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Molecular phylogenetics and biogeography of the Neotropical skink genus *Mabuya* Fitzinger (Squamata: Scincidae) with emphasis on Colombian populations [☆]

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ABSTRACT

Understanding the phylogenetic and geographical history of Neotropical lineages requires having adequate geographic and taxonomic sampling across the region. However, Colombia has remained a geographical gap in many studies of Neotropical diversity. Here we present a study of Neotropical skinks of the genus *Mabuya*, reptiles that are difficult to identify or delimit due to their conservative morphology. The goal of the present study is to propose phylogenetic and biogeographic hypotheses of *Mabuya* including samples from the previously under-studied territory of Colombia, and address relevant biogeographic and taxonomic issues. We combined molecular and morphological data sampled densely by us within Colombia with published data representing broad sampling across the Neotropical realm, including DNA sequence data from two mitochondrial (12S rRNA and cytochrome b) and three nuclear genes (Rag2, NGFB and R35).

To evaluate species boundaries we employed a general mixed Yule-coalescent (GMYC) model applied to the mitochondrial data set. Our results suggest that the diversity of *Mabuya* within Colombia is higher than previously recognized, and includes lineages from Central America and from eastern and southern South America. The genus appears to have originated in eastern South America in the Early Miocene, with subsequent expansions into Central America and the Caribbean in the Late Miocene, including at least six oceanic dispersal events to Caribbean Islands.

We identified at least four new candidate species for Colombia and two species that were not previously reported in Colombia. The populations of northeastern Colombia can be assigned to *M. zuliae*, while specimens from Orinoquia and the eastern foothills of the Cordillera Oriental of Colombia correspond to *M. altamazonica*. The validity of seven species of *Mabuya sensu lato* was not supported due to a combination of three factors: (1) non-monophyly, (2) <75% likelihood bootstrap support and <0.95 Bayesian posterior probability, and (3) GMYC analysis collapsing named species. Finally, we suggest that *Mabuya sensu stricto* may be regarded as a diverse monophyletic genus, widely distributed throughout the Neotropics.

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1. Introduction

The Neotropical realm comprises one of the largest reservoirs of terrestrial biodiversity (Maiti and Maiti, 2011; Santos et al., 2009). Much of the biological diversity in the Neotropics remains undescribed, with large areas still lacking intensive sampling, especially in South America. This sampling gap is particularly evident in Colombia, which remains a 'black box' regarding the systematics of many groups, despite its key geographical position in the

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historical exchange of faunas between North and South America (Simpson, 1940; Cody et al., 2010; Pinto-Sánchez et al., 2012). Sampling Colombian populations may help to clarify the evolutionary history, systematics, and biogeography of Neotropical lineages. In this paper we present new morphological and DNA sequence data from samples of the lizard genus *Mabuya* obtained from Colombia and combine this information with previously published data (Mausfeld, 2000; Carranza and Arnold, 2003; Miralles et al., 2006, 2009; Whiting et al., 2006; Miralles and Carranza, 2010; Hedges and Conn, 2012) in order to provide the most complete combined gene tree hypothesis of the genus.

Mabuya was first described by Fitzinger (1826) as a circumtropical genus of skinks (Squamata: Scincidae). Subsequently, a comprehensive taxonomic and systematic revision of *Mabuya* from the Americas was completed by Dunn (1935), who recognized nine Neotropical species, including *M. mabouya*, a species originally thought to be widely distributed throughout Central America, South America and the Caribbean islands. The genus was subsequently divided into four genera based on congruence between molecular phylogenetic results and the continental distributions of the inferred clades (Mausfeld et al., 2002), restricting *Mabuya* to the Neotropics. The populations from the Antilles, Central America, and much of the South American mainland (aside from Colombia) have been relatively well sampled and well-studied (Miralles et al., 2005a, 2006, 2009b; Vrcibradic et al., 2006; Whiting et al., 2006; Harvey et al., 2008; Miralles and Carranza, 2010; Hedges and Conn, 2012). Based on molecular evidence, Miralles and Carranza (2010) recognized the existence of at least 28 species within *Mabuya*. More recently, Hedges and Conn (2012) reviewed the systematics of *Mabuya* and proposed taxonomic changes involving the splitting of this Neotropical taxon into 16 genera, describing 24 new species, along with a new phylogenetic classification for Scincidae, elevating the genus *Mabuya* (*sensu* Mausfeld et al., 2002) to family level (Mabuyidae). Nevertheless, this last point remains controversial (Pyron et al., 2013; Lambert et al., 2015). Therefore, for present purposes, the name *Mabuya* is used to refer to the whole Neotropical lineage *sensu* Mausfeld et al. (2002).

Despite these recent molecular and taxonomic studies of *Mabuya*, Colombian populations have not been well studied. The Colombian territory is geographically highly heterogeneous, with three Andean mountain ranges, Pacific rainforests, Caribbean deserts and Amazonian jungles. Colombia's geographical position is also crucial to understanding the past biotic exchanges between Central America, South America and Caribbean islands. Four nominal species of *Mabuya* are currently known to occur in Colombia: two mainland species, (1) *M. nigropunctata*, a widely distributed Guyano-Amazonian species, also present in the Colombian Amazonia, (2) *M. falconensis*, endemic to the dry Caribbean coast of South America, present in the Guajira Peninsula, plus two insular species of the San Andrés Archipelago in the western Caribbean, (3) *M. pergravis*, endemic to Providence Island and (4) *M. berengeriae*, endemic to San Andrés Island (Miralles et al., 2005a, 2006). Additional populations from the lowlands of Colombia were originally assigned to *M. mabouya* (Dunn, 1935; Jerez and Ramírez-Pinilla, 2003). Subsequent studies, however, revealed that *M. mabouya sensu lato* was actually a paraphyletic complex of species hardly distinguishable due to their conservative morphology. Currently, *M. mabouya* is recognized as endemic to the Lesser Antilles, leaving several distinct populations from northern South America unassigned to any described species (Miralles et al., 2010). These populations remain enigmatic from a taxonomic point of view, and their relationship to other species in South America, Central America, and the Caribbean region, remains unresolved.

Skinks of the genus *Mabuya* exhibit a highly conservative morphology (Miralles, 2005; Miralles et al., 2006) and species

delimitation within this group is somewhat complicated and controversial. In the present study, we employ a molecular phylogenetic approach, combining samples from Colombia with previously published data to investigate species-level relationships and to infer the timing of diversification and biogeographical patterns within *Mabuya*. We also used new and published morphological character data to compare *Mabuya* species from Colombia. We addressed the following three main objectives: (1) to place populations of *Mabuya* from Colombia within a larger phylogenetic framework, (2) to propose and implement a new interpretation of the GYMC method to detect possible taxonomic alpha-error (type I error, or false positive concerning an hypothetical species boundary), and (3) to propose a biogeographic hypothesis of the origin and spread of the genus *Mabuya* throughout South America, Central America and the Caribbean islands.

2. Materials and methods

2.1. Sampling

Molecular data included DNA sequences from 250 specimens of *Mabuya*, of which 111 were collected for this study (Fig. 1, Appendix A), and 139 were downloaded from GenBank (Appendix A, Supplementary material Fig. S1). Five additional samples were included as outgroups: *Pleistodon egregious*, *P. laticeps*, *Trachylepis capensis*, *T. perrotetii* and *T. vittata*. The two former species were used as outgroup in Miralles and Carranza (2010) and Hedges and Conn (2012), respectively, and in each case were chosen based on a previous phylogenetic study of Scincidae that recovered *Mabuya* as the sister genus of *Trachylepis*, which together formed the sister clade to *Pleistodon* (Carranza and Arnold, 2003). Information on the locality, voucher availability and GenBank accession numbers for all sequences used in this study are provided in Appendix A.

We examined 13 morphological characters from 111 vouchered individuals of *Mabuya*, and preliminarily assigned them to previously described species when possible. Morphological characters examined here were those routinely used in taxonomy of Scincidae: (1) scale counts, (2) presence or absence of homologous scale fusions, and (3) the variability in color patterns. Definition of morphological characters followed Avila-Pires (1995). Collected specimens were deposited in the Museo de Historia Natural of the Universidad Industrial de Santander, Colombia (UIS-R), the Instituto de Ciencias Naturales at the Universidad Nacional de Colombia (ICN-R), and Museo de Historia Natural ANDES at the Universidad de los Andes, Bogotá (ANDES-R). All specimens were fixed in 10% formalin and preserved in 70% ethanol.

2.2. Molecular laboratory methods

We sequenced fragments of two mitochondrial genes, cytochrome b (Cytb) and the 12S ribosomal RNA subunit (12S), and three nuclear genes, the recombination activating gene 2 (Rag2), nerve growth factor beta polypeptide (NGFB) and RNA fingerprint protein 35 (R35). These nuclear genes have proven useful previously to resolve the phylogenetic relationships of skinks at the population and species level (Crottini et al., 2009; Linkem et al., 2011). We obtained DNA from hepatic and muscular tissue stored in 99% ethanol. DNA was isolated using an ammonium acetate extraction protocol (Fetzner, 1999) or DNeasy Blood and Tissue Kit (Qiagen). Polymerase chain reaction (PCR) was performed in 30 µl reaction volumes containing 15 µl GoTaq green master mix, 0.7 µl each of forward and reverse primers at 10 µM, 10.6 µl ddH₂O and 3 µl of extracted DNA (more for low-quality extractions). The primers and PCR conditions used are presented in

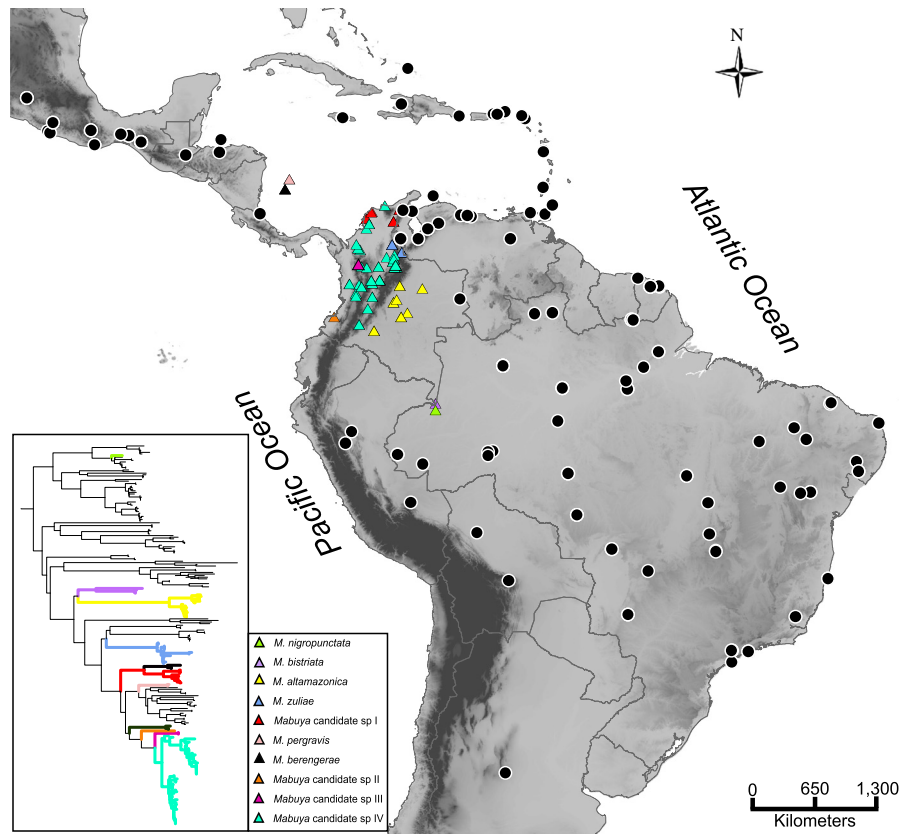


Fig. 1. Map of South America showing sampled localities for *Mabuya*. Colored triangles represent localities from which new data were obtained for the present work, while black circles represent localities corresponding to data obtained from GenBank. Colors of each triangle correspond to colored lineages in phylogenetic tree shown in inset. Tree is same as in Fig. 2, with colored branches corresponding to colored symbols on map. Names of each colored lineage are provided in legend. Darker shading on map indicates increased elevation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Supplementary material Table S1. PCR products were cleaned using ExoI and SAP digestion (Werle et al., 1994). For each individual, the heavy and light chains of each amplicon were sequenced directly using an ABI Prism 3100 automated sequencer (PE Applied Biosystems).

Appendix A includes detailed information with GenBank accession numbers. DNA sequence alignments (see below) are available at TreeBASE (<http://www.treebase.org>) under Study ID SNNN [TreeBASE Study IDs will be made available upon acceptance of MS]. All DNA and collection data may also be found at Barcode of Life Data Systems (<http://www.boldsystems.org>; Ratnasingham and Hebert, 2007) under project code MABUY [BoLD project will be made public upon acceptance of MS].

2.3. Phylogenetic analyses and divergence time estimation

DNA sequences were edited using Geneious 3.7.0 (Biomatters Ltd.). The multiple sequence alignment was performed with MAFFT version 6 (Katoh et al., 2005) using the default parameters. We implemented parsimony, maximum likelihood (ML), and Bayesian criteria to infer phylogenetic relationships. Topologies inferred in preliminary phylogenetic analyses of each gene were compared to detect strongly supported nodes of incongruence among genes prior to multi-locus analyses (Cunningham, 1997).

Parsimony analyses were performed on concatenated gene sequence alignments via heuristic tree searches with 10,000 random addition sequence replicates followed by tree searching using the tree bisection and reconnection (TBR) pruning algorithm as implemented in PAUP* version 4.0b10 (Swofford, 2002) provided by the CIPRES portal (Miller et al., 2010). Clade support values were estimated through 5000 non-parametric bootstrap replicates

(Felsenstein, 1985), each having 20 random addition sequence replicates and TBR branch swapping.

As our combined data set was comprised of one protein-coding mitochondrial gene (Cytb), one ribosomal gene with secondary structure (12S), and three nuclear protein-coding genes (Rag2, NGFB, R35), we used the software PartitionFinder (Lanfear et al., 2012) to select via the corrected Akaike Information Criterion (AICc) substitution models and partitioning schemes prior to ML and Bayesian analyses (Lanfear et al., 2012). Partitions were defined a priori based on gene identity (12S, Cytb, Rag2, NGFB, R35) and codon position. We evaluated four distinct partitioning strategies, including a 2-way partition by genome, 4-way partition with combined mitochondrial and each nuclear gene separately, 5-way partition by gene, and a 14-way partition by gene, codon position and secondary structure (Supplementary material Table S2). The stem and loop secondary structures of the aligned 12S rRNA gene were identified and coded following Titus and Frost (1996).

