

Speciation in the “Várzea” flooded forest: a new *Mabuya* (Squamata, Scincidae) from Western Amazonia

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Abstract

Mabuya altamazonica sp. nov. is described from Peruvian Amazonia. This species is sympatric with *M. nigropunctata*. Despite their superficial similarity, those two Amazonian species could be differentiated both by cephalic scalation characters and molecular results (12S rRNA). *Mabuya altamazonica* sp. nov. differs from all Amazonian and Andean species of *Mabuya* by the combined presence of (1) paired prefrontals and frontoparietals, (2) a single pair of nuchals, (3) four supraoculars, (4) five subequal supraciliaries, (5) seven supralabials with the fifth being the largest and placed under the eye, (6) parietals in contact behind the interparietal and (7) dark palms and soles.

Key words: Scincidae, *Mabuya altamazonica*, new species, *Mabuya bistrriata*, *Mabuya nigropunctata*, molecular phylogeny, Amazonia, Peru

Resumen

Se describe una nueva especie de lagartija, *Mabuya altamazonica* sp. nov. proveniente de la Amazonia de Perú. Esta especie es simpátrica con *M. nigropunctata*, y a pesar de sus similitudes superficiales, tanto la escamación cefálica como los resultados moleculares (12S rRNA) revelan que ambas son especies distintas. *Mabuya altamazonica* sp. nov. se distingue de todas las especies amazónicas y andinas del género *Mabuya* por poseer (1) un par de prefrontales y frontoparietales, (2) un solo par de escamas nucales, (3) cuatro supraoculares, (4) cinco escamas supraciliares subiguales, (5) siete supralabiales, siendo la quinta más grande y ubicada debajo de los ojos, (6) parietales en contacto detrás de la interparietal, y (7) palmas de las manos y plantas de los pies de color negro.

Introduction

The current systematics of the neotropical genus *Mabuya* is very confusing, given both nomenclatural and taxonomic difficulties (Miralles 2005). The taxonomy of the Amazonian *Mabuya* was considerably clarified by Ávila-Pires (1995) who designated a neotype for *M. nigropunctata*, the most common species in the Guyano-Amazonian region (Ávila-Pires 1995, Massary *et al.* 2001).

Mabuya from extreme Western Amazonia (Ecuador, Peru) has been always indiscriminately regarded as belonging to the same species. Lehr (2002) used the nomen *M. bistriata sensu* Rebouças-Spieker (1981) (a chresonym of *M. nigropunctata*; non *Scincus bistriata* [now *Mabuya bistriata*]; see Ávila-Pires 1995) to refer to this alleged single species, whereas Vitt & de la Torre (1996) and Duellman (2005) used the name *M. nigropunctata sensu* Ávila-Pires (1995).

In the present paper, we argue in favour of the existence of another undescribed species of *Mabuya*, living in sympatry with *M. nigropunctata*, and widespread throughout the Peruvian Amazonia. Until now, these two morphologically similar taxa have been confounded, and regarded as a single species. This paper constitutes a further step in the revision of the genus *Mabuya* in the New World. As many other recent studies (Mijares-Urrutia & Arends 1997; Mayer & Lazell 2000; Rodrigues 2000; Miralles 2005, in press; Miralles *et al.* 2005a, 2005b), the present work confirms that the species richness of this genus has been greatly undervalued, given both its conservative morphology, and its confusing taxonomy. That is why such a revision is essential before undertaking a wide comprehensive study on the evolution of this genus which recently crossed the Atlantic ocean from tropical Africa (which happened less than 7–9 million years ago according to Carranza & Arnold (2003)) and to understand how it successfully colonised, dispersed and diversified over all the neotropical world.

Nomenclatural framework

Until recently, the genus *Mabuya* Fitzinger, 1826, included more than 110 species occurring in tropical areas of Africa, Madagascar, Asia and the New World (Greer & Broadley 2000). Mausfeld *et al.* (2002) divided it into four monophyletic genera: *Chinonia* Gray, 1845 (Cape Verdian clade); *Euprepis* Wagler, 1830 (Afromalagasy clade, including *Mabuya atlantica*, from Fernando de Noronha island, offshore Brazil), later replaced by Bauer (2003) for *Trachylepis* Fitzinger, 1843, the oldest valid designation for *Euprepis* placing this genus in the synonymy of *Mabuya sensu stricto*; *Eutropis* Fitzinger, 1843 (Asian clade); and *Mabuya sensu stricto* (American clade). Carranza & Arnold (2003) demonstrated that the Mediterranean species, *M. aurata* and *M. vittata*, constituted a fifth monophyletic lineage, more closely related to the Neotropical *Mabuya* than to the Afrotropical species of the genus *Trachylepis*. Unfortunately, given that Mausfeld *et al.*

(2002) had not included any species of this lineage in their phylogenetical analysis, those authors had not proposed any name for this clade. For this reason, the genus *Mabuya sensu stricto* will be considered in the present paper as an exclusively neotropical lineage (Greer *et al.* 2000; Mausfeld *et al.* 2002; Carranza & Arnold 2003) whereas the Mediterranean species will be referred, for the time being, under the name “*Mabuya*” put between quotes. In order to respect and stabilise the zoological nomenclature, definitions of *M. bistriata* and *M. nigropunctata* are based on Ávila-Pires (1995) (see details in Miralles *et al.* 2005a).

Material and methods

Morphological analysis: The examined specimens, preserved in 70% ethanol, are housed in the American Museum of Natural History, New York, USA (AMNH); Coleção Herpetológica da Universidade de Brasília, Brasília, Brazil (CHUNB); Carnegie Museum, Pittsburgh, USA (CM); Field Museum, Chicago, USA (FMNH); Los Angeles County Museum, Los Angeles, USA (LACM); Museo de Historia Natural La Salle, Caracas, Venezuela (MHNLS); Museum National d’Histoire Naturelle, Paris, France (MNHN); Museum of Comparative Zoology, Cambridge, USA (MCZ); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Nationaal Natuurhistorisch Museum Naturalis, Leiden, Netherlands (RMNH); Sam Noble Oklahoma Museum of Natural History, Norman, USA (OMNH); and University of Michigan Museum of Zoology, Ann Arbor, USA (UMMZ).

We follow Ávila-Pires (1995) in the scale nomenclature, scale counts and measurements used for the description. New characters of first rank in systematics for the genus *Mabuya (sensu lato)* proposed by Greer and Broadley (2000) and Greer and Nussbaum (2000) were also added to the description. Measurements of specimens were recorded to the nearest 0.1 mm with dial callipers. Drawings were made with a stereomicroscope LEICA MS5 equipped with a camera lucida.

