Article

A morphological and molecular revision of lizards of the genus *Marisora* Hedges & Conn (Squamata: Mabuyidae) from Central America and Mexico, with descriptions of four new species

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Abstract

The skink genus *Marisora* ranges from Mexico to northern South America and occurs on some islands in the Caribbean Sea. We conducted a revision of the genus *Marisora* from Mexico and Central America, using new morphological and molecular data, and find support for the five previously described species (*Marisora alliacea, M.aurulae, M. brachypoda, M. magnacornae,* and *M. roatanae*) and describe four new species: *Marisora lineola* **sp. nov.**, *M. aquilonaria* **sp. nov.**, *M. syntoma* **sp. nov.**, and *M. urtica* **sp. nov.** We show that two species previously known only from Central American islands, *M. magnacornae* and *M. roatanae*, also occur on the adjacent mainland and that two species recently placed in *Alinea* belong to this evolutionary clade: *Marisora berengerae* **n. comb.** and *Marisora pergravis* **n. comb**. Together with *M. falconensis* and *M. unimarginata*, these 13 species of *Marisora* arose mostly in the Pliocene and are largely allopatric but are sympatric and nearly sympatric at several locations in Central America where they maintain their morphological and genetic distinctiveness.

Key words: reptile, skink, evolution, systematics, taxonomy, classification, ecology, conservation, reproduction, biogeography, Middle America

Introduction

Skinks of the genus *Marisora* Hedges & Conn in Middle America (Central America and Mexico) occur at low, moderate, and occasionally at lower portions of intermediate elevations (rarely to about 2000 m) from northern Nayarit and central Veracruz, Mexico, into northern South America (Hedges & Conn 2012). That large distribution also includes several Caribbean islands off the coast of Mexico, Central, and South America, and several Pacific Ocean islands in the Golfo de Fonseca in southern Honduras, and on the Archipiélago de las Perlas, Panama. Hedges & Conn (2012) proposed new species names for three Caribbean and South American island populations (*M. aurulae, M. magnacornae,* and *M. roatanae*) and resurrected the Central American mainland *M. alliacea* (Cope) and *M. brachypoda* (Taylor) along with *M. unimarginata* (Cope).

Hedges & Conn (2012) further suggested that several other mainland populations of *Marisora* from Middle America and Colombia likely represent undescribed species. Those authors examined museum specimens and collected new morphological data for all species they recognized. They also conducted a new molecular phylogenetic analysis of the group, but lacked genetic data for several of the species: *M. berengerae, M. magnacornae, M. pergravis,* and *M. unimarginata* (*sensu stricto*). The results of Hedges & Conn (2012) supported the earlier morphological results of Taylor (1956) regarding the distinction of *M. alliacea*, *M. brachypoda*, and *M. unimarginata*. Those results also disagreed with the conclusions of Savage (1973, 2002), who recognized only a single species, *M. unimarginata*. The *M. unimarginata* species description provided by Savage (2002) was taken from the literature, especially from Taylor (1956) and Dunn (1936), including the specific values of characters given by those two authors.

Pinto-Sánchez *et al.* (2015) conducted a molecular phylogenetic analysis of mabuyid skinks of the Americas, with a focus on Colombia, and revised the taxonomy. They contributed new sequence data for Colombian mainland skinks (putative new species), some Middle American skinks, and two Colombian species occurring on Caribbean islands, *Marisora berengerae* and *M. pergravis*. Morphological data for several South American species were presented, but those authors did not morphologically diagnose or describe any new species. In addition, their phylogenetic trees showed that their Colombian specimens were part of the Middle American clade (*Marisora*), but they did not examine museum specimens or present morphological data for Middle American *Marisora*. Although Hedges and Conn (2012) described *Marisora* and presented morphological data that diagnosed species in that genus, Pinto-Sánchez *et al.* (2015) did not refer to those morphological data and instead relied on their molecular phylogeny for taxonomic decisions.

The new sequence data of Pinto-Sánchez *et al.* (2015) had limitations. Although the 12S rRNA and cytochrome B sequence data could be used jointly (concatenated) with available data from earlier studies, the three nuclear genes they sequenced had little or no value. Firstly, those genes were unavailable from the public databases for almost all of the other mabuyid skinks being compared in their tree, and secondly they were nearly invariant, providing only 4% of the total parsimony informative sites according to those authors. For that reason, the nuclear data analysed separately showed essentially no phylogenetic resolution (their figure S4). Lastly, Pinto-Sánchez *et al.* (2015) relied on taxonomic labels applied to Genbank data, which are sometimes problematic, to make taxonomic decisions, instead of examining museum vouchers.

Therefore, the molecular information in the study of Pinto-Sánchez *et al.* (2015) was primarily from two mitochondrial genes: the slow-evolving 12S rRNA and fast-evolving cytochrome b. An additional limitation was that many skink species and specimens lacked one or the other primary mitochondrial gene, which distorted quantitative measures of divergence. For example, the cytochrome b distance separating two species can be several times greater than the 12S rRNA distance separating the same species. Although missing data may not be a major problem for tree building, it can mislead species-level conclusions based on branch length, which happened in the case of Pinto-Sánchez *et al.* (2015), where they made taxonomic decisions based on lengths of branches.

For example, Pinto-Sánchez *et al.* (2015) synonymized *Marisora aurulae* and *M. roatanae* with their closest species because of genetic distances that they perceived as too low. In both cases, they did this without considering diagnostic morphological differences or sequence size. Their *M. aurulae* sequence is a short segment of the slow-evolving gene, 12S rRNA, explaining the low genetic distance. In contrast, the species was shown to be diagnosable from *M. falconensis* by morphological characters (Hedges & Conn 2012) that were not addressed by Pinto-Sánchez *et al.* (2015). We show below that *M. roatanae* is a valid species with a wider distribution that includes museum specimens identified incorrectly as other species (*M. brachypoda* and *M. unimarginata*). Again, the absence of specimen examination by Pinto-Sánchez *et al.* (2015) resulted in taxonomic errors.

The molecular phylogeny of Pinto-Sánchez *et al.* (2015) showed that all but one of the 16 genera erected by Hedges & Conn (2012) for the 61 species of mabuyid skinks in the Americas was monophyletic, corroborating the Hedges & Conn (2012) classification. That was not a surprise because they used virtually the same sequence data set. However, they chose to abandon the generic classification of Hedges & Conn (2012) and recognize a single genus, *Mabuya*, for all 61 species. They based this decision on the clustering of the two newly-added species sequences, *M. berengerae* and *M. pergravis,* with species of the genus *Marisora* instead of *Alinea*, where they had been placed by Hedges & Conn (2012). We reject this decision because a simpler and more stable taxonomic change would be to move those two species from *Alinea* to *Marisora* rather than to deconstruct the entire generic-level classification of mabuyid species in the Western Hemisphere.

Marisora berengerae **n. comb.** and *Marisora pergravis* **n. comb.** differ from the two (remaining) species of *Alinea*, *A. lanceolata* and *A. luciae*, in having a more attenuate body shape (versus heavier-bodied in *Alinea*) and in lacking ventral striping (versus ventral striping present in *Alinea*). In both characters, they agree with species of *Marisora*, supporting the molecular data. Pinto-Sánchez *et al.* (2015) did not comment on those characters, detailed in Hedges & Conn (2012).

The main focus of the study by Pinto-Sánchez *et al.* (2015) was the clade of species known as *Marisora*. Their tree confirmed the work of Hedges & Conn (2012) that this clade, now including the new Colombian material, is monophyletic. However, surprisingly, they synonymized the Middle American species *M. alliacea*, *M. brachypoda*, and *M. roatanae* into a single species *M. unimarginata*. They did so claiming that those three species, particularly *M. brachypoda*, were not monophyletic in their tree. This was a mistake for two reasons. First, they ignored the earlier work of Hedges & Conn (2012), which clarified the taxonomy and provided morphological evidence and diagnostic characters. Secondly, they did not examine the voucher specimens of the tissues they used and therefore used the taxonomic names provided by museums, without scrutiny. However, museums rarely have the resources to guarantee that every specimen is correctly identified according to the latest taxonomic study and instead rely on researchers to study them and revise the taxonomy. In this case, some museums used "*M. brachypoda*" while others "*M. unimarginata*" for all Middle American species simply because the usage had alternated in the literature over decades. In other words, the justification of Pinto-Sánchez *et al.* (2015) for considering *M. brachypoda* and *M. unimarginata* to be non-monophyletic was a data handling error. If they had examined museum specimens of Mexican and Central American populations, they would have found what we found here (see below) that there are multiple new species and all show complete consistency between the molecular and morphological data. Also, Pinto-Sánchez *et al.* (2015) apparently overlooked, entirely, the species *Marisora magnacornae* (Hedges & Conn 2012), as it is not mentioned in their treatment.

Separately, Pinto-Sánchez *et al.* (2015) implemented a molecular method of species delimitation (GMYC) with their molecular phylogeny, and as a result, synonymized several species of threatened skinks on Caribbean islands: *Spondylurus culebrae, S. monitae,* and *S. macleani*. Each of these three species is endemic to a separate, small island and has diagnostic morphological characters (Hedges & Conn 2012). They misused the species delimitation method, which is not intended to be used unilaterally when there is contradictory morphological data (Fujisawa & Barraclough 2013). Pinto-Sánchez *et al.* (2015:191) did this despite acknowledging that limitation of the method, stating "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* [emphasis ours], these named species should likely be synonymized." For these reasons, we reject the decision by Pinto-Sánchez *et al.* to synonymize these three species (also see Hedges *et al.* 2019).

Hedges & Conn (2012) had already examined morphological differences among species of *Marisora*, sufficiently to diagnose seven of them, two of which (*M. alliacea* and *M. unimarginata*) were originally diagnosed by Cope (1862, 1875) and an additional one (*M. brachypoda*) by Taylor (1956). However, it was also clear from molecular phylogenies and specimens that additional (undescribed) species were present, especially in Middle America, and therefore we undertook this revision.

Herein we present a morphological revision of Middle American *Marisora* and an updated molecular phylogeny containing new sequences, including the first of the type species, *M. unimarginata* (*sensu stricto*). We focus on Mexican and Central American populations of these skinks but include genetic material from throughout the region and the geographical distribution of the genus. Our genetic results, supported by morphology, suggest that at least four new names are needed for those Middle American populations.

Material and methods

Morphological analyses

Abbreviations used for measurements and morphometrics in species descriptions include: EAL-ear opening length; FLL-forelimb length; HL-head length; HLL-hind limb length; HW-head width; SVL-snout-vent length; SW-snout width; and TAL-tail length. All measurements, except some SVL, were taken to the nearest 0.1 mm using dial calipers and the aid of a microscope. Some SVL measurements were taken by drawing a line on a tabletop for the snout and making another line at the cloacal opening of the straightened lizard. The distance between those lines were determined to the nearest 0.5 mm with a 12" ruler. All photographs taken by McCranie unless otherwise noted.

We tried to examine specimens from the vicinities of the localities where we had molecular data. Since there is a large hiatus in our molecular data from between Guerrero and the Isthmus of Tehuantepec region, Mexico, there is also that same hiatus in specimens examined. References to all specimens examined are included in the individual new species descriptions (Appendix 1 includes those data for previously described species). All new genetic data are from the laboratory of S.B.H. All color characters given are in preservative. Palm and sole color was considered dark brown or black if they were much darker than the adjacent limb and similar to the adjacent lamella color. Those surfaces were scored as pale brown if they were some shade of brown but were considerably paler than the adjacent lamella. Measuring limb length in these skinks can be difficult because it is normally impossible to completely stretch out a limb in a preserved specimen. Therefore, two measurements were made for each limb. For example, for the forelimb one measurement consisted of the distance between the limb insertion point to the outer edge of the elbow and the second measurement was taken from the outer edge of the elbow to the tip of the longest toe. A similar method was used for the hind limb and all four measurements were combined and divided by the SVL of that individual lizard. All coordinates given are in WGS84 datum.

We generally follow the format used by Hedges & Conn (2012) in their new species accounts for each new name we propose in this study. An exception is that we added two numbered and two unnumbered characters to the opening paragraph of each Diagnosis. We also reproduce a slightly edited version of skink head scalation (Fig. 1) and pattern elements (Fig. 2), from Hedges & Conn (2012; figs. 3, 4). Four described species of *Marisora* that are restricted to islands in the western Caribbean (*M. berengerae* **n. comb.**, *M. pergravis* **n. comb.**) and the South American mainland or the southern Lesser Antilles (*M. aurulae, M. falconensis*) were not examined morphologically for this study. The reader is referred to Hedges & Conn (2012) for recent accounts of those four species. However, Table 1 gives a list of all 13 *Marisora* species we recognize and notes on their geographical distributions. Table 3 gives some morphological variation for the nine species included in this study.

The synonymies included herein for the new species contain those references (beginning with Günther 1885) that include morphological data based on specimens examined, mention museum numbers, or provide specific locality data for the species in question. The synonymies for the previously described species contain the reference to the original description, the reference to the first use of the current name combination as used by Hedges & Conn (2012), and subsequently published data, including the name combination used by Pinto-Sánchez *et al.* (2015).

Unfortunately, many GenBank sequences of *Marisora* lack information on specimen vouchers and the current location of many "vouchers" proved untraceable. Others lack essential locality data. Some specimens sampled for DNA were not preserved, which is understandable given permitting restrictions. Despite the hurdles of poorly documented data, we made an effort to examine all tissue voucher specimens we could track down. We also examined lizard specimens from localities as close as possible to the known locality for each tissue sample. We provide museum vouchers and locality data for as many tissue samples as possible.

The four new species described below were realized as distinct lineages by our genetic results; some of those forms needing names were also previously recovered by Pinto-Sánchez *et al.* (2015) using some of the same tissue sources, but those authors did not discuss those monophyletic clades.

Molecular analyses

The molecular data set comprised 140 individuals (Appendix 2) and 4209 total aligned nucleotide sites from three mitochondrial and three nuclear genes, respectively: 12S ribosomal RNA (rRNA, 871 bp), 16S rRNA (536 bp), cytochrome b (cyt b, 1119 bp), nerve growth factor beta (NGFB, 603 bp), recombination activating protein 2 (RAG2, 429 bp), and RNA fingerprint protein 35 (R35, 651 bp). We contributed 136 new sequences from 52 samples, with other sequence data derived from public sequence databases (Genbank 2018) published in earlier studies (Pinto-

Sánchez *et al.*, 2015; Hedges and Conn, 2012). All of our new sequences come from the three mitochondrial genes (12S rRNA, 16S rRNA, and cyt b). Sequences of the three nuclear genes (NGFB, RAGs, and R35) are from the study of Pinto-Sánchez *et al.* (2015), where those authors acknowledged that they contributed only a small percentage (4 %) of the parsimony-informative sites, and, when analyzed separately (their figure S4), showed essentially no phylogenetic resolution. We include them here only for completeness.

Methods used for the collection of new DNA sequence data are detailed elsewhere (Heinicke *et al.*, 2015). Briefly, DNA extraction was performed with the DNeasy Tissue Kit (Qiagen) with amplification and sequencing performed using these primers: CytBL3 (ATACAYTACACAGCRGAYAT), CytBH3 (TGGGTGTTCK-ACTGGTTGTCC), CytBS1L (GAAAAACCGCYRTTGTWWTTCAACTA), and CytBH15 (ACTGGTTGDC-CYCCRATYCAKGTKAG) for *cytochrome B*; 12L9 (AAAGCAHRRCACTGAARATGYYDAGA), 12H11 (CACTTTCCAGTACGCTTACCATGTTACG), 12L15 (CAAACTGGGATTAGATACCCCACTAT), 12H10 (CA-CYTTCCRGTRCRYTACCRTGTTACGACTT), 12L2 (AAAGCAWRGCACTGAARATGCTWAGAT), 12H3 (CGRGGKKTATCGATTAYAGAACAGGCTCCTCTAG), 12L4 (CAAAGCATAGCACTGAAGATG), 12H8 (GGDKTATCGATTAYAGAACAGGCTCCTCTA), 12L39 (CCTAGACCCCTAAACAGCC), 12H51 (ATTTA-AAAGACAAGTGATTACGC) for *12S rRNA*; and 16L13 (CGACTGTTTACCAAAAACATA), 16 H1 (CTCCG-GTCTGAACTCAGATCACGTAGG) for *16S rRNA*.
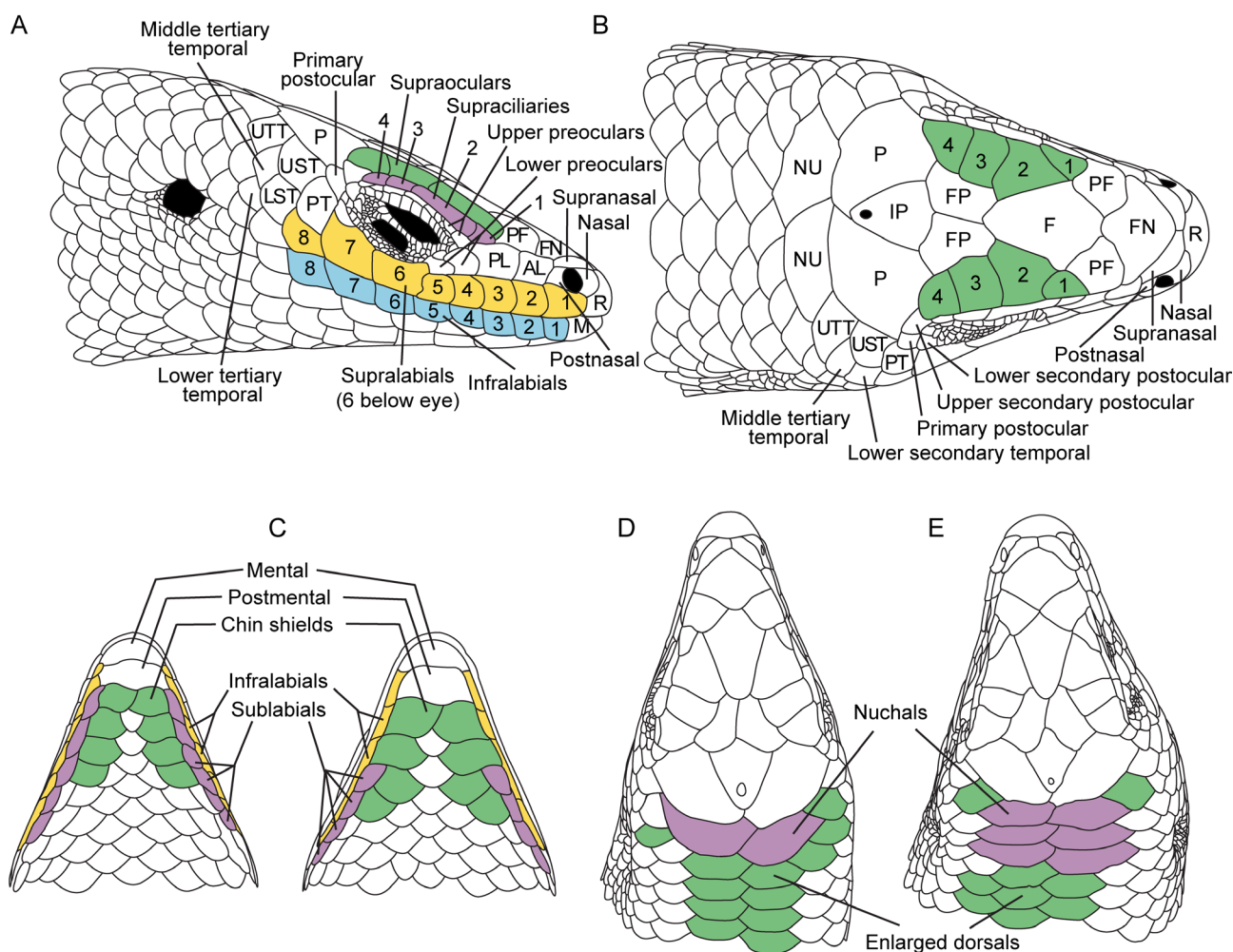

FIGURE 1. Head scalation in Neotropical skinks (Mabuyidae, Mabuyinae, *Marisora*). Locations and names of head scales on side (A) and top (B) of head. Abbreviations are AL (anterior loreal), F (frontal), FN (frontonasal), FP (frontoparietal), IP (interparietal), LST (lower secondary temporal), M (mental), NU (nuchal), P (parietal), PF (prefrontal), PL (posterior loreal), PT (primary temporal), R (rostral), UST (upper secondary temporal), and UTT (upper tertiary temporal). Chin scale configuration: (C) no contact between chin shields and infralabials; (D) two chin shields (each side) in contact with infralabials. In the former case, the sublabials contact the postmental whereas in the latter case they are separated by two chin shields. Nuchal scales: (E) one transverse row; (F) three transverse rows; note presence of enlarged dorsals (not scored as nuchals) in both cases. Adapted from Hedges & Conn (2012).

TABLE 1. A list of the 13 described species of the genus *Marisora* and their geographical distributions. Additional details on distribution are provided in the text for the species covered in this work.

| Species	Distribution
Marisora alliacea (Cope); Middle American Four-lined Skink	Caribbean slope from southeastern Nicaragua, through Costa Rica, to northwestern Panama
Marisora aquilonaria **sp. nov.**; Southern Sierra Madre Skink	Pacific slopes of western Mexico from Nayarit to Guerrero
Marisora aurulae Hedges & Conn; Lesser Windward Skink	St. Vincent, the Grenadines, Grenada, Trinidad, and Tobago.
Marisora berengerae (Miralles) **n. comb.**; San Andrés Skink	San Andrés Island, Colombia
Marisora brachypoda (Taylor); Western Middle America Skink	Pacific versant from southwestern Guatemala, through Honduras and Nicaragua, to west-central Costa Rica; also on Caribbean versant in Río Motagua valley in east-central Guatemala and west-central Honduras
Marisora falconensis (Mijares-Urrutia & Arends); Venezuelan Coastal Skink	Venezuela and Colombia
Marisora lineola **sp. nov.**; Mayan Skink	Caribbean versant from Veracruz, Mexico (including Cozumel), to Belize (including Turneffe Islands), and Guatemala; also on montane slopes of Pacific versant in southeastern Chiapas, Mexico, and southern Guatemala
Marisora magnacornae Hedges & Conn; Eastern Nicaragua Skink	Caribbean lowlands of south-central Nicaragua and Great Corn Island, Nicaragua
Marisora pergravis (Barbour) **n. comb.**; Providencia Skink	Isla de Providencia, Colombia
Marisora roatanae Hedges & Conn; Honduran Skink	Caribbean versant from southeastern Guatemala, much of mainland Honduras, to northeastern Nicaragua; also on Islas de la Bahía, Honduras
Marisora syntoma **sp. nov.**; Tehuantepec Skink	Pacific versant of the Isthmus de Tehuantepec, from southeastern Oaxaca to southwestern Chiapas in southern Mexico
Marisora unimarginata (Cope); Southern Middle America Skink	Pacific versant from northwestern Costa Rica to northwestern Colombia
Marisora urtica **sp. nov.**; Fonseca Islands Skink	Western group of islands in Golfo de Fonseca, Pacific, Honduras
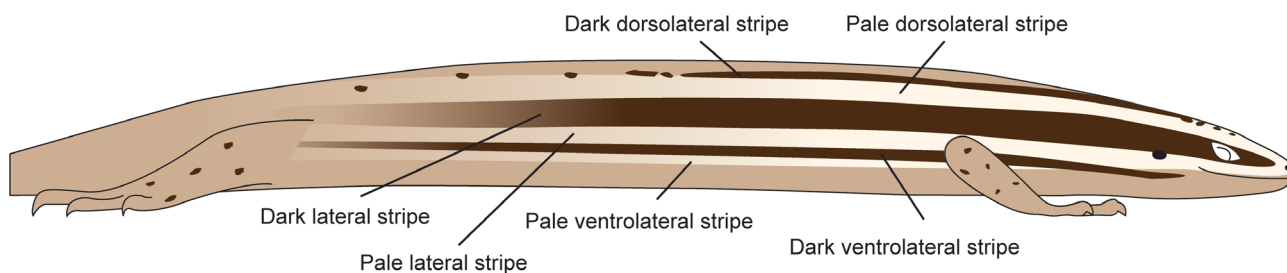
FIGURE 2. General lateral-dorsolateral pattern elements in *Marisora* (Mabuyidae, Mabuyinae). Adapted from Hedges & Conn (2012).

DNA amplification was performed by PCR in a 25μL volume containing 1μL of genomic DNA, 2.5μL of Themopol buffer at 1x, 1μL of dNTPs at 2.5mM, 0.4μL of Taq DNA polymerase, and 1μL of each of the two primers at 10μM. Cycling conditions were as follows: initial denaturation at 94°C for 3 min followed by 35 cycles (3 min at 94°C, 30s at 50–58°C according to the primer pairs, 45s at 72°C) and a final elongation at 72°C for 5 min. Amplification products were purified and sequenced in the forward and reverse directions at Genewiz Scientific (South Plainfield, NJ). Localities, Genbank accession numbers, and museum numbers (if applicable) for all sequences are listed in Appendix 2. Alignments (considering amino acid translations) were performed in Geneious 11.0.4 (https://www.geneious.com) using MAFFT 7.388 with a gap open penalty of 1.53 and offset value of 0.123. In all analyses, gaps were treated as missing data.

Phylogenetic analyses of the concatenated data set were conducted using a maximum likelihood (ML) framework. Model testing was performed with PartitionFinder 2.1.1 (Lanfear, R. *et al.*, 2016). The two best-fitting evolutionary models under the Akaike Information Criterion, TVM + I + Γ (Transversion Model + invariant sites + gamma distribution of changes) and GTR + Γ (General Time Reversible + gamma distribution of changes) were utilized in ML analyses performed with PhyML 2.2.3 (Guindon *et al.*, 2010) and RAxML 8.2.11 (Stamatakis, A., 2014) within Geneious 11.0.4 (https://www.geneious.com), respectively. Trees produced had identical relationships, however the RAxML tree with model GTR + Γ had higher support, according to bootstrap analysis (1000 replicates), and thus it was the tree from which relationships were elucidated.

A Bayesian divergence time estimation was performed to generate a timetree. This was completed in BEAST 2.4.7 (Suchard *et al.*, 2018) using a two-gene subset of the total dataset: 12s and cyt B (1989 bp). Because missing data can impact divergence time estimation in large phylogenies (Filipski *et al.*, 2014) only the most complete gene matrices were included. The xml file was created using BEAUTi 2.4.7 with the following parameters: unlinked GTR + Γ substitution model; relaxed lognormal clock; a yule process to model speciation events; 20 million generations with sampling every 1000 steps, and a 10% burn-in. Convergence was assessed with an infinite sites plot comparing replicate runs, in addition to confirming high ESS values in Tracer 1.6 (Rambaut *et al.*, 2018). No fossil or geological calibrations were available and therefore we used three calibration points corresponding to shared nodes between our timetree and that of Hedges and Conn (2012): 2.8 Ma (4.95–1.4 Ma) for the divergence of *M. alliacea* and *M. roatanae*, 5.2 Ma (8.25–2.5 Ma) for the node joining *M. aquilonaria* with other species (*M. roatanae, M. alliacea, M. lineola, M. brachypoda*, and *M. syntoma*), and 6.8 Ma (7.7–3.5 Ma) for the divergence of *M. aurulae* + *M. falconensis* versus all other *Marisora*.

