



Molecular systematics of Caribbean skinks of the genus *Mabuya* (Reptilia, Scincidae), with descriptions of two new species from Venezuela

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Phylogenetic relationships among the species of *Mabuya* present around the Caribbean Sea (Antilles, Central America, and northern South America) are proposed for the first time. The molecular phylogenetic analyses (based on cytochrome *b* and 12S sequences) give new insights into the diversification of the genus in the New World, its multiple instances of montane habitat colonization, and the multiple waves of colonization towards the Caribbean area. In addition to the molecular analyses, we propose hypotheses about the phylogenetic placement of some rare or possibly extinct species, based on a qualitative analysis of morphological characters. The present article also includes descriptions of two new species from northern Venezuela, *Mabuya nebulosylvestris* sp. nov. (from the highlands of the coastal range and the Andean Cordillera of Mérida) and *Mabuya zuliae* sp. nov. (from the lowlands of the Maracaibo lake basin). *Mabuya luciae* Garman, 1887, a possibly extinct species endemic to St Lucia Island, is resurrected and diagnosed from its supposed sister species, *Mabuya mabouya* (Lacepède, 1788). © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 156, 598–616.

ADDITIONAL KEYWORDS: altitudinal speciation – Andes – Antilles – biogeography – Central America – lizard – phylogeny – Saint Lucia – South America – taxonomy.

INTRODUCTION

The genus *Mabuya* Fitzinger, 1826 formerly included more than 110 species occurring in tropical areas of Africa, Madagascar, Asia, and the New World (Greer

& Broadley, 2000), until Mausfeld *et al.* (2002) restricted the genus solely to the American clade. Recent studies suggest that the common ancestor of this lineage crossed the Atlantic Ocean, from Africa to the Neotropics, less than 7–9 Mya (Mausfeld *et al.*, 2002; Carranza & Arnold, 2003). After colonization, the genus quickly dispersed and diversified across the entire neotropical realm, including South America,

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Central America, and the Antillean Archipelago, with the notable exception of Cuba (Schwartz & Henderson, 1991) and the ABC islands (Aruba, Bonaire, and Curaçao; Buurt, 2005).

As a result of both nomenclatural problems and a lack of sufficient revisionary work, the systematics of neotropical *Mabuya* is highly controversial (Taylor, 1956; Ávila-Pires, 1995; Mausfeld & Lötters, 2001). Confusion is especially apparent for species distributed in the regions peripheral to the Caribbean Sea (Breuil, 2002; Köhler, 2003; Miralles, 2005; Miralles, Rivas & Barrio-Amorós, 2005; Miralles *et al.*, 2006). One of these regions, the Caribbean coast of South America (Colombia and Venezuela), constitutes a key area that has possibly acted as a biogeographical link between Central America, the Antilles, and the South American mainland (Andes and Amazonia). Given that previous studies discovered populations in this region that could not be identified to any known species of *Mabuya* (Miralles, Rivas & Barrio-Amorós, 2005; Miralles *et al.*, 2006), it became obvious that their taxonomic clarification was required before an investigation of the evolutionary history of this group in the Caribbean region (namely the Northern coast of South America, Central America, and the Antillean archipelago) could take place. Thus, the goals of this study are: (1) to delimit species boundaries in the Venezuelan populations/taxa of uncertain taxonomic status discovered by Miralles, Rivas & Barrio-Amorós (2005); (2) to present a molecular phylogeny of the genus *Mabuya*, with special emphasis on the Caribbean taxa; and, (3) to discuss the historical biogeography of the genus *Mabuya* in the Caribbean region, based on the phylogenetic hypothesis generated in this study.

MATERIAL AND METHODS

NOMENCLATURAL AND TAXONOMICAL FRAMEWORK

The genus *Mabuya* Fitzinger, 1826 was recently divided by Mausfeld *et al.* (2002) into four monophyletic genera. In addition, Carranza & Arnold (2003) presented evidence about the existence of a fifth clade in the Mediterranean region, for which a new name seems necessary. Following Mausfeld *et al.* (2002), the genus *Mabuya* Fitzinger, 1826 is considered in the present paper to be an exclusively neotropical taxon. The name *Trachylepis* Fitzinger, 1843 is applied to the African clade (cf. Bauer, 2003), whereas the unnamed Mediterranean clade (the sister group of the genus *Mabuya* s.s.), comprising *Mabuya aurata* (Linnaeus, 1758) and *Mabuya vittata* (Olivier, 1804) (Carranza & Arnold, 2003), is referred to, for the time being, as '*Mabuya*' (see details in Miralles *et al.*, 2006).

Only six Antillean insular species have been frequently recognized [*Mabuya berengeriae* Miralles,

2006; *Mabuya lineolata* Noble & Hassler, 1933; *Mabuya mabouya* (Lacepède, 1788); *Mabuya macleanii* Mayer & Lazell, 2000; *Mabuya pergravis* Barbour, 1921; and *Mabuya sloanii* (Daudin, 1802)]. The taxonomic status of a seventh species, *Mabuya luciae* Garman, 1887, is discussed in the present paper. Examination of the type material of *M. luciae* indeed reveals a combination of morphological characters that are unique within the genus *Mabuya*, whereas the distinctiveness of this species has not been recognized for a long time (Dunn, 1936; Barbour, 1937; Schwartz & Henderson, 1991; Mayer & Lazell, 2000; Breuil, 2002; Miralles, 2005), and it has been regarded as a junior synonym of *M. mabouya*. Definitions of *Mabuya bistriata* (Spix, 1825) and *Mabuya nigropunctata* (Spix, 1825) are based on Ávila-Pires (1995) (see details in Miralles, Rivas & Barrio-Amorós, 2005).

MORPHOLOGICAL STUDY

The specimens examined (all preserved in 70% ethanol) are deposited in 18 international collections (see Appendices S1 and S2). Drawings were made using a stereomicroscope equipped with a camera lucida. Measurements of specimens were recorded to the nearest 0.1 mm using a dial caliper. The scale nomenclature, scale counts, and measurements used in the descriptions follow those of Ávila-Pires (1995). New characters in the systematics of the genus *Mabuya*, proposed by Greer & Broadley (2000), Greer & Nussbaum (2000), and Miralles (2006), were also added to the descriptions. For the new species descriptions, ranges are given for each meristic and mensural character, followed by the mean \pm SD, with the sample size given in parentheses. For some bilateral characters, the sample size has been noted as the number of sides rather than specimens, and this is then indicated after the sample size.

The diagnoses of the two new species are intended to distinguish one from the other, and from all of the 15 neighbouring species of *Mabuya* occurring in the Andean [*Mabuya cochabambae* Dunn, 1936; *Mabuya meridensis* Miralles, Rivas & Schargel, 2005], Guianan [*M. bistriata*; *Mabuya carvalhoi* Rebouças-Spieker & Vanzolini, 1990; the *M. nigropunctata* complex (Spix, 1825)], Central American [the *Mabuya unimarginata* complex Cope, 1862], Northern Venezuelan [*Mabuya croizati* Horton, 1973; *Mabuya falconensis* Mijares-Urrutia & Arends, 1997], and Antillean [*M. berengeriae*; *M. lineolata*; *M. luciae*; *M. mabouya*; *M. macleanii*; *M. pergravis*; *M. sloanii*] regions.

CRITERIA FOR DELIMITING SPECIES

Over the last few decades there has been a lot of debate about what a species is, with many alternative

concepts being proposed (Harrison, 1998; De Queiroz, 1998). Herein we follow Mayden (1997) in recognizing that the evolutionary species concept is perhaps the only purely theoretical concept appropriate for species. Because of its theoretical nature, the evolutionary species concept does not prescribe any specific criteria for species delimitation. In our particular case we combined character-based (morphological data from colour pattern and lepidosis) with tree-based (genetic data from two mitochondrial genes) criteria to delimit species boundaries. For the morphological data, we considered fixed character states as the criteria to support species status; whereas for the molecular data, exclusivity (*sensu* Baum, 1992), was the necessary condition used to recognize a species. Our criteria translate to species being delimited empirically as the smallest mutually exclusive diagnosable group of populations.

MOLECULAR DATA AND PHYLOGENETIC ANALYSES

Sampling

A total of 47 specimens were used in this study (Table 1), including 19 species of *Mabuya* s.s. We focused our sampling effort on the peripheral areas of the Caribbean Sea, obtaining 29 samples from 23 different localities in Northern Venezuela, Central America, and in the Antillean archipelago. Additionally, 15 samples from other neotropical regions (representing 11 different species restricted to, or essentially distributed in, these non-Caribbean regions) were included in order to test the monophyly of both the genus and the Caribbean endemic species of *Mabuya*. Three out-group species were selected: *Eumeces egregius* (Baird, 1859), *Trachylepis quinquetaeniata* (Lichtenstein, 1823), and '*Mabuya*' *vittata*. The latter two species have been chosen based on previous phylogenetic studies of the genus *Mabuya* s.l., '*Mabuya*' *vittata* (a Mediterranean species) and *T. quinquetaeniata*, representing the two closest clades to neotropical *Mabuya*. The phylogenetic relationships between those three taxa and the in-group (after Mausfeld *et al.*, 2002; Carranza & Arnold, 2003; Whiting *et al.*, 2006) are as follows: [*Eumeces* [*Trachylepis* (Mediterranean '*Mabuya*', *Mabuya* s.s.)]].

