In 2011 and 2012, we conducted several expeditions to eastern Panama for the purpose of studying the herpetofauna of the region. We collected numerous specimens, among which were a considerable number of salamanders of the genus *Bolitoglossa*. We found all of the species expected for the area, except for *B. cuna*. After applying an integrative analysis, which included barcoding, morphology, and biogeography, we uncovered specimens that we were unable to assign to any known species. In the following study we revise the subgenus *Eladinea*, to which all of the eastern Panamanian species have been assigned, provide detailed information on these species, and describe a new species from a private reserve (Reserva Natural Privada Cerro Chucantí) in the Cordillera de Majé. © Anand Varma

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A new species of *Bolitoglossa* (Amphibia: Plethodontidae) from eastern Panama, with comments on other members of the *adspersa* species group from eastern Panama

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Abstract: We describe a new species of *Bolitoglossa* from Cerro Chucantí, Cordillera de Majé, Provincia de Darién, Panama. A phylogenetic analysis based on molecular data provides evidence for the assignment of the new taxon to the *Bolitoglossa adspersa* species group. The new species differs in color pattern and morphometrics from all other congeners found in eastern Panama. Additionally, we include comments on the other species of salamanders known to occur in the region.

Key Words: Barcoding, *Bolitoglossa biseriata, Bolitoglossa chucantiensis* sp. nov., Darién, *Eladinea,* morphology, phylogeny.

Resumen: Describimos una nueva especie de *Bolitoglossa* de Cerro Chucantí, Cordillera de Majé, Provincia de Darién, Panamá. Un análisis filogenético basado en datos moleculares proporciona evidencia de la asignación del nuevo taxón al grupo de especies *Bolitoglossa adspersa*. La nueva especie se diferencia en el patrón de color y morfometría de todos los otros congéneres que se encuentran en el este de Panamá. Además, incluimos comentarios sobre las otras especies de salamandras que son conocidas en la región.

Palabras Claves: *Bolitoglossa biseriata*, *Bolitoglossa chucantiensis* sp. nov., códigos de barras, Darién, *Eladinea,* morfología, filogenia.

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INTRODUCTION

The Neotropical salamanders (Plethodontidae) are dominated by the genus *Bolitoglossa*, globally the most diverse salamander genus (128 species) with a distribution extending from northeastern Mexico and across Central America, and into South America (AmphibiaWeb, 2014). With a surface area of only 75,416 km^2 Panama is home to 29 species of plethodontids (AmphibiaWeb, 2014); the highest diversity is in the western part of the country, where 17 species of *Bolitoglossa* are found, but only four of these species are known to occur in eastern Panama (Jaramillo et al., 2010). Two subgenera have been recognized for lower Central America and South America, *Bolitoglossa* (*sensu stricto*) and *Eladinea* (*sensu* Parra-Olea et al., 2004). *Eladinea* is comprised of the *adspersa*, *epimela*, *schizodactyla*, and *subpalmata* species groups. Of these, the distribution of only the *adspersa* species group extends far to the south, reaching central Bolivia (Frost, 2014).

The *adspersa* species group consists of 33 known species, of which four are known from eastern Panama (*B. biseriata*, *B. cuna*, *B. medemi*, and *B. taylori*); two of these are endemic to the Pirre (*B. taylori*) and San Blas (*B. cuna*) mountain ranges (Raffaëlli, 2007; Köhler, 2011; Acosta-Galvis and Gutiérrez-Lamus, 2012; Acevedo et al., 2013). Neotropical salamanders usually are difficult to identify due to their similarities in color pattern variation and morphology (Wake, 1970; Wake and Lynch, 1976; García-París et al., 2000; Wake et al., 2007; Fermin et al., 2012). The few species from eastern Panama, however, are easy to distinguish from each other; the only exceptions are *B. biseriata* Tanner, 1962 and *B. cuna* Wake et al., 1973, which are similar in overall appearance and only can be differentiated by their head width and the number of maxillary teeth (Wake et al., 1973). Wake et al. (1970) noted the occurrence of *B. phalarosoma* Wake and Brame, 1962 in the Jaqué-Imamadó divide of eastern Panama, but this record remains unsubstantiated because the authors did not indicate voucher specimens or provide other supportive data; other authors (e.g., Raffaëlli, 2007; Acosta-Galvis and Gutiérrez-Lamus, 2013) have stated that the identity of the salamanders referred to as *B. phalarosoma* and an undescribed species noted by Wake et al. (1970) needs to be confirmed. At this point, therefore, we do not consider *B. phalarosoma* as a member of the Panamanian herpetofauna. The remaining two species known to occur in eastern Panama are *B. taylori* Wake, et al., 1970 and *B. medemi* Brame and Wake, 1972.

During recent expeditions to the Darién, Jingurudó, Majé, Pirre, and San Blas mountain ranges, we collected specimens of three salamander species known to occur in eastern Panama (*B. biseriata, B. medemi,* and *B. taylori*), as well as a single adult specimen of an undescribed species of salamander from the Cordillera de Majé and a related salamander (an apparent juvenile) from the Cordillera de Jingurudó. We identified both of these specimens as members of the genus *Bolitoglossa* based on the following characteristics: absence of a sublingual fold, presence of well-developed hands and feet, presence of extensive digital webbing, and a count of 13 costal grooves between the limbs (Parra-Olea et al., 2004). Herein we describe the specimen from the Cordillera de Majé as a new species, and discuss its relationship to the juvenile specimen from the Cordillera de Jingurudó. We also provide data on molecular and morphological variation for the four species of *Bolitoglossa* found in the region.

MATERIALS AND METHODS

We conducted our fieldwork in the Darién, Jingurudó, Majé, Pirre, San Blas, and Sapo mountains of eastern Panama, (Fig. 1); see Appendix 2 for details on the collecting areas. We recorded georeferences by using a Garmin GPSmap 60CSx, in the WGS 1984 datum format and given in decimal degrees, and created the maps in ArcGIS 10 (ESRI, 2010). We euthanized the specimens collected with the euthanasia solution T61, fixed them with a preservative solution of 5ml formalin (36%) in 1L ethanol (94%), and subsequently stored them in ethanol (70%).