Molecular Procedures and Phylogenetic Analyses: The aim of the molecular analysis is to constitute a supplementary argument in favour of the fact that the new species of *Mabuya* and *M. nigropunctata* are two distinct species, despite their superficial similarity. It does not intend to discuss the general phylogenetic relationships of the genus *Mabuya*; a more complete analysis implying more marker genes and taxa is being prepared to answer this question.

One sample from the holotype of the new species described here and three samples of *Mabuya nigropunctata* from different South American localities (French Guyana and the Brazilian states of Para and Roraima) were sequenced. Additionally, six others neotropicals species of *Mabuya* have been also included in the analysis (Table 1–2). Three out-group species have been chosen following the phylogenetic studies on the genus *Mabuya sensu lato* published by Mausfeld *et al.* (2002) and Carranza & Arnold (2003): “*Mabuya*” *aurata*, *Trachylepis perrotetii*, and *Eutropis multifasciatus*. Phylogenetic

relationships between those three taxa and the ingroup are as follow: (*Eutropis* (*Trachylepis* (Mediterranean “*Mabuya*”, *Mabuya sensu stricto*))). Only six sequences of all those available on GenBank have been included in this study given that many of them have been erroneously or doubtfully identified (unpublished data).

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

Species	Code	Museum number	GeneBank accession number	reference	locality
Ingroup species					
<i>M. altamazonica</i>	TAR	MNHN 2002.0291 (holotype)	DQ368663	This study	Peru, San Martin
<i>M. bistriata</i>	Bis 00	not collected	DQ368664	This study	French Guyana
<i>M. cochabambae</i>	-	ZFMK 72151	AF202625	Mauslfed & Lötters, 2001	Bolivia, Santa Cruz
<i>M. frenata</i>	E11107	not collected	AF151427	Carranza & Arnold, 2003	Brazil, M. Grosso do Sul
<i>M. macrorhyncha</i>	-	MNRJ 9324	AY070333	Mausfeld <i>et al.</i> , 2002	Brazil, Bahia,
<i>M. nigropunctata</i>	SP26	not collected	DQ368666	This study	French Guyana
<i>M. nigropunctata</i>	H14223	?	DQ368667	This study	Brazil, Para
<i>M. nigropunctata</i>	H12369	OMNH 36318	DQ368668	This study	Brazil, Roraima
<i>M. unimarginata</i>	MSM067	not collected	DQ368665	This study	Guatemala, Zacapa
Outgroup species					
« <i>M.</i> » <i>aurata</i>	E11102	not collected	AY151435	Carranza & Arnold, 2003	Turkey, Kisehir
<i>T. perrotetii</i>	E111019	not collected	AY151440	Carranza & Arnold, 2003	Ghana, Africa
<i>E. multifasciata</i>	E111036	not collected	AY151441	Carranza & Arnold, 2003	Tropical Asia

Total genomic DNA was extracted from 95% ethanol-preserved tissues (muscles, skin or liver) using a CTAB protocol (Winnepenninckx *et al.* 1993). The 12S sequences of studied specimens (approximately 380 pb) were generated by Polymerase chain reaction (PCR) using a couples of primers (of Palumbi *et al.*, 1991): 12SA–L (light chain; 5' – AAA CTG GGA TTA GAT ACC CCA CTA T – 3') and 12SB–H (heavy chain; 5' – GAG GGT GAC GGG CGG TGT GT – 3'). Amplifications were performed in 25µl total reaction

TABLE 2. Summary of the uncorrected p-distances for the 12S data set.

Taxon	1	2	3	4	5	6
1 <i>M. altamazonica</i>	-					
2 <i>M. bistrata</i>	0.05822	-				
3 <i>M. cochabambae</i>	0.09235	0.06632	-			
4 <i>M. frenata</i>	0.07124	0.03975	0.06332	-		
5 <i>M. nigropunctata</i> (F. Guyana)	0.06860	0.04770	0.07124	0.04749	-	
6 <i>M. nigropunctata</i> (Para)	0.06332	0.04503	0.06860	0.04485	0.01847	-
7 <i>M. nigropunctata</i> (Roraima)	0.06596	0.04767	0.07124	0.04749	0.02111	0.00264
8 <i>M. macrorhyncha</i>	0.05277	0.03447	0.07124	0.04222	0.05013	0.04749
9 <i>M. unimarginata</i>	0.07422	0.06913	0.06883	0.07405	0.08204	0.07407
10 « <i>M.</i> » <i>vaillantii</i>	0.09235	0.10068	0.10818	0.08971	0.11082	0.10818
11 <i>T. perrotetii</i>	0.09763	0.12186	0.14776	0.10554	0.12137	0.11609
12 <i>E. multifasciatus</i>	0.14776	0.14572	0.16359	0.13984	0.15040	0.14512

Taxon	7	8	9	10	11	12
7 <i>M. nigropunctata</i> (Roraima)	-					
8 <i>M. macrorhyncha</i>	0.05013	-				
9 <i>M. unimarginata</i>	0.07674	0.06351	-			
10 « <i>M.</i> » <i>vaillantii</i>	0.11082	0.09763	0.10072	-		
11 <i>T. perrotetii</i>	0.11873	0.10818	0.13509	0.12929	-	
12 <i>E. multifasciatus</i>	0.14776	0.14776	0.15634	0.12665	0.16359	-

volumes containing 0.3µl of each primers (25pM/µl), 0.15µl of Taq DNA polymerase (Qbio Appligen) in a buffer supplied by the enzyme manufacturer. Cycling conditions was as follow : 94°C (3 min) / [denaturation: 94°C (30 sec); annealing: 58°C (40 sec); extension: 72°C (50 sec)] x 30 cycles / 72°C (1 min). 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 with 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.). Sequence entry were performed manually with the BioEdit Sequence Alignment Editor program 7. 0. 0. (Hall 1999). Alignment was straightforward as there were no indels. Data were then imported into PAUP* 4.0.b10 (Swofford, 2002) for phylogenetic analyses using Maximum Parsimony (MP). Reconstructions were performed with heuristic search, with random addition of taxa for 1000 replications, and tree bisection reconnection (TBR), all sites were equally weighted. The relative branch support was evaluated with 2000 bootstrap replicates (Felsenstein 1985).

Molecular results

The analysed sequences from the 12S rRNA gene constitute a matrix of 379 characters; 100 sites were variable and 55 of them were parsimony-informative. The heuristic search with MP analysis produced 1 most-parsimonious tree (n tax = 12; tree length = 190; CI = 0.6684; RI = 0.4750; RC = 0.3175). Bootstrap support is shown on the fig 6, and the complete matrix of uncorrected pairwise sequence divergence is presented in Table 2.