We used the molecular species delimitation method ABGD (Puillandre *et al.* 2011) with the caveat that such methods only define isolated populations, not necessarily biological species (Sukumaran and Knowles, 2017). However were unable to use the entire aligned sequence data set because there were substantial amounts of missing data, problematic for delimitation methods. Cyt b was the most complete gene, and therefore we used only that gene, removing some short (incomplete) sequences.

Results

Molecular analyses

Our phylogenetic tree (Fig. 3), now with more samples of *Marisora* than have been analyzed previously, shows that a large amount of genetic differentiation has occurred in the evolution of the clade. Hedges and Conn (2012) found that the initial split in *Marisora* was between the *M. falconensis* Group (*M. falconensis* and *M. aurulae*) and the *M. unimarginata* Group (all other species) and our tree (Fig. 3) shows the same pattern. However, considering the additional sequences and newly resolved relationships here, we further subdivide the former *M. unimarginata* Group into two subclades. The *M. unimarginata* Group (*sensu stricto*) occurs in southern Middle America and northern South America. The *M. alliacea* Group occurs in the core region of Middle America. Samples of skinks from Colombia (extralimital to this current morphological study), sequenced by Pinto-Sánchez *et al.* (2015) but unassigned to species by those authors, appear in the tree within the *M. falconensis* Group and the *M. unimarginata* Group (*sensu stricto*).

Together with the morphological and geographic data we recognize 13 total species of *Marisora* placed in three species groups. The *M. unimarginata* Group (2 species, 81% bootstrap support) includes *M. berengerae* and *M. unimarginata*. Most of the Colombian skinks from the study of Pinto-Sánchez *et al.* (2015) cluster strongly (97%) with *M. unimarginata*, which is why we assign them to that species, pending further investigation. Pinto-Sánchez *et al.* (2015) did not have true *M. unimarginata* (type locality, Panama) in their study, instead referring to species in the *M. alliacea* Group, incorrectly, as "*M. unimarginata*." Also, the large genetic divergence within our restricted *M. unimarginata* (*sensu stricto*) suggests the presence of yet additional undescribed species. The *M. alliacea* Group (9 species, 89% bootstrap support) includes *M. alliacea, M. aquilonaria* **sp. nov.**, *M. brachypoda* (*sensu stricto*), *M. lineola* **sp. nov.**, *M. magnacornae* (no genetic data), *M. pergravis* (extralimital to the current morphological study), *M. roatanae, M. syntoma* **sp. nov.**, and *M. urtica* **sp. nov.** The *M. falconensis* Group (2 species, 99% bootstrap support), extralimital to the current morphological study, includes *M. aurulae* and *M. falconensis*. All of the

FIGURE 3A. Phylogenetic tree of the genus *Marisora* from a maximum-likelihood analysis of DNA sequences of three mitochondrial genes (12S rRNA, 16S rRNA, and cyt b) and three nuclear genes (NGFB, R35, and RAG2) in 140 individuals (4,029 bp). A scale bar (2% sequence divergence) is indicated below. The numbers at left of nodes are bootstrap support values. The tree is rooted with *Mabuya dominicana*. Species delimited using ABGD indicated by black vertical lines at right; samples with horizontal bars missing cytochrome b Figure continues on two pages.
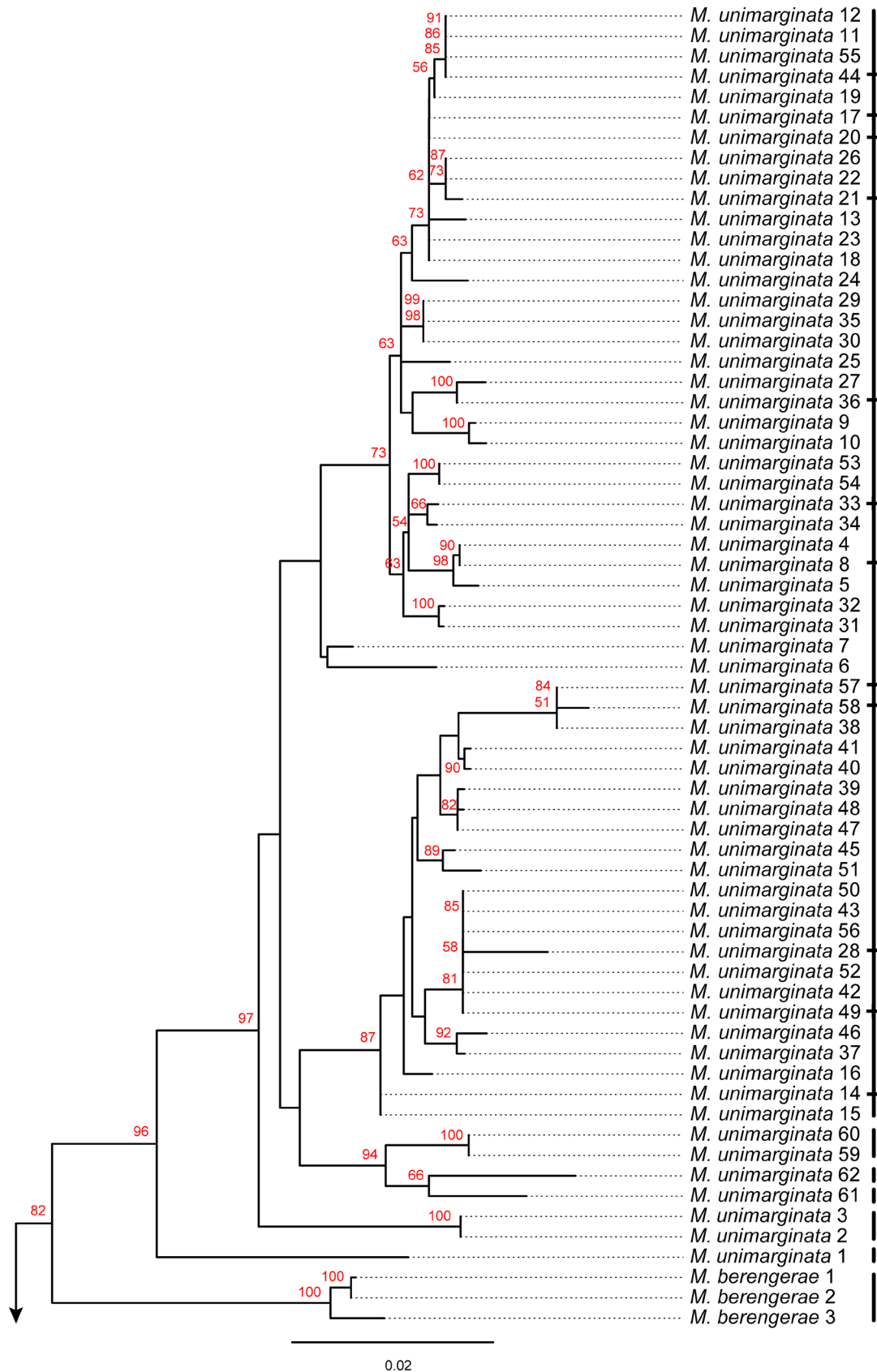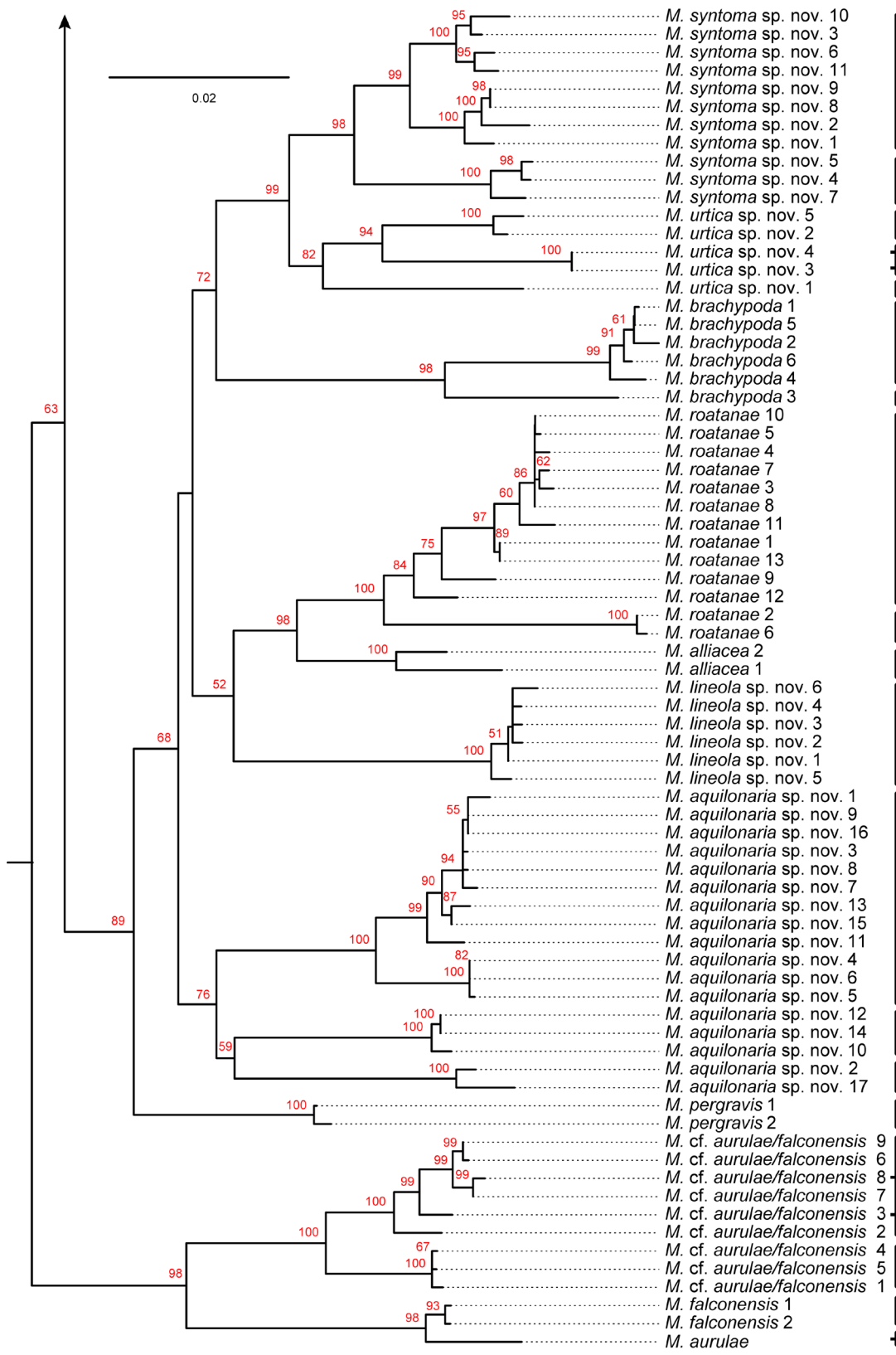
FIGURE 3B. Phylogenetic tree of the genus *Marisora* from a maximum-likelihood analysis of DNA sequences of three mitochondrial genes (12S rRNA, 16S rRNA, and cyt b) and three nuclear genes (NGFB, R35, and RAG2) in 140 individuals (4,029 bp). A scale bar (2% sequence divergence) is indicated. The numbers at left of nodes are bootstrap support values. The tree is rooted with *Mabuya dominicana*. Species delimited using ABGD indicated by black vertical lines at right; samples with horizontal bars missing cytochrome b. Figure continues on two pages.

FIGURE 4A. Timetree of *Marisora* using the most complete data, from two mitochondrial genes (12S rRNA, cyt B). Posterior probabilities for the Bayesian analysis are in red. Nodes show divergence times in millions of years (black, 2 decimal places) followed by uncorrected p-distances (cyt b only; black, precentages) on nodes separating species. A scale bar indicates time (1 million years, Ma). Figure continues on two pages.

FIGURE 4B. Timetree of *Marisora* using the most complete data, from two mitochondrial genes (12S rRNA, cyt B). Poster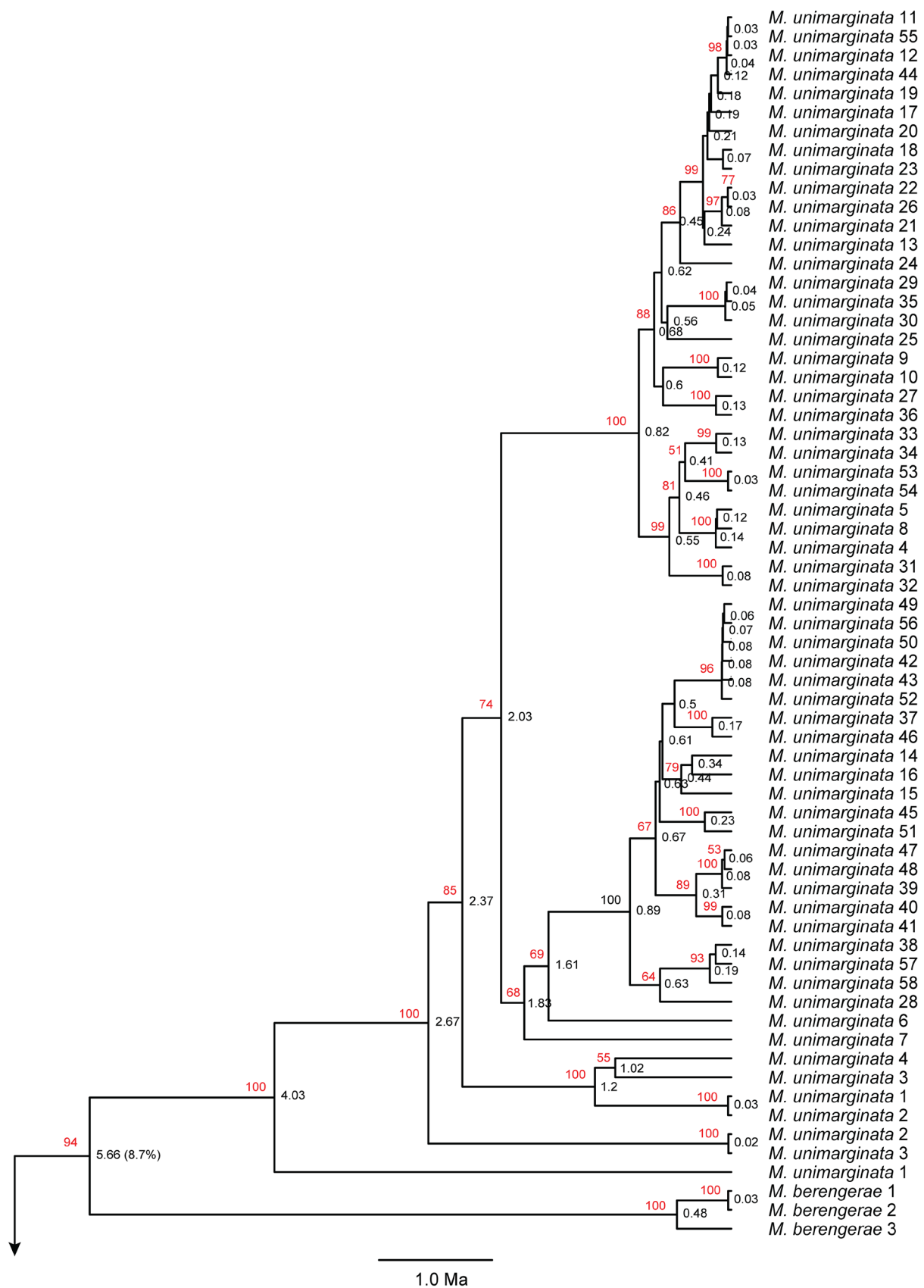ior probabilities for the Bayesian analysis are in red. Nodes show divergence times in millions of years (black, 2 decimal places) followed by uncorrected p-distances (cyt b only; black, precentages) on nodes separating species. A scale bar indicates time (1 million years, Ma). Figure continues on two pages.
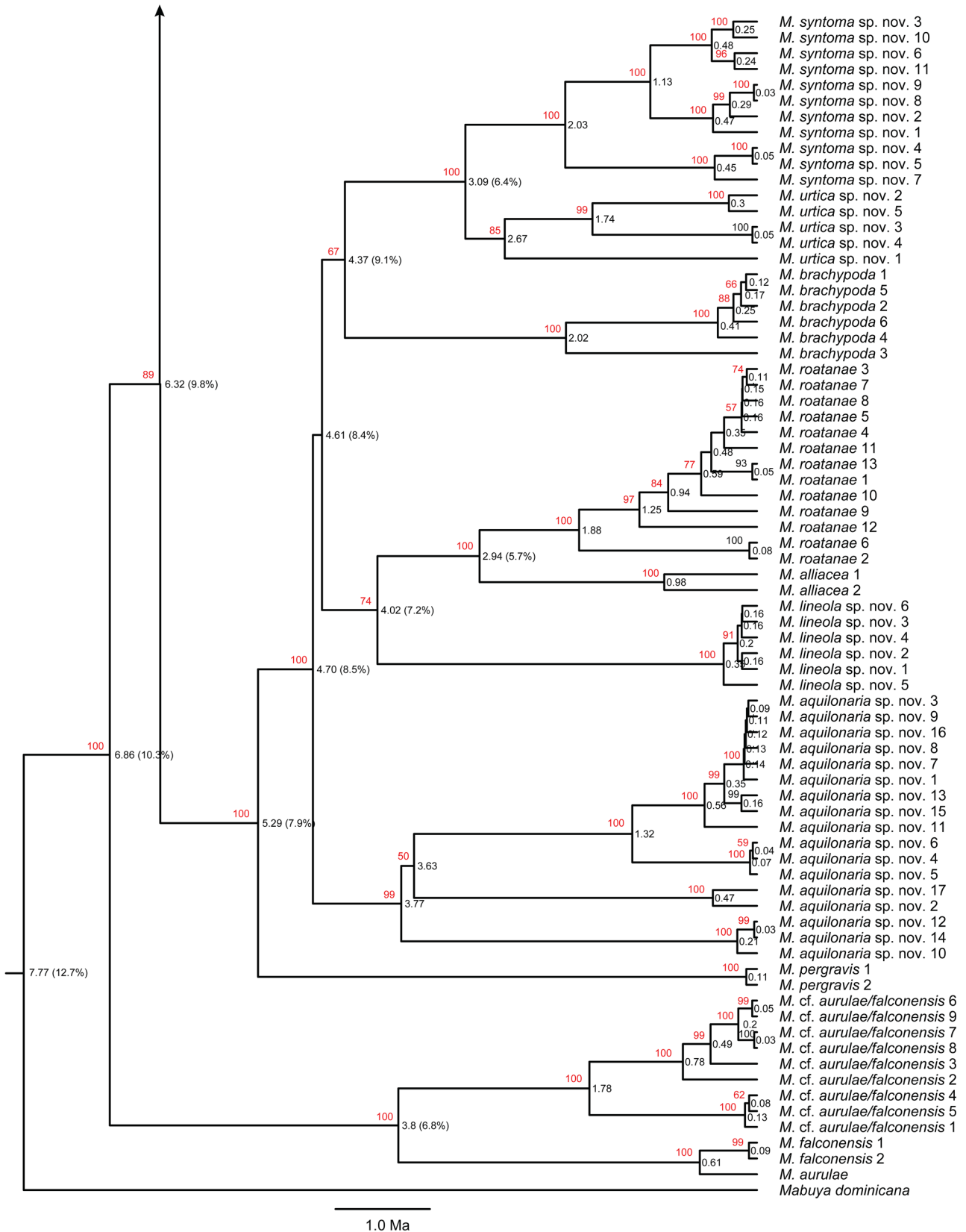
Colombian skinks placed in the *M. falconensis* Group form a subclade (100% bootstrap support) that is separate from the clade containing *M. aurulae* and *M. falconensis*, suggesting that they represent an additional undescribed species, pending further investigation. The *M. alliacea* and *M. unimarginata* species groups, the two groups that have representatives in Central America, are weakly supported as closest relatives (63%).

The molecular species delimitation method, ABGD, identified 25 groups within the ingroup (*Marisora*), as indicated in Fig. 3. None of those groups contain more than one of the 13 species recognized here, and thus there is no conflict with our recognized species. The reason why ABGD delimited more than 13 groups is because there is genetic differentiation among geographically separated populations of several wide-ranging species. Some of these may prove to be undescribed species if further study is undertaken in the future, with additional fieldwork and sampling.

The timetree (Fig. 4) shows that lineage splits leading to each of the species of *Marisora* are dated mostly in the Pliocene (5.3–2.6 Ma) during a time when temperatures were warm and sea levels were relatively high. Exceptions are the split of *M. berengerae* and *M. unimarginata* in the latest Miocene (5.6 Ma) and the split of *M. aurulae* and *M. falconensis* in the Pleistocene (0.61 Ma). However, the latter date probably represents an underestimate resulting from the presence of only a single, slow-evolving gene fragment of 12S rRNA available for the rare species, *M. aurulae*.

A timetree is a better representation of species splits than uncorrected p-distances because it uses a universal measure (time) and corrects for rate and branch length differences. However, past studies have used p-distances as a yardstick for determining whether a divergence is above or below the species level. For comparison, we calculated between-group p-distances (cyt b) among our recognized species (Table 2) and summarize them in Fig. 4, as percentages. They range from 5.7% to 10.3% divergence, typical of different species of reptiles at this gene in past studies (Johns & Avise 1998).

TABLE 2. Uncorrected between-group p-distances (cyt b) among species in this study.

	1	2	3	4	5	6	7	8	9	10	11	12
1. *M. alliacea*												
2. *M. aquilonaria*	0.074											
3. *M. berengerae*	0.091	0.103										
4. *M. brachypoda*	0.082	0.091	0.111									
5. *M.* cf *aurulae-falconensis*	0.104	0.114	0.104	0.118								
6. *M. unimarginata*	0.082	0.101	0.087	0.103	0.096							
7. *M. falconensis*	0.092	0.106	0.095	0.117	0.068	0.096						
8. *M. lineola*	0.069	0.08	0.094	0.091	0.114	0.09	0.106					
9. *M. pergravis*	0.07	0.078	0.079	0.092	0.097	0.09	0.088	0.069				
10. *M. roatanae*	0.057	0.082	0.094	0.09	0.11	0.096	0.105	0.076	0.078			
11. *M. syntoma*	0.067	0.086	0.097	0.087	0.104	0.099	0.101	0.08	0.081	0.084		
12. *M. urtica*	0.072	0.09	0.103	0.098	0.11	0.099	0.102	0.082	0.084	0.085	0.064	
13. *M. dominicana*	0.109	0.115	0.111	0.123	0.127	0.11	0.119	0.109	0.108	0.117	0.115	0.119

Systematic accounts

New Species Descriptions

***Marisora lineola* sp. nov.**
Mayan Skink
Figs. 5A, B, C, D

Mabuia agilis: Günther 1885:33 (in part); Boulenger 1887:190 (in part).
Mabuya agilis: Ruthven 1912:323; Stuart 1934:13; Stuart 1935:47; Gaige 1936:298; Burt & Myers 1942:49 (in part).
Mabuya mabouya: Dunn 1936:539 (in part).
Mabuya mabouya mabouya: Dunn 1936:544 (in part); Gaige *et al.* 1937:11 (in part); Smith 1938:5; Schmidt 1941:496; Smith 1942:344; Stuart 1948:55; Smith & Taylor 1950:156 (in part); Maslin 1963:15.
Mabuya mabouya alliacea: Burger 1952:186 (in part); Werler & Smith 1952:563; Stuart 1954:57; Stuart 1958:23.

Mabuya brachypoda: Webb 1958:1311 (in part); Neill & Allen 1959:45; Smith 1960:223; McCoy & van Horn 1962:182; Neill & Allen 1962:85; Duellman 1965a:603; Neill 1965:98; McCoy 1966:307; Greer 1970:172; Villafuerte & Florés-Villela 1992:47; Campbell 1998:Fig. 104 legend only.

Mabuya unimarginata: Lee 1996:247; Calderón-Mandujano & Mora-Tembre 2004:295; Luja 2006:469.

Mabuya unimarginata complex: Miralles *et al.* 2009a:68 (in part; molecular data only); Pinto-Sánchez *et al.* 2015:204 (by implication only, no specimens examined).

Marisora brachypoda: Hedges & Conn 2012:24 (in part); Lara-Resendiz *et al.* 2017:226 (in part; spot locality map).

Holotype. MVZ 88405, an adult female from El Salto, near Laguna Encantada, Escuintla, Guatemala, 14°16'53"N, -90°42'38"W, elevation 275 m, collected 2 March 1969, by "Woods & Crenshaw."

Paratypes (15). GUATEMALA—MVZ 88406, adult male from the same locality as the holotype; *Jutiapa*: FMNH 68712, adult male, 7 miles W of Jutiapa; *Petén*: USNM 71382, adult female, Chuntuquí; USNM 25116, adult male, Sacluc; USNM 71951, adult female, "Petén." MEXICO—*Campeche*: KU 70560, adult male, 4 km S of Champotón; *Chiapas*: USNM 113656, adult male, USNM 113658–59, 113663, adult females, La Esperanza; USNM 113646, adult female, Palenque 17°32.30'N, 91°59.30'W; *Tabasco*: KU 41604, male, 19 miles N, 10 miles E of Macuspana; USNM 113640–41, adult female and adult male, respectively, Tenosique; *Yucatán*: KU 157475, 13.6 mi E of Mérida.

Referred specimens (62; all examined). BELIZE—*Belize*: USNM 25447, 26074, 31337, 58161–62, Belize City; Orange Walk: USNM 194103–04, Otro Benque; *Stann Creek*: USNM 33092, 29 km SSW of Dangriga; LSUMZ 10282, 1.5 mi W of Mango Creek; *Toledo*: USNM 496705–06, Big Falls 16°15.57'N, 88°52.12'W. GUATEMALA—*Escuintla*: UTA R-37546, Finca Bolivia, km 87.5 on road to Puerto Quetzal; UTA R-39643, Finca el Caobanai, Autosafari; UTA R-22113, 39642, Finca Medio Monte near Palin; *Izabal*: UTA R-9067, 23731, 27268–69, vicinity of El Estor; *Jalapa*: UTA R-39637-41, 40579, Finca Oeste de Volcán Jumay; *Petén*: USNM 71392, Bocomonte; USNM 71395, Flores; *Quezaltenango*: UTA R-27267, km 199 on CA 2, near Coatepeque; *Santa Rosa*: UTA R-37545, between Cuilapa and Chiquimulilla on lower slopes of Volcán Tecuamburro; UTA R-24794, Volcán Jumaytepeque. MEXICO—*Chiapas*: USNM 113657, 113660–62, 113664–65, La Esperanza; USNM 113667–75, Lago Acacoyagua; USNM 113647–55, Palenque; *Quintana Roo*: LSUMZ 33344, 5 mi S of Playa del Carmen; *Tabasco*: USNM 113642–44, Tenosique; *Veracruz*: CM 52754, E of Lago Catemaco; USNM 113645, Paso del Macho; *Yucatán*: USNM 145307, Isla Pérez, Arrecife Alcarán; KU 157476, 13.6 mi E of Mérida.