Morphology

We followed the methodology of Boza-Ovideo et al. (2012) for measuring the morphological characters of the holotype, and used a dial precision caliper under a dissecting microscope (Leica MZ 12) rounded to the nearest 0.1 mm. We examined the following characters: snout–vent length (standard length) from the tip of snout to the posterior end of vent (SVL), tail length from the posterior end of vent to the tip of the tail (TL), distance from the gular fold to the tip of the snout (SG), head width at the greatest width of the head (HW), head depth (height) at the posterior angle of the jaw (HD), eyelid length (EL), eyelid width (EW), distance from the anterior margin of the orbit to the tip of the

snout (ES), horizontal eye diameter (ED), intercanthal distance (IC), interorbital distance between the eyelids (IO), tip of the snout to the point where the forelimb articulates with the body (SF), internarial distance (IN), snout projection (SP), shoulder width (SW), snout to the anterior angle of the vent (SAV), axilla-groin distance (AX), hind limb length from the groin to the tip of longest digit (HLL), forelimb length from the axilla to the tip of the longest digit (FLL), hand width at the widest extent (HAW), foot width at the widest extent (FW), length of the 3rd toe (T3), and length of the 5th toe (T5); we counted premaxillary teeth (PMT), maxillary teeth (MT), and vomerine teeth (VT) by using a dissecting microscope; we provide MT and VT for left and right sides, respectively. We followed Brcko et al. (2013) for the following characters: costal folds between the adpressed limbs of the straightened specimen (limb interval, LI, as a measure of relative limb length), mental gland width (WMG), and mental gland length (LMG). We ran an exploratory analysis among the different morphological characters, since not enough useful morphological information was available (see Table 1) to conduct a statistical test among all the species; we present these diagnostics characters in graphs, showing only the range between the maximum and minimum values. We follow Köhler (2012) for the description of coloration in life and in ethanol. We used the keys to the genus *Bolitoglossa* in Savage (2002) and Köhler (2011) for a preliminary identification of the specimens collected. We obtained data for morphological characters and tooth counts for comparisons within the *adspersa* species group from the following original species descriptions and species revisions: Tanner (1962), Wake and Brame (1962), Brame and Wake (1972), Wake et al. (1973), Wake and Lynch (1976), Acosta-Galvis and Gutiérrez-Lamus (2012), and Acevedo et al. (2013). We derived osteological information on the holotype from radiographs. The capitalized colors and color codes (the latter in parentheses) are those of Köhler (2012). We followed Köhler (2012) for the terminology of markings used in the color descriptions.

Molecular Analysis

We extracted DNA from fresh liver tissue using the protocol of Ivanova et al. (2006). We amplified the mitochondrial 16S mtDNA using a Mastercycler pro S (Eppendorf, Hamburg, Germany), and performed the initial denaturation for 2 min at 94°C, which was followed by 40 cycles with denaturation for 35 s at 94°C, hybridization for 35 s at 48.5°C, and elongation for 60 s at 72°C; the final elongation proceeded for 7 min at 94°C. The reaction mix contained 1 µL DNA template, 2.5 µL Reaction Buffer ×10 (PeqGold), 4 µL 2.5 mM dNTPs, 0.4 µL (containing 2.5 units) Taq Polymerase (PeqLab), 14.1 µL H_2O, 1 µL 25 mM $MgCl_2$, and for 16S 1 µL per primer (containing 10 pmol, forward: L2510, 5'-CGCCTGTTTATCAAAAACAT-3'; reverse: H3056, 5'-CCGGTCTGAACTCAGATCACGT-3'; eurofins MWG Operon); the COI gene was sequenced by the Southern China DNA Barcoding Center; because this project was developed along with a larger barcoding project for the amphibians and reptiles of eastern Panama, we only used the standardized genetic markers 16S and COI (Paz and Crawford, 2012), as financial resources were limited to these markers. We compared the molecular data of our specimens with the available sequences for the species of *Bolitoglossa* present in Central America and South America, which we obtained from recent publications (Boza-Oviedo et al., 2012; Hertz et al., 2013; Elmer et al., 2013; Acevedo et al., 2013). We aligned the obtained sequences with ClustalX (Thompson et al., 1997). We present a list of the specimens included in our genetic analysis, with the corresponding GenBank accession numbers, in Appendix 1. The final alignment of the 16S mtDNA comprised 32 sequences of 439 bp in length, of which 111 sites are variable and 74 are parsimony-informative (excluding outgroups). We computed Kimura 2–parameter (K2P) pairwise genetic distances for 16S and COI separately, using MEGA5 (Tamura et al. 2011). For phylogenetic inference we used 16S mtDNA (we did not include COI, because it was not available for most species of *Bolitoglossa*), and ran a Maximum Likelihood (ML) analysis with 1,000 bootstrap replicates using MEGA5, using the Kimura 2 parameter model. We used JModeltest 0.1.1 (Posada 2008) under the corrected Akaike Information Criterion (AICc) to select the substitution model for the Bayesian analysis. We determined TIM3+G as the best-fitting substitution model, and ran a Bayesian phylogenetic analysis in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001) for 10,000,000 generations with four default chains, sampling every 100 generations and subsequently discarding 5% as burn-in. For the tree including all the species of *Bolitoglossa*, we used *Oedipina complex*, *Nototriton picadoi*, and *N. matama* as outgroups. For the tree including only the *adspersa* species group, we used *B. colonnea* and *B. schizodactyla* as outgroups.