Description

Mabuya altamazonica, new species

Holotype: MNHN 2006.0291, 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 San Martin, Peru.

Paratypes: Thirty one specimens. **Peru**: DEPARTAMENTO DE AMAZONAS: AMNH 57020, confluence between Rio Santiago and Rio Marañón (180 m asl). DEPARTAMENTO DEL CUZCO: 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. 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).

Additional material examined: Three specimens (FMNH 134461–63) were collected in the valley between Palca and Tarma, departamento de Junin, at 1500 m asl. We refrain to include those specimens in the type series given (1) the altitude of this locality which seems to be exceptional for this lowland species, and (2) its uncommon colour pattern with two very dark solid dorsolateral bands.

Moreover, we had also the opportunity to study two specimens (UMMZ 68102, 68103) from the departamento de Santa Cruz, Eastern Bolivia. Those specimens are morphologically very similar to the holotype. Such a locality would extend remarkably the

distribution of this species to the south. However, this data being very approximate, we believe that it needs confirmation.

All latter specimens (from Bolivia and from the Peruvian Andes) are morphologically very close to the type-series and for the time being there are no objective arguments for not considering them as *M. altamazonica*. However, given the lack of reliability about their identification and their uncommon localities, we prefer to discard them herein from the discussion.

Diagnosis

A relatively big sized *Mabuya* having paired prefrontals and frontoparietals, four supraoculars, most frequently five subequal supraciliaries, seven supralabiales with the fifth being the largest and placed under the eyes, parietals in broad contact behind the interparietal and a single pair of nuchals. Two upper and two lower lateral dark stripes; back spotless or covered by many dash-shaped chocolate spots; palms and soles dark.

Mabuya altamazonica differs from the nine species of *Mabuya* occurring potentially in western Amazonian and peri-Andean regions [*M. bistrinata* (Spix 1825), *M. carvalhoi* Rebouças-Spieker & Vanzolini 1990, *M. cochabambae* Dunn 1936, *M. dorsivittata* Cope 1862b, *M. frenata* (Cope 1862a), *M. guaporicola* Dunn 1936, *M. meridensis* Miralles *et al.* 2005b, *M. nigropalmata* Andersson 1918, *M. nigropunctata* (Spix 1825)] by the combined presence of: paired frontoparietals (*versus* frontoparietals fused together in *M. carvalhoi*, *M. frenata* and *M. nigropalmata*), paired prefrontals (*versus* prefrontals fused together in *M. carvalhoi*), a single pair of nuchals (*versus* two to four pairs in *M. carvalhoi* and *M. nigropalmata*), four supraoculars (*versus* three in *M. cochabambae* and *M. dorsivittata*), most often five subequal supraciliaries (*versus* four, with the second largest in *M. bistrinata*, *M. dorsivittata*, *M. guaporicola* and *M. meridensis*), absence of a vertebral thin stripe (contrary to *M. cochabambae*, *M. dorsivittata*, *M. guaporicola* and *M. meridensis*), seven supralabials with the fifth being the largest and placed under the eyes (*versus* eight supralabials with the sixth being the largest and placed under the eyes in *M. frenata* and most specimens of *M. nigropunctata*), parietals in broad contact behind the interparietal (*versus* parietals separated by the interparietal or barely in point contact in *M. nigropunctata*), palms and soles darker than belly (*versus* light palms and soles in *M. bistrinata*, *M. carvalhoi*, *M. cochabambae*, *M. dorsivittata*, *M. frenata* and *M. guaporicola*), and fore- and hind limbs touching (or almost touching) each other when adpressed against body (*versus* fore- and hind limbs distinctly separated from each other when adpressed against body in *M. cochabambae*, *M. dorsivittata*, and *M. guaporicola*).

Description of the holotype

Specimen MNHN 2006.0291 (figs 1, 2, 3a–b) in a perfect state of conservation and coloration, with an abdominal slit.

Snout-vent length 92.1 mm; tail length 91.4 mm (a little piece of tip of the tail was amputated); head length 16.3 mm. Fore- and hindlimbs hardly touching each other when adpressed against body.

Rostral wider than high, contacting first supralabials, nasals and supranasals. Paired

supranasals in median contact, contacting anteriormost loreal. Frontonasal diamond-shaped, wider than long, laterally contacting anterior loreal. Paired prefrontals roughly quadrilateral, medially separated by frontonasal, wider than long, contacting frontonasal, both anterior and posterior loreals, first supraciliaries, first and second supraoculars, and frontal. Frontal lanceolate, approximately twice as long as wide, wider anteriorly, in contact with frontonasal, prefrontals, second supraoculars and frontoparietals. Four supraoculars; the first the smallest, the second the longest and widest. Posteriormost supraocular in contact with the frontal is the second (Greer & Broadley 2000). Five subequal supraciliaries on the right side; on the left side four supraciliaries, the third being the longest and probably resulting from the fusion of two supraciliaries. Paired frontoparietals, longer than wide, in broad contact at midline, in contact with frontal, all supraoculars except the first, parietal and interparietal. Interparietal rhomboid, longer than wide, wider anteriorly. Parietal eye hardly distinct. Parietals larger than interparietal, wider than long, in contact with each other behind interparietal and overlapping the upper temporal scale (Greer & Nussbaum 2000). Single pair of transversely enlarged nuchals, each as wide as three rows of dorsals.

Nasal subrectangular. Nostril located posteriorly. Postnasal small, in contact with supranasal, anterior loreal and first supralabial. Two subrectangular loreals behind nasal, subequal in size, the second slightly higher. First loreal in contact with first, second and third supralabials, second loreal in contact with third supralabial. One presubocular in contact with fourth and fifth supralabials. One preocular, in front of presubocular and behind second loreal, in contact with third and fourth supralabials. Lower eyelid undivided with a transparent disk, one row of small scales across its dorsal edge (Greer & Broadley 2000). Seven supralabials; the fifth is the widest and forms the lower border of the eyelid. Seven infralabials. Temporals imbricate, smooth, cycloid, not distinctly delimited from scales on the nape or sides of the neck. Two pretemporals. One primary temporal, two secondary temporals in contact and three tertiary temporals (Greer & Broadley 2000). Ear-opening relatively small, round, with undulating anterior margin and smooth posterior margin. Auricular lobules absent.

Mental wider than long, posterior margin straight. Postmental wider than long, adjacent to first and half of second infralabials. Two pairs of chin shields, first in contact with postmental, posterior half of second and anterior half of third infralabials. Gulars similar in size and outline to ventrals.