We performed ML phylogenetic inference and non-parametric bootstrapping using the program RAXML v 2.1.3 on the CIPRES portal (Stamatakis, 2006) and assuming the partition scheme recommended by PartitionFinder. We performed Bayesian phylogenetic analysis using BEAST version 2.1.3 (Bouckaert et al., 2014) also implemented in the CIPRES portal and assuming the same partition scheme recommended above with PartitionFinder. We simultaneously inferred the posterior distribution of trees and estimated divergence times assuming a relaxed clock model of evolution, allowing substitution rates to vary among branches according to a lognormal distribution (Drummond et al., 2006) and assuming a calibrated Yule model tree prior, i.e., a constant speciation rate per lineage (Heled and Drummond, 2012).

Following Hedges and Conn (2012), we used three calibration points. The first calibration point corresponded to the divergence of allopatric species between Carrot rock and other Virgin Islands, the second point was the divergence between Greater and Lesser Antillean species, and the third point was the divergence between African and American species (see Supplementary material Table S3). Priors on divergence times for these three nodes were assumed to follow log-normal distributions (Heled and Drummond, 2012), see Supplementary material Table S3 for further details. To explore the sensitivity of the resulting divergence time estimates to our priors placed on each of the three nodes, we performed cross validation by running three additional analyses removing, in turn, one of our three calibration points and observing the changes in the posterior distribution of divergence times at other key nodes of interest on the tree. The problem with using geological events such as island formation to calibrate a phylogenetic tree is that present-day oceanic islands might be just the most recent element of a series of oceanic island formations over time in a particular region, which would invalidate their use as reliable calibration constraints (Heads, 2005). In order to manage this problem we use two strategies: (1) we use a wide prior time interval to provide more conservative age estimation, and (2) we performed cross validation among the calibration points (see above) in order to understand the effect of each calibration point on node ages.

MCMC phylogenetic analyses were run for 100 million generations saving one sampled tree every 10,000 generations. The first 1000 trees were discarded as burn-in. In two searches the convergence and stationarity of the Markov process were evaluated by the stability and adequate mixing of sampled log-likelihood values and parameter estimates across generations, as visualized using Tracer 1.6 (Rambaut and Drummond, 2004). Using Tracer, we also confirmed that our post-burn-in set of trees yielded an effective sample size (ESS) of >200 for all model parameters.

2.4. Species delimitation

The second goal of this study was to reassess species boundaries within the Neotropical genus *Mabuya sensu lato*, using an expanded data set in terms of molecular markers and geographic sampling). We employed the following guidelines for species delimitation, which combined the criteria of monophyly and genetic divergence. First, we used our phylogenetic tree topology to identify non-monophyletic species or genera that we then flagged as unsupported and applied statistical tests of topology (see below). If the group was monophyletic we then looked for groups with high clade support, i.e., parsimony and likelihood bootstrap support $\geq 75\%$ and Bayesian posterior probability ≥ 0.95 , as unconfirmed candidate species (Padiál et al., 2010). We then checked for minimal genetic divergences of 1.0% at 12S and 5% divergence at Cytb. Although the specific levels of statistical support and levels of genetic divergence are arbitrary, our goal was simply to flag well-supported monophyletic clades with a notable genetic divergence as candidate species (Padiál et al., 2010).

To evaluate possible taxonomic over-splitting, we used a new approach to detect 'type I error' or taxonomic overestimation *sensu* Padiál et al. (2010). Two types of errors are possible in taxonomy: the 'true' number of species may be over-estimated by identifying distinct species where there is intraspecific character variation only (type I error or false positive), or on the other hand, the 'true' diversity might be under-estimated by failing to detect cryptic or young species ('type II error' or false negative). A trade-off exists between the risk of type I errors using overly sensitive methods and the risk of type II errors using more stringent methods with lower taxonomic resolving power (Miralles and Vences, 2013).

Monophyletic taxonomic units that were differentiated by very little genetic divergence were further evaluated for possible taxonomic inflation by using the general mixed Yule coalescent (GMYC) method for species delimitation (Pons et al., 2006) as implemented in the SPLITS package for R and applied to a timetree based on mitochondrial DNA sequence data. The timetree was obtained using Bayesian phylogenetic inference implemented in BEAST, as outlined above. The GMYC method was designed for single-locus data, namely mitochondrial DNA markers, and is based on the difference in branching rates between deeper speciation rates (a Yule process) versus within-population rates of coalescence across a genealogy (an exponential process; Pons et al., 2006). We used a likelihood ratio test to compare two GMYC models. The first is the single threshold model which assumes that the point of temporal transition between speciation rates versus coalescence rates is the same within each clade on the tree. The second is a multiple-threshold model (Monaghan et al., 2009) which allows clades to have different transition points between inter and intra-specific branching rates, as determined by re-analyzing each 'cluster' (or potential species) identified by the single-threshold method to evaluate whether better likelihoods may be obtained by dividing clusters or fusing potential sister lineages.

The GMYC method is among the most sensitive methods of species delimitation but is prone to overly splitting lineages and over-estimating the total number of species (Miralles and Vences, 2013; Paz and Crawford, 2012). The number of clusters identified by the GMYC method should therefore be regarded as an upper bound on the estimated number of distinct undescribed species, depending on support from other available taxonomy (Miralles and Vences, 2013; Saltler et al., 2013; Gehara et al., 2014). We therefore propose to use this method to detect type I errors in species delimitation. If multiple named species fall within a single coalescent cluster identified by GMYC, and in the absence of any other supporting evidence, such as diagnostic morphological characters, these named species should likely be synonymized. Quantifying the rate of type I error in taxonomy (false positives or excessive splitting) is more difficult than quantifying the rate of type II error (false negatives or excessive lumping), thus excessive splitting produced by inflationist approaches may be difficult to detect (Carstens et al., 2013; Miralles and Vences, 2013).

A previous study on Malagasy skinks has shown that GMYC minimizes the type II error (false negative) rate while probably causing an increase in the type I error (false positive) rate (Miralles and Vences, 2013). In other words, an appreciable number of valid species tends to be split by GMYC in conflict with several other lines of taxonomic evidence. On the other hand, if GMYC fails to recognize the distinctiveness of two named lineages, such a negative result may be considered strong evidence that only one specific lineage is present, at least from the perspective of mtDNA (Miralles and Vences, 2013). Following a conservative approach to integrative taxonomy (*sensu* Padiál et al., 2010), we prefer type II over type I errors, i.e., better to fail to delimit a couple of species than to falsely circumscribe many evolutionary units that do not represent actual or candidate species (Carstens et al., 2013; Miralles and Vences, 2013). For this reason, we propose to use the GMYC species delimitation method in a slightly different way than usually presented in the literature, i.e., as support for lumping rather than for splitting.

2.5. Topological tests

The present paper also aimed to assess the validity of genera within *Mabuya sensu lato* newly proposed by Hedges and Conn (2012). To test the statistical support for the non-monophyly of all species and genera not recovered as monophyletic in the ML

tree (see above), we conducted constrained ML tree searches in which the genus or species in question was constrained to be monophyletic. Tests of monophyly were conducted independently for each species or genus in question, and constraint trees were made using MacClade 4.08 (Maddison and Maddison, 2005). The likelihood of the constrained topology was compared to that of the unconstrained ML topology using the paired-sites test (SH) of Shimodaira and Hasegawa (1999) and the approximately unbiased (AU) test of Shimodaira (2002) as implemented in PAUP*. The significance of the difference in the sum of site-wise log-likelihoods between constrained and unconstrained ML trees was evaluated by resampling estimated log-likelihoods (RELL bootstrapping) of site scores with 1000 replicates, then calculating how far a given observed difference was from the mean of the RELL sampling distribution (Shimodaira and Hasegawa, 1999). The AU test is based on a multiscale bootstrap (Shimodaira, 2002), and the SH and AU tests are conservative tests of tree topology (Crawford et al., 2007; Felsenstein, 2004).

2.6. Ancestral area reconstruction

We used ancestral area reconstruction to estimate the region of origin of each clade, and the number and direction of dispersal events between Central America, South America and the Caribbean islands (with dispersal dates inferred from the timetree obtain above) using likelihood to infer geographic-range evolution through a model of dispersal, local extinction and cladogenesis (DEC). Biogeographic shifts among nine regions were estimated under maximum likelihood with LAGRANGE version 20130526 (Ree and Smith, 2008). Reconstructions in which the most likely state had a proportional marginal likelihood of 0.95 or greater were considered unambiguous. Because LAGRANGE can accommodate a maximum of nine regions, we assumed and analyzed independently two contrasting sets of nine a priori defined regions. First, we used four regions of high amphibian endemism (Duellman, 1999) to represent South America: (1) Andes, (2) Caribbean Coastal Forest + Llanos, (3) Cerrado-Caatinga-Chaco + Atlantic Forest Domain, (4) Amazonia-Guiana, plus five regions to represent areas outside of South America: (5) Lesser Antilles, (6) Greater Antilles, (7) Central America + Chocó, (8) San Andrés and Providence islands, and (9) Africa. We refer to this a priori set of regions as ‘separate islands’ because we assumed the three Caribbean island regions (Lesser Antilles, Greater Antilles, and San Andrés plus Providence islands) to be independent of each other. The continental islands of Trinidad and Tobago were considered as Caribbean Coastal Forest + Llanos because they were connected to South America 12,000 years ago (Escalona and Mann, 2011). This set of regions allowed us to evaluate possible dispersal among islands. In order to study continental biogeography in more detail, we compared the above set of regions with a ‘fused islands’ model in which Caribbean islands were lumped as one region, the Caribbean Coastal Forest and Llanos were two independent regions, as were Central America and Chocó. Results were congruent and similarly robust under either definition of regions, and we present the results of the ‘separate islands’ scheme here.

3. Results

3.1. Phylogenetic analyses

The complete data matrix contained 250 individuals of *Mabuya sensu Mausfeld et al. (2000)* and five gene fragments for a total of 3211 aligned base pairs (bp), including 388 bp of 12S, 1140 bp of Cytb, 429 bp of Rag2, 603 bp of NGFB and 651 bp of R35. 12S and Cytb data were available for 91% and 96% of samples, respectively.

Nuclear gene sequences were obtained from major mtDNA clades and named species, representing 20 (R35), 16 (NGFB) and 38 taxa (Rag2) of skinks (8%, 6.4%, and 15.2% of samples, respectively). The nodes recovered with each mitochondrial and nuclear genes were represented with boxes in the nodes in Fig. 2. The topology obtained using only mitochondrial data was roughly the same as that obtained using the complete data (including nuclear genes), suggesting the missing data did not strongly affect the topology (see below). Premature stop codons were not detected in any protein-coding gene sequence. Numbers of variable and parsimony-informative characters observed within each gene are given in Table 1.

ML phylogenetic inference based on the complete dataset yielded a consensus tree that was topologically congruent with the Bayesian tree and with MP inference (Fig. 2). The tree including all outgroups is presented in Supplementary material Fig. S2. ML inference based on mitochondrial genes alone is presented in Supplementary material Fig. S3. We provide a nuclear data tree and mitochondrial data tree for the same taxa available for nuclear data; the topologies are presented in Supplementary material Fig. S4. Although the nuclear genes (Rag2, NGFB, R35) were useful at the population or closely related species level of skinks (Crottini et al., 2009; Linkem et al., 2011) we found that parsimony informative characters for species of *Mabuya* are low with 1.4%, 1.2% and 2.5% for Rag2, NGFB and R35 respectively (Table 1, Supplementary material Fig. S4). MP and ML bootstrap support and Bayesian posterior probabilities were relatively consistent among nodes (Fig. 2).

We recovered the genus *Mabuya* as monophyletic, with maximum parsimony bootstrap support (PBS), ML bootstrap support (MLB), and posterior probability support (PP) (PBS:100, MLB:100 and PP:1). Most of the basal relationships within *Mabuya* were poorly resolved (Fig. 2). The basal divergence within *Mabuya* involved the clade *M. crozati* + *M. carvalhoi* versus the sister clade containing the remaining congeneric species. The topology obtained is similar to Miralles and Carranza (2010) and Hedges and Conn (2012). In Fig. 2 we presented the taxonomic names proposed by Hedges and Conn (2012). Additional key phylogenetic results are presented below in Section 3.4 and in Supplementary material Table S4.

3.2. GMYC analyses

Both single and multiple-threshold GMYC models provided a better fit to the mitochondrial ultrametric tree than the null model (likelihood ratio test, $P < 0.0005$), while the multiple threshold model did not fit the data significantly better than the single-threshold model ($\chi^2 = 13.86$, $P = 0.95$), so we report the latter here. The single-threshold model delimited 74 clusters with a confidence interval of 59–93 clusters, including 27 and 40 singletons, respectively (Supplementary material Fig. S5). This method revealed two cases where previously recognized species fell into a single cluster: within *Spondylurus sensu Hedges and Conn (2012)*, the four species, *S. macleani*, *S. monitae*, *S. sloani*, and *S. culebrae* (Fig. 2A, Supplementary material Table S4), and within the *Mabuya unimarginata* complex, the two species *M. brachypoda* and *M. roatanae* formed one coalescent cluster, (Fig. 2C), suggesting the absence of significant differentiation among named species in either group.

3.3. Biogeography

Divergence times estimated under four alternative calibration schemes gave concordant results (Table 2), therefore we presented the dates obtained with the 3-point calibration strategy (column A in Table 2). According to our Bayesian MCMC inference, the genus



Fig. 2. Maximum likelihood phylogenetic tree inferred from the complete data set of two mitochondrial genes (12S, Cytb) and three nuclear genes (R35, Rag2, and NGFB) from samples representing all major clades of the lizard genus *Mabuya* (see Section 2). Branch support is presented for each node as bootstrap support under parsimony (PBS), maximum likelihood (MLB), and posterior probability for Bayesian analyses (PP), respectively, with each score separated by a slash (/). Asterisk indicates support ≥ 0.95 for PP and $\geq 75\%$ for PBS and MLB. Dash indicates support < 0.95 but ≥ 0.5 for PP and $< 75\%$ but $\geq 50\%$ for PBS and MLB. A blank indicates the node received < 0.5 PP support or $< 50\%$ PBS or MLB. Horizontal rectangles under certain nodes contain five boxes that refer from left to right to results for mitochondrial, Rag2, NGFB, R35 genes, and the GMYC analyses, respectively. Black fill indicates that the node was recovered in a single-gene phylogenetic analysis; white indicates that data were unavailable for this node, and 'x' indicates that the node was not recovered with this gene. The number in the fifth box indicates the number of divisions proposed for that clade according to the GMYC results (see text). The symbol (\$) followed by a number and after the specimen name highlights the individuals that were collapsed under GMYC analyses. Specimens are indicated by their field or museum voucher number, or, when not available, by their GenBank accession number for the Cytb gene. The genus and the species name following the proposal by *Hedges and Conn (2012)* are presented before the voucher numbers. Countries or regions are abbreviated as follows: Argentina (AR), Bolivia (BO), Brazil (BR), Colombia (CO), French Guiana (GF), Greater Antilles (GA), Guatemala (GT), Guyana (GY), Lesser Antilles (LA), Mexico (MX), Peru (PE), Trinidad and Tobago (TT), and Venezuela (VE).