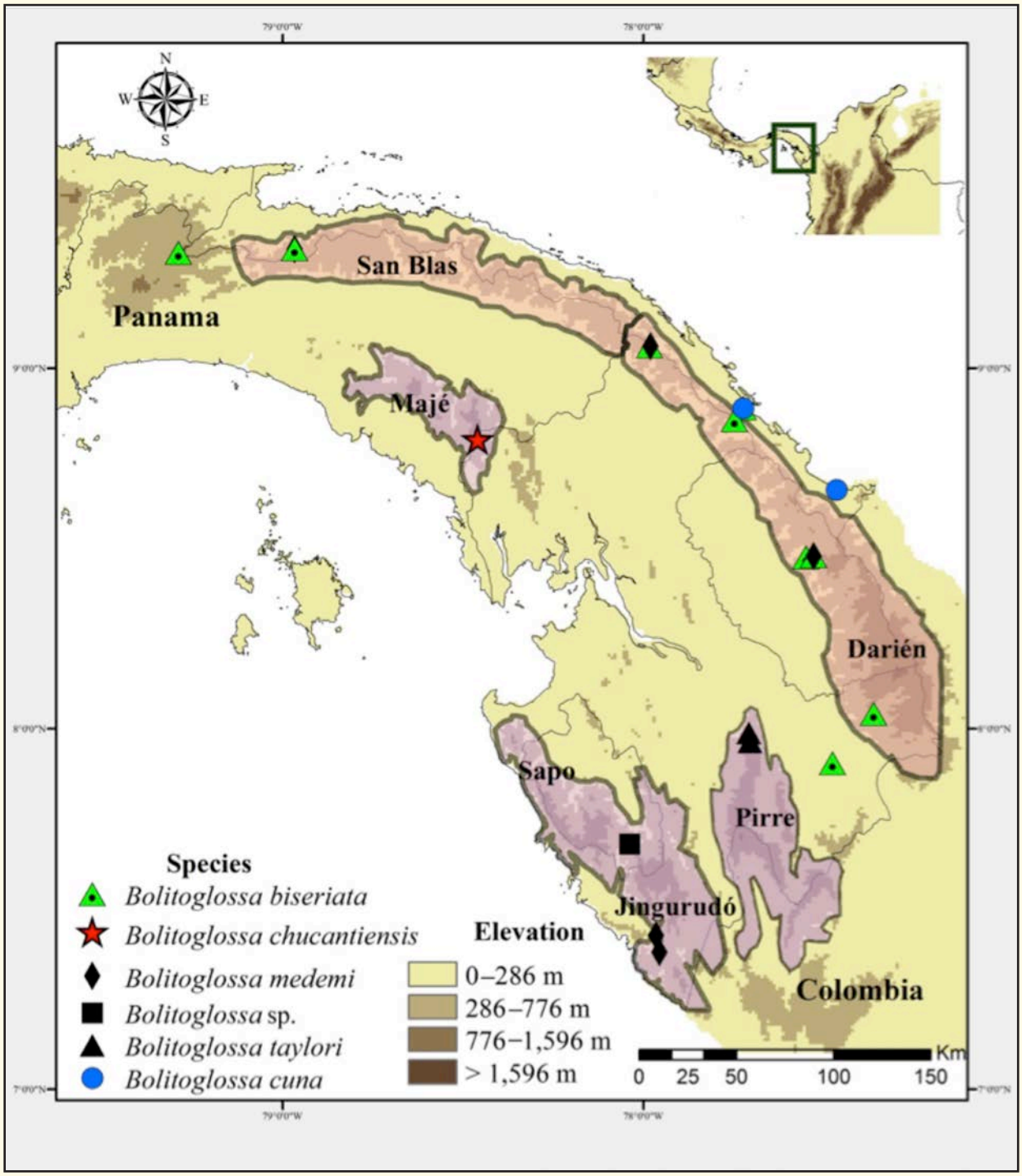

Fig. 1. Distribution of species of *Bolitoglossa* in eastern Panama. *Bolitoglossa* sp. (Black Square) pertains to specimen MHCH 2663 from the Cordillera de Jingurudó; shaded areas with borders represent the principal mountain ranges in eastern Panama, with elevations above 500 m a.s.l. (names of mountain ranges inside the shaded areas).

Table 1. Measurements and morphological proportions for the *Bolitoglossa* spp. from eastern Panama. We included data for *B. medemi, B. taylori,* and *B. cuna* taken from the species descriptions.