Palms and soles covered with small tubercles, subequal in size. Both regions delimited by a row of larger and flatter scales. Subdigital lamellae smooth, single, 11 and 12 under fourth finger, 14 and 15 under left fourth toe. Finger and toes clawed. Relative length of the toes in the following order: $I < II < III = V < IV$.

All scales, except head shields and scales on sole and digits, cycloid, smooth and imbricate. Thirty scale rows around midbody, 52 transverse rows of dorsal scales, 31 transverse rows of ventral scales. Four preanals larger than adjacent ventral scales. Median subcaudal series of scales twice as wide as long on the posterior half of the tail.

Coloration in preservative: background colour of flanks and upper side of the head, neck, back, limbs and tail olive-bronze. Venter, lower side of head, throat, lower side of

limbs and tail immaculate bluish-grey.

Back nearly spotless, just with three widespread little black dots. Lateral and upper sides of limbs spotted with many small, fused dark dots. Palms and soles dark brown-black. Preanals pale cream.

Four dark brown stripes run along body. Two upper lateral stripes; margins darker and strongly contrasted; about three scales wide at midbody; from nostrils, loreals, upper half part of supralabials, around eyes and temporals, along upper half part of ear-openings, on neck, above arms, on sides until insertion of hindlimbs and continuing on the sides of tail. Two lower lateral stripes not well defined; from corner of mouth, below ear-opening, above forelimb until insertion of hindlimb; dorsal margins darker and relatively well contrasted, whereas limits between ventral margins and venter not distinct.

Four whitish stripes run along body; two very thin and hardly distinguishable dorsolateral stripes separating dark dorsolateral stripes from the background colour of the back; and two more contrasting lateral stripes separating the dark upper lateral from lower lateral dark stripes. The coloration in life is slightly lighter than in preservative.

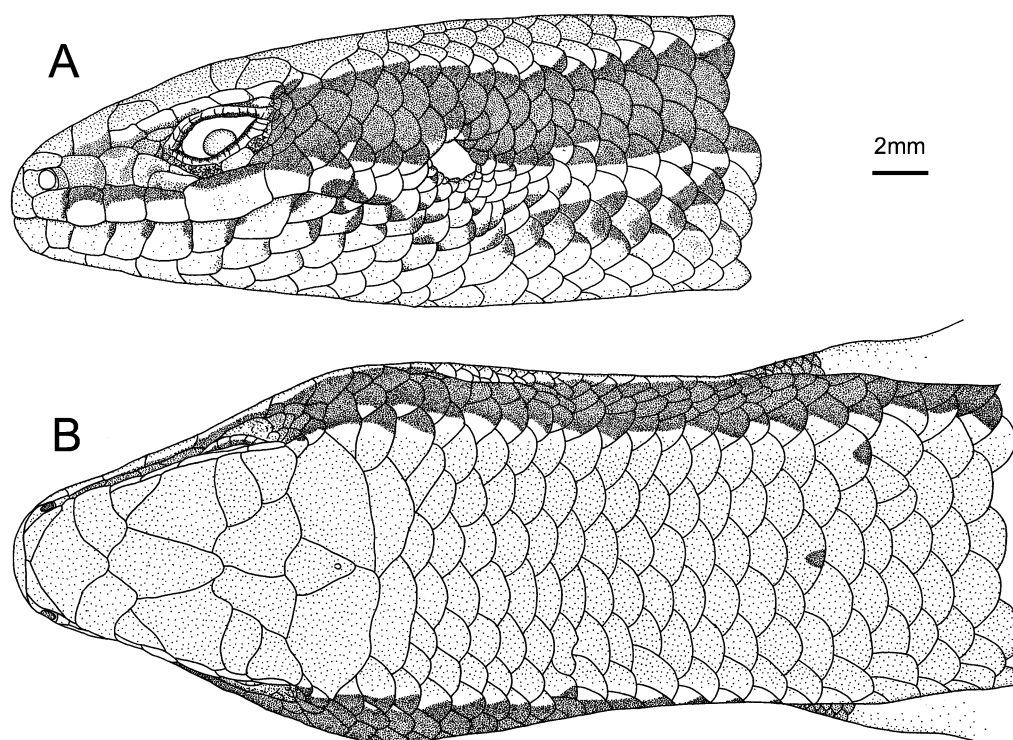


FIGURE 1. Drawings of the holotype of *Mabuya altamazonica* (MNHN 2006.0291): (A) lateral view of the head and (B) dorsal view of the anterior part of the body. Scale bar = 2 mm.

Variation

The following summary of meristic and measurement variation gives the range for each character, followed by the mean, \pm the standard deviation, and sample size in parentheses. For some bilateral characters, the sample size has been noted as the number

of sides rather than specimens, and this is then indicated after the sample size. Dorsal scale rows: 48–55 (52.44 ± 1.98 , 26); midbody scale rows: 26–31 (29.19 ± 1.35 , 26); ventral scale rows: 28–36 (32.12 ± 1.91 , 24); lamellae under fourth finger: 11–15 (12.19 ± 1.04 , 48 sides); lamellae under fourth toe: 13–19 (15.67 ± 1.49 , 46 sides); head length: 14.1–17.7 (15.56 ± 0.86 , 22); snout–vent length: 72.3–97.2 (84.23 ± 7.26 , 21); tail length: 115.0–156.0 (128.94 ± 11.67 , 10).



FIGURE 2. Photograph of the living holotype specimen (MNHN 2006.0291).

Internasals: 96.2% in broad contact and 3.8% separated ($n = 26$). Prefrontals: 7.7% in broad contact, 30.8% in point contact and 61.5% separated ($n = 26$). Parietals 96.0% in contact behind the interparietal ($n = 25$). Fifteen specimens have five subequal supraciliaries on both sides (58%); four specimens have four supraciliaries with second enlarged, on both sides (15%); three specimens have five subequal supraciliaries on one side and four subequal supraciliaries on the other (12%), three specimens have four subequal supraciliaries on both sides (12%), and one specimen has six supraoculars on one side and five on the other. All studied specimen have seven supralabials on both sides ($n = 26$), except the specimen (AMNH 57036) which has eight supralabial on the right side and seven on the left side.

The dorsal coloration of *Mabuya altamazonica* is highly polymorphic (fig 3a–d): some specimens have an homogeneous spotless back (ex. holotype MNHN 2006.0291), whereas some others have a lot of aligned chocolate brown dash-shaped spots on the back, approximately forming two discontinuous and not well defined dorsolateral stripes, running on the back from the prefrontal to the middle of the tail (ex. FMNH 168255). However, most of the specimens are intermediate between those two patterns of coloration. Those different patterns of coloration seem to be randomly distributed in the area of distribution of *M. altamazonica*, and there is no evidence of any biogeographical cline (fig 4).