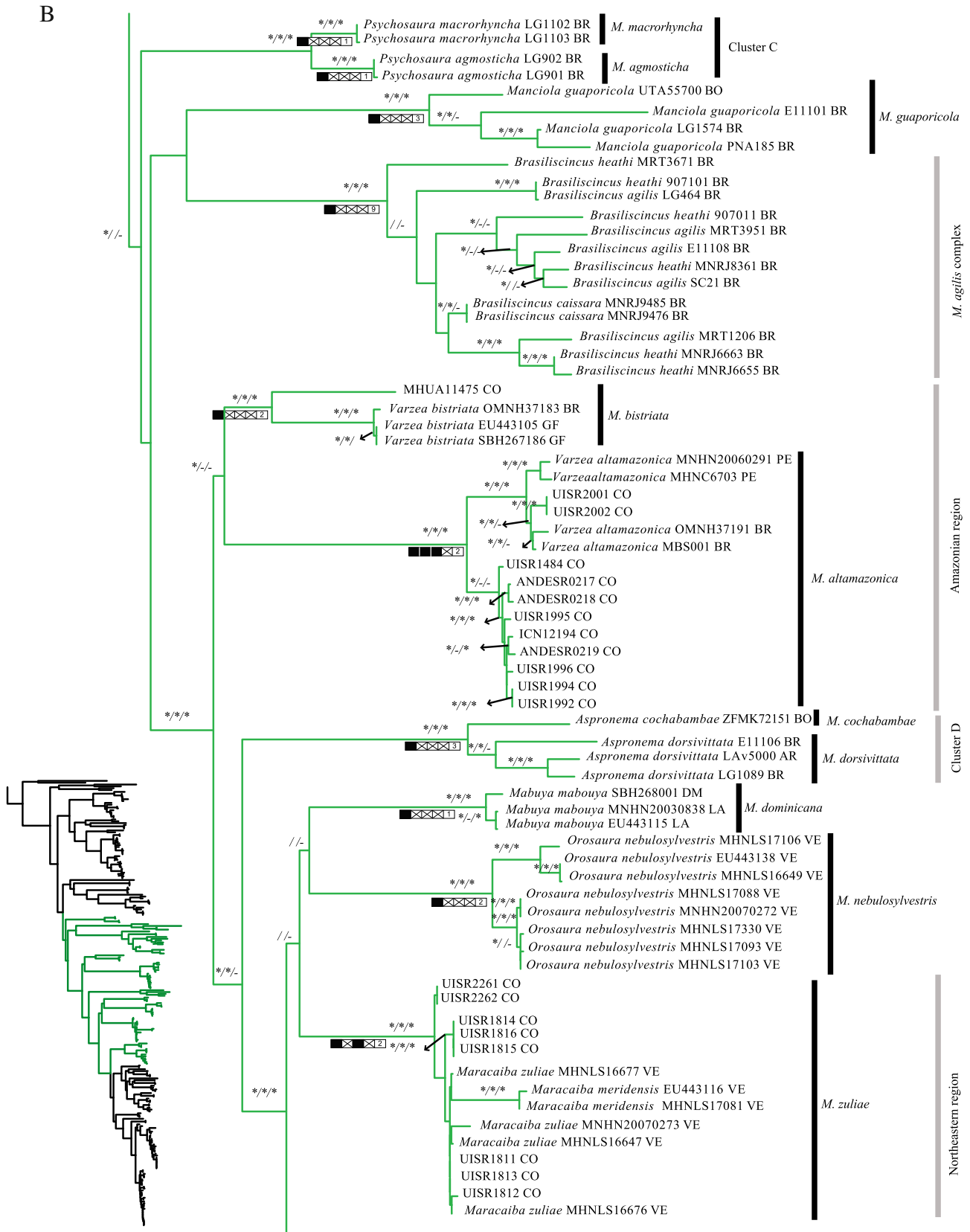


Fig. 2 (continued)

505 *Mabuya* diverged from other skinks in the Eocene around 36.60 Ma
506 (with 95% posterior credibility interval, CI: 16.91–66.59) and began
507 radiating at 21.37 Ma (CI: 9.73–36.71). Fitting the DEC model to

the phylogenetic data left the geographic origin of the genus
Mabuya as ambiguously reconstructed (Fig. 3), although the area
receiving highest likelihood was Amazonia-Guiana.

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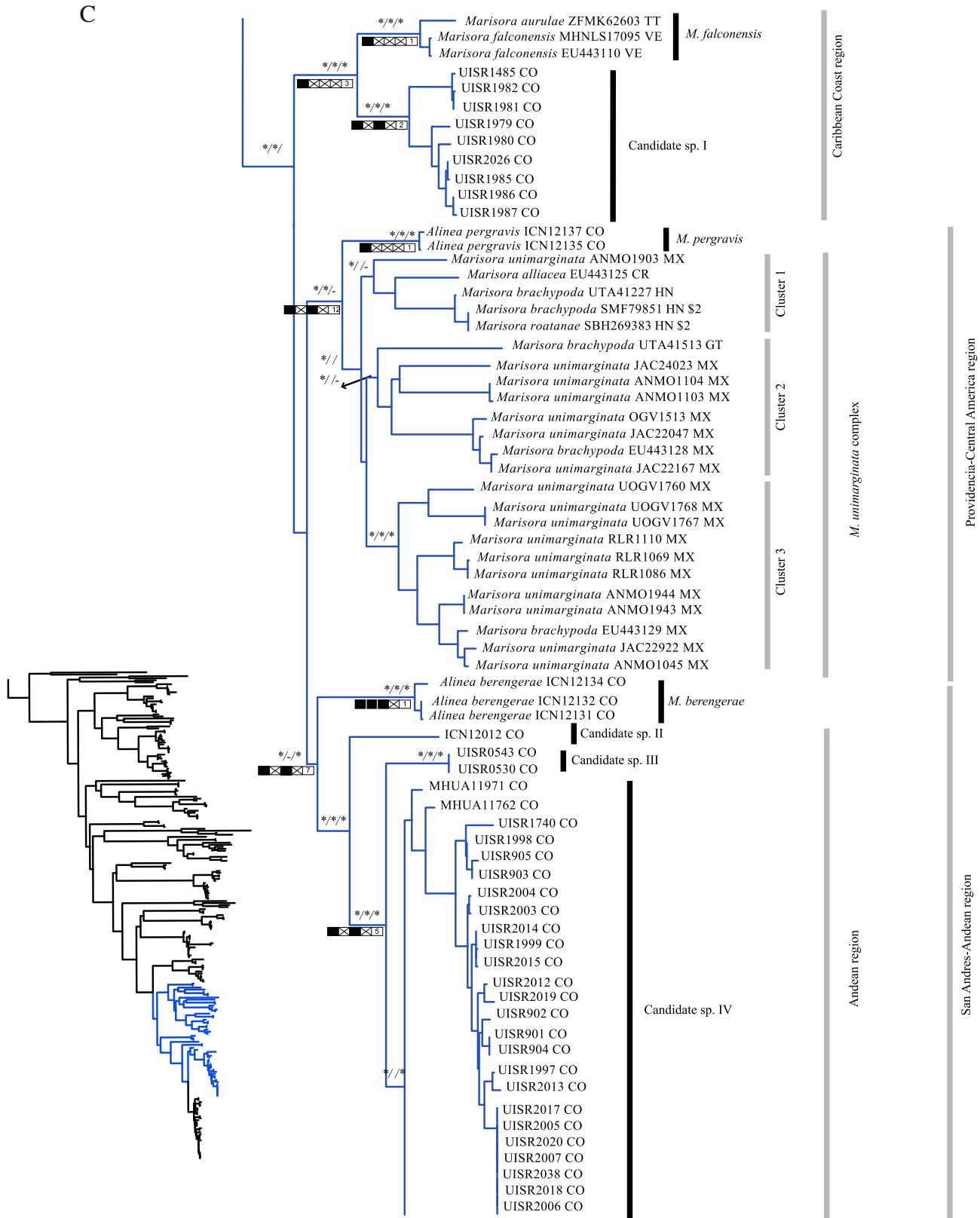


Fig. 2 (continued)

511 The ancestral areas analysis recovered six dispersal events from
 512 the mainland to islands (Fig. 3). The first two events involved the
 513 species in Cluster B that originated in the Miocene (5.95–
 514 21.41 Ma; Table 2) and are distributed in the Greater and Lesser
 515 Antilles. The first dispersal event was from the mainland to

Jamaica (Greater Antilles) and involved *M. fulgidus*, which subse-
 516 quently diversified in the Pleistocene (0.08, CI: 0.06–0.28 Ma).
 517 The second dispersal event from the mainland to the Lesser
 518 Antilles involved the ancestor of *M. powelli*, *M. lineolatus*, *M. caico-*
 519 *sae*, *M. semitaeniatus*, and *M. sloanni*, which then diversified in the
 520

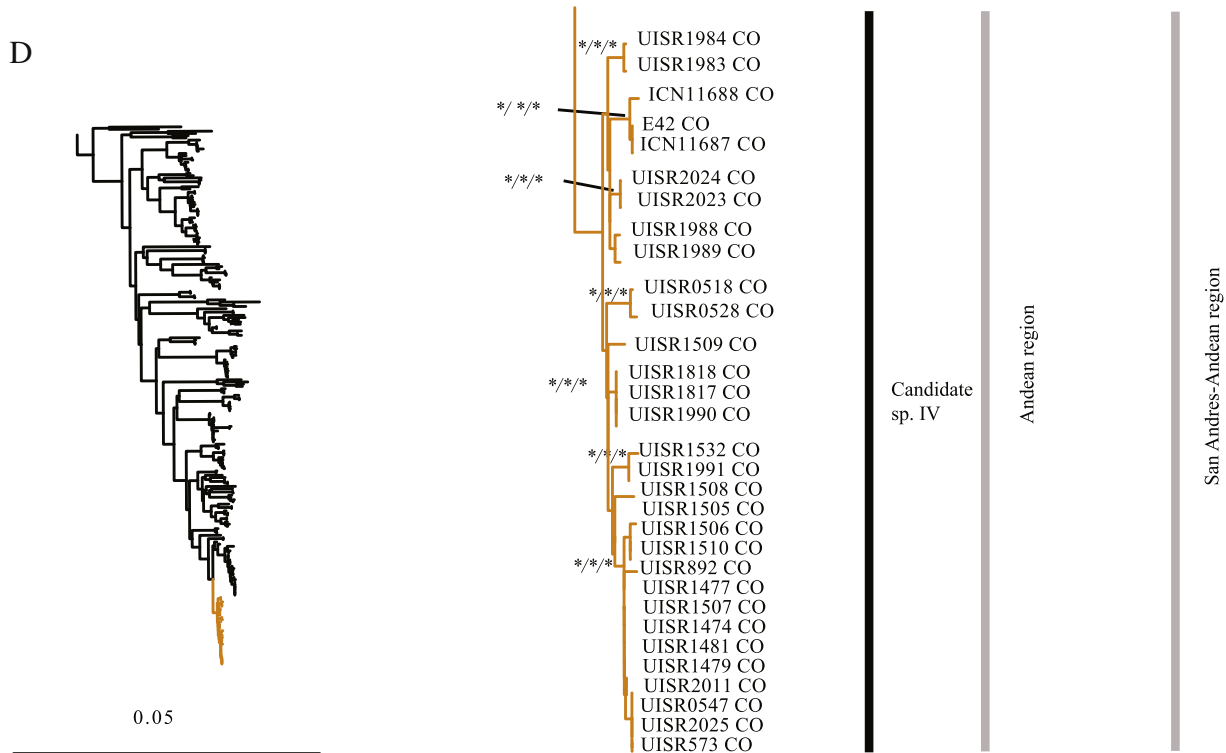


Fig. 2 (continued)

Table 1

Number and proportion of invariant, variable but un-informative (singleton), and parsimony informative (PI) sites for each gene region. In each column the number of sites is given first, with the corresponding proportion of sites in parentheses.

Gene	Aligned position	Invariant sites	Singleton sites	PI sites
12S rRNA	388	219 (0.56)	35 (0.09)	134 (0.35)
Cytb	1140	570 (0.50)	56 (0.05)	514 (0.45)
Rag2	429	415 (0.97)	8 (0.02)	6 (0.01)
NGFB	603	579 (0.96)	17 (0.03)	7 (0.01)
R35	651	622 (0.96)	13 (0.02)	16 (0.02)

Miocene and Pliocene (10.06, CI: 4.76–17.43 Ma). For both dispersal events, the ancestral area reconstruction using the DEC model was ambiguous, but we can nonetheless bound possible dispersal dates as falling before 0.06 Ma but after 0.28 Ma for *M. fulgidus* and prior to 4.76 Ma but after 17.43 Ma for the remaining species of Cluster B, not counting *M. fulgidus*.

The remaining four continent-to-island dispersal events took place in the Quaternary (Table 2): *M. aurae* SBH268935 is distributed in Saint Vincent and Grenadines (Lesser Antilles; arriving around 0.35 Ma, CI: 0.00–0.70 Ma), *M. dominicana* is distributed in Dominica Island (Lesser Antilles; arriving 1.04 Ma, CI: 0.31–2.31 Ma), *M. berengeriae* is endemic to San Andrés Island, Colombia (arriving 0.60 Ma, CI: 0.16–1.32 Ma), and *M. pergravis* in Providence Island, Colombia (arriving 0.22 Ma, CI: 0.03–0.57 Ma). Five of six of the above estimated ages preclude recent anthropogenic dispersal as a possible explanation. No cases of dispersal from islands to mainland were inferred, but the Greater Antilles were colonized from the Lesser Antilles at least three times in the Quaternary (*M. caicosae* at 0.19 Ma, CI: 0.02–0.52 Ma; *M. monitae* at 0.77 Ma, CI: 0–1.54 Ma; and *M. culebrae* at 0.5 Ma, CI: 0–1.0 Ma; Fig. 3).