Characters (mm)	Species				
	***B. chucantiensis* (*n* = 1)**	***B. biseriata* (*n* = 6)**	***B. medemi* (*n* = 16)**	***B. taylori* (*n* = 7)**	***B. cuna* (*n* = 3)**
SVL	47	37–46 (40.88 ± 4.37)	33.7–58 (43.75 ± 6.38)	39.5–64.7 (48.01 ± 6.66)	46.6–55.7 (50.33 ± 4.76)
TL	55	34–44.5 (37.55 ± 4.84)	28.7–54 (39.56 ± 7.8)	40.9–73.3 (55.71 ± 8.74)	45–52.2 (48.6 ± 5.09)
SG	11.74	8.72–10.47 (9.45 ± 0.77)	10.07–12.44 (11.14 ± 1.04)	9.78–15.7 (11.53 ± 1.52)	10.4–11.6 (11.03 ± 0.6)
HW	7.63	5.44–6.89 (5.9 ± 0.68)	6–9.22 (7.46 ± 0.94)	6.6–10.1 (7.65 ± 0.91)	6.8–7.7 (7.3 ± 0.46)
HD	6.41	5.26–6.6 (5.66 ± 0.64)	6.22–8.52 (7.14 ± 0.89)	6.4–8.41 (7.45 ± 0.7)	—
AX	23.18	18.72–24.74 (20.52 ± 2.84)	16.7–27.6 (22.58 ± 3.24)	21.61–36.4 (25.64 ± 3.8)	28.4–32.5 (30.45 ± 2.9)
HLL	10	7.5–10 (8.38 ± 1.11)	8.9–13 (11.19 ± 1.38)	9–13.8 (10.91 ± 1.41)	—
FLL	11	7–10 (8.38 ± 1.25)	8–14 (11.08 ± 1.65)	9–12 (10.33 ± 0.87)	—
HAW	3.67	2.44–3.06 (2.68 ± 0.27)	2.44–3.82 (2.94 ± 0.55)	3.22–4.5 (3.8 ± 0.4)	—
FW	4.63	3.28–4.52 (3.71 ± 0.56)	3.1–5.3 (4.03 ± 0.64)	4.1–6.4 (4.92 ± 0.65)	4.4–5 (4.67 ± 0.31)
LI	13	13–13 (13 ± 0)	13–13 (13 ± 0)	13–13 (13 ± 0)	13–13 (13 ± 0)
PMT	2	1–2 (1.75 ± 0.5)	2–6 (4.17 ± 1.6)	1–5 (3 ± 1.22)	—
MT right	38	10–30 (20 ± 8.52)	20–25 (22.5 ± 2.43)	19–39 (28.33 ± 5.87)	—
MT left	37	8–27 (19.25 ± 8.18)	19–26 (21 ± 2.53)	18–39 (27.89 ± 6.13)	—
MT total	75	18–57 (39.25 ± 16.56)	28–59 (42.13 ± 7.37)	37–78 (58.94 ± 12.17)	66–77 (70.67 ± 5.69)
VT right	13	10–14 (11.5 ± 1.73)	14–23 (17 ± 3.69)	12–18 (14.78 ± 1.72)	—
VT left	12	9–22 (13.75 ± 6.18)	13–19 (15 ± 2.53)	12–20 (14.78 ± 2.28)	—
VT total	25	19–36 (25.25 ± 7.8)	22–50 (31.5 ± 7.38)	18–49 (30.72 ± 6.74)	33–38 (34.67 ± 2.89)
TL/SVL	1.17	0.79–1.01 (0.92 ± 0.09)	0.75–1.03 (0.89 ± 0.09)	1.04–1.28 (1.13 ± 0.08)	0.94–0.97 (0.95 ± 0.02)
HW/SVL	0.16	0.13–0.15 (0.14 ± 0.01)	0.16–0.19 (0.17 ± 0.01)	0.14–0.17 (0.16 ± 0.01)	0.14–0.15 (0.15 ± 0.01)
MT/SVL	1.60	0.49–1.33 (0.94 ± 0.35)	0.8–1.26 (0.97 ± 0.16)	0.8–1.59 (1.23 ± 0.22)	1.38–1.42 (1.41 ± 0.02)
VT/SVL	0.53	0.47–0.78 (0.61 ± 0.15)	0.48–1.06 (0.73 ± 0.2)	0.43–0.89 (0.64 ± 0.13)	0.59–0.82 (0.7 ± 0.11)
HAW/SVL	0.08	0.06–0.07 (0.07 ± 0.01)	0.06–0.07 (0.06 ± 0)	0.07–0.09 (0.08 ± 0.01)	—
FW/SVL	0.10	0.08–0.10 (0.09 ± 0.01)	0.08–0.11 (0.09 ± 0.01)	0.09–0.12 (0.1 ± 0.01)	0.09–0.1 (0.09 ± 0.01)
SG/SVL	0.25	0.22–0.24 (0.23 ± 0.01)	0.21–0.26 (0.24 ± 0.02)	0.20–0.27 (0.24 ± 0.02)	0.2–0.24 (0.22 ± 0.02)
VT/MT	0.33	0.35–1.06 (0.73 ± 0.29)	0.51–1.32 (0.77 ± 0.22)	0.38–0.78 (0.53 ± 0.11)	0.43–0.58 (0.49 ± 0.07)
SVL/HW	6.16	6.49–7.85 (6.95 ± 0.61)	5.24–6.44 (5.86 ± 0.34)	5.75–7.29 (6.27 ± 0.37)	6.58–7.23 (6.89 ± 0.33)

RESULTS

The salamander found on Cerro Chucantí in the Cordillera de Majé differs in color pattern and tooth counts from all its known congeners occurring in eastern Panama (Table 1) and South America. The new species showed a genetic distance to all species in the group of 7.5% (5.5–10.4%; $n = 16$) for 16S and 19.2% (5.6–28.8%; $n = 4$) for COI (only species from eastern Panama were included). In a Bayesian phylogenetic analysis based on all the taxa of *Eladinea* and *Bolitoglossa* available on GenBank (see Appendix 2), the new species clustered together with samples from the *adspersa* species group. In the Cordillera de Jingurudó, a distance of ca. 140 km from the locality of our new species, we found a very small salamander (SVL 17.9 mm) that we were unable to assign to any described species. Based on its disproportionally large head, the specimen apparently is a juvenile, and thus we excluded it from morphological comparisons with other species. According to the mtDNA results, the specimen is closely related to our new species, as it shows a K2P genetic distance of 1.4% for 16S and 5.6% for COI. Our mtDNA analysis shows that the most variable species was *B. biseriata*, with an average within-group genetic distance of 2.4% ($n = 5$) for 16S

(only one sample for COI). A specimen of *B. biseriata* from Río Púcuro (SMF 97139) was 3.5% divergent from one collected on the Cordillera de San Blas (SMF 97127) and another from the Río Tuquesa (MHCH 2659), but showed only 1.2% divergence from a second specimen from the Río Tuquesa (MHCH 2658). *Bolitoglossa biseriata* appears to be a polymorphic species or a complex with several cryptic species, possibly paralleling the high variation in dorsal color pattern (Fig. 8), in hand and foot shapes (Fig. 7 G–L), and genetic distances (Tables 2–3). Genetically, the other two species were less variable: *B. taylori* (0.2 % K2P) and *B. medemi* (1.7 % K2P).

Table 2. Mean genetic distances of 16S mtDNA among the *Bolitoglossa* samples used in the phylogenetic analysis (Fig. 2); numbers below diagonal are for K2P distances, and numbers above are standard error estimates (in percentage).

