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ARTICLE

A new species of *Bolitoglossa* (Amphibia: Plethodontidae) from the central highlands of Guerrero, Mexico

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Abstract: We describe a new species of salamander of *Bolitoglossa* (*Oaxakia*) Parra-Olea, García-París and Wake, 2004 from the cloud forests of the central portion of the Sierra Madre del Sur highlands in the Mexican state of Guerrero. ***Bolitoglossa coaxtlahuacana*** sp. nov. is currently known only from the type locality and can be differentiated from other members of the group by morphological, coloration, and molecular evidence. With the description of this new taxon, the number of species in the subgenus *Oaxakia* increases to six.

Key words: Bolitoglossa coaxtlahuacana, salamander, Sierra Madre del Sur, taxonomy.

Résumé : Nous décrivons une nouvelle espèce de salamandre du sous-genre *Bolitoglossa* (*Oaxakia*) Parra-Olea, García-París et Wake, 2004, des forêts de nuages de la partie centrale des hautes terres de la Sierra Madre del Sur, dans l'État mexicain de Guerrero. ***Bolitoglossa coaxtlahuacana*** sp. nov. n'est actuellement connu que de la localité type et peut être distingué d'autres membres du groupe sur la base d'observations morphologiques, moléculaires et relatives à la coloration. La description de ce nouveau taxon fait passer le nombre d'espèces dans le sous-genre *Oaxakia* à six. [Traduit par la Rédaction]

Mots-clés : Bolitoglossa coaxtlahuacana, salamandre, Sierra Madre del Sur, taxonomie.

Introduction

The Mexican state of Guerrero, although long recognized to harbor an important herpetological diversity, has been less studied when compared with adjoining regions or when considering sampling bias over general distribution patterns of amphibian and reptile species (Palacios-Aguilar and Flores-Villela 2018). Plethodontid salamanders are a good example of how this diversity has been long neglected. During the better part of the last century, the salamander fauna of Guerrero was believed to consist of only one species (*Isthmura belli* (Gray, 1850) (Bell's False Brook Salamander); Günther 1902; Gadow 1905) until Papenfuss et al. (1983) described *Bolitoglossa hermosa* (Guerreran Mushroomtongue Salamander), a member of the *Bolitoglossa macrinii* species group, although *Thorius* Cope, 1862 (Mexican Pigmy Salamanders) specimens were previously reported by Adler (1965). Subsequently, other species of the genera *Pseudoeurycea* Taylor, 1944 (False Brook Salamanders) (Adler 1996) and *Thorius* (Hanken et al. 1999) were described or recorded from the Sierra Madre del Sur and the Trans-Mexican Volcanic Belt portions of the state (Flores-Villela and Hernández-García 1989), increasing the known salamander fauna for the state to 12 described species. During the last two decades, a few new species have been described and additional species have been reported for the state (Pérez-Ramos and Saldaña de la Riva 2003; Campbell et al. 2013, 2014) bringing the total number of described species of plethodontids in Guerrero to 15.

During recent fieldwork in the highlands of central Guerrero, we discovered an isolated population of salamanders of the *B. macrinii* species group (subgenus *Oaxakia*) that upon revision proved to be an unnamed taxon which we describe herein.

Materials and methods

Specimens collected were fixed in 10% buffered formalin, preserved in 70% ethanol, and deposited in the herpetological collection of the Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC). Tissue samples were stored in non-denatured 96% ethanol. Species descriptions follow the format used by Lynch and Wake (1989) for species of Neotropical plethodontids and include the same basic characters and measurements, including coloration and external measurements. We used an electronic Vernier caliper to measure 10 characters: snout–vent length (SVL), tail length (TL), axilla–groin distance (AX), forelimb length (FLL), hind-limb length (HLL), snout to gular fold distance (SG), head length (HL), head width at angle of jaw (HW), shoulder width (SW), internarial distance (IN), and right-foot width (FW). We also counted ankylosed premaxillary (PMT), maxillary (MT), and vomerine (VT) teeth. We present counts for PMT and MT together because of the difficulty in distinguishing them in some specimens. We also measured limb interval (LI) as the number of costal folds between appressed limbs. Positive values equal the number of folds visible between appressed limbs that do not meet or overlap; negative values denote overlap between limbs. We only collected morphological data for males because only males were found for the new species. Finally, 12 additional measurements were obtained for each holo-

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Table 1. Specimen voucher numbers and GenBank accession numbers occupied in the phylogenetic analyses of the salamander genus *Bolitoglossa*.

