



## Three rare and enigmatic South American skinks

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### Abstract

Three enigmatic skinks, *Mabuya nigropalmata* Andersson, 1918, *Tiliqua maculata* Gray, 1839, and *Trachylepis* (*Xystrolepis*) *punctata*, Tschudi, 1845, have been reported from widely separated localities on the South American mainland. They remain the three rarest and most poorly known South American skinks and were known only from type material until recently. In this paper, we comment on recent rediscoveries of *M. nigropalmata* in the western Amazon of Peru and Bolivia. Using cytochrome b and 12S DNA sequences, we resolve this species's phylogenetic position within *Mabuya sensu stricto* and demonstrate its specific distinctiveness, especially from the superficially similar species *M. frenata*. In addition, we show that neither *Trachylepis* (*Xystrolepis*) *punctata* nor *Tiliqua maculata* can be placed within *Mabuya*. A suite of morphological characteristics requires the transfer of these two species to the mostly Afro-Malagasy genus *Trachylepis*. To correct the secondary homonymy of Tschudi's name, we propose a replacement name for *T. punctata*. We designate NRM 23258A as the lectotype of *Mabuya nigropalmata* Andersson and MNHN 2932 as the lectotype of *Trachylepis maculata* (Gray) **new combination**. Finally, we propose an identification key to *Mabuya* of the Amazon basin and adjacent regions.

**Key words:** Scincidae, *Mabuya nigropalmata*, *Trachylepis atlantica*, *Trachylepis maculata* **new combination**, *Trachylepis* (*Xystrolepis*) *punctata*, *Trachylepis tschudii* **new name**, Peru

### Introduction

Recent phylogenetic analyses of the pantropical supergroup *Mabuya sensu lato* (Carranza & Arnold 2003, Mausfeld *et al.* 2002) have identified several monophyletic lineages and allowed its breakup into *Chioninia* (Cape Verdian clade), *Eutropis* (Asian clade), *Trachylepis* (Afro-Malagasy clade, including *Mabuya atlantica*, from Fernando de Noronha island, offshore Brazil) and *Mabuya sensu stricto*, which is restricted to the Neotropics. Prior to the mid 1990s, the systematics of South American *Mabuya* was confusing due to a combination of nomenclatural and taxonomic problems (Ávila-Pires 1995, Mausfeld & Lötters 2001, Miralles 2005). However, a series of recent publications have resolved most persisting problems with this group (Ávila-Pires 1995; Mijares-Urrutia & Arends 1997; Mayer & Lazell 2000; Rodrigues 2000; Massary *et al.* 2001; Miralles 2005, 2006a, 2006b; Miralles *et al.* 2005a, 2005b, 2006, in press, Vrcibradic *et al.* 2006, Whiting *et al.* 2006, Harvey *et al.* 2008).

This paper constitutes one of the last steps in an ongoing taxonomic revision of *Mabuya* begun by the first author many years ago; its aim is essentially to focus on three taxa that could be considered the rarest and most enigmatic South American skinks: (A) *Mabuya nigropalmata* Andersson, 1918, from the western Amazon; (B) *Tiliqua maculata* Gray, 1839, reportedly from Guyana; and (C) *Trachylepis* (*Xystrolepis*) *punctata* Tschudi, 1845, reportedly from Amazonian Peru. All three species have been classified as

Neotropical species of *Mabuya* by several authors (Andersson 1918, Dunn 1936, Horton 1973, Ávila-Pires 1995, Brygoo 1985, Mausfeld & Vrcibradic 2002). Nonetheless, virtually nothing is known about them.

During our previous studies on the genus *Mabuya*, we examined more than 600 specimens from 25 international collections. Although this sample contained numerous specimens from the Amazon Basin, no additional specimens of *M. nigropalmata*, *Trachylepis punctata*, or *Tiliqua maculata* were identified (Miralles 2005, 2006a, 2006b, Miralles *et al.* 2005a, 2005b, 2006, in press). The total absence of these three species understandably raised some doubts about whether they actually occurred in the Neotropics or were really mislabelled specimens from somewhere else. Then in 2004, Moravec & Aparicio published a “note on the herpetofauna of Nacebe” in the Journal of the National Museum of Prague (*Časopis Národního muzea, Řada přírodovědná*), which mentioned two new specimens of *M. nigropalmata*. One year later, one of us (JCC) collected two specimens (MHNC 5121 and 5718) from sandbars along the Manu River, southern Peru. These nearly simultaneous rediscoveries provide an opportunity to redescribe this rare species’s morphology and color in life, to provide additional information on its distribution and ecology, and to analyze DNA samples in order to determine its phylogenetic affinities. Regretably, the other two species remain problematic. Nonetheless, after examining their respective type specimens, we determine their generic allocation and comment on their likely provenance.

## Materials and methods

Museum abbreviations refer to the American Museum of Natural History, New York (AMNH), Natural History Museum, London (NHM), Colección Boliviana de Fauna, Museo Nacional de Historia Natural, La Paz (CBF), Coleção Herpetológica da Universidade de Brasília (CHUNB), Carnegie Museum, Pittsburgh (CM), Estación Biológica de Rancho Grande, Maracay (EBRG), Field Museum of Natural History, Chicago (FMNH), Los Angeles County Museum, Los Angeles (LACM), Museum of Comparative Zoology, Cambridge (MCZ), Museo de Historia Natural, Universidad Nacional de San Antonio Abad del Cusco (MHNC), Museo de Historia Natural La Salle, Caracas (MHNLS), Museum d’Histoire Naturelle de Neuchâtel (MHNN), Museum National d’Histoire Naturelle, Paris (MNHN), Museu Paraense Emilio Goeldi, Belém (MPEG), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), Department of Zoology of the National Museum of Prague (NMP6V), Swedish Museum of Natural History, Stockholm (NRM), Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), Sam Noble Oklahoma Museum of Natural History, Norman (SNOMNH), Laboratorio de Biogeografía, Universidad de Los Andes, Mérida (ULABG), University of Michigan Museum of Zoology, Ann Arbor (UMMZ), and Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK). Specimens examined are listed in the Appendix II.

Drawings were made with a stereomicroscope (LEICA MS5) equipped with a camera lucida and/or with Adobe Illustrator. The scale nomenclature, scale counts and measurements follow Ávila-Pires (1995). Counts of subdigital lamellae do not include the last scale in contact with the claw.

We sequenced approximately 1540 bp of mtDNA [including a 12S gene fragment ( $\approx$  385 bp) and the complete cytochrome *b* gene ( $\approx$  1155 bp)] from a specimen of *M. nigropalmata* from Manu National Park, southern Peru (MHNC 5718) (and additionally from a specimen of *M. altamazonica* (MHNC 6703)). We combined the new sequences with sequences of 31 other samples, previously generated and submitted to GenBank (Mausfeld & Lötters 2001, Carranza & Arnold 2003, Miralles *et al.* 2006, in press, Whiting *et al.* 2006). These samples, representing 20 different species of *Mabuya* (Table 1), include all South American species except for *M. arajara*, a species known only from a few localities in Ceara, Brazil. Thus, all species known from the Amazon Basin were included in the analysis: *M. altamazonica*, *M. bistrriata*, *M. carvalhoi*, *M. guaporicola*, *M. nigropalmata*, and *M. nigropunctata* (Ávila-Pires 1995; Miralles *et al.* 2006). The tree was rooted with *Eumeces egregius* and “*Mabuya*” *vittata* [this last species belongs to an unnamed Mediterranean clade, which is the sister group of *Mabuya sensu stricto* (Carranza & Arnold, 2003). We use quotation marks to indicate that it is unnamed; Miralles *et al.*, 2006).

**TABLE 1.** List of specimens, collection and accession numbers of the sequences with their references, and localities. Genbank accession numbers of new sequences obtained for this study are in bold; all the rest are from Kumazawa & Nishida (1999), Mausfeld & Lötters (2001), Carranza & Arnold (2003), Whiting *et al.* (2006) and Miralles *et al.* (in press); Dash represent missing datas.

Species	Country	Collection number	Locality	Sequences	
				Cyt b	12S
<b>Ingroup:</b>					
<i>M. agilis</i>	Brazil, Pernambuco	not collected <sup>(1)</sup>	Exu	EU443102	AY151428
<i>M. agmosticha</i>	Brazil, Alagoas	LG 902	Xingó (a)	DQ239134	DQ239215
		LG 901	Xingó (b)	DQ239133	DQ239214
<i>M. altamazonica</i>	Peru, San Martin	MNHN	km 34 on road « Tarapoto-	EU443103	DQ368663
		2002.0291 <sup>(2)</sup>	Yurimaguas » (a)		
		MHNC 6703	PN. Rio Abiseo (07°21' 44.9"S; 76°50' 13.8"W) (b)	EU515212	EU515210
<i>M. bistriata</i>	Brazil, Amazonas	SNOMNH 37183	Madeira Scheffer (8°20'47.0''S; 65°42'57.9''W)	EU443104	EU477258
	French Guyana	not collected	Matoury	EU443105	DQ368664
<i>M. carvalhoi</i>	Brazil, Roraima	SNOMNH 36332	junction BR-174 / BR-210	EU443106	EU477259
<i>M. cochabambae</i>	Bolivia, Santa Cruz	ZFMK 72151	vicinity of Pampagrande.	—	AF202625
<i>M. croizati</i>	Venezuela, Antzoátegui	MHNLS 17670	Cerro El Guamal, Turimiquire massif	EU443107	EU477260
<i>M. dorsivittata</i>	Brazil, D.F.	not collected	Brasilia	EU443108	AY151426
	Argentina, Cordoba	LAV-5000	Rio Cuarto city	DQ239149	DQ239230
<i>M. falconensis</i>	Venezuela, Falcón	MHNLS 17095	Peninsula de Paraguaná	EU443109	EU477261
<i>M. frenata</i>	Brazil, M. G. do Sul	not collected	?	EU443111	AY151427
	Brazil, Goias	LG 861	Santa Rita do Argaguia	DQ239128	DQ239209
<i>M. guaporicola</i>	Bolivia, Santa Cruz	UTA 55700	El Refugio	EU443113	EU477263
	Brazil, M. G. do Sul	not collected <sup>(1)</sup>	?	EU443112	AY151434
<i>M. mabouya</i>	Brazil, Mato Grosso	LG 1574	UHE Manso	DQ239250	DQ239169
	Lesser Antilles	MNHN 2003-0838	Dominica island	EU443114	EU477264
<i>M. macrorhyncha</i>	Brazil, Sao Paulo	LG 1102	Ilha da Queimada Grande (a)	DQ239162	DQ239243
		LG 1103	Ilha da Queimada Grande (b)	DQ239132	DQ239213
<i>M. meridensis</i>	Venezuela, Mérida	not collected	Mérida	EU443116	EU477266
<i>M. nigropalmata</i>	Peru, Madre de Dios	MHNC 5718	Manu national park	EU515213	EU515211
<i>M. nigropunctata</i>	Brazil, Pará	LSUMZ H14223	Agropecuaria Treviso LTDA (3°8'56.7''S; 54°50'26.8''W)	EU443118	DQ368667
	Brazil, Roraima	SNOMNH 36318	Fazenda Nova Esperanca (BR-210, 41 km W BR-174)	EU443119	DQ368668
	Colombia, Guainia	not collected	Puerto Inirida	EU443120	AY151438
	Venezuela, Aragua	MHNLS 17080	Turiamo	EU443121	EU477268
<i>M. sloanii</i>	Lesser Antilles	MNHN 2003-0844	St Barthélémy island	EU443122	EU477269
<i>M. unimarginata</i>	Guatemala, Zacapa	UTA 41513	Zacapa	EU443126	EU477272
<i>M. sp. A</i> <sup>(3)</sup>	Venezuela, Zulia	MHNLS 16676	Cerro el Mirador	EU443130	EU477276
<i>M. sp. B</i> <sup>(3)</sup>	Venezuela, Aragua	MNHN 2007.0272	La Colonia Tovar	EU443135	EU477281
<b>Outgroup:</b>					
<i>E. egregius</i>	North America	MVZ 150128	Florida	AB016606 <sup>(4)</sup>	
« <i>Mabuya</i> » <i>vittata</i>	Middle East	BEV 1446	Turkey, Osmandere	EU443142	EU477288

<sup>(1)</sup> Two samples sequenced by Carranza & Arnold (2003) have been here reidentified: *Mabuya agilis* (synonymous with *M. heathi*, E11108); *M. guaporicola* (instead of *M. agilis*, E11101).

