



# A new species of *Amphisbaena* (Squamata: Amphisbaenidae) from the Orinoquian region of Colombia

Juan José Torres-Ramírez<sup>1,2</sup>, Teddy Angarita-Sierra<sup>1,3</sup>, Mario Vargas-Ramírez<sup>2,4</sup>

1 *Yoluka ONG, Fundación de Investigación en biodiversidad y conservación. Carrera 68B No. 23–88. Bogotá, Colombia*

2 *Grupo Biodiversidad y Conservación Genética, Instituto de Genética, Universidad Nacional de Colombia, Carrera 45 # 26–85, Bogotá, Colombia*

3 *Vicerrectoría de Investigación, Universidad Manuela Beltrán. Avenida carrera circunvalar # 60-00, Bogotá, Colombia*

4 *Estación de Biología Tropical Roberto Franco, Universidad Nacional de Colombia. Carrera 33 #33–76, Barrio El Porvenir, Villavicencio, Meta, Colombia*

<http://zoobank.org/EC812295-41EF-4D78-8FCD-CFB2A45DC359>

Corresponding author: Teddy Angarita-Sierra ([tgangaritas@unal.edu.co](mailto:tgangaritas@unal.edu.co))

Academic editor Uwe Fritz | Received 14 October 2020 | Accepted 4 December 2020 | Published 5 March 2021

**Citation:** Torres-Ramírez JJ, Angarita-Sierra T, Vargas-Ramírez MA (2021) A new species of *Amphisbaena* (Squamata: Amphisbaenidae) from the Orinoquian region of Colombia. *Vertebrate Zoology* 71: 55–74. <https://doi.org/10.3897/vz.71.e59495>

## Abstract

In northern South America, amphisbaenians are rarely seen among the herpetofauna. Thus, general knowledge about them is very poor. During a herpetological survey in 2012 at Casanare, Colombia, we found two specimens of an unusual *Amphisbaena*. A third specimen sharing the same morphotype labeled *Amphisbaena* sp. from Vichada department was found deposited in an Colombian reptile collection. Based on morphological analyses together with phylogenetic analyses of 1029 base pairs of the mitochondrial DNA (mtDNA), we describe a new species of *Amphisbaena* that inhabits in the Orinoquian region of Colombia. The new species is part of a phylogenetic clade together with *A. mertensii* and *A. cunhai* (central-southern Brazil), exhibiting a great genetic distance (26.1–28.9%) between the newly identified lineage versus those taxa, and versus the sympatric taxa *A. alba* and *A. fuliginosa*. Morphologically, this new *Amphisbaena* can be distinguished from their congeners by characters combination of number of preocloacal pores, absence of malar scale, postgenital scales and body and caudal annuli counts. *Amphisbaena gracilis* is on morphology grounds the most similar species. However, the new species can be distinguished from it by having higher body annuli counts, angulus oris aligned with the edges of the ocular scales and center of frontal scales, less number of large middorsal segments of the first and second body annulus, and rostral scale visible from above. The description of this new *Amphisbaena* species points out the urgent need to increase the knowledge of worm lizards in Colombia

## Keywords

burrowing habits, cryptic species, fossorial, integrative taxonomy, mtDNA, worm lizard, South America

## Introduction

Amphisbaenians are one of the most enigmatic and unusual squamates. All species have burrowing habits, but some occasionally venture onto the surface or can be

found under objects on the ground (Pough et al. 1998). Thus, due to its fossorial habit, cryptic behavior, secretive microhabitats and lower encounter rate, amphis-

baenians are considered an elusive research objective. About 102 species of the genus *Amphisbaena* Linnaeus, 1758 have been described in South America (Gans 2005; Uetz et al. 2020), with Brazil being the country with the highest diversity with over 80 species (Gans 2005; Gomes and Maciel 2012; Teixeira et al. 2014; Uetz et al. 2020).

Since Gans and Mathers (1977) early efforts to establish species boundaries between *Amphisbaena* from northern South America (sensu Eva and Huber 2005), few researchers have focused on continuing studies on the zoogeography and systematics of these uncommon reptiles (Costa et al. 2018b). The Northern South American *Amphisbaena* currently comprise eight nominal species: *A. alba* Linnaeus, 1758; *A. fuliginosa* Linnaeus, 1758; *A. medemi* Gans & Mathers, 1977; *A. spurrelli* Boulenger, 1915; *A. gracilis* Strauch, 1881; *A. rozei* Lancini, 1963; *A. stejnegeri* Ruthven, 1922 and *A. vanzolinii* Gans, 1963; all inhabiting the tropical lowland ecosystems of Panama, Colombia, Venezuela, Guyana and Surinam.

Colombia is considered to be a megadiverse country in part due to its rich fauna of around 621 species of reptiles (Uetz et al. 2020). However, worm lizards remain poorly represented in the Colombian herpetofauna due to the lack of scientific knowledge. Currently, Colombian worm lizards comprise two genera (*Mesobaena* Mertens, 1925 and *Amphisbaena* Linnaeus, 1758) and five species: *Mesobaena huebneri* Mertens, 1925; *Amphisbaena alba*, *A. fuliginosa*, *A. medemi* and *A. spurrelli*. *Amphisbaena alba* and *A. fuliginosa* (sensu Vanzolini 2002) are the most widely distributed amphisbaenids in the country; *A. alba* is restricted to the Cis-Andean region while *A. fuliginosa* is present in both Cis and Trans-Andean regions, ranging from the sea level to 1300 m. a.s.l. *Amphisbaena spurrelli* was the first amphisbaenid described in Colombia. It is distributed across the Chocó region to Panamá and its type locality corresponds to corregimiento of Andagoyá, Municipality of San Juan, department of Chocó (Boulenger 1915; Gans and Mathers 1977). *Mesobaena huebneri*, the second worm lizard species described, is only known from three disjunct and distant localities: its type locality corresponds to department of Inirida (Amazonian basin, specific locality unknown); the Timbá community, municipality of Mitú, department of Vaupés; and Serranía de la Macarena, department of Meta [specific locality unknown (Gans 1971; Cole and Gans 1987)]. Finally, *Amphisbaena medemi* was erected by Gans and Mathers 33 years ago and is the most recently described worm lizard. This species is distributed across the Caribbean region of Colombia, having as type locality the old Inderena fishing facility at Ciénaga de Amajehuevo, municipality of San Cristóbal, Atlántico.

After the early efforts made by Gans and collaborators during the 20<sup>th</sup> century, few attempts have been made to carry out a comprehensive taxonomic assessment of the *Amphisbaena* species distributed in Colombia, as well as in northern South America (Señaris 1999; Costa et al. 2018a). The most recent studies in Colombia have only provided a check list of the already known *Amphisbaena* species or distributional records obtained from field-

work, ignoring the specimens housed in museums that are waiting for a detailed revision (Rangel-Ch et al. 2012; Angarita-Sierra et al. 2013; Aponte-Gutiérrez et al. 2019; Carvajal-Cogollo 2019).

During a herpetological inventory in the department of Casanare, Colombia (Pedroza-Banda et al. 2014), we found two specimens of an unusual *Amphisbaena* from the municipalities of Paz de Ariporo and Orocué. A third specimen sharing the same morphotype seen in the *Amphisbaena* specimens from Casanare was found in the reptile collection of the Pontificia Universidad Javeriana, labeled as *Amphisbaena* sp., from the municipality of Puerto Carreño, department of Vichada. These three specimens shared unique similarities between them and did not match previous descriptions of any recognized species of the genus (Gonzalez-Sponga and Gans 1971; Gans and Mathers 1977; Gans 2005). Hence, it has become clear that these specimens represent an undescribed evolutionary lineage of amphisbaenians. Therefore, the goal of this paper is to recognize this new species and describe it by integrating molecular and morphological analyses.

## Methods

### Ethics statement

Fieldwork was performed under the scientific research permit for collection of wild specimens of biological diversity for non-commercial purpose issued by CORPORINOQUIA (Research Auto: 500.5712.0380) and the Colombian Ministry of Environment and Sustainable development (MADS) by agreement 083 of 2012. This study was conducted following the Colombian animal welfare law and the collection of wild specimens of the biological diversity acts (Ley 1774, 2016; Decreto 1376, 2013), as well as considering the Universal Declaration on Animal Welfare (UDAW) endorsed by Colombia in 2007.

### Fieldwork and sampling

Fieldwork was carried out in August 2012 in the municipalities of Paz de Ariporo and Orocué, department of Casanare, Colombia. Searches for amphisbaenians were conducted by three researchers from 8:00 to 11:30 and 14:00 to 17:00 for 15 days, with a sampling effort of 97.5 man/hours. We removed covered objects and leaf litter, digging up the ground from 5 to 15 cm deep, during three to five minutes for each event. Particularly, we included piles of palm leaves of moriche palm (*Mauritia flexuosa* L.f., 1782), as part of the microhabitats sampled. Individuals collected were immediately placed into cloth bags for later general procedures of measurement and identification as described by Pedroza-Banda et al. (2014).

## Molecular data collection and laboratory procedures

Molecular distinctiveness and phylogenetic relationships of the new species of *Amphisbaena* were assessed by analyzing molecular data corresponding to 1029 bp of the NADH dehydrogenase subunit 2 (ND2) gene, mtDNA. We assembled a data set by aligning the sequence from the new species and colombian individuals of *A. alba* and *A. fuliginosa*, with homologous sequences from the Antillean and South American amphisbaenian species published in Genbank (Table 1). The homologous ND2 sequence of the lizard species *Anolis auratus* DQ377355 was used as outgroup. Total genomic DNA was extracted using a standard phenol-chloroform method (Sambrook et al. 1989). We amplified the gene fragment using the primer pairs NADHF/NADH R and L4349/H5540 (Measey and Tolley 2013). We carried out PCRs in a total volume of 30  $\mu$ l containing one-unit Taq polymerase (Bioline; Randolph, MA), 1 X of buffer (Bioline), a final concentration of 1.5 mM MgCl<sub>2</sub> (Bioline), 0.5  $\mu$ M of each primer, 0.2 mM of each dNTP (Bioline), 0.2  $\mu$ g of bovine serum albumin (BSA) and approximately 50 ng of total DNA. We purified the PCR products using the ammonium acetate protocol (Bensch et al. 2000), and we sequenced them on an ABI 3130xl genetic analyzer (Applied Biosystems, Foster City, CA, USA) using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) at the Instituto de Genética, Universidad Nacional de Colombia. We stored the remaining DNA extractions at  $-80^{\circ}\text{C}$  in the tissue collection of the Instituto de Genética (for voucher numbers see Table 1). We performed the thermocycling conditions as indicated by Measey and Tolley (2013). The GenBank accession numbers of the obtained sequences are: MT433762, MT433763, MT433764, MT433765, MT433766 (Table 1). The sequences were edited and aligned using Chromas 1.51 (<http://www.technelysium.com.au/chromas.html>) and BioEdit 7.0.5.2 (Hall 1999).

## Phylogenetic analyses and genetic divergence

We analyzed the dataset using the unpartitioned and partitioned (i.e., we treated each codon of the protein-coding gene ND2 as distinct partitions) partition schemes. We assessed the optimal partitioning scheme and best-fit evolutionary models using Partitionfinder v1.1.1 and the Bayesian Information Criterion (Lanfear et al. 2012), resulting in the selection of the partitioned scheme. For this scheme we applied the resulting models in a Bayesian analysis with MrBayes v3.2.1 (Ronquist et al. 2012): ND2 1st and 3rd codons – GTR+I+G and ND2 2nd codon – TVM+G. We incorporated these models into a single tree search mixed model partitioning approach (Nylander et al. 2004). For this analysis, we carried out two parallel runs using four Markov chains, each starting from a random tree. We ran the Markov chains for 20 million generations. The burn-in was set to sample only the plateau of the most likely trees that were used for generating a

50% majority-rule consensus. We then used the software TRACER 1.5.4 (Rambaut and Drummond 2007) to assess an acceptable level of the MCMC chain mixing and to estimate effective sample sizes for all parameters. To assess the genetic differentiation between the new lineage and the other related *Amphisbaena* species (including the sympatric ones *A. fuliginosa* and *A. alba*), we calculated uncorrected *p* genetic distances for the ND2 gene fragment using MEGA 7.0.21 (Kumar et al. 2016).

## Morphology

We compared the collected amphisbaenians and the individual found in the collection of the Pontificia Universidad Javeriana to other preserved specimens housed in the following colombian biological collections: reptile collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN-R, Bogotá); Museo de Historia Natural, Universidad de Antioquia (MHUA, Medellín); Museo de la Universidad La Salle (MLS, Bogotá); Pontificia Universidad Javeriana (MUJ, Bogotá); Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH-R, Villa de Leyva) and the reptile collection of the Universidad Industrial de Santander (UIS-R, Bucaramanga).

We compared the pholidosis of the three specimens analyzed in this study to morphological data available in published references of the 50 nominal four pored *Amphisbaena* species, as well as to the *Amphisbaena* species that inhabit the Orinoquian region (Table 2). The definition and terminology used in the diagnosis, description and comparison sections are, as far as possible, in accordance with the broadly used descriptions of South American amphisbaenians according to Gans (1962, 1963, 1967); Gans and Mathers (1977); Vanzolini (1994); Vanzolini (2002); Teixeira et al. (2014) as follows: number of precloacal pores (P); supralabial scales (SS); infralabial scales (IS); temporal scales (TS); number of segments of the first postgenital scale row (FPG); number of segments of the second postgenital scale row (SPG); malar scales (M); number of segments of the postmalar scale row (PM); body annuli (BA); caudal annuli (CA); number of dorsal segments per annulus at midbody (DS); number of ventral segments per annulus at midbody (VS); number of segments per annulus at anterior edge of the cloaca (SAC); number of segments per annulus at posterior edge of the cloaca (SPC); number of cloacal annuli (CCA) [Cloaca annuli are those between the anterior and posterior edge of the cloaca]; autotomy sites on caudal annuli (AUC). Likewise, we followed the characters used by Gonzalez-Sponga and Gans (1971), particularly, we added to our analyses the angulus oris (i.e. the lateral limit of the oral fissure formed by junction of upper and lower lips), as well as the presence/absence or number of the large middorsal segments of the first and second body annulus.