The Central America species complex was clearly of South American origin, thus *Mabuya* participated in the Great American Biotic Interchange (Marshall et al., 1982). This South to North dispersal took place in the Miocene or Pliocene epoch (6.09 Ma, CI: 2.92–10.62 Ma). Following this dispersal event, *Mabuya*

experienced *in situ* diversification into three clades in Central America (Clusters 1, 2 and 3, in Fig. 2C).

3.4. Molecular identification of the Colombian species of *Mabuya*

Amazonian region. Two named species, *M. altamazonica* and *M. bistrriata*, have been previously recognized in the Amazonian region of Colombia. Eleven specimens were clustered with *M. altamazonica* (Fig. 2), confirming the presence of this species in Colombia as previously postulated by Miralles et al. (2010). The presence of its sister species, *M. bistrriata*, is also confirmed for Colombia based on MHUA 11475, which showed a relatively high genetic divergence of 1.6% at 12S and 8.5–8.9% at Cytb from the remaining specimens of *M. bistrriata* (Fig. 2). Unfortunately, this specimen was poorly preserved, thus it was not possible to compare its morphological characters to the rest of the specimens belonging to this species. Colombian specimens of *M. altamazonica* are easily distinguished from specimens of *M. bistrriata* because they lack two short and thin, light dorsolateral stripes, well defined from the middle of the neck to mid-body, a diagnostic character of *M. bistrriata* (Spix, 1825) (Supplementary material Table S4).

Northwestern region. Specimens from the northern portion of the Cordillera Oriental of Colombia (Santander and Norte de Santander departments) corresponded to *M. zuliae* according to morphology (Supplementary material Table S5) and their geographic distributions (Maracaibo region; Figs. 1 and 2). However, the genetic differentiation between *M. zuliae* and *M. meridensis* at 12S and Cytb was relatively low (0.0–1.3% at 12S and 0.0–4.5% at Cytb) and the latter taxon was nested within the former (bottom of Fig. 2B). We tested the reciprocal monophyly of *M. zuliae* and *M. meridensis*, and found this alternative topology could not be rejected (SH: $P = 0.411$; AU: $P = 0.415$), suggesting that both species may be valid. Therefore, the Colombian populations included in this '*M. meridensis* + *M. zuliae* clade' correspond to *M. zuliae*, while the validity of *M. meridensis* is also supported by

Table 2
Estimated ages in millions of years ago (Ma) for the genus and contained species, with emphasis on species distributed in Colombia and on species involved in dispersal from the mainland to the Caribbean islands. Ages were estimated from Bayesian relaxed clock analyses implemented in the software BEAST (see Section 2.6 for details). Column A shows ages estimated under all three temporal constraints: Africa vs. America, Lesser vs. Greater Antilles, and Carrot Rock vs. Virgin Islands (see text for details). Additional columns present the results of cross validation in which one of three constraints was sequentially lifted, as follows: B = Lesser vs. Greater Antilles constraint removed. C = Carrot Rock vs. Virgin Islands constraint removed. D = Africa vs. America constraint removed. Species and clades distributed in the Caribbean islands are indicated in **bold font**. NR means clade not recovered.

Clade	Bayesian 95% credibility interval (Ma)			
	A	B	C	D
<i>Mabuya</i> genus	9.73–36.7	7.09–33.7	8.03–42.30	NR
Cluster B	5.95–21.41	3.90–18.92	4.97–25.50	5.71–26.18
Cluster B without <i>M. fulgidus</i>	4.76–17.43	2.71–15.18	3.81–20.62	4.15–19.82
<i>M. altamazonica</i>	1.50–6.74	1.07–6.45	1.30–8.26	1.17–8.52
<i>M. aurae</i> SBH 268935	0.00–0.70	0.00–0.67	0.00–0.80	0.00–0.93
<i>M. berengeriae</i>	0.16–1.32	0.13–1.25	0.15–1.71	0.16–1.91
<i>M. bistrata</i>	2.33–13.6	1.64–11.9	1.89–14.7	1.44–15.2
<i>M. falconensis</i>	0.19–2.92	0.69–4.20	0.17–3.47	0.12–3.46
<i>M. fulgidus</i>	0.00–0.28	0.00–0.33	0.00–0.40	0.01–0.45
<i>M. dominicana</i>	0.31–2.31	0.21–2.34	0.24–2.83	0.24–3.01
<i>M. nigropunctata</i>	0.91–4.13	0.61–4.00	0.71–5.18	0.79–5.41
<i>M. pergravis</i>	0.03–0.57	0.03–0.63	0.02–0.99	0.02–0.89
<i>M. unimarginata</i> complex	2.92–10.6	1.81–9.41	2.09–12.1	2.65–12.4
<i>M. zuliae</i>	0.39–1.87	0.26–1.64	0.29–2.17	0.37–2.35
Candidate sp. I	1.01–4.48	0.69–4.20	0.71–5.58	0.80–6.21
Candidate sp. II				
Candidate sp. III	0.00–0.13	0.00–0.12	0.00–0.17	0.00–0.23
Candidate sp. IV	NR	0.75–4.02	0.84–5.21	0.97–5.90

morphological evidence, GMYC analyses, and potentially by the long branch (Fig. 2B).

Providence-Central American region. The Central American clade is composed of *M. pergravis* and the *M. unimarginata* complex. Average within-clade divergence was 0.1–5.0% at 12S and 0.0–9.0% at Cytb. Specimens collected on Providence Island (*M. pergravis*) had palms and soles lightly colored, similar to *M. unimarginata*, but differed strikingly from the latter by exhibiting a very characteristic long snout. The *Mabuya unimarginata* complex contained three main clades (Fig. 2B, Supplementary material Table S4). These clades overlap their distributions in Central America.

San Andrés-Andean region. Haplotypes of the endemic species of San Andrés Island (*M. berengeriae*) appeared related to, but highly divergent from, populations distributed throughout the Andean mountains of Colombia (2.0–4.0% at 12S and 5.0–10.0% at Cytb; Supplementary material Table S4). The Andean clade included at least three new lineages, one of which corresponded to a new taxon currently under description (Candidate sp. II) and two potential new species referred to here as Candidate sp. III and Candidate sp. IV (Fig. 2). Candidate sp. II is the basal-most lineage within the Andean clade, and is distributed in Guapi (Pacific coast of Cauca, Colombia). Candidate sp. III, represented by two individuals collected in the Cauca river depression (Antioquia, Colombia), formed the sister clade to Candidate sp. IV which is widely distributed among mid-elevation sites (from 65 to 1550 m) across the three mountain systems of Colombia (Fig. 2). Individuals of the Candidate sp. III clade exhibited identical mitochondrial haplotypes, and were supported by GMYC analyses, while individuals belonging to the Candidate sp. IV clade showed notable genetic divergences relative to Candidate sp. III (Fig. 2, Supplementary material Table S4). However, the external morphology of vouchered individuals within these clades was homogeneous.

Caribbean Coast region. The clade containing specimens collected in the Colombian departments of Guajira and Cesar on the Caribbean coast corresponded to a new lineage, Candidate sp. I (Fig. 2). This clade appeared as the sister group of the samples of *M. falconensis* from Falcón State in Venezuela. While *M. falconensis* and Candidate sp. I are similar in morphology (Supplementary

material Table S6), they presented a large genetic divergence of 4.0–5.0% at 12S and 6.0–8.0% at Cytb (Supplementary material Table S4) and were supported as two distinct clusters using GMYC analyses (Supplementary material Fig. S5).

4. Discussion

Our molecular phylogenetic analyses of *Mabuya* revealed six important inferences. First, we found evidence of perhaps ten distinct oceanic dispersal events within *Mabuya*, including at least six dispersal events from the mainland to Caribbean islands. The majority (5 of 6) of these events occurred in the Pleistocene. Second, three oceanic dispersal events took place from the Lesser to the Greater Antilles during the Quaternary. Third, minimum divergence times for the crown age of the Providence-Central America region show that the lineage was already present in Central America by 2.9 Ma, suggesting that the species crossed when the isthmus was complete (Coates and Obando, 1996; Montes et al., 2015). Fourth, some species proposed by Hedges and Conn (2012) need to be reevaluated according to our GMYC approach. Fifth, we report two additional species, *M. altamazonica* and *M. zuliae*, to the list of species occurring in Colombia, as supported by molecular and morphological evidence. *Mabuya bistrata* apparently occurs in Colombia as well, but this inference should be confirmed with more specimens. Sixth, at least four candidate species are found in Colombia: one distributed in the Caribbean lowlands (Candidate sp. I), a second distributed along the Pacific coast of Colombia (Candidate sp. II, currently under description), a third is distributed in the Cauca river depression (Candidate sp. III), and a widely distributed fourth taxon (Candidate sp. IV) is found in the foothills of the Andean cordilleras.

4.1. Biogeography

We found at least six dispersal events from the mainland to oceanic islands. The oldest dispersal event involved the arrival from South America of the ancestor of the sister clade to *M. fulgidus* (Cluster B in Fig. 3), which arrived and began diversifying by the Miocene (12.64 Ma, CI: 4.76–17.43 Ma; Fig. 3). Although the

655 confidence intervals on this divergence time are wide, they signif-
656 icantly postdate the time frame proposed for the hypothesized
657 GAARlandia (GAAR = Greater Antilles + Aves Ridge) landspan or
658 archipelago, which may have connected South America briefly
659 with the Antilles around the late Eocene to early Oligocene
660 (Iturralde-Vinent and MacPhee, 1999). Ancestral area reconstruc-
661 tion analysis suggests that the colonization of Jamaica from

South America by *M. fulgidus* was an independent event that could
662 have happened anywhere along the branch leading to the ancestor
663 of Cluster B. We follow the DEC modeling results in suggesting that
664 this dispersal took place around the TMRCA of the *M. fulgidus*
665 samples, i.e., a Pleistocene time frame.
666

The remaining four continent-to-oceanic island colonization
667 events also suggest a Pleistocene time frame. *Mabuya dominicana*
668

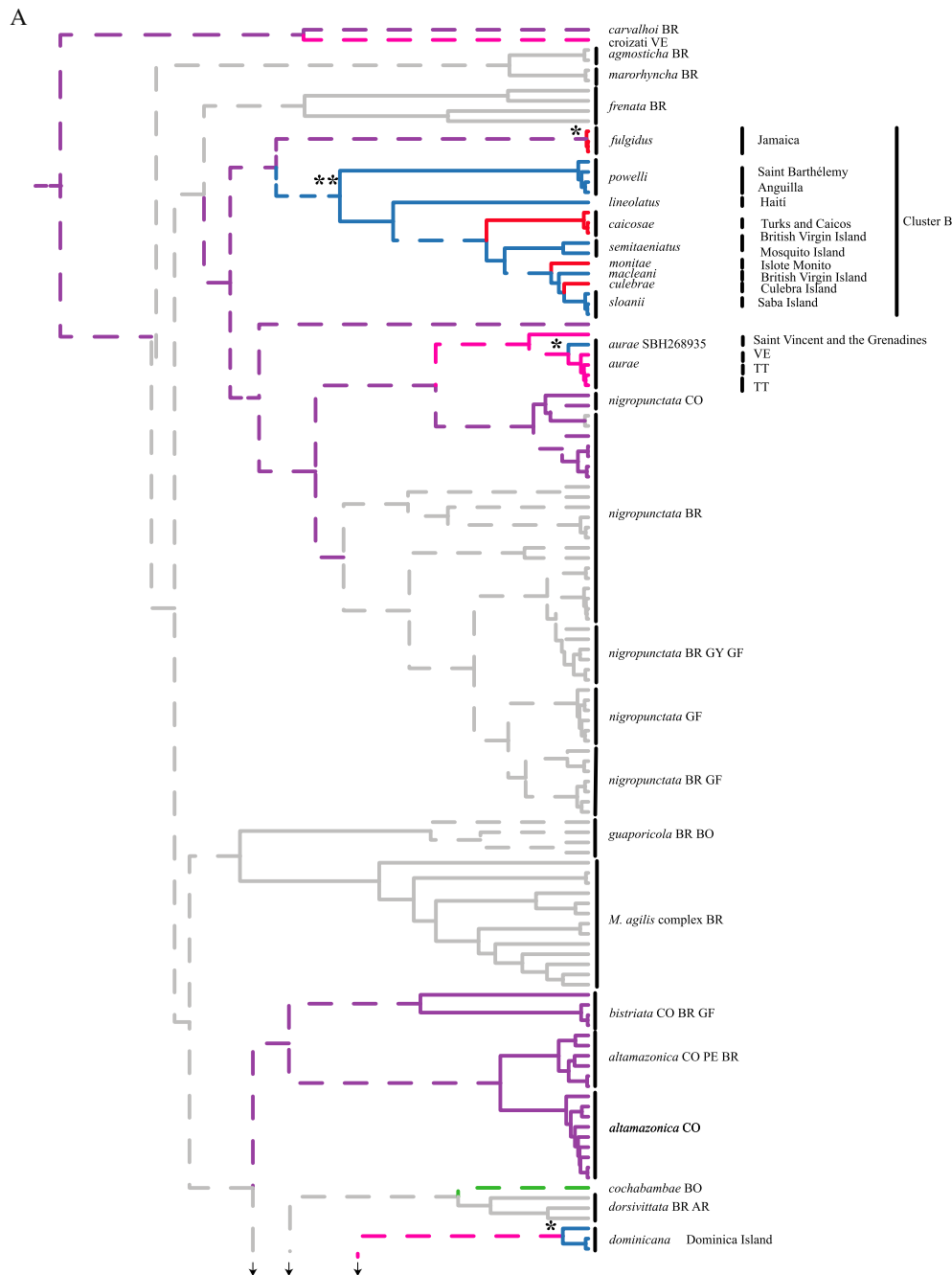
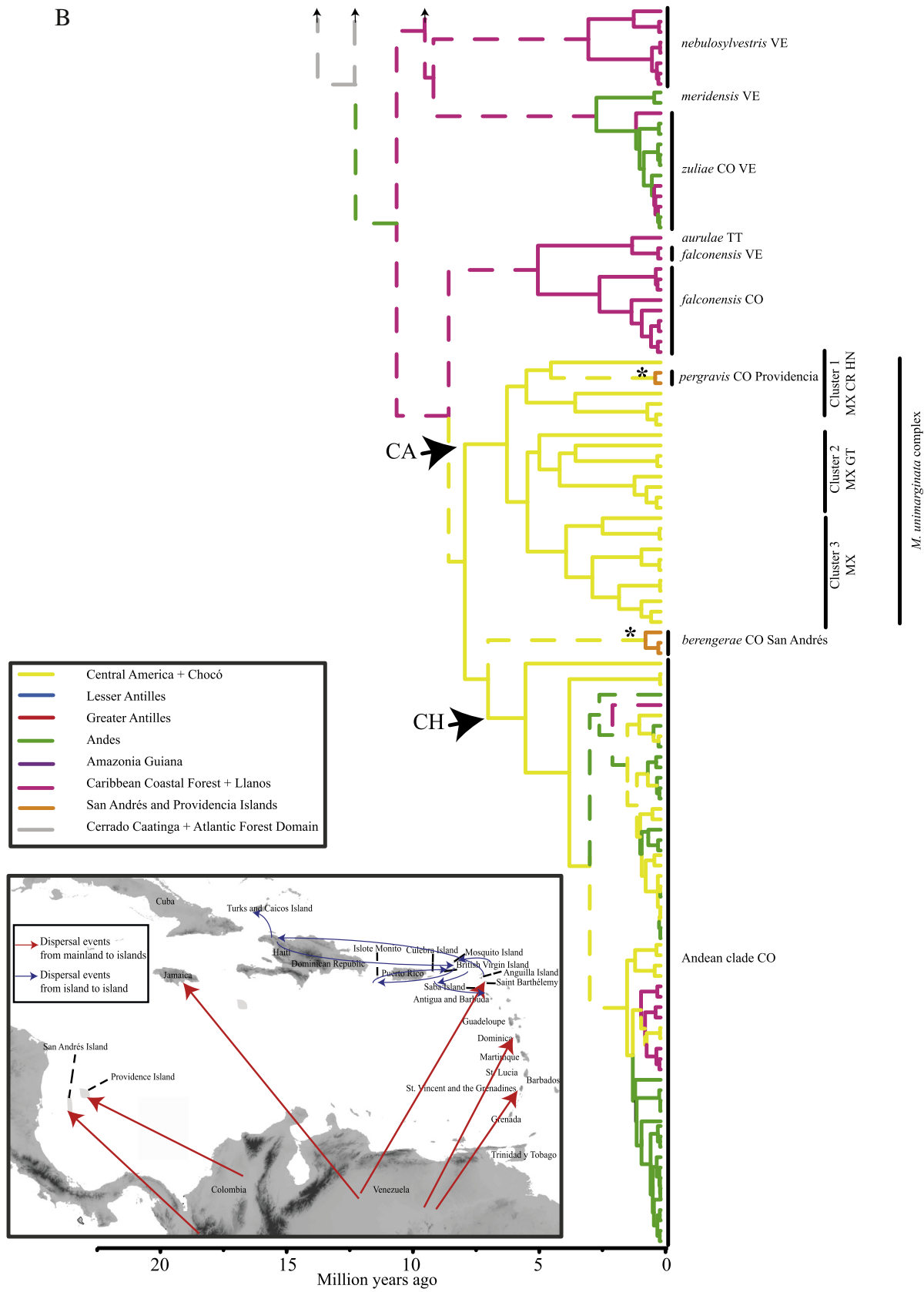