<sup>(2)</sup> Holotype specimens.

<sup>(3)</sup> Undescribed species (to be published, Miralles *et al.*, in press).

<sup>(4)</sup> Complete mitochondrial genome, sequenced by Kumazawa & Nishida (1999).

We extracted total genomic DNA from 95% ethanol-preserved tissues (muscles or liver) using a CTAB protocol (Winnepenninckx *et al.*, 1993). Amplifications were performed in 25 $\mu$ l total reaction volumes containing 0.3 $\mu$ l of each primer (25pM/ $\mu$ l) and 0.15 $\mu$ l of *Taq* DNA polymerase (Qbio Appligen) in a buffer supplied by the enzyme manufacturer. We used the primers 12SA–L and 12SB–H of Köcher *et al.* (1989) to amplify a section of the 12S rRNA gene, with the following PCR cycling procedure: 94°C (3:00); 94°C (0:30), 58°C (0:40), 72°C (0:50) for 30 cycles; 72° (1:00). We amplified the complete cytochrome *b* gene in two fragments, using (1) the primers L15146 and H15915sh of Irwin *et al.* (1991) [(94°C (3:00); 94°C (0:40), 53°C (0:30), 72°C (1:00) for 33 cycles; 72° (1:00)] and (2) the primers MAB1 (5'–AGA ACC ACC GTT GTA TTC AAC TAC–3') and MAB2 (5'–GRG TYA RGG TTG CRT TGT CTA CTG–3') of Miralles *et al.* (in press) [(94°C (3:00); 94°C (0:30), 55°C (0:40), 72°C (0:50) for 30 cycles; 72° (1:00)]. The reaction products were visualised in a 1.5% agarose gel, then purified directly from the PCR mixture and sequenced directly in both forward and reverse directions using an automated DNA sequencer (CEQ 2000 DNA Analysis System, Beckman Coulter Inc.). Both strands obtained for each sequence were aligned and checked using the Sequencher program (Gene Codes Inc.). We entered sequences manually, using the BioEdit Sequence Alignment Editor program 7. 0. 0. (Hall, 1999). Alignment was performed manually and included four indels in 12S.

Phylogenetic reconstruction (Bayesian inference) was carried out on the combined 12S rRNA and cytochrome *b* genes, using MrBayes 3.0 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). Gaps were considered as missing data in both analyses. The substitution model was selected using Modeltest version 3.06 (Posada & Crandall, 1998) using the Akaike Information Criterion (AIC). The analysis was performed using the default priors implemented in MrBayes, version 3.0b4 (Huelsenbeck and Ronquist, 2001) with parameter values for the selected nucleotide substitution model (GTR+G+I) estimated by the program. One 'cold' and three 'heated' chains, with a temperature parameter of 0.2, were started from random topologies, run for 1.5 millions generations, and sampled every 100 generations. The analysis was run twice to ensure that the data included a sampling of the full tree space rather than becoming trapped in local optima. Burn-in was evaluated by examination of the standard deviation of split frequencies (>0.01). Tree samples and parameter estimates from the 375,000 generations of the Bayesian analysis (the first 25% of samples) were designated as burn-in and discarded. The phylogeny inferred from the remaining 1,500,000 generations was represented as a 50% majority rule consensus tree. The frequency of any particular clade among the individual trees contributing to the consensus tree represents the posterior probability of that clade (Huelsenbeck & Ronquist, 2001); only values equal or above 95% were considered to indicate sufficient support (Wilcox *et al.*, 2002).

## Results and discussion

### *Rediscovery of Mabuya nigropalmata and designation of a lectotype*

Until recently, *Mabuya nigropalmata* was known from the five syntypes and its original description. The type series was collected from two different localities, approximately 1000 km apart: four specimens (all originally numbered NRM 23258, formerly 3259) came from Bolivia ("San Fermín, N. W. Bolivia, in the forest district" = San Fermín, Provincia Franz Tamayo, Departamento de La Paz, Bolivia; 13.9055556° S, 68<sup>1</sup>.9722222° W); whereas the fifth (NRM 23259, formerly 3259) came from western Brazil ("Brazil, Amazonas, Rio Curuca, tributary to R. Javary"). Two different collectors, ten years apart, collected the specimens (N. Holmgren in 1904 and V. M. de Oliviera in 1914, respectively). All of the specimens were deposited at the Swedish Museum of Natural History, Stockholm (NRM). In spite of considerable fieldwork, especially in adjacent southern Peru, this species seemed to have never been collected subsequently (Ávila-Pires, 1995). Moravec & Aparicio (2004) recently rediscovered the species at Nacebe (11° 00' S, 67° 25' W, 200 m a.s.l., left bank of the Rio Orthon, Provincia Abuna, Departamento Pando, Bolivia, Fig. 1a). The

following year, one of us (JCC) collected two specimens from Manu National Park, Madre de Dios, Peru: MHNC 5718 (Fig. 1b, 2), sector Cocha Salvador (12°00'12.57"S, 71°14'07.90"W), 329 m a.s.l, 13 October 2005; MHNC 5121, sector of Cocha Juarez (12°09'41.86"S, 71°01'57.51"W), 316 m a.s.l, 20 November 2005. Both the new Bolivian and Peruvian specimens exhibit characters diagnostic of *M. nigropalmata*: prefrontals in contact, frontoparietals fused (hardly verifiable in MHNC 5121, given its poor state of preservation), multiple pairs of nuchals, an acute snout, five subequal supraciliaries on both sides (not verifiable MHNC 5121), fewer than 30 scales around midbody, and very dark palms and soles covered by many small granules (Figs 1, 2; Table 2).

**TABLE 2.** Variations of selected characters of *Mabuya nigropalmata* (n=9 specimens). N = no, Y = yes.

	Type serie		New specimens			
	Bolivia	Brazil	Bolivia		Peru	
	NRM	NRM	NMP6V	CBF	MHNC	MHNC
	23258	23259	72186	2455	5121	5718
	(A to D)					
Number of pair of nuchals (primary + secondary)	1 + 2	1 + 2/1	1+1	1+1	1 + 2/1	1 + 2
Number of ventral scales	39 to 45 (n=5) <sup>(1)</sup>		31	30	47	34
Number of dorsal scales	54 to 55 (n=5) <sup>(1)</sup>		52	46	58	53
Number of scales around midbody	25 to 28 (n=5) <sup>(1)</sup>		24	27	27	28
Supranasals in contact	N	N	N	N	N	N
Prefrontals in contact	Y	Y	Y	Y	Y	Y
Parietals in contact	Y	Y	Y	Y	Y	Y
Frontoparietals fused into a single scale	Y	Y	Y	Y	Y ? <sup>(2)</sup>	Y
Supraciliaries	5/5 <sup>(1)</sup>	5/5 <sup>(1)</sup>	5/5	5/5	? <sup>(2)</sup>	5/5
Number of lamellae under fourth finger	14 to 18 (n=5) <sup>(1)</sup>		16/17	17/16	19/19	18/18
Number of lamellae under fourth toe	19 to 22 (n=5) <sup>(1)</sup>		24/24	20/19	21/21	22/23

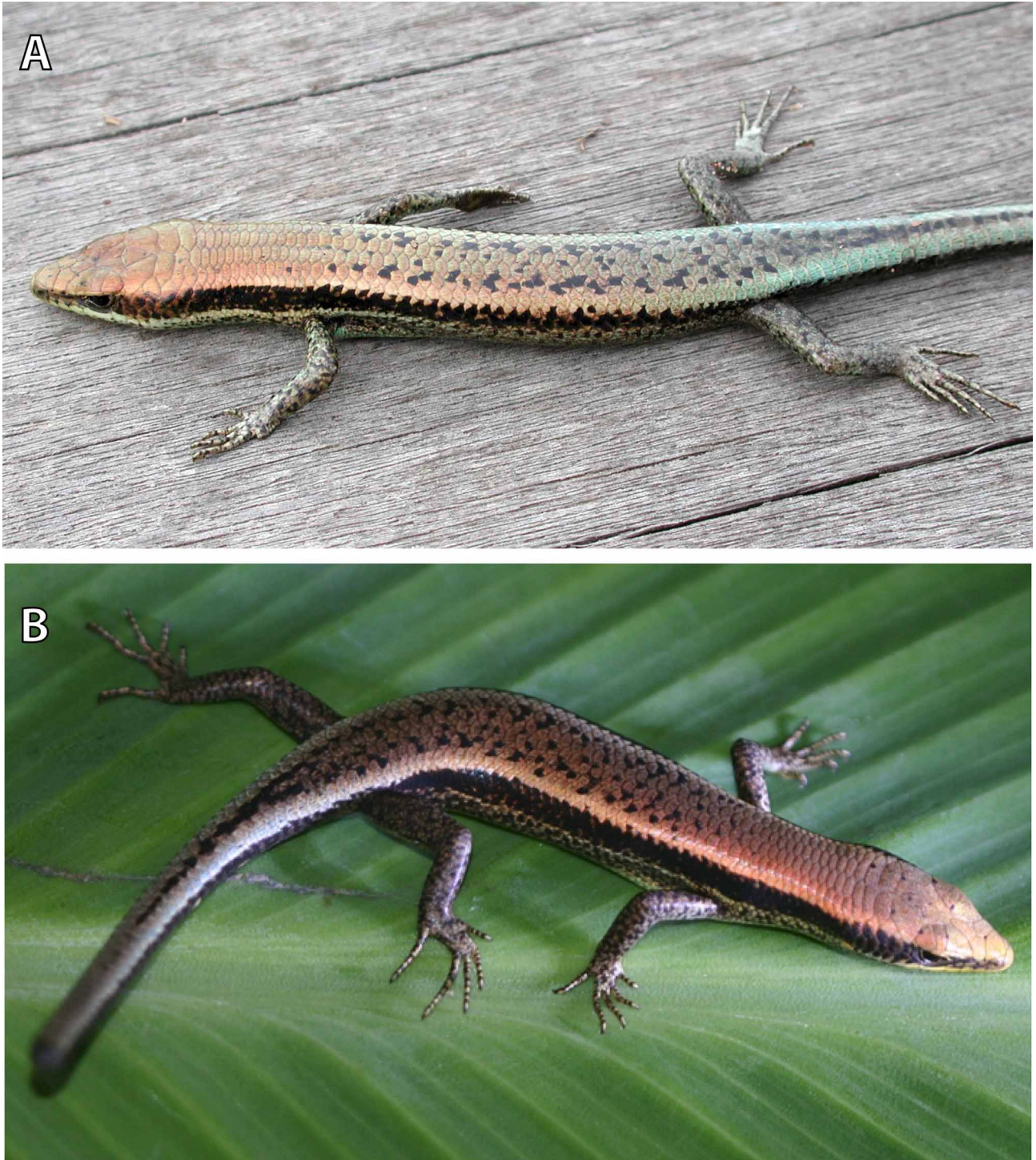
<sup>(1)</sup>Data based both on Ávila-Pires (1995) and material examined in this study.

<sup>(2)</sup>Not counted because of scale damage.