Molecular procedures

We sequenced approximately 1540 bp of mtDNA, including a 12S gene fragment (≈ 385 bp) and the complete cytochrome *b* gene (≈ 1155 bp). A total of 74 newly generated sequences have been submitted to GenBank (Table 1). Total genomic DNA was extracted from 95% ethanol-preserved tissues (muscles or liver) using a cetyl trimethylammonium bromide (CTAB) protocol (Winnepeinnickx, Backeljau & Dewachter,

1993). Amplifications were performed in total reaction volumes of 25 μ L, containing 0.3 μ L of each primer (25 pM μ L⁻¹) and 0.15 μ L of *Taq* DNA polymerase (Qbio Appligen) in a buffer supplied by the enzyme manufacturer. The primers 12SA-L (5'-AAACTGGGATTAGATACCCCACTAT-3') and 12SB-H (5'-GAGGGTGACGGGCGGTGTGT-3') of Köcher *et al.* (1989) were used to amplify a section of the 12S rRNA gene, with the following polymerase chain reaction (PCR) cycling procedure: 94 °C (3 min); 94 °C (30 s), 58 °C (40 s), 72 °C (50 s) for 30 cycles; 72 °C (1 min). The complete cytochrome *b* gene was amplified in two fragments, using: (1) the primers L15146 (5'-CATGAGGACA AATATCATCTCTGAG-3') and H15915sh (5'-TTCTCA GAATGATATCATTCTGAG-3') of Irwin, Kocher & Wilson (1991) [94 °C (3 min); 94 °C (40 s), 53 °C (30 s), 72 °C (1 min) for 33 cycles; 72 °C (1 min)]; and (2) two new primers that were developed for the present work, MAB1 (5'-AGAACCACCGTTGTATTCAACTAC-3') and MAB2 (5'-GRGTYARGGTTGCRTTGTCTACTG-3') [94 °C (3 min); 94 °C (30 s), 55 °C (40 s), 72 °C (50 s) for 30 cycles; 72 °C (1 min)]. The reaction products were visualized in a 1.5% agarose gel, were then purified directly from the PCR mixture, and were sequenced in both forward and reverse directions using an automated DNA sequencer (CEQ 2000 DNA Analysis System; Beckman Coulter Inc.). Both strands obtained for each sequence were aligned and checked using the Sequencer program (Gene Codes Inc.). Alignment was performed manually, and included four indels in 12S.

Phylogenetic analyses

Two methods of phylogenetic reconstruction were carried out on the combined 12S rRNA and cytochrome *b* genes: maximum parsimony (MP), using the program PAUP* 4.0.b10 (Swofford, 2002), and Bayesian analysis, using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Gaps were considered as missing data in both analyses. The MP reconstructions were performed using a heuristic search [i.e. random addition with 100 replications, and tree bisection and reconnection (TBR) branch swapping], with all sites being equally weighted. The relative branch support was evaluated using 1000 nonparametric bootstrap replicates with the heuristic search option, TBR branch swapping, and ten random taxon addition replicates (Felsenstein, 1985). For the Bayesian inference, the substitution model was selected with Modeltest v3.06 (Posada & Crandall, 1998) using the Akaike information criterion (AIC). The analysis was performed using the default priors implemented in MrBayes v3.0b4 (Huelsenbeck & Ronquist, 2001), with parameter values for the selected nucleotide substitution model (GTR + G + I) estimated by the

Table 1. List of *Mabuya* specimens, collection numbers, and accession numbers of the sequences, with their references and localities

| Species | Country | Collection number | Locality | Sequences | |
|--|-----------------------|-------------------|--|-----------------|-----------------|
| | | | | cyt <i>b</i> | 12S |
| Ingroup: | | | | | |
| <i>M. agilis</i> | Brazil, Pernambuco | Not collected* | Exu | EU443102 | AY151428 |
| <i>M. agnosticha</i> | Brazil, Alagoas | LG 902 | Xingó | DQ239134 | DQ239215 |
| <i>M. altamazonica</i> | Peru, San Martin | MNHN 2002.0291† | km 34 on the Tarapoto–Yurimaguas road | EU443103 | DQ368663 |
| <i>M. bistriata</i> | Brazil, Amazonas | SNOMNH 37183 | Madeira Scheffer (8°20'47.0"S, 65°42'57.9"W) | EU443104 | EU477258 |
| | French Guiana | Not collected | Matoury | EU443105 | DQ368666 |
| <i>M. carvalhoi</i> | Brazil, Roraima | SNOMNH 36332 | Junction BR-174/BR-210 | EU443106 | EU477259 |
| <i>M. cochabambae</i> | Bolivia, Santa Cruz | ZFMK 72151 | Vicinity of Pampagrande. | – | AF202625 |
| <i>M. croizati</i> | Venezuela, Anzoátegui | MHNLS 17670 | Cerro El Guamal, Turimiquire massif** | EU443107 | EU477260 |
| <i>M. dorsivittata</i> | Brazil, D.F. | Not collected | Brasília | EU443108 | AY151426 |
| <i>M. falconensis</i> | Venezuela, Falcón | MHNLS 17095 | Península de Paraguaná (A)** | EU443109 | EU477261 |
| | | Not collected | Península de Paraguaná (B)** | EU443110 | EU477262 |
| | Trinidad & Tobago | ZFMK 62603 | Tobago island** | – | AY070339 |
| <i>M. frenata</i> | Brazil, M. G. do Sul | Not collected | ? | EU443111 | AY151427 |
| <i>M. guaporicola</i> | Bolivia, Beni | MBH 5870 | El Refugio | EU443113 | EU477263 |
| | Brazil, M. G. do Sul | Not collected* | ? | EU443112 | AY151434 |
| <i>M. mabouya</i> | Lesser Antilles | MNHN 2003.0838 | Dominica island (A)** | EU443114 | EU477264 |
| | | No number‡ | Dominica island (B)** | EU443115 | EU477265 |
| <i>M. macrorhyncha</i> | Brazil, Sao Paulo | LG 1102 | Ilha da Queimada Grande | DQ239162 | DQ239243 |
| <i>M. meridensis</i> | Venezuela, Mérida | Not collected | Mérida (A)** | EU443116 | EU477266 |
| | | MHNLS 17081 | Monte Zerpa, near Mérida (B)** | EU443117 | EU477267 |
| <i>M. nebulosylvestris</i> sp. nov. | Venezuela, Aragua | MHNLS 17088 | La Colonia Tovar (A)** | EU443134 | EU477280 |
| | | MNHN 2007.0272 | La Colonia Tovar (B)** | EU443135 | EU477281 |
| | Venezuela, Lara | MHNLS 17106 | Cubiro (9°48'29.0"N, 69°33'25.7"W)** | EU443136 | EU477282 |
| | Venezuela, Miranda | MHNLS 17330 | Carrizal, Los Teques** | EU443137 | EU477283 |
| | Venezuela, Trujillo | Not collected | Trujillo (A)** | EU443138 | EU477284 |
| | Venezuela, Vargas | MHNLS 16649 | Trujillo, near the Laguna Negra (B)** | EU443139 | EU477285 |
| | | MHNLS 17093† | Pico Codazzi (A)** | EU443140 | EU477286 |
| | | MHNLS 17103 | Pico Codazzi (B)** | EU443141 | EU477287 |
| <i>M. nigropunctata</i> | Brazil, Pará | LSUMZ H14223 | Agropecuaria Treviso LTDA (3°8'56.7"S, 54°50'26.8"W) | EU443118 | DQ368667 |
| | Brazil, Roraima | SNOMNH 36318 | Fazenda Nova Esperanca (BR-210, 41 km W BR-174) | EU443119 | DQ368668 |
| | Colombia, Guainia | Not collected | Puerto Inirida | EU443120 | AY151438 |
| | Venezuela, Aragua | MHNLS 17080 | Turiamo** | EU443121 | EU477268 |

Table 1. Continued

| Species | Country | Collection number | Locality | Sequences | |
|---------------------------|-------------------|-------------------|---|--------------|----------|
| | | | | cyt <i>b</i> | 12S |
| <i>M. sloanii</i> | Lesser Antilles | MNHN 2003.0844 | St Barthélemy island (A)** | EU443122 | EU477269 |
| | | MNHN 2003.0843 | St Barthélemy island (B)** | EU443123 | – |
| <i>M. unimarginata</i> | Costa Rica | YPM 15082 | British Virgin Islands, Guana Island** | EU443124 | EU477270 |
| | | Not collected | Tortugueros** | EU443125 | EU477271 |
| | Guatemala, Zacapa | UTA 41513 | Zacapa** | EU443126 | EU477272 |
| | Honduras, Olancha | UTA 41227 | Las Trojas, San Esteban** | EU443127 | EU477273 |
| | Mexico, Guerrero | Not collected | Chichihualco (17°39'32"N, 99°42'07"W)** | EU443128 | EU477274 |
| | Mexico, Oaxaca | Not collected | On the El Camaron–Tehuantepec road** | EU443129 | EU477275 |
| <i>M. zuliae</i> sp. nov. | Venezuela, Zulia | MHNLS 16676 | Cerro el Mirador (08°36'45", 72°31'34"W) (A)** | EU443130 | EU477276 |
| | | MHNLS 16677 | Cerro el Mirador (08°36'45", 72°31'34"W) (B)** | EU443131 | EU477277 |
| | | MHNLS 16647† | Río Escalante, Sector El Cañon (C)** | EU443132 | EU477278 |
| | | MNHN 2007.0273 | La Orchila, S. de Perijá (10°48'44"N; 72°21'13"W) (D)** | EU443133 | EU477279 |
| Outgroup | | | | | |
| <i>E. egregius</i> | North America | MVZ 150128 | Florida | AB016606¶ | – |
| <i>T. quinqueaeniata</i> | Africa | MNHN 2004.0102§ | Unknown locality | EU443143 | – |
| | | BEV 7202§ | Egypte, Assouan | – | EU477289 |
| <i>'Mabuya' vittata</i> | Middle East | BEV 1446 | Turkey, Osmandere | EU443142 | EU477288 |

Genbank accession numbers of the new sequences obtained for this study are set in bold; all the rest are taken from Kumazawa & Nishida (1999), Mausefeld & Lötters (2001), Carranza & Arnold (2003), and Whiting *et al.* (2006). Dashes represent missing data.

*Two samples sequenced by Carranza & Arnold (2003) have been reidentified here: *Mabuya agilis* (synonymous with *Mabuya haethi*, E11108); *Mabuya guaporicola* (instead of *Mabuya agilis*, E11101).

†Holotype specimens.

‡Specimen collected but not deposited in an official collection.

§Composite samples, based on cytochrome *b* and 12S sequences from two different specimens.

¶Complete mitochondrial genome, sequenced by Kumazawa & Nishida (1999).

