*Tropidurus itambere* + *Tropidurus psammonastes*) forming the sister group to all remaining *Tropidurus*. In turn, the analysis based on mitochondrial data places *T. hygomi* as sister to the *Tropidurus* from Rondônia + (*T. itambere* + *T. psammonastes*). *Tropidurus oreadicus* was recovered far apart from the *Tropidurus* from Rondônia in all analyses. This core Cerrado lizard appears as the closest relative of *Tropidurus insulanus* in the mitochondrial and combined trees and as the closest relative of *Tropidurus hispidus* in the nuclear tree. Regardless of the relationships with one another, these three taxa form a highly supported monophyletic group in all trees. The *Tropidurus* populations from Rondônia comprise a monophyletic group with maximum statistical support in all analyses; however, most internal clades formed by these samples have only poor or moderate support. Samples from most savannah enclaves fail to show reciprocal monophyly, with the exception of those from Cacoal, Santa Cruz da Serra e FLONA Jamari.

Divergence dating analysis

The chronogram estimated in BEAST using 12S, 16S, and *kif24* (Fig. 4) suggests that tropidurid lineages that are, for the most part, recognized as distinct genera diverged between 33.10 Mya [95% highest posterior density (HPD): 37.95–39.08 Mya] in the Late Eocene and 16.86 Mya (95% HPD: 13.95–20.13 Mya) in the Early Miocene. The split between *T. semitaeniatus* and the *T. torquatus* species group is inferred more recently, at ~12.41 Mya (95% HPD: 10.70–14.20 Mya). Species diversification in the *T. torquatus* species group initiated at ~8.30 Mya (95% HPD: 7.15–9.66 Mya), but most species in this group diverged in the past 5 Myr. Among them, the *Tropidurus* from Rondônia split from their sister group at ~4.46 Mya (95% HPD: 3.72–5.35 Mya), and further lineage divergence involving these lizards took place between the Late Pliocene, ~2.70 Mya (95% HPD: 2.15–3.29 Mya), and the present. Not much earlier, ~3.28 Mya (95% HPD: 2.57–4.01 Mya), *T. hispidus* diverged from *T. insulanus* + *T. oreadicus*, which finally split at ~2.86 Mya (95% HPD: 2.17–3.58 Mya). The latest-diverging species of the *T. torquatus* species group are *Tropidurus chromatops* and *Tropidurus etheridgei*, whose splitting event is inferred at the Mid-Pleistocene ~0.99 Mya (95% HPD: 0.62–1.41 Mya).

Molecular distances

Molecular distances (*p*-distances) calculated for all species analysed in this study are shown in the Supporting Information (File S15). In this section, we concentrate on describing the variation among species of the *T. torquatus* group and, especially, among the *Tropidurus* populations from savannah enclaves from Rondônia (Table 3). In the *T. torquatus* species group, 12S distances vary from 1.65 to 9.37% and 16S distances from 0 to 5.28%. The lowest molecular distances are observed for species pairs *T. hispidus*–*T. oreadicus* and *T. torquatus*–*T. imbituba* (12S) and *T. azurduyae*–*T. chromatops*, *T. azurduyae*–*T. etheridgei*, and *T. chromatops*–*T. etheridgei* (16S), and the highest for *T. erythrocephalus*–*T. hygomi* (12S) and *T. catalanensis*–*T. insulanus* (16S). Within the *Tropidurus* populations from Rondônia, molecular variation is extremely low, with values larger than zero observed exclusively for Flona Jamari (0.10%) and Ariquemes (0.97%) for the 12S locus, and in Ariquemes

(0.59%), Guajará-Mirim (0.09%), and Porto Velho (0.24%) for the 16S locus. In turn, 12S distances calculated among populations vary from 0 to 1.89% and 16S distances from 0 to 1.05%. In all cases, the highest distances are lower than the average molecular distance calculated among species of the *T. torquatus* species group excluding samples from Rondônia (average equal to 5.7% for 12S and 2.68% for 16S). The largest 12S distance is observed between Ariquemes and Cacoal (1.89%) and the largest 16S distance between Ariquemes and Guajará-Mirim (1.04%).

Morphology

Qualitative morphological traits

Mite pockets: Following the 10-type classification of mite pockets defined by Carvalho *et al.* (2016) (adapted from Rodrigues 1987), all *Tropidurus* populations from cerrado enclaves sampled in Rondônia fall under mite pocket Type D, characterized by a single pocket on the each side of the neck and no pockets in the post-humeral (axillary) and prefemoral (inguinal) areas. To date, mite pocket Type D has been reported only for *T. oreadicus* (Carvalho *et al.* 2016). Although the *Tropidurus* populations from Rondônia and *T. oreadicus* share the same mite pocket type, the lateral neck mite pockets of lizards from the savannah enclaves are extremely deep and wide, much larger than those of *T. oreadicus*. The difference in size is so conspicuous that it allows these species to be distinguished without reference to any other morphological features (Fig. 2). The internal surface of the mite pockets of all specimens examined is coated with soft, diminutive, unpigmented, granular scales. Some of the specimens from Rondônia have a poorly developed medial fold internally in their mite pockets, but such a fold never splits the pocket into two distinct compartments.

Chromatic variation and polymorphism: *Tropidurus* specimens from Rondônia have a grey, dark grey, or brownish grey dorsal background, with black spots of variable sizes and smaller cream and/or orangey spots. The dorsal spots often align coarsely, forming wavy rows from side to side; the cream and orangey spots may be absent or nearly imperceptible in some individuals (Figs. S1–S4 in Supporting Information, File S16). All lizards examined have a black nuchal collar outlined (either complete or dorsally interrupted) with a thin, cream border. An orangey dorsal tone often embellishes the head, dorsum, and/or flanks of specimens of both sexes. Overall, chromatic variation encompasses the degree of darkness of the dorsum (with specimens showing a tendency towards melanism) and intensity of orangey tones on the head, dorsum, and flanks, ranging from mild to flame-like. Given the continuous variation in the dorsal coloration, we are unable to determine different circumscribed states of dorsal patterns among the populations from Rondônia. In contrast, the coloration of the ventral surface of the head and the gular region of specimens from all populations is rather invariable. Their anterior ventral surface of the head and chin have cream or orangey-cream circular blotches outlined by a grey or dark grey reticulum, and the gular region is black in almost all individuals (Fig. 5; Figs S1–S4 in Supporting Information, File S16).

Our sample includes individuals with all three flank colour morphs originally identified by Vitt (1993) and Vitt and Caldwell (1993), characterized by a continuous white line with clean edges (morph F1), an uneven white line with interrupted edges giving the impression of a series of large white blotches that overlapped to produce a line effect (morph F2), and lateral surfaces similar to the dorsum with no indication of a line at all (morph F3). Remarkably, it also includes specimens with two flank patterns unreported by previous authors, raising to five the number of colour morphs identified on the basis of flank coloration (Fig. 5). The first of these novel colour morphs shows an uneven black line with interrupted edges giving the impression of a series of large black blotches that overlapped to produce a line effect (morph F4), and the second shows a continuous black line on the mid-flank, running from the inguinal region to near the insertion of the arm (morph F5). Colour morph frequencies vary considerably among populations and between sexes (Fig. 5), but no clear geographical pattern has been identified. Females show a relatively higher frequency of striped morphs, whereas males more often have flank coloration similar to the dorsum. Six of nine populations have at least one male with stripes, and four have at least one female with flanks similar to the dorsum, indicating that none of these morphs is exclusive to one of the sexes or restricted to a single population.

We identified five distinct ventral coloration patterns, referred to as follows: colour morph V1, immaculate, white or cream venter; V2, white or cream venter and mottled chest; V3, postero-midventer white or cream surrounded by ‘smoky’ coloration and mottled chest; V4, greyish venter making up a ‘dirty’ ventral appearance; and V5, black or highly melanic venter. The distribution of these colour morphs between sexes is strikingly distinct, with males showing a much stronger tendency towards melanism than females (Fig. 5). In six of nine sampled populations, all males have a black or highly melanic venter (morph V5), whereas only one of these sites includes a female with that same dark ventral pattern (Fig. 5). Most females in our sample show either a white or cream venter and mottled chest (morph V2) or postero-midventer white or cream surrounded by a ‘smoky’ coloration and mottled chest (morph V3). The geographical distribution of the ventral patterns shows an overall dominance of darker colour morphs across populations; however, only small natural savannah enclaves present highly melanic individuals (e.g. FLONA Jamari and Jaci-Paraná). Samples from anthropic sites include specimens with lighter ventral coloration and show a more diverse and balanced distribution of ventral colour morphs (e.g. EFMM and UNIR).

The association of the flank and ventral chromatic morphs described above results in 20 unique chromatic patterns (Table 4). Besides demonstrating a high degree of chromatic polymorphism, the results summarized in Table 4 also reveal strong sexual dichromatism among the *Tropidurus* from Rondônia. Females exhibit almost double the number of exclusive combinations of chromatic morphs recorded for males. In our sample, patterns F1-V3, F2-V1, F2-V2, F2-V4, F3-V2, F4-V2, F4-V3, F5-V1, F5-V2, and F5-V3 are exclusive to females; F1-V5, F2-V5, F3-V4, F4-V5, F5-V4, and F5-V5 are found only in males; and F1-V1, F2-V3, F3-V3, and F3-V5 are registered for both sexes. Among females, patterns F5-V3 (continuous black line on the mid flank and postero-midventer white or cream surrounded by ‘smoky’ coloration and mottled chest) and F3-V3 (flanks with no stripes and postero-midventer white or cream surrounded by ‘smoky’ coloration and mottled chest) are the most common. In

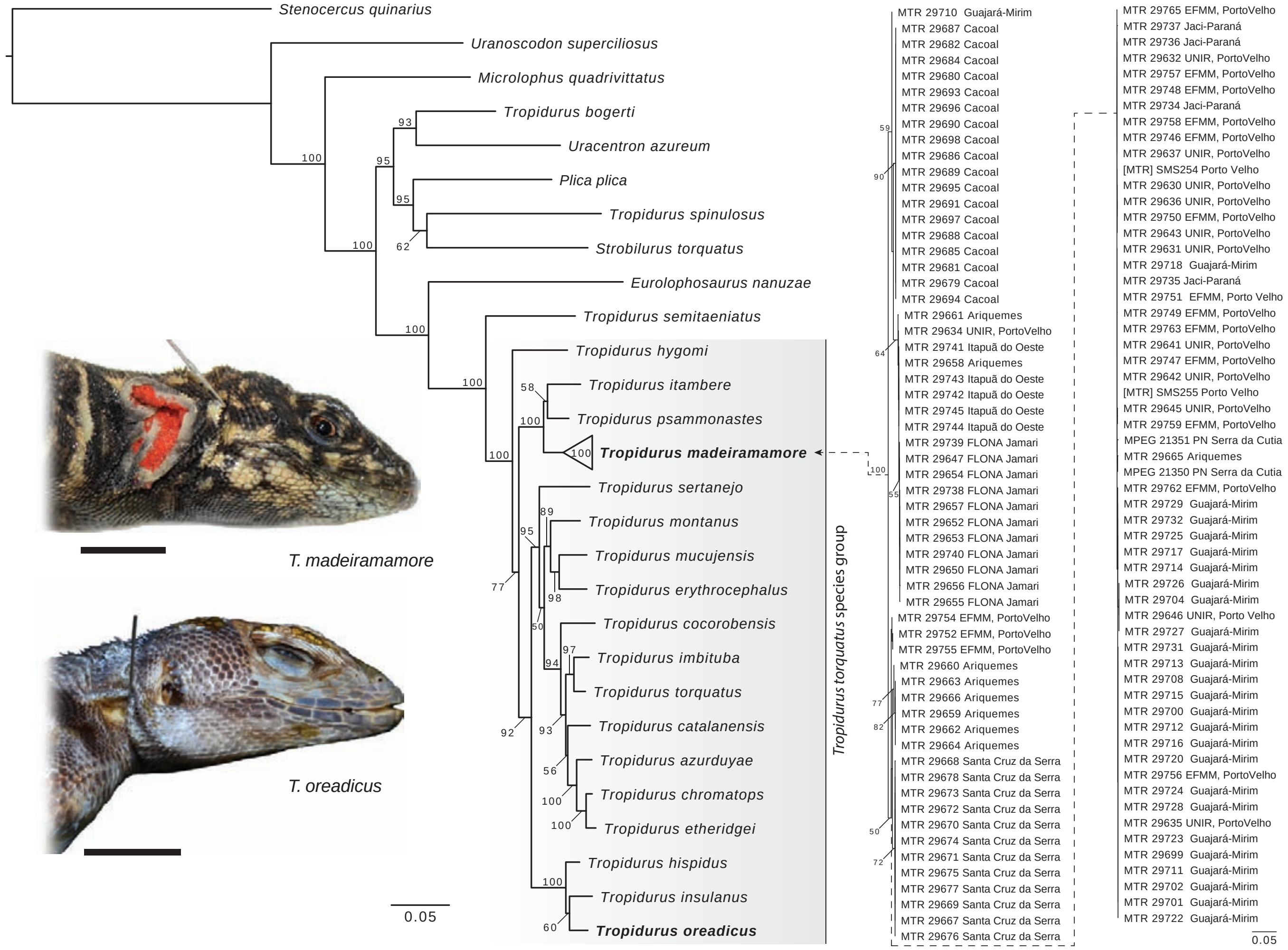

Figure 2. Phylogenetic tree of Tropiduridae based on nuclear plus mitochondrial data combined, showing the distant relationship between the *Tropidurus* from savannah enclaves from Rondônia (*Tropidurus madeiramamore*) and *Tropidurus oreadicus*. Non-parametric bootstrap values (1000 replicates) are shown associated with branches. Dashed lines indicate branches whose lengths were altered for graphical purposes. In the lower left section of the figure, the lateral heads of the holotypes of *T. madeiramamore* (live specimen, *MZUSP 107155*) and *T. oreadicus* (preserved specimen, *MZUSP 9465*) are shown to illustrate the discrepancy in size between their lateral neck mite pockets. This diagnostic character distinguishes the species unambiguously. Scale bar: 1 cm.

males, pattern F3-V5 (flanks with no stripes and black venter) is about five times more frequent than any other.

The quantification of colour morphs detailed above considers only adult specimens. However, analysis of juveniles shows that none of the six juvenile specimens sampled in Rondônia has a colour morph distinct from those reported for adults. Juveniles of both sexes have an orangey coloration at the ventral base of the tail. In males, such coloration fades during development, and it is entirely absent in adults. In females, the orangey coloration is either maintained or intensifies with age (Figs S2, S4 in Supporting Information, File S16). Juveniles show a continuous or interrupted white stripe on the flanks, but none of them has flanks similar to the dorsum or ornamented with a black stripe. We are therefore unable to determine whether the absence of stripes (morph F3) or the presence of black stripes on the flanks (morphs F4 and F5) of adult specimens are conditioned to more advanced ontogenetic stages. Likewise, because none of the sampled juveniles possesses a dark-pigmented or highly melanic venter, it remains unclear when exactly the intensification of skin melanization takes place during ontogenetic development.

Quantitative morphological analysis

Morphometric variation (Table 5): *Tropidurus* populations from Rondônia are morphometrically indistinguishable from *T. oreadicus* (non-parametric MANOVA: males: $r^2 = .00874$, d.f. = 1, sum of squares = 659.00, mean square = 659.10, $F = 0.81144$, $P = .3706$; females: $r^2 = .00536$, d.f. = 1, sum of squares = 122.90, mean square = 122.91, $F = 0.54426$, $P = .4575$). The PCA and LDA capture extensive morphometric overlap for both males and females of these species in analyses including size or size free. Given that size-free analyses were not particularly informative, only results from analyses with size are presented in detail (Fig. 6; Tables 5 and 6). A summary of the results from size-free analyses is provided in the Supporting Information (File S17). For males, SVL and the head measurements HW and EOS have stronger weight in principal component (PC)1, but differences in component loading values in

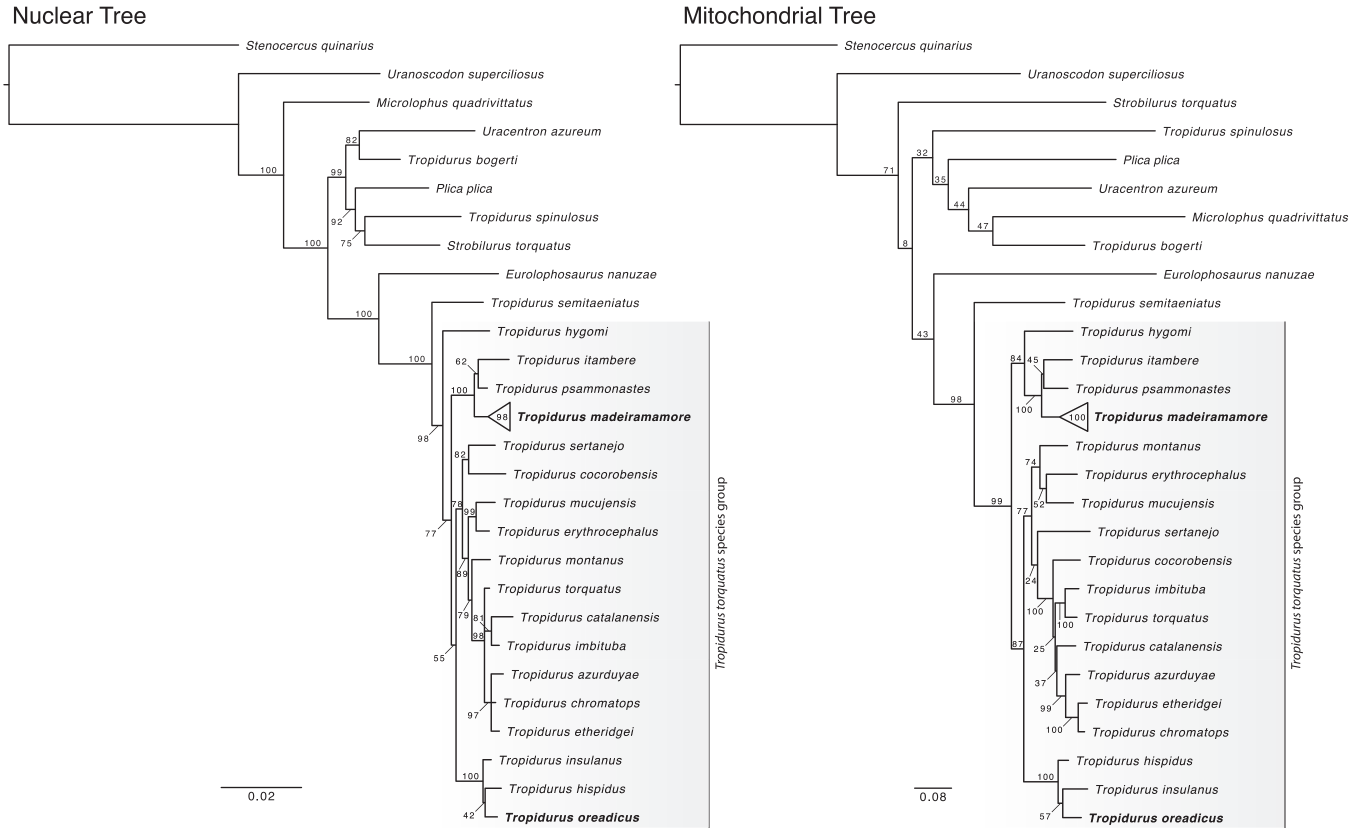

Figure 3. Nuclear and mitochondrial phylogenetic trees produced for Tropiduridae. As shown in the total evidence tree (Fig. 2), *Tropidurus* from savannah enclaves from Rondônia (*Tropidurus madeiramamore*) and *Tropidurus oreadicus* are inferred as distantly related phylogenetically. Non-parametric bootstrap values (1000 replicates) shown associated with branches.

relationship to other variables are not substantial, indicating a similar degree of contribution. The limb measurements FOL and HDL show a more pronounced contribution in PC2. EOS is identified by LDA as a stronger variable in LD1 in order of importance of discriminant coefficients, followed by the forelimb measurements FAL and HDL, whereas the head measurement HW shows a relevant contribution in LD2. Like in males, SVL, EOS, and HW are the most relevant variables discriminating female samples in PC1. On the other hand, body measurement AGD, rather than limb measurements, contribute more strongly for morphometric discrimination in PC2. In the LDA performed for females, head measurements are relevant for group discrimination in both axes, with the highest discrimination coefficients being associated with EOS in discriminant coefficient (LD)1 and with HW and EOS in LD2.

Despite the fact that a subset of *Tropidurus* populations from Rondônia differ statistically from one another regarding morphometric parameters (non-parametric MANOVA: males: $r^2 = .32399$, d.f. = 10, sum of squares = 23562.00, mean square = 2356.18, $F = 3.7861$, $P < .001$; females: $r^2 = .41746$, d.f. = 10, sum of squares = 7163.80, mean square = 716.38, $F = 5.733$, $P < .001$; Table 6), the number of correct LDA-based reclassifications is low in both sexes, and implementation of the cross-validation procedure shows that morphometric variables alone fail to distinguish individuals from most populations accurately (Tables S4 and S5 in Supporting Information, File S17). Given the broad overlap observed among populations, morphometric parameters are uninformative in distinguishing circumscribed groups amongst the *Tropidurus* populations from Rondônia.