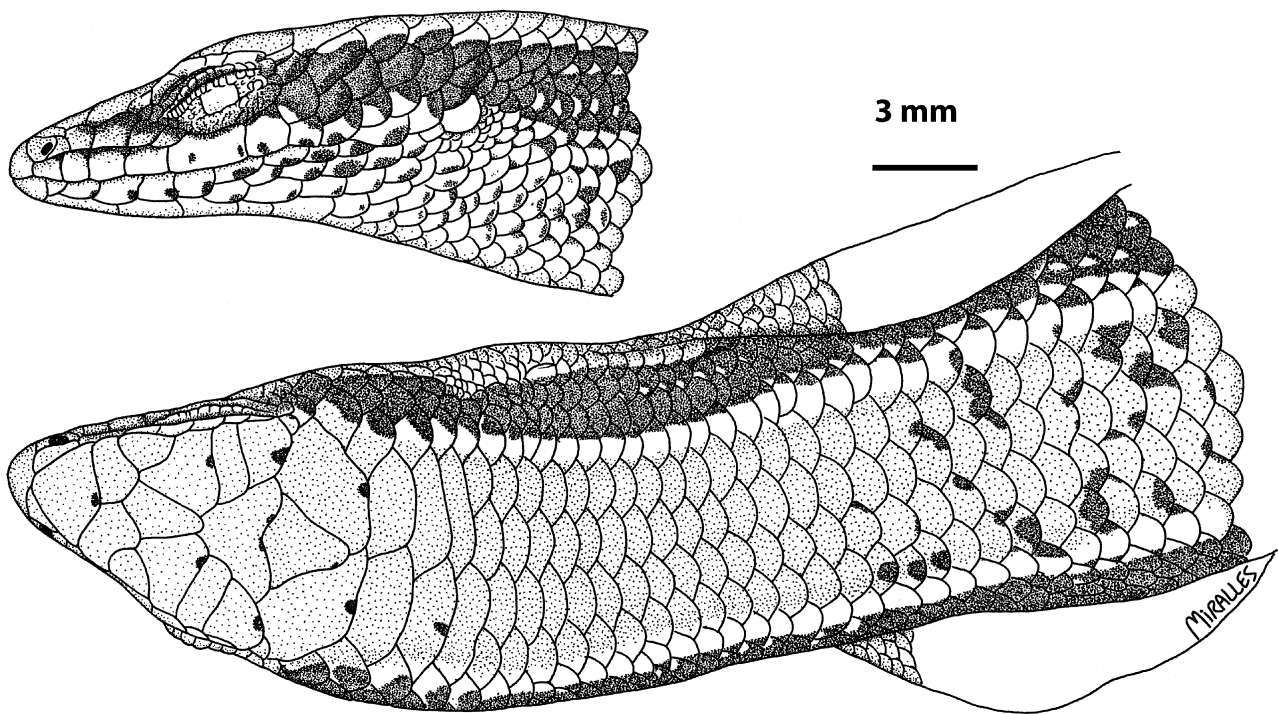
Additionally, another specimen of *Mabuya nigropalmata* was recently discovered, its photograph having been published in the virtual guide of “*Reptiles del Centro Río Los Amigos, Manu y Tambopata, Perú*” (von May *et al.* 2006, plate 3, fig. 44), but it was misidentified as *M. nigropunctata*. Overall, this specimen has a

1. We located San Fermín using the Falling Rain gazateer (Falling Rain Genomics, 2006) and a recent Bolivian atlas (Quiroga, 1999). There seems to be some disagreement as to whether Fermín has an accent. In the gazateer, the name is spelled both ways, whereas, the accent was omitted by Quiroga (1999). Presumably, the name of this town honors Saint Fermin of Amiens and, at least originally, retained the accent as it does in modern Spain. San Fermín is situated within Parque Nacional Madidi in a valley surrounded by low mountains on the humid, eastern slopes of the Andes and across the Río Tambopata from the Peruvian Parque Nacional Bahuaja-Sonene. L. Gonzales A. (from the Museo Noel Kempff Mercado, Santa Cruz) visited San Fermín in 2004; he recorded an elevation of 911 m, latitude 14° 00' 8.5" S, and longitude 68° 57' 15" W. At present, the town is inhabited by about 30 families. Gonzales did not collect any specimens of *Mabuya*, but, in the vicinity of San Fermín, found reptiles typically associated with humid forests of the lowlands and foothill of northern Bolivia such as *Cercosaura ocellata*, *Enyalioides palpebralis*, *Kentropyx altamazonica*, *Imantodes cenchoa*, *Dipsas indica*, and *Xenodon severus*.

darker dorsal pattern than the other known specimens (with larger and more numerous black dots on the back), however, diagnostic characters of *M. nigropalmata* (prefrontals in contact, frontoparietals fused, multiple pairs of nuchal scales) are visible in the photograph. All these recent rediscoveries provide irrefutable proof that *M. nigropalmata* is really a South American species and that it is still present in occidental Amazonia, even if it seems to be rare or, at least, to have a restricted and patchy distribution.



**FIGURE 1.** Living specimens of *Mabuya nigropalmata* from (A) Nacebe, Provincia Abuna, Departamento Pando, Bolivia (NMP6V 72186), and (B) Manu National Park, Peru (MHNC 5718). Photographs by J. Moravec and J. C. Chaparro, respectively.



**FIGURE 2.** Drawings of a recently collected specimen of *Mabuya nigropalmata* (MHNC 5718): (A) lateral view of the head and (B) dorsal view of the anterior part of the body.

It seems appropriate to designate NRM 23258A (San Fermín, La Paz, Bolivia, collected in 1904 by N. Holmgren) as the **lectotype** of *Mabuya nigropalmata* (Fig. 3). This specimen is in excellent condition and appears to be the specimen photographed by Horton (1973:76, his figure 3) and illustrated by Ávila-Pires (1995: 583, her figure 201).

### ***Natural history of Mabuya nigropalmata***

With the exception of San Fermín, localities of *Mabuya nigropalmata* lie within lowland rainforests (from 200 to 329 m) of western Amazonia (Fig. 4). Close to the Peruvian border in extreme northwestern Franz Tamayo province, San Fermín is situated in lower montane rainforest at approximately 1000 m. In Peru, the specimen (MHNC 5718) from Cocha Salvador and the second one (MHNC 5121) from Cocha Juarez were both collected during the day from secondary forest adjacent to sandbars. Tree species of *Tessaria*, *Gynerium*, *Cecropia*, *Salix*, *Ochroma* and *Ficus* dominate these riverine forests. In the same area, we observed (but could not capture) three more specimens foraging and sunning on sandbars, between 1100–1400 hrs. At Nacebe (11° 00' S, 67° 25' W, 200m asl), Moravec & Aparicio (2004) observed *M. nigropalmata* along the sunny margins of roads and trails in secondary or disturbed primary terra firme forest. Usually, this species basked on the ground or on fallen tree trunks, but some specimens were observed climbing up to 5 m aboveground in vegetation (Moravec & Aparicio, 2004). These authors found one specimen inside a wooden house in the settlement and remark that *M. nigropalmata* appears to be more tolerant of open and secondary situations than sympatric *M. nigropunctata*. These largely anecdotal observations agree that *M. nigropalmata* prefers open, sunny areas.



**FIGURE 3.** Photographs of the **lectotype** of *Mabuya nigropalmata* (NRM 23258A). Photographs by B. Kajrup.

#### ***Morphological and molecular characterization of Mabuya nigropalmata.***

Externally, *Mabuya nigropalmata* closely resembles *M. frenata*. In both species, the dorsal field lacks dark stripes and is covered in black to dark brown blotches. They both have fused frontoparietals and relatively long acute snouts. However, *M. nigropalmata* can be distinguished from *M. frenata* by the presence of secondary nuchal scales and by prefrontals in wide contact (secondary nuchal scales absent and prefrontal separated, or slightly in contact in *M. frenata*) (Table 3). Also, with 24–28 scales around midbody, *M. nigropalmata* usually has fewer midbody scales than *M. frenata*. This trait also serves to distinguish *M. nigropalmata* (and *M. carvalhoi*) from most congeners, which usually have midbody counts around 28 to 32 scales (Table 4).



**TABLE 3.** Comparison of selected characters among different specimens of three species of *Mabuya*. Where appropriate means  $\pm$  standard deviation, then sample size, follow ranges. C: in contact, S: separated, P: just in point contact.<sup>(1)</sup>Data based on Ávila-Pires (1995) and material examined in this study.

		<i>M. croizati</i>	<i>M. frenata</i>	<i>M. nigropalmata</i> <sup>(1)</sup>
Supranasals	C :	13.3%	100%	0%
	S :	86.7%	0%	100%
		(15)	(34)	(9)
Prefrontals	C :	100%	5.9%	100%
	S :	0%	82.3%	0%
	P :	0%	11.8%	0%
		(15)	(34)	(9)
Parietals	C :	100%	97.1%	100%
	S :	0%	2.9%	0%
		(15)	(35)	(9)
Frontoparietals fused		100%	100%	100%
		(15)	(28)	(8)
Supraciliaries	n=4 :	3.3%	11.6%	0%
	n=5 :	90%	82.6%	100%
	n=6 :	6.4%	5.8%	0%
		(30 sides)	(69 sides)	(16 sides)
Number of secondary nuchals	n=0 :	0%	100%	0%
	n=1 :	6.7%	0%	25%
	n=2 :	66.6%	0%	75%
	n=3 :	26.7%	0%	0%
		(30 sides)	(35 sides)	(16 sides)
Number of lamellae under fourth finger		10 to 14	10 to 14	14 to 19
		12.4 $\pm$ 1.0 (28 sides)	12.30 $\pm$ 1.0 (65 sides)	(18 sides)
Number of lamellae under fourth toe		13 to 17	13 to 19	19 to 23
		15.1 $\pm$ 1.0 (30 sides)	16.0 $\pm$ 1.2 (66 sides)	(18sides)
Number of dorsal scales		45 to 50	50 to 64	46 to 58
		47.9 $\pm$ 1.6 (15)	53.3 $\pm$ 4.3 (55)	(9)
Number of ventral scales		29 to 36	28 to 39 <sup>(2)</sup>	30 to 47
		32.9 $\pm$ 2.1 (15)	34.9 $\pm$ 29 (50)	(9)
Number of scale around midbody		28 to 30	28 to 33	24 to 28
		29.0 $\pm$ 1.0 (15)	30.4 $\pm$ 1.6 (52)	(9)

Although the two species have different dorsal color patterns, Burt & Burt (1933: 86), Dunn (1936), and Peters & Donoso-Barros (1970) all confused *Mabuya nigropalmata* with *M. croizati*. *Mabuya croizati* has a pair of dark paravertebral stripes extending from the snout to the tail (absent in *M. nigropalmata*). On the basis of cephalic scalation, Horton (1973: 77) suspected that three South American *Mabuya* with fused frontoparietals (namely *Mabuya croizati*, *M. frenata*, *M. nigropalmata*) were closely related. He wrote, “the logical evolutionary sequence would appear to be *frenata* – *nigropalmata* – *croizati* (...) from the condition of the other South American species to the extreme *croizati* condition.” In other words, Horton appeared to conclude that fusion of frontoparietals (in all three species) and presence of multiple nuchal scales (present in *M. nigropalmata* and *M. croizati*) are derived characters within *Mabuya*. His remarks appear to support the following hypothesis of relationships: (*M. frenata* (*M. nigropalmata* + *M. croizati*)) (Figure 4). These characters are now known to occur in other species of *Mabuya*, several described since Horton’s publication. *Mabuya berengerae*, *M. macrorhyncha*, *M. pergravis* and *M. sloanii* have secondary nuchals, but have paired

frontoparietals (Miralles, 2006), whereas both *M. cochabambae* and *M. frenata* lack secondary nuchals and have fused frontoparietals (Harvey *et al.*, 2008). Rebouças-Spieker and Vanzolini (1990) concluded that their new species *M. carvalhoi* is probably the sister species of *M. croizati*, because both species share a distinctive striped color pattern, fused frontoparietals, and secondary nuchals.