Sex determinations were performed by direct dissections. Furthermore, we made measurements of the head scales on fixed specimens, taking digital pictures using a Zeiss Axiocam microscope camera installed on a stereo

**Table 1.** ND2 sequences of *Amphisbaena* species used in the present study.

Species	Locality	Accession number. ND2	Voucher	Source
<i>A. alba</i>	Brazil: Vilhena, Rondônia	FJ441943	CHUNB 12795	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Jalapão, Tocantins	FJ441948	CHUNB 30678	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Minaçu, Goiás	FJ441946	CHUNB 430	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Minaçu, Goiás	FJ441947	CHUNB 435	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Mariana, Minas Gerais	FJ441941	JC 795a	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Uruçuí-Una, Piauí	FJ441942	MTR 5502a	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Manso, Mato Grosso	FJ441940	MZUSP 88618	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Lajeado, Tocantins	FJ441944	MZUSP 94813	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Guarantã do Norte, Mato Grosso	FJ441949	UFMT 3468	Mott and Vieites 2009
<i>A. alba</i>	Brazil: Campo Novo dos Parecis, Mato Grosso	FJ441945	UFMT 3476	Mott and Vieites 2009
<i>A. alba</i>	Colombia: Paz de Ariporo, Casanare	MT433762	MLS 1904	This study
<i>A. anaemariae</i>	Brazil: Brasília, Distrito Federal	FJ441911	CHUNB 38647	Mott and Vieites 2009
<i>A. angustifrons</i>	Argentina: Tucuman	FJ441950	Monteiro 3	Mott and Vieites 2009
<i>A. anomala</i>	Brazil: Igarapé-Açu, Pará	FJ441955	MPEG 22139	Mott and Vieites 2009
<i>A. anomala</i>	Brazil: São Antônio de Tauá, Pará	FJ441956	MPEG 22141	Mott and Vieites 2009
<i>A. arenaria</i>	Brazil: Canudos, Bahia	KY018695	MTR23279	Teixeira et al. 2016
<i>A. bahiana</i>	Brazil: Campo Formoso, Bahia	MG028575	MZUSP106222	Dal Vechio et al. 2018
<i>A. bahiana</i>	Brazil: Campo Formoso, Bahia	MG028574	MZUSP106221	Dal Vechio et al. 2018
<i>A. bolivica</i>	Argentina: Tucuman	FJ441913	Monteiro 11	Mott and Vieites 2009
<i>A. bolivica</i>	Argentina: Salta	FJ441912	Monteiro 8	Mott and Vieites 2009
<i>A. brasiliana</i>	Brazil: Guarantã do Norte, Mato Grosso	FJ441951	UFMT3998	Mott and Vieites 2009
<i>A. caeca</i>	USA: Manati, Puerto Rico	FJ441914	MVZ 232753	Mott and Vieites 2009
<i>A. caiari</i>	Brazil: Porto Velho, Rondônia	KJ669333	MZUSP101602	Teixeira et al. 2014
<i>A. caiari</i>	Brazil: Porto Velho, Rondônia	KJ669334	MZUSP104237	Teixeira et al. 2014
<i>A. camura</i>	Brazil: Aquidauana, Mato Grosso do Sul	FJ441915	MPEG 21463	Mott and Vieites 2009
<i>A. carli</i>	Brazil: São Desiderio, Bahia	KY352335	MTR17848	Teixeira et al. 2016
<i>A. cuiabana</i>	Brazil: Campo Novo dos Parecis, Mato Grosso	FJ441938	UFMT 3545	Mott and Vieites 2009
<i>A. cuiabana</i>	Brazil: Campo Novo dos Parecis, Mato Grosso	FJ441939	UFMT 3546	Mott and Vieites 2009
<i>A. cunhai</i>	Brazil: Manaus, Amazonas	FJ441916	LSUMZH13969	Mott and Vieites 2009
<i>A. darwini</i>	Brazil: São Jerônimo, Rio Grande do Sul	FJ441936	MCP 14723	Mott and Vieites 2009
<i>A. elbakyanae</i> sp. nov.	Colombia: Paz de Ariporo, Casanare	MT433763	MLS 1901	This study
<i>A. fuliginosa</i>	Brazil	JN700169	BPN 988	Genbank
<i>A. fuliginosa</i>	Brazil: Manso, Mato Grosso	FJ441926	MTR 3177	Mott and Vieites 2009
<i>A. fuliginosa</i>	Brazil: Aripuanã, Mato Grosso	FJ441927	MZUSP 82798	Mott and Vieites 2009
<i>A. fuliginosa</i>	Peru: San Jacinto, Loreto	FJ441925	KU 222189	Mott and Vieites 2009
<i>A. fuliginosa</i>	Colombia: San Martín, Meta	MT433765	MLS 1903	This study
<i>A. fuliginosa</i>	Colombia: Bucaramanga, Santander	MT433764	UIS-R 3181	This study
<i>A. fuliginosa</i>	Colombia: Girón, Santander	MT433766	UIS-R 3724	This study
<i>A. hastata</i>	Brazil: Mocambo do Vento, Bahia	FJ441920	MTR 3555	Mott and Vieites 2009
<i>A. hastata</i>	Brazil: Mocambo do Vento, Bahia	FJ441921	MTR 3662	Mott and Vieites 2009
<i>A. ignatiana</i>	Brazil: Santo Inácio, Bahia	FJ441922	MTR 3538	Mott and Vieites 2009
<i>A. ignatiana</i>	Brazil: Santo Inácio, Bahia	FJ441923	MZUSP 93480	Mott and Vieites 2009
<i>A. kingii</i>	Brazil: São Jerônimo, Rio Grande Do Sul	FJ441969	MCP 14720	Mott and Vieites 2009
<i>A. kingii</i>	Brazil: São Jerônimo, Rio Grande Do Sul	FJ441968	MCP 14721	Mott and Vieites 2009
<i>A. kraoh</i>	Brazil: Jalapão, Tocantins	FJ441935	CHUNB 30676	Mott and Vieites 2009
<i>A. leeseri</i>	Brazil: Mateiros, Tocantins	FJ441937	CHUNB 41351	Mott and Vieites 2009
<i>A. leucocephala</i>	Brazil: Santa Maria Eterna, Bahia	KY352337	MTR33126	Teixeira et al. 2016
<i>A. leucocephala</i>	Brazil: Ilheus, Bahia	KY352336	MTR33467	Teixeira et al. 2016
<i>A. mertensii</i>	Paraguay: Itapua, Alto Vera	FJ441917	KU 290721	Mott and Vieites 2009
<i>A. mertensii</i>	Brazil: Marília, São Paulo	FJ441919	MPEG 21462	Mott and Vieites 2009
<i>A. mertensii</i>	Brazil: Campo Novo dos Parecis, Mato Grosso	FJ441918	UFMT 3469	Mott and Vieites 2009
<i>A. mitchelli</i>	Brazil: Belo Monte, Alagoas	KY018696	BM137	Teixeira et al. 2016
<i>A. munoai</i>	Brazil: São Jerônimo, Rio Grande Do Sul	FJ441930	MCP 14749	Mott and Vieites 2009
<i>A. pretrei</i>	Brazil: EEEWG, Bahia	KY352338	MTR22216	Teixeira et al. 2016
<i>A. pretrei</i>	Brazil: Salvador, Bahia	KY352339	TM262	Teixeira et al. 2016
<i>A. roberti</i>	Brazil: Lajeado, Tocantins	FJ441954	MTR 6770	Mott and Vieites 2009

Table 1 continued.

Species	Locality	Accession number. ND2	Voucher	Source
<i>A. roberti</i>	Brazil: Marília	MG028576	TM16	Dal Vechio et al. 2018
<i>A. saxosa</i>	Brazil: Lajeado, Tocantins	FJ441952	MTR 8830	Mott and Vieites 2009
<i>A. saxosa</i>	Brazil: Lajeado, Tocantins	FJ441953	MTR 8831	Mott and Vieites 2009
<i>A. schmidti</i>	USA: Puerto Rico	AY605475	MVZ 232754	Macey et al. 2004
<i>A. schmidti</i>	USA: Puerto Rico, Marchiquita	NC_006284	MVZ 232754	Macey et al. 2004
<i>A. schmidti</i>	USA, Manati, Puerto Rico	FJ441924	MVZ 232756	Mott and Vieites 2009
<i>A. silvestrii</i>	Brazil, Cuiabá, Mato Grosso	FJ441931	UFMT 3996	Mott and Vieites 2009
<i>A. silvestrii</i>	Brazil, Cuiabá, Mato Grosso	FJ441932	UFMT 3997	Mott and Vieites 2009
<i>A. uroxena</i>	Brazil, Mucuge, Bahia	MG028577	MZUSP95987	Dal Vechio et al., 2018
<i>A. uroxena</i>	Brazil, Mucuge, Bahia	MG028578	MZUSP95988	Dal Vechio et al., 2018
<i>A. vermicularis</i>	Brazil, Paranã, Tocantins	FJ441928	CHUNB 35348	Mott and Vieites 2009
<i>A. vermicularis</i>	Brazil, Paranã, Tocantins	FJ441929	CHUNB 35349	Mott and Vieites 2009
<i>A. vermicularis</i>	Brazil, Alagoado, Bahia	MG028579	MTR11246	Dal Vechio et al. 2018
<i>A. vermicularis</i>	Brazil, Santo Inacio, Bahia	MG028583	MTR11294	Dal Vechio et al. 2018
<i>A. vermicularis</i>	Brazil, Serra do Cipo, Minas Gerais	MG028580	MTR20286	Dal Vechio et al. 2018
<i>A. vermicularis</i>	Brazil, Lajeado, Tocantins	MG028582	LAJ403	Dal Vechio et al. 2018
<i>A. xera</i>	—	AY662541	—	Townsend et al. 2004
<i>Amphisbaena</i> sp.	Brazil, Pacoti, Ceara	FJ441933	MTR 169	Mott and Vieites 2009
<i>Amphisbaena</i> sp.	Brazil, Serra das Confusões, Piauí	FJ441934	SC 76	Mott and Vieites 2009

Table 2. Pholidosis comparisons between *Amphisbaena elbakyanae* sp. nov. and all the four-pored *Amphisbaena* species from South America.

Species	P	Head scales							Body and caudal scales								Source
		SS	IS	TS	FPG	SPG	M	PM	BA	CA	DS	VS	SAC	SPC	CCA	AUC	
<i>A. elbakyanae</i> sp. nov.	4	3	3	2–3	4	0	0	6–7	245–257	20–24	13–15	16–18	6–7	11–12	4	6–8	*
<i>A. alba</i> Linnaeus, 1758	4–10	4	3	5	2	2–3	1	12–15	198–248	13–21	30–42	35–46	10			Absent	1, 2, 3, 4, 5, 6
<i>A. albocingulata</i> Boettger, 1885	4	3	3					0	183–204	23–27	12–14	15–18				7–9	4, 5, 7, 8
<i>A. angustifrons</i> Cope, 1861	3–6	4	3					P	190–253	12–18	20–31	21–30				Absent	4, 5, 9
<i>A. arda</i> Rodrigues, 2003	4	4	3				1	P	242	30	23	23				8	5, 10
<i>A. arenaria</i> Vanzolini, 1991	4	3	3		P	P		0	285–307	22–23	12–14	14–16				6–7	4, 5, 6, 11, 12
<i>A. arenicola</i> Perez & Borges-Martins, 2019	4	3–4	3	2	2	3	1	6	199–216	20–22	12–14	15–18	6	11		8–9	8
<i>A. bahiana</i> Vanzolini, 1964	4	3	3						204–223	14–16	12–16	14–20				4–5	5, 13
<i>A. bedai</i> Vanzolini, 1991	4	4	3					P	272–284	22–23	18–20	16–18				6	5, 14
<i>A. bolivica</i> Mertens, 1929	2–6	3	3						200–231	18–26	27–36	26–36				3–5	4, 5, 6, 15, 16
<i>A. borelli</i> Peracca, 1897	4	3	3						239–245	17–19	14–16	16–20				6–8	5, 17
<i>A. brasiliana</i> Gray, 1865	4	3	3						213–229	11–15	18–21	18–22				Absent	5, 6, 18, 52
<i>A. camura</i> Cope, 1862	3–6	4	3						188–207	14–19	28–42	29–46				3–5	4, 5, 6, 19,
<i>A. carvalhoi</i> Gans, 1965	4	3	3					0	231–245	19–22	12–14	16–18				7–8	4, 5, 20
<i>A. cegei</i> Montero, Sáfadez & Álvarez, 1997	4	3	3		3	4–5	1	0	179–199	22	17–22	17–23	6	13–15	3–4	6–8	4, 5, 21, 22
<i>A. cuiabana</i> Strussman & Carvalho, 2001	4	3	3						286–292	18–20	14	16				9–10	5, 23
<i>A. cunhai</i> Hoogmoed & Ávila-Pires, 1991	4	3	3	2	2–3	0	1	7–9	226–239	25–26	14–16	14–18	6	7–11		5–7	4, 5, 6, 24

Table 2 continued.