Species	Voucher	GenBank *16S*	GenBank *cytb*
Bolitoglossa coaxtlahuacana; Coaxtlahuacán Salamander	MZFC 32895	MN567669	MN560182
	MZFC 32896	MN567670	MN560183
Bolitoglossa dofleini (Werner, 1903); Alta Verapaz Salamander	MVZ 161607	AF218497.1	AF212988.1
Bolitoglossa hartwegi Wake and Brame, 1969; Hartweg's Mushroomtongue Salamander	MVZ 263458	KC288004.1	KC288103.1
Bolitoglossa hermosa Papenfuss, Wake and Adler, 1984; Guerreran Mushroomtongue Salamander	MVZ 163690	AF416686.1	AF416678.1
	MVZ 143804	AF416685.1	—
Bolitoglossa macrinii (Lafrentz, 1930); Oaxacan Mushroomtongue Salamander	CNAR 13800	AF416689.1	AF416680.1
	MVZ 158524	AF416688.1	—
	MVZ 158523	AF416687.1	—
Bolitoglossa mexicana Duméril, Bibron and Duméril, 1854; Mexican Mushroomtongue Salamander	MVZ 176839	GU725457.1	GU725470.1
Bolitoglossa morio (Cope, 1869); Cope's Mushroomtongue Salamander	MVZ 257825	GU725452.1	GU725465.1
Bolitoglossa oaxacensis Parra-Olea, García-París and Wake, 2002; Atoyac Salamander	CNAR 13374	AF416690.1	AF416681.1
Bolitoglossa riletti Holman, 1964; Rilett's Mushroomtongue Salamander	MVZ 146774	AF416691.1	—
	MVZ 146775	AF416692.1	—
	MVZ 146777	AF416693.1	—
	MVZ 146778	AF416695.1	—
	MVZ 146767	AF416694.1	—
	MVZ 194328	AF416696.1	AF416682.1
Bolitoglossa rufescens (Cope, 1869); Northern Banana Salamander	MVZ 194333	AY526116.1	AY526159.1
Bolitoglossa subpalmata (Boulenger, 1896); La Palma Salamander	MVZ 229172	AF416697.1	AF212094.1
Bolitoglossa zapoteca Parra-Olea, Garcia-Paris and Wake, 2002; Zapotec Salamander	CNAR 13375	AF416698.1	AF416683.1
	CNAR 13376	AF416699.1	AF416684.1

Note: Museum abbreviations listed in order of appearance within the table are MZFC (Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México), MVZ (Museum of Vertebrate Zoology), and CNAR (Colección Nacional de Anfibios y Reptiles, Universidad Nacional Autónoma de México).

type examined: anterior rim of orbit to snout (snout length), eyelid length, eyelid width, horizontal orbital diameter (eye diameter (ED)), interorbital distance, length of third (longest) toe, length of fifth toe, projection of snout beyond mandible, snout to forelimb, tail depth at base, and tail width at base. We measured most representatives of *Bolitoglossa* (*Oaxakia*) (Appendix A) with the exception of *Bolitoglossa oaxacensis* (Atoyac Salamander) because the male specimen deposited at the Colección Nacional de Anfibios y Reptiles, Universidad Nacional Autónoma de México, (CNAR 13374) could not be located and is presumed lost, and data on the male paratypes were not available. We have used the data on males of this species reported by Parra-Olea et al (2002) for comparisons.

Molecular methods

Genomic DNA was extracted from liver samples using a DNeasy kit (Qiagen, Valencia, California, USA). Polymerase chain reactions (PCR) were performed using the primers 16Sar and 16Sbr for the 16S ribosomal RNA (*16S*) gene (Palumbi et al. 1991), and MVZ15 and MVZ16 for the cytochrome *b* (*cytb*) gene (Moritz et al. 1992). PCR conditions were as follow — *16S*: an initial cycle of 5 min at 94 °C, followed by 35 cycles of 45 s at 94 °C, 30 s at 55 °C, 45 s at 72 °C, plus a final cycle of 3 min at 72 °C; *cytb*: an initial cycle of 2 min at 94 °C, followed by 38 cycles of 30 s at 94 °C, 1 min at 48 °C, 1 min at 72 °C, plus a final cycle of 8 min at 72 °C. PCR products were cleaned with ExoSap-IT (USB Corporation) and sequenced in both directions using the original amplification primers and BigDye termination reaction chemistry (Applied Biosystems). The cycle-sequencing products were column-purified with Sephadex G-50 (GE Healthcare) and run on an ABI 3500xL Genetic Analyzer (Applied Biosystems).