**TABLE 4.** Comparison of the number of scales around midbody from different species of *Mabuya sensu stricto*.

	Mean $\pm$ SD	Range	N specimens
<i>M. agilis</i>	30.1 $\pm$ 1.1	28–33	36
<i>M. agmosticha</i> <sup>(1)</sup>	29.0 $\pm$ 1.2	26–31	31
<i>M. altamazonica</i>	29.2 $\pm$ 1.3	26–31	26
<i>M. bistrriata</i>	30.4 $\pm$ 1.0	28–33	27
<i>M. carvalhoi</i> <sup>(1)</sup>	24.7 $\pm$ 1.0	23–27	14
<i>M. croizati</i>	29.0 $\pm$ 1.0	28–30	15
<i>M. cochabambae</i> <sup>(1)</sup>	30.9 $\pm$ 1.1	28–32	16
<i>M. dorsivittata</i> <sup>(1)</sup>	28.6 $\pm$ 1.8	26–32	13
<i>M. falconensis</i>	30.4 $\pm$ 0.9	29–32	13
<i>M. frenata</i> <sup>(1)</sup>	30.4 $\pm$ 1.6	28–33	52
<i>M. guaporicola</i> <sup>(1)</sup>	31.6 $\pm$ 1.3	29–34	18
<i>M. mabouya</i>	30.4 $\pm$ 2.8	26–34	13
<i>M. macleani</i> <sup>(1)</sup>	32.3 $\pm$ ?	32–34	6
<i>M. macrorhyncha</i> <sup>(1)</sup>	28.1 $\pm$ 0.89	27–30	7
<i>M. meridensis</i>	30.8 $\pm$ 1.3	28–32	10
<i>M. nigropalmata</i> <sup>(1)</sup>	?	24–28	9
<i>M. nigropunctata</i>	30.5 $\pm$ 1.3	27–34	205
<i>M. sloanii</i>	31.9 $\pm$ 1.4	30–34	19
<i>M. unimarginata</i>	30.1 $\pm$ 1.4	28–32	55

<sup>(1)</sup>Data completely or partly based on literature from Rebouças-Spieker & Vanzolini 1990, Ávila-Pires 1995, Mayer & Lazell 2000, Rodrigues 2000, Harvey *et al.* 2008).

Our phylogenetic analysis allows us to objectively test Horton's informal hypothesis and to discover the evolutionary history of the distinctive characters of *M. nigropalmata*. Although our Bayesian tree had relatively low support (Fig. 5a), the topology is at odds with Horton's hypothesis (Fig. 5b). Species of Mediterranean "*Mabuya*" (first outgroup to the Neotropical clade, Carranza & Arnold 2003) and *Trachylepis* (second outgroup) lack fused frontoparietals and secondary nuchals. From the topology of our ingroup, these traits appear to have evolved within the common ancestor of the Neotropical clade and subsequently been lost in various lineages.

Rebouças-Spieker and Vanzolini (1990) appear to have been correct regarding the affinities of *Mabuya croizati*: it is the sister species of *M. carvalhoi*, however these taxa are not related to *M. frenata* or *M. nigropalmata*. The relationships of the two southern Amazonian species remain unresolved; they fall out in an unresolved polytomy at the base of a large clade containing the remaining species of *Mabuya*. Without more data, we cannot know if they are each other's closest relative. However, neither appears to be closely related to *M. cochabambae*, which is the sister species of *M. dorsivittata* and nested within a clade of species lacking both characters.

For the 12S and cytochrome *b* genes, we estimated uncorrected pairwise distances among *Mabuya nigropalmata*, *M. frenata*, and *M. croizati*. Uncorrected p-distances for these genes are comparable to interspecific distances estimated in other studies of *Mabuya sensu lato* (Miralles *et al.* 2006), and support the

distinctiveness of *M. nigropalmata*: 9.70% (12S) and 15.11% (cyt *b*) between *M. nigropalmata* and *M. croizati*; 4.44–5.00% and 14.26–14.64% between *M. nigropalmata* and *M. frenata*; and 8.18–8.77% and 14.81–14.93% between *M. croizati* and *M. frenata*.

### *Status of Trachylepis (Xystrolepis) punctata Tschudi, 1845*

In 1845, Tschudi described *Trachylepis (Xystrolepis) punctata* from the “Waldregion” (= Amazonia) of Peru. Although Roux (1907) later redescribed the holotype and only known specimen, this species has remained enigmatic. Based on its morphology, some authors considered it to be synonymous with *Trachylepis atlantica* (e.g., Travassos, 1946), whereas, based on the type locality, others (e.g., Peters & Donoso-Barros, 1970) concluded that it must be synonymous with one of the Amazonian *Mabuya*. In his “Notes on American *Mabuyas*,” Dunn (1936: 557) remarked that he was “unable to say what it is.” Peters and Donoso-Barros (1970) added Tschudi’s species to the unwieldy synonymy of *M. mabouya mabouya* (Lacépède) where it has remained until the present day. In this section, we consider the generic allocation of Tschudi’s species, correct its secondary homonymy, and propose some possible explanations for its provenance.

During this study, we examined recent photographs of the holotype and only known specimen of *Trachylepis punctata*. The holotype (MHNN 91.2426) is housed in the Museum of Neuchâtel in Switzerland and is in very poor condition. This specimen cannot be assigned to the genus *Mabuya*, because it has 5/5 auricular lobules, tricarinate dorsal scales in 39 rows at midbody, and the third supraocular in contact with the frontal. Species of *Mabuya* lack auricular lobules and have smooth to finely striated scales in 24–34 rows at midbody (Table 4). Among *Mabuya*, the second (in *M. agilis*, *M. agmosticha*, *M. altamazonica*, *M. berengeriae*, *M. bistrinata*, *M. carvalhoi*, *M. croizati*, *M. falconensis*, *M. frenata*, *M. guaporicola*, *M. lineolata*, *M. luciae*, *M. macleani*, *M. macrorhyncha*, *M. meridensis*, *M. nigropalmata*, *M. nigropunctata*, *M. pergravis*, *M. sloanii*, and *M. unimarginata*) or, rarely, the first (in species having the first and second supraoculars fused into a single scale, such as *M. cochabambae*, *M. dorsivittata*, and *M. mabouya*) supraocular contacts the frontal (Greer and Broadley, 2000; personal observation, Fig. 6). These characteristics of *T. punctata* are common among species of the Afro-Malagasy radiation (Hoogmoed 1974; Mausfeld *et al.*, 2002), now comprised of the genera *Trachylepis* and *Chioninia*, and we here formally recognize Tschudi’s species as a member of *Trachylepis*.

In 1845, three different species of *Trachylepis* had been assigned the same specific epithet. Andersson (1900) first noted the homonymy between *Tiliqua punctata* Gray and *Lacerta punctata* Linnaeus [currently considered a junior synonym of *Trachylepis homalocephala* (Wiegmann) from the Cape province, South Africa] and Schmidt (1945) proposed the replacement name *Mabuya atlantica* for Gray’s species (see Mausfeld and Vrcibradic, 2002, for a recent discussion of the nomenclature of the skink on Fernando de Noronha, Brazil). However, the homonymy of Tschudi’s name has never been corrected. In accordance with articles 52 and 60 of the Code (ICZN, 1999), we propose *Trachylepis tschudii* **new name** as a replacement for *Trachylepis (Xystrolepis) punctata* Tschudi. The new name is a patronym for Dr. J. J. von Tschudi, who originally described this species.

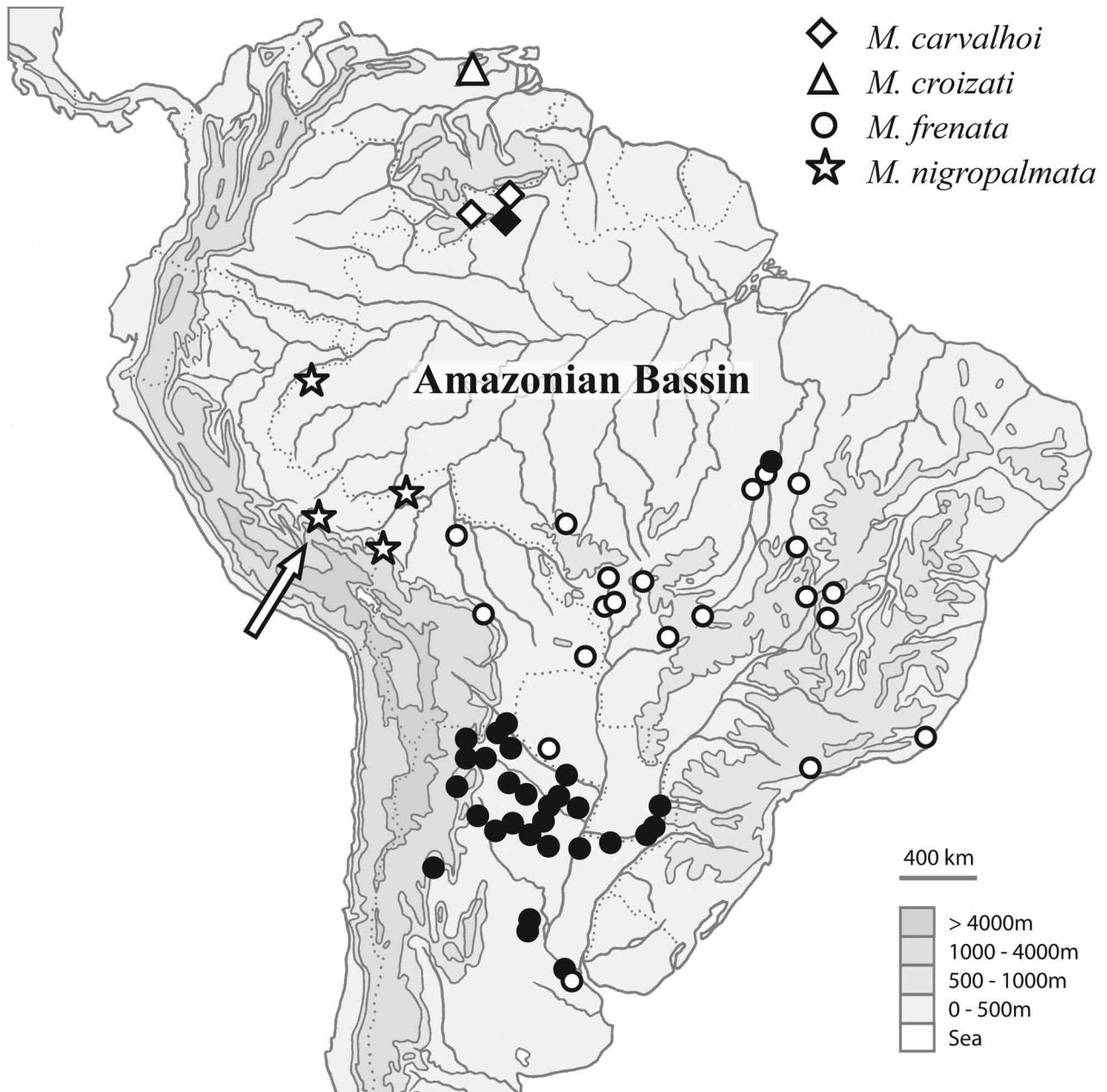
Because of the poor state of the holotype, it may be impossible to unequivocally assign it to an existing species of *Trachylepis*. However, the specimen’s supposed origin in the Peruvian Amazon is difficult to believe, considering that the upper Amazon is so far from the Brazilian coast and no additional specimens of any *Trachylepis* have ever been collected in Amazonia. Three mutually exclusive hypotheses may explain the provenance of the specimen:

(1) *Trachylepis tschudii* is actually a very rare Amazonian species. Skinks from this genus have certainly crossed the Atlantic before (Carranza & Arnold 2003; Mausfeld *et al.* 2002) as demonstrated by the presence of *T. atlantica* on Fernando do Noronha, Brazil, and *T. tschudii* may have dispersed across Amazonia in a manner similar to another African lizard, *Hemidactylus mabouia* (Kluge, 1969; Powell *et al.*, 1998).