Species	P	Head scales							Body and caudal scales							Source	
<i>A. darwini</i> Duméril & Bibron, 1839	2–5	3	3					P	174–199	18–25	13–19	16–23				7–10	4, 5, 8, 25, 26
<i>A. frontalis</i> Vanzolini, 1991	4	3	3					0	252–272	23–24	14–16	14–16				6–7	4, 5, 11
<i>A. fuliginosa</i> Linnaeus, 1758	6–9	2–3	3–4	3–5	2–6	5–7	1–2	10–14	196–218	24–30	19–28	21–28	7–10	10–16	3–6	4–7	1, *
<i>A. gracilis</i> Strauch, 1881	4	3	3	2	4	0	0	7–8	224–248	21–24	13–16	14–17	6	12–13	5	6–7	4, 27, 28, 29, 30
<i>A. hastata</i> Vanzolini, 1991	4	3	3						266–273	40	18	16				12–16	4, 5, 31
<i>A. heathi</i> Schmidt, 1936	4	3	3					0	183–187	32	12	18–20				7–8	4, 5, 32
<i>A. hogei</i> Vanzolini, 1950	4	3	3					P	177–191	15–19	10–13	14–18				4–7	4, 5, 8, 33
<i>A. ibijara</i> Rodrigues, Andrade & Lima, 2003	4	3	3	1	6	6	1	0	239–250	23–25	14–16	14–16				8–11	5, 34,
<i>A. kingii</i> Bell, 1833	4	3	3		P	P		P	214–244	15–23	12–19	14–22				7	5, 35, 36
<i>A. lumbricalis</i> Vanzolini, 1996	2–6	3	3					0	225–247	20–26	12–16	16–20				6–10	4, 5, 26, 37
<i>A. medemi</i> Gans & Mathers, 1977	4	3	3	2	2–3	3–5	1	9	230–235	17–18	14–16	17–18	6–8	12–17		5–7	4, 5, 30, 38
<i>A. munoai</i> Klappenbach, 1960	4	3	3	2	3	0		9	194–221	18–25	10–15	13–20	6–8	7–14		5–9	4, 5, 8, 39
<i>A. myersi</i> Hoogmoed, 1989	4	3	3						221	28	16	16				8	4, 5, 40
<i>A. nigricauda</i> Gans, 1966	0/4–5	3	3					0	192–226	19–24	9–11	13–16				6–10	4, 5, 8, 41, 42
<i>A. occidnetalis</i> Cope, 1875	4	4	3					P	261–279	18–26	16–19	22–27				9	4, 5, 43
<i>A. pericensis</i> Noble, 1921	4	3	3					0	198–218	16–19	12–16	16–20				6–8	4, 5, 44
<i>A. plumbea</i> Gray, 1872	4	4	3					P	210–283	16–21	18–27	20–30				5–9	4, 5, 45
<i>A. polygrammica</i> Werner, 1901	4	3	3		P	0			270	22	18	16				–	4, 5, 36, 46
<i>A. prunicolor</i> Cope, 1885	4	3	3	2	2	0	1	8	180–215	18–27	10–17	14–20				7–11	4, 5, 8, 47
<i>A. ridleyi</i> Boulenger, 1890	4	4	3					P	172–192	14–17	16–18	20–28				Absent	4, 5, 48
<i>A. rozei</i> Lancini, 1963	4	4	3	2	3	0	1	7	205–209	20	15–16	14				6–7	4, 5, 30, 49, 50
<i>A. sanctaeritae</i> Vanzolini, 1994	4	3	3						269		12	12				6–7	5, 51
<i>A. saxosa</i> Castro-Mello, 2003	4	4	3	2	2	0	1	8	253–272	17–21	18–24	16–21	6		4	Absent	5, 6, 52
<i>A. slateri</i> Boulenger, 1907	4	3	3–4	2	2–3	2–4	1	0–7	176–213	20–24	10–14	14–16	6–8	10–12		7–10	4, 5, 36, 53, 54
<i>A. slevini</i> Schmidt, 1936	4	2	2					0	204–211	23–25	10–14	10–12				5–6	4, 5, 32
<i>A. spurrelli</i> Boulenger, 1915	4	4	4	2	2	0	1	7	213–222	18–23	16–18	16–18	6			7	4, 5, 30, 56
<i>A. steindachneri</i> Strauch, 1881	4	3	3						256–266	17–18	14–16	16				7	5, 57
<i>A. stejneri</i> Ruthven, 1922	6	4	2						243–247	13	17–19	16–20	6			9	4, 30, 58
<i>A. supernumeraria</i> Mott, Rodrigues & Dos Santos, 2009	4	3	3	0	2	3	1	0	333–337	22–23	14	17–18				10–12	5, 59
<i>A. talisiae</i> Vanzolini, 1995	4	3	3	2	2	0	1	P	205–234	17–29	10–14	14–18	5–8	7–14		6–8	4, 5, 60, 61
<i>A. townsendi</i> Stejneger, 1911	4	4	3					P	261–279	22–26	16–19	22–27				7–8	5, 62

Table 2 continued.

Species	P	Head scales						Body and caudal scales						Source		
<i>A. trachura</i> Cope, 1885	3–4	3	3				P	168–208	15–25	14–24	16–24	6–8	9–14		5–9	8, 25, 47, 63
<i>A. tragorrhectes</i> Vanzolini, 1971	4	4	3				P	169	31	12	12				12–14	4, 5, 64
<i>A. vanzolinii</i> Gans, 1963	4	2	2					200–231	28–31	12–16	12–18				7–14	4, 24, 30, 3
<i>A. vermicularis</i> Wagler, 1824	4							211–254	23–30	18–26	18–25				6	4, 6, 65
<i>A. xera</i> Thomas, 1966	4	3	3				0	225–234	12–16	12–16	14–16				5–7	5, 30, 55

Preloacal pores (P); supralabial scales (SS); infralabial scales (IS); temporal scales (TS); number of segments of the first postgenial scale row (FPG); number of segments of the second postgenial scale row (SPG); malar scales (M); number of segments of the postmalar scale row (PM); body annuli (BA); caudal annuli (CA); number of dorsal segments perannulus at midbody (DS); number of ventral segments per annulus at midbody (VS); number of segments per annulus at anterior edge of the cloaca (SAC); number of segments perannulus at posterior edge of the cloaca (SPC); number of cloacal annuli [(CCA) Cloaca annuli are those between anterior and posterior edge of the cloaca]; autotomy sites on caudal annuli (AUC). Source: \* = This study, 1= (Linnaeus 1758), 2= (Gans 1962), 3= (Gans 1963), 4= (Vanzolini 2002), 5= (Maciel 2011), 6= (Dal Vecchio et al. 2016), 7= (Boettger 1885), 8= (Perez and Borges-Martins 2019), 9= (Cope 1861), 10= (Rodrigues 2003), 11= (Vanzolini 1991b), 12= (Teixeira et al. 2016), 13= (Vanzolini 1964), 14= (Vanzolini 1991a), 15= (Mertens 1929), 16= (Montero 2019), 17= (Peracca 1897), 18= (Gray 1865), 19= (Cope 1862), 20= (Gans 1965), 21= (Montero et al. 1997), 22= (Montero 2001), 23= (Strussman and Carvalho 2001), 24= (Hoogmoed & Ávila-Pires, 1991), 25= (Duméril and Bibron 1839), 26= (Teixeira et al. 2014), 27= (Gonzalez-Sponga and Gans 1971), 28= (Señaris 1999), 29= (Gans 1971), 30= (Gans and Mathers 1977), 31= (Vanzolini 1991c), 32= (Schmidt 1936), 33= (Vanzolini 1950), 34= (Rodrigues et al. 2003), 35= (Rojas et al. 2016), 36= (Costa et al. 2018b), 37= (Vanzolini 1996), 38= (Meza-Joya 2015), 39= (Klappenbach 1960), 40= (Hoogmoed 1989), 41= (Gans 1966), 42= (Souza e Lima et al. 2014), 43= (Cope 1875), 44= (Noble 1921), 45= (Gray 1872), 46= (Werner 1901), 47= (Cope 1885), 48= (Boulenger 1890), 49= (Lancini 1963), 50= (Costa et al. 2018a), 51= (Vanzolini 1994), 52= (Castro-Mello 2003), 53= (Boulenger 1907), 54= (Gans 1967), 55= (Thomas 1966), 56= (Boulenger 1915), 57= (Strauch 1881), 58= (Ruthven 1922), 59= (Mott et al. 2009), 60= (Vanzolini 1995), 61= (Costa et al. 2019), 62= (Stejneger 1911), 63= (Ruiz-García et al. 2016), 64= (Vanzolini 1971), 65= (Wagler 1824).

microscope Carl Zeiss model stemi 2000c and the software Image-J version 1.52 (Schneider et al. 2012). We measured the following morphometric characters: head length (HL); head width (HW); prefrontal length (PFL); prefrontal width (PFW); frontal length (FL); frontal width (FW); parietal length (PL); parietal width (PW); ocular length (OL); ocular height (OH); postocular length (POL); postocular width (POW); first temporal length (TEL); first temporal height (TEH); mental length (ML); mental width (MW); post mental length (PML); post mental width (PMW). Additionally, we took the following body size measurements using a measuring tape ( $\pm 1$  mm): snout-vent length (SVL) and caudal length (TL). We also took body diameter (BD) at mid-body using a digital caliper ( $\pm 0.01$  mm).

## Results

### Phylogenetic analyses and genetic divergence

The tree-building methods revealed *Amphisbaena elbakyanae* **sp. nov.** with robust support (BA: 0.91) as a sister taxon of a highly supported clade (BA: 0.97), comprising a specimen of *A. cunhai* Hoogmoed & Ávila-Pires, 1991 FJ441916 and specimens of *A. mertensii* Strauch, 1881 FJ441917, FJ441919, and FJ44191 (Fig. 1). Furthermore,

*A. elbakyanae* **sp. nov.** appeared evolutionarily distant from sequences belonging to individuals from the sympatric species *A. fuliginosa* and *A. alba* (Fig. 1). The uncorrected *p* distances for the ND2 gene showed that the sequence differentiation values between *Amphisbaena elbakyanae* **sp. nov.** versus *A. cunhai* and *A. mertensii* were 28.9 % and 26.1%, respectively. Furthermore, sequence differentiation values between the new species versus the individuals of the sympatric species *A. alba* and *A. fuliginosa* were 26.2% and 28.4%, respectively. The sequence divergence ranges of *A. elbakyanae* **sp. nov.** compared to other Antillean and South American taxa was 23.5–30.8% (Table 3).

### New species description

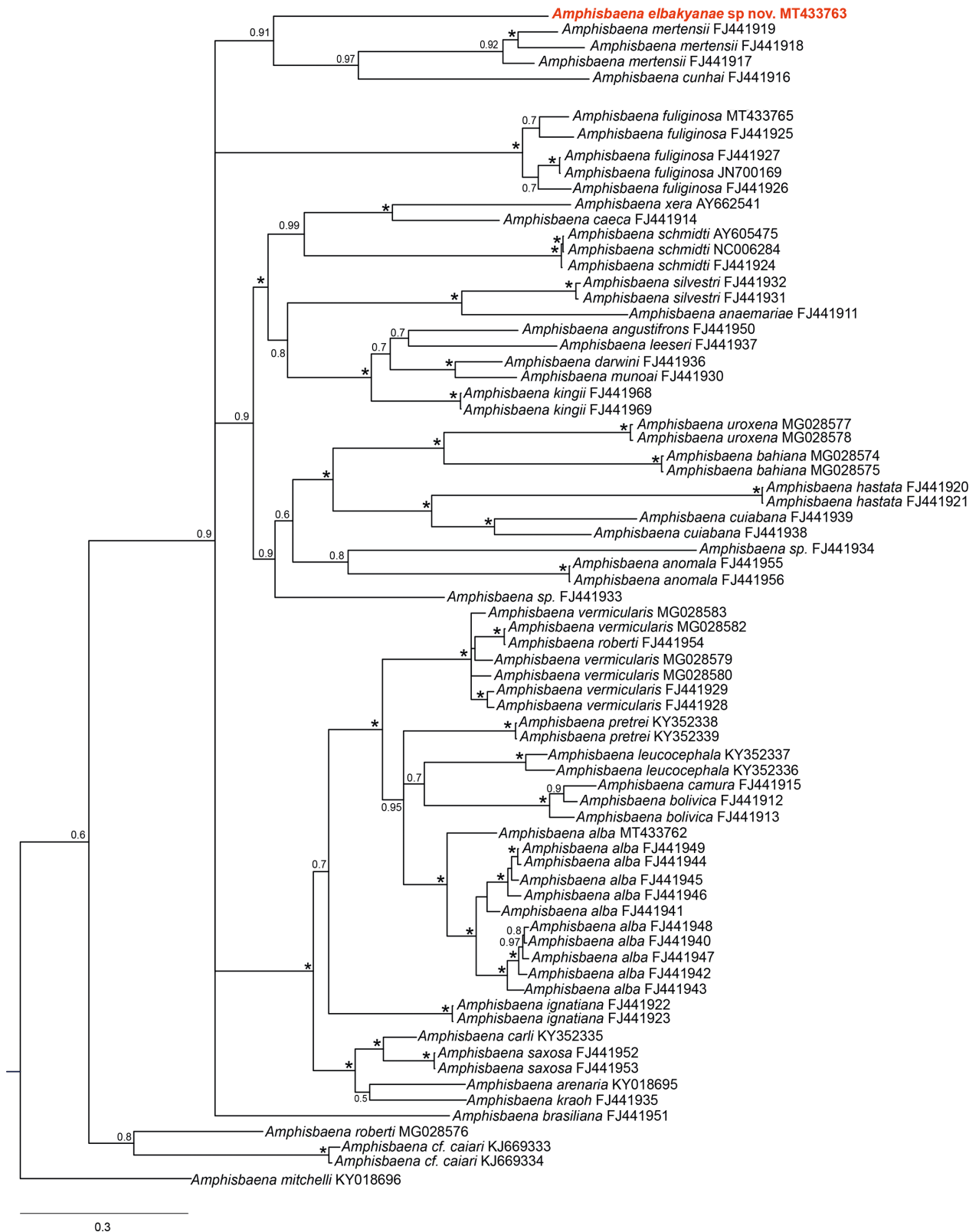
#### *Amphisbaena elbakyanae* **sp. nov.**

<http://zoobank.org/5E06051E-F7CC-4C62-8DCB-05738958-4A65>

Figs 2–4.