**Samples from the Caribbean region (Northern coast of South America, Central America, and the Antillean archipelago).

program. One 'cold' and three 'heated' chains, with a temperature parameter of 0.2, were started from random topologies, and were run for two million generations with sampling every 100 generations. The analysis was run twice to ensure that the resultant data were obtained from sampling the full tree space, rather than from local optima. Burn-in was evaluated by an examination of the standard deviation of split frequencies (> 0.01). Tree samples and parameter estimates from the 500 000 generations of the Bayesian analysis (the first 25% of samples) were designated as burn-in, and were discarded. The phylogeny inferred from the remaining 1 500 000 generations was represented as a 50% majority rule consensus tree. We consider branches supported by posterior probability values greater than or equal to 95% (Wilcox *et al.*, 2002) to be significantly supported by our data.

RESULTS

SPECIES LIMITS AND TAXONOMIC DESCRIPTIONS

In addition to the six insular Antillean species frequently recognized (see Nomenclatural and taxonomical framework), a seventh species, *M. luciae*, is herein considered as valid. The examination of five specimens from St Lucia island (including the holotype MCZ 6046) revealed that *M. luciae* is a morphologically distinct species, and is easily distinguishable from *M. mabouya* by the presence of: (1) several very thin dark stripes running along the throat, venter, and tail, and dark spots on the edge of many supra-cephalic scales; (2) white, brown-edged ocelli on the flanks (unique within the genus); (3) brown marbling on the sides of the neck; (4) four supraoculars; and (5) by the presence of one or two secondary nuchal scales (at least on one side). For these reasons, we consider *M. luciae* to be a valid species diagnosable from *M. mabouya*, as well as from all other neotropical congeners.

Our analysis of species limits also supports the recognition of the recently described *M. falconensis* and *M. meridensis* as valid species. Venezuelan populations that remain under the tentative name of *M. mabouya* represent two different undescribed species, both distinct from true *M. mabouya*. One of these undescribed species is distributed in montane forests of the Coastal and Merida Mountain Range of Venezuela, and is the most basal species of what we call the Caribbean clade in the parsimony analysis (unresolved in the Bayesian analysis). The other undescribed species is sister to *M. meridensis*, and occurs in the lowlands of the Lake Maracaibo Basin. These two new species are described below.

MABUYA NEBULOSYLVESTRIS SP. NOV.

(FIGS 1A, B, 2A)

Holotype: MHNLS 17093. An adult male with extruded hemipenis, from the Hotel Casa de Campo Tovar (10°24'35"N, 67°17'27"W), 1.5 km from Colonia Tovar, Pico Codazzi, Vargas state, Venezuela; collected on 5 May 2005 by G. Rivas, A. Miralles, and O. Lasso-Alcalá.

Paratypes: 30 specimens. Venezuela. Anzoátegui: MHNLS 5887, Valle de Guanape (920 m a.s.l.). Aragua: AMNH 137286–137287, Rancho Grande; MHNLS 17088, 17091, 17092, MNHN 2007.0272, Colonia Tovar. Cojedes: MHNLS 8098, Cerro Azul, Fila la Blanquera. Distrito Capital: MHNLS 719, 720, El Junquito (2000 m a.s.l.); MHNLS 1409, El Junquito (2300 m a.s.l.); MHNLS 2481, 5502, Altigracia, Caracas (980 m a.s.l.), collected, respectively, by J. M. Peláez in 1966 and G. Ramírez in 1971; MHNLS 13262, Quebrada Mariperez, Parque Nacional El Ávila; MHNLS 13337, Parque Zoológico Caricuao, Caracas. Lara: MHNLS 17106, Cubiro (9°48'290"N, 69°33'257"W). Miranda: MHNLS 13734–13735, El Amarillo, San Antonio de Los Altos, collected in May 1997 by G. Colonello; MHNLS 16653, Guatire, Hacienda Santa Rosa (1125 m a.s.l.); MHNLS 16656–16657, Pico Naguayata, El Urquijo (2360 m a.s.l.); MHNLS 17330, Carrizal, Los Teques (specimen in a very poor state of preservation). Trujillo: MHNLS 16649–16650, vicinity of Boconó, front of the Laguna Negra; MHNLS 17082–17083, between Batatal and Río Negro (1100–1500 m a.s.l.), collected in May 2000 by W. Schargel. Vargas: MNHN 2007.0271, from the type locality, collected in May 2005 by G. Rivas, A. Miralles, and O. Lasso-Alcalá; MHNLS 17103, from the type locality, collected in December 2004 by G. Rivas and O. Lasso-Alcalá. Yaracuy: MHNLS 8479, Cerro Azul de Tucuragua; UMMZ 55925, Nirgua.

Additional material: CVULA 4831, an adult from Potosí, Táchira state, Cordillera de Mérida, close to the Colombo–Venezuelan frontier. We refrain from including this specimen in the type series because of its outlying locality and its poor state of preservation.

Diagnosis: A medium-sized *Mabuya* with an undivided lower eyelid, all scales smooth, auricular lobes absent, and with a short and round snout, paired prefrontals and frontoparietals, a single pair of nuchals, four supraoculars, and four supraciliaries, with the second longer than the rest. *Mabuya nebulosylvestris* sp. nov. differs from neighbouring species of *Mabuya* by the combined presence of: six longitudinal dark stripes along the body (versus seven dark stripes in *M. cochabambae* and *M. meridensis*;

between two and four dark stripes in *M. falconensis* and *Mabuya zuliae* sp. nov.; and ten dark stripes in *M. lineolata*); palms and soles dark coloured (versus palms and soles light coloured in *M. bistriata*, *M. berengeriae*, *M. falconensis*, *M. mabouya*, *M. macleani*, *M. luciae*, *M. pergravis*, *M. sloanii*, and the Central American *M. unimarginata* complex species); frontoparietals separated (versus frontoparietals fused in *M. croizati*, *M. carvalhoi*, and *M. cochabambae*); no secondary nuchal scales and a round snout [versus between one and five pairs of nuchal scales, and an acute snout in *M. berengeriae*, *M. carvalhoi*, *M. croizati*, *M. macleani* (variable), *M. luciae*, *M. pergravis*, and *M. sloanii*]; and in having parietals in broad contact behind the interparietal, and four supraciliaries with the second being the longest (versus parietal most often separated by the interparietals, and five or six subequal supraciliaries in *M. nigropunctata*). Moreover, the coloration and the shape of the dorsal stripes, which are very dark, formed by an assemblage of small dots, and which are most often relatively wide, constitute a characteristic peculiar to this species.

Description of the holotype: MHNS 17093 (Fig. 1A, B). In a perfect state of preservation. Snout–vent length 72.1 mm; tail length 112.0 mm; head length 13.2 mm. Fore- and hindlimbs almost touching each other when adpressed against body.

Rostral wider than high, contacting first supralabials, nasals, and supranasals. Paired supranasals in median contact, contacting anteriormost loreal. Frontonasal approximately hexagonal, wider than long, laterally contacting anterior loreal. Paired prefrontals roughly quadrilateral, wider than long, in contact medially, contacting frontonasal, both anterior and posterior loreals, first supraciliaries, first and second supraoculars, and frontal. Frontal lanceolate, as long as wide, wider anteriorly, in contact with prefrontal, second supraoculars, and frontoparietals. Four supraoculars: the first one smallest, and the second one longest and widest. The second supraocular is the posteriormost in contact with the frontal. Four supraciliaries, with the second being the longest. Paired frontoparietals, longer than wide, in broad contact at midline, in contact with frontal, all supraoculars (with exception of the first), parietal, and interparietal. Interparietal roughly triangular, longer than wide, wider anteriorly, separated from nuchals by parietals. Parietal eye distinct. Parietals larger than interparietal, wider than long, overlapping the upper temporal scale. Single pair of transversely enlarged nuchals, each as wide as three rows of dorsals. Nasal subrectangular. Nostril located posteriorly. Postnasal small, in contact with supranasal, anterior loreal, first supralabial, and in point contact with the second

supralabial. Two subrectangular loreals behind nasal, the second slightly larger. First loreal in contact with second supralabials; second loreal in contact with second and third supralabials. One presubocular, in contact with fourth and fifth supralabials. One preocular, anterior to presubocular and posterior to second loreal, and in contact with third and fourth supralabials. Lower eyelid undivided, with a transparent disc, and one row of small scales across its dorsal edge. Seven supralabials, the fifth being the enlarged subocular. Seven infralabials. Temporals imbricate, smooth, cycloid, not distinctly delimited from scales on the nape or sides of the neck. Two pretemporals. One primary temporal, two secondary temporals in contact, and three tertiary temporals. Ear-opening small, round, with inferior and posterior margin bordered by small scales. Auricular lobules absent. Mental wider than long, posterior margin straight. Postmental wider than long, adjacent to first and half of second infralabials. Two pairs of chin shields, in contact with postmental, and the second, third, and fourth infralabials. Gulars similar in size and outline to ventrals. Palms and soles covered with small tubercles, subequal in size. Both regions delimited by a row of larger and flatter scales. Subdigital lamellae smooth, single, 12 under left fourth finger and 11 under right fourth finger, 15 under fourth toe (on each side), right fifth toe missing. Finger and toes clawed. Relative length of the toes in the following order: $I < II < III = V < IV$. All scales, except head shields and scales on palms, soles, and digits, cycloid, smooth, and imbricate. Twenty-eight scale rows around midbody, 53 transverse rows of dorsal scales, and 30 transverse rows of ventral scales. Four preanals larger than adjacent ventral scales. Median supra- and subcaudal series of scales twice as wide as long on the posterior third of the tail.