Phylogenetic analysis

GenBank sequences of all members of the *B. macrinii* species group (subgenus *Oaxakia*) used by Parra-Olea et al. (2002) were downloaded and compared with the small data set that we have generated for this study, as well as species of other subgenera of *Bolitoglossa* Duméril, Bibron and Duméril, 1854 used as outgroups (Table 1). All sequences used were aligned to each other by eye using the program PhyDE. The best fitting evolutionary model was determined using Akaike's information criterion in the software jModelTest (Darriba et al. 2012). Analyses were performed using Bayesian analyses and carried out in the program Mr. Bayes (Ronquist et al. 2012) and consisted of four simultaneous runs, each with four chains (three heated and one cold), sampled every 1000 trees. We ran it for 30 000 000 generation discarding the first 25% of the trees as burn in and visualized the output in the software TRACER version 1.7.0 (Drummond and Rambaut 2007) to verify that the independent runs had converged. Genetic distances (Kimura 2 parameters) were computed using MEGA7 (Kumar et al. 2016).

Results

The morphological data showed that the population from central Guerrero is diagnosable from most members of the *B. macrinii* group based on color pattern and measurements (Table 2). Also, the Bayesian analysis supported the distinctiveness of this population and its close relationship with *Bolitoglossa riletti* (Rilett's Mushroomtongue Salamander) and *B. hermosa*. Based on this evidence, we consider this population to be an unnamed taxon that we describe below.

Bolitoglossa coaxtlahuacana sp. nov.

Coaxtlahuacán Salamander, Salamandra de Coaxtlahuacán

ZOOBANK NO.: urn:lsid:zoobank.org:pub:D44E5B35-88B9-4F66-8C9C-238211F1B354.

HOLOTYPE: MZFC 32985 (field number RPA 217), adult male obtained from 730 m NE Coaxtlahuacán, municipality of Mochitlán (17.39592°N, 99.33838°W), Guerrero, Mexico, 1800 m elevation, collected 24 July 2017 by Ricardo Palacios-Aguilar, J. Diego Arias-

Table 2. Range of morphometric variables from males of *Bolitoglossa coaxtlahuacana* (Coaxtlahuacán Salamander), *Bolitoglossa hermosa* (Guerreran Mushroomtongue Salamander), *Bolitoglossa riletti* (Rilett's Mushroomtongue Salamander), *Bolitoglossa zapoteca* (Zapotec Salamander), and *Bolitoglossa macrinii* (Oaxacan Mushroomtongue Salamander).

Morphometric variable	*B. coaxtlahuacana* (*N* = 1)	*B. hermosa* (*N* = 4)	*B. riletti* (all *N* = 5, except TL where *N* = 4)	*B. zapoteca* (*N* = 3)	*B. macrinii* (*N* = 5)
SVL	41.8	36.0–45.8	39.7–57.2	56.6–60.5	49.2–53.6
TL	32.2	26.6–39.8	35.4–56	45.0–49.2	47.0–52.4
TL/SVL	0.77	0.73–0.86	0.86–0.97	0.79–0.81	0.91–0.99
AX	21.1	18.31–24.22	19.3–27.9	30.4–33.2	24.9–29.4
FLL	9.2	6.8–10.1	9.2–10.5	10.7–13.5	10.3–13.2
HLL	9.8	6.9–10.2	8.1–11.7	12.4–13.3	10.2–12.8
HL	9.1	8.1–10.9	9.4–11.3	12.1–13.7	11.3–12.2
HW	7	4.9–7.1	6.3–8	8.1–8.2	6.9–7.6
SW	5.4	4.1–5.2	4.7–6.4	5.7–6.3	4.7–5.6
IN	2.4	1.42–2.5	2.1–3.2	1.9–2.8	2.1–3.0
FW	3.9	3.4–4.6	4.3–6.3	5.3–6.1	4.5–5.5
LI	2.0	2.0–4.5	2.0–3.50	3.0–4.0	2.0–3.0
PMT + MT	28	9–35	12–30	32–42	14–77
VT	19	18–35	21–38	12–28	21–34
HW/SVL	0.16	0.13–0.16	0.13–0.16	0.13–0.14	0.13–0.15
HLL/SVL	0.23	0.18–0.22	0.19–0.24	0.21–0.22	0.19–0.25
AX/SVL	0.51	0.50–0.55	0.45–0.55	0.54–0.56	0.50–0.55
ED/SG	0.21	0.24–0.27	0.22–0.27	0.21–0.25	0.24–0.28

Note: Morphometric variables are snout–vent length (SVL), tail length (TL), axilla–groin distance (AX), forelimb length (FLL), hind-limb length (HLL), head length (HL), head width at angle of jaw (HW), shoulder width (SW), internarial distance (IN), right-foot width (FW), limb interval (LI), eye diameter (ED), and snout to gular fold distance (SG). We also counted ankylosed premaxillary (PMT), maxillary (MT), and vomerine (VT) teeth. Measurements are given in millimetres, except TL/SVL (proportional value), HW/SVL (proportional value), HLL/SVL (proportional value), AX/SVL (proportional value), ED/SG (proportional value), LI (number of costal folds between appressed limbs), and tooth counts.