Chresonymy: *Amphisbaena* sp. (ICN-TAS 700): Pedroza-Banda et al. (2014).

**Holotype** (Fig. 2). Specimen MLS 1901, a male from El Porvenir farm, Vereda La Colombina, municipality of Paz de Ariporo, department of Casanare, Colombia.



**Figure 1.** Bayesian inference tree showing the evolutionary relationships of *Amphisbaena elbakyaanae* sp. nov. (red) based on 1029 bp of mitochondrial DNA. Numbers before nodes: posterior probability values. Asterisks indicate maximum support.

Coordinates: N 6.043472222, W -71.09283333; elevation 140 m. a.s.l. The specimen was collected by Teddy Angarita-Sierra, Marvin Anganoy-Criollo and John Jairo Ospina-Sarria, on 20<sup>th</sup> August 2012, in a riparian forest near the Ariporo River, under leaf litter of the moriche

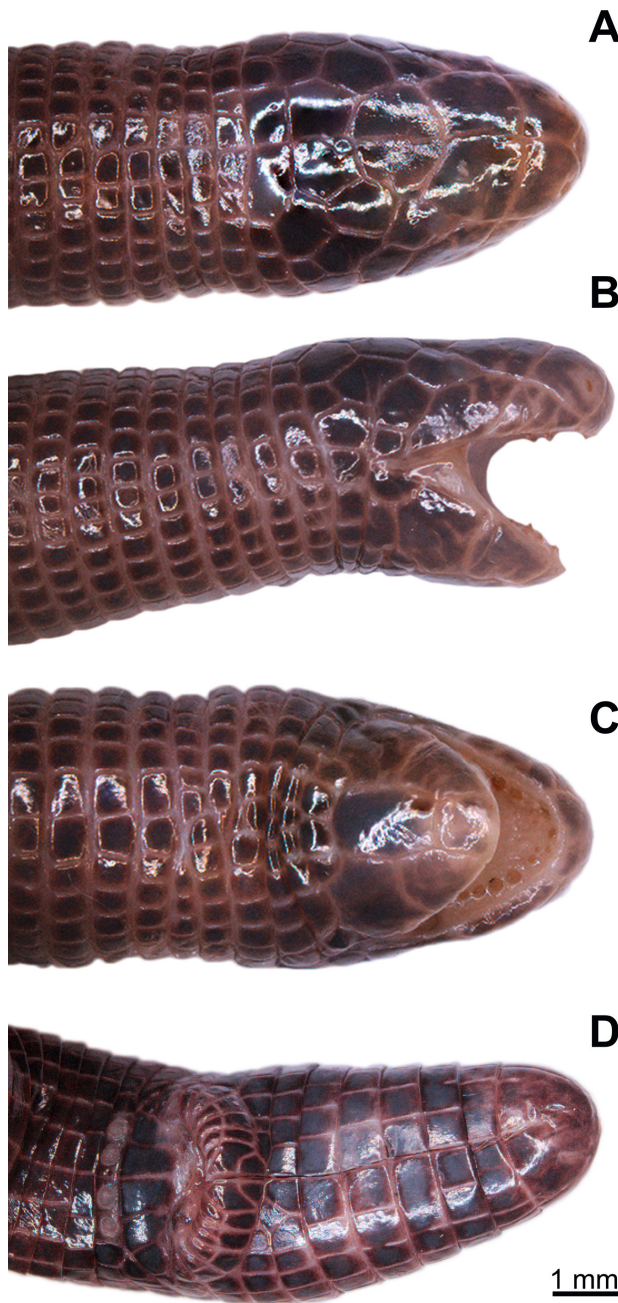
palm (*Mauritia flexuosa*). This specimen was found in sympatry with *A. alba*.

**Paratypes.** Two specimens: MUJ 806, a female from Bojonawi Natural Reserve, Fundación Omacha, municipality of Puerto Carreño, department of Vichada, Colom-



**Table 3.** Uncorrected *p* distances for the fragment of ND2 gene (763 bp) of the species of *Amphisbaena* expressed as percentages (averages). Values below the diagonal represent between lineage divergences. Bold values along the diagonal depict within lineage divergence.

Species	n	elb	alb	ful	ana	ang	ano	are	bah	bol	bra	cae	cam	car	cai	cui	cun	dar	has	ign	kin	kra	lee	leu	mer	mit	mun	pre	rob	sax	sil	sch	uro	ven				
<i>A. elbakyanae</i> sp. nov.	1	—																																				
<i>A. alba</i>	11	26.2	<b>7.2</b>																																			
<i>A. fuliginosa</i>	5	28.4	28.1	<b>7.1</b>																																		
<i>A. anaenariiae</i>	1	27.5	27.1	29.3	—																																	
<i>A. angustifrons</i>	1	28.1	25.7	29.1	24.8	—																																
<i>A. anomala</i>	2	28.7	26.6	30.1	29.2	26.2	<b>0.0</b>																															
<i>A. arenaria</i>	1	27.0	19.4	27.1	26.5	25.1	26.8	—																														
<i>A. bahiana</i>	2	30.8	30.0	30.9	29.9	29.5	28.6	30.2	<b>0.2</b>																													
<i>A. bolivica</i>	2	27.0	18.1	29.9	28.3	27.3	28.3	21.0	28.3	<b>5.8</b>																												
<i>A. brasilitana</i>	1	25.4	25.7	26.5	27.8	26.8	24.8	24.2	29.5	27.8	—																											
<i>A. caeca</i>	1	27.8	26.9	29.8	27.3	24.2	24.6	26.1	28.5	27.7	27.6	—																										
<i>A. camura</i>	1	28.7	19.1	30.1	29.7	28.7	27.9	21.8	29.1	6.8	27.9	28.7	—																									
<i>A. carli</i>	1	23.5	17.7	27.0	26.6	22.4	23.9	12.8	28.8	18.4	21.8	22.6	19.5	—																								
<i>A. cf. caiari</i>	2	29.2	28.6	29.1	29.8	27.4	31.9	28.2	30.7	27.3	28.1	28.8	28.1	25.2	<b>1.7</b>																							
<i>A. cutabana</i>	2	25.8	26.4	28.4	26.0	26.3	26.8	26.2	26.5	26.8	24.9	24.5	28.7	23.0	<b>18.1</b>																							
<i>A. cunhai</i>	1	28.9	30.4	30.3	32.8	30.9	32.8	30.3	32.7	30.1	30.3	31.2	29.8	27.0	31.3	30.4	—																					
<i>A. darwini</i>	1	28.6	24.0	29.8	24.5	18.5	26.4	26.5	27.8	27.6	27.8	23.5	28.6	23.5	27.6	24.8	31.6	—																				
<i>A. hastata</i>	2	32.7	32.7	30.8	33.4	31.1	32.3	30.9	29.8	32.3	30.8	31.2	33.1	28.7	30.8	27.2	32.8	29.7	<b>0.0</b>																			
<i>A. ignatiana</i>	2	26.5	19.4	29.0	27.8	27.0	27.9	16.3	27.6	21.6	24.2	27.2	21.8	15.3	27.5	26.1	27.5	27.6	30.5	<b>0.0</b>																		
<i>A. kangii</i>	2	27.5	24.7	29.6	23.7	17.3	25.4	25.0	28.3	26.1	24.6	23.1	27.9	21.6	27.9	24.2	30.6	16.8	29.8	27.2	0.0																	
<i>A. kraoh</i>	1	25.1	19.8	28.8	27.0	25.9	25.4	14.6	29.1	22.0	25.4	25.3	21.7	13.2	28.7	25.9	28.3	25.7	30.5	19.3	24.6	—																
<i>A. leeseri</i>	1	28.7	27.2	29.4	27.0	19.2	25.1	26.4	29.0	28.0	26.5	25.3	29.4	25.2	28.2	25.6	33.0	20.6	30.8	28.4	18.7	25.9	—															
<i>A. leucocephala</i>	2	28.2	18.0	27.8	28.6	28.0	26.5	20.6	29.5	18.9	26.5	27.0	19.3	19.3	27.9	26.3	31.4	26.9	31.8	21.4	25.0	21.4	28.4	<b>6.1</b>														
<i>A. mertensii</i>	3	26.1	26.5	30.2	30.7	27.3	28.0	26.9	29.3	27.1	27.6	28.4	27.2	23.6	29.9	28.0	25.0	28.0	32.9	24.6	27.0	26.8	29.4	26.4	<b>11.4</b>													
<i>A. mitchelli</i>	1	27.5	26.9	31.2	30.3	27.6	30.0	29.7	31.2	26.8	27.2	28.6	27.9	25.6	27.3	27.3	32.0	27.2	30.3	26.5	27.5	27.2	27.6	26.0	28.0	—												
<i>A. munoai</i>	1	29.8	25.0	29.7	27.5	19.0	25.7	25.9	27.7	28.1	28.9	24.6	28.9	24.5	30.3	25.5	31.9	11.1	30.5	27.9	17.9	26.7	20.7	26.9	29.3	28.1	—											
<i>A. pretrei</i>	2	26.5	16.4	27.3	27.5	28.0	25.9	19.7	29.4	19.1	27.1	25.8	20.2	17.1	28.9	27.6	28.3	26.7	31.2	19.4	26.4	18.9	28.3	16.9	27.0	27.8	<b>0.0</b>											
<i>A. roberti</i>	2	27.9	22.1	29.1	28.6	27.0	28.3	22.5	30.1	23.0	25.9	28.0	24.1	22.0	24.0	26.6	30.5	26.3	31.9	21.9	25.9	22.9	27.9	21.9	27.1	25.5	27.2	21.8	28.3									
<i>A. saxosa</i>	2	25.6	19.2	27.2	25.7	22.9	25.0	14.1	28.1	20.3	23.4	22.4	20.7	8.4	26.5	24.6	29.0	25.1	29.2	16.0	21.8	13.3	23.7	20.2	25.1	27.5	23.9	18.2	21.6	<b>0.0</b>								
<i>A. silvestrii</i>	2	27.6	25.5	28.3	19.4	23.7	27.2	23.8	27.7	26.5	27.6	25.8	26.8	22.0	27.2	25.3	31.6	22.7	28.9	25.1	24.3	23.8	24.4	27.9	28.5	27.8	23.9	27.9	26.5	21.6	<b>0.8</b>							
<i>A. schmidtii</i>	3	27.2	26.8	29.0	27.6	26.1	27.2	25.0	27.2	26.8	26.4	23.7	28.1	22.2	29.7	24.6	29.8	25.9	29.8	25.6	22.9	24.6	25.3	25.9	26.7	27.8	26.1	26.6	26.3	22.9	25.1	<b>0.0</b>						
<i>A. uroxena</i>	2	30.3	29.0	32.8	29.4	28.5	28.5	29.4	25.0	29.4	29.3	28.7	29.5	26.8	31.5	27.8	33.1	27.4	32.9	27.2	26.9	27.9	27.9	28.9	29.9	31.4	28.3	30.1	27.0	26.6	27.7	<b>0.5</b>						
<i>A. ventrimacularis</i>	6	27.1	16.1	27.4	26.9	26.3	27.2	17.7	29.8	18.8	25.2	27.4	19.9	17.2	27.2	24.5	30.5	25.2	31.6	16.9	25.0	19.7	27.0	18.2	25.2	26.7	26.6	18.2	16.3	18.3	24.6	24.8	28.3	<b>0.5</b>				
<i>A. xera</i>	1	29.8	26.3	29.6	27.5	25.6	25.6	25.4	27.0	28.2	25.6	19.6	29.4	23.9	28.2	25.5	32.3	25.6	30.9	25.1	24.6	26.1	25.3	26.8	26.8	28.6	24.2	28.1	26.8	22.8	26.1	23.5	27.9	25.8				



**Figure 2.** Holotype *Amphisbaena elbakyanae* sp. nov. in preservation (MLS 1901, male). (A) Dorsal view of the head; (B) Lateral view of the head; (C) Ventral view of the head; (D) Ventral view of the tail (tail is autotomized).

bia. Coordinates: N 6.097997222, W -67.48321667; elevation 54 m a.s.l., collected by Melissa Cuevas in July 2005. MLS 1902, a female from Caño El Socorro, between veredas Aguaverde and La Virgen, municipality of Orocué, department of Casanare, Colombia. Coordinates: N 5.02901, W -71.18037; elevation 128 m. a.s.l., collected by Marvin Anganoy-Criollo in December 2012, under a pile of palm leaves of moriche palm.