Meristic variation (Table 7*)*: Meristic characters allow more effective discrimination of groups than morphometric ones (Fig. 7; Tables 7 and 8), and statistical comparisons confirmed that female *Tropidurus* from Rondônia are distinct from *T. oreadicus* in terms of meristic traits, and males from the same populations are only marginally distinct (non-parametric MANOVA: males: $r^2 = .04564$, d.f. = 1, sum of squares = 1921.00, mean square = 1920.60, $F = 3.4912$, $P = .0595$; females: $r^2 = .20118$, d.f. = 1, sum of squares = 12775.00, mean square = 12775.10, $F = 21.659$, $P < .001$). Table 7 and the PCA plots show that the *Tropidurus* from Rondônia have an overall higher number of scales compared with *T. oreadicus*, with a stronger contribution of the dorsals, gulars, and tibials in PC1 and of the midbody scales and the number of subdigital lamellae in PC2, determining the structure of the meristic morphospace. In turn, LDA indicates that the dorsals and midbody scales on the first axis and the ventrals, number of subdigital lamellae (for males), and tibials (for females) on the second axis are the most relevant variables for group discrimination.

Some of the *Tropidurus* populations from Rondônia differ statistically in relationship to meristic traits (non-parametric MANOVA: males: $r^2 = .90921$, d.f. = 9, sum of squares = 36436, mean square = 4048.4, $F = 67.878$, $P < .001$; females: $r^2 = .8631$,

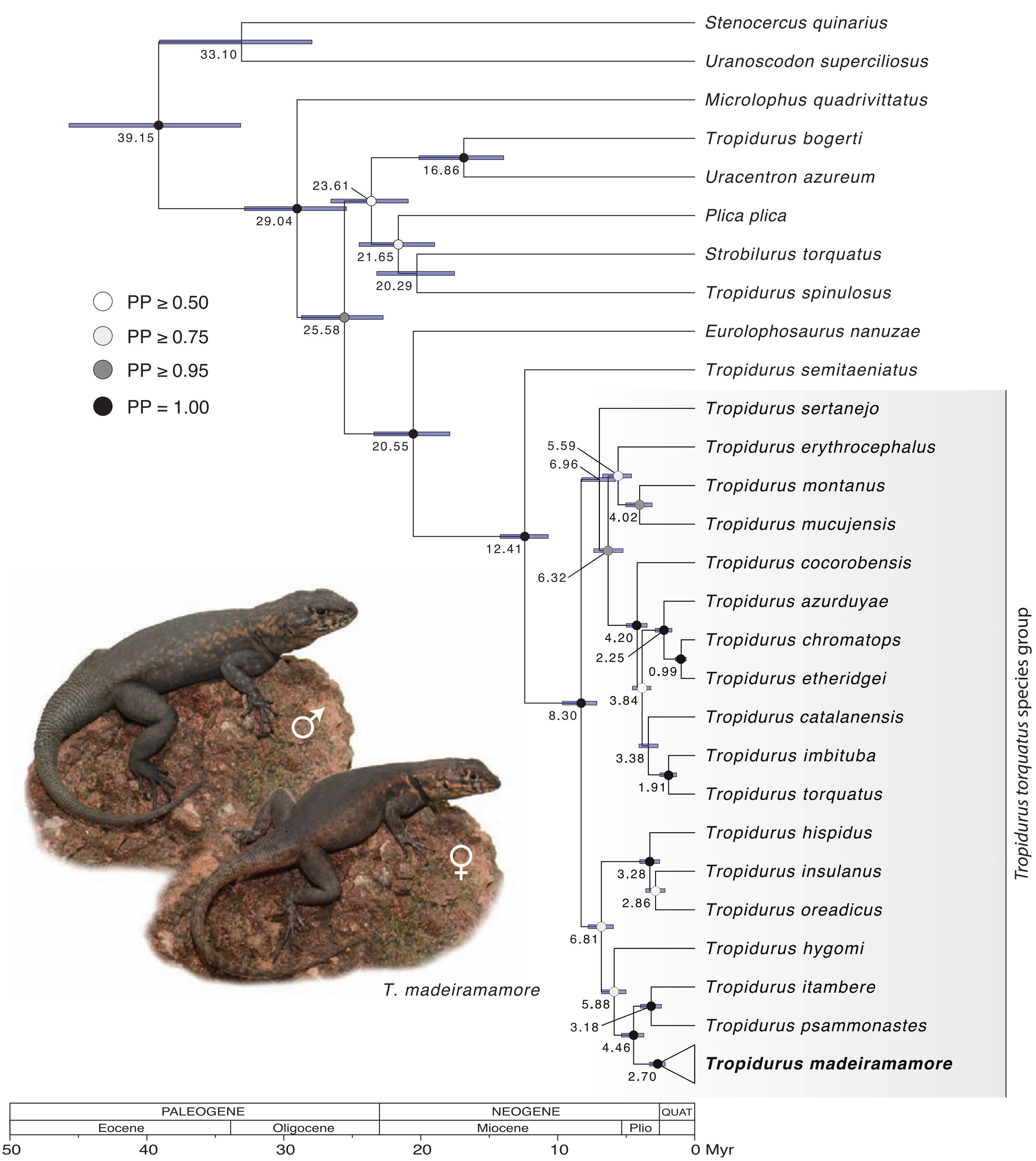

Figure 4. Maximum clade credibility tree showing the phylogenetic relationships and divergence times (median heights) between tropidurid species inferred using BEAST. At the bottom left are shown male (MZUSP 107245) and female (MZUSP 107242) specimens of *Tropidurus madeiramamore* from Jaci-Paraná, Porto Velho, Rondônia. Abbreviation: PP, posterior probability.

d.f. = 10, sum of squares = 42531.00, mean square = 4725.70, $F = 46.236$, $P < .001$). However, PCA and LDA plots fail to reveal groupings structured by geographical proximity (Fig. 7; Tables 7 and 8). Despite the fact that some neighbouring populations do tend to show more similar scale counts (e.g. Santa Bárbara, Itapuã do Oeste, Alto Paraíso, and Ariquemes), this trend is not generalized (e.g. Jaci-Paraná, Guajará-Mirim, and Cacoal). The *Tropidurus* from Rondônia altogether and *T. oreadicus* are consistently reclassified as two different groups using the LDA function based on meristic traits, with 100% correct reclassifications observed even with the adoption of the cross-validation procedure. In contrast, the number of correct

Table 3. Molecular distances (*p*-distances) of 12S (upper right) and 16S (lower left) fragments between *Tropidurus* populations from savannah enclaves from Rondônia, Brazil (*T. madeiramamore*).

Population	1	2	3	4	5	6	7	8	9	10
1. Serra da Cutia										
2. Guajará-Mirim	.0031		.0000	.0000	.0000	.0187	.0165	.0079	.0000	.0165
3. Jaci Paraná	.0000	.0031		.0000	.0000	.0187	.0165	.0079	.0000	.0165
4. UNIR	.0000	.0031	.0000		.0000	.0187	.0165	.0079	.0000	.0165
5. Porto Velho	.0014	.0041	.0014	.0014		.0187	.0165	.0079	.0000	.0165
6. FLONA Jamari	.0062	.0091	.0062	.0062	.0052		.0022	.0184	.0187	.0132
7. Itapuã	.0062	.0091	.0062	.0062	.0052	.0000		.0162	.0165	.0110
8. Ariquemes	.0076	.0105	.0076	.0076	.0077	.0069	.0069		.0079	.0189
9. Jaru	.0031	.0060	.0031	.0031	.0033	.0031	.0031	.0052		.0165
10. Cacoal	.0062	.0088	.0062	.0062	.0064	.0062	.0062	.0083	.0031	

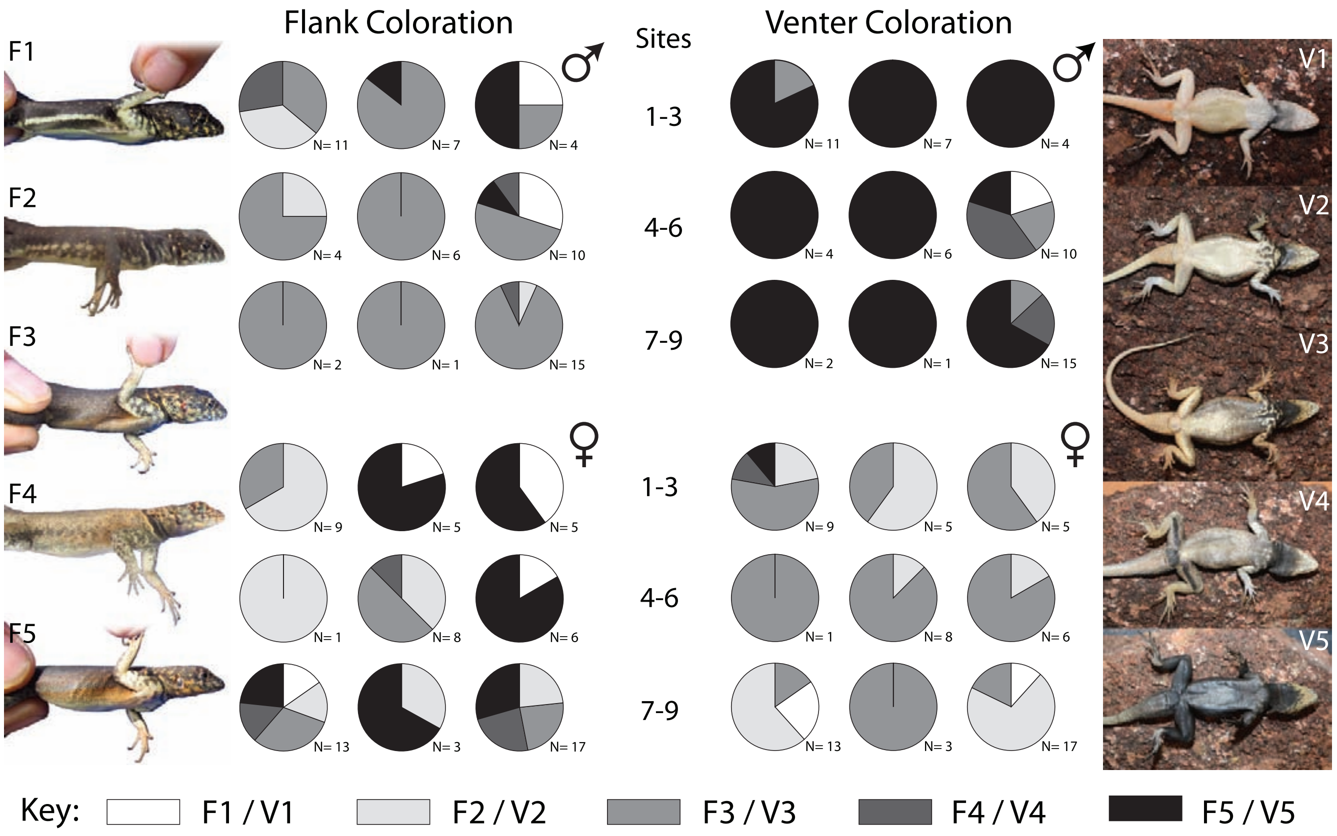

Figure 5. Illustration of the chromatic polymorphism and frequency of the five flank (F1–F5) and ventral body (V1–V5) morphs identified across populations of *Tropidurus* from savannah enclaves from Rondônia (*Tropidurus madeiramamore*). Each shade indicates a different chromatic morph, and each chart represents a different locality, with values for males (top) and females (bottom) shown separately. See Figure 1 for details on the geographical location and characteristics of each site: (1) Cacoal; (2) Santa Cruz da Serra; (3) Ariquemes; (4) Itapuã do Oeste; (5) FLONA Jamari; (6) EFMM; (7) UNIR; (8) Jaci-Paraná; and (9) Guajará-Mirim.

reclassifications among individual populations from Rondônia is moderate overall and drops substantially with the implementation of the cross-validation procedures (Tables S6 and S7 in Supporting Information, File S17). This is expected in the case of the populations being compared pertaining to a single species, and consequently, the populations from savannah enclaves from Rondônia are lumped in a single taxonomic unit on the basis of meristic traits.

Maxent distribution models

Maxent retrodicted climatically suitable areas for the new *Tropidurus* from Rondônia covering at least two vast contiguous zones during the hot and humid periods of the LIG (Fig. 8). The first one stretches diagonally from north-eastern Brazil to northern Bolivia, encompassing a large portion of the area currently occupied by the Cerrado and the Beni savannahs. The second comprises areas to the east of the Andes in north-western

Table 4. Frequency of individual chromatic patterns composed of flank (F1–F5) plus ventral body (V1–V5) morphs identified across populations of *Tropidurus* from savannah enclaves from Rondônia (*T. madeiramamore*). See Figure 1 for details on the geographical location of sites 1–9.

Chromatic patterns	**F1-V2**	**F1-V3**	**F1-V5**	**F2-V1**	**F2-V2**	**F2-V3**	**F2-V4**	**F2-V5**	**F3-V2**	**F3-V3**	**F3-V4**	**F3-V5**	**F4-V2**	**F4-V3**	**F4-V5**	**F5-V1**	**F5-V2**	**F5-V3**	**F5-V4**	**F5-V5**	**Total**
Females																					
1. Cacoal					2	3	1			2		1									9
2. Santa Cruz	1																2	2			5
3. Ariquemes	2																	3			5
4. Itapuã						1															1
5. FLONA					1	2				4				1							8
6. EFMM	1																	5			6
7. UNIR	1	1		1	1				1	3				2		1		2			13
8. Jaci-Paraná						1												2			3
9. Guajará-Mirim				2	2				2	2			4				4	1			17
Total	5	1		3	6	7	1		3	11		1	4	3		1	6	15			67
Males																					
1. Cacoal						2		2				4			3						11
2. Santa Cruz												6								1	7
3. Ariquemes			1									1								2	4
4. Itapuã								1				3									4
5. FLONA												6									6
6. EFMM	2		1							2	3				1				1		10
7. UNIR												2									2
8. Jaci-Paraná												1									1
9. Guajará-Mirim								1		2	3	8								1	15
Total	2		2			2		4		4	6	31			4				1	4	60
Grand total	7	1	2	3	6	9	1	4	3	15	6	32	4	3	4	1	6	15	1	4	127

Table 5. Minimum and maximum values (mean ± SD) of morphometric measurements (in millimetres) of adult specimens of the *Tropidurus madeiramamore* from 12 populations from the State of Rondônia, Brazil, plus the type series of *Tropidurus oreadicus*.

Population	SVL	TL	BH	MB	HH	HL	HW	EOS
Alto Paraíso								
Females (*N* = 5 [0])	70.49–82.39 (76.13 ± 4.91)		11.56–17.88 (14.82 ± 2.75)	23.17–28.09 (26.28 ± 1.90)	8.55–10.51 (9.56 ± 0.85)	17.07–20.34 (19.34 ± 1.34)	12.76–14.64 (13.73 ± 0.73)	16.84–19.19 (18.23 ± 1.01)
Males (*N* = 8 [4])	75.71–99.57 (88.05 ± 8.74)	113.00–131.00 (121.25 ± 7.50)	9.94–16.95 (13.50 ± 2.83)	19.90–29.30 (25.70 ± 3.47)	9.38–13.88 (12.21 ± 1.50)	20.83–24.61 (22.78 ± 1.42)	13.80–20.34 (16.87 ± 2.16)	18.53–25.33 (21.98 ± 1.99)
Ariquemes								
Females (*N* = 5 [5])	65.82–75.66 (72.40 ± 4.11)	88.00–97.00 (93.40 ± 3.36)	13.15–15.33 (14.06 ± 0.87)	22.41–26.51 (24.38 ± 1.53)	7.69–9.19 (8.31 ± 0.62)	15.59–19.69 (17.86 ± 1.62)	11.08–12.54 (12.16 ± 0.62)	14.97–17.31 (16.39 ± 0.98)
Males (*N* = 4 [3])	84.10–92.19 (88.75 ± 3.50)	95.00–129.00 (114.33 ± 17.47)	14.69–19.28 (16.09 ± 2.14)	24.77–27.31 (25.72 ± 1.14)	9.75–14.28 (11.97 ± 1.89)	22.79–25.95 (24.79 ± 1.48)	16.11–17.51 (17.16 ± 0.70)	18.71–21.91 (20.88 ± 1.46)
Cacoal								
Females (*N* = 9 [6])	66.97–76.99 (70.73 ± 3.07)	84.00–96.00 (90.33 ± 4.03)	9.65–14.02 (12.14 ± 1.47)	21.49–26.44 (23.85 ± 1.98)	7.47–9.25 (8.42 ± 0.51)	15.26–19.66 (17.98 ± 1.30)	11.55–13.05 (12.25 ± 0.53)	15.10–17.38 (16.18 ± 0.72)
Males (*N* = 11 [6])	70.28–87.38 (81.26 ± 6.40)	85.00–119.00 (101.83 ± 10.93)	11.74–15.95 (14.02 ± 1.22)	21.71–26.94 (24.06 ± 1.98)	9.05–12.67 (10.59 ± 1.24)	19.76–24.39 (21.75 ± 1.69)	13.24–16.87 (15.31 ± 1.39)	17.74–21.45 (19.60 ± 1.51)
EFMM								
Females (*N* = 9 [6])	68.56–78.05 (72.79 ± 3.92)	96.00–114.00 (102.50 ± 6.41)	7.46–14.94 (12.07 ± 2.63)	21.34–26.73 (24.19 ± 2.25)	7.92–9.21 (8.52 ± 0.47)	18.40–19.97 (19.10 ± 0.60)	12.07–13.54 (12.81 ± 0.62)	16.23–17.75 (16.98 ± 0.55)
Males (*N* = 10 [5])	70.34–103.84 (92.19 ± 7.71)	109.00–142.00 (129.00 ± 15.05)	14.78–18.90 (16.21 ± 1.55)	22.52–32.35 (26.38 ± 3.53)	10.33–14.79 (12.05 ± 1.38)	21.09–27.87 (25.17 ± 2.06)	15.06–20.79 (18.09 ± 1.78)	18.73–24.51 (22.30 ± 1.79)
Guajará-Mirim								
Females (*N* = 16 [12])	62.73–77.04 (70.21 ± 3.63)	90.00–113.00 (98.50 ± 6.30)	10.45–14.30 (11.68 ± 1.13)	20.57–26.97 (24.32 ± 2.24)	7.59–9.73 (8.15 ± 0.57)	17.13–19.82 (18.03 ± 0.81)	11.61–13.56 (12.49 ± 0.65)	14.44–16.79 (15.41 ± 0.79)
Males (*N* = 15 [6])	78.75–93.64 (86.26 ± 4.23)	108.00–126.00 (118.00 ± 7.51)	11.86–17.25 (14.99 ± 1.72)	23.94–28.69 (26.42 ± 1.28)	8.42–12.85 (10.88 ± 1.24)	20.14–26.28 (23.68 ± 1.64)	14.68–17.57 (16.27 ± 0.99)	18.37–22.04 (20.32 ± 1.09)
Itapuã								
Females (*N* = 7 [2])	70.79–81.60 (77.64 ± 4.11)	91.00–93.00 (92.00 ± 1.41)	13.21–17.15 (14.77 ± 1.52)	24.20–30.33 (26.86 ± 2.14)	8.14–11.57 (9.79 ± 1.28)	17.65–20.88 (19.25 ± 1.30)	12.61–15.39 (14.14 ± 1.27)	16.75–19.48 (18.25 ± 1.33)
Males (*N* = 7 [2])	90.17–102.89 (97.69 ± 4.70)	136.00–137.00 (136.50 ± 0.71)	14.37–20.44 (17.21 ± 2.56)	27.25–32.04 (28.47 ± 1.75)	10.06–16.32 (13.62 ± 2.34)	24.32–29.43 (26.31 ± 1.85)	17.25–20.89 (19.19 ± 1.60)	21.80–25.22 (23.90 ± 1.42)
Jaci-Paraná								
Females (*N* = 3 [3])	70.98–72.41 (71.86 ± 0.77)	92.00–102.00 (97.33 ± 5.03)	11.18–14.83 (13.15 ± 1.84)	24.17–26.06 (25.43 ± 1.09)	8.64–8.96 (8.77 ± 0.17)	18.18–19.31 (18.85 ± 0.59)	12.75–13.17 (12.96 ± 0.21)	16.29–16.67 (16.48 ± 0.19)
Males (*N* = 1)	97.75		17.77	28.62	11.86	25.93	19.08	23.17
Mina 14 de Abril								
F males (*N* = 1)	70.52	96.00	9.96	23.87	8.22	17.03	12.45	16.1
Males (*N* = 4 [1])	76.96–98.80 (87.34 ± 10.69)	140.00	9.96–17.73 (13.52 ± 3.63)	20.09–29.51 (24.95 ± 4.55)	8.68–15.00 (11.36 ± 2.79)	18.15–26.33 (22.46 ± 3.98)	13.51–19.40 (16.07 ± 2.90)	18.77–25.12 (21.43 ± 3.18)

