A NEW SPECIES OF MABUYA (REPTILIA, SQUAMATA, SCINCIDAE) FROM THE CARIBBEAN ISLAND OF SAN ANDRÉS, WITH A NEW INTERPRETATION OF NUCHAL SCALES: A CHARACTER OF TAXONOMIC IMPORTANCE

AURÉLIEN MIRALLES

Département d'Ecologie et de Gestion de la Biodiversité, FRE 2696 – Adaptation et évolution des systèmes ostéomusculaires, 55 rue Buffon, Muséum National d'Histoire Naturelle, Paris, France

A new species of *Mabuya* lizard from the isolated Caribbean island of San Andrés is described. This species is closely related to *Mabuya pergravis* Barbour, 1921, another poorly known species from Providencia Island, 87 km NNE of San Andrés. Unfortunately this new species, known from a single specimen, is now probably extinct. It differs from *M. pergravis* in many morphological characters such as a smaller size and very different patterns of coloration, but most importantly in the presence of a very high number of nuchal scales. A new definition of this last character, which is of systematic importance in the genus *Mabuya*, is also given and discussed.

Key words: insular endemism, Mabuya berengerae, San Andrés Archipelago, skink

INTRODUCTION

The San Andrés Archipelago is made up of two major isolated islands in the south-west Caribbean Sea, San Andrés (St. Andrew) and Providencia (Old Providence). These small Colombian islands are situated 197 km and 235 km respectively from the Nicaraguan coasts. Providencia lies at 87 km north-north-east of San Andrés. The latter is situated at 365 km in the north off the coast of Panamá, while Providencia is at 626 km from Jamaica, its nearest neighbour among the Antillean Islands (Fig. 1). Despite their proximity to each other and relationship to the continental landmass, San Andrés and Providencia are thought to have been uplifted independently in the early Tertiary and to have never had a land bridge either between them, or between the mainland (Parsons, 1956). San Andrés is made of uplifted Tertiary and Pleistocene rocks, and Holocene terrestrial and beach deposits (Geister, 1975).

Mabuya pergravis is an endemic species from the Island of Providencia. This species, described in 1921 by Barbour, was recognized by Dunn (1936, 1945) as a full

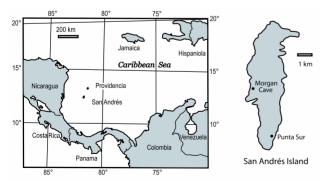


FIG. 1. Localisation of the two Islands of Providencia and San Andrés, with map of San Andrés Island.

Correspondence: A. Miralles, Département d'Ecologie et de Gestion de la Biodiversité, FRE 2696 – Adaptation et évolution des systèmes ostéomusculaires, 55 rue Buffon, Muséum National d'Histoire Naturelle, 75005 Paris, France. E-mail: amiral@mnhn.fr

species, then later regarded as a subspecies of M. mabouya (Dunn & Saxe, 1950; Valdivieso & Tamsitt, 1963). However, I consider M. pergravis as a species in its own right, even though it has some characteristics in common with the two other, widely distributed Caribbean species, M. mabouya and M. sloanii (considered by Dunn & Saxe [1950] as two populations of the same species M. mabouya, the first one being native from the southern Lesser Antilles and the second one from both the northern Lesser Antilles and Greater Antilles). Mabuya pergravis differs from its geographical closest neighbour, M. sloanii, in having a longer snout, a larger size and in the absence of two dorsal stripes. It differs also from M. mabouya in having four supraoculars (versus three) and a longer snout (Miralles, 2005), this last point being highly supported by the very wide gap of about 2200 km which separates their respective geographical distributions.