Diagnosis. *Marisora lineola* sp. nov. is a relatively stout, large species of *Marisora* characterized (data from 8 males, 8 females in type series) by (1) maximum known SVL in males 80.9 mm; (2) maximum known SVL in females 86.2 mm [92.5 mm in specimen not examined by us; see Neill, 1965]; (3) SW 2.6–4.5% SVL in males, 2.2–3.7% in females; (4) HL 17.9–23.8% SVL in males, 16.0–20.5% in females; (5) HW 11.9–13.6% SVL in males, 11.2–12.8% in females; (6) EAL 1.4–2.2% SVL in males, 1.1–2.4% in females; (7) Toe IV length 10.1–12.9% SVL in males, 8.9–11.6% in females; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries four per side in 93.8%, five in 6.2%; (11) frontoparietals one per side; (12) fifth supralabial below orbit in 93.8%, rarely sixth (6.2%); (13) nuchal rows one per side; (14) dorsals 54–59 (56.0 ± 1.7) in males, 57–61 (58.1 ± 1.1) in females; (15) ventrals 61–69 (63.9 ± 2.6) in males, 60–65 (62.1 ± 1.8) in females; (16) dorsals + ventrals 115–126 (119.9 ± 3.7) in males, 117–124 (120.1 ± 2.2) in females; (17) midbody scale rows 30 in 68.8%, 28 in 31.2%; (18) Finger IV lamellae 11–15 (12.4 ± 1.3) per side in males, 11–14 (11.9 ± 1.0) in females; (19) Toe IV lamellae 13–16 per side in both males and females (14.7 ± 1.2, 14.3 ± 1.3, respectively); (20) Finger IV + Toe IV lamellae 26–31 (27.0 ± 2.1) on one side in males, 24–30 (26.1 ± 1.9) in females; (21) supranasals in medial contact in 88.7%, not in medial contact in 11.3%, thus frontonasal in contact with rostral in 13.3%; (22) prefrontals not in contact; (23) supraocular 1-frontal contact absent in 93.3%, point contact made in 6.7%; (24) parietals in contact posterior to interparietal; (25) pale middorsal stripe absent, but dark brown dashes suggestive of a dark brown vertebral line present in some; also dorsal region with several similar rows of dark brown dashes to spots in many, or dark brown dashes or incomplete stripes present in others, especially on posterior third of body; (26) dark brown to black dorsolateral stripe (paired in some), some scales inside stripe with paler brown centers; those dark brown stripes or dashes present above upper edge of pale brown to cream dorsolateral stripe; (27) dark brown lateral stripe present; (28) distinct cream lateral stripe present; (29) palms and soles pale brown or cream, but dark in one (UTA R-22113); (30) total lamellae for five fingers 38–51 (43.9 ± 4.1) in males, 41–49 (45.4 ± 3.2) in females; (31) total lamellae for five toes 51–60 (54.6 ± 3.5) in males, 48–57 (51.7 ± 3.2) in females. In addition, this species is relatively short-limbed with FLL + HLL/SVL 53.7–59.3% in males, 45.1–57.8% in females, and has two or three chinshields contacting infralabials (see Table 3 for some variable characters).

Marisora lineola **sp. nov.** is a member of the *M. alliacea* group of Middle American skinks. *Marisora lineola* is most closely related to *M. alliacea* (Fig. 3), but differs from that species in having shorter limbs (FLL + HLL/SVL 53.7–59.3% in males and 45.1–57.8% in females versus 62.5–74.6% in males and 58.0–67.6% in females in *M. alliacea*). *Marisora lineola* differs from *M. roatanae* in having cream to pale brown palms and soles (versus distinct dark brown to nearly black soles and palms in *M. roatanae*) and in having 2–3 chinshields contacting infralabials (versus one chinshield making that contact in 70.8% in *M. roatanae*). *Marisora lineola* is most easily distinguished from *M. brachypoda* by having one or two dark brown or black dorsolateral body lines or dark brown dashes or spots suggesting lines (versus those dark marks absent or indistinct in *M. brachypoda*). *Marisora lineola* also differs from *M. brachypoda* by having more ventrals (61–69, $x = 63.9 \pm 2.6$ in males and 60–65, $x = 62.1 \pm 1.8$ in females (versus 50–63, $x = 57.9 \pm 3.4$ in males and 55–62, $x = 58.7 \pm 3.2$ in females in *M. brachypoda*). *Marisora lineola* is distinguished from *M. aquilonaria* **sp. nov.** and *M. syntoma* **sp. nov.** (both described below) in being a larger species (maximum known SVL 80.9 mm in males and 92.5 mm in females versus 68.6 mm and 75.2 mm, respectively, in *M. aquilonaria* and 68.5 mm and 75.0 mm, respectively, in *M. syntoma*), having a distinct pale brown dorsolateral stripe (versus that stripe absent or occasionally indistinct in *M. aquilonaria* and *M. syntoma*), and in having one or two dark brown or black dorsolateral body lines or dark brown dashes or spots suggesting lines (versus those dark marks absent or indistinct in *M. aquilonaria* and *M. syntoma*). *Marisora lineola* is further distinguished from *M. syntoma* by having more ventrals in males (61–69, $x = 63.9 \pm 2.6$ versus 56–60, $x = 57.4 \pm 2.3$ ventrals in males of *M. syntoma*). *Marisora lineola* is distinguished from *M. urtica* **sp. nov.** by having pale brown dorsolateral stripes and 2 chinshields contacting infralabials (versus those pale dorsolateral stripes absent and 1 chinshield contacting infralabials in *M. urtica*). *Marisora lineola* differs from *M. magnacornae* in having shorter limbs (FLL + HLL/SVL 53.7–59.3% in males and 45.1–57.8% in females versus 60.8–68.7% in males and 55.8–68.0% in females in *M. magnacornae*). *Marisora lineola* differs from the extralimital to this morphological study *M. pergravis* by having fewer ventrals (60–69 in both sexes combined versus 70–73 in *M. pergravis*), fewer dorsals (54–61 versus 62–63 in *M. pergravis*), and having a dark lateral stripe (versus that stripe absent in *M. pergravis*). *Marisora lineola* has been previously confused with *M. unimarginata* of the *M. unimarginata* group (Fig. 3), but differs from that species by having the fifth supralabial below the orbit in 93.8% (versus sixth supralabial below orbit in 81.9% in *M. unimarginata*), in having 2–3 chinshields in contact with infralabials (versus 1 chinshield contacting an infralabial in 82.9% in *M. unimarginata*), and having shorter limbs (FLL + HLL/SVL 53.7–59.3% in males and 45.1–57.8% in females versus 56.9–66.9% and 55.9–69.1%, respectively, in *M. unimarginata*). *Marisora lineola* is known to differ from the extralimital and poorly known *M. berengerae* (incomplete morphological data available only from the literature of the unsexed holotype) of the *M. unimarginata* group only from genetic data.

Description of the Holotype. An adult female (Figs. 5A, B) in a good state of preservation, except tail broken at base and lost. The tip of the tongue is protruding from the mouth. SVL 86.2 mm; HL 16.3 mm; HW 10.3 mm; SW 3.2 mm; EAL 1.2 mm; ear opening nearly oval; Toe IV length 8.9 mm; toe lengths in descending order I<V<II<III<IV.

Head scalation. Rostral wider than high, contacting first supralabial, nasals, and supranasals. Paired supranasals separated medially by frontonasal-rostral contact, contacting upper edge of anteriormost loreal (only one in entire type series with that contact; also see comments in Variation section below). Frontonasal decagonal, wider than long, laterally in contact with anterior loreal. A pair of pentagonal prefrontals, separated medially, and in contact with frontonasal, anterior and posterior loreals, first supraciliary, frontal, first supraocular, and with point contact with second supraocular on one side. Frontal heptagonal, in contact with first plus point contact with second supraocular on one side, with frontonasal, and with paired frontoparietals. Frontoparietals also in contact with supraoculars 2–4 and with parietals and interparietal. Interparietal tetragonal and lanceolate, separated from nuchals by parietals. Parietal eye not visible externally. Parietals in contact with upper primary, secondary and tertiary temporal scales. Four supraoculars per side. Four (on one side) or five (other side) supraciliaries, second longest. Nostril in posterior part of nasal, forming part of nasal division. A small postnasal bordered by frontonasal, supranasal, anterior loreal, and first supralabial. Anterior and posterior loreals squarish with posterodorsal projection on latter. One upper preocular and one lower preocular. Seven supralabials, the fifth widest and located below the orbit. Three small postoculars, considerably smaller than temporal scales. Two primary temporals, two secondary temporals, and two tertiary temporal scales. All temporal scales imbricate, smooth, cycloid, not distinctly delineated from scales on nape and side of neck. Eight infralabials. Mental scale wider than long, posterior margin straight. Postmental and two pairs of chinshields per side in contact with infralabials. Paired chinshields separated medially by a slightly smaller, somewhat cycloid-shaped scale.

Body and limb scalation. One row of enlarged nuchal scale per side, in contact medially. Other scales on nape similar in size and shape to dorsals. Lateral neck scales slightly smaller than dorsolateral nape scales. Dorsal scales cycloid, imbricate, smooth, 57 in a longitudinal row. Axillary pit absent, but tiny scales present in that region. Ventral scales similar in size and shape to dorsals, 60 in a longitudinal row. Thirty scales around midbody. No distinct boundaries between dorsals, laterals, and ventrals. Scales on base of tail and limbs similar in shape to dorsals, but smaller on limbs. Palmar and plantar surfaces with small, slightly conical scales, subequal in size, and delineated by a surrounding region of slightly larger, flat scales. Subdigital lamellae smooth, single, 14 on Finger IV, 16 on Toe IV. Preanal scales slightly larger than ventrals. No enlarged median subcaudal scales.

Pattern and coloration in preservative. Dorsal ground color dark brown with distinct black lineate spots or dashes, those on dorsolateral portion of body more concentrated and suggesting two relatively thin dark dorsolateral stripes per side, extending from nape region to about level above hind limb insertion. Dark brown dash-like vertebral spots also suggesting a line. Pale middorsal stripe absent. Dark brown lateral stripe present, also with paler brown centers, extending from posterior edge of orbit to level above hind limb insertion. Thin (1/4 scale high) pale brown dorsolateral line bordering upper edge of dark brown lateral stripe. A single, relatively high (ca. 1 1/2 scale rows), white lateral stripe present per side, extending from rostral onto anterior portion of tail, not passing along upper edge of hind limb, passing across lower half of ear opening and with an equal height below ear opening. Lateral white stripe bordered below by a thin (1/3 scale high) dark brown line. A few indistinct dark brown spots present on medium brown dorsal surfaces of limbs. Ventral scales pale brown, with barely indicated slightly darker scale edges. Palmer and plantar surfaces cream, same color as adjacent undersides of limbs. Adjacent lamellae somewhat darker brown.

Variation. All paratypes have the supranasals in median contact, thus medial contact is the normal character state for *Marisora lineola*. The *M. lineola* paratypes are all similar in color and pattern to the holotype in preservative in having dorsal dark lines or dashes. However, some paratypes have less distinct dark lined or striped dorsal patterns. A pale brown to cream dorsolateral stripe is usually evident. Table 3 includes some of the variation recorded for measurements and proportions and scale counts for the entire type series.

Distribution. *Marisora lineola* is known to occur on the Caribbean versant from central Veracruz, Tabasco, and the Yucatán Peninsula, Mexico, to Guatemala and Belize (Fig. 6). The species also occurs on Cozumel Island, Quintana Roo, Mexico, and on the Turneffe Islands of Belize. *Marisora lineola* is also known to occur on the Pacific versant at its type locality, which lies at about 275 m elevation at the edge of the coastal plain. Three Pacific coastal plain localities for this species are also known in the departments of Escuintla and Quetzaltenango, Guatemala. Another Pacific versant locality is at about 1000 m elevation in the upper reaches of a Pacific river in southeastern Chiapas, Mexico. *Marisora lineola* is nearly sympatric with *M. brachypoda* in south-central Guatemala between about 275 and 725 m elevation, with localities for the two species separated from each other by only about 15 km between that of the *M. lineola* type locality and that for *M. brachypoda* near Guanagazapa, Escuintla. The known elevational range is from near sea level to at least 1550 m.

Ecology and conservation. Lee (1996:248) wrote that this "arboreal and terrestrial skink occupies a variety of habitats within the Yucatán Peninsula including savannas, thorn forests, and tall mesic forests." Lee also wrote that they occurred in open habitats and edge situations of those mesic forests. Skinks were found under a variety of objects on the ground and under loose bark of trees (Lee 1996). Werler & Smith (1952) reported *Marisora lineola* individuals were found under loose bark of standing and fallen trees in Veracruz, Mexico. Biogeographic notes, based on his own field experiences, were reported by Stuart (1950). Álvarez del Toro (1983) wrote that Chiapan individuals, a few of which might represent this species, lived under leaves and under rotten logs on the ground, but also lived under loose bark of standing trees and inside roofs of human occupied houses. Neill & Allen (1959, 1962) noted the preference of this species for open habitats in Belize. No conservation studies have been published on any species of *Marisora*, but those species generally adapt well to human presence, even to the point of living inside human inhabited houses (JRM pers. observ. of all nominal forms occurring in Honduras). Thus, *M. lineola* is considered a species of little or no conservation concern at this time. Nonetheless, mabuyid skinks on Caribbean islands also have adapted well to disturbed habitats and coexistence with humans, yet one-third of the species became extinct following introduction of mammalian predators on the islands, in most cases within one or a few decades (Hedges & Conn 2012). Because of their known susceptibility to inavisive predatords, the extinction risk of mabuyid skinks should be continuously monitored.

FIGURE 5. (A) Dorsolateral view of adult female holotype (MVZ 88405) of *Marisora lineola* (Escuintla, Guatemala) in preservative, SVL 86.2 mm; (B) Pale colored palms of same specimen, Toe IV length 8.9 mm; (C) Live *M. lineola* (SMF 99963) from along Bacalar-Reforma road, Quintana Roo, Mexico; image by Gunther Köhler; (D) Live *M. lineola* from El Remate, Petén, Guatemala; image by Jonathan A. Campbell.

Reproduction. Webb (1958) wrote that specimens from Campeche and Yucatán, Mexico, were viviparous. McCoy (1966:307) reported five Yucatán Peninsula females had "six to nine uterine embryos each (average 7.2)." The McCoy collections were made in the last half of August. Álvarez del Toro (1983) reported, in general terms, that Chiapan females (a few might apply to *Marisora lineola*) gave birth to 4–7 young from June to August. Luja (2006:469) reported a Quintana Roo female collected in April had "six totally formed young (mean SVL = 32 mm)," thus implying parturition in May. Hernández-Franyutti & Uribe (2012) studied the seasonal spermatogenic cycle in a population of this species in Tabasco, Mexico. Their recovered evidence demonstrated that spermatogenesis was the result of a single extended spermiation event.

Etymology. The specific name *lineola*, a noun in apposition, is Latin and means a diminutive line. The name is used in reference to the thin dorsolateral dark brown line or dorsal dark brown dashes found in this species.

Remarks. Genetic results in this study recovered *Marisora lineola* as a monophyletic clade (Fig. 3). Thus, we consider it a species distinct from all other named Middle American *Marisora* populations, including those described later in this work. As noted above, *M. lineola* can also be defined by morphological data. Because of the poorly documented previous genetic studies, we were unable to locate a voucher specimen for those samples used in our genetic analysis. Examination of *M. lineola* morphological characters of specimens from nearby localities to those sequenced samples support the genetic results. Even though Pinto-Sánchez *et al.* (2015) recovered this population as a separate clade in their tree Cluster 1 (their ANMO1903), they did not mention those results.

Duellman (1963:246) commented on surprisingly not finding these skinks in southern Petén, Guatemala. Images of *M. lineola* can be found in Acevedo (2006; as *M. unimarginata*), Álvarez del Toro (1983; as *M. brachypoda*), Calderón-Mandujano *et al.* (2008; as *M. brachypoda*), Campbell (1998; as *M. brachypoda*; image legend only, remainder of data a composite of several species in a literature review), García-Vázquez & Feria-Ortiz (2006; second *M. unimarginata*), Köhler (2003, 2008; both as *M. unimarginata*, but Yucatán specimen only), Lee (1996, 2000; both as *M. unimarginata*), (Stafford & Meyer 2000; as *M. unimarginata*), and Werler & Smith (1952; as *M. mabouya alliacea*).
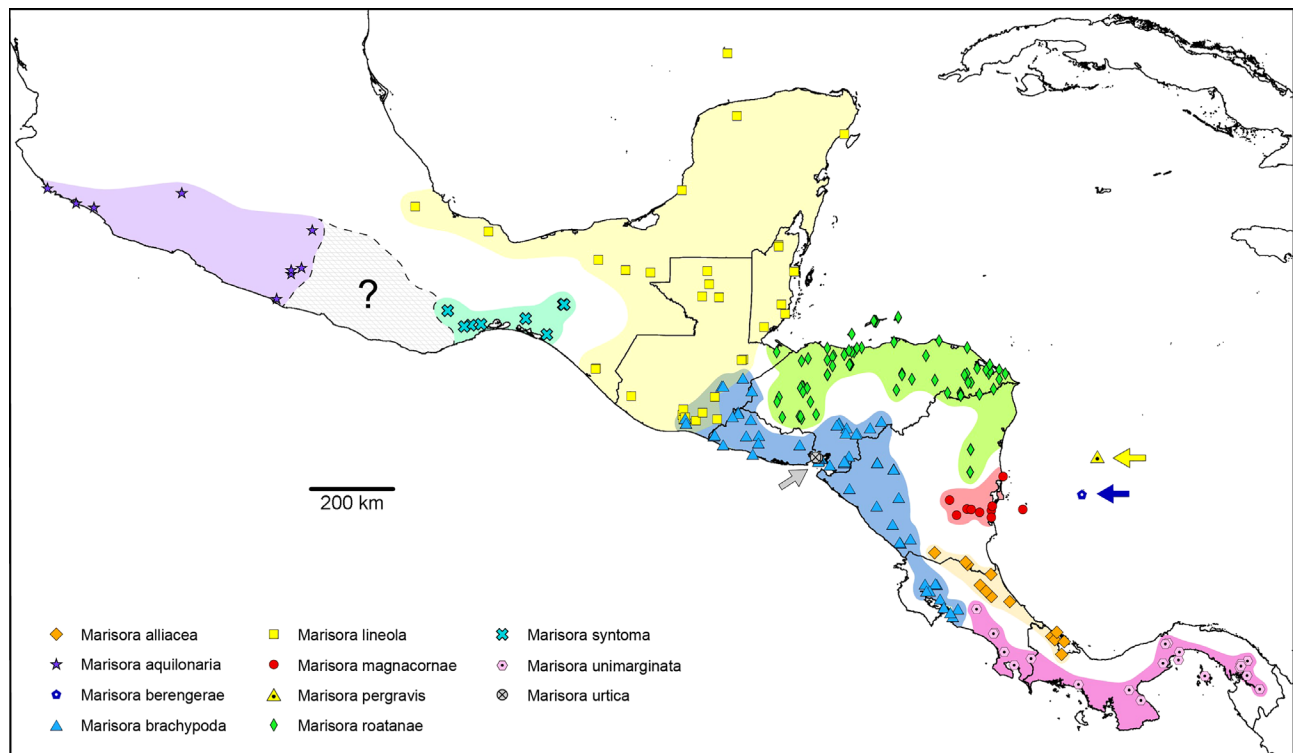

FIGURE 6. Map showing the localities of the *Marisora* specimens examined for this study. The gray arrow points to island record for *M. urtica*. Two extralimital species are also indicated: *M. berengerae* (San Andres, purple arrow) and *M. pergravis* (Providencia, yellow arrow).

Marisora aquilonaria **sp. nov.**
Southern Sierra Madre Skink
Fig. 7A, B, C

Mabuia agilis: Gadow 1905:195 (in part).
Mabuya mabouya: Dunn 1936:537 (in part).
Mabuya mabouya mabouya: Dunn 1936:544 (in part); Gaige *et al.* 1937:11 (in part); Oliver 1937:15; Smith & Taylor 1950:156 (in part); Davis & Smith 1953:105; Flores-Villela *et al.* 1991:161.
Mabuya mabouya alliacea: Burger 1952:186 (in part); Duellman 1954:20; Peters 1954:15; Duellman 1958:16; Peters 1960:331; Flores-Villela *et al.* 1991:161.
Mabuya brachypoda: Webb 1958:1311 (in part); Davis & Dixon 1961:49; Duellman 1961:77; Flores-Villela *et al.* 1991:160.
Mabuya unimarginata: García-Vázquez *et al.* 2006:168; Miralles *et al.* 2009b:602 (tissue sample only); Miralles & Carranza 2010:861 (in part; tissue sample only); Macip-Rios *et al.* 2012:103.
Mabuya unimarginata complex: Miralles *et al.* 2009a:68 (in part; tissue sample only); Pinto-Sánchez *et al.* 2015:204 (in part; by implication only, no specimens examined).
Marisora brachypoda: Hedges & Conn 2012:24 (in part); Lara-Resendiz *et al.* 2017:226 (in part).

Holotype. FMNH 103565, an adult male from Hacienda El Sabino, 30 km S of Uruapan, Michoacán, Mexico, 19°16'59.881"N, -101°58'0.1117"W, 1050 m elevation, collected 21 July 1936, by Hobart M. Smith.

Paratypes (15). MEXICO—*Michoacán*: FMNH 103562, 103575, 103575, 104590, 104592, 104606, 117144, adult males, FMNH 103576, 117129–30, 117132–33, adult females, all from type locality; *Colima*: FMNH 1650, adult female, Manzanillo; FMNH 1673, adult male, Paso del Río; *Guerrero*: USNM 113639, adult female, Paso de Limonaro.

Referred specimens (42; all examined). Mexico—*Michoacán*: FMNH 103563, 103566, 103572, 104595, 104607–09, 117128, 117134–35, 117139–43, 117145–46, all from type locality; *Colima*: USNM 31528, "no further data;" *Distrito Federal*: USNM 12718, "Mexico City" (in error); *Guerrero*: USNM 113620–23, 113625–28, Agua del Obispo; KU 61838, 2.5 mi S of Almolonga; USNM 113629–38, Chilpancingo; *Jalisco*: KU 100514–16, Cuitzmalá; *Morelos*: SMF 81239, Sierra de Huautla.

Diagnosis. *Marisora aquilonaria* **sp. nov.** is a relatively small, short-limbed species of the genus characterized (data from 8 males, 8 females in type series) by (1) maximum known SVL in males 68.6 mm; (2) maximum known SVL in females 75.2 mm; (3) SW 3.1–4.3% SVL in males, 2.8–3.9% in females; (4) HL 19.3–21.6% SVL in males, 16.3–20.9% in females; (5) HW 12.2–14.1% SVL in males, 10.5–12.7% in females; (6) EAL 1.6–2.5% SVL in males, 1.3–2.4% in females; (7) Toe IV length 8.4–10.4% SVL in males, 8.0–9.8% in females; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries 4–5 per side, most often 5 (81.3%); (11) frontoparietals one per side; (12) usually fifth supralabial below orbit (80.0%), occasionally sixth below orbit (20.0%); (13) nuchal rows one per side; (14) dorsals 52–55 (54.3 ± 1.3) in males, 50–59 (54.6 ± 3.1) in females; (15) ventrals 55–62 (57.9 ± 2.0) in males, 55–60 (58.5 ± 1.8) in females; (16) dorsals + ventrals 110–117 (112.6 ± 3.4) in males, 105–120 (113.6 ± 5.0) in females; (17) scales around midbody usually 28 (87.5%), 27 in 12.5%; (18) Finger IV lamellae 12–15 (12.6 ± 1.1) per side in males, 10–15 (12.3 ± 1.4) in females; (19) Toe IV lamellae 14–15 (14.5 ± 0.5) per side in males, 13–15 (14.0 ± 0.8) in females; (20) Finger IV + Toe IV lamellae 26–29 (27.1 ± 1.0) per side in males, 25–30 (26.3 ± 1.6) in females; (21) supranasals usually in medial contact and preventing frontonasal-rostral contact (93.3%); (22) prefrontals not in contact; (23) supraocular 1-frontal contact almost always absent (87.5%), except contact made on both sides in 6.3%, and point contact made on one side in 6.3%; (24) parietals in contact posterior to interparietal; (25) pale middorsal stripe absent, but some have small dark brown dorsal spots; (26) thin, indistinct dark brown dorsolateral stripe usually absent, occasionally present above upper edge of an occasionally present, indistinct, thin, pale dorsolateral stripe; (27) dark brown lateral stripe present; (28) distinct white lateral stripe present; (29) palms and soles pale brown or cream; (30) total lamellae for five fingers 41–50 (45.0 ± 3.1) in males, 41–51 (43.9 ± 3.6) in females; (31) total lamellae for five toes 49–53 (50.3 ± 2.4) in males, 42–53 (49.9 ± 3.4) in females. In addition, this is a short-limbed species with combined FLL + HLL/ SVL 53.4–57.8% in males, 50.8–57.2% in females and has two chinshields contacting infralabials (Table 3).