Table 5. Continued

Population	SVL	TL	BH	MB	HH	HL	HW	EOS
Santa Bárbara (= FLONA Jamari)								
Females (*N* = 14 [9])	61.31–72.23 (67.76 ± 3.08)	83.00–92.00 (87.44 ± 3.71)	9.37–14.91 (11.79 ± 1.38)	20.25–25.61 (22.88 ± 1.78)	7.63–10.66 (8.50 ± 0.83)	14.43–18.95 (17.05 ± 1.19)	11.02–13.74 (12.33 ± 0.85)	13.68–17.13 (15.99 ± 0.90)
Males (*N* = 14 [5])	67.59–102.19 (84.87 ± 11.91)	89.00–118.00 (102.04 ± 11.46)	10.13–21.95 (14.86 ± 4.13)	22.82–32.28 (27.15 ± 3.37)	7.98–14.62 (11.31 ± 2.14)	16.96–29.48 (22.08 ± 4.03)	12.98–20.83 (16.39 ± 2.74)	16.60–25.21 (20.73 ± 2.70)
Santa Cruz								
Females (*N* = 12 [8])	65.06–76.57 (70.77 ± 3.64)	90.00–104.00 (96.12 ± 4.88)	7.43–14.90 (11.89 ± 2.35)	20.21–26.51 (23.62 ± 2.19)	7.57–10.61 (9.01 ± 0.94)	15.94–19.54 (18.17 ± 1.14)	11.34–14.47 (12.82 ± 0.92)	15.23–17.44 (16.37 ± 0.84)
Males (*N* = 14 [6])	78.58–95.55 (86.51 ± 5.07)	100.00–125.00 (117.83 ± 9.33)	12.14–17.75 (14.98 ± 1.90)	20.36–31.25 (25.83 ± 3.29)	10.38–12.91 (11.52 ± 0.80)	19.55–25.78 (22.21 ± 1.77)	14.85–18.26 (16.58 ± 0.95)	18.44–23.13 (20.76 ± 1.19)
UNIR								
Females (*N* = 13 [9])	66.31–81.17 (74.92 ± 4.56)	77.00–113.00 (99.44 ± 14.43)	13.10–17.25 (15.29 ± 1.37)	21.56–29.41 (26.43 ± 2.01)	8.42–10.88 (9.49 ± 0.69)	17.47–20.24 (18.99 ± 0.86)	12.50–14.90 (13.67 ± 0.74)	15.64–18.48 (17.22 ± 0.96)
Males (*N* = 2 [2])	78.06–96.26 (87.16 ± 12.87)	116.00–125.00 (120.05 ± 6.36)	17.35–18.23 (17.79 ± 0.62)	22.82–28.11 (25.46 ± 3.74)	10.94–12.45 (11.70 ± 1.07)	21.50–26.03 (23.76 ± 3.20)	15.94–19.40 (17.67 ± 2.45)	19.23–23.46 (21.34 ± 2.99)
All populations								
Females (*N* = 91 [61])	61.31–82.39 (71.88 ± 4.59)	77.00–114.00 (95.56 ± 8.28)	7.43–17.88 (12.88 ± 2.18)	20.21–30.33 (24.58 ± 2.33)	7.47–11.57 (8.79 ± 0.91)	14.43–20.88 (18.27 ± 1.27)	11.02–15.39 (12.87 ± 0.97)	13.68–19.48 (16.53 ± 1.21)
Males (*N* = 90 [40])	67.59–103.84 (87.48 ± 8.35)	85.00–142.00 (116.62 ± 14.45)	9.94–21.95 (15.10 ± 2.62)	19.90–32.35 (26.15 ± 2.93)	7.98–16.32 (11.57 ± 1.71)	16.96–29.48 (23.28 ± 2.68)	12.98–20.89 (16.80 ± 1.98)	16.60–25.33 (21.14 ± 2.08)
T. oreadicus								
Females (*N* = 12 [3])	61.54–83.90 (71.29 ± 7.27)	116.00–126.00 (122.67 ± 5.77)	8.95–19.59 (13.22 ± 3.19)	18.14–31.12 (24.04 ± 4.19)	6.31–9.44 (8.08 ± 0.87)	14.84–21.60 (18.10 ± 2.13)	10.67–14.71 (12.73 ± 1.34)	15.25–19,34 (16.55 ± 1.36)
Males (*N* = 4 [1])	73.56–94.97 (83.96 ± 8.80)	140.00	12.79–15.71 (14.47 ± 1.42)	19.83–26.95 (23.84 ± 3.02)	9.07–11.42 (10.44 ± 1.01)	18.66- 24.28 (21.85 ± 2.34)	14.58–17.75 (16.15 ± 1.39)	18.00–22.25 (20.32 ± 1.75)

Population	AL	FAL	HDL	THL	SL	FOL	AGD
Alto Paraíso							
Females (*N* = 5)	8.77–14.05 (11.19 ± 2.38)	9.66–11.97 (10.66 ± 1.14)	12.68–15.31 (13.58 ± 1.05)	12.53–17.27 (15.65 ± 1.94)	13.61–16.25 (15.61 ± 1.13)	21.84–24.39 (23.12 ± 1.11)	31.92–39.61 (36.04 ± 3.17)
Males (*N* = 8)	11.91–17.44 (15.06 ± 1.79)	11.67–14.95 (13.53 ± 1.15)	15.36–18.18 (16.91 ± 1.07)	14.30–21.88 (19.06 ± 2.28)	15.69–19.96 (18.33 ± 1.47)	20.24–30.25 (27.22 ± 3.33)	34.76–46.92 (40.64 ± 4.38)
Ariquemes							
Females (*N* = 5)	11.44–13.43 (12.28 ± 0.76)	10.43–11.69 (11.01 ± 0.48)	11.27–12.56 (11.83 ± 0.56)	13.94–15.88 (14.93 ± 0.79)	14.08–15.49 (14.70 ± 0.52)	20.00–21.49 (20.83 ± 0.65)	35.43–38.76 (37.5 ± 1.59)
Males (*N* = 4)	13.09–15.47 (14.43 ± 1.06)	12.35–13.96 (13.28 ± 0.70)	14.45–15.18 (14.80 ± 0.35)	18.06–19.84 (18.95 ± 0.73)	18.16–18.62 (18.47 ± 0.21)	24.64–27.24 (26.00 ± 1.07)	44.17–45.23 (44.64 ± 0.49)

Table 5. Continued

Population	AL	FAL	HDL	THL	SL	FOL	AGD
Cacoal							
Females ($N = 9$)	11.16–12.78 (12.14 ± 0.55)	10.17–11.75 (10.96 ± 0.58)	11.59–13.85 (12.43 ± 0.69)	14.08–17.52 (15.47 ± 0.93)	13.89–15.24 (14.55 ± 0.49)	19.10–21.01 (20.20 ± 0.62)	33.97–41.33 (36.94 ± 2.22)
Males ($N = 11$)	11.59–13.97 (12.99 ± 0.72)	11.34–13.98 (12.76 ± 0.91)	12.89–15.73 (13.95 ± 0.83)	15.88–20.34 (18.12 ± 1.27)	16.04–18.64 (17.35 ± 0.94)	21.98–26.32 (24.33 ± 1.23)	34.59–43.25 (38.88 ± 3.19)
EFMN							
Females ($N = 6$)	11.10–13.50 (12.77 ± 0.93)	10.65–13.03 (11.87 ± 0.85)	12.85–13.93 (13.36 ± 0.43)	13.99–15.82 (15.13 ± 0.74)	14.61–15.86 (15.36 ± 0.57)	21.00–23.92 (22.59 ± 1.04)	36.61–44.01 (39.23 ± 2.88)
Males ($N = 10$)	11.82–19.31 (16.36 ± 2.29)	12.99–17.25 (14.86 ± 1.33)	15.20–17.82 (16.38 ± 0.79)	16.88–22.63 (20.22 ± 1.74)	17.09–21.12 (19.13 ± 1.51)	25.24–29.80 (27.77 ± 1.75)	40.47–55.48 (46.77 ± 5.04)
Guajará-Mirim							
Females ($N = 16$)	10.30–12.79 (11.80 ± 0.74)	9.38–12.21 (10.65 ± 0.73)	10.32–12.33 (11.48 ± 0.57)	12.17–15.58 (14.29 ± 0.85)	12.96–15.76 (13.75 ± 0.80)	18.18–21.56 (19.74 ± 0.86)	30.08–41.51 (38.06 ± 2.46)
Males ($N = 15$)	13.13–16.39 (14.52 ± 0.97)	11.54–13.93 (13.04 ± 0.69)	12.59–16.13 (14.42 ± 0.98)	16.21–20.39 (18.60 ± 1.10)	14.41–18.64 (16.92 ± 1.16)	22.82–25.75 (24.52 ± 0.79)	40.93–49.22 (44.20 ± 2.32)
Itapuã							
Females ($N = 7$)	10.84–13.54 (12.25 ± 1.04)	10.86–12.01 (11.49 ± 0.40)	11.27–14.75 (13.60 ± 1.10)	12.25–18.10 (15.52 ± 1.89)	14.51–15.95 (14.96 ± 0.47)	22.07–24.84 (23.62 ± 1.09)	34.64–40.61 (37.68 ± 2.19)
Males ($N = 7$)	15.55–18.42 (16.79 ± 1.05)	14.23–16.54 (15.35 ± 0.70)	15.34–18.60 (16.79 ± 1.14)	18.68 -23.23 (21.53 ± 1.68)	18.01–21.39 (19.52 ± 1.38)	28.63–30.89 (29.68 ± 0.96)	41.51–51.85 (46.85 ± 3.03)
Jaci-Paraná							
Females ($N = 3$)	12.54–13.56 (13.09 ± 0.52)	11.01–11.37 (11.23 ± 0.19)	11.85–13.60 (12.90 ± 0.93)	15.59–17.07 (16.13 ± 0.81)	13.99–15.59 (14.84 ± 0.80)	21.76–22.54 (22.12 ± 0.39)	35.74–39.87 (38.10 ± 2.13)
Males ($N = 1$)	17.56	15.99	16.89	23.07	20.39	28.2	52
Mina 14 de Abril							
Females ($N = 1$)	12.46	10.68	12.09	14.86	16.78	21.61	37.95
Males ($N = 4$)	13.22–17.25 (14.91 ± 2.00)	12.53–14.89 (13.58 ± 1.15)	13.55–16.46 (14.72 ± 1.41)	18.19–23.53 (20.80 ± 2.58)	16.65–20.65 (18.62 ± 2.10)	24.76–27.66 (26.07 ± 1.50)	37.69–48.47 (42.72 ± 5.09)
Porto Velho							
Females ($N = 2$)	10.34–12.73 (11.54 ± 1.69)	10.71–11.06 (10.89 ± 0.25)	13.69–15.08 (14.38 ± 0.98)	1515–16.01 (15.58 ± 0.61)	15.28–15.37 (15.32 ± 0.06)	22.24–23.38 (22.81 ± 0.81)	35.29–36.51 (35.09 ± 0.86)
Males ($N = 8$)	10.33–14.95 (12.81 ± 1.49)	9.50–15.01 (12.25 ± 1.70)	15.02–17.78 (16.55 ± 1.04)	15.07–21.84 (18.78 ± 2.28)	14.31–19.03 (16.77 ± 1.69)	25.61–30.00 (27.50 ± 1.67)	33.04–46.71 (38.44 ± 4.43)
Santa Bárbara (= FLONA Jamari)							
Females ($N = 14$)	10.73–13.09 (11.71 ± 0.62)	9.17–11.70 (10.75 ± 0.75)	11.16–13.29 (12.01 ± 0.65)	13.68–16.22 (15.16 ± 0.70)	12.99–16.70 (14.32 ± 0.94)	17.70–23.07 (21.10 ± 1.34)	29.99–38.31 (33.78 ± 2.37)
Males ($N = 14$)	10.88–17.40 (13.99 ± 1.85)	11.26–16.00 (13.23 ± 1.43)	12.24–17.18 (14.87 ± 1.65)	15.07–23.30 (18.89 ± 2.52)	14.9–22.41 (18.43 ± 1.90)	21.64–30.26 (26.25 ± 2.24)	32.84–52.33 (41.23 ± 6.85)

Table 5. Continued

Population	AL	FAL	HDL	THL	SL	FOL	AGD
Santa Cruz							
Females (*N* = 12)	10.60–13.71 (11.90 ± 0.86)	9.85–12.67 (11.09 ± 0.79)	10.90–14.05 (12.04 ± 0.89)	13.70–19.50 (15.89 ± 1.78)	13.84–16.64 (14.78 ± 0.76)	20.06–24.61 (22.00 ± 1.39)	32.07–39.05 (35.82 ± 1.79)
Males (*N* = 14)	11.25–17.52 (14.55 ± 1.52)	11.96–14.73 (13.38 ± 0.73)	12.27–16.53 (14.96 ± 1.28)	16.58–22.31 (19.16 ± 1.97)	15.06–19.47 (18.12 ± 1.08)	24.77–29.09 (26.88 ± 1.25)	37.45–46.77 (42.08 ± 2.61)
UNIR							
Females (*N* = 13)	11.49–13.41 (12.47 ± 0.65)	10.07–12.22 (11.17 ± 0.59)	10.56–14.54 (12.84 ± 1.11)	13.45–16.40 (15.01 ± 1.11)	13.44–16.62 (14.68 ± 0.89)	20.90–23.97 (22.59 ± 0.95)	32.73–42.46 (38.41 ± 3.11)
Males (*N* = 2)	10.90–16.82 (13.86 ± 4.19)	11.97–14.63 (13.30 ± 1.88)	14.08–16.17 (15.12 ± 1.48)	16.89–20.03 (18.46 ± 2.22)	15.74–19.53 (17.64 ± 2.68)	23.99–29.12 (26.56 ± 3.63)	38.15–48.26 (43.20 ± 7.15)
All populations							
Females (*N* = 91)	8.77–14.05 (12.07 ± 0.95)	9.17–13.03 (11.01 ± 0.75)	10.32–15.31 (12.40 ± 1.04)	12.17–19.50 (15.18 ± 1.26)	12.96–16.78 (14.61 ± 0.92)	17.70–24.84 (21.53 ± 1.60)	29.99–44.01 (36.96 ± 2.85)
Males (*N* = 90)	10.88–19.31 (14.72 ± 1.87)	11.26–17.25 (13.59 ± 1.27)	12.24–18.60 (15.22 ± 1.48)	14.30–23.53 (19.28 ± 2.03)	14.41–22.41 (18.17 ± 1.57)	20.24–30.89 (26.36 ± 2.25)	32.84–55.48 (42.95 ± 4.82)
T. oreadicus							
Females (*N* = 12)	9.02–14.25 (11.29 ± 1.66)	8.92–12.42 (10.79 ± 1.06)	11.13–14.45 (12.79 ± 1.07)	13.52–17.32 (15.15 ± 1.21)	12.68–16.27 (14.19 ± 1.19)	19.76–23.72 (21.62 ± 1.37)	28.69–44.32 (36.12 ± 4.51)
Males (*N* = 4)	12.68–16.04 (14.08 ± 1.52)	11.34–14.22 (12.39 ± 1.26)	14.12–15.44 (14.48 ± 0.64)	17.03–20.81 (18.28 ± 1.72)	16.19–19.08 (17.49 ± 1.29)	23.49–27.91 (26.25 ± 1.93)	36.79–46.93 (41.72 ± 4.35)

Abbreviations: AGD, armpit–groin distance; AL, arm length; BH, body height; EOS, ear opening–snout distance; FAL, forearm length; FOL, foot length; HDL, hand length; HH, head height; HL, head length; HW, head width; MB, midbody; SL, shank length; SVL, snout–vent length; THL, thigh length; TL, tail length. The number of specimens with fully grown tails [in square brackets] follows the total number of individuals (*N*) from each sex measured for statistical analyses.

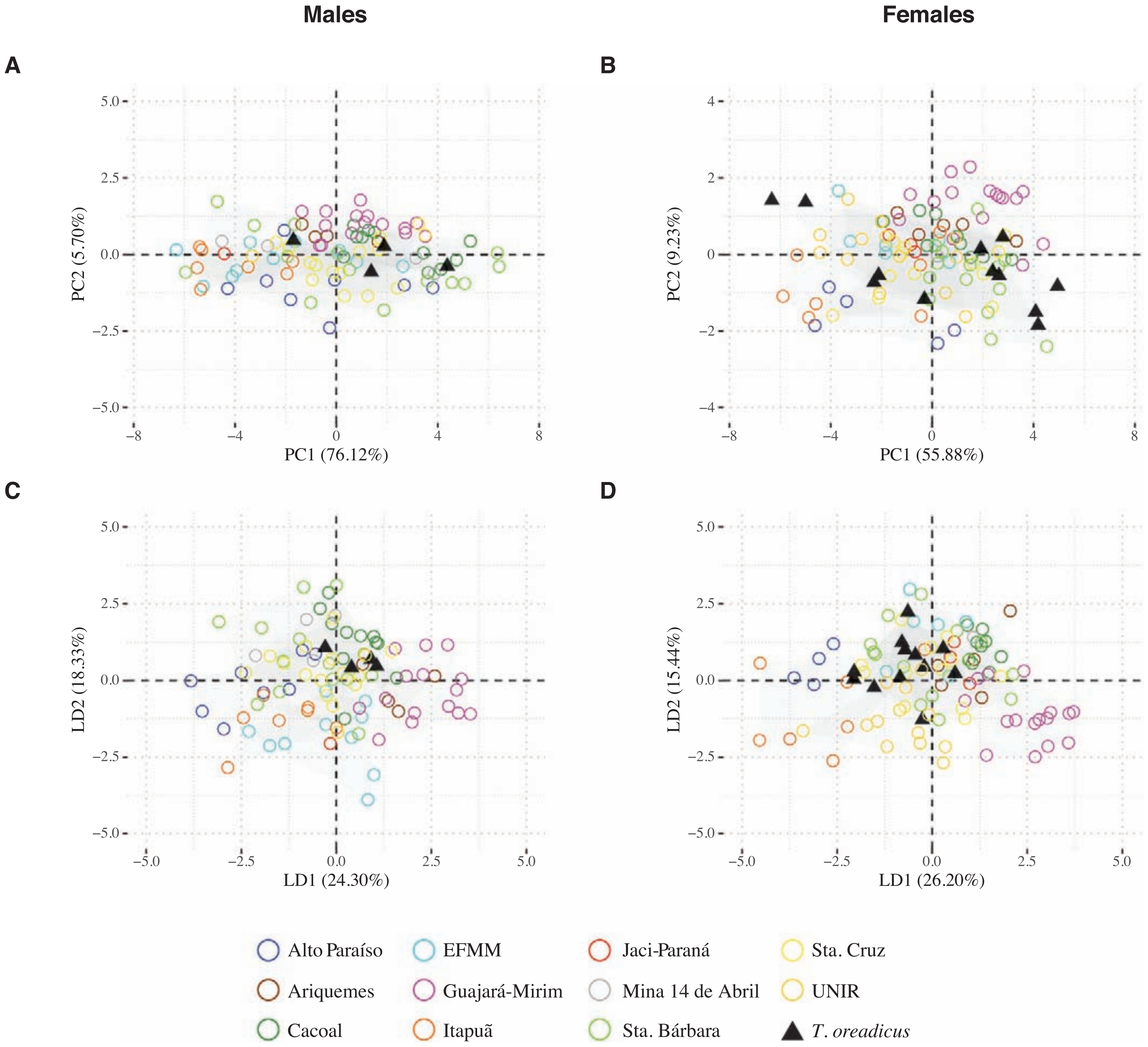

Figure 6. Scatterplots of PC1 and PC2 generated by the principal component analyses and LD1 and LD2 generated by the linear discriminant analyses performed on morphometric variables of males (A, C) and females (B, D). See Table 6 for corresponding summary statistics.

Venezuela, central and south-eastern Colombia, north-eastern Ecuador, northern Peru, and the western portion of the state of Amazonas and most of the state of Acre, in Brazil. Smaller and/or discontinuous areas are inferred as suitable along the margins of the Amazon River in part of the Brazilian states of Amazonas and Pará, and also to the north of that river in the states of Roraima, Pará, and Amapá, reaching the southernmost regions of Guyana, Suriname, and French Guiana. A thin strip of climatically suitable areas is also inferred to the west of the Andes, along the coast of Peru, Ecuador, Colombia, and Venezuela, further entering Central America.