Species		K2P distance\SD (given in %)															
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
1	*B. adspersa*		1.1	1.1	1.4	1.4	1.1	1.5	1.0	1.1	1.1	1.5	1.1	1.4	1.1	1.0	1.4
2	*B. altamzonica*	4.4		1.3	1.3	1.6	1.2	1.6	1.1	1.2	1.0	1.4	0.9	1.6	1.2	1.1	1.5
3	*B. biseriata*	5.2	6.5		1.5	1.6	1.2	1.4	1.1	1.1	1.3	1.5	1.3	1.7	1.0	1.2	1.3
4	*B. chucantiensis* sp. nov.	6.8	5.8	8.2		1.6	1.3	1.5	1.3	1.5	1.5	1.7	1.2	1.6	1.5	1.5	1.5
5	*B. colonnea*	6.9	8.8	9.9	8.3		1.5	1.8	1.4	1.7	1.5	1.7	1.6	1.2	1.6	1.5	1.7
6	*B. leandrae*	4.2	4.7	5.9	5.5	7.8		1.4	0.7	1.1	1.1	1.5	1.1	1.6	1.3	1.1	1.3
7	*B. medemi*	8.3	9.0	8.7	8.5	11.5	7.7		1.5	1.6	1.5	1.7	1.5	1.7	1.5	1.6	1.5
8	*B. nicefori*	3.5	3.8	5.5	5.8	6.6	2.0	7.8		1.0	0.9	1.4	1.0	1.5	1.2	0.9	1.3
9	*B. orestes*	4.1	4.7	5.3	7.1	9.5	4.1	8.8	3.5		1.3	1.5	1.1	1.6	1.2	0.9	1.5
10	*B. palmata*	4.4	3.8	6.6	7.4	8.5	4.4	8.8	3.2	5.4		1.5	1.0	1.6	1.3	1.2	1.3
11	*B. paraensis*	8.2	7.0	8.9	10.4	10.1	7.6	10.5	6.6	7.5	7.6		1.3	1.9	1.6	1.4	1.5
12	*B. peruviana*	5.8	4.2	7.7	6.6	10.1	5.7	9.5	4.9	6.0	5.4	7.4		1.5	1.3	1.1	1.4
13	*B. schizodactyla*	7.2	8.5	10.2	8.7	5.4	9.2	10.6	7.6	9.2	8.9	11.9	9.8		1.6	1.5	1.7
14	*B. sima*	4.1	4.7	4.4	7.1	8.8	5.7	8.0	5.1	4.7	6.0	8.5	6.9	8.5		1.3	1.4
15	*B. tamaense*	3.5	4.4	5.8	7.8	7.5	4.1	9.0	2.6	2.9	4.8	6.3	5.8	7.9	5.4		1.3
16	*B. taylori*	6.4	7.0	7.0	8.2	9.4	5.9	8.2	5.4	7.0	5.7	8.3	8.0	8.9	6.3	5.7	

Table 3. Genetic distances of COI mtDNA gene among the *Bolitoglossa* samples used in the phylogenetic analysis (Fig. 2); numbers below diagonal are for K2P distances, and numbers above are standard error estimates (in percentage).

Species		K2P distance\SD (given in %)													
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
1	*B. chucantiensis* sp. nov. SMF 97141		1.1	2.3	2.4	2.1	2.2	2.2	2.2	2.2	2.1	2.1	2.1	2.1	1.8
2	*B.* sp. MHCH 2663	5.6		2.1	2.4	2.4	2.3	2.3	2.2	2.1	2.2	2.2	2.2	2.2	1.9
3	*B. biseriata* MHCH 2658	20.4	20.1		1.1	2.4	2.3	2.3	2.4	2.3	2.3	2.4	2.3	2.4	2.4
4	*B. biseriata* SMF 97139	21.6	23.5	6.3		2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.4
5	*B. medemi* MHCH 2660	18.5	20.9	22.1	21.5		0.8	0.8	2.2	2.2	2.2	2.2	2.2	2.2	2.4
6	*B. medemi* SMF 97131	19.0	19.8	21.3	21.8	3.6		0.0	2.3	2.2	2.3	2.3	2.3	2.3	2.5
7	*B. medemi* SMF 97130	19.0	19.8	21.3	21.8	3.6	0.0		2.3	2.2	2.3	2.3	2.3	2.3	2.5
8	*B. taylori* MHCH 2666	18.4	20.3	21.0	20.7	18.2	20.1	20.1		0.5	0.5	0.2	0.5	0.2	2.4
9	*B. taylori* MHCH 2665	17.9	18.6	19.6	20.5	17.9	19.3	19.3	1.4		0.2	0.5	0.2	0.5	2.3
10	*B. taylori* SMF 97136	17.6	18.9	19.9	20.7	17.6	19.6	19.6	1.2	0.2		0.4	0.0	0.4	2.3
11	*B. taylori* MHCH 2668	18.1	20.0	20.7	20.5	18.4	20.4	20.4	0.2	1.2	1.0		0.4	0.0	2.4
12	*B. taylori* SMF 97138	17.6	18.9	19.9	20.7	17.6	19.6	19.6	1.2	0.2	0.0	1.0		0.4	2.3
13	*B. taylori* SMF 97137	18.1	20.0	20.7	20.5	18.4	20.4	20.4	0.2	1.2	1.0	0.0	1.0		2.4
14	*B. colonnea* SMF 97128	15.9	16.7	21.5	23.0	21.8	21.8	21.8	20.1	19.0	19.2	19.8	19.2	19.8	