Coloration in preservation: background colour of upper side of the head, neck, back, limbs, and tail dark bronze. Venter, lower side of head, throat, lower side of limbs, and tail immaculate bluish metallic grey colour. Lower half of each supralabial, and each infralabial and mental, yellow–greyish; each infralabial with a brown posterior edge. Lateral and upper sides of limbs spotted with small fused dark dots. Palms and soles black. Preanals pale metallic grey. Six dark stripes run along the body, some of them continuing along the tail. Two wide black dorsal stripes, not well defined, formed by succession of dots, running from the fourth supraocular (with an interruption between the nuchals and fourth dorsal scales) to the first third of the tail, where they fuse together; at midbody, each dorsal stripe is about two scales wide, overlying three rows of scales, and are composed of three longitudinal rows of fused triangular dots. At midbody, dorsal stripes are just separated by

two half dorsal scales. Two dark-brown upper lateral stripes; margins darker and strongly contrasting; about two scales wide at midbody and overlying three rows of scales; from nostrils, loreals, dorsal halves of supralabials, around eyes and temporals, along upper half of ear openings, on neck, above arms, on sides, above hindlimbs, and on sides of the tail. Two black lower lateral stripes, running from below the ear opening, above forelimb, until insertion of hindlimbs; dorsal margins straight, darker, and contrasting with remainder of dorsal coloration, whereas limits between ventral margins and venter not distinct. Four white stripes run along the body. Two white dorsolateral stripes separate dark dorsal stripes from the upper lateral dark stripes: from the fourth supraoculars to the mid-length of the tail. Two very clear whitish lateral stripes separating the dark upper lateral stripes from the dark lower lateral stripes, running from the supralabials to the insertion of the hindlimbs.

Variation: Dorsal scale rows, 48–56 (52.72 ± 1.61 ; 29); midbody scale rows: 26–30 (28.59 ± 1.22 ; 27); ventral scale rows, 27–38 (32.89 ± 2.30 ; 28); lamellae under fourth finger, 10–14 (12.06 ± 1.06 ; 53 sides); lamellae under fourth toe, 13–18 (15.67 ± 1.24 ; 51 sides); head length, 10.3–15.4 (12.68 ± 1.52 ; 23); snout–vent length, 52.1–96.7 (70.14 ± 10.73 ; 23); tail length, 84.5–151.2 (113.27 ± 23.51 ; 9). Internasals: 96.7% in broad contact, 3.3% in point contact, and none separated. Prefrontals: 26.7% in broad contact, 13.3% in point contact, and 60.0% separated. Parietals: 90.0% in broad contact and 10.0% separated ($N = 30$). Number of supraciliaries (n sides = 59): four, with the second being the longest (83.1%); five, with the second being the longest (6.8%); five, subequal in size (6.8%); and six, subequal in size (3.4%). Number of supralabials (n sides = 58): seven with the fifth being the enlarged subocular (29.3%), and eight with the sixth being the enlarged subocular (70.7%).

Etymology: The specific epithet is derived from the Latin *nebulae* (cloud) and *silvae* (forest), *nebulosylvestris* meaning ‘from the cloud forest’.

Distribution: (Fig. 3B) This species is currently known from two separate regions at relatively high elevations (920–2360 m): (1) the central portion of the Venezuelan coastal range (states of Anzoátegui, Aragua, Cojedes, Miranda, Vargas, Yaracuy, and Distrito Capital); and (2) the Cordillera de Mérida (states of Lara, Trujillo, and probably Táchira, but apparently absent in the upper Chama River valley, which is the area of *M. meridensis* endemism).

Natural history: On the summit of the Codazzi Mountain (approx. 2000 m a.s.l.), six *M. nebulosylvestris* sp. nov. were observed, basking together, in an open area at the edge of the cloud forest. On the Pico Naiguata summit (Avila National Park), several individuals were observed on a rock during the early morning, among subparamo shrubby vegetation. In Colonia Tovar, *M. nebulosylvestris* sp. nov. is common in gardens, basking on terraces, piles of wood, and stone walls. In the Mérida Range, specimens were found mostly under rocks in areas where the original forest had been cleared. They were only observed to be active during sunny days around rocky outcrops.

In the coastal range, *M. nebulosylvestris* sp. nov. is sympatric with two endemic lizards present at the same altitude, *Euspondylus acutirostris* Peters, 1863 and *Anadia marmorata* (Gray, 1846) (Gymnophthalmidae). However, both of the latter species are more arboreal, being exclusively found in the cloud forests. In Trujillo, Cordillera de Mérida, we also found individuals of *Liophis epinephelus* Cope, 1862 and *Atractus* spp. under rocks in the same areas where *M. nebulosylvestris* sp. nov. occurred.

MABUYA ZULIAE SP. NOV. (FIGS 1C, D, 2B)

Holotype: MHNLS 16647. An unsexed adult specimen from Rio Escalante (09°03'08"N, 71°55'23"W), south-west lake Maracaibo, sector el Cañon, Zulia state, Venezuela, collected in October 2003 by E. Arrieta.

Paratypes: 13 specimens. Venezuela. Mérida: MHNLS 16671, Finca Onia, 10 km south-west of El Vigía, via San Cristobal. Táchira: UMMZ 55933, río Labatorito San Felix. Trujillo: ULABG 5008, Quebrada Carvajal, 30 min from Valera. Zulia: MBLUZ 190, Aragtoba, Bari indigenous community, Serranía de Abusanki, Sierranía de Perijá, Municipio Machiques (09°34'32"N, 72°55'15"W; 175 m a.s.l.); MBLUZ 254, Frontalia, Río de Oro, Municipio Catatumbo (09°08'17"N, 72°52'17"W; 75 m a.s.l.); MBLUZ 737, Embalse Burro Negro, Municipio Lagunillas; MHNLS 10048–11864, Misión El Tukuko, Sierranía de Perijá, collected by C. Lasso in July 1986 and W. C. Villalobos in November 1983, respectively; MHNLS 11856, carretera Williams, Consejo de Ziruma; MNHN 2007.0273, Fundo La Orchila, Río Maché, Cuenca del Río Cachirí, Serranía de Perijá, Municipio Mara (10°48'44"N, 72°21'13"W; 227 m a.s.l.), collected in November 2003 by G. Rivas and F. Rojas; MHNLS 16676–16677, Cerro el Mirador, km 495 on the Machiques-Colón road, municipality of Jesús Maria Semprún, collected in May 2004 by G. Rivas and T. Barros.

Additional material: Six fetuses (MHNLS 17035–17040) extracted from the uterus of the female MHNLS 16671, at final stage of development (pig-

mented integument). A specimen (MHNLS 9720) from Hacienda El Jaguar, Sierra de Bobare, Yaracuy state, has been excluded from the type series because of its outlying locality (outside of the Maracaibo Basin) and its poor state of preservation.

Diagnosis: A medium-sized *Mabuya* with an undivided lower eyelid, all scales smooth, auricular lobes absent, and with a slightly acute snout, paired prefrontals and frontoparietals, a single pair of nuchals, four supraoculars, four supraciliaries, with the second being longest, and no dark dorsal stripes. *Mabuya zuliae* sp. nov. differs from neighbouring species of *Mabuya* by the combined presence of the following characters: four longitudinal dark stripes along the body (versus six long dark stripes in *M. carvalhoi*, *M. croizati*, *M. nebulosylvestris* sp. nov. and *M. sloanii*; six dark stripes, including a shorter pair of dorsals, in *M. bistrata* and *M. macleani*; seven dark stripes in *M. cochabambae* and *M. meridensis*; and ten dark stripes in *M. lineolata*); palms and soles dark coloured (versus palms and soles light coloured in *M. bistrata*, *M. berengeriae*, *M. falconensis*, *M. mabouya*, *M. macleani*, *M. luciae*, *M. pergravis*, *M. sloanii*, and the Central American *M. unimarginata* complex species); frontoparietals separated (versus frontoparietals fused in *M. croizati*, *M. carvalhoi*, and *M. cochabambae*); no secondary nuchal scales (versus between one and five pairs in *M. berengeriae*, *M. carvalhoi*, *M. croizati*, *M. macleani*, variable, *M. pergravis*, and *M. sloanii*); and in having parietals in broad contact behind the interparietal and four supraciliaries, with the second being the longest (versus parietal most often separated by the interparietals, and five or six subequal supraciliaries in *M. nigropunctata*). Moreover, the presence of small white and black spots on legs and tail, and the distribution pattern of black spots on the back and neck, constitute a characteristic peculiar to this species.

Description of the holotype: MHNLS 16647 (Fig. 1C, D). Good state of preservation. Snout–vent length 83.5 mm; tail length 102.4 mm (partly regenerated); head length 15.0 mm. Fore- and hindlimbs easily touching each other when adpressed against body.

Rostral wider than high, contacting first supralabials, nasals, and supranasals. Paired supranasals in median contact, contacting anteriormost loreal. Frontonasal approximately rhomboid, wider than long, laterally contacting anterior loreal. Paired prefrontals roughly quadrilateral, wider than long, separated medially, contacting frontonasal, both anterior and posterior loreals, first supraciliaries, first supraoculars, and tip of second supraoculars, and frontal. Frontal lanceolate, approximately one and a half

times longer than wide, wider anteriorly, in contact with frontonasal, prefrontal, second supraoculars, and frontoparietals. Four supraoculars: the first being the smallest, and the second being the longest and widest. The posteriormost supraocular in contact with the frontal is the second. Four supraciliaries, with the second being the longest. Paired frontoparietals, longer than wide, in broad contact at midline, in contact with frontal, all supraoculars, except the first, the parietal, and the interparietal. Interparietal rhomboid, longer than wide, wider anteriorly, posterior part rounded and separated from nuchals by parietals. Parietal eye hardly distinct. Parietals larger than interparietal, wider than long, overlapping the upper temporal scale. Single pair of transversely enlarged nuchals, each as wide as three rows of dorsals. Nasal trapezoidal. Nostril located posteriorly. Postnasal small, in contact with supranasal, anterior loreal, and first supralabial. Two subrectangular loreals behind nasal: subequal in size, with the second being slightly longer. First loreal in contact with first and second supralabials; second loreal in contact with second and third supralabials. One small presubocular in contact with fifth and sixth supralabials. Two preoculars in contact, with the anteriormost behind the second loreal, and in contact with the third and fourth supralabials, and with the posteriormost in front of presubocular, and in contact with the fourth and fifth supralabials. Lower eyelid undivided, with a transparent disc, and one row of small scales across its dorsal edge. Eight supralabials, with the sixth being the enlarged subocular. Eight infralabials. Temporals imbricate, smooth, cycloid, and not distinctly delimited from scales on the nape or sides of the neck. Two pretemporals. One primary temporal, two secondary temporals in contact, and three tertiary temporals. Ear opening relatively small, oval, and with inferior and posterior margin bordered by small scales. Auricular lobules absent. Mental wider than long, posterior margin straight. Postmental wider than long, adjacent to the first infralabial, and to two-thirds of the second infralabial. Two pairs of chin shields, in contact with postmental, and second, third, and fourth infralabials. Gulars similar in size and outline to ventrals. Palms and soles covered with small tubercles, subequal in size. Both regions delimited by a row of larger and flatter scales. Subdigital lamellae smooth, single, with 12 under fourth finger (on each side), 17 under left fourth toe, and 18 under right fourth toe. Finger and toes clawed. Relative length of toes in the following order: $I < II < III = V < IV$. All scales, except head shields and scales on palms, soles, and digits, cycloid, smooth, and imbricate. Thirty scale rows around midbody, 52 transverse rows of dorsal scales, 35 transverse rows of ventral scales. Four preanals larger than adjacent

ventral scales. Median supra- and subcaudal series of scales twice as wide as long on the posterior third of the tail.