In comparison with the LIG, a remarkable contraction of suitable areas for the new *Tropidurus* from Rondônia has been estimated for the period corresponding to the LGM (Fig. 8). Reduction of suitable areas is inferred to have occurred, particularly throughout the South American diagonal of open formations, to the extent that a single, relatively small nucleus of suitable areas remained in the area corresponding to the heart of the Brazilian Cerrado. This climatically adequate nuclear area is located hundreds of kilometres apart from the nearest distribution record of the species known presently, indicating that ancestral *Tropidurus* populations might have experienced severe geographical range shifts and geographical isolation around the LGM. Suitable areas located to the north of the Amazon River during the LIG shifted northwards during the LGM, but shrinkage was not as dramatic (Fig. 8). A thin coastal corridor of suitable areas connected north-eastern Brazil and Venezuela, passing through French Guiana, Suriname, and Guiana and extending through a section of the continental shelf that is currently covered by the sea. Discontinuous suitable areas were

Table 6. Summary of the principal component analyses and linear discriminant analyses performed on morphometric variables of *Tropidurus madeiramamore* and *Tropidurus oreadicus*. Abbreviations: EVL, eigenvalues; LD, discriminant coefficients; PC, component loadings; % Variance, explained variance.

Variable	PCA males			LDA males			PCA females			LDA females		
	PC1	PC2	PC3	LD1	LD2	LD3	PC1	PC2	PC3	LD1	LD2	LD3
SVL	−0.3207	0.1531	0.0309	0.1400	0.1692	0.1378	−0.3525	0.1754	−0.2653	−0.0066	−0.2264	0.4015
HH	−0.2772	0.1290	−0.6560	−0.2331	0.0053	−0.1264	−0.2781	−0.2418	−0.0769	−0.1095	−0.4097	0.1975
HL	−0.2866	0.3899	−0.1285	0.4410	−0.2874	0.0511	−0.3089	0.1825	−0.1287	0.0833	−0.2342	−0.4483
HW	−0.3154	0.1613	−0.1559	0.3772	−0.4629	0.1631	−0.3362	−0.0145	−0.2642	0.1101	−1.2833	0.1757
EOS	−0.3194	0.0345	−0.1580	−0.9584	0.3997	0.4070	−0.3472	−0.1414	−0.1400	−1.0971	0.8494	−0.3395
AL	−0.2906	−0.1237	0.4095	0.2646	−0.4306	0.1880	−0.2281	0.3195	0.5847	0.4878	−0.2304	−0.2985
FAL	−0.2939	−0.1154	0.3354	−0.4376	−0.5238	−0.9672	−0.2663	0.2444	0.2446	0.2192	0.5889	−0.2598
HDL	−0.2655	−0.4660	−0.0914	−0.4216	−0.4687	0.6549	−0.2591	−0.3485	−0.1506	−0.3206	0.4715	−0.7007
THL	−0.2933	0.0893	0.0079	−0.1158	0.2834	−0.7108	−0.2425	−0.1232	0.4932	0.1532	0.6336	0.4685
SL	−0.2650	−0.2594	0.1765	−0.2692	0.3172	−0.3391	−0.2614	−0.1788	0.2892	0.1159	0.4467	0.1340
FOL	−0.2553	−0.5334	−0.1628	−0.2635	−0.0465	−0.1204	−0.3009	−0.3958	0.0048	−0.5886	−0.0171	−0.3383
AGD	−0.2720	0.4185	0.3957	0.1034	−0.1306	−0.1268	−0.2483	0.6084	−0.2579	0.2199	0.1462	−0.4900
EVL	9.1342	0.6837	0.5254	3.7754	2.8473	2.2639	6.7055	1.1072	0.8840	4.8291	2.8458	2.7103
SD	3.0223	0.8269	0.7248	1.9431	1.6874	1.5046	2.5895	1.0522	0.9402	2.1975	1.6870	1.6463
% Variance	76.12	5.70	4.38	24.30	18.33	14.57	55.88	9.23	7.37	26.20	15.44	14.70

maintained near the coast of Ecuador, throughout the coast of Colombia and westernmost portion of Venezuela, and towards Central America, but disappeared completely along the coast of Peru.

Species distribution modelling indicates that areas potentially adequate for occurrence of the new *Tropidurus* from Rondônia were again present in South-western Amazonia during the Holocene (Fig. 8). However, the most suitable areas for the species were concentrated to the north, covering the north-westernmost part of the Brazilian state of Amazonas and a large part of the territories of Colombia and Venezuela to the east of the Andes. The second largest block of highly suitable areas is inferred near the mouth of the Amazon River. Given that highly suitable areas were either scarce or absent in South-western Amazonia during the Holocene, it is conceivable that the species had its distribution significantly fragmented around that period or even before. Species distribution modelling suggests that the region currently occupied by the new *Tropidurus* from Rondônia, located between the Madeira and Mamoré rivers, gained more suitable environments around the Holocene and towards the present. Areas estimated as maximally suitable for the species presently are disjunct and concentrated in the core Brazilian Cerrado, in a portion of north-eastern Brazil and near the mouth of the Amazon River in the Brazilian states of Pará and Amazonas, north of the Amazon River towards the Guianas region, and in Venezuela and Colombia to the east of the Andes.

Although extremely large nuclei of climatically suitable areas are predicted for the new *Tropidurus* in the present, not even a single record of this species is currently known outside the savannah enclaves of the state of Rondônia (Fig. 8). The best distribution model selected on the basis of the Akaike information criterion (AICc = 500.102) has a regularization multiplier of 0.5, three resource classes (LPQ), and a 10% training omission rate and minimum training presence omission rate respectively equivalent to .25 and .17 (a summary of MAXENT model selection is provided in Supporting Information, File S14). These later values indicate model overfitting (Muscarella *et al.* 2014) and suggest that even the best species distribution models produced in this study might be overestimating the potential distribution of the new *Tropidurus* from Rondônia to a certain degree.

TAXONOMY

Genetic and morphological evidence supports the recognition of a single, highly polymorphic taxonomic entity assignable to the genus *Tropidurus* Wied, 1825 among the populations sampled in the State of Rondônia, Brazil. Given that no formal names are available for these populations, we herein describe them as a new species unambiguously distinguishable from all 30 valid congeners (*sensu* Carvalho *et al.* 2018).

Tropidurus madeiramamore sp. nov.

(Figs. 2, 9A–C, 10, 11A, B)

LSID: https://zoobank.org/urn:lsid:zoobank.org:pub:740FE136-CE17-4393-85F7-BEEC5CF2837E

Tropidurus torquatus hispidus – Cunha, 1961. *Boletim do Museu Paraense Emílio Goeldi, Zoologia* **39**: 76 [part].

Table 7. Minimum and maximum values (mean ± SD) of scale counts of adult specimens of *Tropidurus madeiramamore* from 10 populations from the State of Rondônia, Brazil, plus the type series of *Tropidurus oreadicus*.

Population	Dorsals to legs	Dorsals to tail	Gulars	Ventrals	Subdigital lamellae finger IV	Subdigital lamellae toe IV	Tibials
Alto Paraíso							
Females (*N* = 4)	81–93 (87.50 ± 5.92)	93–102 (98.25 ± 3.86)	39–43 (41.75 ± 1.89)	75–80 (76.75 ± 2.22)	14–16 (15 ± 0.82)	21–22 (21.25 ± 0.50)	23–26 (24.50 ± 1.29)
Males (*N* = 8)	77–84 (79.75 ± 2.25)	85–93 (88.62 ± 2.50)	38–45 (42.50 ± 2.39)	71–82 (76.38 ± 3.66)	14–16 (15.12 ± 0.83)	20–24 (22.75 ± 1.39)	23–25 (23.88 ± 0.83)
Ariquemes							
Females (*N* = 5)	90–96 (93.60 ± 2.88)	101–110 (105.60 ± 3.65)	41–45 (43.40 ± 1.82)	76–85 (81.00 ± 3.54)	16–17 (16.6 ± 0.55)	23–25 (24.00 ± 1.00)	22–24 (23.60 ± 0.89)
Males (*N* = 4)	80–85 (82.50 ± 2.38)	90–97 (93.00 ± 3.56)	40–47 (43.25 ± 2.99)	74–80 (77.50 ± 2.65)	15–17 (16.50 ± 1.00)	22–25 (24.25 ± 1.50)	23–26 (24.50 ± 1.29)
Cacoal							
Females (*N* = 9)	76–83 (80.00 ± 2.45)	86–95 (90.00 ± 3.24)	37–42 (39.56 ± 1.59)	71–76 (73.33 ± 1.66)	12–14 (12.78 ± 0.67)	18–21 (19.44 ± 1.01)	23–25 (24.00 ± 0.71)
Males (*N* = 11)	70–74 (71.91 ± 1.58)	79–85 (81.09 ± 1.76)	38–42 (40.45 ± 1.29)	67–76 (72.82 ± 2.56)	11–15 (14.09 ± 1.22)	18–22 (19.91 ± 1.14)	23–26 (24.27 ± 1.01)
EFMN							
Females (*N* = 6)	75–83 (78.17 ± 3.43)	83–93 (87.17 ± 4.54)	38–45 (42.00 ± 2.53)	79–91 (84.50 ± 4.51)	15–17 (16.00 ± 0.89)	21–24 (22.33 ± 1.03)	22–27 (24.33 ± 1.75)
Males (*N* = 10)	70–79 (72.30 ± 2.63)	78–84 (79.70 ± 2.00)	40–46 (42.80 ± 1.99)	78–89 (82.60 ± 3.75)	14–17 (15.80 ± 0.79)	21–24 (22.40 ± 1.07)	22–25 (24.10 ± 0.99)
Guajará-Mirim							
Females (*N* = 16)	72–82 (77.25 ± 2.74)	81–90 (86.12 ± 2.85)	36–43 (39.25 ± 1.57)	71–82 (77.19 ± 3.33)	13–17 (15.06 ± 1.12)	20–23 (21.12 ± 0.89)	22–25 (22.06 ± 1.69)
Males (*N* = 15)	67–74 (70.20 ± 1.66)	75–82 (78.60 ± 2.10)	37–44 (40.07 ± 1.91)	69–80 (74.20 ± 3.08)	15–17 (15.47 ± 0.64)	20–24 (21.33 ± 1.05)	21–25 (23.25 ± 0.93)
Itapuã							
Females (*N* = 7)	86–103 (96.00 ± 5.74)	101–114 (108.00 ± 4.76)	48–54 (51.86 ± 2.19)	78–86 (84.00 ± 3.00)	15–18 (16.00 ± 1.15)	23–27 (25.00 ± 1.53)	23–26 (24.57 ± 0.98)
Males (*N* = 7)	86–93 (89.14 ± 2.61)	96–102 (99.86 ± 2.19)	50–53 (51.57 ± 0.98)	77–84 (81.00 ± 2.52)	16–18 (17.43 ± 0.79)	24–27 (25.71 ± 0.95)	23–24 (23.71 ± 0.49)
Jaci-Paraná							
Females (*N* = 3)	90–100 (95.00 ± 5.00)	101–112 (106.33 ± 5.51)	42–45 (43.67 ± 1.53)	82–85 (83.33 ± 1.53)	15–16 (15.67 ± 0.58)	23–25 (24.00 ± 1.00)	24–25 (24.33 ± 0.58)
Males (*N* = 1)	89	101	45	82	17	27	25
Santa Bárbara (= FLONA Jamari)							
Females (*N* = 8)	87–99 (93.75 ± 3.73)	97–110 (104.50 ± 4.04)	48–53 (50.50 ± 2.00)	81–87 (83.62 ± 2.45)	15–17 (15.50 ± 0.76)	22–27 (24.12 ± 1.55)	24–26 (24.75 ± 0.71)
Males (*N* = 6)	84–89 (85.67 ± 2.25)	92–97 (94.60 ± 1.97)	47–53 (50.67 ± 2.73)	80–88 (83.17 ± 2.79)	15–18 (16.17 ± 1.17)	24–27 (25.17 ± 0.98)	23–25 (24.50 ± 0.84)
Santa Cruz							
Females (*N* = 5)	82–87 (84.60 ± 2.51)	94–98 (95.60 ± 1.67)	39–44 (41.40 ± 2.07)	73–84 (76.60 ± 4.39)	12–15 (14.00 ± 1.22)	22–23 (22.40 ± 0.55)	22–25 (23.60 ± 1.14)
Males (*N* = 7)	72–80 (76.43 ± 2.82)	81–89 (85.43 ± 2.76)	38–44 (40.71 ± 2.29)	70–78 (74.14 ± 3.08)	14–16 (15.00 ± 0.58)	21–25 (22.57 ± 1.27)	24–25 (24.14 ± 0.38)
UNIR							
Females (*N* = 13)	69–90 (81.38 ± 5.16)	78–99 (100.33 ± 6.01)	39–44 (41.62 ± 1.80)	79–87 (82.69 ± 2.56)	13–17 (14.85 ± 1.07)	20–24 (21.23 ± 1.36)	24–27 (25.15 ± 0.80)
Males (*N* = 2)	70–70 (70.00 ± 0.00)	79–80 (79.50 ± 0.71)	41–42 (41.50 ± 0.71)	78–78 (78.00 ± 0.00)	15–15 (15.00 ± 0.00)	20–23 (21.50 ± 2.12)	22–25 (23.50 ± 2.12)
All populations							
Females (*N* = 76)	69–103 (84.62 ± 8.02)	78–114 (94.64 ± 9.03)	36–54 (42.97 ± 4.64)	71–91 (79.99 ± 4.77)	12–18 (15.01 ± 1.37)	18–27 (22.11 ± 2.00)	22–27 (24.18 ± 1.14)
Males (*N* = 71)	67–93 (76.58 ± 6.96)	75–102 (85.55 ± 7.68)	37–53 (43.17 ± 4.40)	67–89 (77.24 ± 4.81)	11–18 (15.54 ± 1.24)	18–27 (22.55 ± 2.16)	21–26 (23.90 ± 1.03)
T. oreadicus							
Females (*N* = 12)	67–79 (73.67 ± 3.80)	79–89 (83.92 ± 3.63)	44–54 (49.17 ± 2.92)	57–67 (63.83 ± 2.69)	15–18 (16.17 ± 0.94)	21–23 (21.83 ± 0.83)	18–21 (19.83 ± 0.94)
Males (*N* = 4)	69–73 (70.75 ± 2.06)	78–82 (80.25 ± 1.71)	45–51 (48.00 ± 2.94)	60–67 (64.00 ± 2.94)	15–16 (15.75 ± 0.50)	22–23 (22.25 ± 0.50)	19–23 (21.00 ± 1.63)

Table 7. Continued

(Cont.)	Midbody	Postmentals	Canthals	Supralabials	Infralabials	Loreals	Lorilabials	Superciliaries
Alto Paraíso								
Females ($N = 4$)	92–99 (95.75 ± 2.87)	2–4 (4.00 ± 2.75)	2–3 (2.75 ± 0.50)	4–6 (4.50 ± 1.00)	4–6 (4.75 ± 0.96)	2–6 (4.25 ± 1.71)	7–11 (8.50 ± 1.91)	7–8 (7.25 ± 0.50)
Males ($N = 8$)	77–87 (82.25 ± 3.37)	2–4 (3.00 ± 0.76)	2–3 (2.88 ± 0.35)	4–5 (4.12 ± 0.35)	4–5 (4.75 ± 0.46)	4–7 (4.88 ± 1.13)	6–13 (9.50 ± 2.33)	7–9 (7.62 ± 0.74)
Ariquemes								
Females ($N = 5$)	95–103 (98.40 ± 3.44)	3–4 (3.60 ± 0.55)	2–3 (2.60 ± 0.55)	4–5 (4.80 ± 0.45)	6–6 (6.00 ± 0.00)	2–4 (3.00 ± 0.71)	6–10 (7.80 ± 1.48)	7–9 (7.60 ± 0.89)
Males ($N = 4$)	75–88 (79.25 ± 4.57)	2–4 (3.00 ± 0.82)	2–2 (2.00 ± 0.00)	4–5 (4.75 ± 0.50)	6–6 (6.00 ± 0.00)	3–4 (3.25 ± 0.50)	6–10 (8.25 ± 1.71)	7–10 (8.00 ± 1.41)
Cacoal								
Females ($N = 9$)	88–94 (91.33 ± 2.18)	2–3 (2.78 ± 0.44)	2–3 (2.22 ± 0.44)	4–5 (4.89 ± 0.33)	6–7 (6.11 ± 0.33)	2–5 (2.78 ± 0.97)	10–13 (1.33 ± 0.87)	6–8 (6.89 ± 0.78)
Males ($N = 11$)	74–81 (77.64 ± 2.20)	1–4 (2.91 ± 0.70)	2–2 (2.00 ± 0.00)	4–5 (4.91 ± 0.30)	6–7 (6.09 ± 0.30)	1–4 (2.45 ± 0.93)	9–16 (11.64 ± 1.86)	6–8 (6.91 ± 0.54)
EFMN								
Females ($N = 6$)	88–93 (90.17 ± 1.94)	3–4 (3.67 ± 0.52)	2–3 (2.17 ± 0.41)	4–6 (5.00 ± 0.63)	5–6 (5.83 ± 0.41)	4–6 (4.83 ± 0.75)	9–11 (10.17 ± 0.75)	6–8 (6.50 ± 0.84)
Males ($N = 10$)	74–83 (79.10 ± 3.31)	3–5 (3.70 ± 0.67)	2–2 (2.00 ± 0.00)	5–5 (5.00 ± 0.00)	5–7 (6.00 ± 0.47)	3–8 (5.60 ± 1.43)	8–13 (11.00 ± 2.21)	6–8 (7.10 ± 0.57)
Guajará-Mirim								
Females ($N = 16$)	75–89 (84.88 ± 4.00)	3–4 (3.25 ± 0.45)	2–3 (2.19 ± 0.40)	3–5 (4.19 ± 0.75)	4–6 (5.00 ± 0.37)	3–8 (4.62 ± 1.09)	5–11 (8.06 ± 1.98)	6–9 (7.25 ± 0.86)
Males ($N = 15$)	70–82 (76.47 ± 3.66)	2–4 (3.13 ± 0.64)	2–3 (2.13 ± 0.35)	3–6 (4.33 ± 1.11)	4–6 (5.20 ± 0.56)	3–10 (5.47 ± 1.68)	8–12 (9.73 ± 1.03)	6–9 (7.20 ± 0.94)
Itapuã								
Females ($N = 7$)	98–109 (102.86 ± 3.76)	3–5 (3.86 ± 0.69)	3–3 (3.00 ± 0.00)	4–5 (4.29 ± 0.49)	5–6 (5.29 ± 0.49)	4–9 (5.86 ± 1.86)	9–14 (11.86 ± 1.77)	6–9 (7.29 ± 0.95)
Males ($N = 7$)	86–97 (93.71 ± 3.64)	2–4 (3.43 ± 0.79)	3–3 (3.00 ± 0.00)	4–7 (5.14 ± 1.07)	5–6 (5.57 ± 0.53)	4–9 (5.57 ± 1.72)	9–16 (11.14 ± 2.41)	6–9 (7.57 ± 0.98)
Jaci- Paraná								
Females ($N = 3$)	98–106 (103.00 ± 4.36)	2–3 (2.67 ± 0.58)	2–3 (2.67 ± 0.58)	5–5 (5.00 ± 0.00)	6–7 (6.33 ± 0.58)	5–6 (5.67 ± 0.58)	11–13 (12.00 ± 1.00)	8–10 (9.00 ± 1.00)
Males ($N = 1$)	91	3	3	5	6	6	10	8
Santa Bárbara (= FLONA Jamari)								
Females ($N = 8$)	98–109 (102.00 ± 3.82)	3–4 (3.12 ± 0.35)	2–3 (2.88 ± 0.35)	4–5 (4.88 ± 0.35)	5–6 (5.75 ± 0.46)	5–11 (6.88 ± 2.30)	9–15 (11.50 ± 2.33)	7–8 (7.12 ± 0.35)
Male s ($N = 6$)	87–91 (88.83 ± 1.83)	2–5 (3.33 ± 1.03)	3–3 (3.00 ± 0.00)	5–6 (5.50 ± 0.55)	6–7 (6.17 ± 0.41)	5–8 (6.33 ± 1.03)	10–17 (13.17 ± 2.93)	7–8 (7.50 ± 0.55)
Santa Cruz								
Females ($N = 5$)	89–95 (92.40 ± 2.30)	3–4 (3.20 ± 0.45)	2–3 (2.40 ± 0.55)	4–6 (4.60 ± 0.89)	5–6 (5.80 ± 0.45)	3–4 (3.40 ± 0.55)	6–10 (7.60 ± 1.67)	7–8 (7.60 ± 0.55)
Males ($N = 7$)	79–82 (81.00 ± 1.00)	3–4 (3.43 ± 0.53)	2–3 (2.43 ± 0.53)	4–5 (4.57 ± 0.53)	5–7 (6.00 ± 0.58)	3–5 (3.57 ± 0.79)	4–12 (8.71 ± 2.69)	7–9 (8.00 ± 0.82)
UNIR								
Females ($N = 13$)	78–96 (88.69 ± 4.27)	2–4 (3.31 ± 0.63)	1–3 (2.00 ± 0.41)	4–6 (4.85 ± 0.80)	5–7 (6.00 ± 0.58)	3–8 (4.92 ± 1.38)	7–11 (9.38 ± 1.45)	6–9 (7.08 ± 1.04)
Males ($N = 2$)	75–79 (77.00 ± 2.83)	3–4 (3.50 ± 0.71)	2–3 (2.50 ± 0.71)	5–6 (5.50 ± 0.71)	5–5 (5.00 ± 0.00)	6–7 (6.50 ± 0.71)	10–11 (10.50 ± 0.71)	6–11 (8.50 ± 3.54)
All populations								
Females ($N = 76$)	75–109 (92.84 ± 7.31)	2–5 (3.25 ± 0.61)	1–3 (2.39 ± 0.52)	3–6 (4.64 ± 0.69)	4–7 (5.63 ± 0.65)	2–11 (4.66 ± 1.75)	5–15 (9.68 ± 2.23)	6–10 (7.22 ± 0.90)
Males ($N = 71$)	70–97 (81.30 ± 6.25)	1–5 (3.24 ± 0.73)	2–3 (2.39 ± 0.49)	3–7 (4.76 ± 0.78)	4–7 (5.65 ± 0.66)	1–10 (4.76 ± 1.78)	4–17 (10.45 ± 2.34)	6–11 (7.42 ± 0.95)
T. oreadicus								
Females ($N = 12$)	63–80 (73.92 ± 4.68)	2–4 (3.70 ± 0.67)	3–3 (3.00 ± 0.00)	5–6 (5.25 ± 0.45)	5–6 (5.67 ± 0.49)	2–8 (5.33 ± 1.56)	5–10 (7.58 ± 1.44)	6–10 (8.00 ± 1.04)
Males ($N = 4$)	71–74 (72.75 ± 1.50)	3–4 (3.50 ± 0.58)	3–3 (3.00 ± 0.00)	5–6 (5.50 ± 0.58)	5–6 (5.75 ± 0.50)	4–7 (5.50 ± 1.73)	8–9 (8.25 ± 0.50)	7–9 (7.75 ± 0.96)