Montiel and Gael Palacios (Figs. 1 and 2). Vegetation in the zone consists of cloud forest.

PARATYPE: MZFC 32986 (RPA 218), subadult male, same collecting data as holotype.

DIAGNOSIS: Distinguished from species of all other genera of Neotropical salamander by the lack of a sublingual fold. Distinguished from the rest of the genus *Bolitoglossa* by the presence of discrete digits, including the first, that extends beyond the margins of the webbing; digits expanded distally, with distinct subterminal pads; small size (adult male 41.8 mm SVL); mental gland absent in adult males; and divergence of nucleotide sequences. It can be distinguished from other species of *Bolitoglossa* (*Oaxakia*) as follows.

Bolitoglossa coaxtlahuacana is very similar in body proportions to *B. hermosa* and it differs from it by having smaller eyes (ED/SG 0.21 in one *B. coaxtlahuacana* male vs. 0.24–0.27 in *B. hermosa* males), having longer hind limbs (HLL/SVL 0.23 in one *B. coaxtlahuacana* male vs. 0.18–0.22 in *B. hermosa* males), and by the shape of the snout in lateral view (rounded in *B. coaxtlahuacana* and truncated in *B. hermosa*). Furthermore, it differs from *B. hermosa* in lacking any white or yellowish spots and blotches on the dorsum (vs. presence in *B. hermosa*).

Bolitoglossa coaxtlahuacana differs from *Bolitoglossa macrinii* (Oaxacan Salamander) by its smaller adult body size (SVL 41.8 mm in one *B. coaxtlahuacana* male vs. 49.2–53.6 mm in *B. macrinii* males), shorter tail (TL/SVL 0.77 in one *B. coaxtlahuacana* male vs. 0.91–0.99 in *B. macrinii* males), broader head (HW/SVL 0.16 in one *B. coaxtlahuacana* male vs. 0.13–0.15 in *B. macrinii* males), smaller eyes (ED/SG 0.21 in one *B. coaxtlahuacana* male vs. 0.24–0.28 in *B. macrinii* males), narrower feet (FW 3.9 mm in one *B. coaxtlahuacana* male vs. 4.5–5.5 mm in *B. macrinii* males), and fewer vomerine teeth (VT 19 in one *B. coaxtlahuacana* male vs. 21–34 in *B. macrinii* males).

Bolitoglossa coaxtlahuacana differs from *B. oaxacensis* males by its smaller adult body size (SVL 41.8 mm in one *B. coaxtlahuacana* male vs. 46.1 mm in *B. oaxacensis* males), shorter limbs (LI 2.0 in one *B. coaxtahuacana* male vs. 1.5 in *B. oaxacensis* males), fewer vomerine teeth (VT 19 in one *B. coaxtlahuacana* male vs. 26–38 in *B. oaxacensis* males), and in having a black dorsal coloration (vs. brownish dorsum).

Bolitoglossa coaxtlahuacana differs from *B. riletti* by its shorter tail (TL/SVL 0.77 in one *B. coaxtlahuacana* male vs. 0.86–0.97 in *B. riletti* males), shorter head (HL 9.1 mm in one *B. coaxtlahuacana* male vs. 9.4–11.3 mm in *B. riletti* males), narrower feet (FW 3.9 mm in one *B. coaxtlahuacana* male vs. 4.3–6.3 mm in *B. riletti* males), fewer vomerine teeth (VT 19 in one *B. coaxtlahuacana* male vs. 21–38 in *B. riletti* males), and having a black dorsal coloration (vs. brownish dorsum).