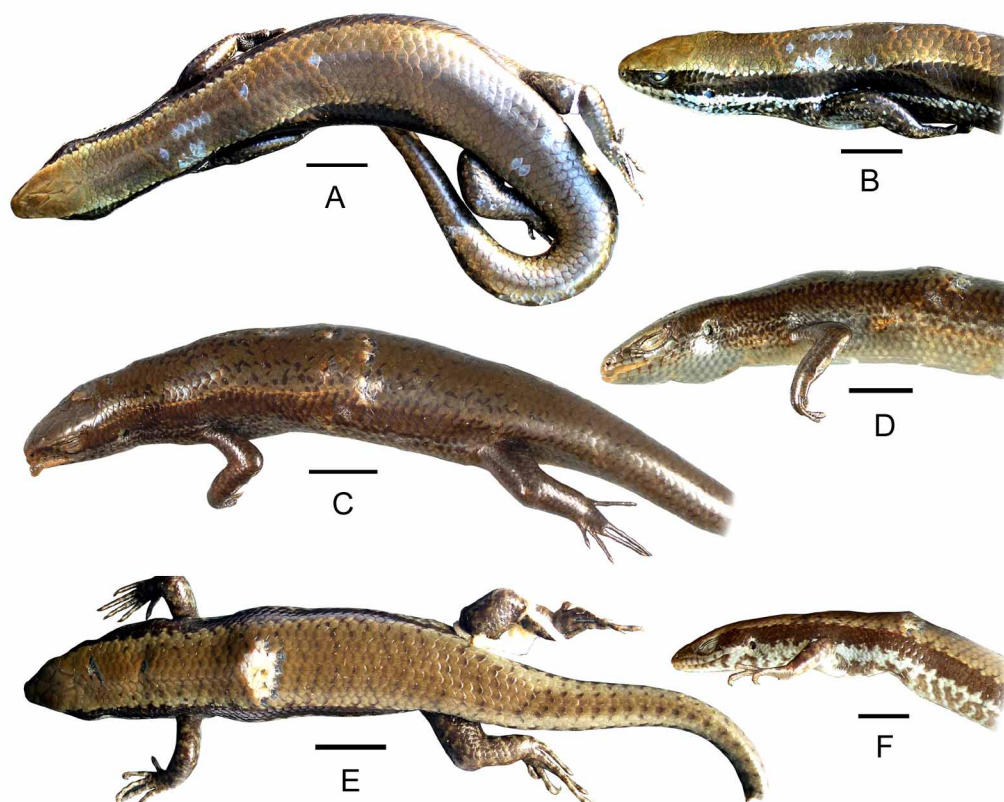


FIGURE 3. Coloration polymorphism in *Mabuya altamazonica* illustrated by specimens having: (A, B) homogeneous spotless back (holotype MNHN 2006.0291) and (C, D) many spot on the back (FMNH 168255); and (E, F) a comparison with a west amazonian specimen of *M. nigropunctata* (OMNH 36514). Scale bar = 1 cm.

Etymology

The specific name refers to the distribution of this taxa, endemic to the extreme occidental part of the Amazon forest, and literally means “from the upper Amazonia”.

Distribution and ecology

Mabuya altamazonica is confined to virtually all the Peruvian Amazonia, extreme western part of the Amazon Basin. The presence in Ecuador is highly probable, as one locality (AMNH 69053, 69054) lies in the border with Peru (fig 4). *Mabuya altamazonica* is a lowland species, all studied specimens having been found at an altitudinal range from 150 to 780 m above sea level.

The holotype was captured in pre-montane forest at 600 m asl. The concession ASPRAVEP have a medium precipitation of 2500 mm/year at the lower valley (R. Schulte, pers. com.).

As all others species belonging to the genus *Mabuya*, *M. altamazonica* is viviparous, embryos having been found in the uterus of the female AMNH 60583.

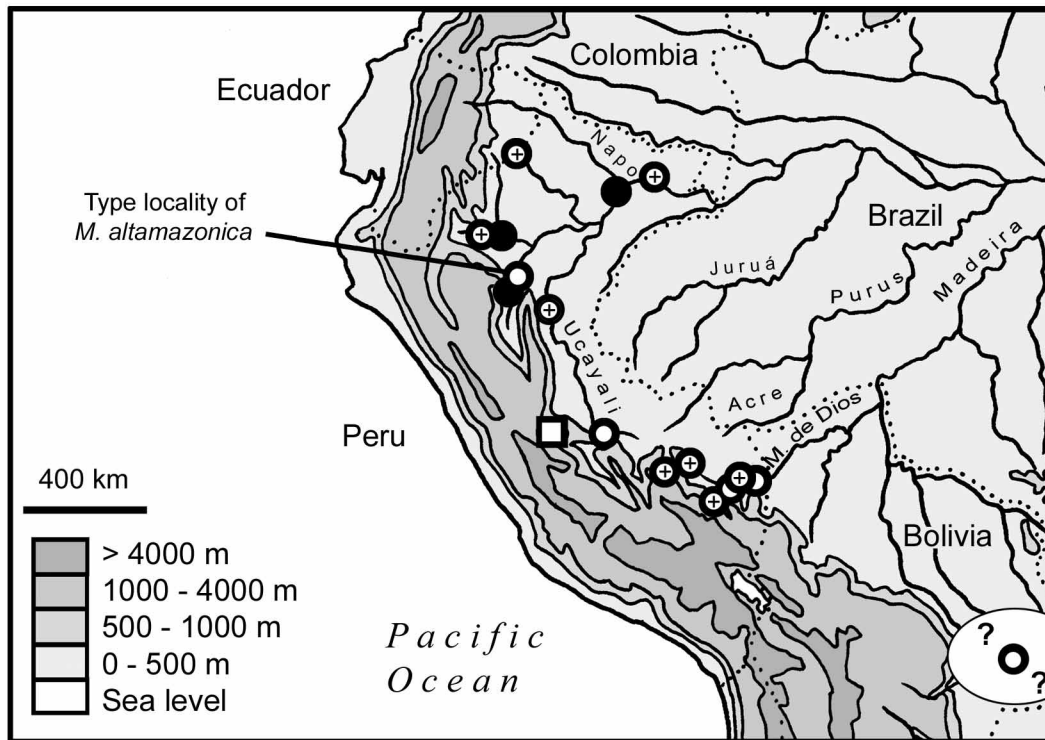


FIGURE 4. Distribution map of *Mabuya altamazonica*. White circles: specimens with a spotless back; Black circles: specimens with a back covered with many spots, more or less aligned in two dorsolateral bands; Circle with cross: intermediate color pattern; White square: specimens (FMNH 134461–63) from the highlands. The white ellipse indicate the very approximate locality of the two supposed Bolivian specimens of *M. altamazonica* (UMMZ 68102–103).