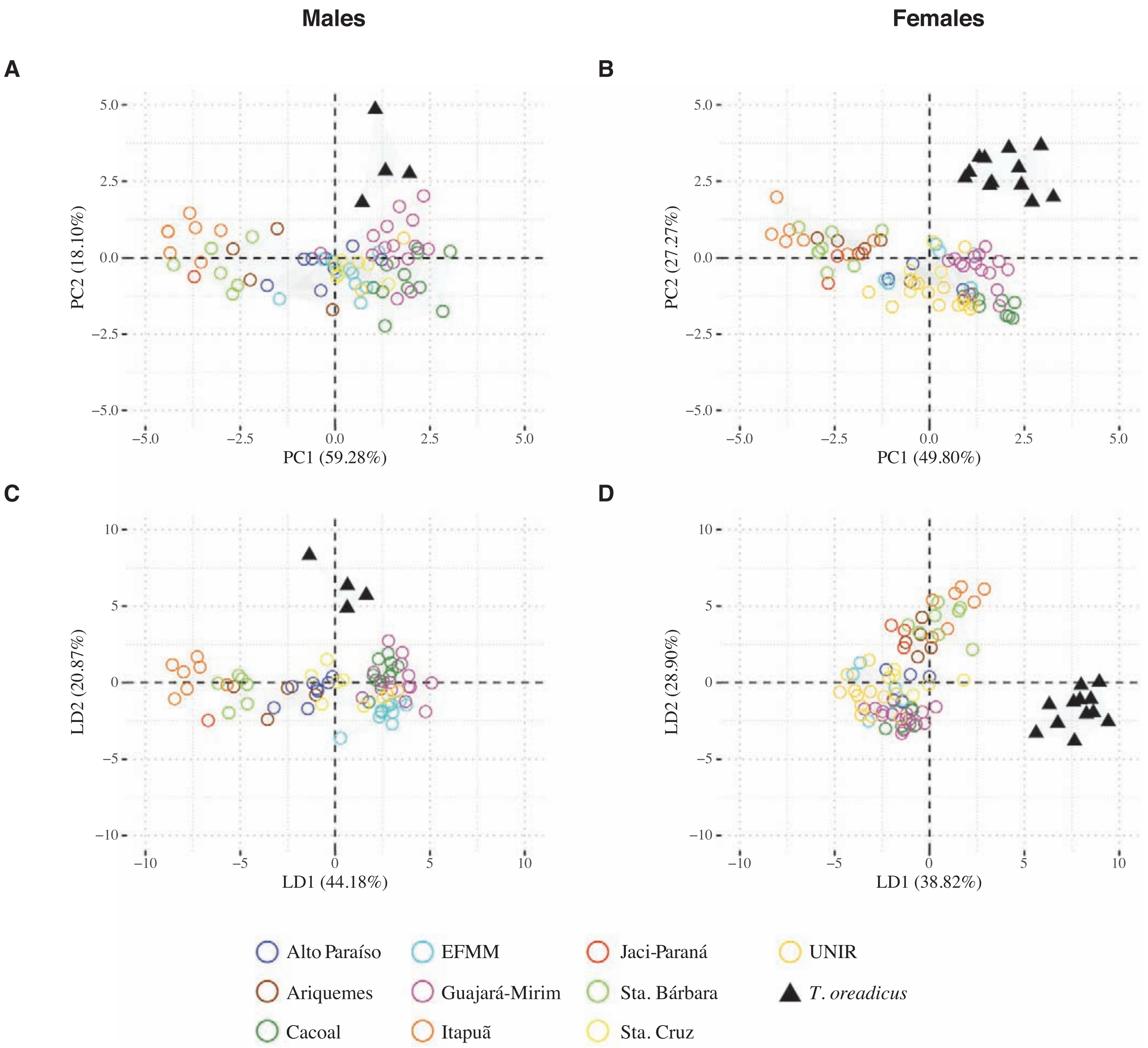

Figure 7. Scatterplots of PC1 and PC2 generated by the principal component analyses and LD1 and LD2 generated by the linear discriminant analyses performed on meristic variables of males (A, C) and females (B, D). See Table 8 for corresponding summary statistics.

Tropidurus oreadicus – Rodrigues, 1987. *Arquivos de Zoologia* **31**: 188 [part].
Tropidurus grupo *torquatus* sp. A – Nascimento *et al.*, 1988. *Boletim do Museu Paraense Emílio Goeldi, Zoologia* **4**: 32 [part].
Tropidurus oreadicus – Vitt, 1993. *Canadian Journal of Zoology* **71**: 2371 [part].
Tropidurus oreadicus – Vitt & Caldwell, 1993. *Journal of Herpetology* **27**: 51 [part].
Tropidurus oreadicus – Ávila-Pires, 1995. *Zoologische Verhandelingen* **299**: 195 [part].
Tropidurus oreadicus – Ribeiro-Júnior, 2015. *Zootaxa* **3983**: 30 [part].

Holotype: MZUSP 107155, adult male from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′21.5″S, 63°04′24.6″W; ~178 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero on 15 November 2017.

Allotype: MZUSP 107158, adult female from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′22.5″S, 63°04′23.6″W; ~167 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero on 15 November 2017.

Paratypes: MZUSP 107156 and 107157, adult females from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′22.9″S, 63°04′24.2″W; ~170 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero on 15 November 2017. MZUSP 107159 and 107160, adult females from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′21.4″S, 63°04′24.5″W; ~162 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero

Table 8. Summary of the principal component analyses (PCAs) and linear discriminant analyses (LDAs) performed on meristic variables of *Tropidurus madeiramamore* and *Tropidurus oreadicus*. Abbreviations: LIV-F, lamellae under finger IV; LIV-T, lamellae under toe IV; EVL, eigenvalue; LD, discriminant coefficients; PC, component loadings; % Variance, explained variance.

Variable	PCA males			LDA males			PCA females			LDA females		
	PC1	PC2	PC3	LD1	LD2	LD3	PC1	PC2	PC3	LD1	LD2	LD3
Dorsal leg	−0.4463	−0.0373	−0.4532	−0.2864	0.0089	−0.3070	−0.4906	−0.0505	0.3619	0.0449	0.1835	−0.2923
Gulars	−0.4533	−0.0496	−0.3926	−0.1368	−0.0675	0.0892	−0.4935	−0.0886	0.3270	−0.0578	−0.0257	0.1169
Ventrals	−0.3929	0.2784	−0.0483	−0.1764	0.3534	0.2967	−0.2686	0.5022	0.2792	0.3635	0.1517	0.2105
LIV-F	−0.3103	−0.4078	0.6032	0.0536	−0.3247	0.1185	−0.3718	−0.3530	−0.4449	−0.2612	0.0792	0.1559
LIV-T	−0.3572	0.3094	0.5121	0.0342	0.0214	0.2518	−0.1863	0.5012	−0.6446	0.0725	−0.0483	0.2077
Tibials	−0.4435	0.1345	0.0870	−0.1535	−0.0972	0.1288	−0.4309	0.2902	−0.1485	0.2095	0.3491	0.0854
Midbody	−0.1425	−0.7991	−0.0662	0.1353	−0.1026	−0.1127	−0.2917	−0.5266	−0.2207	−0.5486	−0.0257	0.1055
EVL	4.1495	1.2667	0.6817	9.9149	4.6846	3.2086	3.4859	1.9092	0.7918	9.9413	7.4005	3.3027
SD	2.0370	1.1255	0.82563	3.1488	2.1644	1.7912	1.867	1.3817	0.8898	3.1530	2.7204	1.8173
% Variance	59.28	18.10	97.38	44.18	20.87	14.30	49.80	27.27	11.31	38.82	28.90	12.90

on 16 November 2017. MZUSP 107161, adult female from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′22.3″S, 63°04′24.3″W; ~178 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero on 16 November 2017. MZUSP 107162, adult female from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′21.8″S, 63°04′24.1″W; ~178 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero on 16 November 2017. MZUSP 107163, adult female from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′21.3″S, 63°04′24.4″W; ~173 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero on 16 November 2017. MZUSP 107164, adult female from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′22.0″S, 63°04′24.0″W; ~176 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero on 16 November 2017. MZUSP 107165, adult male from Floresta Nacional do Jamari, Município de Itapuã de Oeste, Estado de Rondônia, Brazil (09°12′22.5″S, 63°04′23.9″W; ~173 m a.s.l.), collected by A. L. G. Carvalho and R. C. B. Paredero on 16 November 2017.

Common names: 'Lagartixa preta' (black lizard), 'lagartixa', 'calango', South American collared lizard.

Diagnosis: Tropidurus madeiramamore qualifies as a member of *Tropidurus* Wied, 1825 by having a series of morphological characters indicated by Frost *et al.* (2001) as exclusive to the genus: skull not highly elevated at the level of the orbits; presence of 'flash' marks on ventral surface of thighs; circumorbitals distinct from other small supraorbital scales; lateral fringe not developed on both sides of toe IV; enlarged middorsal scale row absent; and tail terete.

The new species fits the definition of the *Tropidurus torquatus* species group (*sensu* Frost *et al.* 2001) by lacking an enlarged middorsal scale row (well marked in species of the *T. spinulosus* group, more pronounced in males), by the black coloration of the 'flash' marks on the underside of the thighs and cloacal flap of adult males (yellow, cream, or orangey 'flash' marks occur in males of the *T. spinulosus* group), and by lacking a dorsoventrally flattened body (strongly flattened in species of the *T. semitaeniatus* group and, more moderately, in *T. bogerti*).

Tropidurus madeiramamore is distinguished from other members of the *T. torquatus* species group by the following combination of traits: a single, extremely wide and deep mite pocket on the lateral neck; post-humeral (axillary) and prefemoral (inguinal) mite pockets absent; posterior ventral head and throat coloration black; venter dark pigmented (light in some females, rarely in males) and/or mottled chest, with a tendency towards melanism observed especially in males; black 'flash' marks on the precloacal flap, underside of thighs, ventral base of the tail, and area near the base of toe I (and non-rarely of finger I) in males; and saxicolous habit.

Comparisons: Tropidurus madeiramamore is distinguished from all its congeners in the *T. torquatus* species group but *T. oreadicus* in having mite pockets Type D (*sensu* Rodrigues 1987), characterized by the presence of a single granular mite pocket on the lateral neck and no post-humeral (axillary) or prefemoral (inguinal) mite pockets. However, the lateral neck mite pocket of *T. madeiramamore* is much wider and deeper than that of *T. oreadicus* (Fig. 2). The new species differs specifically from *T. azurduyae*, *T. catalanensis*, *T. chromatops*, *T. cocorobensis*, *T. etheridgei*, *T. hygomi*, *T. imbituba*, *T. psammonastes*, *T. sertanejo*, and *T. torquatus* in having one mite pocket on the lateral neck (these species have two, except *T. sertanejo*, which lacks lateral neck mite pockets). It also differs from *T. catalanensis*, *T. erythrocephalus*, *T. hispidus*, *T. insulanus*, *T. imbituba*, *T. montanus*, *T. mucujensis*, *T. sertanejo*, and *T. torquatus* in lacking post-humeral mite pockets (present in these species) and from *T. catalanensis*, *T. erythrocephalus*, *T. imbituba*, *T. itambere*, *T. montanus*, *T. mucujensis*, *T. sertanejo*, and *T. torquatus* in lacking prefemoral mite pockets (present and usually well marked in these species).

Tropidurus madeiramamore differs from all congeners in being the only highly chromatically polymorphic species of *Tropidurus* (Fig. 5). The species usually has a dark-pigmented venter (light in some females, rarely in males) and/or mottled chest, tending to intense melanism, a unique condition in the genus. It also differs from all other congeners in the fact that most specimens exhibit a line (white or black) on the mid-flank,

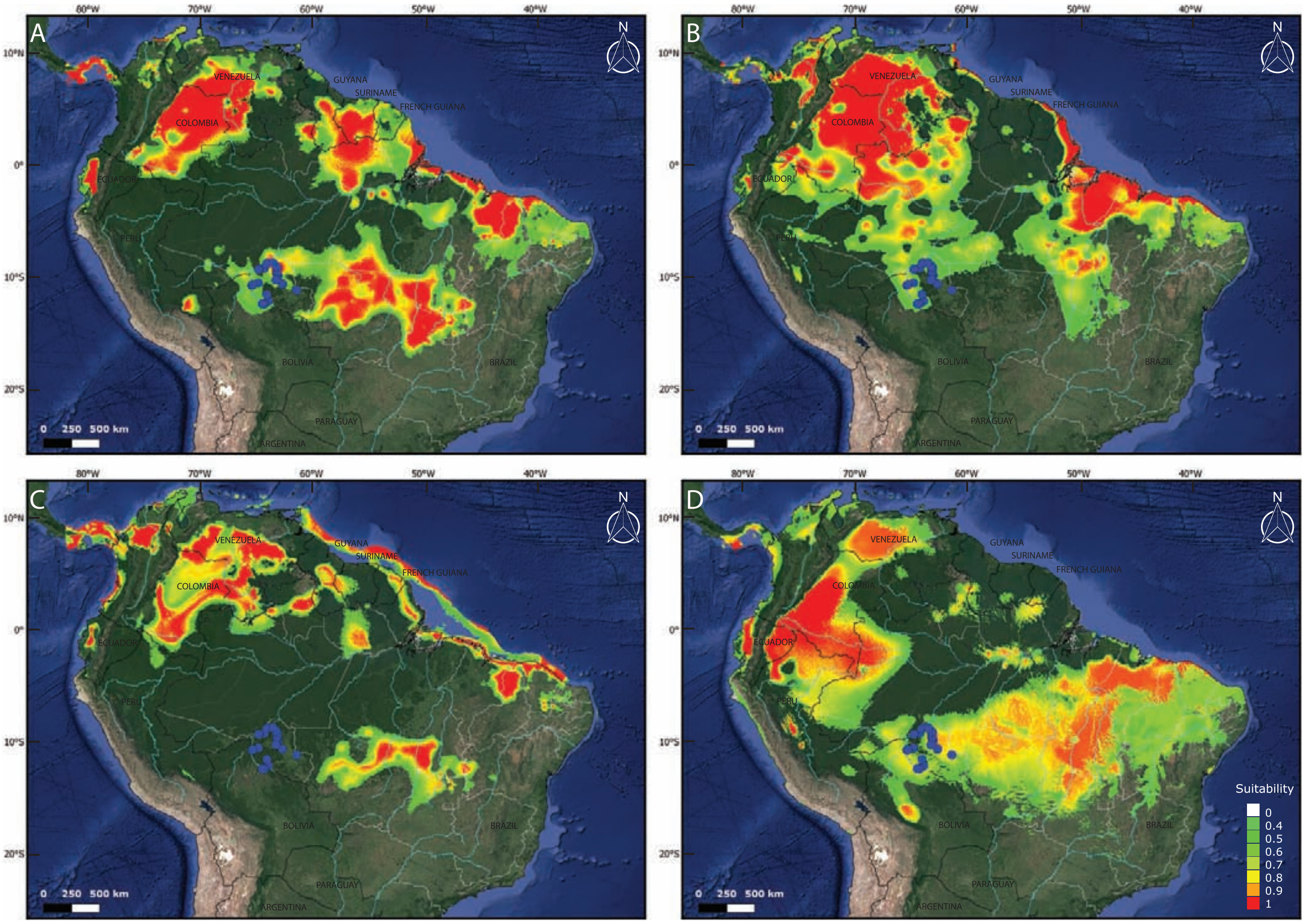

Figure 8. Maxent distribution models produced for *Tropidurus madeiramamore*. A, present. B, Holocene. C, Last Glacial Maximum (LGM). D, Last Interglacial (LIG).

interrupted or continuous. Specimens of the *T. torquatus*–*T. catalanensis*–*T. imbituba* species complex may exhibit a dark longitudinal stripe on the flank (usually present in females) outlined by pale coloration or well-defined white lines, but such a stripe (when present) covers the whole upper flank, differing from the thin dark line observed on the mid-flank of *T. madeiramamore*. The new species is most similar in coloration to *T. oreadicus* but exhibits a grey or brownish grey dorsal background and orange tones embellishing the head, dorsum, and flanks in both sexes, whereas *T. oreadicus* (Figs 9D–F, 11F, 12) has a light brown or greenish brown dorsum (populations with orangey specimens are rare; e.g. Formoso do Araguaia, Tocantins, Brazil). *Tropidurus madeiramamore* is distinguished from all species in the *T. torquatus* group in having large male specimens with black flash marks on the posteriormost portion of the tibial region towards the base of toe I (and sometimes also near the base of finger I). Regarding flash marks, it also differs from most congeners in that group (except *T. itambere* and *T. psammonastes*) in having a black triangular flash mark on the ventral base of the tail, and from *T. azurduyae*, *T. catalanensis*, *T. chromatops*, *T. cocorobenis*, *T. etheridgei*, *T. imbituba*, *T. itambere*, and *T. torquatus* in lacking a midventral 'flash' mark (in some of these species, the midventral flash mark is present only in large adult males).

Tropidurus madeiramamore is a medium-sized lizard (SVL: 67.59–103.84 mm in males and 61.31–82.39 mm in females) that broadly overlaps most species in the *T. torquatus* species group in size (Carvalho *et al.* 2016, 2018) but *T. hygomi* (SVL: 54.15–67.30 mm in males and 60.27–65.37 mm in females), *T. cocorobensis* (SVL: 54.15–67.30 mm in males and 60.27–65.37 mm in females), and *T. itambere* (SVL: 62.28–84.77 mm in males and 58.88–77.43 mm in females). In terms of ecology, the saxicolous habit distinguishes *T. madeiramamore* from *T. cocorobensis*, *T. hygomi*, and *T. psammonastes*, which are strictly psammophilous.