Bolitoglossa coaxtlahuacana differs from *Bolitoglossa zapoteca* (Zapotec Salamander) by its smaller adult body size (SVL 41.8 mm in one *B. coaxtlahuacana* male vs. 56.6–60.5 mm in *B. zapoteca* males), shorter tail (TL/SVL 0.77 in one *B. coaxtlahuacana* male vs. 0.79–0.81 in *B. zapoteca* males), shorter limbs (LI 2 in one *B. coaxtlahuacana* male vs. 3–4 in *B. zapoteca* males), smaller head (HL 9.1 mm in one *B. coaxtlahuacana* male vs. 12.1–13.7 mm in *B. zapoteca* males), narrower head (HW 7 mm in one *B. coaxtlahuacana* male vs. 8.1–8.2 in *B. zapoteca* males), narrower feet (FW 3.87 mm in one *B. coaxtlahuacana* male vs. 5.3–6.1 mm in *B. zapoteca* males), and fewer maxillary and premaxillary teeth (MT + PMT 28 in one *B. coaxtlahuacana* male vs. 32–42 in *B. zapoteca* males).

DESCRIPTION OF THE HOLOTYPE: An adult male (determined by direct examination of the gonads), SVL 41.8 mm. Snout truncated in dorsal view, rounded in profile, projecting beyond mandible; snout length 3.1 mm; nostrils small, located near the tip of the snout; internarial distance 2.4 mm; nasolabial groove distinct extending from the posterior lower margin of the nostril to the lip; labial protuberances absent. Eye diameter 2.3 mm; eyelid length 3.3 mm; eyelid width 1.8 mm; eyes protuberant, not visible beyond the margin of the jaw in ventral view; interorbital distance 2.9 mm; suborbital groove deep; postorbital groove distinct. HW

Fig. 1. Holotype of *Bolitoglossa coaxtlahuacana* (Coaxtlahuacán Salamander) (MZFC 32985): (A) in situ when collected and (B) overall habitus. Color version online.

7 mm; HL 9.1 mm; SG 10.4 mm; snout–forelimb length 12.7 mm. Mental gland absent; other cephalic or dermal glands not visible. VM 19 mm; PMT + MT 28 mm. AX 21.1 mm; 13 costal grooves per side; SW 5.4 mm. TL 32.2 mm; tail depth at base 2.3 mm; tail width at base 2.8 mm. Limbs slender, separated by two costal grooves; digital pads distinct; FLL 9.2 mm; manus width 2.8 mm; HLL 9.8 mm; hind-foot width 3.9 mm; length of third toe 2.4 mm; length of fifth toe 1.6 mm. Webbing of manus and pes moderate, with the distal 1 phalanx free, except on the third finger where 1.5 phalanges are free.

VARIATION: The subadult paratype (MZFC 32986) has the following morphometric values: SVL 35.4 mm, SG 8.2 mm, snout–forelimb length 11.1 mm, snout length 2.3 mm, AX 18.5 mm, HW 5.4 mm, HL 7.9 mm, eye length 2.1 mm, IN 1.8 mm, interorbital distance 2.3 mm, HLL 6.8 mm, FW 3.4 mm, FLL 7.5 mm, manus width 2.6 mm, TL 21.1 mm, tail depth at base 2.3 mm, tail width at base 1.8 mm, and SW 3.5 mm.

COLORATION: Dorsal and tail coloration uniformly black with the dorsal surfaces of the hands and feet, and the tip of the snout and the lips dark brown; iris gold with some reddish flecks in the proximal section; ventral surfaces slightly lighter, with the hands and feet gray and the chin surface dark brown. A degree of metachrosis is present as in many amphibian species; at the moment of capture the holotype and the paratype showed a purplish black coloration in the ventrolateral surfaces and a few days after capture a dark gray hue could be observed on the lips and lateral surfaces of the holotype while active in the afternoon.

Coloration in alcohol is essentially unchanged from that in life, except that the ventral surfaces are more opaque and several small white iridophores are visible in the ventrolateral surfaces with the naked eye.

MOLECULAR DIFFERENTIATION: Our data matrix includes 35 sequences, with a total sequence length of 1170 bp, including gaps: 521 bp for *16S* and 649 bp for *cytb*. Two substitution models were used for each gene: GTR + G for *16S* and HKY + I + G for *cytb*. Genetic distances between the new species and the other members of the *B. macrinii* group ranged from 3% to 4.4% for *16S* and from 13.3% to 15.4% for *cytb*. In the Bayesian analyses, the new species was recovered as divergent and the sister species of a *B. hermosa* + *B. riletti* clade, separated from *B. hermosa* by a genetic distance of 3% for *16S* and 15.4% for *cytb*, and from *B. riletti* by 3.2%–3.4% for *16S* and 14.2% for *cytb*.

ETYMOLOGY: The species name refers to the small village of Coaxtlahuacán, Guerrero, from which the type series was obtained, and honors its inhabitants for their helpfulness and friendliness while conducting our fieldwork since late 2015.