Discussion

Taxonomy

The existence of two species of *Mabuya* looking alike in Peruvian Amazonia was never mentioned in studies dealing with Peruvian *Mabuya* (Burt & Myers 1942, Duellman 2005). Until now *Mabuya altamazonica* has obviously been confused with *Mabuya nigropunctata*, both species having been considered as the same taxa, because of their sympatric distribution. Indeed, morphologically very similar, those two species share a combination of characters which have been until now considered as diagnostic for *M. nigropunctata* (Ávila-Pires 1995): paired prefrontals and frontoparietals, a single pair of nuchals, a relative big size with a big head and a short muzzle, most frequently five supraciliaries and black palms and soles. Their patterns of coloration are also roughly similar in most cases. Two characters of the cephalic scalation, however, can separate the two species: *Mabuya altamazonica* differs from *M. nigropunctata* in having (1) seven supralabials, with the fifth being the subocular one's (versus eight supralabials, the sixth

being the subocular one's) and (2) parietals in broad contact behind the interparietal (versus parietals separated by the interparietals, or barely in point contact) (Table 3). We also observed that Western populations of *Mabuya nigropunctata* from Ecuador, Peru, and Acre state in Brazil (potentially sympatric with *M. altamazonica*), are usually characterised by very wide lower lateral stripes, interrupted by many whitish vertical marblings (fig 3f, see also Duellman 2005: pl. 149, 150), whereas *Mabuya altamazonica* has a thinner and relatively continuous lower lateral stripe (figs 2, 3b, 3d).

TABLE 3. Comparisons of some morphological characteristics of *M. altamazonica* and *M. nigropunctata*.

Characteristics	<i>Mabuya altamazonica</i>	<i>Mabuya nigropunctata</i>		
		western specimens ¹	all specimens	
Number of supralabials, followed by the position of the subocular one in parenthesis	7(5) :	98.1 %	19.2 %	18.7 %
	8(6) :	1.9 %	80.8 %	78.4 %
	other ² :	0 %	0%	2.9 %
	N sides :	52	26	412
Parietals in broad contact ³	% :	96.0 %	18.2 %	9.3 %
	N	25	11	194
	specimens :			
Number of lamellae under fourth fingers	Range :	11–15	13–19	10–16
	mean ± SD :	12.19 ± 1.04	14.35 ± 0.75	12.85 ± 0.98
	N sides :	48	24	412
Number of lamellae under fourth toes	Range :	13–19	15–20	14–20
	mean ± SD :	15.67 ± 1.49	17.90 ± 0.94	16.30 ± 1.26
	N sides :	46	25	404

¹Specimens of *M. nigropunctata* living (or potentially living) in sympatry with *M. altamazonica*. See appendix.

²Abnormal supralabial scalation (ex: subocular supralabial divided; nine supralabials with the seventh being the subocular etc.).

³Parietals scales which are just in point contact behind the interparietal are not included in this category.

On the contrary, *Mabuya bistrriata* could be easily distinguished from *M. altamazonica* by its general appearance and especially by its coloration, but not by the scalation which is very similar (or partially overlapping) in both species. Even if the dorsal coloration of *M. altamazonica* is largely polymorphic, it cannot be confound with the one of *M. bistrriata*, which is highly distinctive and conservative over all its geographic range. The body coloration of *M. bistrriata* is characterised by (1) well defined dark brown lateral stripes (with darker edges), bordered at each side by a relatively large whitish stripe; and (2) two very short and thin dorsolateral stripes, only well defined from the middle of the neck to midbody (fig 5). Moreover, *Mabuya bistrriata* have cream/whitish palms and soles of the

same colour than belly (whereas they are dark in *M. altamazonica*) what probably constitute the most reliable and easily observable difference between these two species.

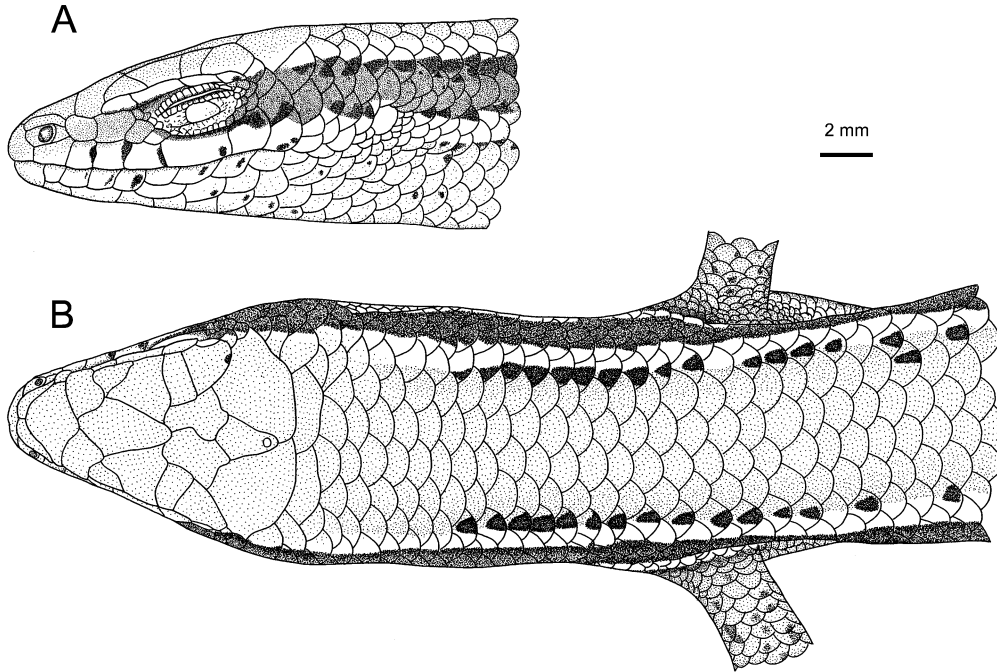


FIGURE 5. Drawings of *Mabuya bistriata* (MPEG 14561): (A) lateral view of the head and (B) dorsal view of the anterior part of the body. The drawing (A) is symmetrically reversed and represent the right side of the head ; scale bar = 2 mm.