During a systematic revision of the genus *Mabuya*, a specimen (UMMZ 127884, firstly identified as a M. pergravis in the collection catalogue of the UMMZ) collected from the Island of San Andrés, was found. The presence of the genus on the island was never mentioned until now. After a comparison with two specimens of *M. pergravis*, USNM 13875 (holotype) and USNM 76947, it became clear the specimen from San Andrés does not conform to the species from the adjacent island of Providencia, nor with any other New World Mabuya. Even though M. pergravis and the specimen from San Andrés share some characteristics, such as a very long and pointed snout, some major characteristics distinguish the two forms easily, such as differences in scalation, size and colour patterns (Fig. 2). Given that (1) San Andrés island was never in contact with Providencia (Parsons, 1956), and is 87 km away from it; and (2) the specimen from San Andrés differs in many morphological characteristics from Mabuya pergravis, I hypothesize that the specimen UMMZ 127884 belongs to a species unknown to science. This paper describes this new species.

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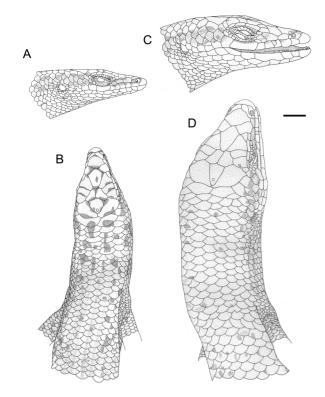


FIG. 2. Drawings of the head of the holotype of *Mabuya berengerae* (UMMZ 127884). A, lateral view of the head; B, dorsal view of the anterior part of the body; and of the holotype of *Mabuya pergravis* (USNM 13875); C, lateral view of the head; D, dorsal view of the anterior part of the body. Scale bar = 3 mm.

MATERIALS AND METHODS

According to its former definition, Mabuya Fitzinger, 1826 was considered as a worldwide distributed genus of tropical Scincidae (with the exclusion of Australia and Pacific islands). However, a recent phylogenetical study (Mausfeld et al., 2002) demonstrated that all Neotropical Mabuya species clearly form a monophyletic lineage (except M. atlantica, an endemic species from Fernando de Noronha Archipelago off Brazil, belonging to the African lineage, firstly classified by Mausfeld et al. (2002) as Euprepis Wagler, 1830, then replaced by Bauer (2003) by Trachylepis Fitzinger, 1843, in accordance with the rules of the Code of Zoological Nomenclature). Following these authors, I consider Mabuya in the present paper as an exclusively Neotropical genus, encompassing Central America, South America, and Caribbean islands.

The specimens examined for this study were preserved in 70% ethanol and deposited at the American Museum of Natural History, New York (AMNH), the Carnegie Museum, Pittsburgh (CM), the Field Museum of Natural History, Chicago (FMNH), the Museo de Historia Natural La Salle of Caracas (MHNLS), the Museum National d'Histoire Naturelle, Paris (MNHN), the Sam Noble Oklahoma Museum of Natural History, Norman (OMNH), the University of Michigan Museum of Zoology, Ann Arbor (UMMZ) and the National Museum of Natural History, Smithsonian Institution, Washington (USNM).

Drawings were made with a stereomicroscope LEICA MS5 equipped with a camera lucida. The scale nomenclature, scale counts and measurements used in the description of specimen are based after Avila-Pires (1995). New characters of first rank in systematics for the genus *Mabuya*, proposed by Greer & Broadley (2000), and Greer & Nussbaum (2000) were also added to the description. Moreover, a new definition of the nuchal scales is given in the discussion of the present paper.

MABUYA BERENGERAE SP. NOV.

Holotype. UMMZ 127884. An unsexed probably subadult or adult specimen from San Andrés Island (between Morgans Cave and Punta Sur), Departamento de Archipielago de San Andrés, Colombia [located between 12° 28' and 12° 36'N, and 81° 40' and 81° 44'W], collected on 6 August 1967 by C. F. Walker. The collector identified this specimen as a M. pergravis, and wrote accompanying field notes "basking on leaf three feet above the ground when first seen" (G. Schneider, pers. comm.).