Marisora aquilonaria **sp. nov.** is a member of the *M. alliacea* Group of Middle American *Marisora* and forms a monophyletic clade (Fig. 3). *Marisora aquilonaria* is a relatively small species as is *M. syntoma* **sp. nov.** (see next Description). *Marisora aquilonaria* can be distinguished from *M. syntoma* in having 5 supraciliaries per side in 81.3% (versus 4 supraciliaries per side in 96.7% in *M. syntoma*) and having combined Finger IV and Toe IV

lamellae per side of 26–29, $x = 27.1 \pm 1.0$ in males and 25–30, $x = 26.3 \pm 1.6$ in females (versus 22–26, $x = 23.7 \pm 1.4$ combined Finger IV and Toe IV lamellae per side in males and 22–27, $x = 24.1 \pm 1.8$ in females in *M. syntoma*). *Marisora aquilonaria* is distinguished from all remaining Mexican and Central American *Marisora* species by being smaller with a maximum known SVL of 68.6 mm in males and 75.2 mm in females (versus 77.0 mm in males of *M. urtica* **sp. nov.** [female *M. urtica* unknown], 81.0 mm in males and 89.0 mm in females of *M. brachypoda*), 80.9 mm in males and 92.5 mm in females of *M. lineola*, 76.1 mm in males and 90.2 mm in females of *M. roatanae*, 85.7 mm in males and 95.1 mm in females of *M. magnacornae*, 79.0 mm in males and 90.3 mm in females of *M. alliacea*, and 84.0 mm in males and 90.3 mm in females of *M. unimarginta*). *Marisora aquilonaria* is further distinguished from *M. urtica* by lacking any indication of dark dorsal lines (versus those lines indicated in *M. urtica* and by having 5 superciliaries per side in 81.3% (versus 4 superciliaries in *M. urtica*). *Marisora aquilonaria* differs further from *M. brachypoda* by having a tiny fifth superciliary scale present posteriorly in 81.3% (versus that small scale absent in 96.7% of *M. brachypoda*). *Marisora aquilonaria* differs further from *M. lineola* by lacking distinct dark and pale dorsolateral stripes (versus dark brown dorsolateral stripe or dashes suggestive of stripes present and a pale brown dorsolateral stripe present in *M. lineola*). *Marisora aquilonaria* differs further from *M. roatanae* by having fewer toe lamellae for five toes (49–53, $x = 50.3 \pm 2.4$ in males and 42–53, $x = 49.9 \pm 3.4$ in females versus 55–62, $x = 60.3 \pm 0.5$ in males and 54–61, $x = 59.0 \pm 2.7$ in females in *M. roatanae*. *Marisora aquilonaria* differs further from *M. magnacornae* and *M. alliacea*) by having shorter limbs (FLL + HLL/SVL 53.4–57.8% in males and 50.8–57.2% in females versus 60.8–68.7% in males and 55.8–68.0% in females of *M. magnacornae* and 62.5–74.6% and 58.0–67.6%, respectively, in *M. alliacea*). *Marisora aquilonaria* differs further from *M. alliacea* in having pale palms and soles (versus palms and soles dark in *M. alliacea*). *Marisora aquilonaria* differs from the extralimital *M. pergravis* by having fewer ventrals (55–62 in both sexes combined versus 70–73 in *M. pergravis*), fewer dorsals (50–59 versus 62–63 in *M. pergravis*), and having a dark lateral stripe (versus that stripe absent in *M. pergravis*). *Marisora aquilonaria* has been previously confused with *M. unimarginata* of the *M. unimarginata* group, but besides the size differences discussed above, also differs from *M. unimarginata* by having shorter limbs (FLL + HLL/SVL 53.4–57.8% in males and 50.8–57.2% in females versus 56.9–66.9% and 55.9–69.1%, respectively, in *M. unimarginata*). *Marisora aquilonaria* is known to differ from the extralimital and poorly known *M. berengerae* (incomplete morphological data available only from the literature of the unsexed holotype) of the *M. unimarginata* group only from genetic data; furthermore a huge geographical hiatus inhabited by other species of *Marisora* occurs between those two species.

Description of the Holotype. An adult male (Fig. 7A) in a good state of preservation with a SVL of 68.6 mm; TAL 116 mm; HL 13.5 mm; HW 9.1 mm; SW 2.4 mm; EAL 1.5 mm; ear opening ovoid; Toe IV length 6.5 mm; toe lengths in descending order I<V<II<III<IV.

Head scalation. Rostral wider than high, contacting first supralabial, anterior nasal, and supranasals. Paired supranasals in median contact, contacting upper edge of anteriormost loreal, anterior and posterior nasals, and frontonasal. Frontonasal decagonal, wider than long, laterally in contact with anterior loreal. A pair of pentagonal prefrontals, separated medially, and in contact with frontonasal, anterior and posterior loreals, first superciliary, first supraocular and point contact with second supraocular, and frontal. Frontal heptagonal, much longer than wide, in contact with second supraocular, frontonasal, and paired frontoparietals. Frontoparietals also in contact with supraoculars 2–4 and with parietals and interparietal. Interparietal tetragonal and lanceolate, separated from nuchals by parietals. Parietal eye visible externally. Parietals in contact with upper primary, secondary, and tertiary temporal scales. Four supraoculars per side, second one largest. Five superciliaries, second longest, fifth tiny. Nostril in posterior part of nasal, forming part of nasal division. A small postnasal bordered by frontonasal, anterior loreal, and first and second supralabials. Anterior and posterior loreals squarish with posterodorsal projection on latter. One upper preocular and one lower preocular. Seven supralabials, sixth widest and located below orbit. Three to four small postoculars, considerably smaller than temporal scales. Three primary, two secondary, and two tertiary temporal scales. All temporal scales imbricate, smooth, cycloid, not distinctly delineated from dorsolateral nape scales and those laterally on neck. Seven and eight infralabials. Mental scale wider than long, posterior margin straight. Postmental and two pairs of chinshields in contact with infralabials. Paired chinshields separated medially by a slightly smaller, somewhat cycloid-shaped scale.

FIGURE 7. (A) Adult male holotype (FMNH 103565) of *Marisora aquilonaria* (Michoacán, Mexico) in preservative, SVL 68.6 mm; (B) Live *M. aquilonaria* from Playa Azul, Michoacán, Mexico, showing essentially unmarked dorsum; (C) Live *M. aquilonaria* from Puerto del Bálsamo, Guerrero, Mexico, showing small dark spots on dorsum; images B, C taken by Jonathan A. Campbell.

Body and limb scalation. One row of enlarged nuchal scale per side, in medial contact. Other scales on nape similar in size to dorsals. Lateral neck scales slightly smaller. Dorsal scales cycloid, imbricate, smooth, 55 in a longitudinal row. Axillary pit absent, but tiny scales present in that region. Ventral scales similar in size and shape to dorsals, 58 in a longitudinal row. Twenty-eight scales around midbody. No distinct boundaries between dorsals, laterals, and ventrals. Scales on base of tail and limbs similar in size to dorsals, except smaller on limbs. Palmar and plantar surfaces with small, slightly conical scales, subequal in size, and delineated by a surrounding region of slightly larger, flat scales. Subdigital lamellae smooth, single, 12 on Finger IV, 15 on Toe IV. Preanal scales slightly larger than ventrals. No enlarged median subcaudal scales.

Pattern and coloration in preservative. Dorsal ground color median brown with a few darker brown spots, especially on dorsolateral portion of body. Tail similar ground color as that of body, but lacking distinct darker markings. Pale middorsal stripe absent. Pale dorsolateral stripe absent. Dark brown lateral stripe (ca. 2 1/2 scales high) extending from posterior edge of orbit to level above hind limb insertion, that lateral stripe without paler brown scales. A single, relatively thin (ca. 2/3 scale row high), white lateral stripe present per side, extending from rostral to level of cloaca, not passing along upper edge of hind limb, passing across lower edge of ear opening. Lateral white stripe bordered below by a thin (3/4 scale high) dark brown line. Indistinct uniformly distributed dark brown spots present on dorsal surfaces of limbs. Ventral scales pale brown, with barely indicated slightly darker scale edges. Palmer and plantar surfaces cream, same color as adjacent undersides of limbs. Adjacent lamellae slightly darker brown.

Variation. Most adults from Guerrero and some from Michoacán have small to tiny dark brown dorsal spots (Fig. 7C; also see Remarks), whereas those from Colima and much of Michoacán mostly lack those spots. Variation in some other characters is shown in Table 3.

Distribution. *Marisora aquilonaria* is known to occur on the Pacific versant of western Mexico from northern Nayarit to at least southeastern Guerrero and southern Puebla and Morelos (Fig. 6). Its known elevational occurrence is from near sea level to 2000 m. The area where its geographical distribution ends is not known since we did not have genetic data for any population between southern Guerrero and just west of the Isthmus of Tehuantepec region of southeastern Oaxaca.

Ecology and conservation. Oliver (1937) reported *Marisora aquilonaria* was usually seen on rock walls in Colima. As usual in *Marisora* species, *M. aquilonaria* prefers open habitats where the large majority of its known localities lie. Duellman (1961) speculated that it probably occurs throughout the coastal region of Michoacán, but museum specimens examined for this study are reported from at least as high as 2000 m elevation. Duellman (1965b), in a fieldwork based biogeographic study in Michoacán, classified what we call *M. aquilonaria* as a lowland species (0–1050 m elevation) living in arid tropical forest and tropical semi-deciduous forest along the Pacific coast. Gadow (1905:218) wrote that this and the following described species were "fond of basking on shrubs and … even climbs trees, hiding under the bark." No conservation studies have been published, but species of *Marisora* generally adapt well to human presence, even living inside human occupied houses (JRM pers. observ.). Thus, this species is almost certainly of little concern regarding its conservation status (although see comments in account of *M. lineola* regarding the susceptibility of mabuyid skinks to invasive predators).

Reproduction. Oliver (1937:15) reported that females from Colima collected in July contained "well-developed young." Webb (1958:1312) reported a Michoacán female, also collected in July, contained "embryos." Davis & Dixon (1961) reported collecting gravid females and recently born individuals in June and July in Guerrero, Mexico.

Etymology. The specific name *aquilonaria* is a Latin feminine adjective derived from aquilonaris, which means north, northern, northerly. The name is used in reference to this nominal form being the most northerly known species of *Marisora*.

Remarks. Recognition of *M. aquilonaria* as a species distinct from all other Middle American nominal forms was first recovered by the genetic results of Pinto-Sánchez (2015; all but the Guatemalan clade in their tree Cluster 2), by our genetic analysis (Fig. 3), and by our morphological study. We were unable to locate voucher specimens for those used in our genetic analysis, based on the available data. Examination of morphological characters of specimens from nearby localities to those sequenced samples support the genetic results.

Our genetic results also contain two monophyletic subclades with the Colima and Michoacán sequences separated from the Guerrero and Morelos subclade. However, morphological characters to support separate nominal forms could not be found. These three subclades diverged 3–4 Ma (Fig. 4), each strongly supported (100% bootstrap) as monophyletic. Given the high level of divergence, the subclades likely represent different species, but such discrimination will require further sampling and analysis.

Duellman (1961:77) corrected the locality data Webb (1958) had given for the large series of *Marisora* from Michoacán, Mexico. The correct locality is "at El Sabino at an elevation of 1050 meters, 30 kilometers south of Uruapan." That locality is also the type locality for this species.

Images of this species can be found in Lara-Resendiz *et al.* (2017) and Ramírez-Bautista (1994).

Marisora syntoma sp. nov.
Tehuantepec Skink
Fig. 8

Mabuia agilis: Günther 1885:33 (in part); Gadow 1905:195 (in part).
Mabuya mabouya mabouya: Hartweg & Oliver 1940:17; Smith & Langebartel 1949:410; Smith & Taylor 1950:156 (in part).
Mabuya mabouya alliacea: Burger 1952:186 (in part); Chrapliwy & Fugler 1955:125.
Mabuya brachypoda: Webb 1958:1304 (in part); Holman 1964:49.
Mabuya unimarginata: Miralles *et al.* 2009b:602 (in part; tissue sample only); Miralles & Carranza 2010:861 (in part; tissue sample only).
Marisora brachypoda: Hedges & Conn 2012:244 (in part); Lara-Resendiz *et al.* 2017:226 (in part; spot locality map).
Mabuya unimarginata complex: Pinto-Sánchez *et al.* 2015:204 (in part; by implication only, no specimens examined).

Holotype. USNM 113677, an adult male from Tehuantepec, Oaxaca, Mexico, 16°19'21.72"N, 95°14'32.39"W, 35 m elevation, collected by Hobart M. Smith, 4 January 1940.

Paratypes (14). MEXICO—*Oaxaca*: USNM 113679–80, 113685, adult males, USNM 113681–83, 113692, 113694, adult females, all from the type locality; USNM 46684, adult male, from Santa Efigenia; USNM 113701, 113705, adult males, USNM 113702–03, 113707, adult females, all from Tres Cruces (NW of Tehuantepec).

Referred specimens (23; all examined). MEXICO. *Chiapas*: USNM 113666, Cruz de Piedra; USNM 47138, Ocozocoautla de la Espinosa; USNM 192534, between Tonala and Arriacaga. *Oaxaca*: KU 33804, 12 miles S, 5 miles E of Nejapa de Madero; USNM 113678, 113684, 113686–91, 113693, 113695–700, Tehuantepec (type locality); USNM 113708–09, Tenango; USNM 113704, 113706, Tres Cruces (NW of Tehuantepec).

Diagnosis. *Marisora syntoma* **sp. nov.** is a relatively small species of *Marisora* characterized (data from 7 males, 8 females in type series) by (1) maximum known SVL in males 68.5 mm; (2) maximum known SVL in females 75.0 mm; (3) SW 3.0–4.6% SVL in males, 3.0–4.6% in females; (4) HL 19.3–22.0% SVL in males, 16.3–21.8% in females; (5) HW 10.4–13.1% SVL in males, 10.1–13.1% in females; (6) EAL 0.8–2.0% SVL in males, 0.7–1.9% SVL in females; (7) Toe IV length 8.7–10.4% SVL in males, 7.4–11.4% in females; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries four per side in 96.7%, five in 3.3%; (11) frontoparietals one per side; (12) fifth supralabial below orbit; (13) nuchal rows one per side; (14) dorsals 53–57 (55.6 ± 1.5) in males, 53–58 (55.4 ± 1.8) in females; (15) ventrals 56–60 (57.4 ± 2.3) in males, 57–63 (59.8 ± 2.0) in females; (16) dorsals + ventrals 108–117 (113.0 ± 3.4) in males, 113–119 (115.1 ± 2.5) in females; (17) midbody scale rows 28 in 80.0%, 26 in 13.3%, 27 in 6.7%; (18) Finger IV lamellae 9–12 (10.4 ± 1.0) per side in males, 9–13 (10.6 ± 1.6) in females; (19) Toe IV lamellae 12–14 (13.3 ± 0.8) per side in males, 13–14 (13.5 ± 0.5) in females; (20) Finger IV + Toe IV lamellae 22–26 (23.7 ± 1.4) on one side in males, 22–27 (24.1 ± 1.8) in females; (21) supranasals in medial contact in 66.7%, not in medial contact in 33.3%, thus frontonasal in contact with rostral in 33.3%; (22) prefrontals almost always not in contact (93.3%), but point contact made in 6.7%; (23) supraocular 1-frontal contact absent in 86.6%, contact made in 6.7%, point contact made in 6.7%; (24) parietals in contact posterior to interparietal; (25) pale middorsal stripe absent; (26) dark dorsolateral stripe absent and a pale dorsolateral stripe at best indistinct; (27) dark brown lateral stripe present; (28) distinct pale lateral stripe present; (29) palms and soles pale brown or cream; (30) total lamellae for five fingers 37–44 (40.0 ± 2.4) in males, 39–46 (41.4 ± 2.3) in females; (31) total lamellae for five toes 41–56 (48.0 ± 4.4) in males, 42–54 (49.5 ± 4.4) in females. In addition, this is a short-limbed species with a FLL + HLL/SVL 47.8–58.3% in males, 42.3–54.3% in females, and has two chinshields contacting infralabials (Table 3).

Marisora syntoma **sp. nov.** is a member of the *M. alliacea* group and is most closely related to *M. urtica* **sp. nov.** (Fig. 3). *Marisora syntoma* differs from all other Mexican and Central American species of *Marisora*, except *M. aquilonaria*, in being a smaller species with a maximum known SVL of 68.5 mm in males and 75.0 mm in females (versus 77.0 mm in males of *M. urtica* [female *M. urtica* unknown], 81.0 mm in males and 89.0 mm in females of *M. brachypoda*), 80.9 mm in males and 92.5 mm in females of *M. lineola*, 76.1 mm in males and 90.2 in females of *M.*

roatanae, 85.7 mm in males and 95.1 mm in females of *M. magnacornae*, 79.0 mm in males and 90.3 mm in females of *M. alliacea*, and 84.0 mm in males and 90.3 mm in females of *M. unimarginta*). *Marisora syntoma* differs further from *M. urtica* in having two chinshields contacting infralabials (versus one chinshield contacting an infralabial in *M. urtica*) and in lacking brown dorsal lines (versus 2–3 fairly distinct to indistinct brown dorsal lines, especially anteriorly, in *M. urtica*). *Marisora syntoma* differs further from *M. magnacornae* in having shorter limbs (FLL + HLL/SVL 47.8–58.3% in males and 42.3–54.3% in females versus 60.8–68.7% in males and 55.8–68.0% in females of *M. magnacornae*) and in lacking distinct dorsolateral stripes (versus pale and dark dorsolateral stripes normally present in *M. magnacornae*). *Marisora syntoma* is further distinguished from *M. alliacea* in having shorter limbs (FLL + HLL/SVL 47.8–58.3% in males and 42.3–54.3% in females versus 62.5–74.6% and 58.0–67.6%, respectively in *M. alliacea*), in lacking distinct dorsolateral and dorsal stripes (versus pale and dark dorsolateral stripes and dark brown dorsal stripes present in *M. alliacea*), and in having pale brown to cream palms and soles (versus palms and soles dark brown to black in *M. alliacea*). *Marisora syntoma* can be distinguished from *M. aquilonaria* by having 4 supraciliaries per side in 96.7% (versus 5 supraciliaries in 81.3% in *M. aquilonaria*) and having 22–26, $x = 23.7 \pm 1.4$ combined Finger IV and Toe IV lamellae per side in males and 22–27, $x = 24.1 \pm 1.8$ in females (versus 26–29, $x = 27.1 \pm 1.0$ in males and 25–30, $x = 26.3 \pm 1.6$ in females in *M. aquilonaria*). *Marisora syntoma* is further distinguished from *M. brachypoda* by having 28 scales around midbody in 80.0% or 26–27 in 20% versus 28 scales around midbody in 35.7%, 30 in 35.7%, or 29 or 31–32 in remainder in *M. brachypoda*). *Marisora syntoma* is further distinguished from *M. lineola* by lacking dark brown dorsolateral stripes or dashes and having 56–60, 57.4 ± 2.3 ventrals in males (versus those stripes or dashes present and male ventrals 61–69, 63.9, ± 2.6 in *M. lineola*). *Marisora syntoma* also differs from *M. roatanae* in having pale palms and soles and 26–28 scales around midbody with 28 in 80% (versus distinct dark brown to nearly black soles and palms almost always present and 30–32 scales around midbody in 76.7% and 28 in only 17.9% in *M. roatanae*). *Marisora syntoma* differs from the extralimital *M. pergravis* by having fewer ventrals (56–63 in both sexes combined versus 70–73 in *M. pergravis*), fewer dorsals (53–58 versus 62–63 in *M. pergravis*). *Marisora syntoma* has sometimes been confused with *M. unimarginata* of the *M. unimarginata* group, but in addition to the size differences discussed above, differs in lacking distinct dark dorsal spots (versus distinct dark dorsal spots present in *M. unimarginata*) and having the fifth supralabial below the orbit (versus sixth in 81.9% in *M. unimarginata*). *Marisora syntoma* is known to differ from the extralimital and poorly known *M. berengerae* (incomplete morphological data available from the literature only from the unsexed holotype) of the *M. unimarginata* group only from genetic data; furthermore a huge geographical hiatus inhabited by other species of *Marisora* occurs between those two species.

Description of the Holotype. An adult male (Fig. 8) in a good state of preservation with a SVL of 55.0 mm; TAL 91.5 mm; HL 12.1 mm; HW 6.2 mm; SW 2.2 mm; EAL 0.5 mm; ear opening nearly oval; Toe IV length 7.6 mm; toe lengths in descending order I<V<II<III<IV.

Head scalation. Rostral wider than high, contacting first supralabial, anterior nasal, and supranasals. Paired supranasals making point contact medially, thus preventing frontonasal-rostral contact, supranasals also contacting upper edge of anteriormost loreal. Frontonasal decagonal, wider than long, laterally in contact with anterior loreal. A pair of pentagonal prefrontals, separated medially, and in contact with frontonasal, anterior and posterior loreals, first supraciliary, frontal, and first supraocular. Frontal heptagonal, in contact with first and point contact with second supraocular, with frontonasal, and with paired frontoparietals. Frontoparietals also in contact with supraoculars 2–4 and with parietals and interparietal. Interparietal tetragonal and lanceolate, separated from nuchals by parietals. Parietal eye not visible externally. Parietals in contact with upper primary, secondary and tertiary temporal scales. Four supraoculars per side, second one largest. Four supraciliaries per side, second longest. Nostril in medial part of nasal, forming nasal division. Postnasal bordered by frontonasal, supranasal, anterior loreal, and first supralabial. Anterior and posterior loreals squarish. One upper preocular and one lower preocular. Seven supralabials, fifth widest and located below orbit. Three small postoculars, considerably smaller than temporal scales. Two primary temporals, two secondary temporals, and two tertiary temporal scales. All temporal scales imbricate, smooth, cycloid, not distinctly delineated from nape scales. Eight infralabials. Mental scale wider than long, posterior margin straight. Postmental and two chinshields per side in contact with infralabials. Chinshields paired, both anterior and posterior in medial contact.

Body and limb scalation. One row of a single enlarged nuchal scale per side, in contact medially (left nuchal scale damaged). Other scales on nape similar in size and shape to dorsals. Lateral neck scales slightly smaller than dorsolateral nape scales. Dorsal scales cycloid, imbricate, smooth, 57 in a longitudinal row. Axillary pit absent,

but tiny scales present in that region. Ventral scales similar in size and shape to dorsals, 60 in a longitudinal row. Twenty-six scales around midbody. No distinct boundaries between dorsals, laterals, and ventrals. Scales on base of tail and limbs similar in shape to dorsals, but smaller on limbs. Palmar and plantar surfaces with small, slightly conical scales, subequal in size, and delineated by a surrounding region of slightly larger, flat scales. Subdigital lamellae smooth, single, 11 on Finger IV, 14 on Toe IV. Preanal scales slightly larger than ventrals. No enlarged median subcaudal scales.

Pattern and coloration in preservative. Dorsal ground color pale brown with scattered indistinct brown spots less than one scale in size. Pale and dark dorsolateral stripes absent. Dark lateral stripe rather indistinct. A single, thin (ca. 1/2 scale row high), cream lateral stripe present per side, extending from rostral onto anterior portion of tail, not passing along upper edge of hind limb, passing across lower half of ear opening and with an equal height below ear opening. Lateral cream stripe bordered below by a thin (1/3 scale high) darker brown line. A few indistinct dark brown spots present on medium brown dorsal surfaces of limbs. Ventral surfaces pale brown, without darker scale edges. Palmer and plantar surfaces pale brown, similar color as adjacent undersides of limbs and adjacent lamellae.

Variation. Little color and pattern variation in preservative was noticed among the paratypes other than the thin dark brown ventrolateral line below the pale lateral stripe can be indistinct or absent. Variation in some important morphometric and meristic characters is presented in Table 3.

Distribution. *Marisora syntoma* is known to occur on the Pacific versant from southeastern Oaxaca just to the west of the Isthmus of Tehuantepec to west-central and southwestern Chiapas, Mexico (Fig. 6). Its known elevational range is from about 30 m to at least 1100 m.

Ecology and conservation. Nothing has been published on the habitats of skinks that we call *Marisora syntoma*, other than the brief notes provided by Gadow (1905) that might pertain to this species (see *M. aquilonaria* section). No conservation information has been published pertaining to this species, but as noted above, species of *Marisora* generally adapt well to human presence. Thus, *M. syntoma* is considered a species of little or no conservation concern (although see comments in account of *M. lineola* regarding the susceptibility of mabuyid skinks to invasive predators).
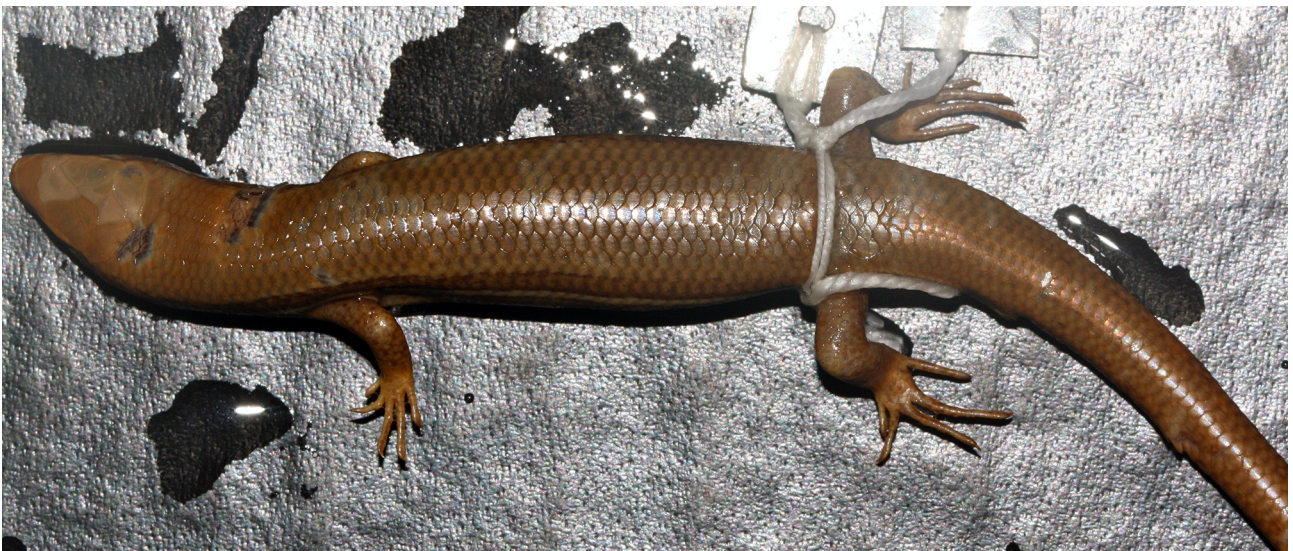
FIGURE 8. Adult male holotype (USNM 113677) of *Marisora syntoma* (Oaxaca, Mexico) in preservative, SVL 55.0 mm.

Reproduction. Nothing has been published on reproduction in *Marisora syntoma*, but the species is certainly viviparous as are other species in the genus.

Etymology. The specific name *syntoma*, a noun in apposition, is taken from the Greek *syntomos*, meaning shortened. The name is used in reference to the short limbs found in this species.

Remarks. Our genetic results (Fig. 3) also support *Marisora syntoma* as a distinct species from all other known Middle American species (also see similar results in Pinto-Sánchez *et al.* 2015; their monophyletic clade containing RLR1110 through ANMO1045MX in their tree Cluster 3). Thus, the distinctiveness of *M. syntoma* was first discov-

ered by genetic-only analyses. We were unable to locate voucher specimens for the genetic data, but examination of morphological characters of specimens from the area of the type locality to those sequenced samples further support the genetic results.

Many of the Oaxaca localities for *Marisora syntoma* were included on a map in Duellman (1960).

Marisora urtica **sp. nov.**
Fonseca Islands Skink
Fig. 9

Marisora brachypoda: McCranie 2015:370 (in part); McCranie & Gutsche 2016:45 (in part); McCranie 2018:339 (in part).