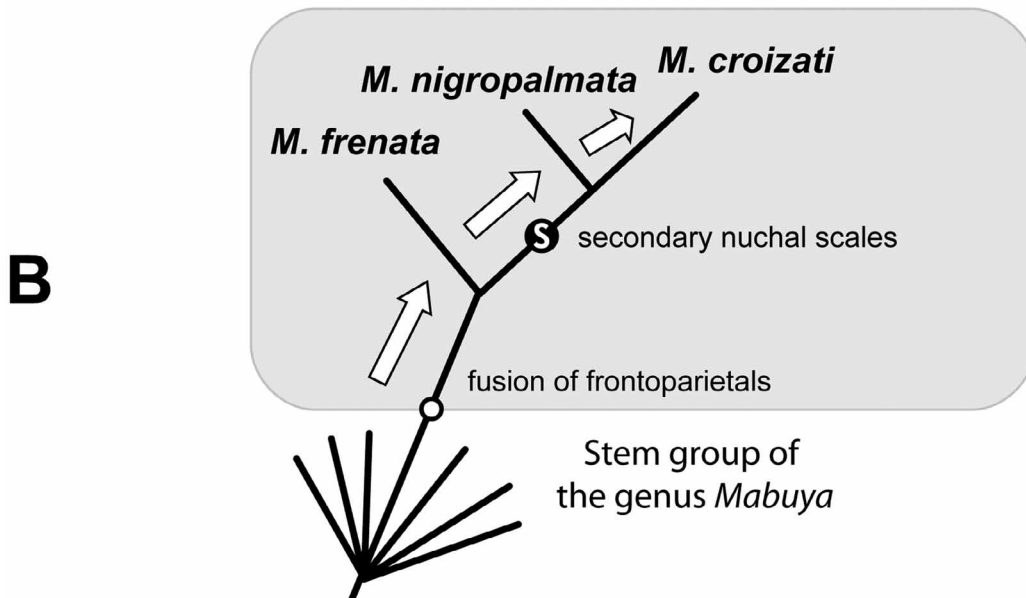
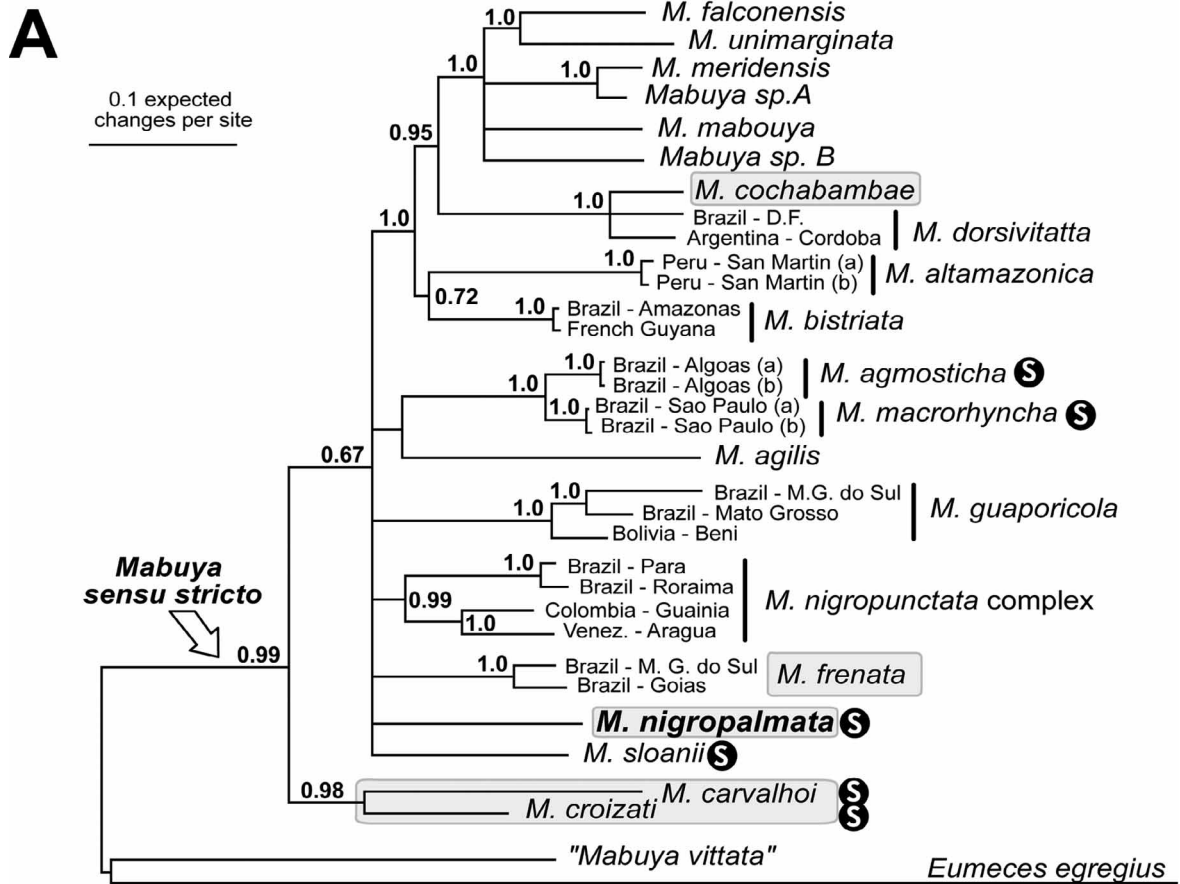
(2) *Trachylepis tschudii* actually occurs somewhere in the Old World and the holotype was mislabeled.

(3) As proposed by Travassos (1946), *Trachylepis tschudii* is a junior synonym of *T. atlantica*. Assuming the specimen was mislabeled, the holotype actually would have been collected on Fernando de Noronha Island, Brazil. Or, if the holotype was actually collected in the Peruvian Amazon, the skinks from Fernando de Noronha have dispersed into Amazonia, again, similar to *Hemidactylus mabouia*.

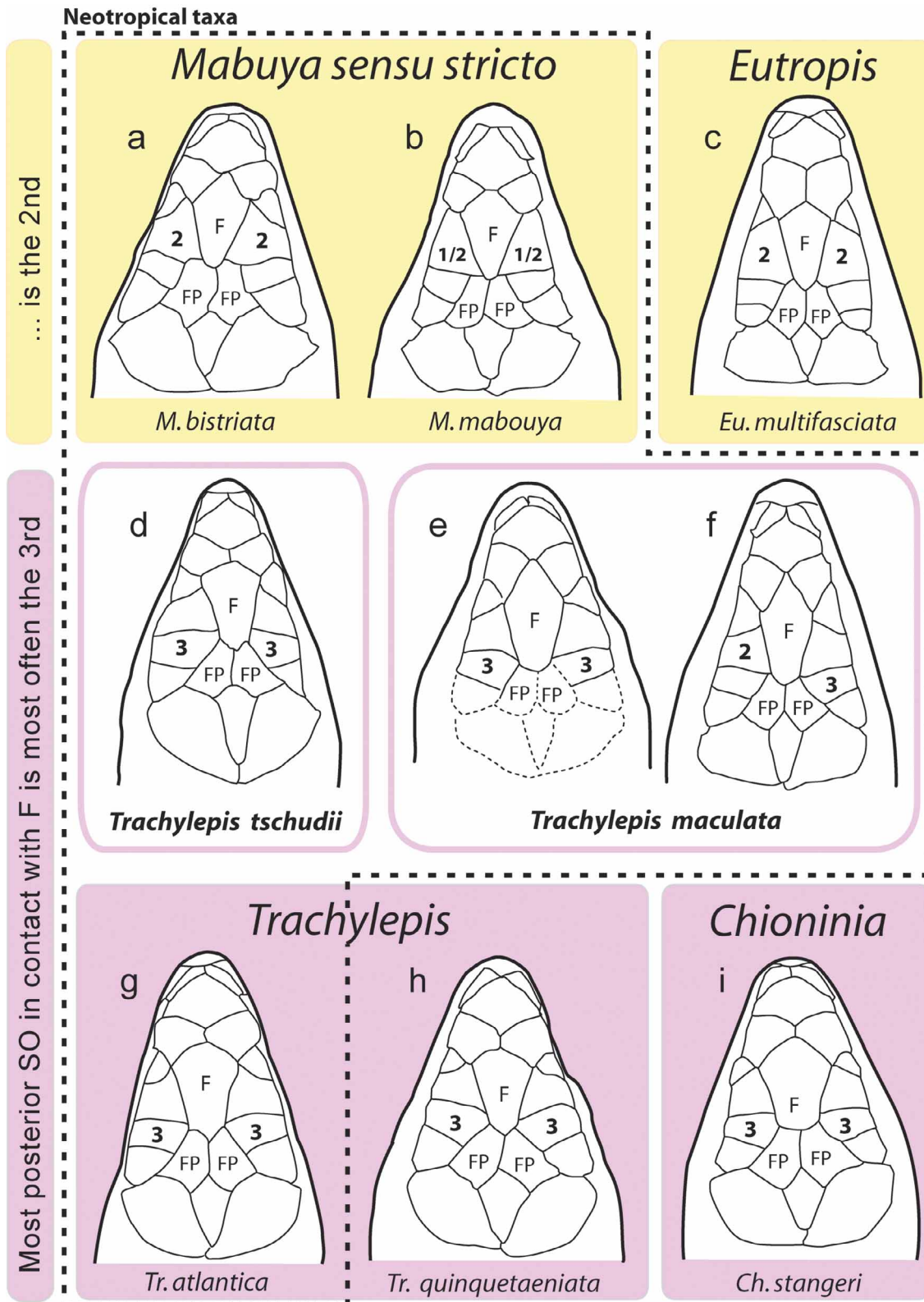
We suspect that the third hypothesis is correct. Like *Trachylepis atlantica*, *T. tschudii* has the supernasals, prefrontals, and parietals in contact. Its body dimensions (SVL 83 mm, tail incomplete, head length 10 mm, head width 6.5 mm, according to Roux 1907), coloration, and scale counts all fall within the variation for this species (Mausfeld and Vrcibradic, 2002; Travassos, 1946). Tschudi's skink is unlikely to be a specimen of *T. maculata* (characteristics in parentheses), because it has three keels on its dorsals (five), 39 scales at midbody (32–34), and its parietals in contact (separate).