Diagnosis. Mabuya berengerae is a particularly uncommon species which can be easily distinguished from all other Mabuya species, including its closest relative M. pergravis, by the following combination of characters: an extremely long, slender and pointed snout, the highest number of enlarged nuchal scales of any known species of Mabuya (Table 1), a high number of subdigital lamellae under the fourth toes (19) and a contrasting reticulated pattern on the upper side of the head, the neck and the back, also unique in the genus (Fig. 2B, 3).

Description of the holotype. UMMZ 127884 (Fig. 2A-B, 3). Very good state of preservation. Snout-vent length 52.8 mm, tail (regenerated) length 28.8 mm, Head length 11.7 mm. Rostral wider than high. Fore and hind limbs easily touching each other when adpressed against body. A pair of internasals in median contact. A frontonasal, approximately hexagonal, as wide as long, laterally in contact with anterior loreal scale. A pair of quadrilateral prefrontals, separated medially, and in contact with frontonasal, both anterior and posterior loreals, first supraciliary, first and second supraoculars, and frontal. Frontal rhomboid (almost triangular), in contact with all the length of the second supraocular. A pair of frontoparietals, each in contact with frontal, the supraoculars except the first, parietal and interparietal. Interparietal triangular, separated from nuchals by parietals; parietal eye distinct. Parietal overlapping the upper temporal scale. Four supraoculars, the second one being the longest and largest. The posteriormost supraocular in contact with the frontal is the second one. Four supraciliaries, the second the longest. Nostril in posterior part of the nasal. A small postnasal, bordered by supranasal, anterior loreal and first supralabial. An anterior and a posterior loreal, both elongate. A frenocular and two pre-suboculars. Lower eyelid undivided, with a transparent disk. A single row of small

TABLE 1. Number of primary and secondary pairs of enlarged nuchals (nuchals I and II) in some species of *Mabuya*. The table is divided in two parts: species without pair of secondary enlarged nuchal (upper part), and species with them (lower part). When specimens had an asymmetric number of nuchals on each side of the nape, the highest number of the two was scored. Data for species followed by an asterisk (*) are entirely or partly based on literature (Dunn & Saxe, 1950; Rebouças-Spieker & Vanzolini, 1990; Avila-Pires, 1995 and Hoge, 1946).

Species	Presence of nuchals I		Number of nuchals II				
	none	1	none	1	2	3	<u>≥</u> 4
M. bistriata (n=23)	_	23	23	_	_	_	_
M. falconensis (n=5)	_	5	5	_	-	_	-
M. frenata (n=6)	_	6	6	-	-	-	-
M. heathi (n=4)	_	4	4	-	-	-	-
M. nigropunctata (n=91)	2	89	90	1	-	-	-
<i>M. mabouya</i> (<i>n</i> =11)	-	11	11	-	-	-	-
M. pergravis (n=20)*	-	20	15	5	-	-	-
M. unimarginata (n=18)	_	18	18	-	-	-	-
M. berengerae (n=1)	-	1	-	-	-	-	1
$M. \ carvalhoi \ (n=4)*$	-	4	-	-	3	1	-
M. croizati (n=14)	-	14	-	1	8	5	-
$M. \ nigropalmata \ (n=5)*$	-	5	-	-	5	-	-
M. macrorhyncha (n=3)*	-	3	-	3	-	-	-
M. sloanii (n=19)	-	19	-	13	4	1	-

scales across the dorsal edge of the eyelid window. Eight supralabials, the sixth being the widest and forming the lower border of the eyelid. Two pretemporal scales, a single primary temporal, two secondary temporals in contact and three tertiary temporals. Temporal scales imbricate, smooth, cycloid, not distinctly delimited from the scales on the nape and the sides of the neck. Ear-opening relatively small, oval, with undulating anterior margin and smooth posterior margin. Mental scale wider than long, posterior margin straight. Postmental scales and a pair of chin shields in contact with infralabials. First pair of chin shields in contact medially, second pair separated by a smaller cycloid scale. Gulars similar to ventrals. Eight infralabials. One pair of primary nuchal scales, the left one being laterally fused with the left upper tertiary temporal; number of secondary nuchal scales asymmetric: five on the right side, four on the left one (see Discussion). Other scales on nape similar to dorsals. On lateral sides of neck, scales