Coloration in preservative: background colour of upper side of the head, neck, back, limbs, and tail olive-greyish. Venter, lower side of head, throat, lower side of limbs, and tail immaculate cream/light-grey, lighter medially than laterally. Lower half of rostral and each supralabial white; each infralabial grey with a black posterior edge. A dark spot on the posterior edge of each fourth supraocular. Lateral and upper sides of limbs spotted with small black and white spots, often in contact together. Supradigital lamellae white, most of them with a black dot on each lateral side. Palms and soles dark grey. White and black triangular dots on the tail. Preanals pale cream. No dorsal stripes. Two dark upper lateral stripes, with irregular margins on each side; margins darker and better defined on the anterior part; about three scales wide at midbody; from nostrils, loreals, dorsal halves of supralabials, around eyes and temporals, along upper half of ear openings, on neck, above arms, and on sides extending to insertion of hindlimbs. Two lower lateral dark stripes formed by a succession of more or less aligned dark dots; extending from below ear opening, above forelimb, to insertion of hindlimbs. Four white stripes run along the body. Two white dorsolateral stripes nearly imperceptible, very short, and only present on the neck (from the parietal to the 15th dorsal). Two white lateral stripes clearly defined from supralabials to forelimbs, continuing in a succession of aligned spots to the hindlimbs. Numerous dark triangular dots on the dorsum, each one of them in the middle of a dorsal scale, and in contact with its posterior edge; on the neck, only present in two longitudinal scale rows, edging the dorsolateral white stripe dorsally, but present in all of the dorsal scale rows.

Variation: Dorsal scale rows, 47–53 (51.53 ± 1.50 ; 19); midbody scale rows, 28–30 (29.24 ± 0.97 ; 17); ventral scale rows, 29–36 (31.72 ± 1.84 ; 18); lamellae under fourth finger, 13–16 (15.38 ± 0.66 ; 40); lamellae under fourth toe, 16–19 (18.22 ± 0.85 ; 37); head length, 10.4–16.9 (14.89 ± 1.77 ; 12); snout–vent length, 65.7–100.9 (81.04 ± 12.04 ; 12); tail length, 118.3–155.3 (136.31 ± 13.91 ; 7). Internasals: 95.0% in broad contact and 5.0% separated. Prefrontals: all separated. Parietals: 95.0% in broad contact and 5.0% separated ($N = 20$). Number of supraciliaries (n sides = 40): four, with the second being the longest (87.5%); five, with the second being the longest (10.0%); five, subequal in size (2.5%). Number of supralabials (n sides = 40): eight, with the sixth being the enlarged subocular (97.5%); nine, with the seventh being enlarged subocular (2.5%).

Etymology: The name of this species is given in reference to the state of Zulia, where this species is relatively common.

Distribution (Fig. 3B): *Mabuya zuliae* sp. nov. is widespread in Zulia state, and also marginally in the neighbouring states of Mérida and Trujillo. It is distributed around the Lake Maracaibo Basin, including the lowlands, foothills, and mountainous areas of the eastern slope of the Serranía de Périjá (under 1500 m a.s.l.).

Natural history: *Mabuya zuliae* sp. nov. is a diurnal species that can be found associated with rural houses, ranches, and farms with moderate intervention of the surrounding habitat. This species is a good climber, and is frequently observed higher than 1 m above ground, basking on tree trunks or shrubs, and also in debris associated with agricultural areas. Many specimens have been found foraging in mangrove areas, close to water (lakes, lagoons, or rivers). At Cerro Mirador, a young specimen was observed, apparently active (or just escaping) at night. Given the extensive distribution of this species in the Maracaibo Basin, and the high diversity of habitat spanning its distribution, a great diversity of lizards are to be found in sympatry with *M. zuliae* sp. nov., such as *Norops annectens* (Williams, 1974), *Norops auratus* (Daudin, 1802), *Norops biporcatus* (Wiegmann, 1834), *Norops tropidogaster* (Hallowell, 1856), *Basiliscus basiliscus* (Linnaeus, 1758), *Iguana iguana* (Linnaeus, 1758), *Polychrus marmoratus* (Linnaeus, 1758), *Gonatodes petersi* Donoso-Barros, 1967, *Gonatodes vittatus* (Lichtenstein, 1856), *Thecadactylus rapicauda* (Houttuyn, 1782), and *Phyllodactylus ventralis* O'Shaughnessy, 1875.

MOLECULAR RESULTS

The combined analysis of the mitochondrial 12S rRNA and cytochrome *b* genes constitutes a matrix of 1539 characters: 670 sites were variable, and 534 of them were parsimony informative. The heuristic search using MP analysis produced 20 equally most-parsimonious trees (n taxa = 47; tree length = 2791; consistency index, CI = 0.363; retention index, RI = 0.594; rescaled consistency index, RC = 0.216). The monophyly of the genus *Mabuya* is strongly supported, but most of the basal relationships are poorly resolved when examining the strict consensus tree (Fig. 4A). *Mabuya carvalhoi* and *M. croizati* are resolved as sister species, and are placed at the base of the genus. Most species around the Caribbean Sea constitute a strongly supported clade (referred to as the Caribbean clade in the present study, and composed of *M. falconensis*, *M. mabouya*, *M. meridensis*,

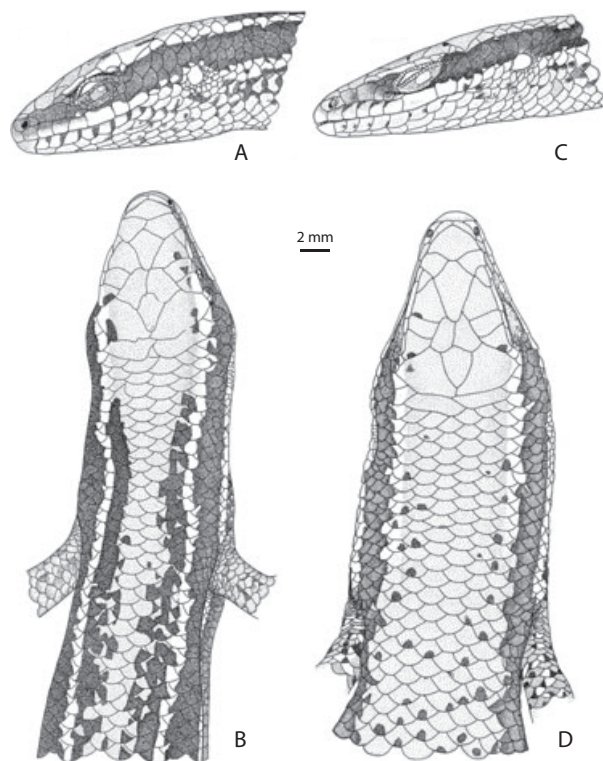


Figure 1. A, B, holotype of *Mabuya nebulosylvestris* sp. nov. (MHNLS 17093). C, D, holotype of *Mabuya zuliae* sp. nov. (MHNLS 16647). The drawing (A) is symmetrically reversed, and represents the right side of the head. Scale bar: 2 mm. Illustrations by AM.

M. unimarginata, and the two new species), with the notable exceptions of *M. sloanii* (an Antillean species) and *M. croizati* (a species endemic to the Turumiquire massif in north-eastern Venezuela). The Central American *Mabuya* (*M. unimarginata* complex) also represents a strongly supported monophyletic unit. The Bayesian tree topology is very similar to the MP tree (Fig. 4B), but with a higher support for the monophyly of the neotropical lineage, the Caribbean clade (with the exclusion of *M. sloanii*), and the basal position of the clade (*M. carvalhoi* + *M. croizati*).

HYPOTHETICAL PHYLOGENETIC POSITION OF RARE CARIBBEAN SPECIES

Most of the insular Antillean species of *Mabuya* appear to be extremely rare, if not extinct (e.g. *M. berengerae*, *M. luciae*, or *M. pergravis*). Consequently, it was not possible to obtain tissue samples of five of the seven insular *Mabuya* so as to include those species in the molecular analyses. The genus *Mabuya* is morphologically too conserved to obtain sufficient phylogenetically informative characters to generate a phylogenetic tree including those species for which genetic data is not

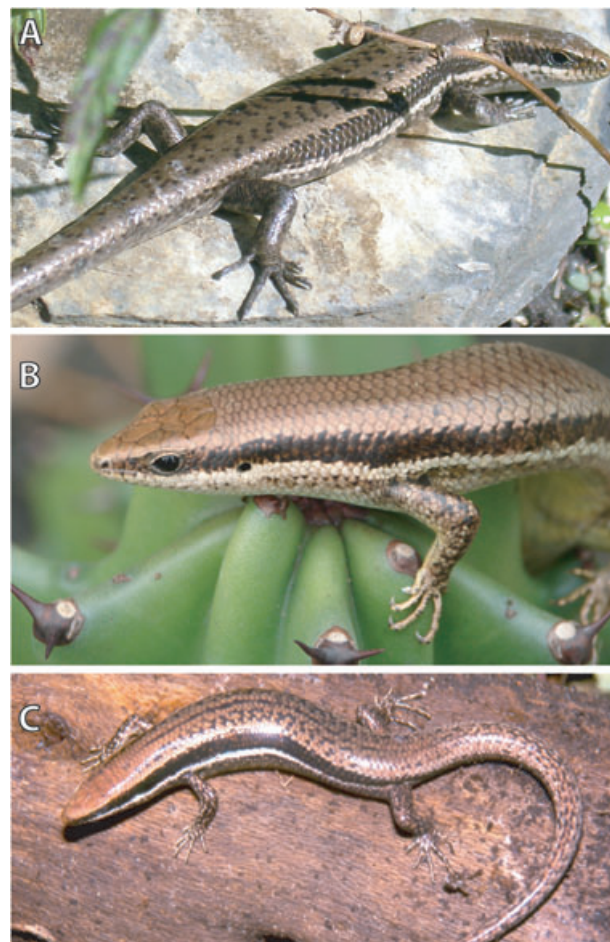


Figure 2. Uncollected specimens of (A) *Mabuya nebulosylvestris* sp. nov. (from the type locality, Colonia Tovar, Aragua, Venezuela), (B) *Mabuya zuliae* sp. nov. (from Cerro El Mirador, km 495 on the Machiques-Colón road, Zulia, Venezuela), and (C) *Mabuya meridensis* (in the vicinity of Mérida city, Mérida, Venezuela). Photographs by AM, TB, and CLB-A, respectively.