**Generic placement.** *Amphisbaena elbakyanae* sp. nov. belong to the genus *Amphisbaena* Linnaeus, 1758 (sensu Mertens 1925; Vanzolini 1951; Gans and Alexander 1962) by having the following characters: (1) Snout

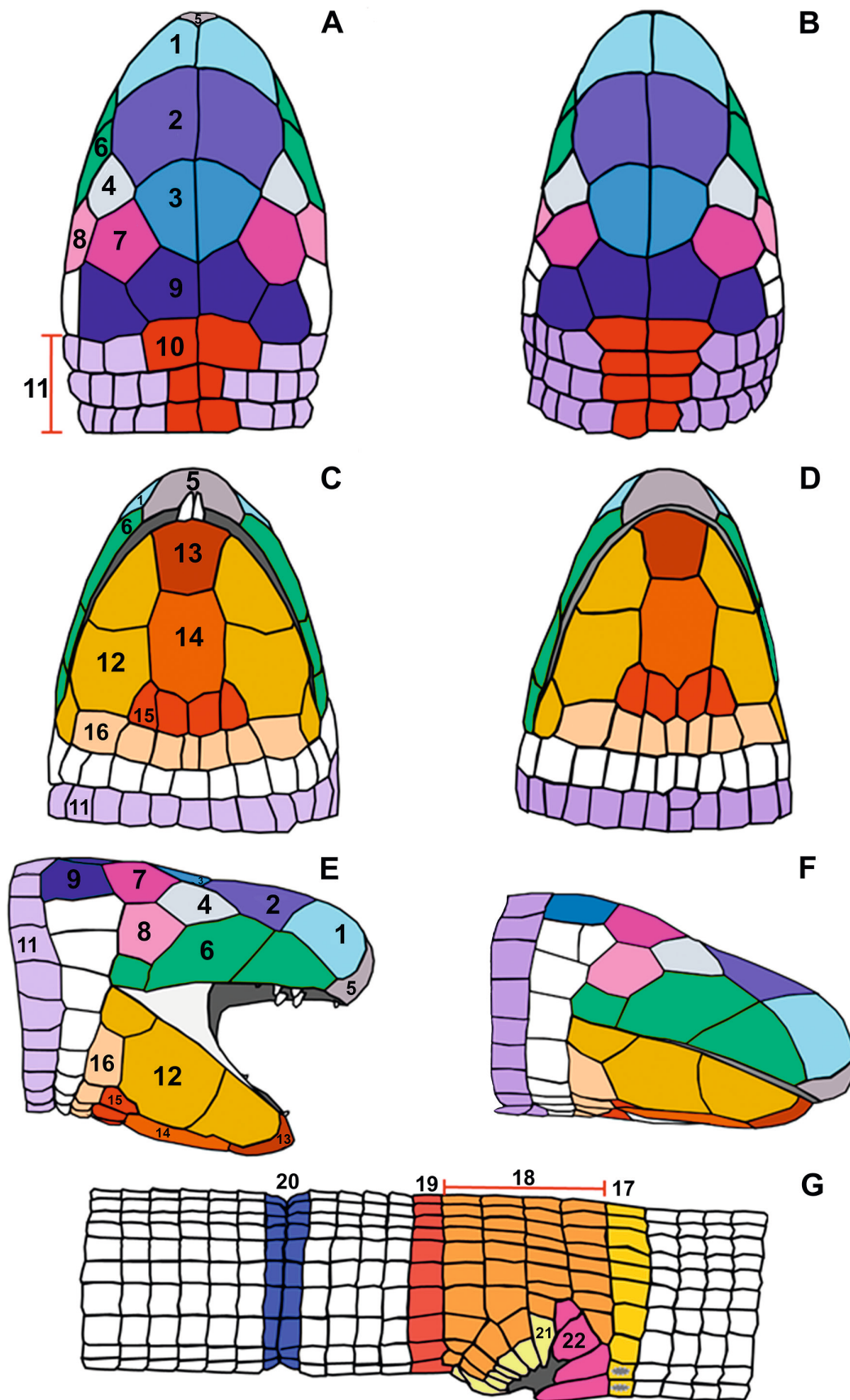
**A** rounded, flattened or slightly convex above; (2) upper head scales paired; (3) rostral scale short, subtriangular, ventrally expanded and posteriorly without contact with prefrontal scales; (4) nasal scales in broad contact; (5) six premaxillary teeth; (6) ten maxillary teeth.

**B** **Diagnosis.** *Amphisbaena elbakyanae* sp. nov., can be distinguished from all its congeners by the following combination of characters: (1) three supralabial scales; (2) three infralabial scales; (3) second supralabial scale longer than first and third supralabial scales, contacting first and third supralabial, temporal, ocular and prefrontal scales; (4) angulus oris lies in transverse plane passing through the posterior edges of the ocular scales and the center of the frontal scales; (5) second infralabial scale in contact with postmental scales; (6) six premaxillary teeth; (7) ten maxillary teeth; (8) one temporal scale; (9) absence of malar scale; (10) a single postgenial scale row with four segments; (11) postmalar scale rows with six to seven segments; (12) first body annulus includes one large segment on each side lying immediately posterior to inner parietal scales, abutting onto posterolateral edge of the outer parietal scales; (13) middorsal segments of second and third body annulus non-enlarged; (14) 245–257 body annuli; (15) 13–15 dorsal segments per annulus at mid-body; (16) 16–18 ventral segments per annulus at mid-body; (17) four precloacal pores; (18) autotomy sites located on sixth to eighth caudal annuli, (19) 20–24 caudal annuli, (20) rostral scale visible from above, (21) dorsal and ventral surfaces homogeneously dark brown or dark brown-reddish, (22), and small body size 211–237 mm (Fig. 3).

**C**

**D**

**Comparisons** (Table 2). Among all four-pored *Amphisbaena* species from South American, *Amphisbaena cunhai*, *A. frontalis*, *A. gracilis*, *A. medemi*, *A. talisiae* and *A. slateri* are the most similar species. Nonetheless, *A. elbakyanae* sp. nov. can be distinguished by having 245–257 body annuli (versus 226–239 in *A. cunhai*, 252–272 in *A. frontalis*, 224–248 in *A. gracilis*, 230–235 in *A. medemi*, 205–234 in *A. talisiae*, and 176–213 in *A. slateri*); 20–24 caudal annuli (versus 25–26 *A. cunhai*, 17–18 in *A. medemi*); a single postgenial scale row composed by four segments (versus two postgenial scale rows in *A. medemi* and *A. slateri*); absence of malar scales (versus a single malar scale in *A. cunhai*, *A. slateri* and *A. talisiae*); postmalar scale row composed by six to seven segments (versus nine segments in *A. medemi*); rostral scale visible from above (versus rostral scale non-visible from above in *A. gracilis*, Fig. 3A–B), first body annulus includes one large segment on each side lying immediately posterior to inner parietal scales, abutting onto posterolateral edge of the outer-parietal scales (versus first body annulus including two or three, large segments on each side lying immediately posterior to inner parietal scales, abutting onto posterolateral edge of the outer parietal scales in *A. gracilis*, Fig. 3A–B); middorsal segments of second and third body annuli non-enlarged (versus three or four middorsal segments of second and third body annuli enlarged in *A. gracilis*, Fig. 3A–B) and angulus oris lies in trans-



**Figure 3.** Comparison of the head scutellation between the holotypes of *Amphisbaena elbakyanae* sp. nov. and *A. gracilis*. (A, C, E) Dorsal, lateral and ventral view of the head of *A. elbakyanae* sp. nov. (B, D, F) Dorsal, lateral and ventral view of the head of *A. gracilis*. (G) Lateral view of the caudal scutellation of *A. elbakyanae* sp. nov. Scales: 1 = nasals, 2 = prefrontals, 3 = frontals, 4 = oculars, 5 = rostral, 6 = supralabials, 7 = posoclulars, 8 = temporals, 9 = parietals, 10 = middorsals segments of the body annulus, 11 = first, second and third body annulus, 12 = infralabials, 13 = mental, 14 = postmentals, 15 = postgenials, 16 = postmalars, 17 = precloacal annulus, 18 = cloacal annuli, 19 = postcloacal annulus, 20 = autotomus annulus, 21 = postcloacal lip, 22 = precloacal lip.

**Table 4.** Measurements (in mm) of holotype and paratype series of *Amphisbaena elbakyanae* sp. nov.

Trait (mm)	MLS 1901*	MLS 1902	MUJ 806
Sex	Male	Female	Female
SVL	211	237	224
TL	incomplete	27	20
BD	5.3	5.6	5.9
HL	7.1	7.0	6.4
HW	5.5	5.3	5.2
PFL	1.9	2.2	2.5
PFW	1.8	1.7	1.4
FL	1.8	2.0	1.8
FW	1.1	1.2	1.1
IPL	1.4	1.5	1.6
IPW	1.3	1.3	1.3
OPL	1.2	1.2	1.5
OPW	1.3	1.3	1.4
OL	1.6	1.3	1.2
OH	1.0	0.9	0.9
POL	1.4	1.6	1.6
POW	1.2	1.0	0.8
TEL	1.6	1.3	1.4
TEH	1.1	1.2	1.2
ML	1.2	1.4	1.3
MW	1.1	1.2	1.1
PML	2.0	1.9	1.9
PMW	1.4	1.4	1.5

Snout ventral length (SVL), caudal length (TL), head length (HL), head width (HW), prefrontal length (PFL), prefrontal width (PFW), frontal length (FL), frontal width (FW), inner parietal scales length (IPL), inner parietal scales width (IPW), outer parietal scales length (OPL), outer parietal scales width (OPW), ocular length (OL), ocular height (OH), postocular length (POL), postocular width (POW), first temporal length (TEL), first temporal height (TEH), mental length (ML), mental width (MW), postmental length (PML), postmental width (PMW). Asterisk (\*) indicates the holotype.

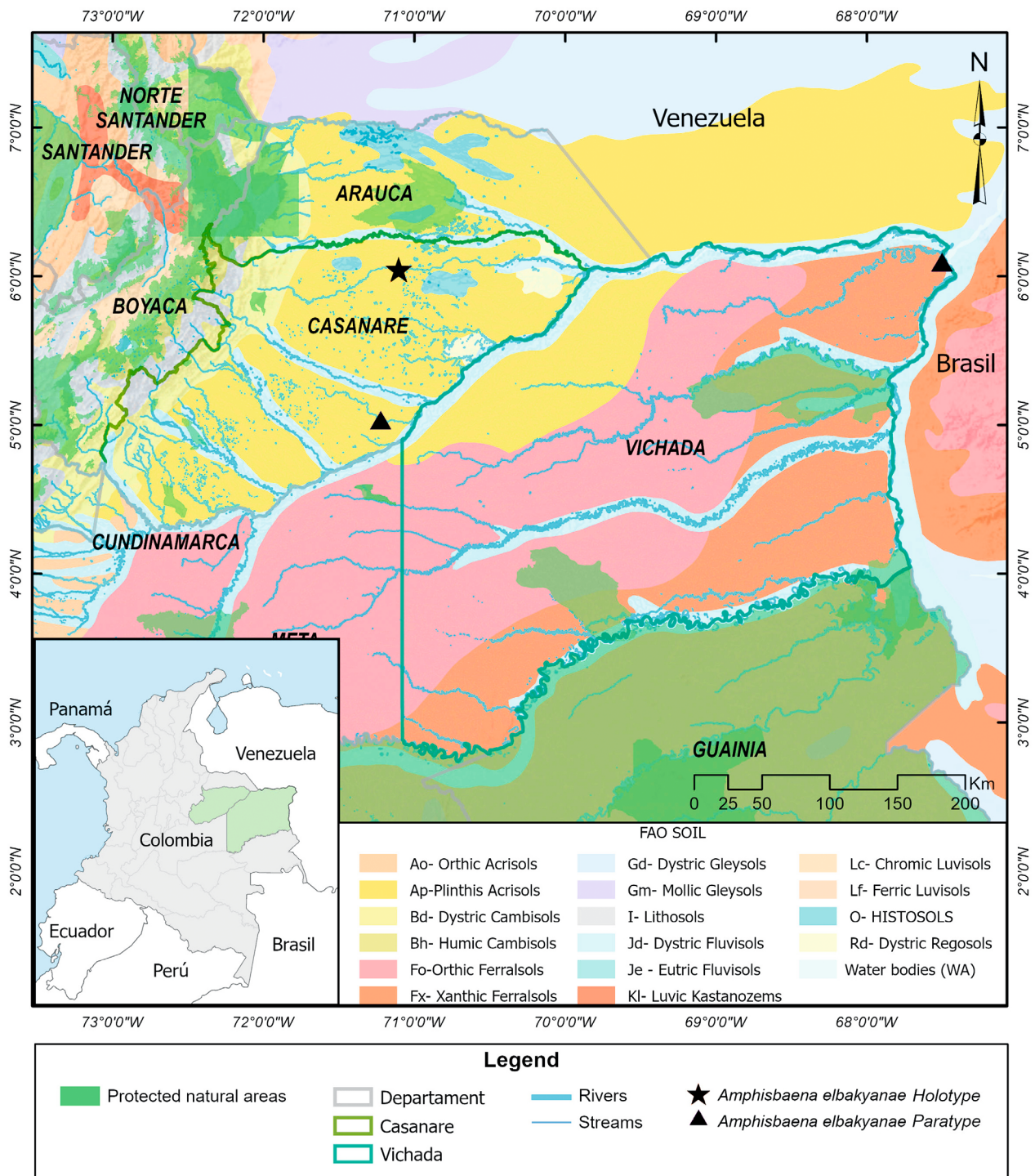
verse plane that passes through posterior edges of the ocular scales and center of frontal scales [versus angulus oris lies in transverse plane that passes through posterior edges of the postocular scales and center of parietal scales in *A. gracilis*, Fig. 3E–F (Gonzalez-Sponga and Gans 1971)]. Additionally, *Amphisbaena elbakyanae* sp. nov. can be distinguished from *A. mertensii* (one of phylogenetically closely related species, Fig. 1) by having four pre-cloacal pores and 245–257 body annuli (versus 6–8 and 210–250 in *A. mertensii*, respectively). Comparisons with the remaining four-pored *Amphisbaena* species are summarized in Table 2.