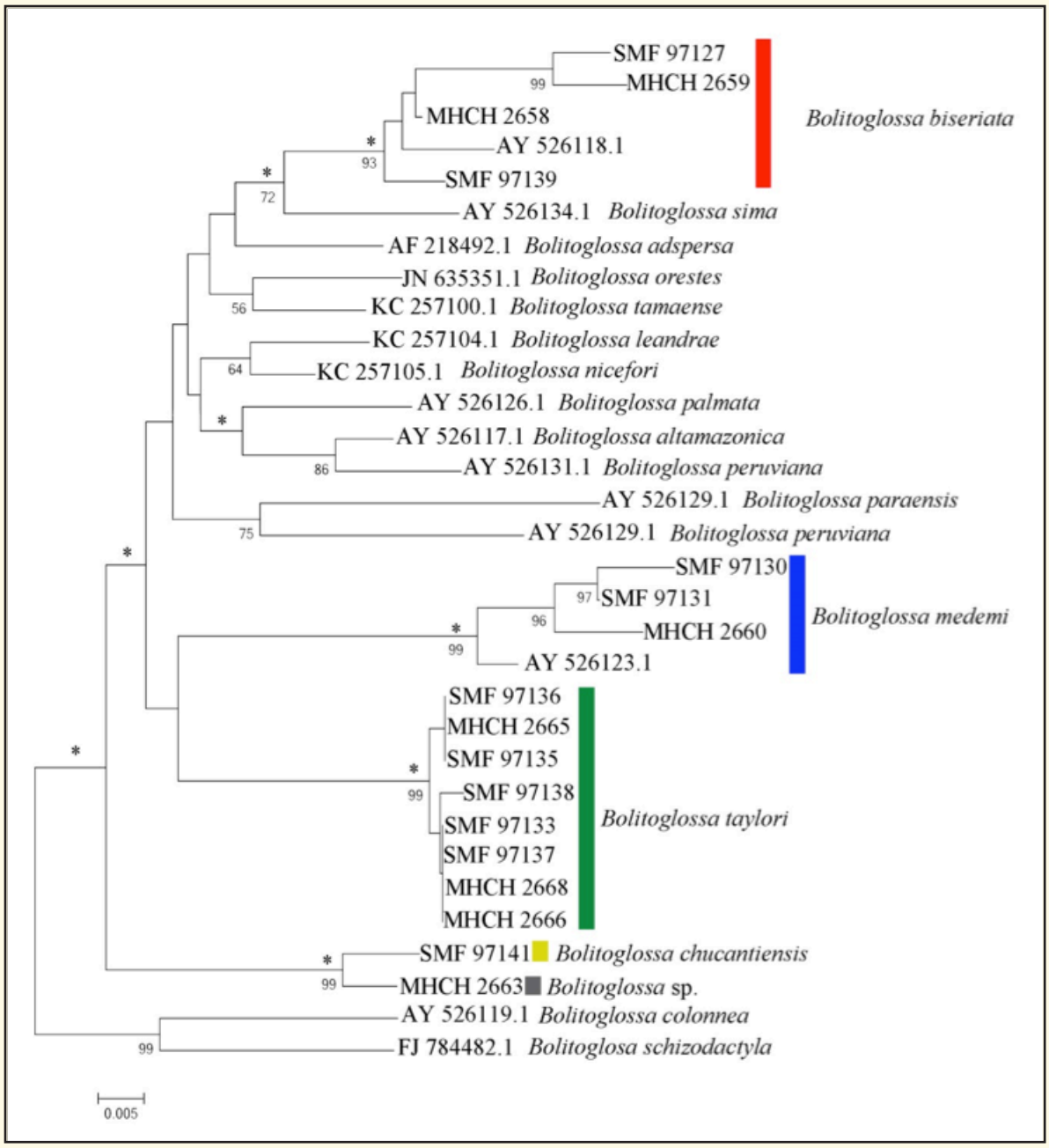

Fig. 2. Maximum likelihood consensus tree of 16S mtDNA, for the *Bolitoglossa adspersa* species group; specimen labels refer to the collection or museum number; scale bars refer to the number of substitutions per site. Maximum likelihood bootstrap values are shown below the branch, Bayesian posterior probabilities ≥ 0.95 are shown with an asterisk above the branch, ≤ probabilities are not shown. We used *B. colonnea* and *B. schizodactyla* as outgroups.

Our new species is most similar to *Bolitoglossa taylori* in body proportions, but the two species can be distinguished from one another by their color pattern and shape of their hands and feet (Fig. 7). We provide a formal description of the new species below.

Bolitoglossa chucantiensis sp. nov.

***Common names*:** Chucantí Salamander (English); Salamandra de Chucantí (Spanish). Fig. 3, Fig. 4, Fig. 7 A–B.

***Holotype*:** SMF 97141 (original field number AB 1063), an adult male from Panama, Provincia de Darién, Cordillaera de Majé, Distrito de Chepigana, Río Congo Arriba, Reserva Natural Privada Cerro Chucantí, (8.8034°N, 78.4601°W; 1,424 m elev.), collected 3 December 2013 by Abel Batista and Konrad Mebert.

***Diagnosis*:** A salamander of the genus *Bolitoglossa* and the subgenus *Eladinea* (as evidenced by the presence of a first caudal vertebra that bears unbranched transverse processes, and a prominent mental gland in males; Parra-Olea et al., 2004; Fig. 4). Our mtDNA sequence data show that this species is nested within the *adspersa* group. *Bolitoglossa chucantiensis* can be distinguished from all other eastern Panamanian and South American species of *Eladinea* by the presence of a higher number of maxillary teeth in proportion to the SVL, by the presence of completely webbed feet and hands, by its unique color pattern, and by a mtDNA genetic distance > 5.5%. *Bolitoglossa chucantiensis* is a small salamander (SVL 47 mm) with a slight indentation evident between the toe and fingertips, and in which only the longest toe and finger are pointed; the tail is relatively long (TL/SVL = 1.2); the dorsal coloration is brown, with patches of yellow speckling; and a prominent rounded hedonic mental gland and a postiliac glands are present in males. *Bolitoglossa chucantiensis* can be distinguished from other species in the *adspersa* group by the following characteristics (with contrasting features for *B. chucantiensis* in parentheses or brackets; see Table 1 for additional details): it differs from all the South American species (Acevedo et al., 2013; Brcko et al., 2013; García-Gutiérrez et al., 2013) by the presence of a higher number of maxillary teeth in males; and it differs from its closest relatives in South America by more than 5.5% of K2P pairwise genetic distance (*B. adspersa*, *B. altamazonica*, *B. leandrae*, *B. nicefori*, *B. orestes*, *B. palmata*, *B. paraensis*, *B. peruviana*, *B. sima*, *B. tamaense*, and *B. mucuyensis*). *Bolitoglossa chucantiensis* can be distinguished from the closely related *B. guaneae* by several characters. In *B. guaneae* the SVL is shorter (31.53–41.56 mm [vs. 47.3]), the 3rd finger and toe tips are pointed and protruding (vs. a slight indentation is evident between the toe and fingertips), its coloration is pale brown to gray in preservative, and in life the coloration is dark brown, sometimes mottled or streaked with white (vs. the dorsal ground color is dark brown and contains patches of yellow speckling); similarly, *B. chucantiensis* can be differentiated from *B. biseriata* because the head of this species is shorter (an HL/SVL ratio of 8.7–10.5 [vs. 11.74]), the hand and foot are narrower (vs. a broad hand and foot), the dorsal ground color is brown, cream, or red and sometimes is patterned with single small dark or yellow dots (vs. the dorsal ground color is dark brown, and contains patches of yellow speckling that are paler toward the head; Fig. 3); although males are not available for comparison, 33–38 vomerine teeth are present in female *B. cuna* (vs. 25), the head and hands of this species are narrower in relation to the body length, and fewer maxillary teeth are present (Fig. 6). Additionally, *B. cuna* is a lowland species (vs. a highland species) found near sea level (see Discussion), and the body is more slender than that of *B. chucantiensis*. *Bolitoglossa medemi* is a species with 28–59 maxillary teeth (vs. 75), generally contains fewer teeth in relation to the body length (0.8–1.3 vs. 1.6), and the head is broader. *Bolitoglossa taylori* is a species with extensive webbing (vs. completely webbed), and its dorsal coloration usually consists of small or large blotches (vs. patches of yellow speckling).