Fig. 3. A timetree of *Mabuya* derived from a relaxed-clock Bayesian MCMC analysis using the software BEAST and assuming three calibration points which correspond to the divergence between Carrot Rock and other Virgin Islands, Greater and the Lesser Antilles, and African versus South American species (see Supplementary material Table S3). Scale bar along the bottom indicates time in millions of years ago. Branch colors reflect ancestral areas estimated under the DEC model of Ree and Smith (2008). The outgroup (not shown) is endemic to Africa. DEC analysis assumed an a priori division of the Neotropics into nine regions and corresponds to the 'separated island analyses' (see Section 2). Dashed lines indicate uncertain reconstruction of ancestral states, while solid lines indicate that all alternative reconstructions fell >2 log-likelihood units lower than the maximum likelihood estimate (Ree and Smith, 2008), typically much lower. Asterisks highlight six dispersal events from the mainland to oceanic islands. One asterisk corresponds to Quaternary events and two asterisks correspond to dispersal events in the Miocene. Inset map shows the Caribbean region with arrows corresponding to dispersal events from the mainland to islands or among islands. CA and CH indicate Central America and Chocó respectively. Countries and regions are abbreviated as follows: Argentina (AR), Bolivia (BO), Brazil (BR), Colombia (CO), Costa Rica (CR), French Guiana (GF), Guatemala (GT), Guyana (GY), Honduras (HN), Mexico (MX), Peru (PE), Trinidad and Tobago (TT), and Venezuela (VE). We considered the continental islands of TT as belonging to the region Caribbean Coastal Forest + Llanos. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



672 is found only in Dominica Island, while *M. pergravis* and *M. berengerae* are endemic to Providence Island and San Andrés Island, respectively. The minimum crown ages of diversification on these

672 three islands (0.31 Ma, 0.03 Ma, and 0.16 Ma, respectively) predate the arrival of humans in the Caribbean roughly 0.015 Ma, therefore, we argue that oceanic dispersal could be explained by rafting

672
673
674

on floating mats of vegetation (Calsbeek and Smith, 2003; Censky et al., 1998; De Queiroz, 2005). *Mabuya aurae* SBH268935 is found in Saint Vincent and Grenadines, but the credibility interval on the crown age of samples for this species includes zero, thus anthropogenic transport remains a viable alternative explanation for its presence on these islands. Vicariance via sea level rise following Pleistocene glacial maxima provides an alternative explanation to dispersal among some Lesser Antillean islands, but cannot explain dispersal from the continent to oceanic islands (Pregill, 1981).

Five of six of the dispersal events from continent to island were supported statistically. The nodes corresponding to dispersal events by the ancestors of *M. fulgidus*, *M. dominicana*, *M. pergravis*, and *M. berengerae* had strong support according to PBS, MLB and PP measures. Cluster B (excluding *M. fulgidus*) had strong support according to MLB and PP. In contrast, the phylogenetic placement of the sample, SBH268935 from Saint Vincent and Grenadines, relative to conspecific samples of mainland *M. aurae*, received no statistical support. The timing of this mainland–island dispersal event is therefore difficult to estimate, and could be consistent with either human-mediated dispersed or rafting (Calsbeek and Smith, 2003).

The minimum estimate of the crown age of the Central America clade of *Mabuya* (2.9 Ma) is compatible with the traditional hypothesis that the Isthmus of Panama was closed as recently as 3.1 Ma (Coates and Obando, 1996). Our point estimate, however, centers around 8 Ma, which coincides with the time of dispersal from South to North estimated for eight lineages of terraranan frogs (Pinto-Sánchez et al., 2012), and with the second of three shifts in the increasing rate of terrestrial dispersal between North and South America estimated at roughly 5–8 Ma (Bacon et al., 2015). The upper limit of the credibility interval for dispersal of *Mabuya* into Central America was 10.62 Ma, which is compatible with the 10–15 Ma proposed by Montes et al. (2012, 2015) for the completion of the Isthmus of Panama. Skinks may not be the best faunal system for testing hypotheses of early land connections, however, given the surprising number of oceanic dispersal events we inferred here for the Caribbean islands.

4.2. Molecular identification of the Colombian species of *Mabuya*

Amazonian region. This region includes two species, *M. altamazonica* and *M. bistrriata*. Divergence observed here between *M. altamazonica* and *M. bistrriata* was 5.0–7.0% at 12S and 10.0–13.0% at Cytb, i.e., similar to the 5.8% at 12S found by Miralles et al. (2006). Therefore, our molecular evidence supports the distinctiveness of populations from the Orinoquia and Cordillera Oriental foothills of Colombia as *M. altamazonica*, a species previously reported for Peruvian and Ecuadorean Amazonia (Fig. 2; Miralles et al., 2006). Thus, Colombian specimens assigned here to *M. altamazonica* represent the first records of this species in Colombia. The southernmost known locality of *M. altamazonica* in Colombia (Caquetá Department, Morelia municipality) is separated from the nearest reported locality in Tarapoto, San Martín, Peru by 890 km straight-line distance. This species is typical of lowland habitats and occurs at an altitudinal range of 175–260 m. Individuals of this species collected in Colombia were observed next to rural houses, ranches, and farms with moderate intervention of the surrounding habitat.

The specimen of *M. bistrriata* collected in the Colombian Amazon (MHUA 11475) shows high genetic divergence from the remaining specimens of *M. bistrriata*. This specimen could also correspond to a new species closely related to *M. bistrriata*. We considered this sample as *M. bistrriata*, however, but hope to collect other specimens in order to better characterize the morphological and genetic variation. Although this species was not previously reported in Colombia, Avila-Pires (1995) reviewed the distribution of Amazonian lizards and included records of *M. bistrriata* from three

localities very close to the Amazonian border of Colombia [Cucuí (on the Rio Negro), La Varre (Jaguararé, Vaupés river), and Lago Ucayali, 16 km down the Amazon River from Leticia, Colombia], and suggested that this taxon should be present in Colombia and Venezuela. This species predominantly inhabits the borders of large rivers and várzea forest (Miralles and Carranza, 2010).

Northeastern region. Samples from the northeastern region of Colombia comprised a clade containing *M. zuliae* and *M. meridensis*. The divergence between Colombian and Venezuelan samples of *M. meridensis* was low (0.5–1.3% at 12S and 2.8–4.5% at Cytb), and between Colombian samples and Venezuelan *M. zuliae* were lower still (0.0–0.8% at 12S and 0.0–1.2% at Cytb). Thus, genetic data suggest that *M. zuliae* and *M. meridensis* are present in Colombia. Colombian samples of *M. zuliae* also match the morphological characters diagnosing *M. zuliae*: four dark stripes along the body, and palms and soles darkly colored. The geographic distribution of *M. zuliae* was previously restricted to Venezuela around the Lake Maracaibo Basin in the State of Zulia, and the neighboring states of Mérida and Trujillo, although only marginally (Miralles et al., 2009), while *M. meridensis* has been reported in the vicinity of Mérida (Miralles et al., 2005a). While *M. zuliae* was restricted to the lowlands and foothills of Lake Maracaibo, *M. meridensis* was reported as a montane species above 1300 m. Thus, specimens reported here represent the first record of *M. zuliae* in Colombia (Fig. 1), and expand its distribution to an altitudinal range of 1100–2300 m in Colombia (previously the maximum altitude was below 1500 m). The Colombian populations of both species can be found associated with rural houses, ranches, and farms with moderate intervention of the surrounding habitat.

Providencia-Central American and San Andrés-Andean regions. We found that *M. pergravis*, an endemic taxon of Providence Island, is closely related to *M. unimarginata* from Central America, whereas *M. berengerae*, endemic to the neighboring San Andrés Island, is more closely related to the Chocoan and Andean clade from mainland Colombia (Fig. 3). Qualitative analyses of the morphology and geographic distribution of *M. pergravis* and *M. berengerae sensu Miralles et al. (2009)* suggested that *M. pergravis* and *M. berengerae* were sister species, and were grouped with *M. unimarginata* and *M. falconensis* (Hedges and Conn, 2012). Molecular evidence (12S, Cytb, and NGFB genes, Fig. 2) presented here showing that *M. pergravis* and *M. berengerae* are not closely related, suggests that their similar and derived phenotypes, including an extremely elongated and pointed snout and a high number of secondary nuchal scales, likely resulted from a convergent evolution to their similar island habitats. One possible scenario for how *M. berengerae* could have arrived would be that floating mats of vegetation containing *Mabuya* from the Chocoan and Andean clade were ejected between 11.86 and 3.13 Ma from an early Atrato River in the Colombian Chocó or early Magdalena River on the Caribbean coast, both of which flow south to north into the Caribbean Sea (Fig. 3).

High genetic variation within Central American populations of *M. unimarginata* at 0.0–5.0% at 12S and 0.0–9.0% at Cytb was indicated previously by Miralles et al. (2009) and Castiglia et al. (2010) using mitochondrial markers, and suggests that samples assigned to this taxon represent a species complex (Miralles et al., 2009). *Mabuya unimarginata* is widely distributed from central Mexico to Panama and has a long history of taxonomic confusion (Dunn, 1935; Burger, 1952; Taylor, 1956; Webb, 1958; Lee, 1996). Hedges and Conn (2012) recognized four species in this complex: *M. alliacea*, *M. rotanae*, *M. brachypoda*, and *M. unimarginata*. We did not recover *M. brachypoda* and *M. unimarginata sensu Hedges and Conn (2012)* as monophyletic (Fig. 2). Therefore, we propose that the *M. unimarginata* complex contains three main clades (Fig. 2, Supplementary material Table S4), which are concordant with its biogeographical distribution in Central America. Genetic divergence observed among haplotypes of the Andean region

suggests that populations represented by these haplotypes correspond to three potential new species. Candidate sp. II represents the only species of *Mabuya* endemic to the trans-Andean region of South America, and the southern-most locality for the genus *Mabuya* on the Pacific coast. Candidate sp. III is distributed in the Cauca river depression (Antioquia department), and Candidate sp. IV occurs in the foothills of the Colombian Andes. All three candidate species were collected during the day in open areas, with most individuals found in anthropogenic habitats.

Caribbean coast region. The presence of *M. falconensis* in the Caribbean coast of Colombia was previously suggested based on the morphology of one specimen from La Guajira Department (Miralles et al., 2005a). Our morphological revision included seven specimens from Cesar and Guajira departments and revealed no morphological differences between the Colombian and Venezuelan samples. However, the molecular divergence between our sampled individuals and *M. falconensis* from Venezuela is high (4.0–5.0% at 12S rRNA, 6.0–8.8% at Cytb). We suggest, therefore, that the Colombian populations distributed in the Caribbean region correspond to a candidate species (Candidate sp. I). *Mabuya falconensis* is endemic to xerophytic areas of the Caribbean coast of Venezuela. Individuals of Candidate sp. I were collected in similar environments in the Guajira and Cesar, Colombia, between 40 and 131 m.