**Description of holotype** (Figs 2–4; Table 4). Male, small body size (SVL = 211 mm; TL = Incomplete tail); slender body (BD = 5.3 mm); head and body slightly differentiated by a small nuchal constriction; head longer than



**Figure 4.** Color in life of *Amphisbaena elbakyanae* sp. nov. (A) Holotype of *A. elbakyanae* sp. nov., recently euthanized (MLS 1901, male). (B) Specimen in life of *A. elbakyanae* sp. nov. from paratype locality: Bojonawi Natural Reserve, Fundación Omacha, municipality of Puerto Carreño, Vichada Department, Colombia (N 6.097997222, W - 67.48321667; elevation 54 m. a.s.l.). Photo by Beiker Castañeda.

wide (HW/HL 77.7%); snout rounded; six premaxillary teeth beginning with two large, anteromedian teeth that are flanked on either side by a posteriorly directed row of two slightly recurved teeth that gradually diminish in size; ten maxillary slightly recurved teeth that gradually diminish in size arrayed in an oblique row; rostral scale visible from above, subtriangular, ventrally expanded, wider and concave posteriorly, narrowly contacting first supralabial and broadly contacting with nasal scales; nasal, prefrontal, frontal and parietal scales from both sides contacting along the midline of the head forming a longitudinal suture (Figs 2A, 3A); nasal scale quadrangular, contacting the first supralabial, prefrontal and rostral scales; nostrils lateral in the anteroventral part of nasal scale; prefrontal scales roughly pentagonal, wider than long (PFW/PFL 92.9%), broadly contacting nasal, frontal, ocular, first and second supralabial scales, hav-



**Figure 5.** Geographic distribution of *Amphisbaena elbakyanae* sp. nov. detailing the soil type where each specimen was collected. The black star represents the holotype locality. The black triangles represent the localities of the paratypes. Background map was retrieved from the Esri open database accessing the following sources: DeLorme, USDS, NPS; USGS, NOAA.

ing a narrow contact with first supralabial scale and a broad contact with second supralabial scale (Figs 2A, 3A); frontal scales trapezoidal, longer than wide (FW/FL 63.0%), in broad contact with prefrontal, postocular and inner parietal scales and in narrow contact with ocular scale. Four parietal scales roughly pentagonal; inner parietal scales longer than wide (IPW/IPL 91.4%), in broad contact with frontal, postocular, and outer-parietal scales, as well as with the middorsal enlarged segments of the first body annulus; outer parietal scales wider than long

(OPL/OPW 91.8%), in broad contact with inner-parietal and postocular scales; first body annular non-enlarged scales, but in narrow contact with middorsal enlarged segments of the first body annulus; angulus oris lies in transverse plane that passes through posterior edges of the ocular scales and center of frontal scales (Figs 2B, 3E); three supralabial scales, first subtriangular, longer than wide in broad contact with nasal and second supralabial scales, in narrow contact with prefrontal and rostral scales; the second supralabial larger than the first one and



**Figure 6.** Habitat of *Amphisbaena elbakyanae* sp. nov. (A) Panoramic view of savanna flood forest dominated by moriche palm at the Bita River, Department of Vichada, Colombia. (B) Microhabitats inside of moriche palm's forest. (C) Moriche palm (*Mauritia flexuosa*).

third supralabial scales, contacting first and third supralabial, temporal, ocular and prefrontal scales; third supralabial scale smaller than first and second supralabial scales, contacting second supralabial, temporal and in posterior contact with first body annulus; ocular scales rhomboidal, longer than high (OH/OL 62.4%), in broad contact with prefrontal, postocular, temporal and second supralabial scales, in narrow contact with frontal scales; eye slightly visible in the anterior corner of the ocular scale; postocular scales roughly hexagonal, longer than wide (POW/POL 84.8%), broadly contacting frontal, parietal, ocular, temporal and in posterior contact with first body annulus; one temporal scale roughly pentagonal longer than wide (THE/TEL 68.1%) broadly contacting second and third supralabial and ocular scales, as well as the first body annular scales.

Mental scales quadrate, smaller and narrower than rostral scale, longer than wide (MW/ML 94.8%), in

broad contact with postmental and first infralabial scales; postmental scale oblong, longer than wide (PMW/PML 70.3%), visible longer than and in broad contact with mental scale, first and second infralabials and postgenial scale row; three infralabial scales, first trapezoidal, longer than wide and in broad contact with mental, postmental and second supralabial scales; second infralabial scale larger than first and third infralabial scales, broadly contacting first and third infralabial and postmalar scale rows; third infralabial scale smaller than first and second infralabial scales, in contact with second infralabial scale, postmalar scale row and in posterior contact with first body annulus; malar scales absent; postgenial scale row composed by four segments, in contact with second infralabial, postmental, and in posterior contact with postmalar row of scales; postmalar row of scales composed by seven segments (Figs 2C, 3C).

Body annuli demarcated; lateral and middorsal sulci present, beginning from 16<sup>th</sup> (left) or 18<sup>th</sup> (right) body annulus; 245 body annuli, 13 dorsal segments per annulus at midbody, 16 ventral segments per annulus at midbody; first body annulus with one enlarged middorsal segment on each side contacting with posterior edge of the inner parietals, abutting onto posterolateral edge of the outer parietal scales; middorsal segments of second and third body annulus non-enlarged (Figs 2A, 3A); four precloacal pores rounded; anal flap semicircular; four cloacal annuli, six caudal annuli (incomplete tail), caudal autotomy site between sixth to seventh caudal annuli (Figs 2D, 3G).

**Color of the holotype in life** (Fig. 4). Dorsal and ventral surfaces from dark brown to dark brown-reddish; occipital, parietal, frontal, temporal, third supralabial, third infralabial, postmental scales, as well as postgenial and postmalar scale rows dark brown highly pigmented; rostral, prefrontal, ocular, nasal, first and second supralabial, mental and first infralabial scales dark brown faded.

**Color of the holotype in preservative** (Fig. 2). After seven years in preservative, dorsal and ventral surfaces, as well as head scales maintained dark brown coloration having slight differences with color in life, such as a faint grey coloration on dorsal and ventral surfaces, and a few unpigmented scales.

**Etymology.** We dedicate this species to the Kazakhstani scientist Alexandra Asanovna Elbakyan (Russian: Александра Асановна Элбакян), creator of the web site Sci-Hub, for her colossal contributions for reducing the barriers in the way of science, as well as her reclamation that “everyone has the right to participate and share in scientific advancement and its benefits, freely and without economic constraints”.

**Distribution and natural history.** The known localities of *Amphisbaena elbakyanae* **sp. nov.**, are distributed in the flooded savanna ecosystem of the Orocué and Ariporo River basin, as well as in the drained savanna ecosystem of the Bitá River basin in the department of Vichada (Fig. 5). *Amphisbaena elbakyanae* **sp. nov.** seems to be highly associated with the leaf litter of the savanna flood forest dominated by moriche palm (*Mauritia flexuosa*), which are commonly known as “morichales” or “cananguales” in Colombia (Fig. 6). The new species was found in sympatry with *A. alba* and *A. fuliginosa*.

## Discussion

In this research, molecular and morphological evidence allowed us to confirm that *Amphisbaena elbakyanae* **sp. nov.** represents a new species of amphisbaenian from northern South America (sensu Eva and Huber 2005). Our phylogenetic analysis suggests that *Amphisbaena elbakyanae* **sp. nov.** together with *A. cunhai* and *A. mer-*

*tensii* from central-southern Brazil, is part of the same monophyletic clade (Fig. 1). However, great genetic distances for the ND2 gene fragment were revealed between *Amphisbaena elbakyanae* **sp. nov.** versus *A. cunhai* and *A. mertensii* (28.9% and 26.1%, respectively). Currently, molecular data of several species from northern South America is lacking (e.g. *A. medemi*, *A. spurrelli*, *A. gracilis*, *A. vanzolinii*, and *A. steinegeri*), limiting the understanding of the evolutionary relations of northern-South American amphisbaenians. Therefore, it is crucial to include many more taxa, to formulate a complete phylogenetic hypothesis that may reduce spurious phylogenetic relationships, basal polytomies and poorly supported nodes (Teixeira et al. 2014). Despite the scarcity of the molecular data, our analyses revealed that the new taxon is not closely related to the sympatric species *A. alba* or *A. fuliginosa* (Fig. 1), confirmed by the great genetic distances between them (Table 3). The morphological evidence analyzed allowed us to clearly diagnose *Amphisbaena elbakyanae* **sp. nov.** as a different lineage compared to the 50 nominal four pored *Amphisbaena* species, demonstrating that it was an undescribed species of worm lizard from Colombia.

Furthermore, both molecular and morphological evidence agreed with Gans and Mathers (1977) group’s division of the amphisbaenians from northern South America: The first group included two larger and wide-ranging species (*A. alba* and *A. fuliginosa*), and the second group comprised six smaller narrow-ranging species (*A. gracilis*, *A. medemi*, *A. rozei*, *A. spurrelli*, *A. steinegeri* and *A. vanzolinii*). Based on the morphological characters of *Amphisbaena elbakyanae* **sp. nov.**, this taxon can be allocated into Gans and Mathers’ second group. Interestingly, *Amphisbaena elbakyanae* **sp. nov.**, exhibited a close morphological similarity with both closely distributed taxon (e.g. *A. gracilis*) and geographically distant taxa (e.g. *A. cunhai*, *A. frontalis*, *A. talisiae* and *A. slateri*). Moreover, *Amphisbaena elbakyanae* **sp. nov.** and *A. gracilis* are the continental worm lizards that seem to have the greatest affinity with the Antillean *Amphisbaena* species by showing a lack of malar scales, four precloacal pores, relatively small size and uniform dorsal and ventral pigmentation. Additionally, *A. elbakyanae* **sp. nov.** together with *A. gracilis* and *A. medemi* are the only forms of the northern mainland that have fewer dorsal rather than ventral segments to a midbody annulus closely resembling the Antillean *Amphisbaena* species (Gans and Alexander 1962; Gonzalez and Gans 1971; Gans and Mathers 1977).

This situation leaves open the question of whether such morphological similarities are due to evolutionary ancestry or could be due to convergent evolution of characters, a product of adaptation to similar habitats (Harmon et al. 2005; Edwards et al. 2012). Some authors have claimed that parallelism, understood as the independent evolution of similar traits, starting from a similar ancestral condition, could be another possibility for morphological similarities between *Amphisbaena* species (Mott and Vieites 2009). Vidal et al. (2008) dated the split between African and South American Amphisbaenidae at 40 Mya ago (Eocene), proposing that transatlantic dispersal from Africa

to South America + West Indies could explain this divergence. According to Gonzalez and Gans (1971), the West Indies species may be the ancestors of the northern South American *Amphisbaena* species. Consequently, the similarities between some Antillean and South American species may have resulted from the retention of a primitive character pattern in a zone geographically peripheral to the range of the genus. Although we cannot assess directly Gonzalez-Sponga and Gan's hypothesis, the distant evolutionary relationship between *Amphisbaena elbakyanae* **sp. nov.** and the Antillean species *A. caeca* and *A. xera* revealed by our phylogenetic and genetic distance analyses (Fig. 1; Table 3), as well as the distant relationships showed by Pyron et al. (2013; Fig 12K) between *A. cunhai* and *A. mertensii* (species that form a monophyletic clade together with *Amphisbaena elbakyanae* **sp. nov.**) and the Antillean species (i.e. *A. bakeri*, *A. caeca*, *A. cubana*, *A. fenestrata*, *A. manni*, *A. schmidtii* and *A. xera*), suggest that recent evolutionary ancestry may not be the cause of the morphological similarities. Those and many more questions concerning northern South American worm lizards remain open, evidence that the state of knowledge for many fields is still extremely fragmentary.

## Conclusions

*Amphisbaena elbakyanae* **sp. nov.**, described as a new species from the Orinoquia savanna ecosystem of Co-

lombia, seems to be related to *A. cunhai* and *A. mertensii* from central-southern Brazil. This species of *Amphisbaena* is one of the several still-unrecognized evolutionary lineages of worm lizards that are deposited in Colombian museum shelves waiting to be described. We think that the lack of worm lizard studies in Colombia is derived from three main factors. First, insufficient funding for field and museum research; second, large areas still lack intensive sampling and third, there are few investigators searching for worm lizards and few experts and trained personnel capable of describing species (Gascon et al. 2007; Ospina-Sarria and Angarita-Sierra 2020). Therefore, the description of this new *Amphisbaena* species points out the urgent need to generate a research grant program that could support field surveys and research on several disciplines to increase our knowledge of worm lizards, as well as help to train researchers to describe species including the known but yet-undescribed species currently housed in Colombian biological collections. Studies of taxonomy and species descriptions in a megadiverse country like Colombia play a substantial role in the conservation of our natural heritage. Thus, encouraging these activities will allow an evaluation of biodiversity loss and the development of systematic conservation planning and practices, as well as a scientific focus on value judgments that make up environmental policies and laws.