Description of holotype (MZUSP 107155; Figs 2, 9A–C, 10, 11A, B): Medium-sized male specimen of *Tropidurus*, SVL 96.25 mm; head subtriangular, length 28% of SVL and width 72% of head length; skull not compressed, not strongly elevated at level of orbits; snout rounded in dorsal view, rostrum not noticeably shortened relative to most other species in the genus; scales of frontonasal region tumescent, not imbricating posteriorly; lenticulate scale organs distributed on the head, more abundant on the rostral, frontonasal, supraocular, lorilabial, and labial areas; rostral tall, approximately three times (in lateral view) as high as first supralabial, contacting first supralabials, first lorilabials, nasals, and postrostrals; 2/1 postrostrals; nasal single,

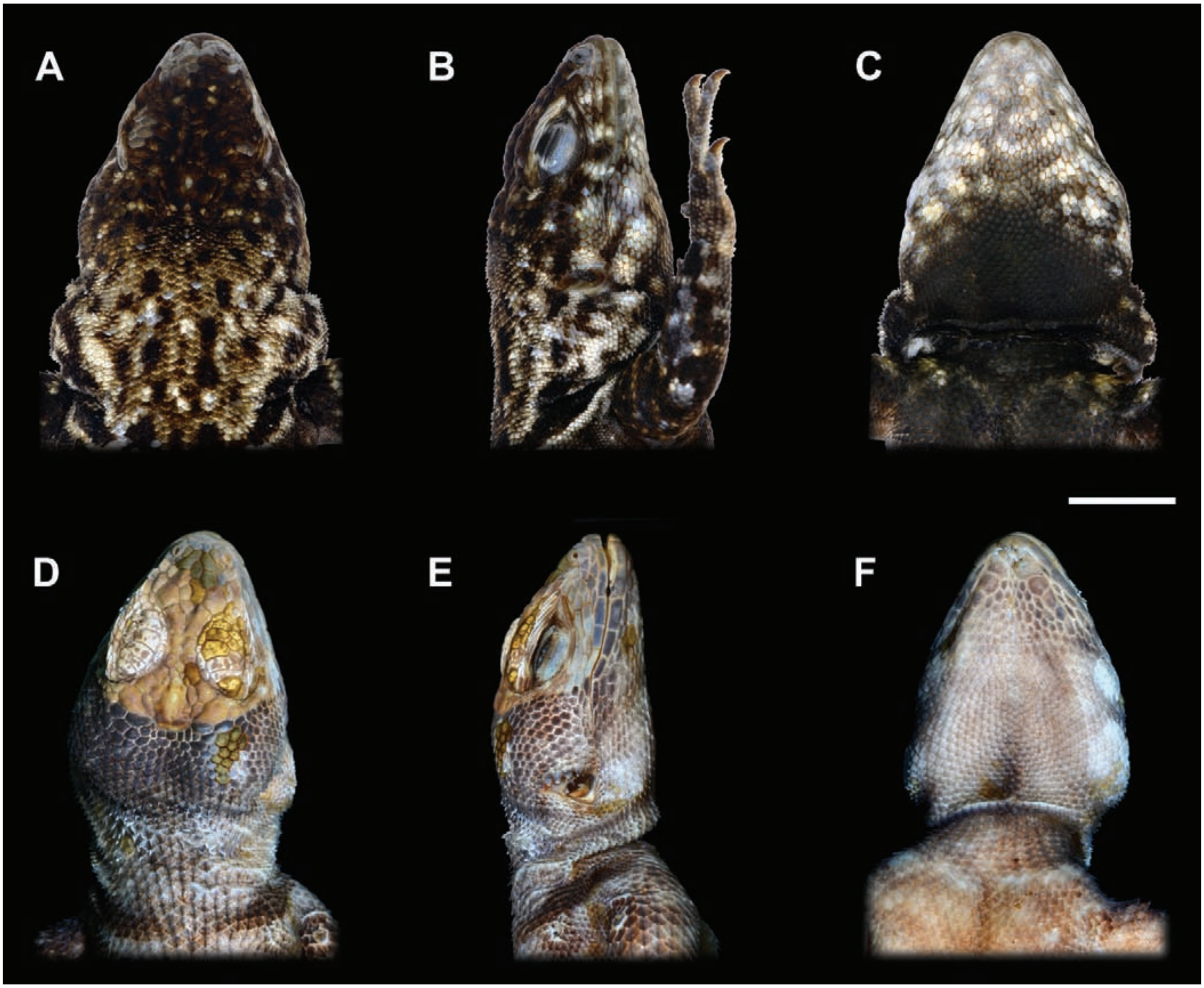

Figure 9. Dorsal head, lateral head, and ventral head of the preserved holotypes of *Tropidurus madeiramamore* (adult male, *MZUSP 107155*; A–C) and *Tropidurus oreadicus* (*MZUSP 9465*; D–F). Scale bar: 1 cm.

protruding, pentagonal, elongated anteroposteriorly, with the tip of the pentagon directed anteriorly, in contact with rostral, 1/1 post-rostral, anteriormost canthal, and 5/5 smaller scales separating it posteriorly from larger scales of the frontonasal area; nostril elliptical, occupying ~20–25% of nasal area, positioned posteriorly, directed dorsolaterally; 3/3 canthals, anteriormost separated from supralabials by 1/1 row of lorilabials, third one not in contact with anteriormost superciliary and anteriormost preocular; 9/8 laminate superciliary scales weakly produced vertically; 1/1 row of short semilaminate scales separating superciliaries from palpebrals; palpebrals subgranular, central ones forming the upper eyelid pigmented, lower eyelid poorly pigmented, semi-translucent; first row of palpebrals larger, squarish; scales of second row of palpebrals smaller than those on the first row, subconical, tumescent, 1–3 (usually 1–2) scale organs on tip; pupil circular; 4/4 main rows of supraoculars, the enlarged medial ones occupying less than half the width of the supraocular area; 1/1 irregular row of elongate, angulate circumorbitals; 1/1 row of short semilaminate scales separating circumorbitals from superciliaries; interparietal enlarged, subcordiform, ~1.3× longer than wide, anterior and posterior margins indented; parietal eye distinct, medially positioned right after the posterior limit of the first one-third of the interparietal scale; 1/1 preocular, about one-quarter the size of subocular, dorsally keeled, in contact with 4/3 loreals and 1/1 supernumerary scale separating it from posteriormost canthal; 1/1 suboculars, elongate, dorsally keeled, separated from supralabials by 2/1 row of lorilabials posteriorly; 3/2 rows of loreals, first row with four scales and second with two scales on both sides, third row with single scale on left side, absent on right side; 2/2 rows of lorilabials, first row with 8/8 scales and second row with 4/5 scales; 5/5 enlarged supralabials, followed by 6/5 smaller scales reaching the rictus oris; temporals slightly imbricate, keeled, slightly mucronate, wider than longer, at least three times larger than lateral neck scales and smaller than dorsals and parietals, lower temporals slightly smaller than upper temporals; four short rows of occipitals right after interparietal, subconic in shape, much smaller than parietals; ear shaped like an inverted keyhole, ~6.3 mm × 2.5 mm, canal deep; tympanum translucent; preauricular fringe consisting of a row of 7/9 smooth,

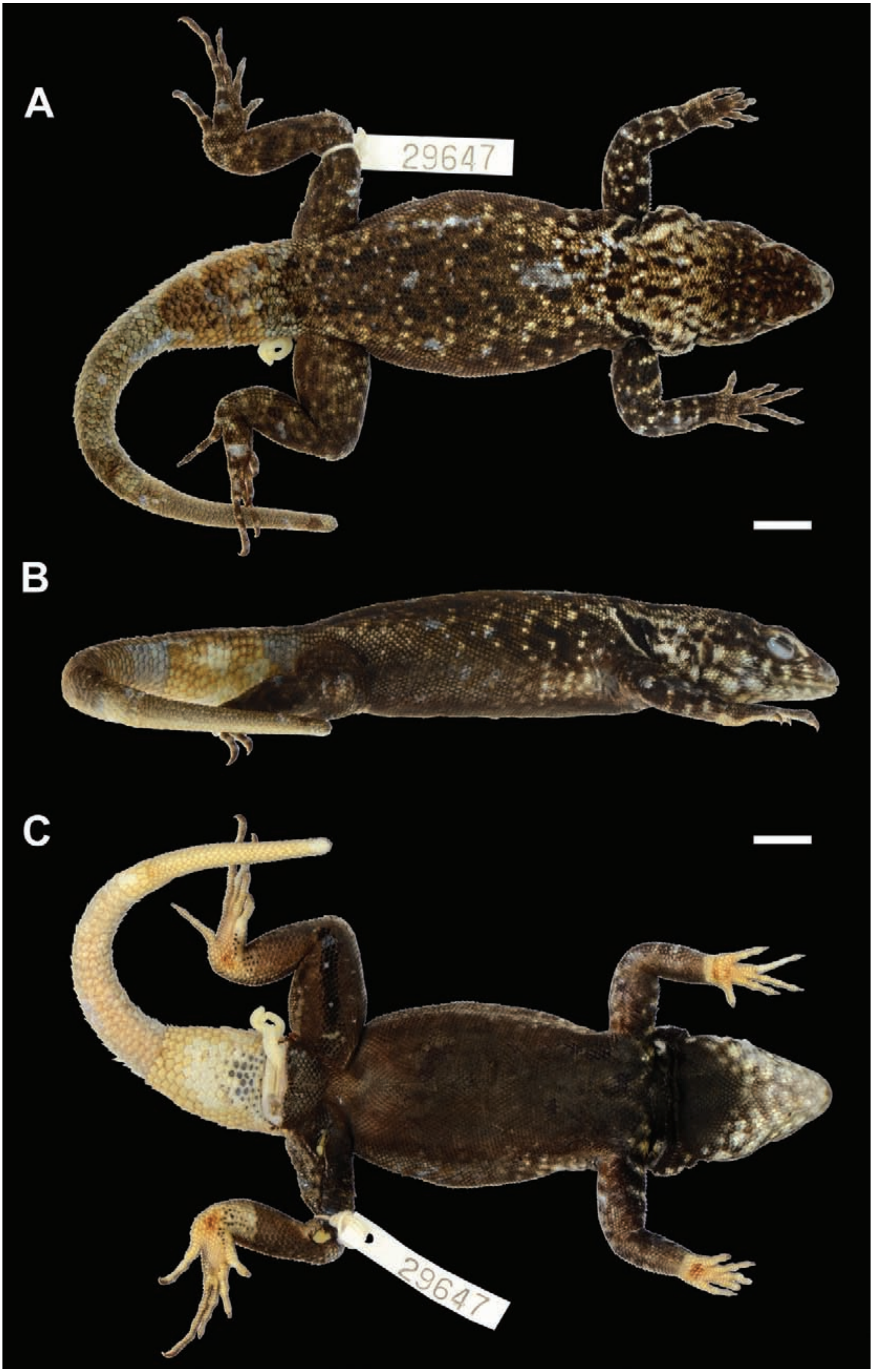

Figure 10. Preserved holotype of *Tropidurus madeiramamore* (adult male, *MZUSP 107155*). A, dorsal body. B, lateral body. C, ventral body. Scale bar: 1 cm.

sublanceolate scales, much shorter than half the ear opening width, about the same size as upper temporals; mental extending posteriorly to the level of the first one-third of the first adjacent infralabials; 4/4 angulate, enlarged postmentals, first pair of postmentals not in contact with one another, 1/1 postmentals in contact with first infralabial; 5/5 enlarged infralabials followed by 3/3 smaller scales reaching the rictus oris; 7/8 sublabials; 46 gular scales, smooth, non-mucronate, longer than wide anteriorly, wider than long posteriorly, becoming imbricated posteriorly.

Vertebral crest absent; 88 dorsals, keeled, mucronate, wider than long; keels on dorsal and caudal scales align to form continuous, longitudinal, slightly oblique lines observable macroscopically; scales on the lateral neck keeled, mucronate, at least three times smaller than dorsals; post-humeral region with small, subgranular, smooth, non-mucronate scales, increasing in size, intensity of keels, and mucronation towards the flanks; 86 scale rows around midbody; 83 ventrals, smooth, non-mucronate, imbricate, about half the size of the largest dorsals; 17 cloacal scales; dark-pigmented 'flash' marks present on the ventral surface of thighs, precloacal flap, ventral base of tail, and distalmost, ventral portion the tibial region and base of feet towards base of toe I, absent in the midventer; femoral 'flash' marks formed by a patch of 6/6 rows of dark glandular scales; precloacal 'flash' marks formed by 12 rows of dark glandular scales, and that on the base of the tail by nine rows of dark, glandular scales organized in a triangular shape (base of triangle facing the cloacal slit); supracarpal scales smooth, non-mucronate, subrhomboidal in shape; supratarsals mostly smooth, non-mucronate, rhomboidal or subrhomboidal in shape, slightly keeled and mucronate towards base of toe IV; one or two (usually one) scale organ positioned on the distal end of supracarpals and supratarsals; proximal infracarpals and infratarsals mostly smooth (those reaching the base of fingers slightly keeled and mucronate), rhomboidal or subrhomboidal in shape; scales covering the anterior portion of palm of hand and sole of foot tumescent, apparently glandular, with strong signs of abrasion; fingers and toes thin, cylindrical, compressed laterally, fingers III and IV of left hand amputated; supradigital lamellae smooth, rhomboidal, scale organ positioned on the distal end of the scales; infradigital lamellae tricarinate and mucronate, –/15 under finger IV + ungual, 23/25 under toe IV + ungual, medial careen larger and more projected than laterals; claws long, curved, brown in colour; scales of forearm keeled and strongly mucronate anteriorly and dorsally, grading to smooth scales with no or short mucrons and smaller size posteriorly and ventrally; scales on preaxial axis of thigh smooth, with sensorial organ on tip of scale, grading into keeled and mucronate dorsally, and strongly keeled and mucronate posteriorly, scales on posterior axis smaller than anterior and dorsal thigh; 24/25 tibial scales, keeled, mucronate, more intensely keeled and mucronate distally; rictal and postauricular folds present; nuchal, supra-auricular, and dorsolateral folds absent; oblique neck fold well marked, defining a single lateral neck mite pocket on each side of the neck, extremely broad and deep, starting above the level of the dorsal margin of ear-opening and reaching the head venter, coated with granular, unpigmented scales, internal folds not forming full subcompartments; antegular fold present, gular fold incomplete medially; antehumeral fold present and well marked, covered with imbricate scales similar to or smaller than those on lateral neck; post-humeral (axillary) and prefemoral (inguinal) mite pockets absent; tail slightly compressed laterally, broken; caudal verticils absent; scales of tail imbricate, keeled, mucronate, anterior ones 2.5× larger than dorsals or more, progressively reducing in size towards the tip; ventral caudal scales smooth, poorly mucronate or non-mucronate.

Coloration in life (*Fig. 11A*, *B*)*:* Dorsal body with an overall brindled pattern and extremely subtle orangey tone towards the anterior flanks; snout and dorsal head dark brown, with sparse light tan spots, smaller than one scale in size; first two rows of (enlarged) palpebral scales, labial, lorilabial, and loreal areas with touches of cream, bluish grey, and sparse light tan spots; nape and lateral neck background with light tan and brownish tones conspicuously lighter than dorsal head and body background, ornamented with irregular black spots, some of which are connected, forming short, irregular, anteroposterior, oblique stripes on the lateral neck; black nuchal collar well marked, slightly oblique, two to five scales wide, starting immediately before the insertion of forelimbs, dorsally incomplete, dorsal limit attaining paravertebral region, outlined by light tan contour nearly half the width of nuchal collar; background of dorsal body and flanks dark brown, sprinkled with small, irregular black spots of variable sizes; paired series (one on each side of the body) of ~12 irregular paravertebral black blotches from nape to base of tail, distinctly larger (6–11 scales in size) than small black spots scattered on dorsum, clearly visible from nape to post-scapular level, barely distinct from background posteriorly; dorsum ornate, with a series of eight wavy rows of light tan spots, one to four scales in size, from side to side of the body; fore- and hindlimbs with background similar to dorsum, marked with irregular black spots of variable sizes; forelimbs ornate, with thin (one scale wide), transverse, light tan streaks (five discernible along the right arm and forearm, and one on the left forearm, near the wrist) combined with randomly distributed light tan spots, one to four scales in size; hindlimbs without transverse streaks, light tan spots present but inconspicuous; hand, feet, fingers, and toes with overall coloration similar to limbs but less conspicuous; fingers and toes transversely crossed by thin, light tan bands; dorsum of tail light brown, with irregular black pigmentation concentrated anteriorly, sparse towards the end; flanks of tail light brown, small bluish grey area noticeable at the base, more evident immediately after insertion of thighs. Ventral surface of head with touches of cream and bluish grey anteriorly, mottled with a dark reticulum delineating cream blotches medially and towards the chin, cream markings progressively assuming rounded shape towards the posterior part of chin; coloration changes abruptly to solid black on the posterior ventral portion of the head, followed by similar fully melanic throat, neck, chest, venter, and underside of limbs; palm of hands and sole of feet cream; black patches of α-gland scales on the underside of thighs, precloacal flap, and ventral base of feet charcoal in colour, discernible even against the melanic background; ventral surface of tail light greyish cream, except for the area immediately posterior to the vent, marked by a triangular patch of α-gland scales charcoal in colour.

Coloration in preservative (Figs 9A–C, 10)*:* Overall coloration pattern of head and body preserved; subtle orangey tone originally discernible on the dorsal head and towards the anterior flanks lost; brown dorsal coloration became a little darker,

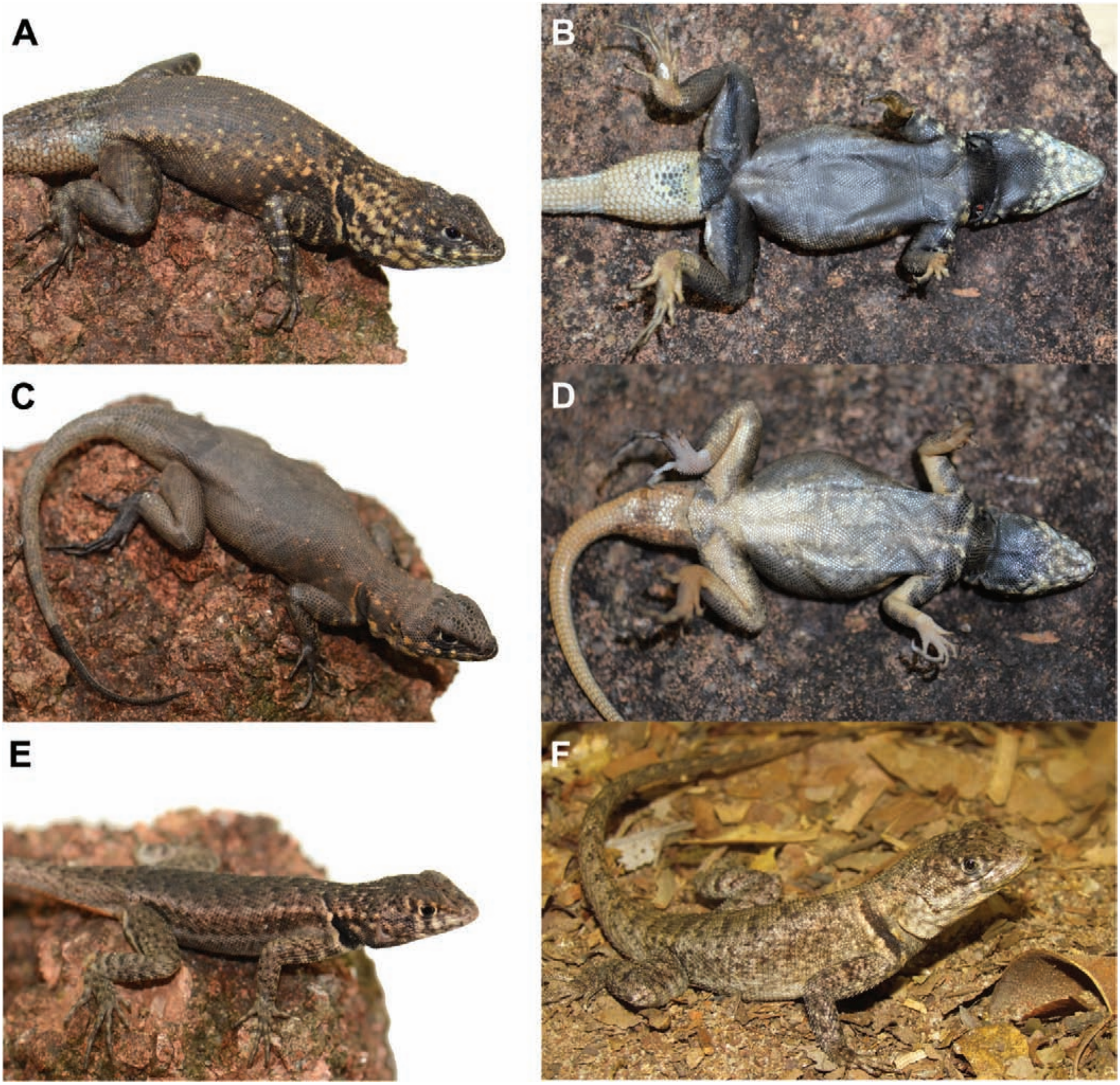

Figure 11. *Tropidurus madeiramamore* and *Tropidurus oreadicus* in life. A, B, general and ventral views of the holotype of *T. madeiramamore* (*MZUSP 107155*). C, D, general and ventral views of the allotype of *T. madeiramamore* (MZUSP 107158). E, juvenile of *T. madeiramamore* (MZUSP 107267) from the margin of the Madeira River near the Museu da Estrada de Ferro Madeira-Mamoré (EFMM), Porto Velho. F, general view of a topotype of *T. oreadicus* (MTR 33325) from Primeira Cachoeira do Rio Urucuia, Buritis, Minas Gerais, Brazil (16°05′49.3080″S, 46°14′57.9840″W). Photograph F is by courtesy of M. A. Sena.