4.3. Taxonomic implications

We inferred as clades most of the genera proposed by Hedges and Conn (2012). Only *Marisora* and *Alinea* were recovered as non-monophyletic groups. The type species of *Alinea* is *A. lanceolata*, for which molecular data do not exist. *Alinea lanceolata* is from Barbados in the Lesser Antilles, and based on our phylogenetic and biogeographic findings we predict that *A. lanceolata* is not phylogenetically closely related to the other two species of '*Alinea*' from San Andrés and Providence *Mabuya*. Therefore, we likely have three distinct clades of '*Alinea*': *berengerae* from San Andrés, *pergravis* from Providence, and *lanceolata* from Barbados (and maybe a fourth if *luciae* is not related to *lanceolata*, which needs to be tested in the future). Thus, we do not know which if any of the two *Alinea* clades in our tree (Fig. 2) should keep the generic name. In absence of any other phylogenetic information, based on geography, it would be more parsimonious to consider all the southern Lesser Antillean *Mabuya* as being phylogenetically related (*M. mabouya*, *M. dominicana*, *M. lanceolata*, *M. luciae*, among others) until all species can be tested with molecular data. Our proposed solution would be to synonymize *Alinea* with *Mabuya*, pending further evidence. We note that no single morphological character state is shared among the four species of *Alinea* (Hedges and Conn, 2012, page 31), and that Hedges and Conn (2012) had no DNA data for this genus, whereas we offer DNA data for two species. Therefore, we preferred to maintain the taxonomy proposed by Mausfeld et al. (2002) because the main focus of the present paper is the phylogeny and biogeography of species distributed in Colombia.

The main taxonomic results are presented in Supplementary material Table S4. Seven species were classified as invalid species according to the following evidence. *Mabuya agilis*, *M. heathi*, and *M. brachypoda* are considered invalid as they are not monophyletic according to our mitochondrial and nuclear evidence, and they lack clade support. *Mabuya roatanae* has low genetic divergence (0.0% at 12S) from its sister clade, *M. brachypoda*, and these species were collapsed by our GMYC inference. *Mabuya monitae*, *M. macleani*, and *M. culebrae* were collapsed within *M. sloanii* according to our GMYC approach.

In summary, we propose to maintain the genus *Mabuya* as a diverse taxon widely distributed throughout Central America, South America and several Caribbean islands. According to our appraisal of species delimitation and diversity, there are 58 species

within *Mabuya* including four candidate species revealed in the present study plus one candidate species proposed by Miralles et al. (2010). Of these, 23 named species do not have molecular data and were not evaluated here, suggesting the total species could still be higher. For Colombia we present the first record of three species: *M. altamazonica* from the Orinoquia and the eastern foothills of the Cordillera Oriental, *M. bistrata* from Amazonia and *M. zuliae* from the northeastern region. This study thus filled a long-standing geographic sampling gap that is Colombia and revealed a plentitude of lineages of *Mabuya*. This work also highlights the broader importance of complete sampling before reviewing and revising the taxonomy of a widespread and complex taxon. Therefore, we urge researchers to have as complete a geographic sampling design as possible, combined with an explicit a priori methodology for species delimitation, before revising taxonomy and erecting new taxonomic names.

5. Uncited references

Austin et al. (2011), Bermingham and Martin (1998), Brown et al. (2000), Drummond and Rambaut (2007), Haffer (1967), Miralles (2006), Miralles et al. (2005b), Moritz et al. (2000) and Vences et al. (2013).

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Appendix A

List of specimens of *Mabuya* used in the present study. For each specimen the museum voucher, locality, latitude, longitude, and GenBank accession numbers are reported. Acronyms for museums are: ANDES-R = Reptiles collection, Museo de Historia Natural ANDES, Bogotá, Colombia; ICN-R = Reptiles collection, Instituto de Ciencias Naturales, Universidad Nacional, Colombia; MHUA-R = Reptiles collection Museo de Herpetología de la Universidad de Antioquia, Colombia, UIS-R = Colección Herpetológica, Museo de Historia Natural, Universidad Industrial de Santander, Colombia. Species names in **bold** indicate to specimens sequenced in the present study. N/A means sequence not available. *Mabuya* sp. I, *Mabuya* sp. II, *Mabuya* sp. III, and *Mabuya* sp. IV refer to candidate species.

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
<i>Mabuya altamazonica</i>	UIS-R-2001	Colombia	Caquetá	Morelia	1.49	–74.75	KJ493240	KJ492287	KJ493000	N/A	N/A
<i>Mabuya altamazonica</i>	UIS-R-2002	Colombia	Caquetá	Morelia	1.49	–74.75	KJ493241	KJ492288	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	UIS-R-1484	Colombia	Casanare	Orocué	4.8	–71	KJ493242	KJ492289	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	ANDES-R 0217	Colombia	Meta	San Carlos de Guaroa	3.72	–73.25	KJ492290	KJ493001	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	ANDES-R 0218	Colombia	Meta	San Carlos de Guaroa	3.72	–73.25	KJ493243	KJ492291	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	UIS-R-1995	Colombia	Guaviare	San José del Guaviare	2.57	–72.65	KJ493244	KJ492292	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	ICN-R-12194	Colombia	Meta	Pachaquiario	3.94	–73.01	KJ493245	KJ492293	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	ANDES-R 0219	Colombia	Meta	Mapiripan	2.9	–72.17	KJ493246	KJ492294	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	UIS-R-1996	Colombia	Guaviare	San José del Guaviare	2.57	–72.65	KJ493247	KJ492295	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	UIS-R-1994	Colombia	Casanare	Tauramena	5.02	–72.75	KJ493238	KJ492285	N/A	KJ492964	KJ492980
<i>Mabuya altamazonica</i>	UIS-R-1992	Colombia	Casanare	Tauramena	5.02	–72.75	KJ493239	KJ492286	N/A	N/A	N/A
<i>Mabuya berengeriae</i>	ICN-R-12134	Colombia	San Andres	No information	12.55	–81.71	KJ493250	KJ492298	KJ493003	N/A	N/A
<i>Mabuya berengeriae</i>	ICN-R-12132	Colombia	San Andres	Shingle Hill	12.56	–81.72	KJ493248	KJ492296	N/A	KJ492965	KJ492982
<i>Mabuya berengeriae</i>	ICN-R-12131	Colombia	San Andres	Harmony Hall Hill	12.56	–81.71	KJ493249	KJ492297	KJ493002	N/A	KJ492983
<i>Mabuya bistrata</i>	MHUA-R-11475	Colombia	Amazonas	Leticia	–4.17	–69.95	KJ493251	KJ492299	N/A	N/A	KJ492984
<i>Mabuya sp. I</i>	UIS-R-1485	Colombia	Guajira	Cerrejón	11.09	–72.67	KJ493253	KJ492302	N/A	N/A	N/A
<i>Mabuya sp. I</i>	UIS-R-1981	Colombia	Guajira	Barrancas	10.96	–72.79	KJ493254	KJ492303	N/A	N/A	N/A
<i>Mabuya sp. I</i>	UIS-R-1982	Colombia	Guajira	Barrancas	10.96	–72.79	KJ493255	KJ492304	KJ493005	KJ492966	KJ492985
<i>Mabuya sp. I</i>	UIS-R-1979	Colombia	Cesar	Codazzi	10.04	–73.23	KJ493256	KJ492305	N/A	KJ492967	KJ492986
<i>Mabuya sp. I</i>	UIS-R-1980	Colombia	Cesar	Codazzi	10.04	–73.23	KJ493257	KJ492306	N/A	N/A	N/A
<i>Mabuya sp. I</i>	UIS-R-1986	Colombia	Bolívar	Arjona	10.26	–75.35	KJ493258	KJ492307	KJ493006	N/A	N/A
<i>Mabuya sp. I</i>	UIS-R-1987	Colombia	Bolívar	Arjona	10.26	–75.35	N/A	KJ492300	KJ493004	N/A	N/A
<i>Mabuya sp. I</i>	UIS-R-1985	Colombia	Atlántico	Baranoa	10.8	–74.92	KJ493259	KJ492308	N/A	N/A	N/A
<i>Mabuya sp. I</i>	UIS-R-2026	Colombia	Atlántico	Usiacuri	10.75	–74.98	KJ493252	KJ492301	N/A	N/A	N/A
<i>Mabuya meridensis</i>	UIS-R-2261	Colombia	Norte de Santander	Chinácota	7.61	–72.6	KJ493262	KJ492311	KJ493007	KJ492969	KJ492988
<i>Mabuya meridensis</i>	UIS-R-2262	Colombia	Norte de Santander	Chinácota	7.61	–72.6	KJ493263	KJ492312	N/A	N/A	N/A
<i>Mabuya meridensis</i>	UIS-R-1814	Colombia	Norte de Santander	Chinácota	7.61	–72.6	KJ493264	KJ492313	N/A	N/A	KJ492989
<i>Mabuya meridensis</i>	UIS-R-1815	Colombia	Norte de Santander	Chinácota	7.61	–72.6	N/A	KJ492314	N/A	N/A	N/A
<i>Mabuya meridensis</i>	UIS-R-1816	Colombia	Norte de Santander	Chinácota	7.61	–72.6	KJ493265	KJ492315	N/A	N/A	N/A
<i>Mabuya meridensis</i>	UIS-R-1811	Colombia	Norte de Santander	Chinácota	8.23	–73.36	KJ493260	KJ492309	N/A	N/A	N/A
<i>Mabuya meridensis</i>	UIS-R-1812	Colombia	Norte de Santander	Chinácota	8.23	–73.36	KJ493266	KJ492316	KJ493008	N/A	N/A
<i>Mabuya meridensis</i>	UIS-R-1813	Colombia	Norte de Santander	Chinácota	8.23	–73.36	KJ493261	KJ492310	N/A	KJ492968	KJ492987
<i>Mabuya nigropunctata</i>	Not catalogued	Colombia	Amazonas	Leticia	–4.69	–69.96	KJ493267	KJ492317	N/A	KJ492970	KJ492990
<i>Mabuya pergravis</i>	ICN-R-12135	Colombia	Providencia	South West Bay	13.34	–81.37	KJ493269	KJ492319	KJ493010	KJ492971	KJ492991

(continued on next page)

Appendix A (continued)

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
Mabuya pergravis	ICN-R-12137	Colombia	Providencia	Camino de terracería a Kan Kan Ha	13.34	−81.37	KJ493268	KJ492318	KJ493009	N/A	N/A
Mabuya sp. II	ICN-R12012	Colombia	Cauca	Guapi	2.57	−77.89	N/A	KJ492340	N/A	KJ492973	KJ492993
Mabuya sp. III	UIS-R-0530	Colombia	Antioquia	Santa Fé de Antioquia	6.56	−75.83	KJ493285	KJ492341	N/A	KJ492974	KJ492994
Mabuya sp. III	UIS-R-0543	Colombia	Antioquia	Santa Fé de Antioquia	6.56	−75.83	KJ493286	KJ492342	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-0902	Colombia	Cundinamarca	Yacopi	5.46	−74.34	KJ493287	KJ492343	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-0904	Colombia	Cundinamarca	Yacopi	5.46	−74.34	KJ493288	KJ492344	KJ493016	N/A	N/A
Mabuya sp. IV	UIS-R-0901	Colombia	Cundinamarca	Yacopi	5.46	−74.34	KJ493289	KJ492345	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1997	Colombia	Tolima	Espinal	4.15	−74.89	KJ493290	KJ492346	KJ493017	N/A	N/A
Mabuya sp. IV	UIS-R-2013	Colombia	Tolima	Mariquita	5.2	−74.9	KJ493291	KJ492347	KJ493018	N/A	N/A
Mabuya sp. IV	UIS-R-1740	Colombia	Santander	Lebrija	7.12	−73.22	KJ493292	KJ492348	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2005	Colombia	Valle del Cauca	Roldanillo	4.42	−76.16	KJ493293	KJ492349	KJ493019	KJ492975	KJ492995
Mabuya sp. IV	UIS-R-2020	Colombia	Risaralda	Apia	5.11	−75.94	N/A	KJ492350	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2017	Colombia	Risaralda	Marsella	4.94	−75.74	KJ493294	KJ492351	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2006	Colombia	Valle del Cauca	Bugalagrande	4.21	−76.16	KJ493295	KJ492352	KJ493020	N/A	N/A
Mabuya sp. IV	UIS-R-2018	Colombia	Risaralda	Marsella	4.94	−75.74	KJ493296	KJ492353	KJ493021	N/A	N/A
Mabuya sp. IV	UIS-R-2038	Colombia	Antioquia	Sopetrán	6.51	−75.75	KJ493297	KJ492354	KJ493022	N/A	N/A
Mabuya sp. IV	UIS-R-2012	Colombia	Tolima	Mariquita	5.2	−74.9	KJ493298	KJ492355	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2014	Colombia	Caldas	Samaná	5.42	−74.99	KJ493299	KJ492356	KJ493023	N/A	N/A
Mabuya sp. IV	UIS-R-1999	Colombia	Huila	Aipe	3.22	−75.25	KJ493300	KJ492357	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2015	Colombia	Caldas	Samaná	5.42	−74.99	KJ493301	KJ492358	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2003	Colombia	Huila	Timana	1.98	−75.93	KJ493302	KJ492359	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2004	Colombia	Huila	Timana	1.98	−75.93	KJ493303	KJ492360	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1998	Colombia	Tolima	Espinal	4.15	−74.89	KJ493304	KJ492361	KJ493024	N/A	N/A
Mabuya sp. IV	UIS-R-903	Colombia	Cundinamarca	Yacopi	5.46	−74.34	N/A	KJ492362	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-905	Colombia	Cundinamarca	Yacopi	5.46	−74.34	N/A	KJ492363	N/A	N/A	N/A
Mabuya sp. IV	MHUA-R-11971	Colombia	Antioquia	Barbosa	6.44	−75.34	N/A	KJ492364	KJ493025	N/A	N/A
Mabuya sp. IV	ICN-R-11687	Colombia	Córdoba	Monte líbano	7.81	−75.85	KJ493305	KJ492365	KJ493026	N/A	N/A
Mabuya sp. IV	ICN-R-11691	Colombia	Córdoba	Tierra Alta	7.96	−76.01	N/A	N/A, N/A	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1988	Colombia	Bolívar	San Jacinto	9.84	−75.13	KJ493306	KJ492366	KJ493027	N/A	N/A
Mabuya sp. IV	MHUA-R-11762	Colombia	Sucre	Colosó	9.5	−75.36	KJ493307	KJ492367	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1983	Colombia	Magdalena	Tayrona	11.28	−73.93	KJ493308	KJ492368	N/A	KJ492976	KJ492996
Mabuya sp. IV	UIS-R-1984	Colombia	Magdalena	Tayrona	11.28	−73.93	KJ493309	KJ492369	KJ493028	N/A	N/A
Mabuya sp. IV	UIS-R-1989	Colombia	Bolívar	San Jacinto	9.84	−75.13	KJ493310	KJ492370	KJ493029	N/A	N/A
Mabuya sp. IV	UIS-R-2023	Colombia	Chocó	Itsmina	5.16	−76.68	KJ493311	KJ492371	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2024	Colombia	Chocó	Itsmina	5.16	−76.68	KJ493312	KJ492372	N/A	N/A	N/A
Mabuya sp. IV	ICN-R-11688	Colombia	Córdoba	Tierra Alta	7.96	−76.01	KJ493313	KJ492373	N/A	N/A	N/A
Mabuya sp. IV	Not collected	Colombia	Córdoba	Valencia	8.26	−76.15	KJ493314	KJ492374	KJ493030	N/A	N/A
Mabuya sp. IV	UIS-R-0518	Colombia	Antioquia	Puerto Berrio	6.5	−74.41	KJ493315	KJ492375	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-0528	Colombia	Antioquia	Puerto Berrio	6.5	−74.41	KJ493316	KJ492376	KJ493031	N/A	N/A