## Key to the Colombian worm lizard species

- (1) Snout prognathous; rostral scale large, elongate and coniform in broad contact with prefrontal scales, separating nasal scales ..... (Genus *Mesobaena*) *Mesobaena huebneri*
- Snout non-prognathous; rostral scale short, subtriangular, ventrally expanded and posteriorly without contact with prefrontal scales; nasal scales in broad contact (Genus *Amphisbaena*) ..... **2**
- (2) Robust body; 30–42 dorsal segments per annulus at midbody, 35–46 ventral segments per annulus at midbody, caudal autotomy absent ..... *Amphisbaena alba*
- Robust or thin body, less than 29 dorsal and ventral segments per annulus at midbody, caudal autotomy present ... **3**
- (3) Robust body; 19–28 dorsal segments per annulus at midbody, 21–28 ventral segments per annulus at midbody; 6–9 preloacal pores, postmalar scale row composed by 10–14 segments ..... *Amphisbaena fuliginosa*
- Thin body, four preloacal pores, postmalar scale row composed by 6–9 segments ..... **4**
- (4) 245–257 body annuli, 13–15 dorsal segments per annulus at midbody, three supralabial and infralabial scales ..... *Amphisbaena elbakyanae* **sp. nov.**
- Less than 244 body annuli ..... **5**
- (5) 230–235 body annuli, 14–16 dorsal segments per annulus at midbody, three supralabial and infralabial scales ..... *Amphisbaena medemi*
- 213–222 body annuli, 16–18 dorsal segments per annulus at midbody, four supralabial and infralabial scales ..... *Amphisbaena spurrelli*

## Acknowledgments

We thank John Jairo Ospina-Sarria, Marvin Anganoy-Criollo and Juan Carlos Gómez (Chigüi) for their help and support during the fieldwork.

We give special thanks to Esperanza Parales, who hosted us in her farm (El Porvenir) during the fieldwork. We thank Rebeca Morantes-Zamora for her help with the distribution map. We thank Beiker Castañeda, Brayan Marín, Carlos Lasso, as well as Fundación Omacha for pro-



vide us a photograph of specimen in life of *Amphisbaena elbakyanae* from Bojonawi Natural Reserve. We also thank the researchers of the Biodiversity and Conservation Genetics Group of the Genetics Institute, National University of Colombia for their assistance in the DNA lab. We thank Martha Calderón-Espinosa and John D. Lynch (ICN), Julio Mario Hoyos (MUJ), Andres R. Acosta-Galvis (IAVH), Fernando Sarmiento-Parra and Julieth S. Cardenas-Hincapie (MLS), Juan Manuel Daza (MHUA), Matha Patricia Ramirez and Elson Meneses-Pelayo (UIS) for allowing us to examine specimens of *Amphisbaena* under their care.

## References

- Angarita-Sierra T, Ospina-Sarria JJ, Anganoy-Criollo M, Pedroza-Banda R, Lynch JD (2013) Guía de campo de los Anfibios y Reptiles del departamento de Casanare (Colombia). Serie Biodiversidad para la Sociedad No. 2. YOLUKA ONG, Fundación de Investigación en Biodiversidad y conservación; Universidad Nacional de Colombia, Bogotá, 117 pp.
- Aponte-Gutiérrez AF, Niño-Cárdenas IL, Arias-Escobar A, Lynch JD (2019) Diversidad de anfibios y Reptiles en la región de la Serranía de Manacías, Municipio de San Martín, Meta, Orinoquía Colombia. In: Rangel-Ch OJ, Andrade-C MG, Jarro-F C, Santos-C G (Eds) Colombia diversidad biótica XVII: La región de la Serranía de Manacías (Meta), Orinoquía colombiana. Universidad Nacional de Colombia, Bogotá, 431–448.
- Bensch S, Stjernman M, Hasselquist D, Ostman O, Hansson B, Westerdahl H, Pinheiro RT (2000) Host specificity in avian blood parasites: a study of *Plasmodium* and *Haemoproteus* mitochondrial DNA amplified from birds. *Proceedings of the Royal Society of London B* 7: 1583–1589. <https://doi.org/10.1098/rspb.2000.1181>.
- Boettger O (1885) Liste von Reptilien und Batrachiern aus Paraguay. *Zeitschrift für Naturwissenschaften* 58: 213–248. <https://www.biodiversitylibrary.org/part/69906#/summary>.
- Boulenger GA (1890) Reptilia. In: Ridley HN, Notes on the zoology of Fernando Noronha. *Journal of the Linnean Society* 20: 481–482. <https://doi.org/10.1111/j.1096-3642.1886.tb02243.x>
- Boulenger GA (1907) Descriptions of new lizards in the British Museum. *Annals and Magazine of Natural History* 7(19): 486–489. <https://doi.org/10.1080/00222930709487278>
- Boulenger GA (1915). Descriptions of a new *Amphisbaena* and a new snake discovered by Dr. H. G. F. Spurrell in southern Colombia. *Proceedings Zoological Society of London* 1915: 659–661. <https://www.biodiversitylibrary.org/part/69958#/summary>
- Carvajal-Cogollo JE (2019) Biología de los anfibios y reptiles en el bosque seco tropical del norte de Colombia. In: Vargas-Salinas F, Uñoz-Avila JA, Morales-Puentes ME (Eds) Catálogo de anfibios y reptiles de Colombia. Editorial UPTC, Tunja: 97–162.
- Castro-Mello C (2003) Nova espécie de *Bronia* Gray, 1845, do estado do Tocantins, Brasil (Squamata: Amphisbaenidae). *Papéis Avulsos de Zoologia* 43: 139–143. <https://doi.org/10.1590/S0031-1049200-3000700001>
- Cole CJ, Gans C (1987) Chromosomes of *Bipes*, *Mesobaena*, and other amphisbaenians (Reptilia) with comments on their evolution. *American Museum Novitates* 2869: 1–9. <http://hdl.handle.net/2246/5205>
- Cope ED (1861) Some remarks defining the following species of Reptilia Squamata. *Academy of Natural Sciences of Philadelphia* 1861: 75–76. <https://www.biodiversitylibrary.org/part/10878#/summary>
- Cope ED (1862) Catalogues of the reptiles obtained during the Explorations of the Parana, Paraguay, Vermejo and Uruguay Rivers, by Capt. Thos. J. Page, U.S.N.; and of those procured by Lieut. N. Michler, U.S. Top. Eng., Commander of the Expedition conducting the survey of the Atrato River. *Proceedings of the Academy of Natural Sciences of Philadelphia* 14: 346–359. <https://www.biodiversitylibrary.org/part/16874#/summary>
- Cope ED (1875) Report on the Reptiles brought by Professor James Orton from the middle and upper Amazon and western Peru. *Journal of the Academy of Natural Sciences of Philadelphia* 2: 159–183. [https://archive.org/details/cbarchive\\_55553\\_copeed1876reportonthereptilesb1952/page/n3/mode/2up](https://archive.org/details/cbarchive_55553_copeed1876reportonthereptilesb1952/page/n3/mode/2up).
- Cope ED (1885) Twelfth contribution to the herpetology of tropical America. *Proceedings of the American Philosophical Society* 22: 167–194. <https://www.jstor.org/stable/982675>
- Costa HC, Graboski R, Zaher H (2019) *Amphisbaena mensae* Castro-Mello, 2000 is a synonym of *Amphisbaena talisiae* Vanzolini, 1995 (Squamata: Amphisbaenia: Amphisbaenidae). *Zootaxa*, 4559: 166–174. <https://doi.org/10.11646/zootaxa.4559.1.7>
- Costa HC, Senáris JC, Rojas-Runjaic FJM, Zaher H, Garcia PCA (2018a) Redescription of the rare South American worm lizard *Amphisbaena rozei* (Squamata: Amphisbaenidae). *Amphibia Reptilia* 39: 21–30. <https://doi.org/10.1163/15685381-00003136>
- Costa HC, Welton LJ, Hallermann J (2018b) An updated diagnosis of the rare *Amphisbaena slateri* Boulenger, 1907, based on additional specimens (Squamata, Amphisbaenia, Amphisbaenidae). *Evolutionary Systematics* 2: 125–135. <https://doi.org/10.3897/evolsyst.2.28059>
- Dal Vechio FD, Teixeira M, Mott T, Rodrigues MT (2018) Rediscovery of the poorly known *Amphisbaena bahiana* Vanzolini, 1964 (Squamata, Amphisbaenidae), with data on its phylogenetic placement, external morphology and natural history. *South American Journal of Herpetology* 13: 238–248. <https://doi.org/10.2994/SA-JH-D-16-00053.1>
- Dal Vechio F, Teixeira M, Sena M, Argôlo A, Garcia C, Rodrigues MT (2016) Taxonomic status and the phylogenetic placement of *Amphisbaena leucocephala* Peters, 1878 (Squamata, Amphisbaenidae). *South American Journal of Herpetology* 11: 157–175. <https://doi.org/10.2994/SAJH>
- Duméril AM, Bibron G (1839) *Erpétologie générale ou histoire naturelle complète des reptiles*. Vol. 5. Roret, Paris, 880 pp.
- Edwards S, Vanhooydonck B, Herrel A, Measey GJ, Tolley KA (2012) Convergent evolution associated with habitat decouples phenotype from phylogeny in a clade of lizards. *PLoS One* 7: 1–9. <https://doi.org/10.1371/journal.pone.0051636>
- Eva HD, Huber O (2005) A proposal for defining the geographical boundaries of Amazonia. Office for Official Publications of the European Communities, Luxembourg, 53 pp.
- Gans C (1962) Notes on amphisbaenids (Amphisbaenia, Reptilia), 5. A redefinition and a bibliography of *Amphisbaena alba* Linne. *American Museum Novitates* 2105: 1–31. <http://hdl.handle.net/2246/3410>
- Gans C (1963) Notes on amphisbaenids (Amphisbaenia, Reptilia), 8. A redescription of *Amphisbaena stejneri* and the description of a new species of *Amphisbaena* from British Guinea. *American Museum Novitates* 2128: 1–18. <http://hdl.handle.net/2246/3374>
- Gans C (1965) On *Amphisbaena heathi* Schmidt and *A. carvalhoi*, new species, small forms from the northeast of Brazil (Amphisbaenia: Reptilia). *Proceedings of the California Academy of Sciences* 4th Series 31: 613–630. <https://archive.org/details/biostor-545>