***Description of holotype*:** Male, SVL 47.3 mm; 75 MT, 2 PMT, the PMT do not pierce the lip, 23 VT; trunk length 23.18 mm between the levels of the axilla and groin; the head is moderately broad with an SVL/HW ratio of 6.2; the head is distinctly wider than the neck; the distance across shoulders is 6.0 mm; the horizontal orbit diameter is 75% of the snout length; the eyes protrude beyond the lateral margins of the head and are visible in dorsal view; the nasolabial protuberances are evident and developed; the snout is truncate in dorsal view and slightly rounded to truncate in lateral view; the canthus rostralis is indistinct; the nostrils are small and located near the tip of the snout; a mental gland is present, oval, WMG 3.1 mm, LMG 2.6 mm; the body is cylindrical, with 13 costal grooves; the hands and feet are moderately broad (HAW = 7%, HFW = 10% of SVL), the feet are completely webbed, subterminal pads are evident on digits 2–3–4 on the foot and 2–3 on the hand; the fingers, in order of decreasing length, are III–II–IV–I; the toes are III–IV–II–V–I (Figs. 3F, 7 A–B); the tail is long, 55.0 mm and exceeding the standard length 1.17 of SVL; the hind limb is 10.0 mm, the forelimb is 11.0 mm; the maxillary teeth are relatively numerous, MT/SVL 1.6 times, and extend to about the level of the end of the eye; the vomerine teeth border the anterior orbit shape in the roof of mouth; paravomerine teeth are present and numerous; the tongue is enlarged and rounded in its anterior tip, with a concavity in the center; the prevomer clearly projects from the level of the palate, bearing

vomerine teeth in long, slightly arched series, and extends laterally almost to the center of the roof of the mouth. We include other measurements and counts in Table 1.

Coloration of the holotype in life (Fig. 3)**:** The color pattern of the holotype was recorded the day after capture (at 1730 h), as follows: the upper dorsum is Crimson (62); the flanks, tail, and limbs are Maroon (39), strongly speckled with Straw Yellow (53); the iris is Light Yellow Ocher (13) with Hazel (26) reticulations, and the eyelids are Straw Yellow (53); the venter is translucent with Warm Sepia (40) pigment, with the throat Straw Yellow (53); the ventral surfaces of the limbs are speckled with Straw Yellow (53).

***Coloration of the holotype in alcohol*:** The color pattern of the holotype was recorded after the specimen spent about two years in ethanol (70%), as follows: the upper dorsum is Verona Brown (37); the head region is Vandyke Brown (282); the flanks and limbs are Grayish Olive (274), speckled with Glaucous (272); the tail is Dusky Brown (285); the eyelids are Brownish Olive (292); and the venter is Smoke Gray (267).

Osteology (Fig.4)**:** The vertebral column consists of one atlas, 14 trunk vertebrae, one sacral, two caudosacral vertebrae, and 39 caudal vertebrae, with the first caudal process directed frontally; ribs are present on all the trunk vertebrae except for the last one, and are directed forwardly; the skull is well formed, and the visible structures of the head are the following: premaxilla, maxilla, nasals, vomer bodies, orbitosphenoids, and parasphenoid; the otic capsules are well developed and attached to the squamosals, the quadrates are barely visible and connected to the squamosals; the limbs are well developed; the digits are visible on all the limbs; the phalangeal formula for the hand is 1–2–3–2, and for the foot 1–2–3–3–2; and the metacarpal IV and metatarsal V are broader than the others (Fig. 4).

***Habitat and natural history notes*:** *Bolitoglossa chucantiensis* is known only from the type locality in the eastern Panamanian montane forest (*sensu* Fund and Hogan, 2012; Fig. 1) comprised of trees attaining heights of about 15 m, with their branches densely covered with bromeliads and other epiphytes (e.g., orchids, Loranthaceae), and with palms, vines, and bromeliads dominating the understory. The holotype was found at 2200 h, active on a palm leaf about 1 m above the ground, along a trail 200 m southwest from the ridge top. A drizzling rain had fallen between 1830 and 2100 h, but the conditions had turned calm, with only a slight breeze. Other species of amphibians and reptiles observed in the area that day were: *Oedipina* aff. *complex*, *Diasporus* sp., *Colostethus* aff. *pratti, Pristimantis moro*, *P. caryophyllaceus*, *P. cruentus*, *Espadarana prosoblepon*, *Silverstoneia* sp., *Ptychoglossus festae*, *Dendrophidion percarinatum*, and *Geophis* sp.

***Etymology*:** The species name is derived from the name of the mountain (Cerro Chucantí) where the holotype was found, with the Latin suffix *-ensis* indicating a place or locality. Chucantí is the highest point in the Cordillera de Majé, with an elevation of 1,439 m, and is part of the Chucantí Private Cloudforest Reserve, a protected area owned by Guido Berguido.