making the light tan coloration on the nape and lateral neck proportionally lighter; cream and bluish grey tones on the first two rows of (enlarged) palpebral scales, labial, lorilabial, and loreal areas turned pale cream; black coloration of nuchal collar preserved, outline turned pale cream; background of dorsum and flanks dark brown, irregular black spots spread all over preserved; series of wavy rows of light tan spots reaching from side to side of the body turned pale cream; light tan streaks and spots on fore- and hindlimbs became pale cream, resulting in increased contrast against the dark brown background coloration; same observed for coloration of hands, feet, fingers, and toes; background coloration of the dorsum and flanks of tail became lighter brown, making the dark pigmentation seen anteriorly more conspicuous, small bluish grey area at the base of tail, immediately after insertion of thighs, nearly unaltered; touches of cream and bluish grey anteriorly on ventral head turned pale cream; dark reticulum delineating cream blotches medially and towards the chin became more evident; solid black coloration on the posterior ventral head, throat, neck, chest, venter, and underside of limbs became slightly lighter, developing a dark brownish appearance; palm of hands and sole of feet cream, unchanged; all patches of charcoal α-gland scales on ventral body became

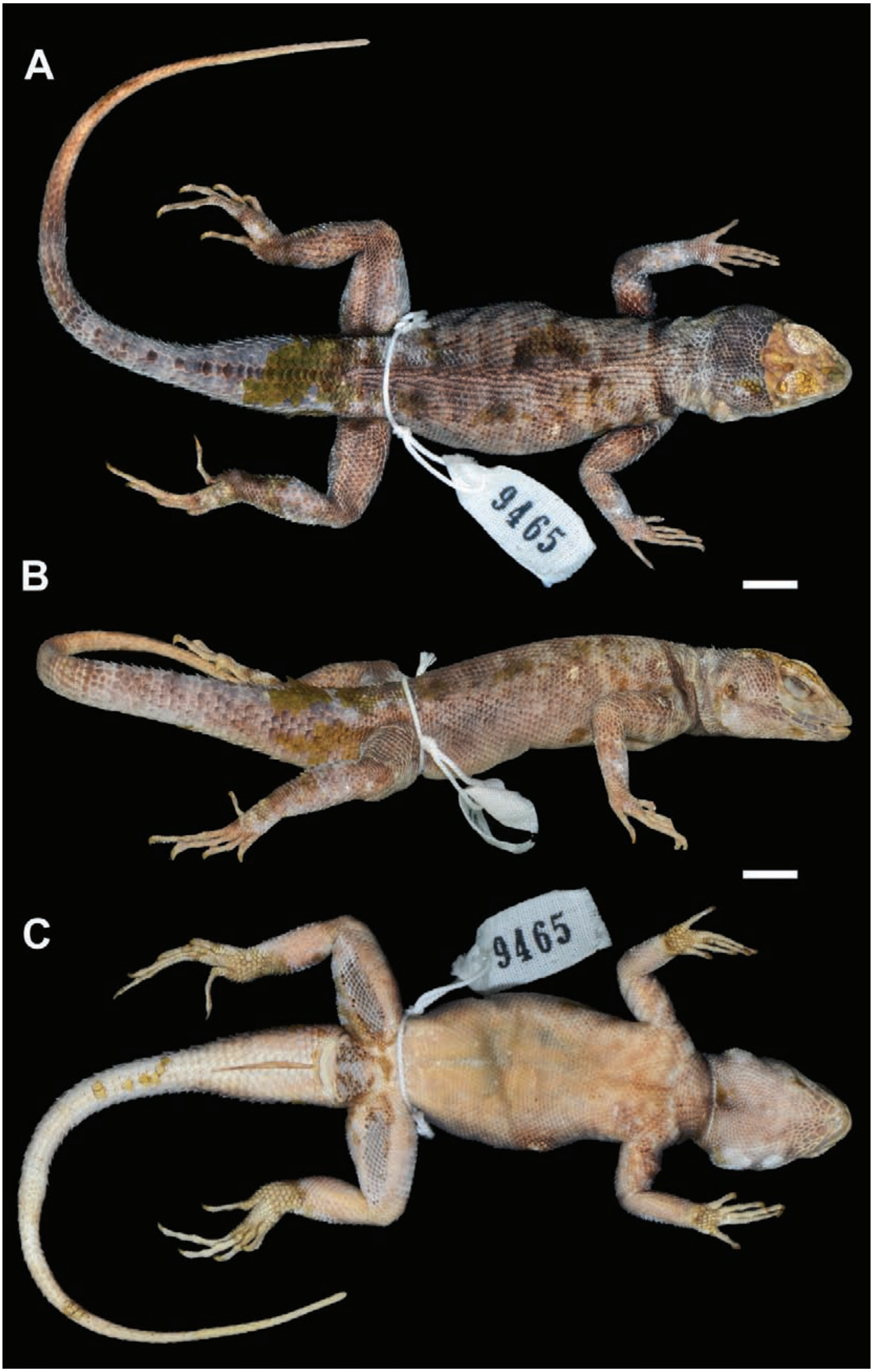

Figure 12. Preserved holotype of *Tropidurus oreadicus* (adult male, *MZUSP 9465*). A, dorsal body. B, lateral body. C, ventral body. Scale bar: 1 cm.

slightly lighter; original light greyish cream ventral surface of tail lost the greyish tone and turned cream.

Measurements of holotype (in millimetres): AGD, 50.84; AL, 15.96; BH, 20.52; EOS, 23.61; FAL, 14.55; FOL, 26.91; HDL, 16.56; HH, 12.95; HL, 26.60; HW, 19.20; MB, 31.82; SL, 18.59; SVL, 96.25; THL, 20.96.

Taxonomic remarks: Despite the chromatic polymorphism and body size variation identified by Vanzolini (1986), and subsequently described by Vitt (1993) and Vitt and Caldwell (1993), as potential evidence of multiple *Tropidurus* species associated with the savannah enclaves of the state of Rondônia, Rodrigues (1987) chose to allocate those populations under the name *T. oreadicus* Rodrigues, 1987. In contrast to these studies, our results support a single polymorphic species associated with the savannah enclaves from Rondônia, which differs remarkably in most morphological parameters from *T. oreadicus*, except for the presence of a single mite pocket on the lateral neck (Type D, *sensu* Rodrigues 1987). Thus, we assign all *Tropidurus* populations distributed in the state of Rondônia confidently to *T. madeiramamore*, including those treated by Cunha (1961), Rodrigues (1987), Nascimento *et al.* (1988), Vitt (1993), Vitt and Caldwell (1993), and Ávila-Pires (1995), and some of the populations listed by Ribeiro-Júnior (2015). This latter author informed on the occurrence of '*T. oreadicus*' in five localities in the state of Amazonas and one in the state of Acre, both in northern Brazil (Fig. 13). Our sampling does not include specimens from those areas; nonetheless, given the large geographical gap with respect to the closest confirmed occurrence records of *T. oreadicus* in the core Brazilian Cerrado (~870 km in a straight line), the assignment of the specimens reported by Ribeiro-Júnior (2015) from Amazonas and Acre to *T. oreadicus* seems unlikely. It is possible that the reported specimens from the Parque Estadual do Guariba, in Novo Aripuanã, and from the vicinities of Rio dos Marmelos, in Manicoré, are assignable to *T. madeiramamore*; however, the corresponding voucher material requires revision. The identification of samples from Puruzinho and Lábrea, located to the west of the Madeira River, is more doubtful, as is the record from Porto Acre (Fig. 13). These records might be inaccurate or in error, given that, to our knowledge, the region lacks rocky outcrops.

Etymology: The specific epithet that makes up the name *Tropidurus madeiramamore* is an indeclinable word formed by the juxtaposition of the proper nouns Madeira (Portuguese language) and Mamoré (Tupi-Guarani language). These are the names of the Amazonian rivers that appear to circumscribe the northern and western distribution limits of the species in the State of Rondônia, Brazil. Madeira-Mamoré is also the name of the world-famous railroad built between 1907 and 1912 to export rubber and other goods produced in the western Brazilian and Bolivian Amazonia (Bennitt 1913). During the field expedition carried out in November 2017, A.L.G.C. and R.C.B.P. followed part of the historical path of the 'Madeira-Mamoré Railway' searching for lizards, among other areas in the state of Rondônia. This was the most important terrestrial connection between the Brazilian territories of Porto Velho and Guajará-Mirim until 1966, when the Madeira-Mamoré Railway was officially shut down, after 54 years of service. During the field trip, A.L.G.C. and R.C.B.P. witnessed intense environmental degradation in the region, fuelled synergistically by population growth, logging, mining, farming, and ranching (Pedlowski *et al.* 2005). Conservation issues in the area have been aggravated by the recent development of some of the largest hydroelectric dams and power plants ever built in the Brazilian Amazonia (2008–2016), namely Santo Antônio and Jirau (Fearnside 2014). By naming *T. madeiramamore* after two of the most magnificent rivers of Western Amazonia, we aim to call attention to the critical conservation threats currently faced by the areas drained by these rivers and their tributaries. These areas include the highly vulnerable cerrado enclaves that harbour populations of the new species.

Distribution and endemism: Tropidurus madeiramamore is spread over a large portion of the State of Rondônia, Brazil, but mostly restricted to small and historically isolated savannah (cerrado) enclaves surrounded by the Amazon forest (or currently deforested areas) (Fig. 13). Together, our fieldwork, museum work, and literature analysis has expanded the previously known distribution of *T. madeiramamore* (Vanzolini 1986, Vitt 1993, Vitt and Caldwell 1993) to ≥ 34 areas in 11 municipalities of the State of Rondônia. For instance, the species is currently known from sites in the Parque Nacional Serra da Cutia, Guajará-Mirim; Parque Natural Municipal Serra dos Parecis, Guajará-Mirim; Jaci-Paraná, Porto Velho; campus of the Universidade Federal de Rondônia – UNIR, Porto Velho; south margin of the Madeira River, near the Museu da Estrada de Ferro Madeira-Mamoré, Porto Velho; Floresta Nacional Jamari and neighbouring rock outcrops along the highway BR-364, Itapuã do Oeste; and also from cerrado enclaves in the municipalities of Alto Paraíso, Ariquemes, Cacaulândia, Cacoal, Candeias do Jamari, Costa Marques, Jaru, and Rio Crespo. *Tropidurus madeiramamore* is likely to be present in other enclaves located between these areas. For instance, in the early 1990s, A.L.G.C. observed the species in the backyard of a house in the neighbourhood Casa Preta, in Ji-Paraná (10°52′19.6428″S, 61°57′04.6224″W; ~154 m a.s.l.), a municipality located halfway between Jaru and Cacoal. During the expedition carried out in November 2017, A.L.G.C. and R.C.B.P. visited Ji-Paraná but failed to locate *T. madeiramamore* in the searched areas, possibly owing to the expanded urban development that eliminated the natural habitats used by the species.

Since the early 1960s, the Amazon forest of the State of Rondônia has been largely destroyed, especially after the expansion of highway BR-364 to connect the municipalities of Vilhena, in the eastern limit of the state, to Porto Velho, in its north-western part (Fearnside and Ferreira 1984, Piontekowski *et al.* 2019), and implementation of colonization projects and settlements by the Instituto Nacional de Colonização e Reforma Agrária (INCRA) (Fearnside 1986). Together with the Amazon rainforest, savannah enclaves along highway BR-364 were wiped out or exposed after removal of the surrounding forest matrix and subsequent conversion of the original landscapes into pastures for cattle, agricultural fields, mining sites, or urban areas. Today, the last patches of natural habitats are mostly restricted to a few conservation units and indigenous territories (Pedlowski *et al.* 2005). In these areas, enclaves of variable sizes that potentially harbour populations of *T. madeiramamore* are inaccessible by land. Examples of such areas

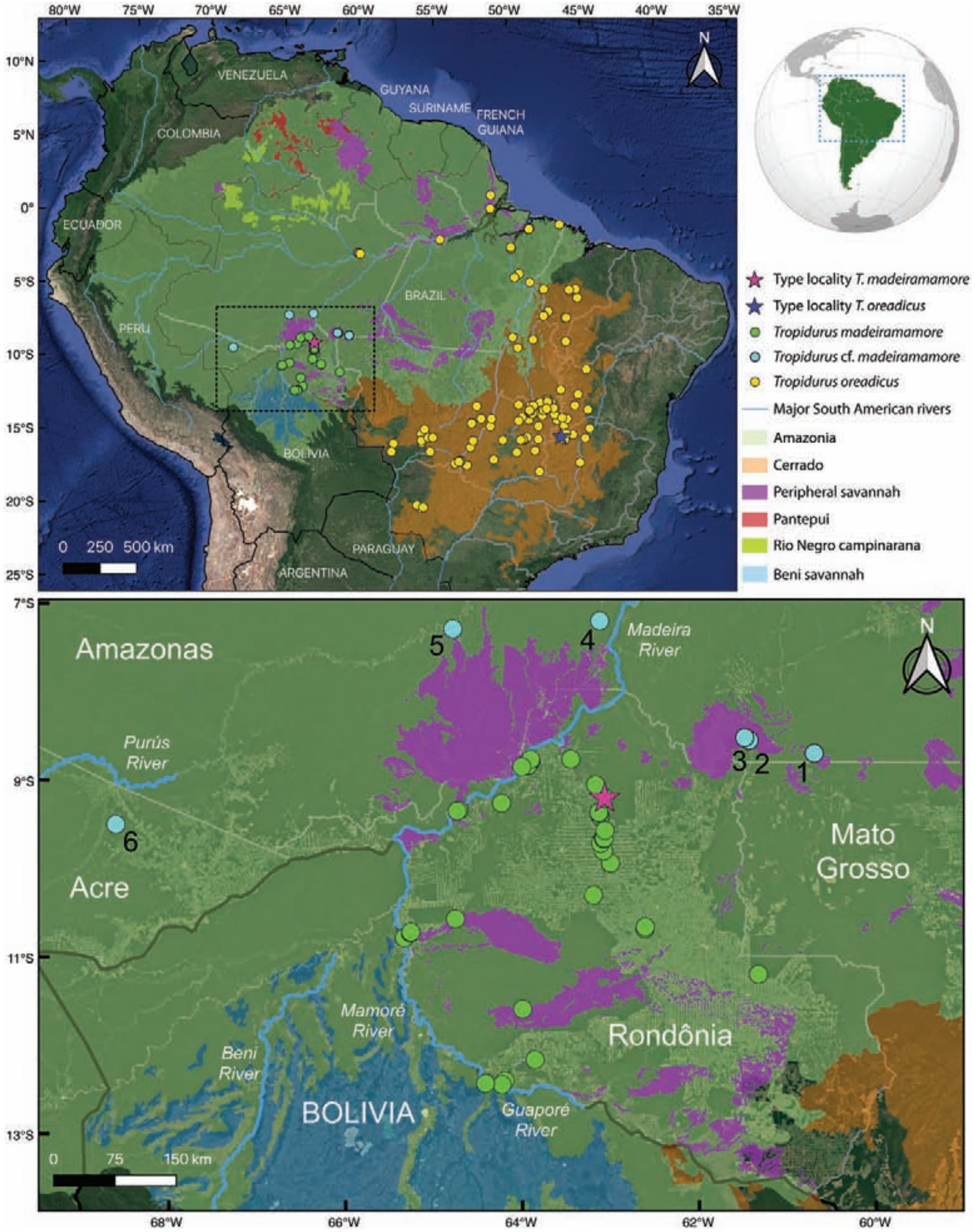

Figure 13. Distribution of *Tropidurus madeiramamore* and *Tropidurus oreadicus*. Top map shows the fully allopatric range of the species. *Tropidurus oreadicus* is a typical Cerrado endemic, with distribution advancing northwards through the Tocantins River Basin. Bottom map is a blown-up view of the area delimited by the dashed rectangle in the top map. It shows the distribution of *T. madeiramamore* in savannah enclaves of the state of Rondônia, in addition to unconfirmed records of this species in the states of Amazonas and Acre (indicated by numbers 1–6), originally published by Ribeiro-Júnior (2015) as pertaining to '*T. oreadicus*'. Locality names: (1) Parque Estadual do Guariba, Novo Aripuanã, Amazonas; (2) Arredores da Fazenda Passo Formoso, Manicoré, região do Rio dos Marmelos, Amazonas; (3) Rodovia do Estanho, região do Rio dos Marmelos, Manicoré, Amazonas, Brazil; (4) BR-319 km 620, Puruzinho, Amazonas; (5) Lábrea, Amazonas, Brazil; and (6) Porto Acre, Acre. Refer to the Supporting Information (File S18) for a full list of geographical coordinates associated with the distribution records shown in the maps.

are found in the Parque Nacional da Serra da Cutia and Indigenous Territory Uru-Eu-Wau-Wau, which contains the Parque Nacional de Pacaás Novos. These are some of the last continuous preserved areas in the heart of the State of Rondônia. During an expedition carried out by M.T.R. to the Parque Nacional de Pacaás Novos in April 2013, a few individuals of *Tropidurus* were observed at 911 m a.s.l., on a cliff at the Pico do Tracoá (10°50′35.5128″S, 63°37′41.7266″W), located at the easternmost limit of the park, in the municipality of Campo Novo de Rondônia. This record of *T. madeiramamore* corresponds to the highest elevation where the species has been registered to date.

The management plan of the Parque Estadual da Serra dos Reis provides information on the occurrence of '*Tropidurus hispidus*' (SEDAM—RO 2019). However, the photograph of a sampled specimen included in the document (p. 197) shows that the species has been misidentified. *Tropidurus hispidus* is associated with open landscapes in Brazil, French Guiana, Guyana, Suriname, Venezuela, and part of the Brazil–Colombia border (Carvalho 2013). In Brazil, it occupies the domains of the semi-arid Caatinga and the Espinhaço mountain range, with additional records in transitional areas towards the Cerrado and in coastal sand dunes and restingas (Rodrigues 1987, Carvalho 2013). Because the management plan lacked information on voucher material, we were unable to revise the specimen sampled at Serra dos Reis. However, the photograph included in the management plan (their fig. 139) sufficed to confirm that the 'lagartixa preta' (black lizard) registered in that state park corresponds to *T. madeiramamore*. The Reserva Biológica do Guaporé and Parque Estadual de Corumbiara, located at the extreme south of Rondônia, at the border with Bolivia, and ~50 and ~200 km to the south-east of Serra dos Reis (in a straight line), respectively, are additional areas where *T. madeiramamore* might occur. However, to our knowledge, comprehensive herpetological surveys have not been carried out in the southern portion of the State of Rondônia, resulting in very little information being available on the lizards present in the area.

In summary, the confirmed distribution of *T. madeiramamore* is limited to the central, north-western, and western portions of the State of Rondônia. Its occurrence in the extreme north of the state (to the east of Porto Velho and Itapuã do Oeste) is uncertain because most collection records are restricted to the margins of highway BR-364. In turn, the inventories carried out by Gainsbury and Colli (2003) recorded *T. madeiramamore* (their *Tropidurus* sp.) in Guajará-Mirim but not in Pimenta Bueno and Vilhena, located in the southern portion of the State of Rondônia. Given that the sampling efforts reported in that study were substantial, we tend to believe that the species does not reach areas to the south-east of the collection site visited by A.L.G.C. and R.C.B.P. in Cacoal. Nevertheless, the geographical, ecological, and historical factors limiting the eastern-, southern-, and south-easternmost distribution of the species remain to be verified. At this point, as the specific epithet *madeiramamore* indicates, the Madeira and Mamoré rivers are assumed to limit the north-western and western distribution of *T. madeiramamore*, respectively. Interestingly, although these massive rivers have been thought to act as effective geographical barriers for a number of animal groups, this idea was found to be inappropriate for > 99% of the 1952 species analysed by Santorelli *et al.* (2018), at least in the case of the Madeira river. Nevertheless, Peixoto *et al.* (2020) did find evidence that lizard assemblages in South-western Amazonia are structured by the upper Madeira River, with 29.62% of the 27 species sampled in that study being isolated historically at one of the river banks. The known distribution of *T. madeiramamore* seems to reinforce these findings. However, for us to ascertain this, the unverified records of *Tropidurus* to the west of the Madeira river by Ribeiro-Júnior (2015) must be confirmed (see 'Taxonomic remarks'; Fig. 13). Given that *Tropidurus* populations morphologically similar to *T. madeiramamore* have never been reported to the Bolivian Amazonia (e.g. Parker and Bailey 1991, Parker *et al.* 1993, Killeen and Schulenberg 1998, Chernoff and Willink 1999, Dirksen and De la Riva 1999, Montambault 2002, Carvalho *et al.* 2018), the species is recognized herein as endemic to Brazil, and more specifically, endemic to savannah enclaves of the state of Rondônia.