slightly smaller. Dorsal scales cycloid, imbricate, smooth; 56 in a longitudinal row. Ventrals similar to dorsals; 37 in a longitudinal row. No distinct boundaries between dorsals, laterals and ventrals; 28 scales around midbody. Preanal plate with scales similar to ventral. Scales on tail similar to dorsals, except for its posterior part which is regenerated. Palms and soles light coloured, covered with small tubercles, subequal in size. Both regions delimited by a row of larger and flatter scales. Subdigital lamellae smooth, single, under fourth finger 14 (right) and 15 (left), under fourth toe 19 (on each side). Finger and toes clawed; toes length in the following order: I < II < III = V < IV.

The colour in life is unknown. In preservative, the background colour of the flanks and the upper side of the head, neck, back, legs and tail is bronze, with six very narrow and slightly darker dorsal lines running from the middle of the nape to the base of the tail. Supraciliaries, supranasals and lips are very light cream



FIG. 3. Photograph of the holotype of *Mabuya berengerae* (UMMZ 127884). Scale bar = 1 cm.

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coloured. A brown lateral strip, itself spotted with darker dots, extends each side from the nostril (loreals, upper third part of the supralabials, around eyes and temporals), along the upper half part of the ear-opening, and continues in a lighter reticulated gradation on the neck to above the arms (width on neck about three scale rows). Three nearly imperceptible light lines are supposed to have been more discernible in the living animal: a vertebral line, running from nape to the tail, and two dorsolateral ones, on each side along the lateral brown strips, from the lateral part of the parietals to above the arms. Many dark brown symmetric spots accentuate posterior sutures of nearly all supracephalic scales, others elongate spots run on the neck. The back, sides and upper side of the legs are spotted with small fused dark dots, forming many transverse narrow stripes. The ventrum, lower side of head, neck, lower side of the limbs and tail are cream-coloured with some grey marks due to the transparency of the ventral skin.

Etymology. The name has been given in honour of my wife Bérengère, for her invaluable support during all my studies.

Remark. It appears quite probable that this species, known from a single specimen, is now extremely rare. For this reason, I avoided the dissection of the holotype that would be necessary to determine its sex.

DISCUSSION

CONSERVATION, ENDEMISM AND BIOGEOGRAPHY

During the seventeenth and eighteenth centuries, San Andrés apparently supported extensive natural stands of "Cedar" (possibly Cedrela odorata), which were decimated by early colonists (Emmel, 1975). Most of the island is presently devoted to the cultivation of coconut palms, Cocos nucifera (covering the southern half of the island) and Colombian tourism. The human population of San Andrés increased from 17 000 in 1967 (Emmel, 1975) to over 50 000 in 1984 (Johnson, 1988) and is likely growing still. Gonzalez et al. (1995) comment on the state of conservation of the original biotopes on San Andrés and Providencia islands "It has been an unequal struggle: so many hectares of Primary forest mainly from San Andrés, have been sacrificed to give space for hundreds of cement tons". Unfortunately, Mabuya berengerae is only known from a single specimen caught in 1967. Given the small size of the island, its very damaged ecosystem (Emmel, 1975; Barriga et al., 1985; Johnson, 1988; Gonzalez et al., 1995) and the fact that this specimen is the only one known, it appears highly probable that this species is now endangered, if not extinct. For those reasons, a faunistic survey on this island seems to be urgently needed, in particular for a reassessment of the current conservation status of M. berengerae, but also in a more general perspective, to have an accurate assessment of the degree of endemism on this island and to elaborate preservation strategies to protect it.