DISTRIBUTION AND HABITAT: *Bolitoglossa coaxtlahuacana* is known only from the type locality in a small mountain range that we call herein as Sierra de Mochitlán because it covers most of the municipality of Mochitlán, Guerrero (Fig. 3). The main vegetation formation at the type locality consists of humid oak forests with distinct degrees of perturbance. However, in many ravines and trails mostly in the southward slopes of this small mountain range, a more "cloud forest like" vegetation is present where ferns, mosses, orchids, and bromeliads abound (either in epiphytic and saxicolous situations) and dominant tree species show a mixture of both tropical and temperate representatives.

NATURAL HISTORY: The specimens were found crawling at night on thin bushes near the edge of a small mountain stream at an approximate elevation of 1 m above the ground after moderate to heavy rains. They showed very slow movements when first discovered and helped themselves with their tails to move among leaves (Fig. 1A). We could observe that they have very strong prehensile tails which can support their mass; even when the holotype was found, it was holding itself from a leaf with its prehensile tail.

Upon dissection, large fat bodies were observed in the male holotype (MZFC 32985) suggesting reproductive activity. Both specimens were found after heavy rains, but after considerable field effort both during rainy and dry seasons, no other specimens have been secured. Rains during summer of 2018 were particularly scarce at the type locality, which may explain our failure to obtain additional specimens.

Discussion

The salamanders from Guerrero are poorly studied and are poorly represented in scientific collections. Most literature concerning the plethodontid salamanders of the state is focused on species descriptions and the overall information on biology and ecology of many is scarce, incomplete, and consists only on what original descriptions report. According to Adler (1996), the salamander fauna of the Sierra Madre del Sur in Guerrero and Oaxaca has a mountain-specific distribution where lower elevation valleys and depressions effectively isolate populations, resulting in a high degree of endemism. This seems particularly true for the Sierra de Mochitlán, which is a small uplift of approximately 25 km wide located in the middle of the Sierra Madre del Sur portion of Guerrero bordered to the north and to the east by the dry lowlands of the Río Huacapa, and Río Azul drainages; and to the west and south by the humid and warmer lowlands of the Río Escondido–Apetlanca–Zintlanapa drainages (Fig. 3).

Allopatric speciation by vicariance is the most common speciation mode in bolitoglossines (Rovito 2017), and has been recognized as the main process involved in the speciation in some of the members of the *B. macrinii* species group (Parra-Olea et al. 2004; Rovito 2017), particularly those that are closely related to

Fig. 2. Bayesian inference tree based on partial sequences of the mitochondrial genes *16S* and *cytb*. Values in front of the internal nodes represent Bayesian support and asterisks represent those with a support of 1.