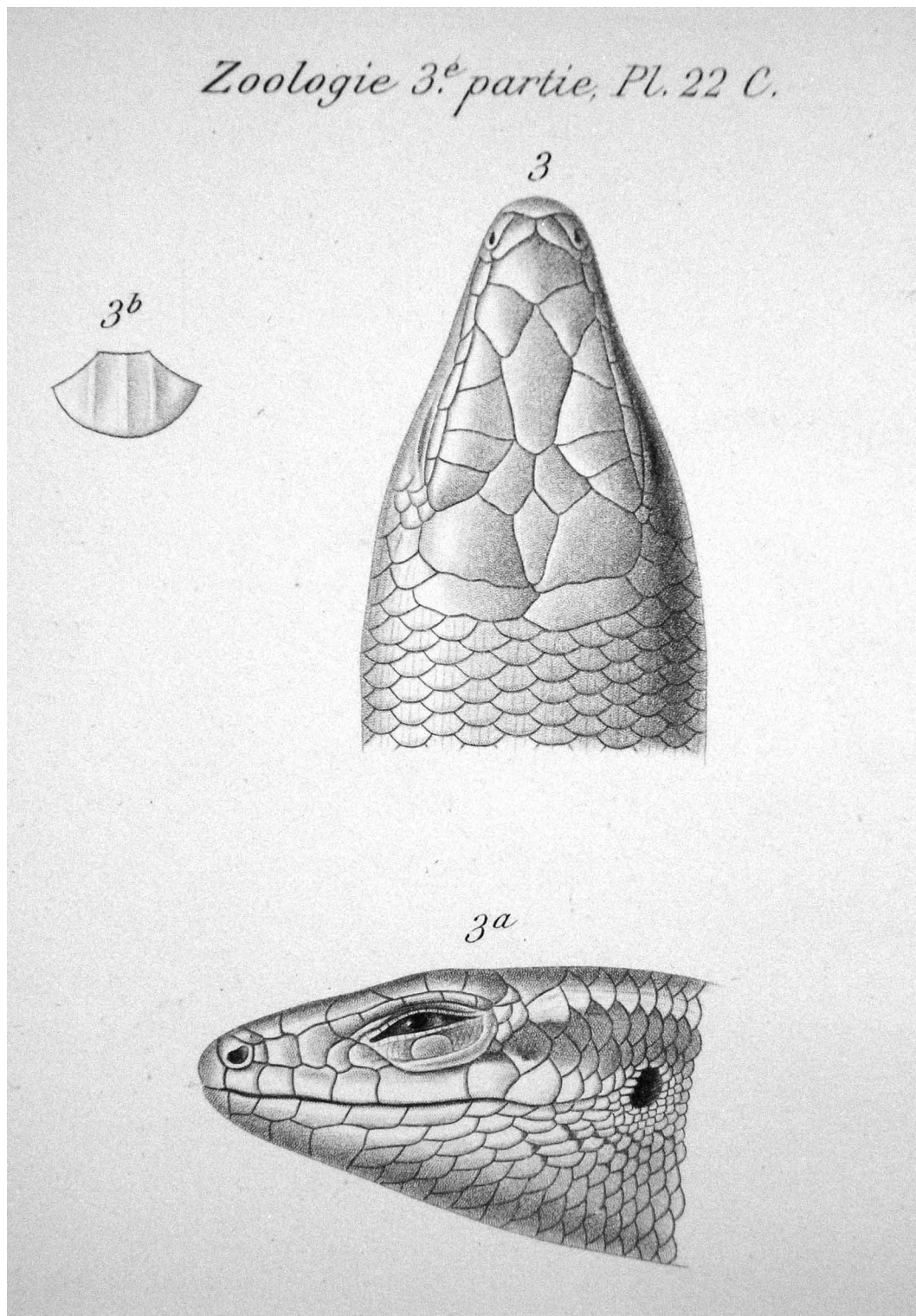
**FIGURE 4.** Locality records of four species of *Mabuya* in South America. Arrow indicates new record for Manu National Park, Peru. Open symbols represent specimens examined during this study, whereas closed symbols reflect published localities (Andersson, 1918; Cei 1986, 1993; Moravec & Aparicio 2004; Pinto & Araujo 2000; Rebouças-Spieker & Vanzolini 1990).



**FIGURE 5.** (A) Phylogeny of *Mabuya* (Bayesian analysis of 12S and cytochrome b sequences, 50% majority rule consensus) compared to (B) Horton's (1973) hypothesis of the «logical evolutionary sequence» between *M. frenata*, *M. nigropalmata*, *M. croizati* and the other South American *Mabuya*, based on characteristics of cephalic scalation (grey square represent species with fused frontoparietals ; « S » mark represent species with secondary nuchal scales).



**FIGURE 6.** Cephalic morphology of *Mabuya sensu lato*, showing diagnostic features of supraocular and frontal contact in *M. bistrinata* (a, MPEG 14561), *M. mabouya* (b, Holotype MNHN 5421), *Eutropis multifasciata* (c, representing the Asian clade, redrawn from Boulenger 1890: 181), *Trachylepis tshudii* (d, Holotype MHNN 91.2426) and *T. maculata* (e, NHM 1946.8.18.6, and f, lectotype, MNHN 2932, redrawn from Bocourt 1879), *T. atlantica* (g, MNR 1175, redrawn from Travassos, 1946: plate III, fig. 5), *Trachylepis quinquetaeniata* (h, RMNH 17427b, redrawn from Hoogmoed, 1974: 48), and *Chioninia stangeri* (i, syntype NHM 1946.8.2). Numbered scales are the most posterior supraoculars contacting the frontal (F) and frontoparietals (FP).



**FIGURE 7.** Lectotype (MNHN 2932) of *Trachylepis maculata* as illustrated by Bocourt (1879, Plate XXII C)

#### **Status of *Tiliqua maculata* Gray, 1839, and designation of a lectotype**

Gray (1839) described *Tiliqua maculata* from Demerara, Guyana. Since its original description, various authors (Boulenger 1887, Travassos 1946, 1948) considered it as synonymous with *Trachylepis atlantica*. Recently, Mausfeld & Vrcibradic (2002) examined two syntypes (NHM 1946.8.18.5–6) and strongly

suspected that *T. maculata* is a species distinct from *T. atlantica*. Comparing the two species, they noted differences in number of dorsal keels, midbody scales, dorsals, ventrals and subdigital lamellae under Finger IV and Toe IV. These authors also concluded that, “*the type locality of maculata should be considered dubious*” as “*some other specimens of lizards and snakes from ‘Demerara’ collected by Capt. Sabine turned out to be restricted to certain Caribbean islands such as St. Kitts and Nevis and Santa Lucia (Underwood 1993),*” and, consequently, “*it is likely that the type locality of maculata is St. Lucia or Barbados.*” These author also speculated that *T. maculata* might be synonymous with *Mabuya falconensis*.

When Travassos (1948 : 206) reconsidered the status of Gray’s names, he designated a lectotype of *Tiliqua punctata*. Regrettably, this author did not reference the specimen by its museum number stating only, « *aproveito a oportunidade para designar o exemplar macho, com 16,5 mm depositado no Museu Britânico como lectótipo [...]* ». This imprecise text misled some subsequent authors such as Bauer (2003) to conclude that a lectotype of *T. maculata* had been chosen. The measurement Travassos (1948) used to reference the specimen is its head length as indicated in the table he presents on page 207. The head measurement corresponds to the larger syntype ; thus Travassos (1948) designate NHM 1946.8.27.47 as the lectotype of *Tiliqua punctata* Gray. He did not designate a lectotype of *T. maculata*, which he considered synonymous with *T. punctata*.

During this study, we examined two of the three types of *Tiliqua maculata*: NHM 1946.8.18.6 (one of the two NHM types examined by Mausfeld & Vrcibradic, 2002) and MNHN 2932 (a third type housed at the MNHN) and compared them to *Trachylepis atlantica*, *Mabuya falconensis*, and various species of *Mabuya* from the Caribbean (Appendix II). Both specimens are in a very poor state of preservation, a fact noted by Boulenger (1887). Fortunately, Bocourt (1879) illustrated and redescribed MNHN 2932 (Fig. 7). For this reason, it seems appropriate to designate this specimen as the **lectotype** of *Tiliqua maculata* Gray, even if it is in a very poor state. The lectotype has 7 supralabials, the fifth below the eye, 15/15 lamellae under the fourth finger, 20/20 lamellae under the fourth toe, 37 ventrals, 58 dorsals, 32 scales around midbody, a pair of primary nuchals (secondary nuchals absent), and 5/5 supraciliaries. To avoid damaging this delicate specimen, we did not measure it, however Brygoo (1985) reported that it has a SVL of 219 mm and an incomplete tail, 125 mm.

Although number of dorsals at midbody falls within the range of *Mabuya*, Gray’s species has auricular lobules and heavily keeled dorsals. Contact between the third supraocular and frontal also excludes *Tiliqua maculata* from *Mabuya*. In the types, these scales narrowly contact one another (Fig. 6e, f), whereas they never contact one another in *Mabuya*. On the other hand, this suite of characters allies Gray’s species with the Afro-Malagasy radiation and we formally transfer it to *Trachylepis* as *Trachylepis maculata* (Gray) **new combination**. This same suite of characters serves to distinguish *T. maculata* from *Mabuya falconensis* and its congeners from both the Caribbean and mainland Neotropics. We agree completely with Mausfeld & Vrcibradic (2002) that *T. maculata* is a species distinct from *T. atlantica*. However, we do not know if it is synonymous with a species from the Afro-Malagasy region or if it actually once occurred in Guyana. We often think of exotic species as a 20–21st century problem. It is certainly possible that *T. maculata* was accidentally introduced to the port of Demerara during the transatlantic slave trade period and has since gone extinct. Both Bocourt (1879: 412) and Duméril (Duméril & Duméril 1851) argued that *T. maculata* is most similar to the African species *T. perrotettii*: « *Nous trouvons parfaitement juste l’appréciation suivante donnée par M. Aug. Duméril (Cat. Méth. 1851, p. 159) : « C’est avec l’Euprépis de Perrottet, originaire de la côte occidentale d’Afrique, que cette espèce a le plus de rapport par l’ensemble de ses caractères »* (Bocourt 1879).

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## Appendix I. Key to the skinks (*Mabuya*) from the Guianas, Amazonia, and adjacent regions

*Mabuya* can be easily distinguished from all other South American lizard genera by the presence of a translucent disk (or window) in the lower eyelid, two supranasals, and uniform cycloid body scales. The following key is intended to identify Amazonian species, many of which extend into the Guianas, the Andean slopes, and adjacent dry formations such as the Cerrados of Brazil and Bolivia. *Trachylepis tschudii* has also been included in the key, even if its presence in South America is doubtful. [Brasil (Br), Bolivia (Bo), Colombia (Co), Ecuador (Ec), French Guyana (Fg), Guyana (Gu), Peru (Pe), Surinam (Su), Venezuela (Ve)].

1. Auricular lobules present, number of scales around midbody relatively high (39), last supraocular in contact with the frontal is the third ..... *Trachylepis tschudii* (Pe?).
- 1'. Auricular lobules absent, scales around midbody relatively few (34 or less), last supraocular in contact with the frontal is the first or second ..... 2 (*Mabuya sensu stricto*).
2. Frontoparietals fused into a single scale ..... 3
- 2'. Frontoparietals paired ..... 4
3. Single pair of nuchal scales (secondary nuchals absent) ..... *M. frenata* (Br, Bo)
- 3'. More than a single pair of nuchal scales (secondary nuchals present) ..... 5
4. Parietals in broad contact behind interparietal scale ..... 6.
- 4'. Parietals separated by interparietal, or barely in point contact ..... *M. nigropunctata* complex (Br, Bo, Co, Ec, Fg, Gu, Pe, Su, Ve).
5. Frontonasals fused into a single scale, two well-defined dark stripes running down the back from snout to tail ..... *M. carvalhoi* (Ve, Br).
- 5'. Frontonasals paired, back lacking dark stripes ..... *M. nigropalmata* (Bo, Br, Pe)
6. Four supraciliaries with second longest, palms and soles light coloured (same colour as belly) ..... 7.
- 6'. Five or six supraciliaries subequal in size, palms and soles dark coloured (darker than belly) . *M. altamazonica* (Pe).
7. Paravertebral stripes present; dorsals in a longitudinal row more than 60; subdigital lamellae under fourth toe 12–16 (open grasslands of central Bolivia and Brazil south of Amazonia) ..... *M. guaporicola* (Bo, Br).