Indeed, the San Andrés Archipelago appears to have a unique evolutionary history. Despite the fact that few studies were published on the fauna of San Andrés Island, five endemic taxa of terrestrial vertebrates have been described in addition to Mabuya berengerae, from it: three reptiles out of thirteen known from the Archipelago (Valdivieso & Tamsitt, 1963), including a dipsadine snake species, Coniophanes andresensis Bailey, 1937, a species of polychrotid (also present on Providencia), Norops concolor (Cope, 1862), and a subspecies of gekkonid lizard, Sphaerodactylus argus andresensis Dunn & Saxe, 1950; but also two passerines birds including a species of mimid, Mimus magnirostris Cory, 1887 and a species of vireonid, Vireo caribaeus Bond & Meyer de Schauensee, 1942. On the other hand, no amphibian or mammal species appears to be endemic to the island. So high a degree of endemism in so small an area (about 44 km²) strongly suggests a unique history and a prolonged isolation of this island.

Given the large distance that separates the San Andrés Archipelago from the other Caribbean islands, its biogeographical affinities are not clear. Its original fauna and flora seem to be a mix of both Mesoamerican and Caribbean elements (Riley, 1975; Smith et al., 1989; Gonzalez et al., 1995). Although it seems certain that M. berengerae and M. pergravis are sibling species (their extremely elongate and pointed snout being the most remarkable synapomorphy of their monophyletic lineage), the origin of this clade on the archipelago is still unresolved. On the basis of their scale characters, Dunn & Saxe (1950) conclude that the Mabuya from Providencia seemed to be more closely related to the Lesser Antillean populations than to those from the adjacent mainland. Indeed, M. pergravis and M. berengerae share with M. mabouya (present in the southern Lesser Antilles from Dominica, Guadeloupe, Martinique and Saint Lucia) a slender muzzle and a short lateral strip from snout to above arms. They share also with M. sloanii (present in northern Lesser Antilles and in the Great Antilles) the presence of secondary nuchal scales. Contrary to the biogeographical trends based on botanical or entomological studies, no affinities seem to be shared by Mesoamerican species of Mabuya and the San Andrés Archipelago's clade.

However, species belonging to the genus *Mabuya* are often very similar and external morphological characters are usually used for studying their taxonomy. Unfortunately, most of these characters could easily result from convergence. For this reason, only a real phylogenetical approach would precisely determine the relationships of this small clade.

WHAT IS A NUCHAL SCALE?

The organisation of the nuchal scales, transversally enlarged dorsal scales of the nape, is a major characteristic in the systematics of the genus *Mabuya*, and more generaly in all the lygosomines skinks. Notably, it represents one of the most important diagnostic characters for

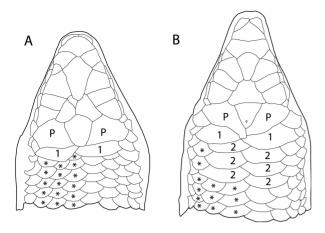


FIG. 4. Details of scales on the nape of two specimens of *Mabuya*: (A) specimen with only a pair of primary nuchals (*M. nigropunctata*, OMNH 36834) and (B) specimen with a pair of primary nuchals and three pairs of secondary nuchals (*M. carvalhoi*, AMNH 13732). P: parietal scale; 1: primary nuchal scale; 2: secondary nuchal scale; *: rows of cycloid scales homologue to nuchals ones (only showed for the left side).

the new species described in the present paper. Until now, no real definition was given to explain what a nuchal scale is, this point being somewhat unclear in the literature. Most of the authors who worked on the systematic of the genus *Mabuya* considered more or less implicitly nuchal scales as any scales present on the nape, in contact with parietals, and larger than other cycloid scales (= small scales covering the body) present on the back, (Dunn, 1936; Hoogmoed, 1973; Avila-Pires, 1995; Rodrigues, 2000). Recently, Mayer & Lazell (2000: 872) proposed that the pair of scales on the nape as a pair of nuchal scales if their combined width is more than 75% the width of the parietals.