- Gans C (1966) Studies on amphisbaenids (Amphisbaenia, Reptilia). 3. The small species from southern South America commonly identified as *Amphisbaena darwini*. Bulletin of the American Museum of Natural History 134: 185–260. <http://hdl.handle.net/2246/1983>
- Gans C (1967) Redescription of *Amphisbaena slateri* Boulenger, with comments on its range extension into Bolivia. Herpetologica 23: 223–227. <https://www.jstor.org/stable/3890860>
- Gans C (1971) Redescription of three monotypic genera of amphisbaenians from South America: *Aulura* Barbour, *Bronia* Gray, and *Mesobaena* Mertens. American Museum Novitates 2475: 1–32. <http://hdl.handle.net/2246/2683>
- Gans C (2005). Checklist and Bibliography of the Amphisbaenia of the World. Bulletin of the American Museum of Natural History 289: 1–130 [https://doi.org/10.1206/0003-0090\(2005\)289<0001:cabota>2.0.co;2](https://doi.org/10.1206/0003-0090(2005)289<0001:cabota>2.0.co;2)
- Gans C, Alexander A (1962) Studies on amphisbaenids (Amphisbaenia, Reptilia), 2. On the amphisbaenids of the Antilles. Bulletin of the Museum of Comparative Zoology 128: 65–148. <https://www.biodiversitylibrary.org/part/29249#/summary>
- Gans C, Mathers S (1977) *Amphisbaena medemi*, an interesting new species from Colombia (Amphisbaenia, Reptilia), with a key to the amphisbaenians of the Americas. Fieldiana Zoology 72: 21–46. <https://www.biodiversitylibrary.org/bibliography/5131#/summary>
- Gascon C, Collins JP, Moore RD, Church DR, McKay JE, Mendelson JR (2007) Amphibian Conservation Action Plan (III). IUCN/ SSC Amphibian Specialist Group, Gland, Switzerland and Cambridge, UK, 64 pp.
- Gomes JO, Maciel AO (2012) A new species of *Amphisbaena* Linnaeus (Squamata, Amphisbaenidae) from the state of Maranhão, northern Brazilian Cerrado. Zootaxa 54: 43–54 <https://doi.org/10.11646/zootaxa.3572.1.6>
- Gonzalez-Sponga MA, Gans C (1971) *Amphisbaena gracilis* Strauch rediscovered (Amphisbaenia: Reptilia). Copeia 1971: 589–595. <https://doi.org/10.2307/1442627>
- Gray JE (1865) A revision of the genera and species of amphisbaenians with the descriptions of some new species now in the collection of the British Museum. Proceedings Zoological Society of London 16: 442–455. <https://www.biodiversitylibrary.org/part/61439#/summary>
- Gray JE (1872) Catalogue of shield reptiles in the collection of the British Museum. Part II. Emydosaurians, rhynchocephalians, and amphisbaenians. British Museum (Natural History), London, 41 pp.
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. In Nucleic Acids Symposium Series 41: 95–98. <https://www.scienceopen.com/document?vid=8b59b929-3c37-49f6-936b-f8bf6dd92ace>
- Harmon LJ, Kolbe JJ, Cheverud JM, Losos JB (2005) Convergence and the multidimensional niche. Evolution 59: 409–421. <https://doi.org/10.1111/j.0014-3820.2005.tb00999.x>
- Hoogmoed MS (1989) A new species of *Amphisbaena* (Amphisbaenia: Amphisbaenidae) from Suriname. Notes on the herpetofauna of Suriname. Uitgaven Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen 123: 65–73.
- Hoogmoed MS, Ávila-Pires TCS (1991) A new species of small *Amphisbaena* (Reptilia: Amphisbaenia: Amphisbaenidae) from western Amazonian Brazil. Boletim do Museu Paraense Emilio Goeldi Serie Zoologia 7: 77–94. <http://repositorio.museu-goeldi.br/handle/mgoeldi/740>
- Klappenbach M (1960) Notas herpetológicas, I. *Amphisbaena munoai* n. sp. (Amphisbaenidae). Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo 4: 3. <https://lib.ugent.be/catalog/ejn01:110975506068969>
- Kumar S, Stecher G, Tamura K (2016) Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Lancini AR (1963) Una nueva especie del género *Amphisbaena* (Sauria: Amphisbaenidae) de Venezuela. Publicaciones Museo de Ciencias Naturales de Caracas (Zoología) 6: 1–3. <https://eurekamag.com/research/024/071/024071190.php>
- Lanfear R, Calcott B, Ho SY, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701. <https://doi.org/10.1093/molbev/mss020>
- Linnaeus, C. (1758). Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I (Editio decima). Laurentius Salvius, Holmia, 823 pp.
- Maciel RP (2011) Revisão do status taxonômico de *Amphisbaena prunicolor* (Cope, 1885) e *Amphisbaena albocingulata* Boettger, 1885 (Amphisbaenia: Amphisbaenidae). PhD thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre.
- Macey JR, Papenfuss TJ, Kueh JVI, Fourcade HM, Boore JL (2004) Phylogenetic relationships among amphisbaenian reptiles based on complete mitochondrial genomic sequences. Molecular Phylogenetics and Evolution 33: 22–31. <https://doi.org/10.1016/j.ympev.2004.05.003>
- Measey GJ, Tolley KA (2013) A molecular phylogeny for sub-Saharan amphisbaenians. African Journal of Herpetology 62: 100–108. <https://doi.org/10.1080/21564574.2013.824927>
- Mertens R (1925) Eine neue EidechsenGattung aus der Familie der Leposterniden. Senckenbergiana 7: 170–171.
- Mertens R (1929) Herpetologische Mitteilungen. XXIII. Über einige Amphibien und Reptilien aus Süd-Bolivien. Zoologischer Anzeiger 86: 57–62.
- Meza-Joya FL (2015) New records of *Amphisbaena medemi* Gans & Mathers, 1977 (Squamata: Amphisbaenidae) from the Caribbean region of northern Colombia. Check List 11: 10–12. <https://doi.org/10.15560/11.1.1526>
- Montero R (2001) *Amphisbaena cegei*. Catalogue of American Amphibians and Reptiles 726: 1–3. <https://ri.conicet.gov.ar/handle/11-336/78671>
- Montero R (2019) Universo Tucumano 38 – *Amphisbaena bolivica* (Montero). In: Srocchi GJ, Szumik C (Eds) Universo Tucumano. Fundación Miguel Lillo y Unidad Ejecutora Lillo, Tucuman, 21 pp.
- Montero R, Sáfadez IF, Álvarez LG (1997) A new species of *Amphisbaena* from Bolivia. Journal of Herpetology 31: 218–220. <https://www.jstor.org/stable/1565389>
- Mott T, Rodrigues MT, Dos Santos EM (2009) A new *Amphisbaena* with chevron-shaped anterior body annuli from state of Pernambuco, Brazil (Squamata: Amphisbaenidae). Zootaxa 58: 52–58. <https://doi.org/10.5281/zenodo.189069>
- Mott T, Vieites DR (2009) Molecular phylogenetics reveals extreme morphological homoplasy in Brazilian worm lizards challenging current taxonomy. Molecular Phylogenetics and Evolution 51: 190–200. <https://doi.org/10.1016/j.ympev.2009.01.014>
- Noble GK (1921) Two new lizards from northwestern Peru. Annals of the New York Academy of Sciences 29: 141–143. <https://doi.org/10.1111/j.1749-6632.1920.tb55354.x>

- Nylander JA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey J (2004) Bayesian phylogenetic analysis of combined data. *Systematic Biology* 53: 47–67. <https://doi.org/10.1080/10635150490264699>
- Ospina-Sarria JJ, Angarita-Sierra T (2020) A new species of *Pristimantis* (Anura: Strabomantidae) from the eastern slope of the Cordillera Oriental, Arauca, Colombia. *Herpetologica* 76: 83–92. <https://doi.org/10.1655/Herpetologica-D-19-00048>
- Pedroza-Banda R, Ospina-Sarria JJ, Angarita-Sierra T, Anganoy-Criollo M, Lynch JD (2014) Estado del conocimiento de la fauna de anfibios y reptiles del departamento de Casanare, Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 38(146): 17–34. <https://doi.org/10.18257/raccefyn.37>
- Peracca MG (1897) Rettili e Anfibi. Viaggio del Dott. Alfredo Borelli nel Chaco boliviano e nella Repubblica Argentina. *Bollettino dei Musei di Zoologia* 12(274): 1–19.
- Perez R, Borges-Martins M (2019) Integrative taxonomy of small worm lizards from Southern South America, with description of three new species (Amphisbaenia: Amphisbaenidae). *Zoologischer Anzeiger* 283: 124–141. <https://doi.org/10.1016/j.jcz.2019.09.007>
- Pough FH, Andrews R, Cadle JE, Crump ML, Savitzky AH, Wells KD (1998) *Herpetology*. Prentice-Hall, Upper Saddle River, NJ, 544 pp.
- Pyron R, Burbrink FT, Wiens JJ (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 1471–2148. <https://doi.org/10.1186/1471-2148-13-93>
- Rambaut A, Drummond AJ (2007) Tracer v1.4. <http://beast.bio.ed.ac.uk/software/tracer>
- Rangel-Ch OJ, Aguirre-Ceballos J, Carvajal JE (2012) La Biodiversidad de Municipios del Caribe de Colombia. Instituto de Ciencias Naturales Universidad Nacional de Colombia, Bogotá, 713 pp.
- Rodrigues MT (2002) Herpetofauna of the quaternary sand dunes of the checkerboard patterned *Amphisbaena* (Squamata, Amphisbaenidae). *Phyllomedusa* 1: 51–56. <https://doi.org/10.11606/issn.2316-9079.v1i2p51-56>
- Rodrigues MT, Andrade GV, Lima JD (2003) A new species of *Amphisbaena* (Squamata, Amphisbaenidae) from state of Maranhão, Brazil. *Phyllomedusa* 2: 21–26. <https://doi.org/10.11606/issn.2316-9079.v2i1p21-26>
- Rojas Murcia LE, Cabrejo Bello JA, Carvajal Cogollo JE (2016) Reptiles from the seasonal dry forest of the Caribbean region: distribution of habitat and use of food resource. *Acta Biologica Colombiana* 21: 365–377. <https://doi.org/10.15446/abc.v21n2.49393>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Ruiz-García JA, Curi LM, Lamas MF, Céspedes JA (2016). *Amphisbaena trachura* Cope, 1885 (Amphisbaenia: Amphisbaenidae): new record for the northeast of Argentina José. *Check List* 12: 10–13. <https://doi.org/10.15560/14949>
- Ruthven AC (1922) A new species of *Amphisbaena* from British Guiana. *Occasional Papers of the Museum of Zoology University of Michigan* 122: 1–2. <http://hdl.handle.net/2027.42/56561>
- Sambrook J, Fritsch EF, Maniatis T (1989) *Molecular cloning: a laboratory manual* (No. Ed. 2). Cold Spring Harbor Laboratory Press, Cold Spring Harbor, 1659 pp.
- Schmidt KP (1936) Notes on Brazilian amphisbaenians. *Herpetologica* 1: 28–32. <https://doi.org/10.2307/3889998>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*. 9(7):671–675. <https://doi.org/10.1038/nmeth.2089>
- Señaris JC (1999) Contribution to the taxonomic and ecologic knowledge of *Amphisbaena gracilis* Strauch, 1881 (Squamata: Amphisbaenidae) in Venezuela. *Memoria de la Fundación La Salle de Ciencias Naturales* 152: 115–120.
- Souza e Lima FA, Gasparini JL, Almeida AP, Vital MV, Mott T (2014) Dimorfismo sexual em *Amphisbaena nigricauda* (Reptilia, Squamata, Amphisbaenidae) do Sudeste do Brasil. *Iheringia Serie Zoologia* 104: 299–307. <https://doi.org/10.1590/1678-476620141043299307>
- Stejneger L (1911) Description of a new amphisbaenoid lizard from Peru. *Proceedings of the United States National Museum* 41: 283–284. <https://doi.org/10.5479/si.00963801.1856.283>
- Strauch A (1881) Bemerkungen über die Eidechsenfamilie der Amphisbaeniden. *Bulletin de l'Académie impériale des Sciences de St.-Petersbourg* 11: 355–479.
- Strussman C, Carvalho MA (2001) Two new species of *Cercolophia* Vanzolini, 1992 from the state of Mato Grosso, western Brazil (Reptilia, Amphisbaenia, Amphisbaenidae). *Bulletin Museo Regionale di Scienze Naturali Torino* 18: 487–505.
- Teixeira M, Dal Vechio F, Neto AM, Rodrigues MT (2014) A new two-pored *Amphisbaena* Linnaeus, 1758, from Western Amazonia, Brazil (Amphisbaenia: Reptilia). *South American Journal of Herpetology* 9: 62–74. <https://doi.org/10.2994/sajh-d-14-00004.1>
- Teixeira M, Vechio FD, Rodrigues MT (2016) Diagnostic clarification, new morphological data and phylogenetic placement of *Amphisbaena arenaria* Vanzolini, 1991 (Amphisbaenia, Amphisbaenidae). *Zootaxa* 4205: 293–296. <https://doi.org/10.11646/zootaxa.4205.3.9>
- Thomas R (1966) Additional notes on the amphisbaenids of Greater Puerto Rico. *Breviora* 249: 1–23. [https://mczbase.mcz.harvard.edu/SpecimenUsage.cfm?action=search&publication\\_id=10619](https://mczbase.mcz.harvard.edu/SpecimenUsage.cfm?action=search&publication_id=10619)
- Uetz P, Freed P, Hošek J (2020) Reptile Database. Reptile Database News, August 2020. <http://www.reptile-database.org/>
- Townsend TM, Larson A, Louis E, Macey M (2004) Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology* 53:735–757. <https://doi.org/10.1080/10635150490522340>
- Vanzolini EP (1950) Contribuições ao conhecimento dos lagartos Brasileiros da família Amphisbaenidae Gray, 1825. I. Sobre uma nova subespecie insular de *Amphisbaena darwini* D. and B., 1839. *Papéis Avulsos de Zoologia* 9: 69–77.
- Vanzolini EP (1951) *Amphisbaena fuliginosa*. Contribution to the knowledge of the Brazilian lizards of the family Amphisbaenidae Gray, 1825. 6, On the geographical distribution and differentiation of *Amphisbaena fuliginosa*. *Bulletin of the Museum of Comparative Zoology* 106: 1–67.
- Vanzolini EP (1964) *Amphisbaena bahiana* species nov. In: Brown P (Ed.) *Pilot Register of Zoology*. Cornell University, Ithaca, 1.
- Vanzolini EP (1971) New Amphisbaenidae from Brasil. *Papéis Avulsos de Zoologia* 24: 191–195.
- Vanzolini EP (1991a) A third species of *Bronia* Gray, 1865 (Reptilia, Amphisbaenia). *Papéis Avulsos de Zoologia* 37: 379–388.
- Vanzolini EP (1991b) Two further new species of *Amphisbaena* from the semi-arid northeast of Brasil (Reptilia, Amphisbaenia). *Papéis Avulsos de Zoologia* 37: 347–361.
- Vanzolini EP (1991c) Two new small species of *Amphisbaena* from the fossil dune field of the middle Rio São Francisco, State of Bahia, Brasil (Reptilia, Amphisbaenia). *Papéis Avulsos de Zoologia* 37: 259–276.

- Vanzolini EP (1994) New species of *Amphisbaena* from State of Sao Paulo, Brasil. *Papéis Avulsos de Zoologia* 39: 29–32.
- Vanzolini EP (1995) A new species of *Amphisbaena* from the state of Mato Grosso, Brasil (Reptilia: Amphisbaenia: Amphisbaenidae). *Papéis Avulsos de Zoologia* 39: 217–221.
- Vanzolini EP (1996) On slender species of *Amphisbaena*, with the description of a new one from northeastern Brasil (Reptilia, Amphisbaenia). *Papéis Avulsos de Zoologia* 39: 293–305.
- Vanzolini EP (2002) An aid to the identification of the South American species of *Amphisbaena* (Squamata, Amphisbaenidae). *Papeis Avulsos de Zoologia* 42: 351–362. <http://dx.doi.org/10.1590/S0031-10492002001500001>
- Vidal N, Azvolinsky A, Cruaud C, Hedges SB (2008) Origin of tropical American burrowing reptiles by transatlantic rafting. *Biology Letters* 4: 115–18. <https://doi.org/10.1098/rsbl.2007.0531>
- Wagler J (1824) *Serpentum brasiliensium species novae ou Histoire Naturelle des espèces nouvelles de serpens, recueillis et observées pendant le voyage dans l'intérieur du Brésil dans les années 1817, 1818, 1819, 1820 executé par ordre de Sa Majesté le Roi de Bavière, publiée par Jean de Spix, écrite d'après les notes du voyageur.* FS Hübschmann, Monachium, VIII, 75 pp., errata, 26 pls. <https://www.biodiversitylibrary.org/bibliography/4269#/summary>
- Werner F (1901) Reptilien und Batrachier aus Peru und Bolivien. *Abhandlungen und Berichte des Königlichen Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden* 9(2): 1–14. <https://www.biodiversitylibrary.org/part/144760#/summary>