Holotype. USNM 589196, an adult male from Playa de Exposición, on east-southeast side of Isla Exposición, Golfo de Fonseca, Valle, Honduras, 7 m elevation, 13°18.891'N, -87°40.447'W, collected by Alexander Gutsche & James R. McCranie, 15 July 2010. Laboratory sample number SBH 269996.

Paratypes (3). HONDURAS—*Valle*: USNM 589197, adult male, Punta El Molina, north portion of Isla Exposición 13°19.826'N, -87°40.485'W; USNM 589194–95, adult males, Isla Garrobo, 13°20.002'N, -87°42.795'W, 30 m elevation, Golfo de Fonseca.

Diagnosis. *Marisora urtica* **sp. nov.** is a relatively large, short-limbed species of *Marisora* characterized (data from four males in type series; females not known) by (1) maximum known SVL 77.0 mm; (3) SW 3.1–4.4% SVL; (4) HL 16.6–18.4% SVL; (5) HW 10.0–13.3% SVL; (6) EAL 1.4–1.9% SVL; (7) Toe IV length 10.0–11.2% SVL; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries four per side; (11) frontoparietals one per side; (12) fifth supralabial below orbit; (13) nuchal rows one per side; (14) dorsals 52–58 (54.5 ± 2.6); (15) ventrals 53–59 (56.3 ± 2.8); (16) dorsals + ventrals 106–117 (110.8 ± 4.6); (17) midbody scale rows 26 in one (25.0%), 28 in three (75.0%); (18) Finger IV lamellae 11–12 (11.8 ± 0.5) per side; (19) Toe IV lamellae 15–16 (15.8 ± 0.5) per side; (20) Finger IV + Toe IV lamellae 26–28 (27.0 ± 1.2) on one side; (21) supranasals in medial contact, thus frontonasal not in contact with rostral; (22) prefrontals not in contact; (23) supraocular 1-frontal contact absent; (24) parietals in contact posterior to interparietal; (25) pale middorsal stripe absent, but 3–4 brown dorsal stripes present, especially anteriorly on body; (26) dark and pale dorsolateral stripes absent; (27) dark brown lateral stripe present; (28) distinct pale lateral stripe present; (29) palms and soles cream to pale brown; (30) total lamellae for five fingers 42–46 (42.8 ± 2.2); (31) total lamellae for five toes 47–55 (51.8 ± 2.9). In addition, this is a short-limbed species with FLL + HLL/SVL 48.2–57.5% that has only one chinshield per side (100.0%) contacting the infralabials (Table 3).

Marisora urtica **sp. nov.** is a member of the *M. alliacea* group of Middle American skinks and is most closely related to *M. syntoma* (Fig. 3). *Marisora urtica* differs from *M. syntoma* in having one chinshield contacting an infralabial (versus two chinshields contacting infralabials in *M. syntoma*), reaching a larger size (maximum SVL 77.0 mm in males [females unknown] versus 68.5 mm SVL in males of *M. syntoma*), and by having 2–3 fairly distinct to indistinct brown dorsal lines, especially anteriorly (versus those lines absent, but occasionally small dark spots or dashes present in *M. syntoma*). *Marisora urtica* differs from *M. aquilonaria* in having one chinshield contacting an infralabial (versus two chinshields contacting infralabials in *M. aquilonaria*), is a larger species (maximum SVL 77.0 mm in males [females unknown] versus 68.6 mm SVL in *M. aquilonaria*), by having 2–3 fairly distinct to indistinct dark brown dorsal lines, especially anteriorly (versus those lines absent, but occasionally small dark spots or dashes present in *M. aquilonaria*), and in having 4 supraciliaries per side (versus 5 superciliaries in 81.3% in *M. aquilonaria*). *Marisora urtica* differs from *M. brachypoda* by the combination of having fairly distinct to indistinct brown dorsal lines, especially anteriorly (versus those lines normally absent in *M. brachypoda*) and having 1 chinshield contacting an infralabial in all (versus 2 chinshields contacting infralabials in 77.8% of *M. brachypoda*). *Marisora urtica* is distinguished from *M. lineola* by lacking pale and dark dorsolateral stripes and having 1 chinshield contacting an infralabial (versus those pale and dark dorsolateral stripes usually present and 2–3 chinshields contacting infralabials in *M. lineola*). *Marisora urtica* differs from *M. roatanae* in having cream to pale brown palms and soles (versus distinct dark brown to nearly black soles and palms almost always present in *M. roatanae*) and having 26–28 scales around midbody (versus 30–32 in 76.7% in *M. roatanae*). *Marisora urtica* differs from *M. magnacornae* in having shorter limbs (FLL + HLL/SVL 48.2–57.5% in males [females unknown]

versus 60.8–68.7% in male *M. magnacornae*), in lacking pale and dark brown dorsolateral stripes (those stripes present in *M. magnacornae*), and having 1 chinshield contacting an infralabial (versus 2 chinshields contacting infralabials in *M. magnacornae*). *Marisora urtica* is distinguished from *M. alliacea* by having shorter limbs (FLL + HLL/SVL 48.2–57.5% in males [females unknown] versus 62.5–74.6% in male *M. alliacea*) and in having pale palms and soles (versus dark in *M. alliacea*). *Marisora urtica* differs from the extralimital *M. pergravis* by having fewer ventrals (53–59 in males versus 70–73 in *M. pergravis*), fewer dorsals (52–58 versus 62–63 in *M. pergravis*). *Marisora urtica* would be confused with *M. unimarginata* of the *M. unimarginata* group of *Marisora* using the Pinto-Sánchez *et al.* (2015) taxonomy, but differs from that species in having shorter limbs in males [females unknown] (FLL + HLL/SVL 48.2–57.5% versus 56.9–66.9% in *M. unimarginata*), having pale palms and soles (versus dark in *M. unimarginata*), having fifth supralabial below the orbit (versus sixth in 81.9%), and having less male ventrals (53–59, x = 56.3 ± 2.8 versus 60–65, x = 63.0 ± 2.3 in *M. unimarginata*). *Marisora urtica* is known to differ from the extralimital and poorly known *M. berengerae* (incomplete morphological data available only from the unsexed holotype) of the *M. unimarginata* group only from genetic data; furthermore a huge geographical hiatus inhabited by other species of *Marisora* occurs between those two species.

Description of the Holotype. An adult male (Fig. 9) in a good state of preservation. Tail broken near base, but with a short, poorly developed regenerated portion. A ventral incision present on left side for liver extraction. SVL 77.0 mm; HL 12.8 mm; HW 9.0 mm; SW 2.4 mm; EAL 1.5 mm; ear opening laterally ovoid; Toe IV length 7.9 mm; toe lengths in descending order I<V<II<III<IV.

Head scalation. Rostral wider than high, contacting first supralabial, anterior nasal, and supranasals. Paired supranasals in contact medially, preventing frontonasal-rostral contact, each supranasal also contacting upper edge of anterior loreal. Frontonasal decagonal, about as wide as long, laterally in contact with anterior loreal. A pair of pentagonal prefrontals, separated medially, and in contact with frontonasal, anterior and posterior loreals, first supraciliary, frontal, and first and second supraoculars. Frontal heptagonal, in contact with second supraocular, with frontonasal, and with paired frontoparietals. Frontoparietals also in contact with supraoculars 2–4 and with parietals and interparietal. Interparietal tetragonal and lanceolate, separated from nuchals by parietals. Parietal eye indistinct externally. Parietals in contact with upper primary, secondary and tertiary temporal scales. Four supraoculars per side, second one largest. Four supraciliaries per side, second longest. Nostril in posterior third of nasal, forming nasal division. Postnasal bordered by frontonasal, supranasal, anterior loreal, and first supralabial. Anterior loreal squarish, posterior loreal with posterodorsal projection. One upper preocular and one lower preocular. Seven supralabials, the fifth the longest and located below orbit. Four small postoculars, considerably smaller than temporal scales. Three primary temporals, two secondary temporals, and two tertiary temporal scales. All temporal scales imbricate, smooth, cycloid, not distinctly delineated from scales on nape and side of neck. Eight infralabials. Mental scale wider than long, posterior margin straight. Postmental and one chinshield per side in contact with infralabials. Anterior chinshield paired, in contact medially. Second chinshield paired, separated medially by a slightly smaller, somewhat cycloid-shaped scale.

Body and limb scalation. One row of enlarged nuchal scale per side, in contact medially. Other scales on nape similar in size and shape to dorsals. Lateral neck scales slightly smaller than dorsolateral nape scales. Dorsal scales cycloid, imbricate, smooth, 58 in a longitudinal row. Axillary pit absent, but small scales present in that region. Ventral scales similar in size and shape to dorsals, 59 in a longitudinal row. Twenty-six scales around midbody. No distinct boundaries between dorsals, laterals, and ventrals. Scales on base of tail and limbs similar in shape to dorsals, but smaller on limbs. Palmar and plantar surfaces with small, slightly conical scales, subequal in size, and delineated by a surrounding region of slightly larger, flat scales. Subdigital lamellae smooth, single, 12 on Finger IV, 14 on Toe IV. Total subdigital lamellae on fingers I–V 43, total on toes I–V 53. Preanal scales slightly larger than ventrals, slightly wider and close to rectangular. No enlarged median subcaudal scales.

Pattern and coloration in preservative. Dorsal ground color dark brown with distinct dark brown longitudinal dashes or 3–4 incomplete lines, those lines more evident anteriorly. Pale and dark dorsolateral stripes or lines absent. Dark brown lateral stripe distinct, solid color, 3 scale rows high, extending from posterior edge of orbit to level above hind limb insertion. A single, relatively broad (ca. 2 scale rows high) white lateral stripe present per side, extending from rostral onto anterior portion of tail, not passing along upper edge of hind limb, passing across lower half of ear opening and with an equal height below ear opening. Scattered distinct dark brown spots present on medium brown dorsal surfaces of limbs. Indistinct dark brown ventrolateral stripe plus an indication of a single white ventrolateral line present on one side. Ventral surface of body cream, occasional darker brown spots present

ventrolaterally. Palmer and plantar surfaces cream, same color as adjacent undersides of limbs. Adjacent lamellae a darker grayish-brown.

Variation. All paratypes are rather similar in color and pattern as that described for the holotype. Table 3 shows some of the more important variation recorded for measurements and proportions and some scale counts for the entire type series.

Distribution. *Marisora urtica* is known to occur on two islands in the western portion of the Golfo de Fonseca in the Pacific Ocean in southern-most Honduras (Fig. 6; but see Remarks). Its known elevational distribution is from near sea level to about 30 m. The species has not been reported from any of those nearby islands in the Golfo de Fonseca belonging to El Salvador. *Marisora urtica* is replaced by *M. brachypoda* on three eastern-most Honduran islands in that gulf (Fig. 6).

Ecology and conservation. McCranie & Gutsche (2016:874) discussed the general habitats of a combination of *Marisora urtica* and *M. brachypoda* on the Golfo de Fonseca islands. Those authors wrote that these skinks were "diurnal, terrestrial, or arboreal species that is highly adaptable and can be found in a variety of habitats, including edificarian situations. Although frequently active on the ground, it also climbs to bask on tree trunks, fence posts, brush piles, or other elevated objects." As is the case with all *Marisora* species, no conservation studies have been published pertaining to this species, but other Middle American species adapt well to human presence, even living inside human inhabited houses (JRM pers. observ.). Thus, *M. urtica* is considered a species of little or no conservation concern (although see comments in account of *M. lineola* regarding the susceptibility of mabuyid skinks to invasive predators).

FIGURE 9. Adult male holotype (USNM 589196) of *Marisora urtica* (Isla Exposición, Valle, Honduras) in preservative showing indistinct lines on anterior portion of body, HL 12.8 mm, SVL 77.0 mm.

Reproduction. Nothing has been published on reproduction in *Marisora urtica*, and McCranie & Gutsche (2016) did not recover any reproductive information during their collections of this species. Species of *Marisora* are viviparous.

Etymology. The specific name *urtica*, a noun in apposition, is Latin for nettle. The name is used in reference

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to the abundance of stinging nettles that at some places on Isla de Exposición seemed impossible to avoid contact with. The usage of *urtica* for this species name refers to the first author's memories of those contacts with shrubs and small trees of those nettles while in pursuit of these fast moving skinks.

Remarks. *Marisora urtica* was recovered as a separate clade by our genetic analysis of tissues from the holo-type (USNM 589196). As a result, close morphological examination of that tissue voucher specimen and three other adults of that and another nearby island population revealed supporting morphological characters to distinguish this species from the other members of the *M. alliacea* group. Our genetic results also recovered two subclades (four tissue sequences) from Pluma Hidalgo, Oaxaca, Mexico, that cluster with *M. urtica*. Unfortunately, and because of the poorly documented literature, we were unable to locate any museum specimens from Pluma Hidalgo to examine their morphology. As a result, we only tentatively include that Oaxaca population as *M. urtica*. Pluma Hidalgo lies about 90 km south-southwest of the nearest *M. syntoma* locality (southeast of Nejapa de Madero). Also, according to Binford (1989: his fold out map), Pluma Hidalgo lies in Tropical Semideciduous Forest, whereas the remaining Oaxaca localities (= *M. syntoma*) for this skink complex are in Tropical Deciduous Forest.

No images of *Marisora urtica* have been previously published.

Discussions of Previously Described *Marisora* Species Occurring in Middle America

Marisora alliacea (Cope)
Middle American Four-lined Skink
Fig. 10A, B, C

Mabuia alliacea Cope 1875:115 (no holotype designated, but Dunn 1936:539 and Cochran 1961:125b listed USNM 30619–20 as syntypes; no type locality given, but Taylor 1956:298 gave "Costa Rica" "low country" [= Caribbean lowlands] as the type locality).
Marisora alliacea: Hedges & Conn 2012:119; Sunyer *et al.* 2015:384; HerpetoNica 2015:220; Sunyer *et al.* 2016:1052.
Mabuya unimarginata complex: Pinto-Sánchez *et al.* 2015:195 (in part).

Diagnosis. *Marisora alliacea* is a long-limbed, relatively large species of the genus characterized (data from five males and nine females [marked by an * in Appendix 1], plus data from Taylor 1956, where noted) by (1) maximum known SVL in males 79.0 mm; (2) maximum known SVL in females 90.3 mm; (3) SW 2.6–4.7% SVL in males, 2.4–5.1% in females; (4) HL 17.7–22.8% SVL in males, 16.0–22.8% in females; (5) HW 11.3–19.2% SVL in males, 11.3–17.3% in females; (6) EAL 1.1–2.0% SVL in males, 1.0–2.4% in females; (7) Toe IV length 11.4–13.3% SVL in males, 9.5–12.6% in females; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries 4 per side; (11) frontoparietals one per side; (12) usually sixth supralabial below orbit (73.8%), fifth below orbit in 26.2% (includes our data and that from Taylor); (13) nuchal rows one per side; (14) dorsals 51–60 (53.6 ± 1.4) in males, 50–60 (56.0 ± 2.5) in females (includes our data and that from Taylor); (15) ventrals 59–62 (60.6 ± 1.3) in males, 56–65 (58.5 ± 3.3) in females; (16) dorsals + ventrals 112–115 (113.6 ± 1.1) in males, 107–123 (114.0 ± 4.6) in females; (17) scales around midbody 28 in 48.5%, 26 in 40.0%, rarely 27 or 29 (includes data from Taylor); (18) Finger IV lamellae 12–15 (13.4 ± 1.1) per side in males, 13–15 (13.4 ± 0.7) in females; (19) Toe IV lamellae 15–18 (16.6 ± 1.1) per side in males, 15–18 (15.6 ± 1.3) in females; (20) Finger IV + Toe IV lamellae 28–31 (30.0 ± 1.2) per side in males, 28–31 (29.0 ± 1.4) in females; (21) supranasals only occasionally (17.0%) in medial contact, thus frontonasal-rostral contact in 83.0% (includes our data and that from Taylor); (22) prefrontals not in contact medially; (23) supraocular 1-frontal contact absent; (24) parietals in contact posterior to interparietal; (25) pale middorsal stripe absent; (26) distinct dark brown to black dorsolateral stripe or lines present above a pale brown to cream dorsolateral stripe; supplemental thin dorsal stripes or lines present, those supplemental lines sometimes broken into dashes; (27) dark brown lateral stripe present, broad (3–4 scale rows high), at least in shoulder region; (28) distinct white lateral stripe present; (29) palms and soles dark brown to black; (30) total lamellae for five fingers 46–51 (47.8 ± 2.2) in males, 42–53 (47.6 ± 4.2) in females; (31) total lamellae for five toes 53–62 (56.3 ± 4.4) in males, 52–55 (53.6 ± 1.1) in females. In addition, this is a long-limbed species with the combined FLL + HLL/SVL 62.5–74.6% in males, 58.0–67.6% in females (includes data from Taylor), and 2 chinshields contacting infralabials in 84.4% and one in 15.6% (Table 3).

Marisora alliacea is a member of the *M. alliacea* Group of Middle American mabuyids and is apparently most

closely related to *M. roatanae* (Fig. 3) [but tissues not available for the also Caribbean lowland *M. magnacornae*]. *Marisora alliacea* differs from *M. roatanae* in having longer limbs (FLL + HLL/SVL 62.5–74.6% in males and 58.0–67.6% in females versus 53.5–58.4% and 47.8–57.7%, respectively, in *M. roatanae*), having 26–28 scales around midbody in 88.5 % (versus 30–32 in 76.7% in *M. roatanae*), and having the frontonasal contacting the rostral in 83.0% (versus that contact absent in *M. roatanae*). *Marisora alliacea* differs from *M. magnacornae* by the combination of having the sixth supralabial below the orbit in 73.8% (versus fifth supralabial below orbit in 85.5% of *M. magnacornae*), having the frontonasal contacting the rostral in 83.0% (versus frontonasal separated from rostral in 96.9% of *M. magnacornae*), and having 28 in 48.5%, 26 in 40.0%, or rarely 27 or 29 scales around midbody (versus 30 scales around midbody in 93.1% and 28 in 6.9% of *M. magnacornae*). *Marisora alliacea* differs from all remaining Middle American *Marisora* species of the *M. alliacea* group studied herein by having long limbs (FLL + HLL/SVL 62.5–74.6% in males and 58.0–67.6% in females versus <60% in males and <58% in females of those species). *Marisora alliacea* differs from the extralimital *M. pergravis* in having dark dorsolateral stripes (versus those stripes absent in *M. pergravis*). *Marisora alliacea* has been confused with *M. unimarginata* of the *M. unimarginata* Group of the genus in several poorly documented, incomplete studies. *Marisora alliacea* differs from *M. unimarginata* in having the frontonasal contacting the rostral in 83.0% (versus frontonasal separated from rostral by supranasal medial contact in all *M. unimarginata* examined), having two chinshields per side contacting infralabials in 84.7% (versus one chinshield per side contacting infralabials in 82.9% in *M. unimarginata*), and in having dark brown dorsal stripes or lines, or dashes suggesting lines (versus dark brown to black dorsal spots present in *M. unimarginata*). *Marisora alliacea* is known to differ from the extralimital and poorly known *M. berengerae* (incomplete morphological data available only from the unsexed holotype) of the *M. unimarginata* group only from genetic data; furthermore a large geographical hiatus occurs between those two species.

Distribution. *Marisora alliacea* is a Caribbean versant lowland species that is known to occur from southeastern Nicaragua to Bocas del Toro Province in northwestern Panama (Fig. 6). All specimens of this species we examined are from below 300 m elevation. The specimens examined by Taylor (1956) also are from localities below 300 m elevation. Savage (2002) plotted numerous Costa Rican Caribbean versant localities that are certainly from higher elevations but did not provide supporting locality data or museum specimen numbers for those localities.

Remarks. Our genetic results (Fig. 3) support the morphological studies of Taylor (1956), Hedges & Conn (2012), and this study that *Marisora alliacea* is a valid species. Pinto-Sánchez *et al.* (2015) also recovered *M. alliacea* as a separate clade in their phylogenetic analysis, but, oddly, did not recognize that species or comment on that result.

A tissue sample from northeastern Costa Rica presumed to be of this species was sequenced by Miralles *et al.* (2009b) and included in studies by Miralles & Carranza (2010), Hedges & Conn (2012), Pinto-Sánchez *et al.* (2015), and in the current study. Unfortunately, the voucher specimen for that sequence apparently was not collected (Miralles & Carranza 2010:861). A second *Marisora alliacea* sequenced for this study from southeastern Nicaragua does have a voucher (MVZ 269259) that upon examination proved to be typical in morphological characters with *M. alliacea*.

The reproductive data presented by Goldberg (2009; as *Mabuya unimarginata*) are not informative at the species level because the summary data provided therein are a complex of *Marisora alliacea, M. brachypoda*, and *M. unimarginata*.

Images of *Marisora alliacea* are in HerpetoNica (2015), Köhler (2003, 2008; both as *M. unimarginata* from Bartola), Sunyer *et al.* (2016), Taylor (1956), and Vences *et al.* (1998; as *M. unimarginata*). Fitch (1985) reported three *M. alliacea* from Costa Rica gave birth to 2, 2, 1 young (no dates given), but Fitch (1975) reported that one of those females was found in March.

FIGURE 10. (A) Adult (MVZ 269259) of *Marisora alliacea* in preservative showing striped dorsal pattern, SVL 83.5 mm; (B) Live *M. alliacea* from Dos Bocas del Río Indio, Atlántico Sur, Nicaragua (SMF 86751); image by Sebastian Lotzkat; (C) Live *M. alliacea* from Río Pijibaye, Atlántico Sur, Nicaragua; image by Milton Salazar.

Marisora brachypoda (Taylor)
Western Middle America Skink
Fig. 11A, B, C

Mabuya brachypodus Taylor 1956:308 (holotype KU 36528; type locality: "4 km. ESE of Los Angeles de Tilarán, Guanacaste" [Costa Rica]).
Marisora brachypoda: Hedges & Conn 2012:119 (in part); McCranie 2015:370 (in part); HerpetoNica 2015:219; McCranie & Gutsche 2016:45 (in part); Lara-Resendiz *et al.* 2017:226; McCranie 2018:339 (in part).
Mabuya unimarginata: Chacón & Johnston 2013:97; Miralles *et al.* 2017:72.
Mabuya unimarginata complex: Pinto-Sánchez *et al.* 2015:195 (in part; genetic data only).

Diagnosis. *Marisora brachypoda* is a large species of the genus characterized (data from 17 males, 19 females; [those marked by * in Appendix 1]) by (1) maximum known SVL in males 81.0 mm; (2) maximum known SVL in females 89.0 mm; (3) SW 3.4–5.1% SVL in males, 2.8–4.1% in females; (4) HL 15.7–19.7% SVL in males, 14.9–19.5% in females; (5) HW 11.2–13.5% SVL in males, 10.8–13.0% in females; (6) EAL 1.2–2.3% SVL in males, 1.1–1.9% in females; (7) Toe IV length 9.4–10.7% SVL in five males, 6.3–9.5% in nine females; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries 4 per side in 96.7%, rarely 5; (11) frontoparietals one per side; (12) normally fifth supralabial below orbit (96.7%), rarely sixth below orbit; (13) nuchal rows one per side; (14) dorsals 50–56 (53.3 ± 1.8) in males, 49–61 (52.6 ± 3.2) in females; (15) ventrals 50–63 (57.9 ± 3.4) in males, 55–62 (58.7 ± 3.2) in females; (16) dorsals + ventrals 107–123 (113.1 ± 3.4) in males, 104–129 (116.3 ± 7.0) in females; (17) scales around midbody usually 28 or 30 (each with 35.7%), occasionally 31 (12.9%), or rarely 29 (10.2%) or 32 (5.5%); (18) Finger IV lamellae 10–15 (12.4 ± 1.5) per side in males, 10–16 (12.5 ± 1.8) in females; (19) Toe IV lamellae 12–18 (15.4 ± 1.8) per side in males, 13–18 (14.9 ± 1.7) in females; (20) Finger IV + Toe IV lamellae 23–32 (27.9 ± 3.1) per side in males, 24–32 (27.3 ± 3.3) in females; (21) supranasals in medial contact and preventing frontonasal-rostral contact in 87.1%; (22) prefrontals not in medial contact; (23) supraocular 1-frontal contact absent in 96.4%, rarely point contact made on one side in 3.6%; (24) parietals in contact posterior to inter-parietal; (25) pale middorsal stripe absent; (26) thin, indistinct dark brown dorsolateral stripe present or absent; pale dorsolateral stripe usually absent, or indistinct if present; (27) dark brown lateral stripe present; (28) distinct white lateral stripe present; (29) palms and soles almost always pale brown or cream (96.4%), rarely dark brown (3.6%); (30) total lamellae for five fingers 43–46 (45.7 ± 1.8, $n = 5$) in males, 38–49 (48.8 ± 3.1, $n = 6$) in females; (31) total lamellae for five toes 52–55 (53.5 ± 1.3, $n = 3$) in males, 45–54 (48.8 ± 3.1, $n = 6$) in females. In addition, this is a short-limbed species with combined FLL + HLL/SVL 51.5–57.7% in males, 47.6–53.9% in females and normally having two chinshields contacting infralabial (77.8%) (Table 3).

Marisora brachypoda is a member of the *M. alliacea* Group of Middle American *Marisora* and forms a clade nested between two clades containing the remaining Middle American species of the *M. alliacea* group (Fig. 3). *Marisora brachypoda* has been diagnosed from the four species of *Marisora* described herein (*M. lineola, M. aquilonaria, M. syntoma,* and *M. urtica*) in their respective diagnosis above. *Marisora brachypoda* differs from *M. roatanae* in having pale colored palms and soles (versus palms and soles dark brown to black in *M. roatanae*), having 43–46, $x = 45.7 ± 1.8$ total lamellae for five fingers in males (versus 48–55, $x = 50.5 ± 3.1$ total lamellae for five fingers in male *M. roatanae*), and having 52–55, $x = 53.5 ± 1.3$ total lamellae for five toes in males, (versus 55–62, $x = 60.3 ± 0.5$ total lamellae for five toes in males in *M. roatanae*). *Marisora brachypoda* has shorter limbs than do *M. magnacornae* and *M. alliacea* (FLL + HLL/SVL 51.5–57.7% in males and 47.6–53.9% in females versus 60.8–68.7% in males and 55.8–68.0% in females in *M. magnacornae* and 62.5–74.6 and 58.0–67.6, respectively in *M. alliacea*). *Marisora brachypoda* differs from the extralimital *M. pergravis* by having fewer ventrals (50–63 in both sexes combined versus 70–73 in *M. pergravis*), fewer dorsals (49–61 in both sexes combined versus 62–63 in *M. pergravis*). *Marisora brachypoda* has frequently been confused with *M. unimarginata*, but differs from that species of the *M. unimarginata* Group of Middle American mabuyids by having shorter limbs (FLL + HLL/SVL 51.5–57.7% in males and 47.6–53.9% in females versus 56.9–66.9% and 55.9–69.1%, respectively, in *M. unimarginata*) and in lacking distinct dorsal spots (versus those dorsal spots present in *M. unimarginata*). *Marisora brachypoda* is known to differ from the extralimital and poorly known *M. berengerae* (incomplete morphological data from literature available only from the unsexed holotype) of the *M. unimarginata* group only from genetic data; furthermore a large geographical hiatus inhabited by other species of *Marisora* occurs between those two species.