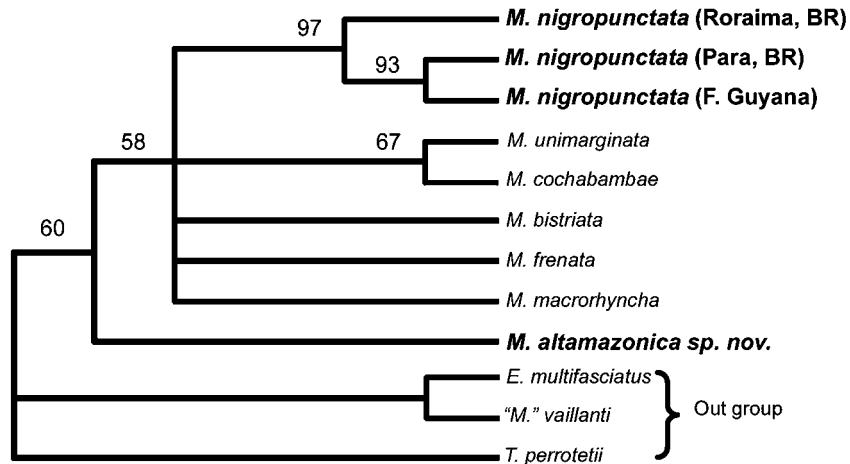


FIGURE 6. Cladogram of the maximum parsimony tree (MP) obtained from 12S sequences, with MP bootstrap values (2,000 replicates; bootstrap proportions less than 50% are not shown).

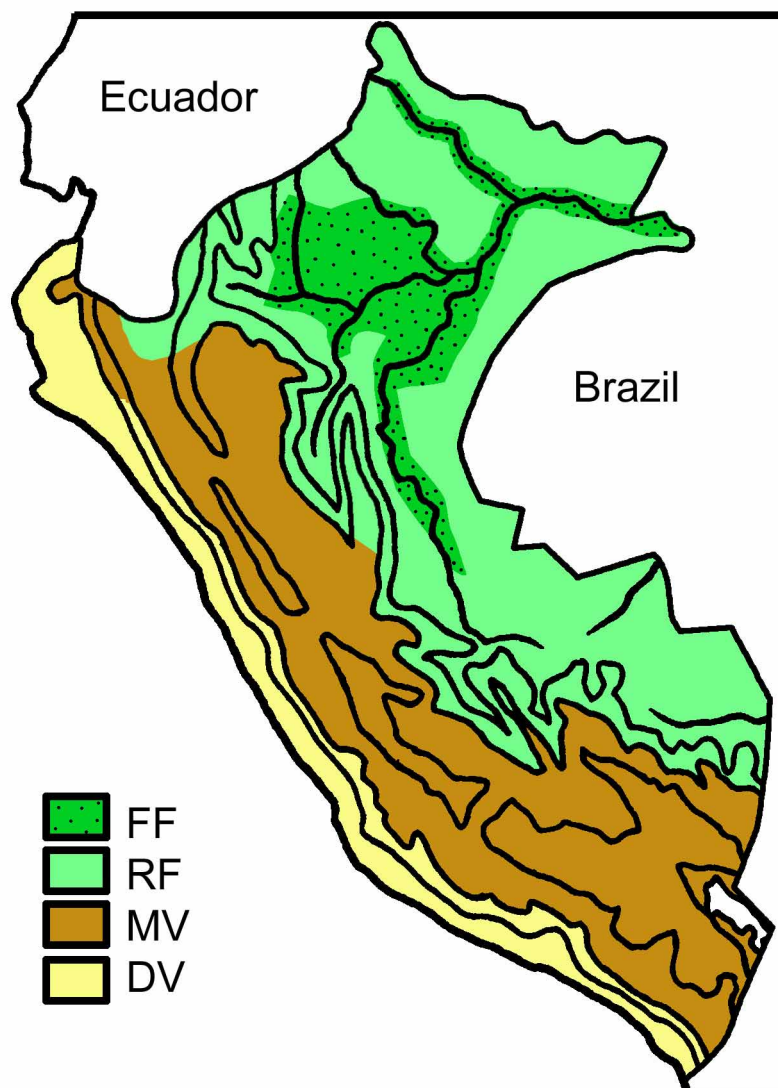


FIGURE 7. Schematic ecoregions map of Peru, simplified after Zamora (1997) and Olson & Dinerstein (2002). FF: periodically flooded rainforest (Várzea forest); RF: lowland rainforest; MV: mountain vegetation (Puna, Yunga, mountain forest etc.); DV: desert vegetation (Atacama desert).

Molecular results do not reject conclusions previously based on morphology. Despite a relative low support of the MP tree obtained (fig 6), *Mabuya altamazonica* is clearly excluded from the *M. nigropunctata* clade, whereas the monophyly of the latter is strongly supported by the bootstrap score (97%). The uncorrected pairwise distances between *M. altamazonica* and *M. nigropunctata* varied from 6.33% to 6.86%, and the distance between *M. altamazonica* and *M. bistrinata* was 5.82%. Both values are above the one observed between *M. bistrinata* and *M. nigropunctata* (4.50–4.77%). In comparison, the average interspecific distance obtained within the genus *Mabuya sensu stricto* was 5.95% (3.45–8.20%). Similar results (based on the same gene) have been obtained by Günther *et*

al. (2005) on the African genus *Trachylepis*, with a divergence of 5.14% between *T. brevicollis* and *T. dichroma*, two sister taxon morphologically very close. So, thought limited, molecular results also support the distinctiveness of *Mabuya altamazonica*.

Biogeography

Mabuya altamazonica is found both in the Marañón-Ucayali subbasin (from the confluence of Rio Ampiyacu with the upper Rio Amazonas, the Rio Napo, Rio Marañón, Rio Huallaga and running along the Rio Ucayali valley (Rio Shehua, Rio Pachitea, Rio Aguaytia, Rio Blanco and Rio Pacaya)) and the Madre de Dios subbasin (from the upper Rio Madre de Dios, Rio Manú and Rio Inambari). This pattern of distribution is shared by ten species of amphibians and two species of reptiles (Duellman 2005: 146, pattern F). According to the map of ecological regions from Peru (Zamora 1997) and the Global 200 ecoregions map of Peru (Olson & Dinerstein 2002) the distribution of *M. altamazonica* is situated along the tropical forest of the Rio Ucayali valley and in the hydromorphic tropical humid forests (also called *Várzea*, periodically flooded riverine forest) (fig 7).

Ávila-Pires (1995) mentioned the occurrence of five species of *Mabuya* in the Amazon forest. Three of them (*M. carvalhoi*, *M. guaporicola* and *M. nigropalmata*) have peripheral and restricted distributions. Only the two other species are really widespread in this region: (1) *Mabuya nigropunctata* is present everywhere in Amazonia, from the Atlantic coast to the piedmont of the Andes, and (2) *Mabuya bistrriata* has also a wide Amazonian distribution, but with the notable exception of the western part of the basin, this species having never been found in Colombia, Ecuador and Peru (fig 8).