- 7' Paravertebral stripes absent; dorsals in a longitudinal row fewer than 60; subdigital lamellae under fourth toe 15—20 (Avila-Pires, 1995)..... *M. bistrriata* (Br, Fg)

## Appendix II. Specimens examined.

*Mabuya agilis* (n = 38). — **Brazil**: ALAGOAS: UMMZ 209950, Olho D'Agua. BAHIA: CHUNB 25287, Itacare. ESPIRÍTO SANTO: CHUNB 9285, 9288, São Matheus; CHUNB 9361, 9362, 9364, 25042, Presidente Kennedy; CHUNB 36488, Domingos Martins. GOIÁS: CHUNB 33197, 33199, Alvorada do Norte. RIO DE JANEIRO: CHUNB 9358, 9359, Rio de Janeiro; CHUNB 9351, 9353, 9355, 9356, 24186, Maricá; FMNH 177632, 177633, Rio de Janeiro, parc de Tijuca; MNHN 1999.8020 (735a) (paralectotype of *Eumeces spixii*, Duméril & Bibron, 1839), probably from Rio de Janeiro (instead of “Cayenne”, this locality seeming to have been inversed with the locality of the *M. bistrriata* MNHN 0000.0734, also paralectotype de *E. spixii*). PARAIBA: CHUNB 29027, 29491, Mamanguape; FMNH 64393, Independencia. PERNAMBUCO: CHUNB 9264, Petrolina; CM 65379, Agrestina; FMNH 42089, 42090, Garanhuns; UMMZ 149027, 149042, Exu. TOCANTINS: CHUNB 26999, 27011, Mateiros; CHUNB 33193, Dianópolis; CHUNB 33198, Paranã. NO LOCALITÉ: CHUNB 9363, 13585 to 13587.

*Mabuya agmosticha* (n = 1). — **Brazil**: ALAGOAS: MZUSP 79189 (holotype) (photograph only), Xingó.

*Mabuya altamazonica* (n = 35). — **Ecuador**: ZAMORA CHINCHIPE: NHM 1933.6.24.92-93, Zamora (990m asl). **Peru**: DEPARTAMENTO DE AMAZONAS: AMNH 57020, confluence between Rio Santiago and Rio Marañón (180 m asl). DEPARTAMENTO DEL CUSCO: FMNH 81376, 81377, Prov. Paucartambo, Hda Villacarmen (around 550 m asl); FMNH 168240, 168255, Quincemil, on the Rio Marcapata (780 m asl). DEPARTAMENTO DE LORETO: AMNH 57035, Yarina, Rio Huallaga valley (180 m asl); AMNH 60583, 60584, Quache (?), Rio Pastaza valley, frontier Peru-Ecuador (around 130 m asl); AMNH 73472 (= 3 embryos), FMNH 45523, Iquitos (around 100 m asl); MNHN 1978.2141, Colonia, Bora tribe's village on the Rio Zumun, tributary of Rio Yahuashacu, coll. in 1978 by M. T. Rodrigues; MNHN 1999.4827, 1999.4828, 1999.4829, Estiron, coll. in 1978 by J. P. Gasc. DEPARTAMENTO DE MADRE DE DIOS: FMNH 40429, Candamo (around 450 m asl); FMNH 168227, Manu, between Rio Madre de Dios and Rio Manu (400 m asl); FMNH 168344, 168349, 168418, 168452, Avispas, near Rio Inambari, 145 km W Puerto Maldonado (480 m asl); MCZ 183676, Tambopata (around 230 m asl), coll. in 1996 by J. E. Cadle. DEPARTAMENTO DE PASCO: LACM 76853 to 76855, no exact locality. DEPARTAMENTO DE SAN MARTIN: AMNH 126375, Tarapoto farms; MHNC 6703, Distrito de Juanjui, Prov. Mariscal Caceres, Parque Nacional Rio Abiseo, PV. Churo (07°21' 44.9"S; 76°50' 13.8"W), coll. by J.C. Chaparro, J.A. Ochoa & R. Gutierrez; MNHN 2006.0291 (holotype), an adult female, May 2005, collector undetermined. Type-locality: Kilometer 34 on road Tarapoto-Yurimaguas (600 m asl), Concesión de Manejo de Fauna Silvestre ASPRAVEP (Asociación de Productores de Ranas Venenosas Progreso), Rio Cainarachi. DEPARTAMENTO DE UCAYALI: AMNH 57036, at mouth of Rio Tambo (confluence between Rio Tambo and Rio Bajo Urubamba = Upper Rio Ucayali (260 m asl); AMNH 57037, Orellana, Rio Ucayali valley (150 m asl).

*Mabuya bistrriata* (n = 26). — **Brazil**: AMAPÁ: CHUNB 9339, 9542, 9550, Amapá. AMAZONAS: CHUNB 32337, Humaitá; FMNH 64391, Manaus (= Manaus); MPEG 1656, 1659, Jauareté (= Iaguaréte, = Yaruareté), Rio Uaupés; MPEG 13816, 13819, Cucui; SNOMNH 37183, Rio Ituxi, Madeira Scheffer. PARA: MPEG 14561, 14564, MPEG camp, Belém; MPEG 1987, 1986, 15499, 15666, Cachoeira do Arari, Marajó; RMNH 2512 (lectotype of both *Scincus bistrriatus* (Spix 1825) and *Eumeces spixii* Duméril & Bibron, 1839), Belém. RONDONIA: FMNH 64392, Porto Velho. **French Guyana**: MNHN 0000.0735 (paralectotype of *Eumeces spixii* Duméril et Bibron, 1939), Cayenne; MNHN 1902.0266, 1997.2264, no exact locality; MNHN 1902.0267, 1902.0268, Oyapock, near St Georges; MNHN 1902.0272, Camopi; MNHN 1903.0022, La Mère Islet; MNHN 1999.8349, Macouria.

*Mabuya carvalhoi* (n = 2). — **Brazil**: RORAIMA: AMNH 137372 (paratype), Ilha de Maracá. **Venezuela**: AMAZONAS: MHNLS 14471, Coyowa-Terri.

*Mabuya cochabambae* (n = 2). — **Bolivia**: SANTA CRUZ: UMMZ 68098 (paratype). COCHABAMBAE: MCZ 46532, Pocono (= Pocona ?), coll. par F. B. Steinback.

*Mabuya croizati* (n = 21). — **Venezuela**: ANZOATEGUI: MHNLS 17670–17675, Cerro El Guamal, sector occidental del Macizo del Turimiquire, municipio Freites. SUCRE: AMNH 29314 (holotype), Turumiquire massif; CM 7978, 7982, 7988, Elvecia, Turumiquire massif; EBRG 3797; FMNH 17796–17797, 17798–428 to 17798–430, 17799–434 to 17799–438, Turumiquire massif

*Mabuya dorsivittata* (n=14). — **Argentina**: SANTA FE: CM 147881, San Javier. **Brazil**: DISTRITO FEDERAL: CHUNB 27614, 28892, Brasília; GOIÁS: CHUNB 11557, 23760, Mineiros. MATO GROSSO DO SUL: CHUNB 27736, Alcinópolis. MINAS GERAIS: CHUNB 23840, 23842, Unai; CHUNB 26408, Paracatu; MNHN 0000.5342, 1879.0048, 1879.0049 (all three syntypes of *M. joberti* Thominot, 1884), Itathia (= Itatiaia). NO LOCALITY: MNHN 1886.0049. **Uruguay**: MONTEVIDEO: MNHN 0000.5422, Montevideo.

*Mabuya falconensis* (n = 17). — **Colombia**: GUAJIRA: UMMZ 54793, Rio Barbacoa Arroyo de Arenas. **Lesser Antilles**: MCZ 38196, Young's Island (off St Vincent island). **Trinidad & Tobago**: ZFMK 62602, 62603, Tobago island,

Buccoo. **Venezuela:** CARABOBO: MHNLS 5511, 5512, Lago de Valencia; MHNLS 6087, 6302, Patanemo bay. FALCON: MHNLS 9526, Sierra San Luis, Curimagua; MHNLS 17095, Paraganá peninsula, biological reserve of Monte Cano; UMMZ 55927, 55932, Tucacas. MIRANDA: MHNLS 16654, Higuero. SUCRE: MHNLS 9040, Chacoptata. YARACUY: UMMZ 55924, Boqueron.

*Mabuya frenata* (n = 41). — **Argentina:** DISTRITO FEDERAL: MNHN 0000.2899 (paralectotype of *Eumeces spixii*, Duméril & Bibron, 1939), Buenos Aires. **Paraguay:** PRESIDENTE HAYES: CM 94064, 134 km W of Pozo Colorado, road to General Diaz, then 18 km toward S-SW. **Bolivia:** BENI: FMNH 140191, San Joaquin. SANTA CRUZ: CM 35862, Province of Chiquitos, El Carmen; FMNH 21518, Buenavista. **Brazil:** DISTRITO FEDERAL: CHUNB 8608, 8941, 9083, 9621, 25589, 32739, Brasília. ESPÍRITO SANTO: CHUNB 25337, Presidente Kennedy. GOIÁS: CHUNB 26514, Mineiros; CHUNB 29555, 29596, Minaçu. MATO GROSSO: CHUNB 10478, 10479, Santa Terezinha; CHUNB 19829, 19850, Chapada dos Guimarães; FMNH 9128, Yucca, W of Descalvados; FMNH 10820, Sucury; FMNH 10821, Descalvados, Sucury; MNHN 1971.0180, Alto Xingu; MPEG 14312, Serra das Araras, Barra dos Bugres. MATO GROSSO DO SUL: CHUNB 25660, 27737, 27739, 27743, 27745, Alcinópolis. MINAS GERAIS: CHUNB 30407, 30408, Unai; CHUNB 26413, 26420, Paracatu. RONDÔNIA: CHUNB 11443, 11444, Vilhena. SÃO PAULO: FMNH 69957, vicinity of Fazenda Ipanema, Varnhagem. TOCANTINS: CHUNB 13892, Caseara; CHUNB 16146, 37468, Palmas. NO LOCALITY: MNHN 0000.8773, 1946.0003.

*Mabuya guaporicola* (n = 17). — **Bolivia:** SANTA CRUZ: UMMZ 83171, Buena Vista. **Brazil:** DISTRITO FEDERAL: CHUNB 9283, 29318, Brasília. GOIÁS: CHUNB 23762, 23763, 23765, 23766, Mineiros. MINAS GERAIS: CHUNB 26419, Paracatu. MATO GROSSO: CHUNB 10470, 10475, Santa Terezinha; CHUNB 15796, 15837, 19608, 19677, Chapada dos Guimarães. MATO GROSSO DO SUL: CHUNB 9304, Corumbá. PARÁ: CHUNB 9345, 9346, Novo Progresso.

*Mabuya mabouya* (n = 11). — **Lesser Antilles:** DOMINICA: MNHN 2003.0838, Pointe Baptiste; UMMZ 83323, between Roseau and Grand Bay. GUADELOUPE: MNHN 1889.0664; MNHN 0000.2902. Martinique: MNHN 0000.5110, 0000.5421 (neotype of *M. mabouya*), 0000.0738, 0000.0739, 0000.1785. UNKNOWN ORIGINE: MNHN 0000.2903, 0000.5423.

*Mabuya macrorhyncha* (n = 7). — **Brazil:** BAHIA: CHUNB 25288, Itacare. ESPÍRITO SANTO: CHUNB 8631, 8634, 8635, 8637, 25015, Presidente Kennedy. RIO DE JANEIRO: CHUNB 24187, Maricá.

*Mabuya meridensis* (n = 12). — **Venezuela:** MÉRIDA: AMNH 13405–13408 (paratypes), Rios Albarregas y Milla; AMNH 13526; MHNLS 923, Mérida; MHNLS 1393, Mérida; MHNLS 17081, vicinity of Mérida city, on the road to the Mount Zepa; ULABG 1570 (holotype); Mérida; ULABG 4153, 4281, Mérida (paratypes); UMMZ 57435, Mérida.