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Appendix A (continued)

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
Mabuya sp. IV	UIS-R-1509	Colombia	Santander	Simacota	6.45	−73	KJ493317	KJ492377	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1818	Colombia	Santander	Betulia	6.9	−73.29	KJ493318	KJ492378	KJ493032	N/A	N/A
Mabuya sp. IV	UIS-R-1817	Colombia	Santander	Betulia	6.9	−73.29	KJ493271	KJ492321	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1990	Colombia	Santander	Sogamoso	7.25	−73.78	KJ493272	KJ492322	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1532	Colombia	Santander	Sabana de Torres	7.4	−73.16	N/A	KJ492323	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1991	Colombia	Santander	Lebrija	7.12	−73.22	N/A	KJ492324	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1508	Colombia	Santander	Simacota	6.45	−73	KJ493273	KJ492325	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1477	Colombia	Santander	Pinchote	6.53	−73.17	KJ493274	KJ492326	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1507	Colombia	Santander	Curití	6.61	−73.07	KJ493275	KJ492327	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1505	Colombia	Santander	Valle de San José	6.45	−73.15	N/A	KJ492328	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1506	Colombia	Santander	Valle de San José	6.45	−73.15	KJ493270	KJ492320	KJ493011	N/A	N/A
Mabuya sp. IV	UIS-R-1510	Colombia	Santander	Valle de San José	6.45	−73.15	KJ493276	KJ492329	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-0892	Colombia	Santander	Curití	6.61	−73.07	KJ493277	KJ492330	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1474	Colombia	Santander	Curití	6.61	−73.07	N/A	KJ492331	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-1481	Colombia	Santander	Valle de San José	6.45	−73.15	KJ493278	KJ492332	KJ493012	N/A	N/A
Mabuya sp. IV	UIS-R-1479	Colombia	Santander	Valle de San José	6.45	−73.15	KJ493279	KJ492333	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2011	Colombia	Santander	Curití	6.61	−73.07	KJ493280	KJ492334	KJ493013	N/A	N/A
Mabuya sp. IV	UIS-R-2025	Colombia	Santander	Curití	6.61	−73.07	KJ493281	KJ492335	KJ493014	KJ492972	KJ492992
Mabuya sp. IV	UIS-R-0547	Colombia	Santander	Curití	6.61	−73.07	N/A	KJ492336	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-0573	Colombia	Santander	Curití	6.61	−73.07	KJ493282	KJ492337	N/A	N/A	N/A
Mabuya sp. IV	UIS-R-2019	Colombia	Caldas	Samaná	5.42	−74.99	KJ493283	KJ492338	KJ493015	N/A	N/A
Mabuya unimarginata complex	ANMO 1903	Mexico	Chiapas	Lázaro Cárdenas-Manzanillo	16.14	−92.78	N/A	KJ492385	N/A	N/A	N/A
Mabuya unimarginata complex	ANMO 1103	Mexico	Michoacán	Lázaro Cárdenas-Manzanillo	19.57	−101.71	N/A	KJ492386	N/A	KJ492978	KJ492998
Mabuya unimarginata complex	ANMO 1104	Mexico	Michoacán	No information	19.57	−101.71	N/A	KJ492387	KJ493034	N/A	N/A
Mabuya unimarginata complex	JAC 24023	Mexico	Michoacán	No information	19.57	−101.71	KJ493321	KJ492388	KJ493035	N/A	N/A
Mabuya unimarginata complex	UOGV 1513	Mexico	Guerrero	Coyuca de Benitez	17.01	−100.09	N/A	KJ492389	N/A	N/A	N/A
Mabuya unimarginata complex	JAC 22047	Mexico	Guerrero	Ejido de Bahia	16.86	−99.91	N/A	KJ492390	N/A	KJ492979	KJ492999
Mabuya unimarginata complex	JAC 22167	Mexico	Guerrero	Area alrededor de Chichihualco	17.66	−99.67	N/A	KJ492391	KJ493036	N/A	N/A
Mabuya unimarginata complex	UOGV 1760	Mexico	Oaxaca	Pluma Hidalgo	15.93	−96.42	N/A	KJ492392	N/A	N/A	N/A
Mabuya unimarginata complex	UOGV 1768	Mexico	Oaxaca	Pluma Hidalgo	15.93	−96.42	N/A	KJ492393	KJ493037	N/A	N/A
Mabuya unimarginata complex	UOGV 1767	Mexico	Chiapas	No information	16.14	−92.78	N/A	KJ492394	N/A	N/A	N/A
Mabuya unimarginata complex	RLR 1069	Mexico	Chiapas	No information	16.14	−92.78	KJ493322	KJ492395	N/A	N/A	N/A
Mabuya unimarginata	RLR 1086	Mexico	Chiapas	No information	16.14	−92.78	KJ493323	KJ492396	N/A	N/A	N/A

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Appendix A (continued)

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
complex											
<i>Mabuya unimarginata</i> complex	RLR 1110	Mexico	Chiapas	No information	16.14	−92.78	KJ493324	KJ492397	N/A	N/A	N/A
<i>Mabuya unimarginata</i> complex	ANMO 1943	Mexico	Chiapas	Cintalapa	16.64	−93.76	N/A	KJ492381	N/A	N/A	N/A
<i>Mabuya unimarginata</i> complex	ANMO 1944	Mexico	Chiapas	Cintalapa	16.64	−93.76	N/A	KJ492382	N/A	N/A	N/A
<i>Mabuya unimarginata</i> complex	ANMO 1045	Mexico	Oaxaca	Pie de la Sierra Madre Al N de Zanatepec	16.75	−94.38	N/A	KJ492383	KJ493033	KJ492977	KJ492997
<i>Mabuya unimarginata</i> complex	JAC 22922	Mexico	Oaxaca	Col. Rudolfo Figueroa	17.05	−96.71	N/A	KJ492384	N/A	N/A	N/A
<i>Mabuya agilis</i>	E11108	Brazil		Pernambuco	−8.81	−36.95	AY151428	EU443102	N/A	N/A	N/A
<i>Mabuya agilis</i>	LG 464	Brazil	Bahia	Jacobina	−11.19	−40.54	DQ239256	DQ239175	N/A	N/A	N/A
<i>Mabuya agilis</i>	MRT 1206	Brazil	Espírito Santo	UHE Rosal	−20.92	−41.72	DQ239233	DQ239152	N/A	N/A	N/A
<i>Mabuya agilis</i>	SC 21	Brazil	Piauí	Serradas Confusoes	−7.07	−40.88	DQ239251	DQ239170	N/A	N/A	N/A
<i>Mabuya agilis</i>	MRT 3951	Brazil	Tocantins	Peixe	−12.04	−48.54	DQ239207	DQ239126	N/A	N/A	N/A
<i>Mabuya agmosticha</i>	LG 902	Brazil	Algoas	Xingó	−9.57	−36.78	DQ239215	DQ239134	N/A	N/A	N/A
<i>Mabuya agmosticha</i>	LG 901	Brazil	Algoas	Xingó	−9.57	−36.78	DQ239214	DQ239133	N/A	N/A	N/A
<i>Mabuya alliacea</i>	Not collected	Costa Rica		Tortugueros	10.54	−83.51	EU477271	EU443125	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	MNHN 2006.0291	Peru		San Martín	−6.48	−76.36	DQ368663	EU443103	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	MBS 001	Brazil	Acre	Estirão do Panela, PNSD	−8.99	−70.81	DQ239210	DQ239129	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	OMNH 37191	Brazil	Amazonas	Rio Ituxi, Madeirera Scheffer	−8	−65.33	GQ982525	GQ982545	N/A	N/A	N/A
<i>Mabuya altamazonica</i>	MHNC 6703	Peru	San Martín	PN. Rio Abiseo	−7.36	−76.84	EU515210	EU515212	N/A	N/A	N/A
<i>Mabuya aurae</i>	E11103	Trinidad and Tobago	Trinidad	Talparo	10.51	−61.27	AY151436	GQ982565	N/A	N/A	N/A
<i>Mabuya aurae</i>	E11104	Trinidad and Tobago	Trinidad	Talparo	10.51	−61.27	AY151437	GQ982566	N/A	N/A	N/A
<i>Mabuya aurae</i>	CAS 231775	Trinidad and Tobago		Manzanilla Beach			N/A	JN246081	N/A	N/A	N/Af
<i>Mabuya aurae</i>	SBH 268935	Lesser Antilles	Saint Vincent and the Grenadines	Grenadines, Union Island	12.6	−61.43	JN227576	JN227555	N/A	N/A	N/A
<i>Mabuya aurae</i>	WES 636	Venezuela		Sucre, Península de Paria	10.63	−62.41	GQ982544	GQ982567	N/A	N/A	N/A
<i>Mabuya aurae</i>	MHNLS 17080	Venezuela		Aragua	10.45	−67.84	EU477268	EU443121	N/A	N/A	N/A
<i>Mabuya aurulae</i>	ZFMK 62603	Trinidad and Tobago		Tobago island	11.23	−60.65	AY070339	N/A	N/A	N/A	N/A

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Appendix A (continued)

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
<i>Mabuya bistrata</i>	Not collected	Francia		Guiana	4.85	−52.33	DQ368664	EU443105	N/A	N/A	N/A
<i>Mabuya bistrata</i>	OMNH 37183	Brazil		Amazonas	−8.05	−65.72	EU477258	EU443104	N/A	N/A	N/A
<i>Mabuya bistrata</i>	SBH 267186	Fr. Guiana		Macouria	4.92	−52.37	JN227577	JN227556	N/A	N/A	N/A
<i>Mabuya brachypoda</i>	UTA 41513	Guatemala		Zacapa	15.12	−89.32	EU477272	EU443126	N/A	N/A	N/A
<i>Mabuya brachypoda</i>	SMF 79851	Honduras		I. de la Bahía Isla de Útila	16.34	−86.5	AB057378	N/A	N/A	N/A	N/A
<i>Mabuya brachypoda</i>	UTA 41227	Honduras		Olancho Las Trojas	15.36	−86.7	EU477273	EU443127	N/A	N/A	N/A
<i>Mabuya brachypoda</i>	Not collected	Mexico		Guerrero	17.66	−99.67	EU477274	EU443128	N/A	N/A	N/A
<i>Mabuya brachypoda</i>	Not collected	Mexico		Oaxaca	17.06	−96.72	EU477275	EU443129	N/A	N/A	N/A
<i>Mabuya caicosae</i>	SBH 266355	Greater Antilles	Turks and Caicos Islands	North Caicos	21.87	−71.98	JN227578	JN227557	N/A	N/A	N/A
<i>Mabuya caicosae</i>	SBH 266356	Greater Antilles	Turks and Caicos Islands	North Caicos	21.87	−71.98	JN227579	JN227558	N/A	N/A	N/A
<i>Mabuya caicosae</i>	SBH 266357	Greater Antilles	Turks and Caicos Islands	North Caicos	21.87	−71.98	JN227580	JN227559	N/A	N/A	N/A
<i>Mabuya caissara</i>	MNRJ 9485	Brazil	Sao Paulo	Caraguatatuba, Massaguassu beach	−23.62	−45.41	AF548788	N/A	N/A	N/A	N/A
<i>Mabuya caissara</i>	MNRJ 9476	Brazil	Sao Paulo	Caraguatatuba, Massaguassu beach	−23.62	−45.41	AF548787	N/A	N/A	N/A	N/A
<i>Mabuya carvalhoi</i>	OMNH 36332	Brazil		Roraima	2.74	−62.08	EU477259	EU443106	N/A	N/A	N/A
<i>Mabuya cochabambae</i>	ZFMK 72151	Bolivia		Santa Cruz	−18.09	−64.12	AF202625	N/A	N/A	N/A	N/A
<i>Mabuya croizati</i>	MNHN 17670	Venezuela	Antzoátegui	Cerro El Guamal	8.59	−63.96	EU477260	EU443107	N/A	N/A	N/A
<i>Mabuya culebrae</i>	SBH 268453	Puerto Rico		Culebra	18.32	−65.29	JN227581	JN227560	N/A	N/A	N/A
<i>Mabuya dorsivitata</i>	E 11106	Brazil		D.F.	−15.78	−47.93	AY151426	EU443108	N/A	N/A	N/A
<i>Mabuya dorsivitata</i>	LG 1089	Brazil		Sao Paulo	−23.55	−46.64	DQ239257	DQ239176	N/A	N/A	N/A
<i>Mabuya dorsivitata</i>	Lav-5000	Argentina	Cordoba	Rio Cuarto City	−33.13	−64.35	DQ239230	DQ239149	N/A	N/A	N/A
<i>Mabuya falconensis</i>	MHNLS 17095	Venezuela		Falcón	11.92	−70	EU477261	EU443109	N/A	N/A	N/A
<i>Mabuya falconensis</i>	Not collected	Venezuela		Falcón	11.92	−70	EU477262	EU443110	N/A	N/A	N/A
<i>Mabuya falconensis</i>	ZFMK62603	Trinidad and Tobago		Trinidad and Tobago	11.23	−60.7	AY070339	N/A	N/A	N/A	N/A
<i>Mabuya frenata</i>	E 11107	Brazil		Mato Grosso Do Sul	−20.77	−54.79	AY151427	EU443111	N/A	N/A	N/A
<i>Mabuya frenata</i>	LG 861	Brazil	Gois	Santa Rita do Araguaia	−17.33	−53.2	DQ239209	DQ239128	N/A	N/A	N/A
<i>Mabuya frenata</i>	SC 28	Brazil	Piaui	Serra das Confusoes	−6.18	−41.84	DQ239254	DQ239173	N/A	N/A	N/A
<i>Mabuya frenata</i>	PNA 77	Brazil	Tocantins	Parque Nacional do Araguaia	−9.92	−50.21	DQ239246	DQ239165	N/A	N/A	N/A
<i>Mabuya fulgidus</i>	SBH 267953	Jamaica		St. Catherine	18.04	−77.06	JN227583	JN227562	N/A	N/A	N/A
<i>Mabuya fulgidus</i>	SBH 267954	Jamaica		St. Catherine	18.04	−77.06	JN227584	JN227563	N/A	N/A	N/A
<i>Mabuya fulgidus</i>	SBH 267955	Jamaica		St. Catherine	18.04	−77.06	JN227585	JN227564	N/A	N/A	N/A
<i>Mabuya guaporicola</i>	UTA 55700	Bolivia		Beni	−14.37	−66.58	EU477263	EU443113	N/A	N/A	N/A
<i>Mabuya guaporicola</i>	E 11101	Brazil		Mato Grosso Do Sul	−20.77	−54.79	AY151434	EU443112	N/A	N/A	N/A
<i>Mabuya guaporicola</i>	LG 1574	Brazil	Mato Grosso	UHE Manso	−15.63	−56.06	DQ239250	DQ239169	N/A	N/A	N/A