Natural history and conservation: Tropidurus madeiramamore is not sympatric with any congener. Rather, Vitt (1993) reports on it coexisting with eight other lizard species in savannah enclaves from Rondônia, namely *Ameiva ameiva* (Linnaeus, 1758), *Anolis ortoni* Cope, 1898, *Hoplocercus spinosus* Fitzinger, 1843, *Cnemidophorus leminiscatus* (Linnaeus, 1758), *Kentropyx calcarata* Spix, 1825, *Uranoscodon superciliosus* (Linnaeus, 1758), *Iguana iguana* (Linnaeus, 1758), and *Copeoglossum nigropunctatum* (Spix, 1825). During fieldwork carried out in 2017, A.L.G.C. and R.C.B.P. observed *Cnemidophorus cryptus* Cole & Dessauer, 1993, *Tupinambis* gr. *teguixin* (*sensu* Murphy *et al.* 2016), *A. ameiva*, and *I. iguana* in syntopy with *T. madeiramamore* in Guajará-Mirim (former three) and Porto Velho (last species), but there were no field observations of interactions among them. Most lizards registered by Vitt (1993) and observed by A.L.G.C. and R.C.B.P. are widespread in Amazonia (Ribeiro-Júnior 2015; Ribeiro-Júnior and Amaral 2016). *Hoplocercus spinosus* is the only one besides *T. madeiramamore* that is a typical Cerrado lizard; however, this species dwells in sandy sites within the savannah enclaves, whereas *T. madeiramamore* uses granitic outcrops (Vitt 1993, Vitt and Caldwell 1993).

Tropidurus madeiramamore expends most of its time on the rocks, performing territorial defence, thermoregulation, foraging, and reproductive activities, in addition to using crevices and the spaces underneath boulders as shelters and escape routes. As noted by Vanzolini (1986) and Vitt (1993), and confirmed by our field observations, even when approached by a potential predator, *T. madeiramamore* never enters the forest surrounding the enclaves. Adult males form harems and fiercely defend their territories from other males; these are visited by females and juveniles, which show submissive behaviours. When a dominant male approaches a female, it arches the body, and the female lifts the tail, exposing its orangey ventral surface. The same behaviour is displayed by other species of the *T. torquatus* species group (e.g. Carpenter 1977). *Tropidurus madeiramamore* can lay one to five eggs and are reproductive all year round (Vitt 1993). Most females collected in all nine localities sampled in November 2017 were gravid, indicating that reproduction is synchronic among populations. The diet of *T. madeiramamore* is composed mainly of ants and termites; however, specimens also feed on plant material, such as flowers (Vitt 1993, Gainsbury and Colli 2003). Vitt (1993) suggested that the ingestion of plants in this species is not accidental, given that some lizards had only this food item in the stomach, with no evidence of insect fragments.

Populations of *T. madeiramamore* are susceptible to the impacts of economic activities that have grown rapidly in Rondônia, including mining, hydroelectric production in large power plants, industrial farming, and illegal logging (Fearnside 2014, 2017, Piontekowski *et al.* 2019). For instance, mining greatly affected the habitat used by the species in at least two localities sampled in 2017, the Floresta Nacional do Jamari (type locality) and Jaci-Paraná. Mining pits are expected to have strong detrimental effects on populations of *T. madeiramamore* because the species is strictly rupicolous. However, assessments of population size and population size fluctuation over time have not been published, even for populations located within conservation units (e.g. Floresta Nacional do Jamari and Parque Estadual Serra dos Reis). Deforestation (Fearnside and Salati 1985, Fearnside 2017) and expansion of the paved road network in Rondônia (Fearnside and Ferreira 1984) are expected to contribute synergistically to form open corridors capable of reconnecting lizard populations from otherwise isolated savannah enclaves. No studies have been performed thus far to evaluate the dispersion potential of *T. madeiramamore* through paved roads and other human-modified environments, although concrete-rich habitats are known to provide suitable thermal conditions that facilitate lizard colonization (Hulbert *et al.* 2020, Mitchell *et al.* 2021), including *Tropidurus* (de Andrade 2019). All we know at this point is that populations of *T. madeiramamore* are established in a few urban sites in the municipality of Porto Velho (e.g. UNIR and EFMM) and at least one other in the municipality Itapuã do Oeste.

In summary, although natural habitats in the state of Rondônia have been reduced extensively over the years, and simulations have shown that 32–47% of the native forest of the State of Rondônia could be fully deforested by 2050 (Piontkowski *et al.* 2019), an evaluation of the degree of threat currently faced by *T. madeiramamore* is hindered by the limited biological information available for most populations throughout its range. An informed conservation assessment would require the estimation of parameters such as population size, number of mature individuals, gestation length, population decline over time, degree of fragmentation of the populations, and distribution range (IUCN 2022). Given that this information is currently missing, we have no option but to recommend *T. madeiramamore* be classified as 'Data Deficient', following IUCN rules. Nonetheless, it is impossible to stress enough that the accelerated rates of habitat loss registered in Rondônia make an informed conservation assessment of *T. madeiramamore* absolutely critical.

DISCUSSION

Unexpected phylogenetic relationships

To help unveil the origins of the biota associated with peripheral savannah enclaves of South-western Amazonia, we focused on resolving the taxonomic identity and phylogenetic relationships of a long-overlooked species from the State of Rondônia, Brazil, a member of the South American collared lizards. Phylogenetic analyses recovered a paraphyletic *Tropidurus*, a monophyletic *T. torquatus* species group, and grouped all samples from Rondônia in a single clade. Although the paraphyly of *Tropidurus* is unquestionably an acute systematic problem, it is being addressed somewhere else (Carvalho 2015; A.L.G. Carvalho, unpubl. data). The placement of the newly described *T. madeiramamore* in a clade positioned as sister to all other members of the *T. torquatus* species group, and therefore distantly related to *T. oreadicus*, is among the most significant phylogenetic findings of this contribution. Rodrigues (1987) allocated all *Tropidurus* populations from South-western Amazonia under *T. oreadicus* on the basis of morphology alone, and mostly because these are the only *Tropidurus* that share mite pockets Type D (*sensu* Rodrigues 1987). The distant phylogenetic placement of these species indicates that mite pocket morphology is not completely tied to phylogeny, even in the *T. torquatus* species group (for an appreciation of other tropidurid clades, see Frost 1992, Harvey and Gutberlet 2000, Frost *et al.* 2001). Nevertheless, despite exhibiting some degree of phylogenetic lability, mite pockets remain relevant for species identification in *Tropidurus*, as demonstrated by the diagnosis of *T. madeiramamore*.

Tropidurus madeiramamore is endemic to South-western Amazonia but closely related to *T. itambere* and *T. psammonastes*, respectively distributed in the core Brazilian Cerrado and in the field dunes of the São Francisco River in north-eastern Brazil (Carvalho 2013). Their close association was unanticipated for several reasons: (i) because these taxa have fairly distinct body proportions and robustness (Carvalho *et al.* 2016), whilst closely related species of *Tropidurus* tend to have overall conserved morphology and body size (Grizante *et al.* 2010); and (ii) because their phylogenetic proximity suggests that their common ancestor possibly had a vast distribution in the Cerrado and entered the domains of the Caatinga. No extant *Tropidurus* has such a large geographical range, and most (if not all) of them that have been considered widespread taxa represent complexes of incompletely delimited species (e.g. Werneck *et al.* 2015, Domingos *et al.* 2017, Carvalho *et al.* 2018). *Tropidurus itambere* itself might comprise up to five undescribed entities (Domingos *et al.* 2017), rendering the number of species forming the sister clade of *T. madeiramamore* substantially larger than recognized at present. Interestingly, the morphological disparity and asymmetry in the number of lineages forming this focal clade could indicate that extinction eroded this section of the tropidurid tree, perhaps severely, eliminating lineages of *Tropidurus* from peripheral savannahs that were engulfed by the expanding Amazon Forest.

The absence of reciprocal monophyly among populations of *T. madeiramamore* located up to hundreds of kilometres apart from one another is striking, and at least three scenarios (the first two non-mutually exclusive) can potentially explain this lack of phylogeographical structure: (i) the populations examined do not exhibit complete geographical isolation, and gene flow has persisted over time; (ii) human-induced translocation of individuals has facilitated gene flow among otherwise isolated populations; and (iii) the history of isolation of the enclave populations is fairly recent. Among these possibilities, we deem the first scenario the most likely. Most sampled populations of *T. madeiramamore* are located at least several kilometres apart and, like all other congeners, this species is incapable of crossing forests with closed canopy (Vanzolini 1986, Vitt 1993, Vitt and Caldwell 1993). However, past connections and reconnections among enclaves, rather than constant movement of specimens across densely forested habitats, might have facilitated the maintenance of gene flow among populations. Although the second scenario cannot be ruled out, especially in the case of urban populations (e.g. Porto Velho), absence of strong (or at least moderate) geographical structure in the grouping of samples from undisturbed and highly isolated savannah enclaves further supports the historical (and perhaps cyclical) connections among areas. The lack of geographical compartmentalization and low clade support observed in our trees are therefore interpreted as reflexes of a complex biogeographical history influenced by changes in landscape structure dictated by large-scale geoclimatic processes (see the following sections).

A preliminary assessment of divergence times

Chronological investigations of tropidurids are plagued by the absence of fossils for node calibration. For that reason, our analysis relied solely on molecular data to produce a temporal hypothesis of species divergence. The fact that the inferred date for the split between *T. semitaeniatus* and the *T. torquatus* species group more than doubled the estimate proposed in a phylogeographical study of the *T. semitaeniatus* species group (Werneck *et al.* 2015) is striking but not unexpected. We analysed sequence data of 12S, 16S, and *kif24*, and we used the 12S rate estimated by Olave *et al.* (2015) to set the global substitution rate of the mitochondrial DNA (0.6339×10^{-2} substitutions/sites/Myr), whereas Werneck *et al.* (2015) analysed the 16S and *Cyt-b* loci, and adopted the *Cyt-b* rate (1.94×10^{-2} substitutions/sites/Myr) estimated in the same study. Although both analyses adopted similar analytical approaches implemented in BEAST, the fairly distinct mitochondrial rates used to parameterize the molecular clocks are likely to be responsible for the disparate estimates of divergence times. Given that independent sources of temporal references (e.g. fossils) are unavailable to help validate the most appropriate estimates, the results of the dating analyses produced thus far are deemed tentative. For that reason, it remains unfeasible to pinpoint specific geoclimatic events responsible for individual lineage splits. Nevertheless, these are the first temporal assessments of tropidurid lineages and, as such, they provide important preliminary references for further exploration of the diversification history of this lizard group.

For instance, our results suggest that genus-level splits in Tropiduridae date back to the Late Eocene and Early to Mid-Miocene, whereas diversification in *Tropidurus* took place, for the most part, much later, during the Late Miocene, Pliocene, and Early to Mid-Pleistocene. Lineage splitting in the genus has been hypothesized to be linked to large-scale vicariance events, including the establishment of humid forest corridors that connected the Amazon and Atlantic Forest segregating open–dry biomes along the South American diagonal, the uplift of the Brazilian Plateau in the Late Pliocene–Early Pleistocene along the Espinhaço, Serra do Mar, and Serra da Mantiqueira mountain ranges, the subsidence of the Chaco and Pantanal owing to the Andean uplift, and (more recently proposed) changes in the course of one of the largest South American rivers, the São Francisco River (Carvalho *et al.* 2013, Werneck *et al.* 2015). If so, as suggested by Carvalho *et al.* (2013), the Quaternary represented only the apex of a long history of diversification in South America. Assuming that our dating analysis produced minimally accurate estimates, the split of *T. madeiramamore* from its sister group at ~4.46 Mya implies that landscape changes driven by glaciation cycles of Pleistocene age cannot underlie its origin in peripheral savannah enclaves of the State of Rondônia. Consequently, the scenario proposed by Vanzolini (1986), which posits that speciation took place in allopatry following landscape changes in the State of Rondônia during the Late Pleistocene, still holds from a spatial standpoint but not temporally. Nonetheless, we would hardly be surprised if subsequent divergence dating analyses supported by fossil evidence shifted this estimate towards the Pleistocene.

The estimated divergence of *T. insulanus* from *T. oreadicus* at ~2.86 Mya points again to pre-Pleistocene vicariance events promoting speciation in peripheral Amazonian savannah enclaves. However, equally relevant is the observation that the latest-diverging species of the *T. torquatus* species group are *T. chromatops* and *T. etheridgei*, with splitting dated to the Mid-Pleistocene ~0.99 Mya. This estimated divergence date implies that independent historical events underlie the evolution of the species endemic to savannah enclaves distributed along the edges of the Brazilian Amazonia. More precisely, *T. insulanus* is endemic to savannah enclaves distributed between Serra do Cachimbo, in the State of Pará, and Almas, in the State of Mato Grosso (Ribeiro-Júnior 2015), and *T. oreadicus* is widespread in the Brazilian Cerrado, open formations throughout the course of the Tocantins River in the state of Pará, and savannah enclaves in the states of Pará and Amazonas (Rodrigues 1987, Ávila-Pires 1995, Carvalho 2013). In turn, *T. chromatops* is found only in rock outcrops surrounded by the Amazon rainforest in south-eastern Bolivia and western border in the Brazilian state of Mato Grosso, and *T. etheridgei* is widespread in the Chaco biome (Carvalho *et al.* 2018). The distribution pattern of these species is clearly similar, and the same geoclimatic processes might have played a role in the divergence of the aforementioned savannah enclave endemics. Although we agree that their evolution was probably driven by large-scale shifts in the range and structure of open and forested South American biomes, as suggested by Vanzolini (1986), Rodrigues and (1987), and Vitt (1993), distinct climatic cycles, both pre-Pleistocene and of Pleistocene age, must be invoked as triggers of allopatric speciation.

A chromatically very polymorphic species

Although the disjunct distribution of *Tropidurus* populations in savannah enclaves from South-western Amazonia and the morphological variation observed across areas sampled in Rondônia might suggest the occurrence of multiple events of allopatric differentiation (Vanzolini 1986, Vitt 1993, Vitt and Caldwell 1993), the evidence gathered thus far allowed the recognition of a single, very polymorphic lizard species. The chromatic polymorphism of *T. madeiramamore* has no parallel in the *T. torquatus* species group or even in *Tropidurus* altogether. Flank coloration patterns originally identified by Vanzolini (1986), Vitt (1993), and Vitt and Caldwell (1993) occur indistinctly in most sampled locations, without any instance of geographical segregation that would allow objective diagnoses. Additionally, our sample revealed an even greater polymorphism represented by newly described chromatic morphotypes. The evolution of chromatic polymorphism in lizards is often assumed to have an adaptive function linked to camouflage and apostatic selection (Bond 2007, Marshall *et al.* 2015), enhancement of thermoregulatory efficiency (Smith *et al.* 2016), or establishment of alternative reproductive strategies (Sinervo and Lively 1996). However, the fact that the size of the populations from savannah enclaves is in general small suggests that genetic drift alone might account for discrepant frequencies of colour morphs (Oxford 2005). It is perhaps even more likely that the nearly generalized distribution of chromatic morphotypes across areas has been shaped by historical contact and gene flow among populations, counterbalancing the effects of genetic drift. Although these are exciting evolutionary hypotheses that deserve proper investigation, testing them is beyond the scope of this study.

Amazonian open formations as refugia

Epitomizing several decades of intense research on climate and landscape changes, Colinvaux (2007: 73) posited concisely that whatever caused the climatic upheaval of continental glaciers in the north also had impacts on the warmer climates further south. The theory of Pleistocene refugia (Haffer 1969) originally attempted to explain such impacts in terms of the conversion of the lush tropical rainforests into drier and more open landscapes and its further effects on the associated biodiversity. However, disproportionate attention has been given to forest refugia. This is one of very few recent studies (e.g. Da Silva *et al.* 1997, Gainsbury and Colli 2003, Mittermeier *et al.* 2010, Ritter *et al.* 2021) to have considered the historical nature and evolutionary significance of isolated patches of savannah vegetation enclosed in the periphery of Amazonia. Moreover, the discovery of *T. madeiramamore*, a new lizard species endemic to savannah enclaves from Rondônia, highlights the contribution of these refugia to the formation of extant South American biodiversity. The fact that *T. madeiramamore* has remained obscured for so long is remarkable, especially because this is a locally abundant vertebrate species with disjunct distribution but widespread in a relatively vast portion of South-western Amazonia. Regardless, given that *T. madeiramamore* has a distribution restricted to rock outcrops in savannah enclaves and is incapable of crossing the surrounding forest (Vanzolini 1986, Vitt 1993, Vitt and Caldwell 1993), our interpretation of current records and historical distribution models produced for the species is that the recent expansion of the Amazon forest fragmented its formerly wider, and perhaps contiguous or partially contiguous, distribution range.

Although the extent to which the forested habitats of South America were affected by climate changes during the Pleistocene remains a subject of debate (reviewed by Hooghiemstra and van der Hammen 1998, Colinvaux 2007, Bush *et al.* 2011, Rocha and Kaefer 2019), it has been assumed that the connectivity between open vegetation landscapes in Rondônia and Central Brazil was interrupted after the Amazon forest expanded during the current interglacial (humid) period, leading to both extinction (more prominently) and formation (less prominently) of new species and lineages (Gainsbury and Colli 2003). In fact, historical distributional modelling of South American landscapes has supported that the savannah enclaves from South-western Amazonia are relicts of Cerrado vegetation that were formerly connected with the north-westernmost portion of the homonymous biome (Werneck *et al.* 2012, Bueno *et al.* 2017). Furthermore, palynological and geological evidence, including sedimentological and carbon isotope data, suggests that these open–dry refugia became isolated only in the Late Pleistocene and Holocene (van der Hammen 1972, 1974, Absy and van der Hammen 1976, Burbridge *et al.* 2004, Mayle *et al.* 2007) as a result of the southward expansion of the Amazon forest. The historical distribution models of *T. madeiramamore* suggest that, after the LIG, the expansion of the Amazon rainforest split populations of this (and presumably other erstwhile contiguously distributed) species, isolating them in savannah enclaves. However, it is important to emphasize that, different from previously thought, our divergence date analysis indicates that the split between this species and its relatives distributed in the core Cerrado biome is likely to have taken place much before the Pleistocene (see above).

Landscape models produced for South America disagree with classical refugial theory by suggesting that, instead, the LIG (between 130 000 and 115 000 years BP) and LGM (between 31 000 and 16 000 years BP) were, respectively, the periods of widest and narrowest extension of the Cerrado (Werneck *et al.* 2012, Bueno *et al.* 2017, Costa *et al.* 2018), and these historical inferences of landscape limits seem to be corroborated by palynological evidence (for a summary, see appendix S3 of the paper by Werneck *et al.* 2012, Costa *et al.* 2018). Although the specific historical context and biological significance of savannah enclaves inhabited by *T. madeiramamore* remain for the most part unknown, these and other similar areas in South-western Amazonia have been destroyed systematically before scientists have had the chance to catalogue their species diversity (Fearnside and Ferreira 1984, Fearnside 1986, Piontekowski *et al.* 2019). Perhaps similarly catastrophic is the fact that recent deforestation-induced contact among otherwise isolated savannah enclave populations might be facilitating introgressive hybridization or even fusion of recently evolved lineages (Seehausen *et al.* 2008, Todesco *et al.* 2016). To date, published assessments of Amazonian biodiversity have not addressed these phenomena from either an evolutionary or conservationist standpoint. An appreciation of this issue potentially affecting *T. madeiramamore* is certainly desirable.

CONCLUSION

This study has raised the number of formally described *Tropidurus* species to 31 and shed light on a taxonomic problem identified almost 40 years ago (Vanzolini 1986). Perhaps more importantly, rather than supporting previous suggestions about the existence of multiple *Tropidurus* species in savannah enclaves from Rondônia (Vanzolini 1986, Vitt 1993, Vitt and Caldwell 1993), our results revealed a highly polymorphic species, whose populations became trapped in savannah relicts surrounded by the Amazon forest. The unanswered question, however, is for how much longer these lizards will remain isolated. *Tropidurus* from Rondonian savannah enclaves have been isolated for thousands of years, perhaps since the LGM. However, intense deforestation in Rondônia in recent decades, in addition to the construction of large roads dissecting the state, might facilitate range expansion and secondary contact among populations in close geographical proximity. Anthropogenic landscape modifications have also been hypothesized to promote dispersion and range expansion of other lizard lineages (e.g. whiptails) that occupy open–dry environments throughout Amazonia (Martins *et al.* 2021). These issues have not been explored in this study but should be addressed in future studies. Human-induced reconnection of enclave populations is worrisome for at least two main reasons: (i) because the secondary contact among lineages with incomplete reproductive isolation might promote genetic homogenization; and (ii) because the genetic signature of the historical processes that shaped lineage divergence will be lost irreversibly, eliminating our chances of testing biogeographical scenarios in the future. In South-western Amazonia, from only 2002 to 2020, the total area of primary rainforest in Rondônia decreased by 22%, which corresponds to 3.35 Mha of humid primary forest and 79% of the total loss of tree cover for the state in that period (https://www.globalforestwatch.org; see also Piontekowski *et al.* 2019). We, therefore, urge that studies of enclave populations be prioritized, and preferably executed employing genomic-level sampling and comparative analyses of the largest number of species possible. We hope this assessment has demonstrated successfully that *T. madeiramamore* is among the taxa that should be on that priority list.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

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