Distribution. *Marisora brachypoda* is known to occur on the Pacific coastal lowlands and into adjacent lower

mountain slopes, from south-central Guatemala to west-central Costa Rica, including some of the islands in the Golfo de Fonseca, Honduras. *Marisora brachypoda* also occurs in the subhumid portion of the Caribbean versant Río Motagua Valley in eastern Guatemala, and in a subhumid tributary of that river valley that extends into west-central Honduras to the vicinity of Copán (Fig. 6). Its known elevational distribution is from near sea level to about 1400 m, but most localities lie below 1000 m.

Remarks. Our genetic analyses support recognition of *Marisora brachypoda* as a distinct species as originally proposed by Taylor (1956) and confirmed by Hedges & Conn (2012) with new morphological data. Three new specimens sequenced for this study that have voucher specimens are listed herein (Appendix 1). Morphological examination of those vouchers, plus examination of another voucher previously sequenced (UTA R-41513) from Zacapa, Guatemala, confirm the distinctiveness of *M. brachypoda*. Miralles *et al.* (2006) appear to have first sequenced tissues from UTA R-41513 but said that specimen was not collected. *Marisora brachypoda* was also recovered as a separate clade (UTA R-41513 in tree Cluster 2) in the phylogenetic only Pinto-Sánchez *et al.* (2015) study.

FIGURE 11. (A) Subadult male (UF 190316) of *Marisora brachypoda* (Granada, Nicaragua) showing dorsal color in preservative, SVL 58.5 mm; (B) Adult male (USNM 589193) of *M. brachypoda* (Isla del Tigre, Valle, Honduras) in life, SVL 60.4 mm; (C) Live *M. brachypoda* from El Arenal, Zacapa, Guatemala, essentially the site of a tissue sample; image by Jonathan A. Campbell.

Duellman & Berg (1962) listed the type series from the KU collection, but also included the collectors and dates of collection, which was not given for all by Taylor (1956). An adult female (USNM 589174) from Orealí, El Paraí-

so in southern Honduras deposited three living young (UNAH 256405, USNM 589175–76 in the collecting bag on 28 November. The SVL of those young on the same day was 29.6–29.7 mm and their tail length was 32.9–33.7 mm. Another female (UTA R-41513) from Zacapa, Guatemala, collected on 30 June deposited five young (UTA R- 41514–18) on the same day. Images of *M. brachypoda* are in Chacón & Johnston (2013; as *M. unimarginata*), Fitch (1983; *M. unimarginata*), Guyer & Donnelly (2005; as *M. unimarginata*), HerpetoNica (2015); Köhler (2003, 2008; as *M. unimarginata* from Guatemala and Isla Ometepe, Nicaragua), Köhler *et al.* (2005; as *M. unimarginata*), McCranie (2018), Mertens (1952; as *M. unimarginata*), Savage (2002; as *M. unimarginata*), Taylor 1956, and Villa *et al.* (1988; as *M. unimarginata*).

Marisora magnacornae Hedges & Conn
Eastern Nicaraguan Skink
Fig. 12

Marisora magnacornae Hedges & Conn 2012:129 (holotype MCZ R26976; type locality "Great Corn Island, Nicaragua"); Sunyer *et al.* 2013:1386; HerpetoNica 2015:220.
Marisora brachypoda: Hedges & Conn 2012:244 (in part).

Diagnosis. *Marisora magnacornae* is a long-limbed, relatively stout, large species of *Marisora* characterized (21 males, 14 females; marked with an * in specimens examined; data incomplete for some specimens) by (1) maximum known SVL 85.7 mm in males; (2) maximum known SVL 95.1 mm in females; (3) snout width 3.4–4.2% SVL in males, 2.6–4.1% in females; (4) HL 17.8–21.6% SVL in males, 16.4–20.9% in females; (5) HW 12.3–15.5% SVL in males, 11.0–14.8% in females; (6) EAL 1.3–2.3% SVL in males, 1.2–1.4% in females; (7) Toe IV length 10.9–13.3% SVL in males, 10.7–13.3% in females; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries four per side; (11) frontoparietals one per side; (12) supralabial five below orbit on 53 sides, 6 on 9 sides; (13) nuchal rows one per side, except 1–2 in one (longitudinally divided by insertion of tiny scale for most of division); (14) dorsals 52–59 in males, 54–59 in females; (15) ventrals 57–65 in males, 57–62 in females; (16) dorsals + ventrals 109–122 in males, 111–121 in females; (17) midbody scale rows 30 in 27, 28 in 2; (18) Finger IV lamellae 12–15 per side in males, 11–15 in females; (19) Toe IV lamellae 15–18 per side in males, 15–17 females [17]; (20) Finger IV + Toe IV lamellae 28–33 per side in males, 28–31 in females; (21) supranasals in medial contact in 31, not in contact in 1, preventing frontonasal-rostral contact in 96.9%; (22) prefrontals widely separated in 30, in contact with each other in 2; (23) supraocular 1-frontal contact absent in 26, present in 5; (24) parietals in contact posterior to interparietal; (25) pale middorsal stripe absent; (26) dark, thin dorsolateral dark stripe of dashes present in 15, absent in 18, pale brown to cream dorsolateral stripe present in 29 of 33; (27) dark lateral stripe present, about 2 scale rows high; (28) each side of body with distinct white lateral stripe; (29) palms and soles cream to dark brown; (30) total lamellae for five fingers 47–55 in males, 44–54 in females; (31) total lamellae for five toes 56–66 in males, 54–62 in females. In addition, this is a long limbed species with a combined FLL + HLL/SVL 60.8–68.7% in males, 55.8–68.0% in females, and usually has 2 chinshields contacting infralabials (Table 3).

Marisora magnacornae is apparently a member of the *M. alliacea* Group of Middle American *Marisora* (no genetic data available). *Marisora magnacornae* has been diagnosed from the four species of *Marisora* described herein (*M. lineola, M. aquilonaria, M. syntoma,* and *M. urtica*) in their respective diagnoses above. *Marisora magnacornae* differs from the more southern and also Caribbean lowland *M. alliacea* in having 30 scales around midbody in 93.1% and 28 in 6.9% (versus 28 in 48.5%, 26 in 40.0%, or rarely 27 or 29 midbody scales in *M. alliacea*) and having the fifth supralabial below the orbit in 85.5% (versus sixth supralabial below orbit in 73.8% of *M. alliacea*). *Marisora magnacornae* is distinguished from the slightly more northern Caribbean *M. roatanae* in having longer limbs (FLL + HLL/SVL 60.8–68.7% in males, 55.8–68.0% in females versus 53.5–58.4% in males and 47.8–57.7% in females in *M. roatanae*). *Marisora magnacornae* differs from *M. brachypoda* by having longer limbs (FLL + HLL/SVL 60.8–68.7% in males and 55.8–68.0% in females versus FLL + HLL/SVL 51.5–57.7% in males and 47.6–53.9% in females and in having a pale brown dorsolateral stripe (versus distinct pale brown dorsolateral stripe absent in *M. brachypoda*). *Marisora magnacornae* differs from the extralimital *M. pergravis* by having fewer ventrals (57–65 in males versus 70–73 in *M. pergravis*), fewer dorsals (52–59 versus 62–63 in *M. pergravis*). *Marisora magnacornae* differs from *M. unimarginata* of the *M. unimarginata* group by having the fifth supralabial below the orbit in 85.5% (versus sixth supralabial below orbit in 81.9% in *M. unimarginata*), 2 chinshields in con-

tact with infralabials in 87.3% (versus 1 chinshield contacting an infralabial in 82.9% in *M. unimarginata*), and having only scattered and slightly darker brown dorsal spots (versus numerous dark brown dorsal spots present in *M. unimarginata*). *Marisora magnacornae* is known to differ from the extralimital and poorly known *M. berengerae* (incomplete morphological data from literature available only from the unsexed holotype) of the *M. unimarginata* group only from genetic data; furthermore a large geographical hiatus inhabited by other species of *Marisora* occurs between those two species.

Distribution. *Marisora magnacornae* was described based on a single specimen from Big Corn Island, but is now better known from several mainland localities along the environs of the Río Escondido and tributaries, Atlántico Sur, Nicaragua (Fig. 6). Those mainland localities lie to the north, west, and south of Bluefields and lie in the lowlands on the Caribbean versant in eastern and south-central Nicaragua (about 4 to about 100 m elevation).

Remarks. Barbour & Loveridge (1929) evasively reported a single specimen (MCZ R 26976) of *Mabuya* (= *Marisora*) from one of the Corn Islands; those authors did not refer to either of the two Corn Islands. Subsequently, no publication ever associated the Corn Islands with any discussion of these mabuyid skinks until Hedges & Conn (2012) described the MCZ specimen as the new species *Marisora magnacornae* (including all of those references listed in the synonymy of this species by Hedges & Conn). No specimens of *Marisora* have been collected on the Corn Islands since that original specimen in 1927–1928 (see Sunyer *et al.* 2013). Those circumstances might suggest that the single Corn Island specimen could have been introduced to that island by a boat carrying cargo from the mainland port of Bluefields, from which this skink is now known to occur to the north, west, and south.

Marisora magnacornae might be most closely related to *M. alliacea*. Both species are similar in limb length and occur in mesic Caribbean lowland habitats. Unfortunately, genetic data for *M. magnacornae* remain unknown.

Images of *Marisora magnacornae* are in Hedges & Conn (2012).

FIGURE 12. Adult female (USNM 19872) of *Marisora magnacornae* (Atlántico Sur, Nicaragua) in preservative showing dorsolateral pattern, SVL 83.5 mm.

Marisora roatanae **Hedges & Conn**
Honduran Skink
Figs. 13A, B, C

Marisora roatanae Hedges & Conn 2012:132 (in part) (holotype TCWC 21955; type locality: "Jonesville, Isla de Roatán, Islas de la Bahía, Honduras, 3 m"); McCranie 2015:370 (in part); McCranie 2018:344 (in part).
Mabuya unimarginata complex: Pinto-Sánchez *et al.* 2015:195 (in part).
Marisora brachypoda: McCranie 2018:344 (in part).

Diagnosis. *Marisora roatanae* is a relatively large, relatively short-limbed, species of *Marisora* characterized (data from 11 males, 20 females; with * in Appendix 1) by (1) maximum known SVL in males 76.1 mm; (2) maximum known SVL in females 90.2 mm; (3) SW 2.7–4.4% SVL in males, 2.4–4.7% in females; (4) HL 16.4–20.8% SVL in males, 15.7–19.5% in females; (5) HW 11.4–12.7% SVL in males, 11.8–14.0% in females; (6) EAL 1.3–2.2% SVL in five males, 1.1–2.0% in ten females; (7) Toe IV length 9.9–12.5% SVL in five males, 9.0–12.1% in ten females; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries four per side; (11) frontoparietals one per side; (12) usually fifth supralabial below orbit (80.4%), rarely sixth below orbit (19.6%); (13) nuchal rows one

per side; (14) dorsals 55–59 (57.0 ± 1.6) in males, 50–59 (56.2 ± 2.4) in females; (15) ventrals 55–64 (59.7 ± 2.5) in males, 58–67 (60.4 ± 2.6) in females; (16) dorsals + ventrals 113–123 (116.7 ± 3.2) in males, 109–125 (116.6 ± 3.8) in females; (17) scales around midbody most often 30 (57.1%), occasionally 32 (25.0%) or 28 (17.9%); (18) Finger IV lamellae 10–16 (13.2 ± 1.7) per side in males, 11–16 (13.4 ± 1.4) in females; (19) Toe IV lamellae 13–18 (15.8 ± 1.6) per side in males, 11–18 (15.8 ± 1.5) in females; (20) Finger IV + Toe IV lamellae 23–34 (29.0 ± 3.2) per side in males, 22–34 (29.3 ± 2.7) in females; (21) supranasals in medial contact, preventing frontonasal-rostral contact; (22) prefrontals not in contact medially; (23) supraocular 1-frontal contact present (55.4%) or absent (44.6%); (24) parietals in contact posterior to interparietal; (25) pale middorsal stripe absent; (26) thin, indistinct dark brown dorsolateral stripe and pale dorsolateral stripe present or absent; (27) dark brown lateral stripe present; (28) distinct white lateral stripe present; (29) palms and soles dark brown to nearly black in almost all populations; (30) total lamellae for five fingers 48–55 (50.5 ± 3.1, *n* = 4) in males, 44–52 (48.8 ± 3.4, *n* = 6) in females; (31) total lamellae for five toes 55–62 (60.3 ± 0.5, *n* = 4) in males, 54–61 (59.0 ± 2.7, *n* = 6) in females. In addition, this is a relatively short-limbed species with combined FLL + HLL/SVL 53.5–58.4% in males, 47.8–57.7% in females that usually has 1 (70.8%) or occasionally 2 (29.2%) chinshields contacting infralabials (Table 3).

Marisora roatanae is a member of the *M. alliacea* Group of Middle American *Marisora* and is apparently most closely related to *M. alliacea* (99% confidence level [Fig. 3], but no genetic data are available for the geographically closer *M. magnacornae*). *Marisora roatanae* is a short-limbed species with a FLL + HLL/SVL of 53.5–58.4% in males and 47.8–57.7 in females (versus 62.5–74.6% and 58.0–67.6%, respectively, in the long limbed *M. alliacea*), lacks frontonasal-rostral contact (versus that contact present in 83.0% in *M. alliacea*), and has 30 or 32 scales around midbody in 76.7% (versus 26 or 28 in 88.5% in *M. alliacea*). Those same short limbs will also distinguish *M. roatanae* from the long limbed *M. magnacornae* (HLL + FLL/SVL 60.8–68.7% in males and 55.8–68.0% in females in *M. magnacornae*). *Marisora roatanae* has been diagnosed from the four species of *Marisora* described herein (*M. lineola, M. aquilonaria, M. syntoma,* and *M. urtica*) in their respective diagnosis above. *Marisora roatanae* is most easily distinguished from *M. brachypoda* in almost always having dark brown to black palms and soles (versus pale brown or cream palms and soles in *M. brachypoda*) and having 55–62, *x* = 60.3 ± 0.5 total lamellae for five toes and 48–55, *x* = 50.5 + 3.1 for five fingers in males (versus 52–55 *x* = 53.5 ± 1.3 total lamellae for five toes and 43–46, *x* = 45.7 ± 1.8 for five fingers in males in *M. brachypoda*). *Marisora roatanae* differs from the extralimital *M. pergravis* by having fewer ventrals (55–64 in both sexes combined versus 70–73 in *M. pergravis*) and fewer dorsals (50–59 versus 62–63 in *M. pergravis*). *Marisora roatanae* has been confused with *M. unimarginata* of the *M. unimarginata* group (Fig. 3), but differs from that species in normally lacking distinct dorsal spots (versus distinct dorsal spots present in *M. unimarginata*), having the fifth supralabial below the orbit in 80.4% (versus sixth in 81.9% in *M. unimarginata*), and in almost always having shorter limbs with a FLL + HLL/SVL of 53.5–58.4% in males and 47.8–57.7 in females (versus 56.9–66.9% and 55.9–69.1%, respectively, in *M. unimarginata*).

Distribution. *Marisora roatanae* is known to occur on the Honduran Bay Islands (Guanaja, Roatán, and Utila) and on the mainland of the Caribbean versant from extreme southeastern Guatemala across northern to north-central Honduras and the southwestern portion (with the exception of the Copán region) to northeastern Nicaragua (Fig. 6). Its known elevational range is from near sea level to about 1510 m, but it appears most common below 600 m.

Remarks. *Marisora roatanae* was thought to be restricted to Isla de Roatán in Hedges & Conn (2012), but the new genetic data recovered from this study (Fig. 3), and then a closer look at the morphology of numerous specimens, including tissued voucher specimens (Appendix 1) plus the previously sequenced voucher UTA R-41227, discovered the species as occurring widely on the Honduran mainland as far south as the Caribbean headwaters in the southwestern portion. It is also distributed on the extreme southeastern Guatemalan mainland (based only on morphology), as well as in northeastern Nicaragua (voucher of tissued UF 190315). *Marisora roatanae* was also recovered as a monophyletic clade in the Pinto-Sánchez *et al.* (2015) genetic study, but not recognized as a species or commented upon. The specimens from the southwestern portion (still Caribbean versant) of Honduras from Intibucá, La Paz, and Lempira are assigned to *M. roatanae* because of the tissue results from FMNH 283593, which clusters with *M. roatanae*. However, those specimens differ from typical *M. roatanae* by having paler palms and soles. Also, some Honduran specimens of *M. roatanae* from Yoro and near Lago de Yojoa, Cortés and Santa Bárbara, can also have less pigmented palms and soles.

FIGURE 13. *Marisora roatanae* showing dorsal pattern. (A) In preservative, USNM 578839 (Atlántida, Honduras), adult female, SVL 79.0 mm; (B) In life, USNM 589206 (Isla de Roatán, Islas de la Bahía, Honduras), adult female, SVL 87.9 mm; (C) Live adult (Warunta, Gracias a Dios, Honduras; not collected).

Hedges & Conn (2012) believed *Marisora roatanae* occurred in "unnaturally low abundance" on Roatán Island, but that does not appear to be the case. This species appears to frequently inhabit the fronds of coconut palms on that island. At least seven were seen on one such palm on a largely overcast afternoon, but none could be captured

at that time because of their reluctance to sufficiently leave their hiding places. However, two were collected at that site the following morning during sunny conditions before heavy rains began. Given the number of coconut palms on Roatán, this is likely a quite common lizard on the island. Also, an American living on a small key off the southern coast of Roatán, who owns a copy of the Bay Island book (McCranie *et al.* 2005) told JRM these lizards are commonly seen on the ground on his property. That resident also said he generally sees those skinks only during the rainy season. That was also the opinion of the man and woman on whose property the coconut palm discussed above was on.

Summaries of the Honduran lizard fauna have recorded these lizards in Honduras as *Mabuya agilis* (see Dunn & Emlen 1932), *M. mabouya* (see Meyer & Wilson 1973), or *Marisora brachypoda* or *M. roatanae* (see McCranie 2015, 2018). Images of *M. roatanae* are in Hedges & Conn (2012), Köhler (2000, 2003; both as *M. unimarginata*), McCranie (2018), and McCranie *et al.* (2002, 2005, 2006; as *M. unimarginata* in all three). The study of endoparasites by Goldberg and Bursey (2003; as *M. unimarginata*) represent *M. roatanae.*

TABLE 3. Select characters for the species of the genus *Marisora* included in this work. Abbreviations used are: Ch = chinshields; D + V = dorsals plus ventrals; FLL = forelimb length; FN = frontonasal; HLL = hind limb length; Infra = infralabials; Lam = lamellae; M = male; Max. = maximum; mm = millimeters; N = no; Num. = number; R = rostral; SAM = scales around midbody; SC = supraciliary; SL = supralabial; SVL = snout-vent length; and Y= yes. The toe lamellae counts and limb lengths are for one side only. The superscript + means that data are from this study and the superscript T means that some of that data (except ventrals, dorsals plus ventrals, and toe lamellae) are from Taylor (1956). The asterisk means that data are for both sexes combined. A row is also included for each species for both sexes combined (BSC) for the more variable characters.

Marisora Species	Sex, Num	Max. SVL	FN-R Contact	SC Num.	SL below Orbit	Dorsals
M. lineola	M (8[+])	80.9 mm	N (88.7%)	4 (93.8%)	5 (93.8%)	54–59 (56.0)
M. lineola	F (8[+])	86.2 mm	Y (11.3%)*	5 (6.2%)*	6 (6.2%)*	57–61 (58.1)
M. lineola-BSC	16					54–61 (57.1)
M. aquilonaria	M (8[+])	68.6 mm	N (93.3%)	5 (81.3%)	5 (80.0%)	52–55 (54.3)
M. aquilonaria	F (8[+])	75.2 mm	Y (6.7%)*	4 (18.7%)*	6 (20.0%)*	50–59 (54.6)
M. aquilonaria-BSC	16					50–59 (54.5)
M. syntoma	M (7[+])	68.5 mm	N (66.7%),	4 (96.7%),	5 (100%)*	53–57 (55.6)
M. syntoma	F (8[+])	75.0 mm	Y (33.3%)*		5 (3.3%)*	53–58 (55.4)
M. syntoma-BSC	15					53–58 (55.5)
M. urtica	M (4[+])	77.0 mm	N (100%)	4 (100%)	5 (100%)	52–58 (54.5)
M. urtica-M						
M. alliacea	M (5[+], 10[T])	79.0 mm	Y (83.0%)	4 (100%)*	6 (73.8%)	51–60 (53.6)
M. alliacea	F (9[+], 7[T])	90.3 mm	N (17.0%)*		5 (26.2%)*	50–60 (56.0)
M. alliacea-BSC	31					50–60 (54.9)
M. brachypoda	M (17[+])	81.0 mm	N (87.1%)	4 (96.7%)	5 (96.7%)	50–56 (53.3)
M. brachypoda	F (19[+])	89.0 mm	Y (12.9%)*	5 (3.3%)*	6 (3.3%)*	49–61 (52.6)
M. brachypoda-BSC	36					49–61 (53.0)
M. magnacornae	M (21[+])	85.7 mm	N (96.9%)	4 (100%)*	5 (85.5%)	52–59 (56.1)
M. magnacornae	F (14[+])	95.1 mm	Y (3.1%)*		6 (14.5%)*	54–59 (56.1)
M. magnacornae-BSC	35					52–59 (56.1)
M. roatanae	M (11[+])	76.1 mm	N (100%)*	4 (100%)*	5 (80.4%),	55–59 (57.0)
M. roatanae	F (20[+])	90.2 mm			6 (14.5%)*	50–59 (56.2)
M. roatanae-BSC	31					50–59 (56.5)
M. unimarginata	M (4[+], 17[T])	84.0 mm	N (100%)*	4 (100%)*	6 (81.9%)	51–56 (54.8)
M. unimarginata	F (8[+], 14[T])	90.3 mm			5 (18.1%)*	53–60 (57.3)
M. unimarginata-BSC	43					51–60 (55.8)

TABLE 3 (Continued).

Marisora Species	Ventrals	D + V	SAM	Toe I–V LAM	FLL+HLL/ SVL	CH/INF
M. lineola-M	61–69 (63.9)	115–126 (119.9)	30 (68.8%)	51–60 (54.6)	53.7–59.3%	3 (63.6%)
M. lineola-F	60–65 (62.1)	117–124 (120.1)	28 (31.2%)*	48–57 (51.7)	45.1–57.8%	2 (36.4%)*
M. lineola-BSC	60–69 (63.0)	115–126 (120.0)		48–60 (52.9)	45.1–59.3%	
M. aquilonaria-M	55–62 (57.9)	110–117 (112.6)	28 (87.5%)	49–53 (50.3)	53.4–57.8%	2*
M. aquilonaria-F	55–60 (58.5)	105–120 (113.6)	27 (12.5%)*	42–53 (49.9)	50.8–57.2%	
M. aquilonaria-BSC	55–62 (58.1)	105–120 (113.1)		42–53 (50.1)	50.8–57.8%	
M. syntoma-M	56–60 (57.4)	108–117 (113.0)	28 (80.0%)	41–56 (48.0)	47.8–58.3%	2*
M. syntoma-F	57–63 (59.8)	113–119 (115.1)	26,27 (20.0%)*	42–54 (49.5)	42.3–54.3%	
M. syntoma-BSC	56–63 (58.6)	108–119 (114.1)		41–56 (48.9)	42.3–58.3%	
M. urtica-M	53–59 (56.3)	106–117 (110.8)	28 (75.0%)	47–55 (51.8)	48.2–57.5%	1
M. urtica-M			26 (25.0%)*			
M. alliacea-M	59–62 (60.6)	112–115 (113.6)	28 (48.5%)	53–62 (56.3)	62.5–74.6%	2 (84.7%)
M. alliacea-F	56–65 (58.5)	107–123 (114.0)	26 (40.0%)*	52–55 (53.6)	58.0–67.6%	1 (15.6%)*
M. alliacea-BSC	56–65 (59.3)	107–123(113.8)		52–62 (55.4)	58.0–74.6%	
M. brachypoda-M	50–63 (57.9)	107–123 (113.1)	28,30 (77.4%)	52–55 (53.5)	51.5–57.7%	2 (77.8%)
M. brachypoda-F	55–62 (58.7)	104–129 (116.3)	29,32 (23.1%)*	45–54 (48.8)	47.6–53.9%	1 (22.2%)*
M. brachypoda-BSC	50–63 (58.3)	104–129 (114.1)		45–55 (49.9)	47.6–57.7%	
M. magnacornae-M	57–65 (59.4)	109–122 (115.3)	30 (93.1%)	56–66 (59.7)	60.8–68.7%	2 (87.3%)
M. magnacornae-F	57–62 (59.2)	111–121 (115.4)	28 (6.9%)*	54–62 (57.9)	55.8–68.0%	3 (9.5%)*
M. magnacornae-BSC	57–65 (59.3)	109–122 (115.4)		54–66 (58.9)	55.8–68.0%	
M. roatanae-M	55–64 (59.7)	113–123 (116.7)	30 (51.7%)	55–62 (60.3)	53.5–58.4%	1 (70.8%)
M. roatanae-F	58–67 (60.4)	109–125 (116.6)	32 (25.0%)*	54–61 (59.0)	47.8–57.7%	2 (29.2%)*
M. roatanae-BSC	55–64 (60.2)	109–125 (116.7)		54–62 (59.5)	47.8–58.4%	
M. unimarginata-M	60–65 (63.0)	112–125 (118.8)	30 (77.1%)	55–62 (58.3)	56.9–66.9%	1 (82.9%)
M. unimarginata-F	59–66 (62.9)	112–131 (120.6)	32 (11.4%)*	53–60 (57.0)	55.9–69.1%	2 (17.1%)*
M. unimarginata-BSC	59–66 (62.9)	112–131 (119.4)		53–62 (57.7)	55.9–69.1%	

Marisora unimarginata (Cope)
Southern Middle America Skink
Fig. 14A, B, C, D

Mabuia unimarginata Cope 1862:187 (no holotype designated; type locality: "Panama").
Marisora unimarginata: Hedges & Conn 2012:119.
Mabuya unimarginata complex: Pinto-Sánchez *et al.* 2015:195 (in part).