*Mabuya nigropalmata* (n = 7). — **Bolivia:** LA PAZ: NRM 23258a–d (four syntypes, previously NRM 3258, photographs only), San Fermín, coll. in 1904 by N. Holmgren. **Brazil:** AMAZONAS: NRM 23259 (syntype, previously NRM 3259, photographs only), Rio Curuca, tributary to R. Javary, coll. in 1914 by V. M. de Oliveira. **Peru:** MADRE DE DIOS: MHNC 5121: Provincia Manu, Distrito Fitzcarrald, Cocha Juarez, coll. by J.-C. Chaparro (20<sup>th</sup> november 2005); MHNC 5718, Provincia Manu, Distrito Fitzcarrald, Cocha Salvador, coll. by J.-C. Chaparro (13<sup>th</sup> october 2005).

*Mabuya nigropunctata* (n = 215). — **Brazil:** ACRE: SNOMNH 37048 to 37051, 5 km N Porto Walter, Rio Jurua. AMAPÁ: CHUNB 8582, Tartarugalzinho; CHUNB 9538, 9541, 9543, 9551, Amapá. AMAZONAS: CHUNB 8611 to 8616, Humaitá; CHUNB 13332, 13333, São Gabriel da Cachoeira; CM 55650, Lago Ucayali, Terezina; SNOMNH 37184 to 37192, Rio Ituxí, Madeirera Scheffer (8°20'S–65°43'W), coll. in march 1997 by L. J. Vitt; SNOMNH 37681 to 37698, Castanho, 40 km S Manaus (3°30,9'S–59°54,2'W), coll. in December 1998 by L. J. Vitt. BAHIA: CHUNB 9266, 9347, Correntina. DISTRITO FEDERAL: CHUNB 8832, 9208, 9577, 13710, Brasília. GOIÁS: CHUNB 9341, Pirenópolis; CHUNB 9622, 13058, 13113, 13114, 29557, Minaçu; CHUNB 12631, Caldas Novas; CHUNB 17519, Alto Paraíso de Goiás. MARANHÃO: MPEG 10690, 10691, 10693, 10695, 10698, Nova Vida, 25 km of Rio Gurupi, BR 316. PARA: CHUNB 9276, Maracajá; CHUNB 29825, 31146, 31150, 31151, 31153, Monte Alegre; CHUNB 34517, 34521, 34524, Novo Progresso; MPEG 8605, 8608, 8611, 8616, 8642, Bela Vista, Viseu; MPEG 12194, 12196, 12199, 12200, 12218, between Rio Tocantins and Rio Mojú, 12 miles of the barrage Tucuruí; SNOMNH 36828 to 36842, CEMEX, Agropecuaria Trevico LTDA, 101 km S and 18 km E of Santarém (3°8'44,4"S–54°50'22,5"W), coll. in April 1995 by L. J. Vitt. MATO GROSSO: CHUNB 19405, 19420, 19438, 19441, Chapada dos Guimarães. MATO GROSSO DO SUL: CHUNB 27735, Alcinópolis. MINAS GERAIS: CHUNB 24734, 24735, 30893, Unai; CHUNB 26401, Paracatu. PERNAMBUCO: CHUNB 9297, Exu. RONDÔNIA: CHUNB 9818, Vilhena; CHUNB 18714, Pimenta Bueno; CHUNB 22841 to 22846, Guajará-Mirim; CHUNB 28976, Costa Marques; SNOMNH 37411 to 37417, Rio Formoso, Parque Estadual Guajara-Mirim, 90 km N Nova Mamoré (10°19'17,2"S–64°33'47,9"W), coll. in April 1998 by L. J. Vitt. RORAIMA: SNOMNH 36313 to 36322, 7 km E Rio Ajaraní, BR 210, coll. in June and July 1993 by L. J. Vitt. TOCANTINS: CHUNB 12546, 12547, 14530, Palmas; CHUNB 27015, 27016, 27018, 27019, Mateiros; CHUNB 37512, 37515, 37517, 37520, 38312, Paranã. Colombia: AMAZONAS: CM 55601, 55602, Leticia. Ecuador: NAPO: UMMZ 84742, San Francisco, Rio Napo (200 m asl). SUCUMBIOS: FMNH 165292, Santa Cecilia, Rio Aquarico, tributary of Rio Napo; SNOMNH 36514, Reserva faunística

Cuyabeno (RPF-Cuyabeno), coll. en March 1994 by L. J. Vitt. **Guyana:** CUYUNI-MAZARUNI: AMNH 15120 to 15122, 18183, 21326, Kartabu, on the Mazaruni-Potaro. **French Guyana:** MNHN 1902.0265, no exact locality, coll. between 1899 and 1901 by F. Geay; MNHN 1996.4630, 1996.4570, St Eugène, coll. by I. Ineich; MNHN 1996.4572, St Eugène, coll. in 1995 by G. Dubost; MNHN 1996.4571, 1997.2206 to 1997.2213, St Eugène, coll. in 1995 and 1996 by J. C. De Massary; MNHN 2001.0827, Piton Baron, layon sud, coll. by Ph. Gaucher; MNHN 2002.0612, 2002.0613, St Marcel; MNHN 2004.0103 to 2004.0105, Bakra mountains, forest at the foot of the peak Coudreau (500 m asl), coll. in November 2004 by J. C. De Massary & A. Miralles. **Paraguay:** ALTO PARAGUAY: CM 109111, Estancia Dona Julio, 5 km N Bahia Negra. **Peru:** AMAZONAS: AMNH 57025, at mouth of Rio Santiago, Rio Marañón (180 m asl). LORETO: MNHN 1978.2412, 1978.2413, Rio Yubinetto (=Yavineto), tributary of the Rio Putumayo, coll. in 1978 by M. T. Rodrigues and J. P. Gasc. MADRE DE DIOS: FMNH 168137, Avispas, near Rio Inambari, 145 km W Puerto Maldonado (480 m asl). **Suriname:** RMNH 15593, Brokopondo district, Afobaka; RMNH 15629, airstrip Paloemeu; RMNH 15633, Paramaribo district; RMNH 15648, Sipaliwini district; RMNH 16453, Awarra savannah, Marataka river; RMNH 16468, 16469, district de Nickerie, Blanche Marie; RMNH 28080, 10 km N Wanekreek; RMNH 28580, km 117 on the road to Amotopo, Kabalebo. **Trinidad & Tobago:** AMNH 64528, Trinidad; CM 6565, Trinidad, County of St George, Manzilla Beach; FMNH 49901 to 49908, Trinidad, San Rafael; UMMZ 79919, Trinidad, County of St George, Chaguaramas. **Venezuela:** AMAZONAS: MHNLS 16389, Parima B (960 m asl), (02°48'00"N-64°18'00"W). ARAGUA: MHNLS 17080, Quebrada, right margin of Río San Miguel, National Park Henri Pittier; BOLIVAR: MHNLS 11544, 11545, foot of the mount Roraima, La Gran Sabana (5°10'N-60°47'W), coll. en February 1990 by M. J. Praderio; MHNLS 15532, Serranía del Supamo, Cerro Santa Rosa. DELTA AMACURO: LACM 31469, 31470, Managas; MHNLS 4543, Burojoida. MIRANDA: MHNLS 4971, La Toma, Capaya; MHNLS 16652, S-W of Araira, Hacienda La Ceiba; MHNLS 16651, 16655, 16658, Guatire (300 m asl). NUEVA ESPARTA: MHNLS 3401 3402, Cerro Copey, Margarita island. SUCRE: MHNLS 15533, Las Melenas, Paria peninsula; MHNLS 16203, Macuro, Paria peninsula.

*Mabuya sloanii* (n = 20). — **Bahamas:** TURKS AND CAICOS: UMMZ 117393, West Caicos, west side. **Greater Antilles:** BRITISH VIRGIN ISLANDS: CM 17357, 17358, Anegada; UMMZ 80582, VIRGIN GORDA. U. S. Virgin Islands: MNHN 0000.0554 (holotype of *Scincus sloanii*); MNHN 0000.1088, St Thomas; UMMZ 73821, St Thomas, Buck Island; UMMZ 80586, St Thomas, Capella Island. JAMAICA: MNHN 0000.2904 (syntype of *Mabuia fulgida*, Cope 1862), no locality; UMMZ 85861, Portland Point. PUERTO RICO: CM 23775, 23776, Mona Island, Sardinera; FMNH 215, Mona Island; SNOMNH 32878, no locality; UMMZ 124819, Mona Island, on the road between Lighthouse and Landing Pier. **Lesser Antilles:** ANGUILLA: CM 115480, Brimegin, W. of Foutain Hill; CM 115481, no locality. ST BARTHÉLEMY: MNHN 1997.6064; MNHN 2003.0843, 2003.0844.

*Mabuya unimarginata* complex species (n = 40). — **Belize:** BELIZE: CM 90965, Northern Highway between Ladyville and Sand Hill; CM 105799, 1 Mile W Burrel Boom road on road to Double Head Cabbage. CAYO: CM 105699, 4 Miles S Georgeville on road to San Antonia. **Colombia:** CHOCO: AMNH 18262, 18263, Quibdo; FMNH 43829, 43830, Pizarro. **Costa Rica:** PUNTARENAS: UMMZ 145875, 16 km S San Vito, on highway 16, Las Cruces field station; UMMZ 117575, 1 Mile E of Volcán de Buenos Aires cone finca. **El Salvador:** SAN SALVADOR: UMMZ 117649, San Salvador. **Guatemala:** ALTA VERAPAZ: UMMZ 91144, Panzos. RETALHULEU: UMMZ 107661, Haciendas Cas Blanca, 1–3 km N of Casa Grande. **Honduras:** ISLA DE LA BAHIAS: CM 65381, Utila. **Mexico:** CAMPECHE: UMMZ 99882, Calcehtok. CHIAPAS: UMMZ 94916, 11 km W Tuxtla Gutierrez; UMMZ 117648, Arriaga. GUERRERO: UMMZ 104431, 6 Miles E of San Luis, 200 FT. MICHOACAN DE OCAMPA: UMMZ 121662, 3.6 MI S of Tzitzio. OAXACA: CM 41258, Valle Nacional, Cerro Pelon; UMMZ 115089, 1.2 Miles SE of Tlacolulá, 5400 FT. QUINTANA ROO: UMMZ 78594, Mujeres Island. TABASCO: UMMZ 113774, 14 Miles N of Teapa. VERACRUZ-Llave: UMMZ 121171, Cienega de Macuile. YUCATAN: AMNH 38863–65, Chichen Itza; CM 47214, Merida; CM 65371, 6.7 km E of Chuburna Puerto; UMMZ 113548, Calcehtok. **Nicaragua:** LEON: OMHN 36173–75, Vulcan Momotombo. RIO SAN JUAN: SNOMNH 36177–79, by Isla de Diamante on Rio San Juan. RIVAS: SNOMNH 36176, Chococente. **Panama:** LOS SANTOS: CM 43593–94, Los Santos; CM 43595, Santa Maria. PANAMA: UMMZ 135354, Gorgas Memorial Laboratory Field Station on the Rio Bayano.

*Trachylepis maculata* (n=2). — **Guyana:** DEMERARA-MAHAICA: NHM 1946.8.18.6 (paralectotype of *Tiliqua maculata* Gray, 1839) and MNHN 2932 (lectotype of *Tiliqua maculata* Gray, 1839, gift of the NHM), both from “*Demerara*”, collected by the “*Col. Edward Sabine*”.

*Trachylepis tschudii* (n=1). — **Peru:** MHNN 91.2426 (photograph only), from the “*Waldregion*” (=Amazonia), holotype of *Trachylepis (Xystrolepis) punctata* Tschudi 1845.