available. However, some hypothetical phylogenetic groupings of these species, based on a qualitative analysis of their morphology (including notions of overall similarity and some putative synapomorphies) and geographical distribution are proposed as follows: (1) *M. luciae* is placed as a sister species of *M. mabouya*; (2) *M. berengerae* and *M. pergravis* are regarded as sister species (San Andrés clade), and are grouped with *M. unimarginata* and *M. falconensis* in a trifurcate consensus; (3) *M. macleani* is placed as a sister species of *M. sloanii*; and (4) *M. lineolata* is placed as a sister species of the *M. sloanii* group (*M. sloanii* + *M. macleani*). These hypothetical groupings, combined with our molecular results, are presented in a hypothetical consensus tree (Fig. 5).

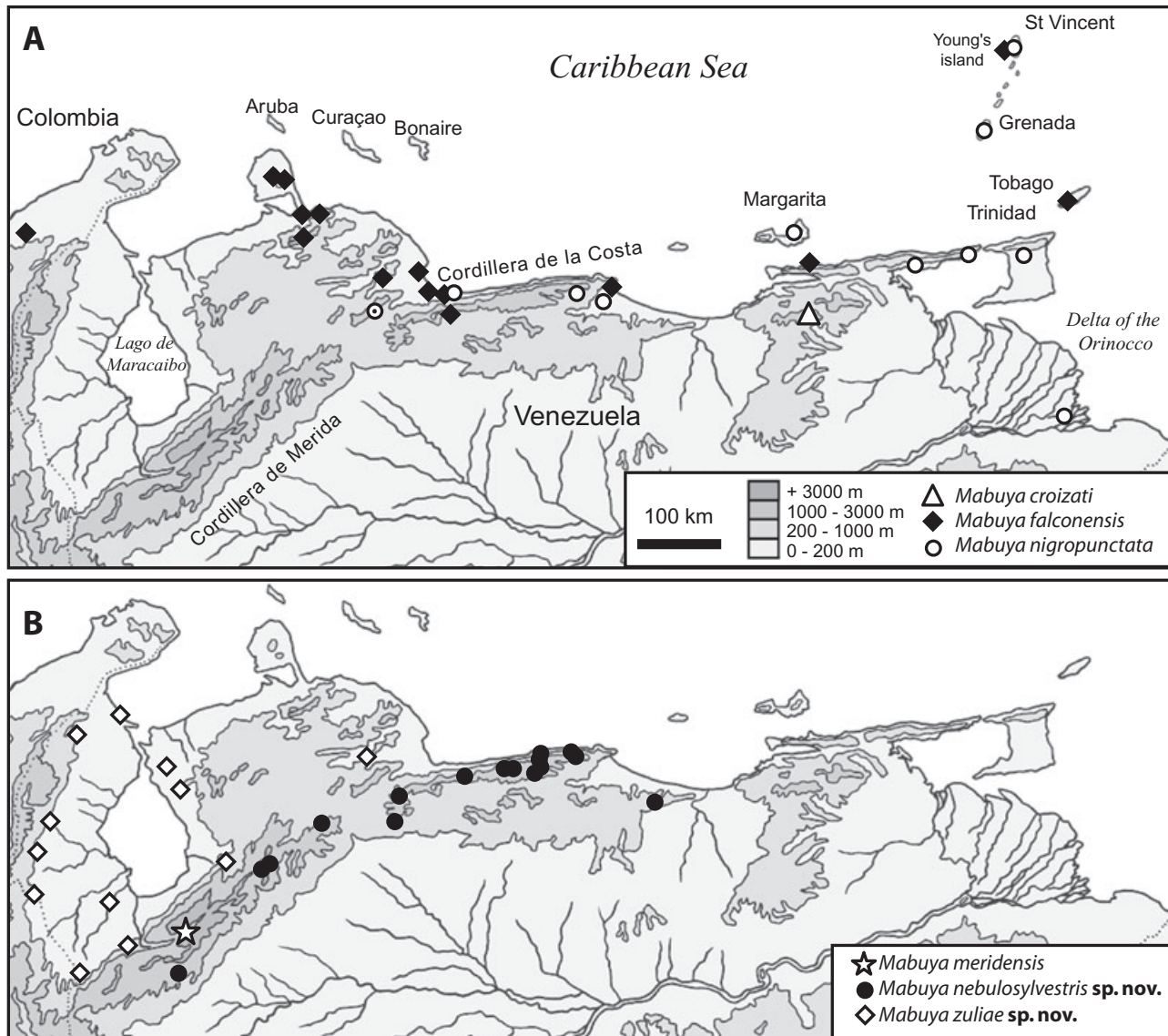


Figure 3. Distribution of (A) *Mabuya croizati*, *Mabuya falconensis*, *Mabuya nigropunctata* (in part; the only locality, based on the bibliography of Lotzkat, 2007, is represented by a white circle with a black dot), and (B) distribution of *Mabuya meridensis*, *Mabuya nebulosylvestris* sp. nov., and *Mabuya zuliae* sp. nov.

DISCUSSION

MOLECULAR TAXONOMY OF THE GENUS *MABUYA*

Central American *Mabuya* (*M. unimarginata* complex) represent a strongly supported monophyletic unit. However, the genetic divergence observed within this clade is relatively high, and, surprisingly, the highest divergence value observed for cytochrome *b* (9.29%) was between two geographically proximate populations, from the states of Guerrero and Oaxaca, Mexico (Table 2). These data suggest that *M. unimarginata* constitutes a species complex, which would explain in part the taxonomic confusion for this group

(Burger, 1952; Taylor, 1956; Lee, 1996; Köhler, 2003). A molecular and morphological revision focusing on this complex is currently in preparation to clarify its problematic status.

Mabuya falconensis, endemic to the xerophytic area of the Caribbean coast of South America (Venezuela and Colombia; Miralles, Rivas & Barrios-Amorós, 2005), is the sister species of the Central American *M. unimarginata* complex. A previously published 12S sequence for a specimen from Tobago Island (ZFMK 62603, assigned to *M. mabouya* by Mausfeld *et al.* 2002) is herein reallocated to *M. falconensis* (Fig. 4; Table 2). The examination of the specimen ZFMK