However, the width of dorsal scales can vary gradually in some specimens, from the small cycloid scales of the back to the wide scales of the nape. Consequently, it becomes impossible to distinguish the limit between these two categories of scales, the count becoming subjective. Therefore, I propose to present here a more accurate definition for the nuchal scales. This one is based on a hypothesis of homology. A nuchal scale is regarded as an enlarged scale of the nape, occupying transversally the place of two or more rows of dorsal cycloid scale. Thus, the antero-posterior transition from nape to back, between nuchal and dorsal scales is sharp, one longitudinal row of nuchals giving rise to two rows of cycloïds. In the case of a gradual variation of width between a single row of small dorsal scale and a single row of large scale on the nape, all those scales will be considered as "enlarged dorsal cycloid ones", not as nuchals. Additionally, I have distinguished two categories of nuchals (Fig. 4). The "primary pair of enlarged nuchals, or nuchals I" (Fig. 4A-B) is in contact with the posterior border of the parietal scales. Each scale of this always singular pair occupies the equivalent of three transverse rows of dorsal cycloid scales (sometimes two). The nuchals I are present in all species belonging to the genus Mabuya sensu lato. The "secondary pairs of

enlarged nuchals, or nuchals II" (Fig. 4B) are aligned along the vertebral axis, posterior to the "nuchals I". Their number could vary from one to four/five pairs (holotype of *M. berengerae*) depending on the species. Each "nuchal II" occupies the equivalent of two transverse rows of dorsal cycloid scales. They are always present in six species, M. berengerae, M. carvalhoi, M. croizati, M. nigropalmata, M. macrorhyncha and Mabuya sloanii. They are nearly always absent in M. arajara, M. bistriata (sensu Avila-Pires, 1995), M. caissara, M. cochabambae, M. dorsivittata, M. falconensis, M. frenata, M. guaporicola, M. heathi, M. pergravis, M. mabouya (sensu Miralles, 2005), M. nigropunctata (sensu Avila-Pires, 1995) and M. unimarginata (sensu Savage, 2002), (Avila-Pires, 1995; Dunn, 1936; Mausfeld & Lötters, 2001; Mijares-Urrutia & Arends, 1997; Rebouças-Spieker, 1981; Rodrigues, 2000). On the other hand, they seem to be occasionally present in only four species, M. agmosticha, M. lineolata, M. macleani and M. pergravis (Cochran, 1941; Dunn & Saxe, 1950; Mayer & Lazell, 2000; Rodrigues, 2000). In conclusion, the characteristic "presence or absence of secondary nuchals scales" constitutes a new useful diagnostic character given its very low intraspecific variability for the majority of Mabuya species.

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APPENDIX

SPECIMENS EXAMINED AND LOCALITIES (*N*=159):

Mabuya berengerae sp. nov. (*n*=1): COLOMBIA: San Andrés Island: UMMZ 127884 (holotype), between Morgans Cave and Punta Sur (= South End).

Mabuya carvalhoi (*n*=1): BRAZIL: Roraima: AMNH R-137372 (paratype), Ilha de Maraca.

Mabuya croizati (*n*=14): VENEZUELA: Sucre: AMNH R-29314 (holotype), Turumiquire massif; CM 7978, 7982, 7988, Elvecia, Turumiquire massif; FMNH 17796, 17797, 17798-428 to 17798-430, 17799-434 to 17799-438, Turumiquire massif.

Mabuya falconensis (n=5): VENEZUELA: Carabobo: MHNLS 5511, 5512, Lago de Valencia; FALCÓN STATE: 5526, Sierra San Luis, Curimagua; UMMZ 55927, 55932, Tucacas.

Mabuya mabouya (n=11): LESSER ANTILLES: Dominica: MNHN 2003-0838, UMMZ 83323. Guadeloupe: MNHN 2902, 1889-0664. Martinique: MNHN 738, 739, 1785, 5110, 5421, 5424. Unspecified island: MNHN 2903.