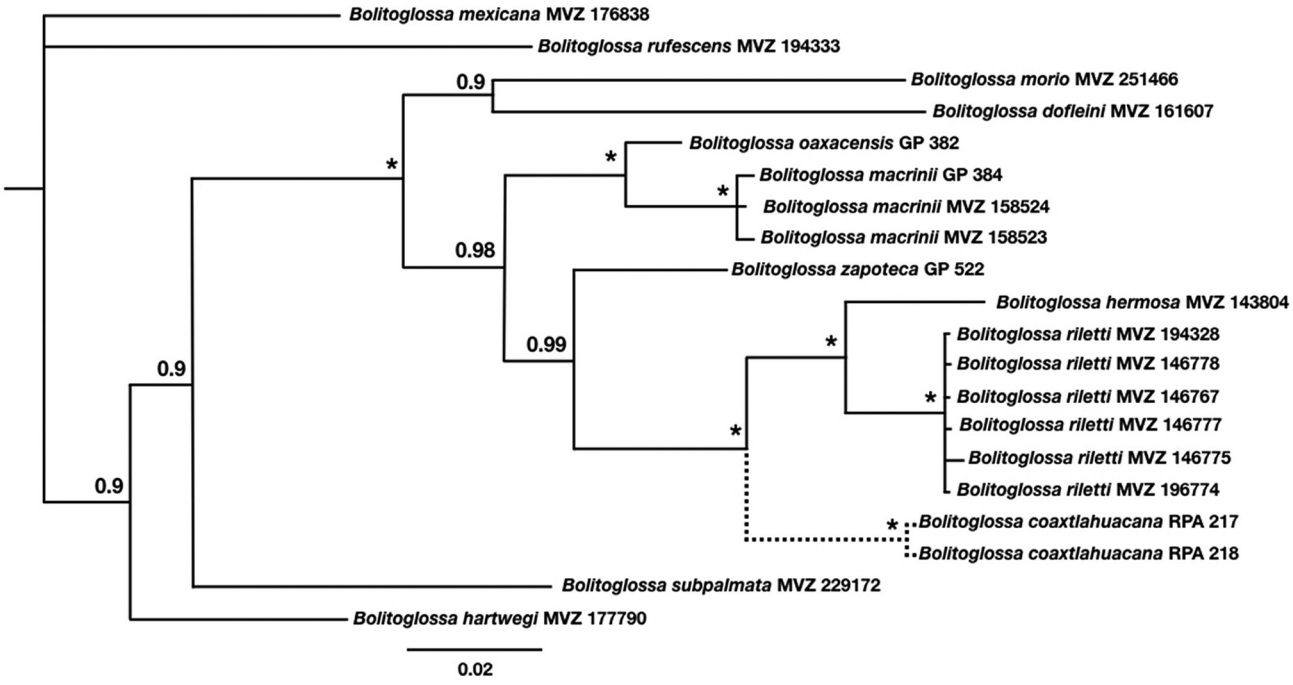
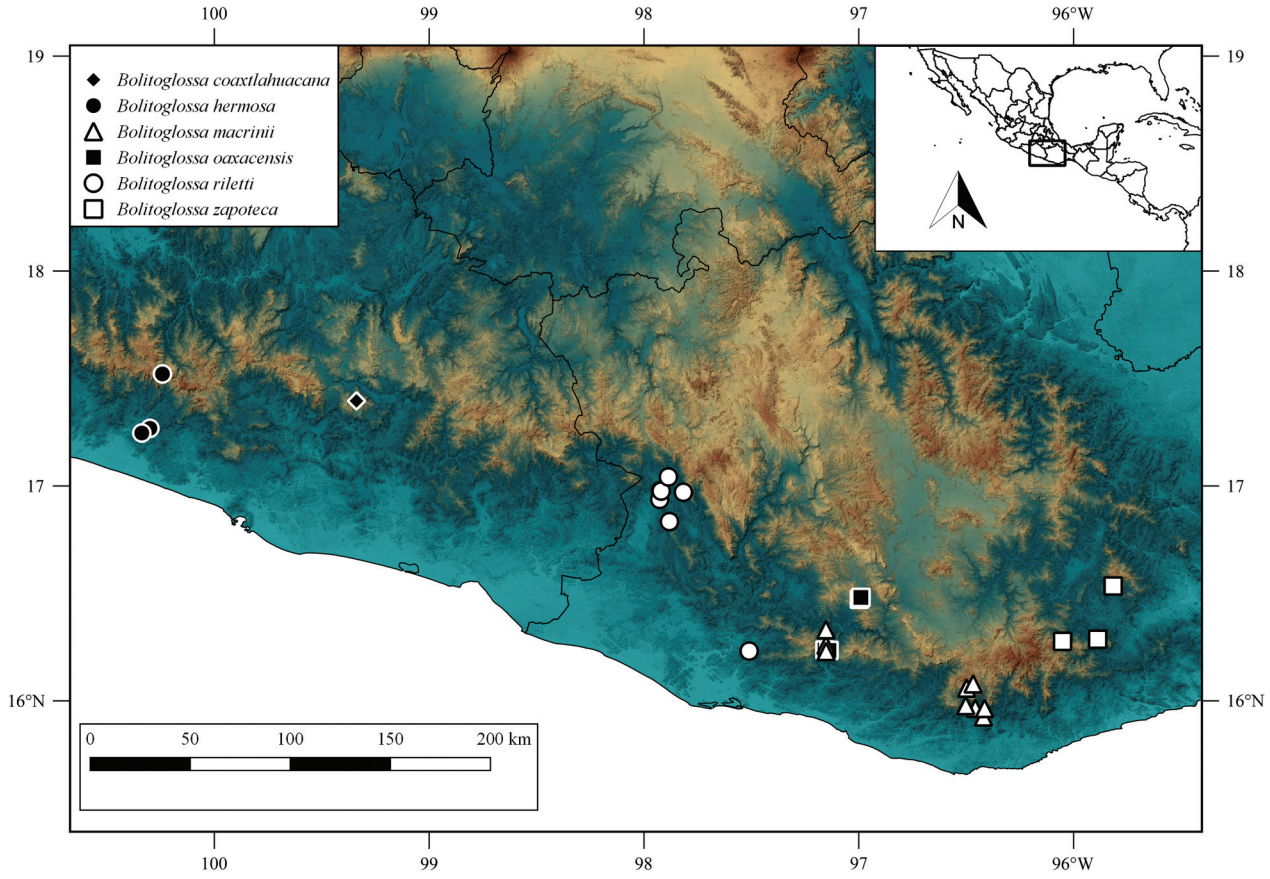