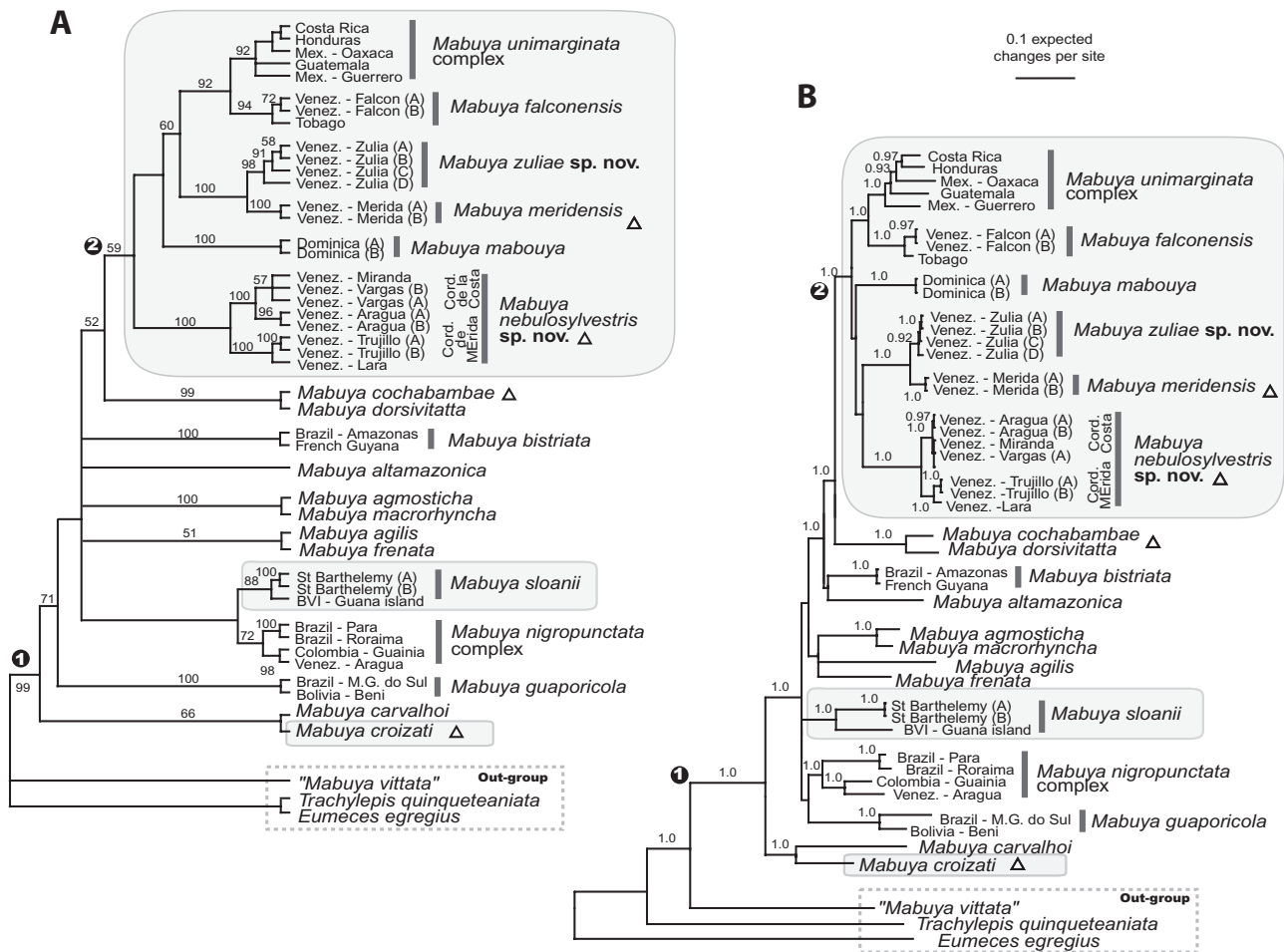


Figure 4. Phylogenetic trees of the genus *Mabuya* obtained from 12S and cytochrome *b* sequences. A, cladogram of the strict consensus maximum parsimony (MP) tree with bootstrap values (1000 replicates; bootstrap proportions less than 50% are not shown). B, Bayesian analysis, with 50% majority rule consensus (posterior probabilities below 0.90 are unmarked). The most remarkable nodes are: (1) the genus *Mabuya* s.s. (exclusively neotropical clade) and (2) the Caribbean clade. Grey rectangles represent clades endemic to the Caribbean region. Mountain species are marked with triangles so as to be distinguishable from lowland species. Abbreviations: Mex., Mexico; Venez., Venezuela.

62603 (plus ZFMK 62602, from the same locality) strongly supports these molecular results, with both specimens exhibiting a combination of characteristics conspicuously attributable to *M. falconensis* (paired prefrontals and frontoparietals, parietal plates in contact with each other behind the interparietal plate, a single pair of nuchals, four light-coloured supraciliaries, with the second being the longest, a faded coloration, with ill-defined dark lateral stripes, and with dorsolateral light stripes being absent, the presence of some roughly triangular brown dots on the back, and palms and soles light in colour; Mijares-Urrutia & Arends, 1997; Miralles, Rivas & Barrios-Amorós, 2005). The Tobago record considerably extends the distribution of this putative mainland species to the east (Fig. 3A). Although puzzling, such

a pattern of discontinuous geographic distribution (presence on the mainland and Tobago, but absence from the intermediate island of Trinidad) is apparently shared by another reptile, *Atractus univittatus* (Jan, 1862), and an amphibian, *Hyalinobatrachium orientale* (Rivero, 1968) (Murphy, 1997). The historical and/or ecological factors that have produced this repeated pattern remain unclear, but are worthy of investigation. Additionally, a single specimen (MCZ 38196) collected on Young's Island (an islet off St Vincent Island, Lesser Antilles) fits remarkably well with the description of *M. falconensis*. This locality is relatively far from Tobago (more than 200 km away), and as such represents a remarkable extension for the range of *M. falconensis* to the north, and would need to be confirmed by additional specimens.

Table 2. Summary of the genetic divergence (uncorrected p distances) for the cytochrome *b* and 12S rRNA sequences

| Taxa | | cyt <i>b</i> | 12S |
|----------------------------------|-----------------------|--------------------|-------------------|
| Interspecific distances | Min–max: | 4.08–17.51 | 0.53–12.03 |
| within the genus | Mean \pm σ : | (13.71 \pm 1.76) | (7.11 \pm 1.99) |
| <i>Mabuya</i> | <i>N</i> : | (153) | (174) |
| Distances between <i>M.</i> | Min–max: | 8.76–11.10 | 2.94–5.08 |
| <i>falconensis</i> and <i>M.</i> | <i>N</i> : | (10) | (10) |
| <i>unimarginata</i> | | | |
| Distances between <i>M.</i> | Min–max: | 4.08–4.40 | 0.53–1.07 |
| <i>meridensis</i> and <i>M.</i> | <i>N</i> : | (8) | (8) |
| <i>zuliae</i> sp. nov. | | | |
| Distances within the | Min–max: | 5.28–9.29 | 2.41–4.03 |
| <i>M. unimarginata</i> | <i>N</i> : | (10) | (10) |
| complex species | | | |
| Distances between the | Min–max: | 4.01–4.55 | 1.34–1.61 |
| ‘cordillera de Merida’ | | | |
| clade and the | | | |
| ‘cordillera de la | <i>N</i> : | (15) | (15) |
| costa’ clade of <i>M.</i> | | | |
| <i>nebulosylvestris</i> sp. | | | |
| nov. | | | |
| Distances between | Value: | – | 0.81 |
| Venezuelan <i>M.</i> | | | |
| <i>falconensis</i> and the | <i>N</i> : | | (2) |
| specimen from | | | |
| Tobago island. | | | |

N, number of comparisons; min and max: minimal and maximal values.

The Antillean skinks, *M. mabouya* and *M. sloanii* clearly represent distinct species, given that they are not in the same clade. This result, together with the morphological observations by Miralles (2005), categorically rejects treating these two taxa as conspecific, as was previously suggested by Mayer & Lazell (2000).

Recently, a molecular phylogeny of the South American *Mabuya* was published by Whiting *et al.* (2006). One part of this study dealt with the relationships within the Guyano–Amazonian *M. nigropunctata* species complex (incorrectly called *M. bistriata* by Whiting *et al.* 2006; see nomenclatural explanations in Miralles, Rivas & Barrio-Amorós, 2005). Their study, contrary to what we expected based on morphology (see below), suggested that the *M. nigropunctata* complex was not monophyletic with the inclusion of *M. carvalhoi*. On the contrary, our molecular results show that *M. carvalhoi* is not nested within the *M. nigropunctata* complex, but is rather the sister species to *M. croizati*, forming the basalmost clade of the genus (*s.s.*). Furthermore, our results support the monophyly of the *M. nigropunctata* complex, although we acknowledge that better sampling is needed to test this notion rigorously. A close relationship between *M. carvalhoi* and *M. cro-*

izati was previously hypothesized, based on putative synapomorphies including an acute snout, the presence of secondary nuchal scales, the fusion of frontoparietals, and the presence of two wide dark dorsal stripes (Rebouças-Spieker & Vanzolini, 1990; Miralles, Rivas & Barrio-Amorós, 2005). Interestingly, the close relationship between *M. carvalhoi* and *M. croizati* is consistent with Steyermark’s (1966, 1974) observations (see also Schargel, Fuenmayor & Myers, 2005), who noted that many plant species in montane habitats of the Coastal mountain range of Venezuela, and especially in mount Turimiquire (from where *M. croizati* is endemic) are closely related to species in the Guiana Shield (to which *M. carvalhoi* is restricted). Steyermark (1974) first suggested a past connection between the biota of these two regions, which supposedly began during the Cretaceous, but later indicated that this connection was likely to have occurred during one of the humid phases of the Pleistocene (Steyermark, 1979). The contradiction between our results and those published by Whiting *et al.* (2006) prompted us to start a wide molecular phylogeographic study, focusing on these Guyano–Amazonian taxa. We are currently working on another paper, which endeavours to determine the main causes of incongruence between both studies.

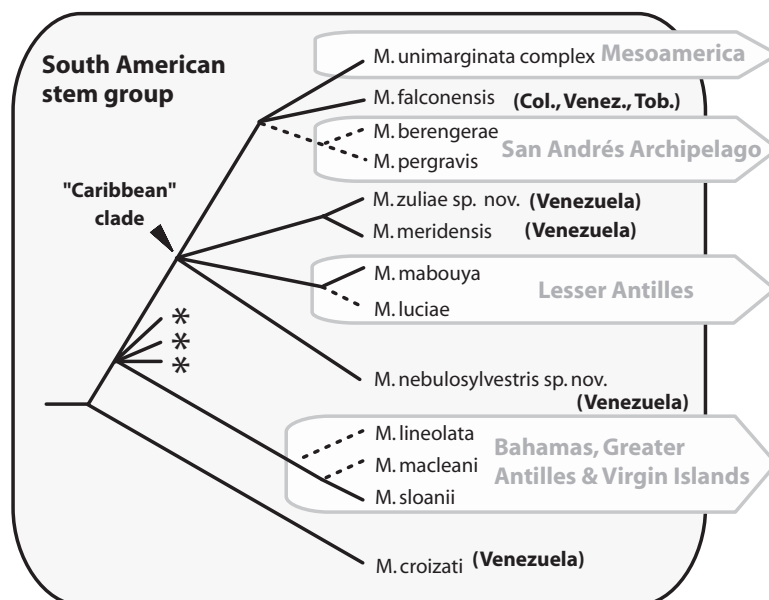


Figure 5. Hypothetical phylogenetic relationships between the species of *Mabuya* endemic to different subregions of the Caribbean area (white arrows) and the South American stem group (shown on the grey background). Asterisks represent all the other South American species that are not restricted to the Caribbean coast. This synthetic tree was realized by combining molecular results and both biogeographical and morphological data. Both categories of groupings should be distinguished, according to their respective reliability: (1) black lines, groupings supported by molecular data; (2) dashed lines, hypothetical groupings, based on overall similarity, putative synapomorphies, and biogeographic distributions (Mayer & Lazell, 2000; Miralles, 2005, 2006; this study). Abbreviations: Col., Colombia; Tob., Tobago; Venez., Venezuela.

DISPERSAL OF THE GENUS *MABUYA* THROUGHOUT THE NEOTROPICS

Many recent molecular studies have supported the monophyly of the genus *Mabuya* s.s. (Mausfeld *et al.*, 2002; Carranza & Arnold, 2003; Whiting *et al.*, 2006). However, these studies had limited South American representation. Herein, we complement previous studies by showing that *Mabuya* s.s. remains a strongly monophyletic group when middle American and Caribbean taxa are included. Based on the topologies recovered here, the first diversification of the genus *Mabuya* is likely to have occurred in South America, because all species from this continent constitute the stem group of the genus (progression rule principle, Humphries, 1992).