Contrary to *Mabuya nigropunctata*, which is a species living in unflooded (*terra firme*) forest, *M. altamazonica* and *M. bistrriata* inhabit predominantly borders of large rivers and várzea forest. Moreover these two species have a remarkable complementary distribution, and there is no evidence of overlapping area (fig 8). So, we consider that such a combination of both ecological and biogeographical characteristics indicates a probable competitive exclusion between those two species (Mayr 1970). The watershed separating the Marañón-Ucayali and the Madre de Dios subbasins from the Acre subbasin (and more largely from the rest of the Amazonian basin) could represent a putative biogeographical frontier between those two parapatric species.

On the *Mabuya*-like species of Lizards described from Peru by J. J. Tschudi

In 1845, Tschudi described two species of Lizards collected in the “*Waldregion*” (litteraly “Forest region”, designated here as the Peruvian Amazonian forest). Those two species, “*Copeoglossum cinctum*” and “*Trachylepis (Xystrolepis) punctata*”, were later supposed to belong to the genus *Mabuya* (Roux 1907, Dunn 1936, Mausfeld *et al.* 2002). Unfortunately, we had not the opportunity to study the type materiel housed at the Museum of Neuchâtel (Switzerland), those specimens being in a too poor state of conservation to be loaned (B. Mulhauser, *pers. com.*). Despite this fact, we can assume here that *Mabuya altamazonica* does not fit morphologically any of those two taxa because:

(A) according to the original description and the drawing published by Tschudi (Plate

III, fig 1) and also to the very accurate redescription of the type made by Roux (1907), *Trachylepis (Xystrolepis) punctata* has a long and acuminate snout, parietals in broad contact behind the interparietal, a single pair of nuchals, keeled dorsal scales, five auricular lobules, and both white and black dots aligned on the back. Given this uncommon combination of characters, this species cannot be confounded with any known species of *Mabuya*. Dunn (1936: 557) explained that he was “unable to say what it is”. So, we believe that this binomen should probably refer to a very rare species of *Mabuya* only known from the type specimen, as it is the case for *M. nigropalmata*. However, we cannot exclude that this species belongs to an other genus of Scincidae, perhaps more closely related to the African lineages (ex. *Trachylepis*, a genus largely represented in tropical Africa, but having also colonized the Brazilian island of Fernando de Noronha) than to the genus *Mabuya sensu stricto*. Indeed, very few *Mabuya* have keeled dorsal scales, and none have auricular lobules, whereas both those characteristics are very common in the genus *Trachylepis*.

(B) the drawing of the type of *Copeoglossum cinctum* published by Tschudi (Plate III, fig 2) represents a specimen with parietals clearly separated behind the interparietals.

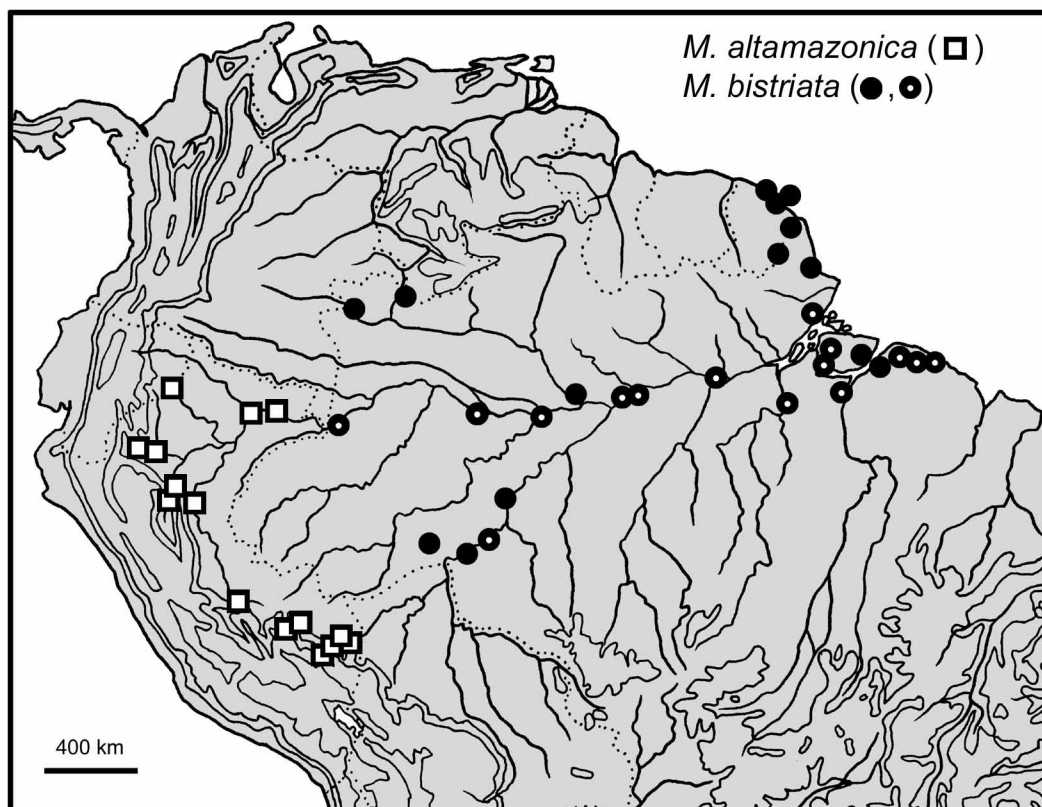


FIGURE 8. Comparative distribution map of *Mabuya altamazonica* (white square) and *M. bistrriata* (Black circle). Black circles with a white dot are localities of *M. bistrriata* based after Ávila-Pires (1995).

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Appendix. List of other examined specimens

Mabuya bistrriata (n = 26)

Brazil: AMAPÁ: CHUNB 9339, 9542, 9550, Amapá. AMAZONAS: CHUNB 32337, Humaitá; FMNH 64391, Manaus (= Manaus); MPEG 1656, 1659, Jauareté (= Iguarete, = Yaruareté), Rio Uaupés; MPEG 13816, 13819, Cucui; OMNH 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 nigropunctata (n total = 215; specimens sympatric (or potentially) with *Mabuya altamazonica* are in bold (n = 13)).

Brazil: ACRE: **OMNH 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; OMNH 37184 to 37192, Rio Ituxí, Madeirera Scheffer (8°20'S-65°43'W), coll. in march 1997 by L. J. Vitt; OMNH 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 Tucurui; OMNH 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, Alcinoópolis. 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; OMNH 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: OMNH 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,

Paraná. **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; **OMNH 36514**, Reserva faunistica 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, Peninsula de Paria.