Diagnosis. *Marisora unimarginata* is a long-limbed, relatively large species of *Marisora* characterized (data for four males and eight females examined for this work or data from Hedges & Conn 2012 [those marked by an * in Appendix 1], plus data from Taylor 1956 where noted) by (1) maximum known SVL in males 84.0 mm; (2) maximum known SVL in females 90.3 mm; (3) SW 2.7–3.9% SVL in males, 2.2–4.9% in females; (4) HL 19.5–25.0% SVL in males, 17.3–23.6% in females; (5) HW 12.1–16.9% SVL in males, 11.3–16.0% in females; (6) EAL 1.5–2.0% SVL in males, 1.1–1.7% in females; (7) Toe IV length 10.9–11.9% SVL in males, 9.0–13.6% in females; (8) prefrontals one per side; (9) supraoculars four per side; (10) supraciliaries four per side; (11) frontoparietals one per side; (12) normally sixth (81.9%) supralabial below orbit, rarely fifth below orbit on one or both sides (18.1%; includes our data and that from Taylor); (13) nuchal rows one per side; (14) dorsals 51–56 (54.8 ± 1.2) in males, 53–60 (55.8 ± 1.4) in females (includes our data and that from Taylor); (15) ventrals 60–65 (63.0 ± 2.3) in males, 59–66 (62.9 ± 5.8) in females; (16) dorsals + ventrals 112–125 (118.8 ±5.0) in males, 112–131 (120.6 ± 5.8) in females; (17)

scales around midbody usually 30 (77.1%), occasionally 32 (11.4%), rarely 29 or 31 (includes our data and that from Taylor); (18) Finger IV lamellae 13–14 (13.4 ± 0.5) per side in males, 11–15 (13.0 ± 1.9) in 11 females; (19) Toe IV lamellae per side 14–18 (16.4 ± 1.7) in males, 15–17 (16.0 ± 1.8) in 11 females; (20) Finger IV + Toe IV lamellae 28–32 (30.2 ± 1.6) per side in males, 26–32 (29.0 ± 2.4) in 11 females; (21) supranasals in medial contact, preventing frontonasal-rostral contact; (22) prefrontals not in contact medially; (23) supraocular 1-frontal contact absent; (24) parietals in contact posterior to interparietal; (25) pale middorsal stripe absent, but numerous dark brown spots present dorsally; (26) thin, indistinct dark brown dorsolateral stripe usually absent; pale dorsolateral stripe absent or indistinct; (27) dark brown lateral stripe present, about 2 1/2–3 scale rows high; (28) distinct white lateral stripe present; (29) palms and soles dark brown; (30) total lamellae for five fingers 51–54 (52.7 ± 1.5) in males, 44–54 (50.5 ± 4.5) in females; (31) total lamellae for five toes 55–62 (58.3 ± 3.5) in males, 53–60 (57.0 ± 2.9) in females. In addition, this species has a combined FLL + HLL/SVL 56.9–66.9% in males, 55.9–69.1% in females (includes data from Taylor), and usually only 1 chinshield contacting infralabials (82.9%) (Table 3).

Marisora unimarginata is a member of the *M. unimarginata* Group of Middle American *Marisora*. All other Middle American species of the genus with genetic data available are members of the *M. alliacea* group (Fig. 3). *Marisora unimarginata* differs from *M. magnacornae* in usually having the sixth supralabial below the orbit (81.9% versus fifth supralabial below orbit in 85.5% of *M. magnacornae*), usually only one chinshield contacting an infralabial in 82.9% (versus 2 chinshields per side in contact with infralabials in 87.3% of *M. magnacornae*), and having numerous dark brown to black spots on the body (versus only scattered and slightly darker brown dorsal scales in *M. magnacornae*). *Marisora unimarginata* differs from *M. alliacea* in having the frontonasal separated from the rostral (versus frontonasal contacting rostral in 83.0% in *M. alliacea*), usually only first chinshield per side contacting infralabials (82.9%; versus 2 chinshields in 84.7% in *M. alliacea*), in having the dark lateral stripe 2 1/2 to 3 scale rows high (versus dark lateral stripe 3–4 scale rows high, at least in shoulder region, in *M. alliacea*), and in having dark brown to black dorsal spots (versus dorsal dark brown to black lines or dashes suggestive of lines in *M. alliacea*). *Marisora unimarginata* differs from *M. brachypoda* by having longer limbs (FLL + HLL/SVL of 56.9–66.9% in males and 55.9–69.1% in females versus 51.5–57.7% in males and 47.6–53.9% in females of *M. brachypoda*), having dark brown palms and soles (versus pale brown to cream palms and soles in *M. brachypoda*), and in having distinct dorsal dark spots (versus dorsal spots, if present small and indistinct in *M. brachypoda*). *Marisora unimarginata* is diagnosed from the four species of *Marisora* described herein (*M. lineola, M. aquilonaria, M. syntoma*, and *M. urtica*) in the respective diagnosis of those species above. *Marisora unimarginata* differs from *M. roatanae* by the combination of having distinct dark spots on the dorsum (versus dark large spots absent or indistinct in *M. roatanae*), having the sixth supralabial below the orbit in 81.9% (versus fifth in 80.4% in *M. roatanae*), and in almost always having longer limbs with a FLL + HLL/SVL of 56.9–66.9% in males and 55.9–69.1% in females (versus 53.5–58.4% and 47.8–57.7%, respectively, in *M. roatanae*). *Marisora unimarginata* differs from the extralimital *M. pergravis* by having distinct dark dorsal spots (versus those markings absent in *M. pergravis*).

Distribution. *Marisora unimarginata* is known to occur on the Pacific versant from northwestern Costa Rica to at least eastern Panama (Fig. 6). This species is also known to occur on the Caribbean versant in the Canal Zone region of central Panama. Its known elevational range is from near sea level to about 1500 m, but most localities are below 600 m. Because of the geographic restriction of this study, we do not plot the distribution of specimens in South America tentatively assigned to this species.

Remarks. Recognition of *Marisora unimarginata* is also supported by our genetic results (Fig. 3) and morphological studies. Tissues of *M. unimarginata* (*sensu stricto*) were not available for previous genetic studies, thus are sequenced for the first time in the current study. Photographs in life of three of those four vouchers are presented herein (Figs. 14B, C, D).

Fitch (1985) indicated seven Costa Rican females, apparently of this species, gave birth to 2–7 (5.2) young, apparently in March and August (also see reproduction remarks for *M. alliacea*). Images of *Marisora unimarginata* are in Leenders (2001) and Taylor (1956).

FIGURE 14. *Marisora unimarginata* showing dorsal pattern. (A) Adult male (FMNH 178691) (near San Isidro del General, San José, Costa Rica) in preservative, SVL 75.0 mm; (B) Live adult male (SMF 89582) from Café de Eleta, Chiriquí, Panama; (C) Live adult female (Museo Herpetológico de Chiriquí 2349) from Café de Eleta, Chiriquí, Panama; (D) Live adult (SMF 91565) from Guayabito, Veraguas, Panama. These images show the known range of variation in dorsal spotting in *M. unimarginata*, with the least spotted specimen also being the considerably least common phase. Images B, C, and D by Sebastian Lotzkat.

Discussion

We have shown here that the mabuyid skinks of Middle America are more diverse than previously thought and represent a radiation of species including some that are known to be sympatric and others nearly sympatric. With the four new species described herein, the genus *Marisora* now numbers 13 species, most of which (nine species) occur in Middle America, including adjacent islands in the Caribbean and Pacific. In addition, the molecular phylogeny suggests that undescribed species exist in mainland Colombia. The molecular phylogeny also shows that the genus includes three evolutionary clades (species groups), with the largest being the *M. alliacea* Group of eight Middle American species plus one extralimital named island species. The undescribed Colombian species belong to the two smaller species groups: the *M. falconensis* Group (two species) of northern South America, Trinidad and Tobago, and the southern Lesser Antilles; and the *M. unimarginata* Group (two named species) of southern Middle America, mainland Colombia, and San Andrés Island (Colombia) in the western Caribbean.

Besides exploring the genetic relationships of species in the genus, we have examined morphological differences among the Middle American species, with emphasis on the nine species of the *M. alliacea* Group. Considering the 36 pairwise comparisons of those species, we were able to identify completely non-overlapping morphological differences in 34 pairs. Even in the two remaining pairs, *M. alliacea*/*M. magnacornae* and *M. aquilonaria*/*M. syntoma*, we identified several nearly non-overlapping characters that, in combination, will permit identification of specimens of those species. Geographic information will also permit identification.

The biogeographic history of *Marisora* outlined by Hedges & Conn (2012) still largely applies, suggesting that the origin of *Marisora* occurred in the Miocene by dispersal from northern South America to Middle America 5–7 million years ago (Ma), before the two land masses became permanently connected 3 Ma. Considering the updated phylogeny (Fig. 3) and timetree (Fig. 4) here, that initial dispersal led to the *M. alliacea* Group (Middle American Clade) that diversified in isolation. Two subsequent over-water dispersals from the Middle American Clade led to *M. pergravis* (Providencia) and *M. urtica* (Golfo de Fonseca). The Pliocene was a major time of speciation in the Middle American Clade. The northern South American Clade (*M. unimarginata* Group) probably evolved in isolation over the last seven million years in what is now Colombia, invading Panama and western Costa Rica after the Isthmus of Panama arose 3 Ma. A species from this clade, *M. unimarginata*, then became essentially sympatric with a species of the *M. alliacea* Group (*M. brachypoda*) in western Costa Rica. Separately, a long-distance dispersal from this clade led to *M. berengerae* on Isla San Andrés in the Caribbean. The NE South America Clade (*M. falconensis* Group) also evolved in isolation over the last seven million years in what is now Venezuela, dispersing during the Pleistocene to Trinidad and Tobago and the southern Lesser Antilles (*M. aurulae*).

With the new species described here, we have identified additional cases of sympatry and near sympatry. *Marisora lineola* and *M. brachypoda* are sympatric across a zone in south-central Guatemala (although not yet known to be syntopic), with some localities of the two species as close as 15 km. In addition, two pairs of species, *M. roatanae*-*M. magnacornae* and *M. magnacornae*-*M. alliacea*, are currently known to be separated by only 60 and 50 km, respectively, in continuous lowland rainforest, without losing their diagnostic characters or showing evidence of intergradation. Additional collections from intervening areas are likely to reduce those separations. Additionally, *M. urtica* occurs only about 2–3 km from localities of *M. brachypoda*, but on different islands. The co-occurrence (sympatry or near-sympatry) of species retaining their diagnostic differences is one of the hallmarks that two populations are not exchanging genes and are good species.

Cope (1875) was the first to recognize that multiple species of these skinks (in his case, *M. alliacea* and *M. unimarginata*) occurred in the same region (southern Middle America), although locality information was not as precise in those days as it usually is today. A century later, Taylor (1956) confirmed that *M. brachypoda* and *M. unimarginata* essentially co-occur, within ~10 km, in western Costa Rica, also close to the range of a third species, *M. alliacea*. Hedges & Conn (2012) re-examined Taylor's evidence and collected new morphological data on these species, confirming the findings of Cope (1875) and Taylor (1956) and suggesting the existence of additional species confused within *M. brachypoda,* although Savage (1973, 2002) later chose not to recognize multiple species of these Middle America skinks.

Miralles *et al.* (2009) and Pinto-Sánchez *et al.* (2015) presented molecular analyses showing deep divergences in Middle America, consistent with species-level differences in the literature, but they did not examine pertinent museum specimens of those Mexican and Central American populations in their study. As a result, they made taxonomic errors by using only their molecular phylogeny as a guide, collapsing several valid species into a single

species (*M. unimarginata*). In the case of Pinto Sánchez *et al.* (2015), this was especially surprising after Hedges & Conn (2012) had identified diagnostic characters for seven species in that genus, laying the groundwork for any further revision. Ironically, one of the main conclusions of Pinto Sánchez *et al.* (2015) was the discovery of putative new species of skinks from Colombia. However, we show here that most of their specimens are genetically close to, and possibly conspecific with, a described species, *M. unimarginata*, which they did not include in their study. Instead, they labelled other species, incorrectly, as *M. unimarginata*, leading them to conclude that *M. unimarginata* was distant to their putative new species. These errors could have been avoided by the joint use of morphological (e.g., museum specimens) and molecular data.

The increasing ease of obtaining molecular sequence data and availability of computational tools for conducting evolutionary analyses has led to a renaissance in systematics. At the same time, we must not forget that sequences belong to real organisms that have traits and names. Failing to consider these two types of information can lead to errors in evolutionary conclusions and in taxonomy. Museum collections and specimen examination are a critical and necessary part of systematics and will continue to be so into the future.

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APPENDIX 1. Specimens examined

A specimen number with a following * (asterisk) signifies that their morphological data, at least in part, were utilized in their species accounts. Coordinates for many Honduran collecting localities can be found in McCranie (2011) and updated in McCranie (2018: supplemental data). Coordinates for the remaining collecting localities are given when provided by the museum curators.

Marisora alliacea (29). COSTA RICA. FMNH 188802*, "no further data." *Heredia*: KU 67386*, 7.5 km W of Puerto Viejo; UF 30454*, 30459*, 30460, 30467, 30471*, Standard Fruit Company, Río Frio; *Limon*: KU 34332, Batán; FMNH 103150*, KU 34328, Los Diamantes. NICARAGUA. *Atlántico Sur*: MVZ 269259, Dos Bocas de Río Indio. *Río San Juan*: SMF 79804, 80902*, 82735*, 82736–37, 82739, Bartola; USNM 19542, Colorado Junction; SMF 82740, Islas Solentiname, Isla Mancarrón; KU 174109–10, Islas Solentiname. PANAMA. *Bocas del Toro*: USNM 142304*, Almirante; USNM 348007, Cayo Garcia; USNM 338240, Isla Colón; USNM 348217*, Isla Cristobal; USNM 347294*, Isla Popa; USNM 38690* 38691, Punta de Peña; USNM 58160, "no further data."

Marisora brachypoda (101). COSTA RICA. *Alajuela*: USNM 36997–98, San Mateo; *Guanacaste*: USNM 219871, Cañas; USNM 245018, 34 km S of Cañas; RT 1729, UF 143817*, Hacienda Taboga; TCWC 80536*, Los Angeles de Tilarán; *Puntarenas*: TCWC 17165*, 6.5 mi N, 2 mi W of Puntarenas; TCWC 84023*, 84025*, 1 mi S of Río Tarcoles; USNM 36996, Tivives. EL SALVADOR. *Ahuachapán*: SMF 81342*, El Refugio; SMF 79021*, 79023–26 (23*, 25*, 26*), Mariposario near San Francisco Menéndez; KU 289839, Parque Nacional El Imposible; *Chalatenango*: SMF 44390, Hacienda El Morito; *Cuscatlán*: KU 184348, Tenancingo; *La Libertad*: KU 184350, 1.8 km NE of Quetzaltepeque; *La Paz*: KU 184351, 184354, La Zunganera; *Morazán*: FMNH 10972, El Divisadero; *San Salvador*: KU 184349*, 184356–57, 184359, 184361–62, SMF 42416*, Lago de Ilopango; *Santa Ana*: SMF 43131*, Hacienda San José; SMF 44389*, Laguna de Güija; KU 184364*, 6 km S of Metapán; *Sonsonate*: SMF 51999*, 52000, 5 km S of San Julián. GUATEMALA. *Escuintla*: SMF 82694*–95*, near Guanagazapa; UTA R-45953, km 86 on road to El Salvador 14°6.50'N, 90°37.85'W; *Zacapa*: UTA R-28957–58, 41513, 41515, Cabañas, Aldea El Rosario; TCWC 17163, 13 km N, 27 km E of El Progresso. HONDURAS. *Choluteca*: UMMZ 123017, 21.1 km W of Choluteca; KU 200581, El Banquito; CAS 152979, El Despoblado; USNM 589170*, Finca Monterrey; SDSNH 72728, La Fortunita; *Copán*: USNM 570299–301, AMNH 70339–40, 140273, UMMZ 83029 (3), 1 km S of Copán; *El Paraíso*: USNM 589171*, Mapachín; USNM 589172*–73*, El Rodeo; USNM 589174*, 589175–76, 589177*, Orealí; AMNH 70380, Valle de Jamastrán; *Francisco Morazán*: USNM 570302*, El Picacho; AMNH 70338, El Zamorano; UF 143819, 8.0 km W of Maraita; BYU 18226, Río Yeguare near Tegucigalpa; Tegucigalpa, FMNH 5064*–65; *Valle*: UMMZ 94040, USNM 589192, Isla de Pájaros; USNM 589193*, near summit of Isla del Tigre; KU 194267, LSUMZ 36578, Isla Zacate Grande; SDSNH 72727, Playa Negra, Isla del Tigre; USNM 589198, Punta Novillo, Isla Zacate Grande. NICARAGUA. USNM 16145, "no further data"; *Boaco*: KU 103268, SMF 79351–52, 79665, La Cruz de Teustepe; *Estelí*: SMF 79668, El Carizo; *Granada*: UF 190316–17, SMF 78546*, 83067*, Volcán Mombacho; *León*: UMMZ 79912 (3), León; *Managua*: SMF 83064*, Laguna de Apoyeque; *Matagalpa*: UMMZ 116423–24, near Matagalpa; *Rivas*: SMF 82741–45 (all*), Isla de Ometepe, Lago de Nicaragua; TCWC 55590*, 1.5 km SE of La Virgén.

Marisora magnacornae (38). NICARAGUA. *Atlántico Sur*: KU 113017–19 (all *), El Recreo, Río Mico; AMNH 16417*, Kukra; AMNH 16412*, Masalina Creek; TCWC 55585–86 (both *), Muelle de las Buyes; TCWC 55587–89 (all *), 2 mi NW of Rama; USNM 19872*, Río Escondido, 50 river miles from Bluefields; USNM 19873*, Río Escondido, 16 river miles from Bluefields; AMNH 16413–14 (both *), 16417*, mouth of Río Grande; UMMZ 78942* (7 specimens; MJA 416–419, 422–424), 78943* (10 specimens; MJA 425–427, 487–493), 78944* (6 specimens; MJA 517, 523, 534, 541, 553, 610), Río Siquia NW of Rama.

Marisora roatanae (203). GUATEMALA. *Izabal*: UTA R-39644–48, 39649–51, 52217, Puerto Barrios. HONDURAS. *Atlántida*: USNM 62968, Carmelina; LACM 47753–54, Corozal; USNM 589167*, El Naranjal; USNM 578839*, Es-

tación Forestal CURLA; USNM 578840*, Jilamito Nuevo; LACM 47755–56, 13 km E of La Ceiba; INHS 4488, La Ceiba; ANSP 28120, 33147, MCZ R29888, Lancetilla; USNM 589168, near Pico Bonito Lodge; USNM 589169*, MCZ R21150, 21768, 27326–27, San José de Texíguat; MCZ R21150, Tela; *Colón*: ANSP 28121, Barranco; CM 65385–87 (all*), LSUMZ 22428, Trujillo; *Comayagua*: FMNH 5063, UF 124824 Siguatepeque; *Cortés*: AMNH 70337, MCZ R49966–67 (+ 3 unnumbered), TCWC 19211*–12*, Agua Azul; LSUMZ 52317–18, 1.6 km NW of El Jaral; FMNH 5062, El Jaral; FMNH 5061, Laguna Ticamaya; USNM 573175, 1 km N of Los Pinos; FMNH 5060, San Pedro Sula; *Gracias a Dios*: USNM 570303*–04*, Awasbila; USNM 20306–09, Barra Patuca; UF 150308, Cauquira; USNM 570305, Dursuna; USNM 589178*, Finca Nakunta; USNM 573961, SW end of Isla del Venado; USNM 573169, Kakamuklaya; LACM 16860, Kisalaya; USNM 570306, 573958–60, Krahkra; USNM 589179, 589180*, 589181, Leimus (Río Warunta); USNM 589182*–83*, Mavita; UTA R-42650–51, 42653, near Mocorón; UTA R-42652, 46175–78, 53521–24, Mocorón; BMNH 1985.1293–94, Palacios; USNM 589178, Puerto Lempira; LACM 16859, Quiguastara; USNM 559560, 570307, 570308*, 570309, 570310*, 589184*, Rus Rus; USNM 573957, 589185, Samil; UF 150307, 150312, Swabila; LACM 47726–28, USNM 573171, Tánsin; UF 150309, 150322, 150328, Tikiraya; USNM 573953–56, Usus Paman; USNM, 589186–89 (all*), Warunta; USNM 573172–74, Yahurabila; *Intibucá*: USNM 570311, 15.0 km SE of La Esperanza; FMNH 236393, 17.0 km N of Marcala; *Islas de la Bahía*: USNM 589202, Isla de Guanaja, Posada del Sol hotel ruins; USNM 589203*, Isla de Guanaja, Savannah Bight; LSUMZ 21883, "Isla de Guanaja"; TCWC 21955*, Isla de Roatán, Jonesville; UTA R-55232*, Isla de Roatán, Oak Ridge; USNM 589204*, Isla de Roatán, 1 km E of Pollytilly Bight; USNM 589205*–06*, 589207, Isla de Roatán, entrance to Turquoise Bay; SMF 77097*, Isla de Utila, 2.5 km N of Utila; LSUMZ 22309, SMF 79851, Isla de Utila, Utila; CM 65381, "Isla de Utila"; *La Paz*: USNM 570312–14, 13.7 km N of Marcala; FMNH 283593, Potrerillos; *Lempira*: USNM 573170, El Rodeito; CM 65382–83, Erandique; CM 65384, Gracias; *Olancho*: LACM 47720, 1 km WNW of Catacamas; LACM 45165, 47721–25, 4.5 km SE of Catacamas; LACM 45151, 12.1 km E of Dulce Nombre de Culmí; UTA R-41227, Las Trojas; USNM 570315, confluence of Quebrada Siksatara and Río Wampú; USNM 589190, near Río Catacamas; KU 200580, 10.5 km S of San Esteban; *Santa Bárbara*: AMNH 70341, El Sauce; USNM 589191*, SW corner of Lago de Yojoa; *Yoro*: LACM 47729, 5 km E of Coyoles; LACM 47730–52, Coyoles; USNM 589199, Río San Lorenzo; MVZ 52416, San Francisco; USNM 589200, 5.5 km ESE of San Lorenzo Arriba; USNM 570316*, 4.7 km ESE of San Lorenzo Arriba; USNM 589201*, San Patricio; FMNH 21784–85, 21787, 21826–28, MCZ R32037–39, 38934–36, 38936, UMMZ 77848 (6), Subirana Valley. NICARAGUA. *Atlántido Norte*: UF 190315, SMF 79830, Alamikamba; AMNH 16415–16, Cooley Plantation.

Marisora unimarginata (43). COSTA RICA. *Puntarenas*: KU 67387*, Golfito; SMF 92610, USNM 287721, Palmar Norte; *San José*: FMNH 178691*, 188801*, 4 miles NW of San Isidro del General; RT 1764*, TCWC 17164*, 4 mi N of San Isidro del General. PANAMA. *Chiriquí*: FMNH 60130*, 60131, Río Fonchico near highway 29; SMF 85445*, 8 km N of Río Sereno; *Colón*: USNM 54322, Canal Zone; *Darién*: USNM 50133, Caña; UF 143888–90 (all*), 1.0 mi W of El Real; FMNH 170158, Ortega Camp; FMNH 170117–18, 170120, vicinity of Santa Fé Camp; *Herrera*: CM 43595, Santa María Institute of Agriculture; *Islas de las Perlas*: USNM 120624–30, Isla San José; *Los Santos*: CM 43593–94 (both*), Los Santos; *Panamá*: USNM 50398, Ancón; FMNH 13363, 13364*, 56473, 123787, 176988, 176989*, 188782–83, Barro Colorado Island, Canal Zone; FMNH 195522, Cerro Campana; FMNH 152159, 170050, Panama City; *Veraguas*: USNM 148092, Río Corobo; UPRRP 6495*, "no further data".

APPENDIX 2. Sequences used in the molecular analyses

We summarize sample vouchers and locality data in the text below, and list Genbank numbers (if applicable) in the table, where samples and sequences new to this study are in bold. The Genbank database (Genbank 2018) provides other information on sequences, including the original submitter, authors of publications, and citations; the original articles contain additional information. Laboratory and sample numbers from earlier studies, listed here, are only for reference. NA = not applicable (no sequences available).