Invasion of the Antillean Archipelago by the genus *Mabuya* represents a minimum of two distinct south-to-north dispersal events that have resulted in diversification: (1) the *M. sloanii* lineage, which is only present in the Bahamas, the Greater Antilles, and the extreme northern part of the Lesser Antilles; and (2) the *M. mabouya* clade (with inclusion of its sister species, *M. luciae*), which is (or was) present in the Lesser Antilles, from St Lucia to Anguilla.

Additionally, some invasions of Caribbean islands by species widely distributed in the mainland have also occurred: the Guyano–Amazonian *M. nigropunc-*

tata species complex has successfully invaded Isla Margarita, Trinidad, Grenada, and St Vincent Island (Miralles, Rivas & Barrio-Amorós, 2005; this study), whereas *M. falconensis* has reached Tobago (and presumably Young's Island). These last two invasions seem to be more recent, given that the insular populations do not seem to have differentiated at the species level, based on both molecular and morphological evidence, and are restricted to the southernmost islands of the Archipelago, which are relatively close to the mainland (Fig. 3A).

EVOLUTION OF THE ALTITUDINAL DISTRIBUTION OF THE GENUS *MABUYA*

Genetic divergences between *M. meridensis* and *M. zuliae* sp. nov. vary from 3.87 to 4.42% at cytochrome *b*, and from 0.54 to 1.07% at 12S. Such values are relatively low, and are usually obtained with intraspecific rather than interspecific comparisons (Table 2). However, these two closely related species have diverged substantially in their respective ecological niches. The altitudinal distribution of both species is disjunct: *M. meridensis* is a montane species (always found above 1300 m a.s.l., and reaching at least 2300 m a.s.l.) endemic to the upper drainage of the Chama River, whereas *M. zuliae* sp. nov. is restricted

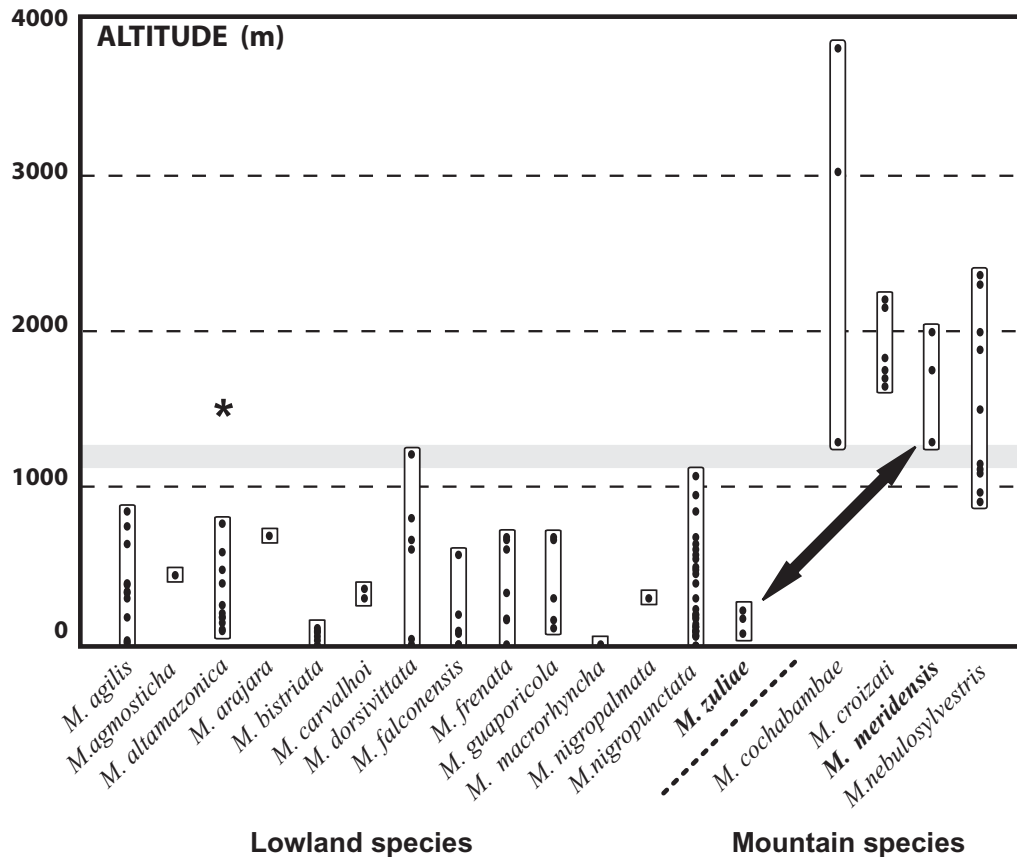


Figure 6. Altitudinal distribution of the South American species of *Mabuya*. Each dot corresponds to the altitude of a locality of specimens examined, or to data found in the following references: De la Riva, Castroviejo & Cabot, 1992; Dunn, 1936; Rebouças-Spieker & Vanzolini, 1990; Mijares-Urrutia & Arends, 1997; Rodrigues, 2000; Mausfeld & Lötters 2001. *'Unexpected' locality of a putative specimen of *Mabuya altamazonica* Miralles, Barrio-Amorós, Rivas & Chaparro-Auza, 2006.

to the lowlands and foothills of the Lake Maracaibo Basin, which is one of the warmest Venezuelan regions (annual, mean monthly minimum–maximum temperatures in Maracaibo city of 22.8–35.0 °C, versus 14.4–26.6 °C at Mérida city; <http://www.worldweather.org>). Interestingly, examination of the altitudinal distributions of the different species in the genus clearly shows a bimodal distribution (Fig. 6): lowland species rarely surpass 1000–1200 m a.s.l., whereas montane species are rarely found below this elevation. No known species of *Mabuya* is distributed across both ranges of altitude. This suggests that such a hypothetically broad ecological niche is constrained in this group, and it supports the distinctiveness of *M. meridensis* and *M. zuliae* sp. nov. Furthermore, examination of the topologies obtained here (Fig. 4) reveals that the common ancestor of the genus was likely to have been a lowland species, and that the colonization of montane habitats occurred at least three (perhaps four) times, independently, generally corresponding to each species of montane

Mabuya: (1) *M. cochabambae*, (2) *M. croizati*, (3) *M. meridensis*, and possibly (4) *M. nebulosylvestris* sp. nov. We cannot determine here if *M. meridensis* and *M. nebulosylvestris* sp. nov. represent two distinct events of altitudinal colonization, or a single event having been followed by a return to the ancestral condition for *M. zuliae* sp. nov. (the sister species of *M. meridensis*, which is restricted to the lowlands), as both hypotheses are equally parsimonious. It is possible that an exceptional degree of placentotrophy in *Mabuya* (type IV), which is very close to that of eutherian mammals (Blackburn & Vitt, 1992), has allowed this group to easily colonize a wide spectrum of thermally different environments, because it eliminates the constraints determined by the availability of microhabitats with suitable temperatures for egg incubation. This idea is consistent with the proposal that the evolution of viviparity in lizards has been driven by the selective advantages accruing from the maternal regulation of incubation temperatures (Webb, Shine & Christian, 2006).

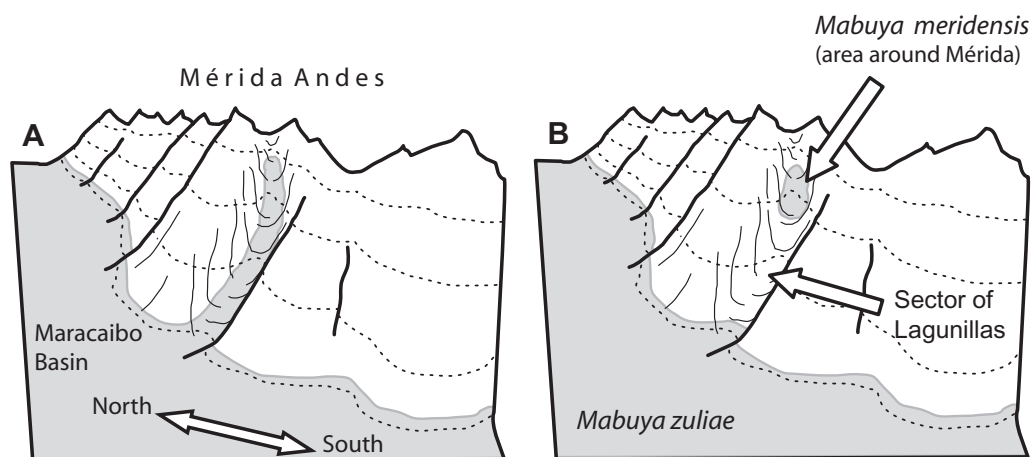


Figure 7. Scenario of allopatric speciation along the valley of Mérida: (A) putative distribution (in grey) of the common ancestor of *Mabuya meridensis* and *Mabuya zuliae* sp. nov., and (B) present-day distribution of both species, separated by the xerophytic enclave of Lagunillas.

A hypothesis restricted to the region of the Chama River valley is proposed here to explain the divergence of *M. meridensis* and *M. zuliae* sp. nov. This valley is a long and narrow corridor between two elevated mountainous ridges (> 4000 m a.s.l.), which progressively decline in elevation from the hills above Mérida city (\pm 3000 m a.s.l.) to the Maracaibo Lake Basin lowlands (at sea level). This river drainage valley may have served as a bridge between the distributions of *M. meridensis* (surrounding Mérida) and *M. zuliae* sp. nov. (Maracaibo Basin). Currently, the genus is unknown from the intermediate central portion of the valley (called the 'semi-arid enclave of Lagunillas' by La Marca & Soriano, 2004), which is probably because of its characteristic xerophytic microclimate (both *M. meridensis* and *M. zuliae* sp. nov. are restricted to moister biotopes). We hypothesize here that the common ancestor of both species would have been continuously distributed from the Maracaibo Basin to within the vicinity of the present-day city of Mérida, located 50 km uphill from the valley (Fig. 7A). Then, a confined climatic change would have induced xerification of the Lagunillas sector, and consequently isolated the two populations by vicariance (Fig. 7B). The cause of this putative climatic change is undetermined, but the low genetic divergence observed between these species suggests that it would have been relatively recent on the geological time scale.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Abbreviations of the museums collections cited.

Appendix S2. Additional specimens examined (*N* total = 266).

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