Fig. 3. Distribution map of the members of the *Bolitoglossa macrinii* group in southern Mexico. Figure was created using QGIS version 2.18.19 and assembled from the following data sources (shapefiles): Continuo de Elevaciones Mexicano 3.0 (CEM 3.0) (INEGI); Estados Unidos Mexicanos, División estatal (INEGI); MapSurfer ASTER GDEM-SRTM Hillshade (MapSurfer.NET); World Country Boundaries (DIVA–GIS); and locality records of each species compiled consulting electronic (VertNet) and museum (MZFC) databases and specialized literature (see text). Color version online.



the new species described herein. It is logical to consider that the same speciation mode which acted over these taxa also has acted over *B. coaxtlahuacana* because it is in the middle of a former distributional hiatus of approximately 265 km between the known populations of the *B. macrinii* group in Guerrero and Oaxaca (Fig. 3). The addition of *B. coaxtlahuacana* to the analysis performed by Parra-Olea et al. (2002) recovered it as the sister taxon to a clade formed by *B. hermosa* and *B. riletti*. Also, worth noting is that this clade is more closely related to *B. zapoteca*, which is distributed in the distal portion of the Sierra Madre del Sur in Oaxaca rather than to the geographically closer congeners; a similar tree topology was recovered by the analysis performed by Parra-Olea et al. (2002) (Figs. 2 and 3). Although largely unexplored, the Guerrero highlands have been recognized by some authors to harbor an important number of endemic species and to have their closest relatives east in the Oaxaca highlands (Nieto-Montes de Oca et al. 2001; Campbell et al. 2013). In the case of *B. coaxtlahuacana*, it is possible that this taxon had evolved in isolation and hence it is more distantly related to its closest relatives than they are to each other.

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Appendix A

Material examined

Specimens examined for morphological data and to generate the molecular data set are included. Abbreviations are as follow: MVZ (Museum of Vertebrate Zoology), MZFC (Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México), and RSB (Rufino Santos Bibiano field numbers).

Bolitoglossa hermosa

MEXICO — **Guerrero**: Atoyac de Álvarez: 4.2 km (by road) E of Rio Santiago, elevation 825 m (MVZ 143804, holotype); 11.3 mi NE (Puerto del Gallo Rd.) Atoyac, Sierra Madre del Sur (MVZ 143805, 143808, 158489, 158498, 158500, 150502–150503, 158505–158506); Tecpan de Galeana: Sierra de Tecpan, elevation 700 m (RSB 127–128).

Bolitoglossa macrinii

MEXICO — **Oaxaca**: San Gabriel Mixtepec (MVZ 158523–158525); San Marcial Ozolotepec: 40 km N San Pedro Pochutla along road to Suchixtepec, Mexico Hwy. 175 (MVZ 158507, 158511–158513, 158520); San Miguel Suchixtepec: 4.4 km S of [by Mexico Hwy. 175] San Miguel Suchixtepec (MVZ 161077–161078); San Pedro el Alto: Candelaria Loxicha-San Miguel Suchixtepec, 16°03′01.7″N, 96°30′12.6″W (MZFC 28202–28203).

Bolitoglossa oaxacensis

MEXICO — **Oaxaca**: Villa Sola de Vega: 9.4 km S Sola de Vega (MVZ 158533).

Bolitoglossa riletti

MEXICO — **Oaxaca**: Villa Putla de Guerrero: 3.8 mi S (by road) Putla (MVZ 138887, 138889, 138892); 6 km S of Putla (MVZ 132567);

6.1 km S (via Mexico Hwy. 125) of Putla (MVZ 146778); 6 mi S of Putla (MVZ 106359, 106360, 106362); 13.3 km S (by road) Putla (MVZ 115291); 19.5 km NE (via Mexico Hwy. 125) of Putla (MVZ 146773); San Pedro Reyes, Putla Villa de Guerrero (MZFC 28428); Santa María Yucuhiti, 16°58′15″N, 97°49′0.6″W (MZFC 28427); Santa María Zacatepec: Corral de Piedra, Santa Ana del Progreso (MZFC 13412–13414).

Bolitoglossa zapoteca

MEXICO — **Oaxaca**: Santa María Ecatepec: 0.7 km E (by road) Santa Maria Ecatepec on road to Mexico highway 190 (MVZ 272310); 3.0 km ENE (by road) Santa Maria Ecatepec on road to Mexico highway 190 (MVZ 272311–272312).