Mabuya nigropunctata (n=98): BRAZIL: Acre: OMNH 37048 to 37051, 5 Km N Porto Walter, inland from the Rio Juruá. Amazonas: OMNH 37681 to 37698, Município de Castanho, 40 Km S Manaus at Km 12 on road to Autazes. Maranhão: MPEG 10690, 10691, 10693, 10695, 10698, Nova Vida, 25 Km dist. of Rio Gurupi, BR 316. Para: MPEG 8605, 8608, 8611, 8616, 8642, Bela Vista, Viseu; MPEG 12194, 12196, 12199, 12200, 12218 between the rivers Tocantins and Mojú, 12 miles of the barrage Tucurui; OMNH 36828 to 36842, CEMEX, Agropecuaria Treviso LTDA, 101 Km S and 18 Km E Santarém. Rondonia: OMNH 37411 to 37417, Rio Formoso, Parque Estadual Guajará-Mirim, 90 Km N Nova Mamoré. Roraima: OMNH 36313 to 36322, 7 km E Rio Ajaraní, BR 210. FRENCH GUIANA: MNHN 1996-4570 to 1996-4572, 1997-2206 to 1997-2213, St Eugene; MNHN 2002-0612, 2002-0613, St Marcel. TRINIDAD & TOBAGO: AMNH R-64528, Trinidad island FMNH 49901 to 49908, Trinidad island, San Rafael, UMMZ 79919, Trinidad island. VENEZUELA: Amazonas: MHNLS 16389, Parima B, Bolívar: MHNLS 15532, Serranía del Supamo, Cerro Santa Rosa; MHNLS 11545, foot of the Roraima Moutain. Delta Amacuro: MHNLS 4543, Burojoida. Sucre: MHNLS 15533, Peninsula de Paria, Las Melenas; MHNLS 16203, Peninsula de Paria, Macuro.

Mabuya lineolata (n=1): GREATER ANTILLES: Dominican Republic: AMNH R-42145 (Holotype), Monte Cristy province, not far from Monte Cristy, near the bank of the Rio Yaque del Norte.

Mabuya pergravis (n=2): COLOMBIA: Providencia island: USNM 13875 (Holotype), USNM 76947

Mabuya sloanii (n=19): BAHAMAS: Turks and Caicos islands: UMMZ117393, West Caicos, on W side. GREATER ANTILLES: Jamaica: UMMZ 85861, Portland Point. Puerto Rico: CM 23775, 23776, FMNH 215, UMMZ 124819, Mona Island; OMNH 32878, unspecified locality. LESSER ANTILLES: Anguilla: CM 115480, Brimegin, W of Foutain Hill, CM 115481, unlocalised locality. British Virgin Islands: CM 17357, 17358, Anegada: UMMZ 80582 Virgin Gorda, Saint-Barthélemy: **MNHN** 1997-6064, 2003-0843. 2003-0844, unlocalised locality. US Virgin Islands: MNHN 554 (holotype), 1088, St Thomas; UMMZ 73821, St Thomas, Buck Island; UMMZ 80586, St Thomas, Capella Island.

Mabuya unimarginata complex (n=7): COSTA RICA: Puntarenas: UMMZ 117575, 1 Mile E of Volcan de Buenos Aires cone finca; UMMZ 145875, 16 Km S San Vito, on Highway 16 Las Cruces field station, 1250m. MEXICO: Yucatan: AMNH R-38863 to R-38865, Chichen Itza; UMMZ 113548, Calcehtok. NICARAGUA: Leon: OMNH 36173 to 36175, Vulcan Momotombo. Rio San Juan: OMNH 36177 to 36179, by Isla de Diamante on Rio San Juan. Rivas: OMNH 36176, Chococente. PANAMA: Bocas del Toro: UMMZ 142636, Bocas del Toro. Los Santos: CM 43593 to 43594, Los Santos; CM 43595, Santa Maria. Panama: UMMZ 135354, Gorgas Memorial Laboratory Field Station on the Rio Bayano, 250 m alt.