(continued on next page)

Appendix A (continued)

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
<i>Mabuya guaporicola</i>	PNA 185	Brazil	Tocantins	Parque Nacional do Araguaia	−9.92	−50.21	DQ239222	DQ239141	N/A	N/A	N/A
<i>Mabuya heathi</i>	MRT 3671	Brazil	Bahia	Mocambo do Vento	−10.8	−42.9	DQ239244	DQ239163	N/A	N/A	N/A
<i>Mabuya heathi</i>	907101	Brazil	Bahia	Jacobina	−11.19	−40.54	DQ239232	DQ239151	N/A	N/A	N/A
<i>Mabuya heathi</i>	907011	Brazil	Bahia	Alagoado	−11.28	−41.3	DQ239231	DQ239150	N/A	N/A	N/A
<i>Mabuya heathi</i>	MNRJ 6655	Brazil	Bahia	Abrolhos archipelago, Siriba island	−17.93	−39.18	AF548785	N/A	N/A	N/A	N/A
<i>Mabuya heathi</i>	MNRJ 6663	Brazil	Bahia	Abrolhos archipelago, Siriba island	−17.93	−39.18	AF548786	N/A	N/A	N/A	N/A
<i>Mabuya heathi</i>	MNRJ 8361	Brazil	Rio Grande do Norte	Natal	−5.79	−35.21	AF548784	N/A	N/A	N/A	N/A
<i>Mabuya lineolatus</i>	USNM 329347	Haiti		l'Artibonite	19.12	−72.48	JN227586	JN227565	N/A	N/A	N/A
<i>Mabuya dominicana</i>	Not collected	Lesser Antilles		Dominica island	15.49	−61.37	EU477265	EU443115	N/A	N/A	N/A
<i>Mabuya dominicana</i>	Not collected	Lesser Antilles		Dominica island	15.49	−61.37	EU477264	EU443114	N/A	N/A	N/A
<i>Mabuya macleani</i>	USNM 576303	British Virgin Islands		Carrot Rock	18.32	−64.57	JN227587	JN227566	N/A	N/A	N/A
<i>Mabuya macrorhyncha</i>	LG 1102	Brazil		Ilha da Queimada Grande	−24.48	−46.68	DQ239243	DQ239162	N/A	N/A	N/A
<i>Mabuya macrorhyncha</i>	LG 1103	Brazil	Sao Paulo	Ilha da Queimada Grande	−23.54	−46.7	DQ239213	DQ239132	N/A	N/A	N/A
<i>Mabuya meridensis</i>	Not collected	Venezuela		Mérida	8.6	−71.15	EU477266	EU443116	N/A	N/A	N/A
<i>Mabuya meridensis</i>	MHNLS 17081	Venezuela	Mont Zerpa	Near Mérida	8.6	−71.15	EU477267	EU443117	N/A	N/A	N/A
<i>Mabuya monitae</i>	USNM 576301	Puerto Rico		Islote Monito	18.16	−67.95	JN227588	JN227567	N/A	N/A	N/A
<i>Mabuya nebulosylvestris</i>	MHNLS 17088	Venezuela		Aragua	10.41	−67.29	EU477280	EU443134	N/A	N/A	N/A
<i>Mabuya nebulosylvestris</i>	Not collected	Venezuela		Aragua	10.41	−67.29	EU477281	EU443135	N/A	N/A	N/A
<i>Mabuya nebulosylvestris</i>	MHNLS 17106	Venezuela		Lara	9.79	−69.58	EU477282	EU443136	N/A	N/A	N/A
<i>Mabuya nebulosylvestris</i>	MHNLS 17330	Venezuela		Miranda	10.34	−67.04	EU477283	EU443137	N/A	N/A	N/A
<i>Mabuya nebulosylvestris</i>	Not collected	Venezuela		Trujillo	9.37	−70.43	EU477284	EU443138	N/A	N/A	N/A
<i>Mabuya nebulosylvestris</i>	MHNLS 16649	Venezuela		Trujillo	9.37	−70.43	EU477285	EU443139	N/A	N/A	N/A
<i>Mabuya nebulosylvestris</i>	MHNLS 17093b	Venezuela		Vargas	10.42	−67.33	EU477286	EU443140	N/A	N/A	N/A
<i>Mabuya nebulosylvestris</i>	MHNLS 17103	Venezuela		Vargas	10.42	−67.33	EU477287	EU443141	N/A	N/A	N/A

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Appendix A (continued)

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
<i>nebulosylvestris</i>											
<i>Mabuya nigropalmata</i>	MHNC 5718	Peru	Madre de Dios	Manu National Park	−12.01	−71.76	EU515211	EU515213	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LSUMZ H-14223	Brazil		Pará	−3.15	−54.84	DQ368667	EU443118	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 36318	Brazil		Roraima	2.82	−60.68	DQ368668	EU443119	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	E111016	Colombia		Guanía	3.88	−67.9	AY151438	EU443120	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LSUMZ H-13610	Brazil	Acre	5 km N. Port Walter, inland from the Rio Juruá	−8.26	−72.78	DQ238269	DQ239188	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LSUMZ H-13900	Brazil	Acre	5 km N. Port Walter, inland from the Rio Juruá	−8.26	−72.78	DQ239190	DQ239109	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MRT 6300	Brazil	Amapá	Igarapé Camaipi	−0.25	−52.4	DQ239211	DQ239130	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MRT 6303	Brazil	Amapá	Igarapé Camaipi	−0.25	−52.4	DQ239212	DQ239131	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LSUMZ H-16446	Brazil	Amazonas	Castanho, S. Manaus	−3.05	−59.9	GQ982526	GQ982546	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 37687	Brazil	Amazonas	Castanho, S. Manaus	−3.05	−59.9	GQ982527	GQ982547	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LSUMZ H-16489	Brazil	Amazonas	Castanho, S. Manaus	−3.05	−59.9	DQ239192	DQ239111	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LSUMZ H-16490	Brazil	Amazonas	S. Manaus	−3.05	−59.9	DQ239193	DQ239112	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 37186	Brazil	Amazonas	Rio Ituxí, Madeirera Scheffer	−8.35	−65.72	GQ982528	GQ982548	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	CHUNB 9624	Brazil	Brazil DF	Brazilía	−15.83	−47.92	AF548783	N/A	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MRT 154	Brazil	Ceara	Mulungú	−4.3	−39	DQ239240	DQ239159	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MRT 097	Brazil	Ceara	Pacoti	−4.22	−38.93	DQ239238	DQ239157	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LG 1085	Brazil	Goiás	Niquelandia	−14.46	−48.45	DQ239249	DQ239168	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	967956	Brazil	Mato Grosso	Aripuaña	−9.73	−59.48	DQ239255	DQ239174	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	967904	Brazil	Mato Grosso	Aripuaña	−9.73	−59.48	DQ239261	DQ239180	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LG 1561	Brazil	Mato Grosso	UHE Manso	−15.63	−56.06	DQ239253	DQ239172	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 36830	Brazil	Pará	Agropecuaria Treviso LTDA	−3.15	−54.84	GQ982529	GQ982549	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MRT 916872	Brazil	Pará	Alter do Chao	−2.52	−54.95	DQ239258	DQ239177	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LG 756	Brazil	Pará	Vai-Quem-Quer	−1.43	−53.56	DQ239239	DQ239158	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MRT 2502	Brazil	Piauí	Urucuí-uma	−7.23	−44.55	DQ239248	DQ239167	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 37414	Brazil	Rondonia	Parque Estadual Guajara-Mirim	−1.32	−64.55	GQ982530	GQ982550	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 37417	Brazil	Rondonia	Parque Estadual Guajara-Mirim	−1.32	−64.55	GQ982531	GQ982551	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 37416	Brazil	Rondonia	Parque Estadual Guajara-Mirim	−1.32	−64.55	GQ982532	GQ982552	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 37413	Brazil	Rondonia	Parque Estadual Guajara-Mirim	−1.32	−64.55	GQ982533	GQ982553	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LSUMZ H17864	Brazil	Rondonia	Parque Estadual	−1.32	−64.55	DQ239194	DQ239113	N/A	N/A	N/A

(continued on next page) 21

Appendix A (continued)

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
<i>Mabuya nigropunctata</i>	OMNH 36316	Brazil	Roraima	Guajara-Mirim Fazenda Nova Esperança	−12.99	−58.76	GQ982534	GQ982554	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	OMNH 36317	Brazil	Roraima	Fazenda Nova Esperança	−12.99	−58.76	GQ982535	GQ982555	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	LSUMZ H12311	Brazil	Roraima	Fazenda Nova Esperança	−12.99	−58.76	DQ239268	DQ239187	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	BPN 160	Guyana			−5.63	−60.25	GQ982536	GQ982556	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	Not collected	Fr. Guiana		Mitaraka a	2.27	−54.52	GQ982537	GQ982557	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	Not collected	Fr. Guiana		Mitaraka b	2.27	−54.52	GQ982538	GQ982558	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MNHN 2005-9719	Fr. Guiana		St Eugene	4.85	−53.06	DQ368666	GQ982559	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MNHN 2005.9721	Fr. Guiana		St Eugene	4.85	−53.06	GQ982539	GQ982560	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MNHN 2005.9717	Fr. Guiana		St Eugene	4.85	−53.06	GQ982540	GQ982561	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MNHN 2005.9720	Fr. Guiana		St Eugene	4.85	−53.06	GQ982541	GQ982562	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	Michel Blanc	Fr. Guiana		Summit of the Pic Coudreau	2.25	−54.39	GQ982542	GQ982563	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	MNHN 2004.0103	Fr. Guiana		Summit of the Pic Coudreau	2.25	−54.39	GQ982543	GQ982564	N/A	N/A	N/A
<i>Mabuya nigropunctata</i>	SBH 267187	French Guiana		St. Eugene	5.5	−54.03	JN227589	JN227568	N/A	N/A	N/A
<i>Mabuya powelli</i>	Not collected	Lesser Antilles	St Barthélémy island		17.94	−62.84	EU477269	EU443122	N/A	N/A	N/A
<i>Mabuya powelli</i>	Not collected	Lesser Antilles	St Barthélémy island		17.94	−62.84	N/A	EU443123	N/A	N/A	N/A
<i>Mabuya powelli</i>	SBH 267292	Lesser Antilles	Anguilla island	Junk's Hole	18.2	−63.07	JN227590	JN227569	N/A	N/A	N/A
<i>Mabuya powelli</i>	SBH 267291	Lesser Antilles	Anguilla island	Junk's Hole	18.2	−63.07	JN227591	JN227570	N/A	N/A	N/A
<i>Mabuya roatanae</i>	SBH 269383	Honduras		Roatan	16.32	−86.54	JN227592	JN227571	N/A	N/A	N/A
<i>Mabuya semitaeniatus</i>	YPM 15082	Lesser Antilles		British Virgin Islands	18.42	−64.64	EU477270	EU443124	N/A	N/A	N/A
<i>Mabuya semitaeniatus</i>	MCZ R 185692	British Virgin Islands		Mosquito Island	18.51	−64.39	JN227593	JN227572	N/A	N/A	N/A
<i>Mabuya sloanii</i>	USNM 576305	USA	Saint Thomas	Saba Island	18.31	−65	JN227594	JN227573	N/A	N/A	N/A
<i>Mabuya sloanii</i>	USNM 576306	USA	Saint Thomas	Saba Island	18.31	−65	N/A	JN227574	N/A	N/A	N/A
<i>Mabuya sloanii</i>	USNM 576307	USA	Saint Thomas	Saba Island	18.31	−65	N/A	JN227575	N/A	N/A	N/A
<i>Mabuya zuliae</i>	MHNLS 16676	Venezuela		Zulia	8.61	−72.53	EU477276	EU443130	N/A	N/A	N/A
<i>Mabuya zuliae</i>	MHNLS 16677	Venezuela		Zulia	8.61	−72.53	EU477277	EU443131	N/A	N/A	N/A
<i>Mabuya zuliae</i>	MHNLS 16647	Venezuela		Zulia	10.73	−71.65	EU477278	EU443132	N/A	N/A	N/A

Appendix A (continued)

Species	Source	Country	Department	Specific locality	Latitude	Longitude	12S rRNA	Cytb1, Cytb2	Rag2	NGFB	R35
<i>Mabuya zuliae</i>	MNHN 2007.0273 SBH 268001	Venezuela		Zulia	10.81	-72.35	EU477279	EU443133	N/A	N/A	N/A
<i>Mabuya dominicana</i>		Lesser Antilles	Dominica island	Jimmits	15.38	-61.39	JN227582	JN227561	N/A	N/A	N/A
<i>Plestiodon egregius</i>	MVZ 150128	North America	Florida	Florida	27.61	-81.54	N/A	AB016606	N/A	N/A	N/A
<i>Trachylepis vittata</i>	BEV 1446	Turkey	Northern Cape Prov	Osman Dere Richtersveld Nat. Park	38.93	40.53	EU477288	EU443142	N/A	N/A	N/A
<i>Trachylepis capensis</i>	AMB 4765	South Africa			28.11	17.02	DQ239259	DQ239178	N/A	N/A	N/A
<i>Trachylepis perrotetii</i>	FMNH 262227	Ghana		USFWS	5.65	-0.17	DQ239227	DQ239146	N/A	N/A	N/A
<i>Plestiodon laticeps</i>	S8	USA	Florida	Duval Co., Little Talbot Island	30.46	-81.42	AY218039	EU116510	N/A	N/A	N/A

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympbev.2015.07.016>.

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