Specimen vouchers (if known), lab numbers, and localities of samples used in molecular analyses. *Mabuya dominicana* (SBH 268001; Dominica, St. Paul, Jimmit), *Marisora alliacea* 1 (not collected; Costa Rica, Limón, Tortuguero), *M. alliacea* 2 (MVZ 269259, SBH 274986; Nicaragua, Río San Juan, Dos Bocas del Río Indio), *M. aquilonaria* **sp. nov.** 1 (not collected; Mexico, Guerrero, Chichihualco), *M. aquilonaria* **sp. nov.** 2 (UOGV 709, SBH 274899; Mexico, Colima, El Paraíso), *M. aquilonaria* **sp. nov.** 3 (ANMO 2659, SBH 274902; Mexico, Morelos, approximately 0.8 km NW off of road between Coatetelco-Mazatepec near limit of Coatetelco), *M. aquilonaria* **sp. nov.** 4 (ENS 11812, SBH 274903; Mexico, Guerrero, Sierra Madre del

Sur, Carretera El Guayalo-La Laguna), *M. aquilonaria* **sp. nov.** 5 (ENS 11812, SBH 274904; Mexico, Guerrero, Sierra Madre del Sur, Carretera El Guayalo-La Laguna), *M. aquilonaria* **sp. nov.** 6 (ENS11811, SBH 274905; Mexico, Guerrero, Sierra Madre del Sur, Carretera El Guayalo-La Laguna), *M. aquilonaria* **sp. nov.** 7 (ANMO 3051, SBH 274913; Mexico, Guerrero, Chilacayapa, El Peral, on road between Chilpancingo-Chilapa), *M. aquilonaria* **sp. nov.** 8 (ANMO3045, SBH 274914; Mexico, Guerrero, between Chilpancingo and Zumpango del Río), *M. aquilonaria* **sp. nov.** 9 (ANMO 3647, SBH 274915; Mexico, Guerrero, Municipality of Olinalá), *M. aquilonaria* **sp. nov.** 10 (ANMO 1103, SBH 274916; Mexico, Michoacán, approx. 151 km on Mex Hwy 200 between Lazaro Cardenas and Manzanillo), *M. aquilonaria* **sp. nov.** 11 (UOGV 1513, SBH 274918; Mexico, Guerreo, Coyuca de Benítez), *M. aquilonaria* **sp. nov.** 12 (ANMO 1104, SBH 274919; Mexico, Michoacán, approx. 151 km on Mex Hwy 200 between Lazaro Cardenas and Manzanillo), *M. aquilonaria* **sp. nov.** 13 (IDF 67, SBH 274927; Mexico, Guerrero, Tixtla Road), *M. aquilonaria* **sp. nov.** 14 (ISZ619, SBH 274930; Mexico, Michoacán, approx. 22 km E of Caleta de Campos), *M. aquilonaria* **sp. nov.** 15 (JAC 22047; Mexico, Guerrero, Ejido de Bahia), *M. aquilonaria* **sp. nov.** 16 (JAC 22167; Mexico, Guerrero, Area above Chichihualco), *M. aquilonaria* **sp. nov.** 17 (JAC 24023; Mexico, Michoacán, Mex Hwy 200), *M. aurulae* (ZFMK 62603; Trinidad and Tobago, Tobago, Buccoo), *M. berengerae* 1 (ICN-R-12131; Colombia, San Andrés, Harmony Hall Hill), *M. berengerae* 2 (ICN-R-12132; Colombia, San Andrés, Shingle Hill), *M. berengerae* 3 (ICN-R-12134; Colombia, San Andrés, Harmony Hall Hill), *M. brachypoda* 1 (UF 190315; Nicaragua, Atlántido Norte, Alamikamba), *M. brachypoda* 2 (UF 190317; Nicaragua, Granada, Volcán Mombacho), *M. brachypoda* 3 (MF 6419, SBH 274912; Costa Rica, Guanacaste, Guanacaste Conservation Area, near Cacao station, on road to Cacao between Río Gongora and station), *M. brachypoda* 4 (UTA 41513; Guatemala, Zacapa, Zacapa), *M. brachypoda* 1 (UF 190316; Nicaragua, Granada, Volcán Mombacho), *M. brachypoda* 6 (SBH 274736; Honduras, Valle, Isla del Tigre), *M.* cf. *aurulae/falconensis* 1 (UIS-R-1485; Colombia, Guajira, Cerrejón), *M.* cf. *aurulae/falconensis* 2 (UIS-R-1979; Colombia, Cesar, Codazzi), *M.* cf. *aurulae/falconensis* 3 (UIS-R-1980; Colombia, Cesar, Codazzi), *M.* cf. *aurulae/falconensis* 4 (UIS-R-1981; Colombia, Guajira, Barrancas), *M.* cf. *aurulae/falconensis* 5 (UIS-R-1982; Colombia, Guajira, Barrancas), *M.* cf. *aurulae/falconensis* 6 (UIS-R-1985; Colombia, Atlántico, Baranoa), *M.* cf. *aurulae/falconensis* 7 (UIS-R-1986; Colombia, Bolívar, Arjona), *M.* cf. *aurulae/falconensis* 8 (UIS-R-1987; Colombia, Bolívar, Arjona), *M.* cf. *aurulae/falconensis* 9 (UIS-R-2026; Colombia, Atlántico, Usiacuri), *M. falconensis* 1 (not collected; Venezuela, Falcón, Península de Paraguaná), *M. falconensis* 2 (MHNLS 17095; Brazil, Distrito Federal, Brasília), *M. lineola* **sp. nov.** 1 (SBH 274907; Mexico, Tabasco), *M. lineola* **sp. nov.** 2 (SBH 274908; Mexico, Tabasco, Tapotzingo), *M. lineola* **sp. nov.** 3 (SBH 274909; Mexico, Tabasco, Tapotzingo), *M. lineola* **sp. nov.** 4 (SBH 274910; Mexico, Chiapas), *M. lineola* **sp. nov.** 5 (SBH 274911; Mexico, Chiapas), *M. lineola* **sp. nov.** 6 (ANMO 1903, SBH 274928; Mexico, Chiapas, dirt road to Kan Kan Ha), *M. pergravis* 1 (ICN-R-12135; Colombia, Providencia, South West Bay), *M. pergravis* 2 (ICN-R-12137; Colombia, Providencia, South West Bay), *M. roatanae* 1 (SBH 269383; Honduras, Islas de la Bahía, Roatán, Politilly Bight), *M. roatanae* 2 (SBH 269991; Honduras, Santa Bárbara, SW corner of Lago de Yojoa), *M. roatanae* 3 (SBH 269992; Honduras, Gracias a Dios, Mavita—4 km N Rus Rus), *M. roatanae* 4 (SBH 269993; Honduras, Gracias a Dios, Mavita—4 km N Rus Rus), *M. roatanae* 5 (SBH 269995; Honduras, Olancho, near Catacamas), *M. roatanae* 6 (SBH 269997; Honduras, Cortes, Los Pinos—visitors' center for PN Cerro Azul Meámber), *M. roatanae* 7 (SBH 274396; Honduras, Gracias a Dios, near Puerto Lempira), *M. roatanae* 8 (SBH 274397; Honduras, La Paz, Potrerillos), *M. roatanae* 9 (SBH 274416; Honduras, Islas de la Bahía, Guanaja), *M. roatanae* 10 (SMF 79851; Honduras, Islas de la Bahía, Isla de Utila), *M. roatanae* 11 (UTA 41227; Honduras, Olancho, Las Trojas, San Esteban), *M. roatanae* 12 (SBH 269994; Honduras, Yoro, San Lorenzo Arriba), *M. roatanae* 13 (SBH 274737; Honduras, Islas de la Bahía, Roatan), *M. syntoma* **sp. nov.** 1 (UOGV 872, SBH 274900; Mexico, Oaxaca, Approx 5 km SE Tapanatepec; km post 175 on road between Zanatepec-Pijijiapan (Mex 195-200)), *M. syntoma* **sp. nov.** 2 (UOGV 901, SBH 274901; Mexico, Chiapas, Chamic), *M. syntoma* **sp. nov.** 3 (ANMO 1045, SBH 274917; Mexico, Oaxaca, foot of the Sierra Madre, north of Zanatepec), *M. syntoma* **sp. nov.** 4 (RLR 1069, SBH 274920; Mexico, Chiapas, Ejido Conquista Campesina, Tapachula), *M. syntoma* **sp. nov.** 5 (RLR1086, SBH 274921; Mexico, Chiapas, Huixtla—Cantón La Ceiba), *M. syntoma* **sp. nov.** 6 (ANMO 2760, SBH 274923; Mexico, Oaxaca, Approx. 30 km on the road from Mitla toward Ayutla), *M. syntoma* **sp. nov.** 7 (RLR 1110, SBH 274925; Mexico, Chiapas, Acapetahua, Ejido Barra 2.51 km SE Zacapulco), *M. syntoma* **sp. nov.** 8 (ANMO 1944, SBH 274926; Mexico, Chiapas, Ranchería la Victoria, Cintalapa), *M. syntoma* **sp. nov.** 9 (ANMO 1943; Mexico, Chiapas, Ranchería la Victoria, Cintalapa), *M. syntoma* **sp. nov.** 10 (JAC 22922; Mexico, Oaxaca, Colonia Rodulfo Figueroa), *M. syntoma* **sp. nov.** 11 (not collected; Mexico, Oaxaca, on El Camaron-Tehuantepec road), *M. unimarginata* 1 (ICN-R12012; Colombia, Cauca, Guapi), *M. unimarginata* 2 (UIS-R-0530; Colombia, Antioquia, Santa Fé de Antioquia), *M. unimarginata* 3 (UIS-R-0543; Colombia, Antioquia, Santa Fé de Antioquia), *M. unimarginata* 4 (ICN-R-11687; Colombia, Córdoba, Montelíbano), *M. unimarginata* 5 (ICN-R-11688; Colombia, Córdoba, Tierra Alta), *M. unimarginata* 6 (MHUA-R-11762; Colombia, Sucre, Colosó), *M. unimarginata* 7 (MHUA-R-11971; Colombia, Antioquia, Barbosa), *M. unimarginata* 8 (not collected; Colombia, Córdoba, Valencia), *M. unimarginata* 9 (UIS-R-0518; Colombia, Antioquia, Puerto Berrio), *M. unimarginata* 10 (UIS-R-0528; Colombia,

Antioquia, Puerto Berrio), *M. unimarginata* 11 (UIS-R-0547; Colombia, Santander, Curití), *M. unimarginata* 12 (UIS-R-0573; Colombia, Santander, Curití), *M. unimarginata* 13 (UIS-R-0892; Colombia, Santander, Curití), *M. unimarginata* 14 (UIS-R-0901; Colombia, Cundinamarca, Yacopí), *M. unimarginata* 15 (UIS-R-0902; Colombia, Cundinamarca, Yacopí), *M. unimarginata* 16 (UIS-R-0904; Colombia, Cundinamarca, Yacopí), *M. unimarginata* 17 (UIS-R-1474; Colombia, Santander, Curití), *M. unimarginata* 18 (UIS-R-1477; Colombia, Santander, Pinchote), *M. unimarginata* 19 (UIS-R-1479; Colombia, Santander, Valle de San José), *M. unimarginata* 20 (UIS-R-1481; Colombia, Santander, Valle de San José), *M. unimarginata* 21 (UIS-R-1505; Colombia, Santander, Valle de San José), *M. unimarginata* 22 (UIS-R-1506; Colombia, Santander, Valle de San José), *M. unimarginata* 23 (UIS-R-1507; Colombia, Santander, Curití), *M. unimarginata* 24 (UIS-R-1508; Colombia, Santander, Simacota), *M. unimarginata* 25 (UIS-R-1509; Colombia, Santander, Simacota), *M. unimarginata* 26 (UIS-R-1510; Colombia, Santander, Valle de San José), *M. unimarginata* 27 (UIS-R-1532; Colombia, Santander, Sabana de Torres), *M. unimarginata* 28 (UIS-R-1740; Colombia, Santander, Lebrija), *M. unimarginata* 29 (UIS-R-1817; Colombia, Santander, Betulia), *M. unimarginata* 30 (UIS-R-1818; Colombia, Santander, Betulia), *M. unimarginata* 31 (UIS-R-1983; Colombia, Magdalena, Tayrona), *M. unimarginata* 32 (UIS-R-1984; Colombia, Magdalena, Tayrona), *M. unimarginata* 33 (UIS-R-1988; Colombia, Bolívar, San Jacinto), *M. unimarginata* 34 (UIS-R-1989; Colombia, Bolívar, San Jacinto), *M. unimarginata* 35 (UIS-R-1990; Colombia, Santander, Sogamoso), *M. unimarginata* 36 (UIS-R-1991; Colombia, Santander, Lebrija), *M. unimarginata* 37 (UIS-R-1997; Colombia, Tolima, Espinal), *M. unimarginata* 38 (UIS-R-1998; Colombia, Tolima, Espinal), *M. unimarginata* 39 (UIS-R-1999; Colombia, Huila, Aipe), *M. unimarginata* 40 (UIS-R-2003; Colombia, Huila, Timana), *M. unimarginata* 41 (UIS-R-2004; Colombia, Huila, Timana), *M. unimarginata* 42 (UIS-R-2005; Colombia, Valle del Cauca, Roldanillo), *M. unimarginata* 43 (UIS-R-2006; Colombia, Valle del Cauca, Bugalagrande), *M. unimarginata* 44 (UIS-R-2011; Colombia, Santander, Curití), *M. unimarginata* 45 (UIS-R-2012; Colombia, Tolima, Mariquita), *M. unimarginata* 46 (UIS-R-2013; Colombia, Tolima, Mariquita), *M. unimarginata* 47 (UIS-R-2014; Colombia, Caldas, Samaná), *M. unimarginata* 48 (UIS-R-2015; Colombia, Caldas, Samaná), *M. unimarginata* 49 (UIS-R-2017; Colombia, Risaralda, Marsella), *M. unimarginata* 50 (UIS-R-2018; Colombia, Risaralda, Marsella), *M. unimarginata* 51 (UIS-R-2019; Colombia, Caldas, Samaná), *M. unimarginata* 52 (UIS-R-2020; Colombia, Risaralda, Apia), *M. unimarginata* 53 (UIS-R-2023; Colombia, Chocó, Itsmina), *M. unimarginata* 54 (UIS-R-2024; Colombia, Chocó, Itsmina), *M. unimarginata* 55 (UIS-R-2025; Colombia, Santander, Curití), *M. unimarginata* 56 (UIS-R-2038; Colombia, Antioquia, Sopetrán), *M. unimarginata* 57 (UIS-R-903; Colombia, Cundinamarca, Yacopí), *M. unimarginata* 58 (UIS-R-905; Colombia, Cundinamarca, Yacopí), *M. unimarginata* 59 (SLK 156, SBH 274671; Panama, Chriquí, Hacienda Café de Eleta (citrus plantation between utility shed and Río Candela), *M. unimarginata* 60 (SLK 157, SBH 274672; Panama, Chriquí, Hacienda Café de Eleta (citrus plantation between utility shed and Río Candela)), *M. unimarginata* 61 (SLK 754, SBH 274673; Panama, Comarca Ngöbe Buglé, Guayabito (central soccer field)), *M. unimarginata* 62 (CH 4952, SBH 274924; Panama), *M. urtica* **sp. nov.** 1 (SBH 269996; Honduras, Valle, Isla Exposición), *M. urtica* **sp. nov.** 2 (ENS 12027, SBH 274906; Mexico, Oaxaca, La Alejandria—Puerto Escondido), *M. urtica* **sp. nov.** 3 (UOGV 1767; Mexico, Oaxaca, Finca El Carmen, municipality of Pluma Hidalgo, on the Pluma Hidalgo-Huatulco road), *M. urtica* **sp. nov.** 4 (UOGV 1768; Mexico, Oaxaca, Finca El Carmen, municipality of Pluma Hidalgo, on the Pluma Hidalgo-Huatulco road), *M. urtica* **sp. nov.** 5 (UOGV 1760, SBH 274922; Mexico, Oaxaca, Finca El Carmen, municipality of Pluma Hidalgo, on the Pluma Hidalgo-Huatulco road).

Species	12S rRNA	16S rRNA	Cyt b	RAG2	NGFB	R35
Mabuya dominicana	**MK395704**	JN227601	JN227561	NA	NA	NA
Marisora alliacea 1	EU477271	NA	EU443125	NA	NA	NA
M. alliacea 2	**NA**	**MK395749**	**MK395654**	NA	NA	NA
M. aquilonaria **sp. nov.** 1	EU477274	NA	EU443128	NA	NA	NA
M. aquilonaria **sp. nov.** 2	**MK395705**	**MK395704**	**MK395655**	NA	NA	NA
M. aquilonaria **sp. nov.** 3	**MK395756**	**MK395705**	**MK395656**	NA	NA	NA
M. aquilonaria **sp. nov.** 4	**MK395707**	**MK395706**	**MK395657**	NA	NA	NA
M. aquilonaria **sp. nov.** 5	**MK395708**	**MK395707**	**MK395658**	NA	NA	NA
M. aquilonaria **sp. nov.** 6	**MK395709**	**MK395708**	**MK395659**	NA	NA	NA
M. aquilonaria **sp. nov.** 7	**MK395710**	**MK395709**	**MK395660**	NA	NA	NA
M. aquilonaria **sp. nov.** 8	**MK395711**	**MK395710**	**MK395661**	NA	NA	NA
M. aquilonaria **sp. nov.** 9	**MK395712**	**MK395711**	**MK395662**	NA	NA	NA
M. aquilonaria **sp. nov.** 10	**MK395713**	**MK395712**	**MK395663**	NA	KJ492978.1	KJ492998.1

Species	12S rRNA	16S rRNA	Cyt b	RAG2	NGFB	R35
M. aquilonaria **sp. nov.** 11	**MK395714**	**MK395713**	**MK395664**	NA	NA	NA
M. aquilonaria **sp. nov.** 12	**MK395715**	**MK395714**	**MK395665**	KJ493034	NA	NA
M. aquilonaria **sp. nov.** 13	**MK395716**	**MK395715**	**MK395666**	NA	NA	NA
M. aquilonaria **sp. nov.** 14	**MK395717**	**MK395716**	**MK395667**	NA	NA	NA
M. aquilonaria **sp. nov.** 15	NA	NA	KJ492390	NA	KJ492979.1	KJ492999.1
M. aquilonaria **sp. nov.** 16	NA	NA	KJ492391	KJ493036	NA	NA
M. aquilonaria **sp. nov.** 17	KJ493321	NA	KJ492388	KJ493035	NA	NA
M. aurulae	AY070339	NA	NA	NA	NA	NA
M. berengerae 1	KJ493249	NA	KJ492297	KJ493002	NA	KJ492983
M. berengerae 2	KJ493248	NA	KJ492296	NA	KJ492965	KJ492982
M. berengerae 3	KJ493250	NA	KJ492298	KJ493003	NA	NA
M. brachypoda 1	**MK395718**	**MK395717**	**MK395668**	NA	NA	NA
M. brachypoda 2	**MK395719**	**MK395718**	**MK395669**	NA	NA	NA
M. brachypoda 3	**MK395720**	**MK395719**	**MK395670**	NA	NA	NA
M. brachypoda 4	EU477272	NA	EU443126	NA	NA	NA
M. brachypoda 5	**NA**	**MK395750**	**MK395671**	NA	NA	NA
M. brachypoda 6	**NA**	**MK395751**	**MK395672**	NA	NA	NA
M. cf. aurulae/falconensis 1	KJ493253	NA	KJ492302	NA	NA	NA
M. cf. aurulae/falconensis 2	KJ493256	NA	KJ492305	NA	KJ492967	KJ492986
M. cf. aurulae/falconensis 3	KJ493257	NA	KJ492306	NA	NA	NA
M. cf. aurulae/falconensis 4	KJ493254	NA	KJ492303	NA	NA	NA
M. cf. aurulae/falconensis 5	KJ493255	NA	KJ492304	KJ493005	KJ492966	KJ492985
M. cf. aurulae/falconensis 6	KJ493259	NA	KJ492308	NA	NA	NA
M. cf. aurulae/falconensis 7	KJ493258	NA	KJ492307	KJ493006	NA	NA
M. cf. aurulae/falconensis 8	NA	NA	KJ492300	KJ493004	NA	NA
M. cf. aurulae/falconensis 9	KJ493252	NA	KJ492301	NA	NA	NA
M. falconensis 1	EU477262	NA	EU443110	NA	NA	NA
M. falconensis 2	EU477261	NA	EU443109	NA	NA	NA
M. lineola **sp. nov.** 1	MK395721	**MK395720**	**MK395673**	NA	NA	NA
M. lineola **sp. nov.** 2	**MK395722**	**MK395721**	**MK395674**	NA	NA	NA
M. lineola **sp. nov.** 3	**MK395723**	**MK395722**	**MK395675**	NA	NA	NA
M. lineola **sp. nov.** 4	**MK395724**	**MK395723**	**MK395676**	NA	NA	NA
M. lineola **sp. nov.** 5	**MK395725**	**MK395724**	**MK395677**	NA	NA	NA
M. lineola **sp. nov.** 6	**MK395726**	**MK395725**	**MK395678**	NA	NA	NA
M. pergravis 1	KJ493269	NA	KJ492319	KJ493010	KJ492971	KJ492991
M. pergravis 2	KJ493268	NA	KJ492318	KJ493009	NA	NA
M. roatanae 1	**MK395727**	JN227610	**MK395679**	NA	NA	NA
M. roatanae 2	**MK395728**	**MK395726**	**MK395680**	NA	NA	NA
M. roatanae 3	**MK395729**	**MK395727**	**MK395681**	NA	NA	NA
M. roatanae 4	**MK395730**	**MK395728**	**MK395682**	NA	NA	NA
M. roatanae 5	**MK395731**	**MK395729**	**MK395683**	NA	NA	NA
M. roatanae 6	**MK395732**	**MK395730**	**MK395684**	NA	NA	NA
M. roatanae 7	**MK395733**	**MK395731**	KU587600	NA	NA	NA

Species	12S rRNA	16S rRNA	Cyt b	RAG2	NGFB	R35
M. roatanae 8	**MK395734**	**MK395732**	**MK395685**	NA	NA	NA
M. roatanae 9	**MK395735**	**MK395733**	**MK395686**	NA	NA	NA
M. roatanae 10	AB057378	NA	NA	NA	NA	NA
M. roatanae 11	EU477273	NA	EU443127	NA	NA	NA
M. roatanae 12	**NA**	**MK395752**	**MK395687**	NA	NA	NA
M. roatanae 13	NA	**MK395753**	**MK395688**	NA	NA	NA
M. syntoma **sp. nov.** 1	**MK395736**	**MK395734**	**MK395689**	NA	NA	NA
M. syntoma **sp. nov.** 2	**MK395737**	**MK395735**	**MK395690**	NA	NA	NA
M. syntoma **sp. nov.** 3	**MK395738**	**MK395736**	**MK395691**	KJ493033	KJ492977	KJ492997
M. syntoma **sp. nov.** 4	**MK395739**	**MK395737**	**MK395692**	NA	NA	NA
M. syntoma **sp. nov.** 5	**MK395740**	**MK395738**	**MK395693**	NA	NA	NA
M. syntoma **sp. nov.** 6	**MK395741**	**MK395739**	**MK395694**	NA	NA	NA
M. syntoma **sp. nov.** 7	**MK395742**	**MK395740**	**MK395695**	NA	NA	NA
M. syntoma **sp. nov.** 8	**MK395743**	**MK395741**	**MK395696**	NA	NA	NA
M. syntoma **sp. nov.** 9	NA	NA	KJ492381	NA	NA	NA
M. syntoma **sp. nov.** 10	NA	NA	KJ492384	NA	NA	NA
M. syntoma **sp. nov.** 11	EU477275	NA	EU443129	NA	NA	NA
M. unimarginata 1	NA	NA	KJ492340	NA	KJ492973	KJ492993
M. unimarginata 2	KJ493285	NA	KJ492341	NA	KJ492974	KJ492994
M. unimarginata 3	KJ493286	NA	KJ492342	NA	NA	NA
M. unimarginata 4	KJ493305	NA	KJ492365	KJ493026	NA	NA
M. unimarginata 5	KJ493313	NA	KJ492373	NA	NA	NA
M. unimarginata 6	KJ493307	NA	KJ492367	NA	NA	NA
M. unimarginata 7	NA	NA	KJ492364	KJ493025	NA	NA
M. unimarginata 8	KJ493314	NA	KJ492374	KJ493030	NA	NA
M. unimarginata 9	KJ493315	NA	KJ492375	NA	NA	NA
M. unimarginata 10	KJ493316	NA	KJ492376	KJ493031	NA	NA
M. unimarginata 11	NA	NA	KJ492336	NA	NA	NA
M. unimarginata 12	KJ493282	NA	KJ492337	NA	NA	NA
M. unimarginata 13	KJ493277	NA	KJ492330	NA	NA	NA
M. unimarginata 14	KJ493289	NA	KJ492345	NA	NA	NA
M. unimarginata 15	KJ493287	NA	KJ492343	NA	NA	NA
M. unimarginata 16	KJ493288	NA	KJ492344	KJ493016	NA	NA
M. unimarginata 17	NA	NA	KJ492331	NA	NA	NA
M. unimarginata 18	KJ493274	NA	KJ492326	NA	NA	NA
M. unimarginata 19	KJ493279	NA	KJ492333	NA	NA	NA
M. unimarginata 20	KJ493278	NA	KJ492332	KJ493012	NA	NA
M. unimarginata 21	NA	NA	KJ492328	NA	NA	NA
M. unimarginata 22	KJ493270	NA	KJ492320	KJ493011	NA	NA
M. unimarginata 23	KJ493275	NA	KJ492327	NA	NA	NA
M. unimarginata 24	KJ493273	NA	KJ492325	NA	NA	NA
M. unimarginata 25	KJ493317	NA	KJ492377	NA	NA	NA
M. unimarginata 26	KJ493276	NA	KJ492329	NA	NA	NA

Species	12S rRNA	16S rRNA	Cyt b	RAG2	NGFB	R35
M. unimarginata 27	NA	NA	KJ492323	NA	NA	NA
M. unimarginata 28	KJ493292	NA	KJ492348	NA	NA	NA
M. unimarginata 29	KJ493271	NA	KJ492321	NA	NA	NA
M. unimarginata 30	KJ493318	NA	KJ492378	KJ493032	NA	NA
M. unimarginata 31	KJ493308	NA	KJ492368	NA	KJ492976	KJ492996
M. unimarginata 32	KJ493309	NA	KJ492369	KJ493028	NA	NA
M. unimarginata 33	KJ493306	NA	KJ492366	KJ493027	NA	NA
M. unimarginata 34	KJ493310	NA	KJ492370	KJ493029	NA	NA
M. unimarginata 35	KJ493272	NA	KJ492322	NA	NA	NA
M. unimarginata 36	NA	NA	KJ492324	NA	NA	NA
M. unimarginata 37	KJ493290	NA	KJ492346	KJ493017	NA	NA
M. unimarginata 38	KJ493304	NA	KJ492361	KJ493024	NA	NA
M. unimarginata 39	KJ493300	NA	KJ492357	NA	NA	NA
M. unimarginata 40	KJ493302	NA	KJ492359	NA	NA	NA
M. unimarginata 41	KJ493303	NA	KJ492360	NA	NA	NA
M. unimarginata 42	KJ493293	NA	KJ492349	KJ493019	KJ492975	KJ492995
M. unimarginata 43	KJ493295	NA	KJ492352	KJ493020	NA	NA
M. unimarginata 44	KJ493280	NA	KJ492334	KJ493013	NA	NA
M. unimarginata 45	KJ493298	NA	KJ492355	NA	NA	NA
M. unimarginata 46	KJ493291	NA	KJ492347	KJ493018	NA	NA
M. unimarginata 47	KJ493299	NA	KJ492356	KJ493023	KJ492972	NA
M. unimarginata 48	KJ493301	NA	KJ492358	NA	NA	NA
M. unimarginata 49	KJ493294	NA	KJ492351	NA	NA	NA
M. unimarginata 50	KJ493296	NA	KJ492353	KJ493021	NA	NA
M. unimarginata 51	KJ493283	NA	KJ492338	KJ493015	NA	NA
M. unimarginata 52	NA	NA	KJ492350	NA	NA	NA
M. unimarginata 53	KJ493311	NA	KJ492371	NA	NA	NA
M. unimarginata 54	KJ493312	NA	KJ492372	NA	NA	NA
M. unimarginata 55	KJ493281	NA	KJ492335	KJ493014	NA	KJ492992
M. unimarginata 56	KJ493297	NA	KJ492354	KJ493022	NA	NA
M. unimarginata 57	NA	NA	KJ492362	NA	NA	NA
M. unimarginata 58	NA	NA	KJ492363	NA	NA	NA
M. unimarginata 59	**MK395744**	**MK395742**	**MK395697**	NA	NA	NA
M. unimarginata 60	**MK395745**	**MK395743**	**MK395698**	NA	NA	NA
M. unimarginata 61	**MK395746**	**MK395744**	**MK395699**	NA	NA	NA
M. unimarginata 62	**MK395747**	**MK395745**	**MK395700**	NA	NA	NA
M. urtica **sp. nov.** 1	**MK395748**	**MK395746**	**MK395701**	NA	NA	NA
M. urtica **sp. nov.** 2	**MK395749**	**MK395747**	**MK395702**	NA	NA	NA
M. urtica **sp. nov.** 3	NA	NA	KJ492394	NA	NA	NA
M. urtica **sp. nov.** 4	NA	NA	KJ492393	KJ493037	NA	NA
M. urtica **sp. nov.** 5	**MK395750**	**MK395748**	**MK395703**	NA	NA	NA