DISCUSSION

Bolitoglossa chucantiensis is a member of the *adspersa* group of the subgenus *Eladinea***,** the only group of the subgenus distributed in eastern Panama and northern South America. The new species can be distinguished from other members of the group by external features (TL/SVL and MT/SVL ratios, a brown dorsal coloration containing patches of yellow speckling) and by its relatively large genetic distance from other species in the group (> 5.5% in 16S and > 16% in COI). Herein we combined morphology and molecular genetics to compare the species of *Bolitoglossa* occurring in eastern Panama. Within the *adspersa* group, several examples of distinct species exhibit a smaller sequence divergence. For example, we analyzed sequences of *B. nicefori*, *B. tamaense*, and *B. leandrae* from Colombia and found a genetic divergence of 2.6% of p and K2P for 16S between the first two species, and only 2.0% of p and K2P for 16S between *B. nicefori* and *B. leandrae*. The mean genetic divergence among these species is 3.0% of K2P (Acevedo et al., 2013). While *B. tamaense* can be distinguished from *B. nicefori* by the different amount of webbing, *B. leandrae* is morphologically similar to *B. tamaense* but shows high maxillary tooth counts (29–30 vs. 35–40) and a distinct elevational distribution (Acosta-Galvis and Gutiérrez-Lamus, 2012; Acevedo et al., 2013). Nevertheless, an even lower genetic divergence (0.5% K2P) has been found for some morphologically well-defined sister species of the genus *Bolitoglossa* (Parra-Olea et al., 2004). Finally, the minimum threshold of 3% of pairwise genetic divergence applied in barcoding analyses of 16S mtDNA of amphibians (Vieites et al., 2009;

Crawford et al., 2010; Jansen et al., 2011) is not consistent to delineate among *Bolitoglossa* spp., as the morphological differences noted above justify the use of an even lower %-divergence to recognize separate species.

Although *B. chucantiensis* can be well differentiated from other species of *Bolitoglossa*, we refrain from assigning our second specimen from the Cordillera de Jingurudó to any recognized taxon. Initially, we treated it as conspecific with *B. chucantiensis* due to their low pairwise genetic distance (1.4% K2P). The recently described species, *B. guaneae* Acosta-Galvis and Gutiérrez-Lamus, 2012, from the Cordillera Oriental of the Colombian Andes, however, appears to exhibit a similar phenotype to our Jingurudó specimen. Unfortunately, neither molecular data nor tissue samples of *B. guaneae* were available for a genetic comparison. Thus, a taxonomic assignment of our Jingurudó specimen must await a proper analysis that includes more Colombian material and/or more specimens from the Cordillera de Jingurudó.

Among the other taxa of *Bolitoglossa* we collected in eastern Panama, we detected exceptionally high variation in morphological and molecular characters in specimens of *B. biseriata*, even within geographically close metapopulations or from the same locality. As already mentioned, the sample from Río Púcuro (SMF 97139) is unusual by showing a genetic distance of 3.5% K2P to samples from Río Tuquesa and San Blas (SMF 97127, MHCH 2659), which exceed the suggested threshold of genetic distance for species level within the genus (> 3.0%). The Río Púcuro specimen also possesses fully webbed feet (Fig. 7 K–L), which is strikingly different from other specimens of *B. biseriata* sampled in the area. In the context of a sample size too low to reveal the full morphological variation of foot webbing, we provisionally consider this an anomaly. The sample was collected relatively close to the type locality of *B. biseriata* (19.7 km NE) and its genetic distance from other conspecifics (MHCH 2658, S13236) with typical *biseriata* webbing on the feet (Fig. 7 I–J) is much lower (1.7 % of K2P). These facts, together with other morphological similarities, allocate the Río Púcuro specimen to *B. biseriata*. Another case of high variation is evident among three *B. biseriata* collected within the Cordillera de San Blas: almost twice as many maxillary teeth are present in SMF 97641 and SMF 97129 that in SMF 97127, found at the same locality (57–61 vs. 36), whereas the typical counts for other specimens collected in Panama range from 18 to 46. Furthermore, molecular distances also are quite variable, as the specimen with high tooth counts, SMF 97641, exhibits 3.1% K2P distance to the syntopic SMF 97127, which has a low tooth count, but only 1.0% K2P distance to MHCH 2658 (an adult male from Río Tuquesa) whose maxillary tooth count is even lower (18 maxillary teeth) and was found at a distance of about 82 km to the northwest. Although SMF 97641 was not included in the phylogenetic analysis due to an incomplete sequence of 16S mtDNA (only 192 bp, no sequence was obtained for COI), its morphological appearance corresponds well to that of other *B. biseriata* from the region (Fig. 8). Due to these incongruences in geographic pattern of molecular and morphological data, we treat *B. biseriata* as a species complex harboring deep conspecific lineages (Vieites et al., 2009; Padial et al., 2010). Therefore, we suggest treating it as a species complex until a larger sample size allows for a more detailed comparative analysis to better understand the extent of morphological and genetic variation. In the view of these data, the validity of *B. cuna* needs to be evaluated. Although Wake et al. (1973) state that the head of *B. cuna* is narrower than that of *B. biseriata,* we did not find any differences in HW/SVL ratio between these species (Fig. 6). The only character that might be useful to differentiate between them is maxillary tooth count (see key below). Since *B. cuna* is known only for the vicinity of the type locality (Solis et al. 2004), molecular data from this locality still are needed to clarify its status in relation to the *B. biseriata* complex, whose members are similar in overall appearance.

Bolitoglossa taylori was the least genetically variable species (average genetic distance within species = 0.2% K2P), but it showed considerable variation in coloration and skin texture (Fig. 10). This variation was documented by Wake et al. (1970: 9), who stated that the dorsal surfaces of *B. taylori* can be "light grayish brown, light brown, yellowish brown, orange-brown, or rich red-brown sometimes with extensive dark brown or black dorsal markings, and often with a dark brown lateral stripe". Such variability also has been described for other members of the genus (e.g., Vial, 1966; García-París et al., 2000, 2008). We summarize the morphological variation for the species reported from eastern Panama in the key below, and emphasize the importance of conserving Panama's primary rainforests to enable the survival and long-term persistence of these beautiful and valued amphibians.

Fig. 3. *Bolitoglossa chucantiensis* holotype. A–C = head and dorsal color pattern; D = ventral coloration; E = left foot; F = right hand; and G–H = internal parts of mouth.

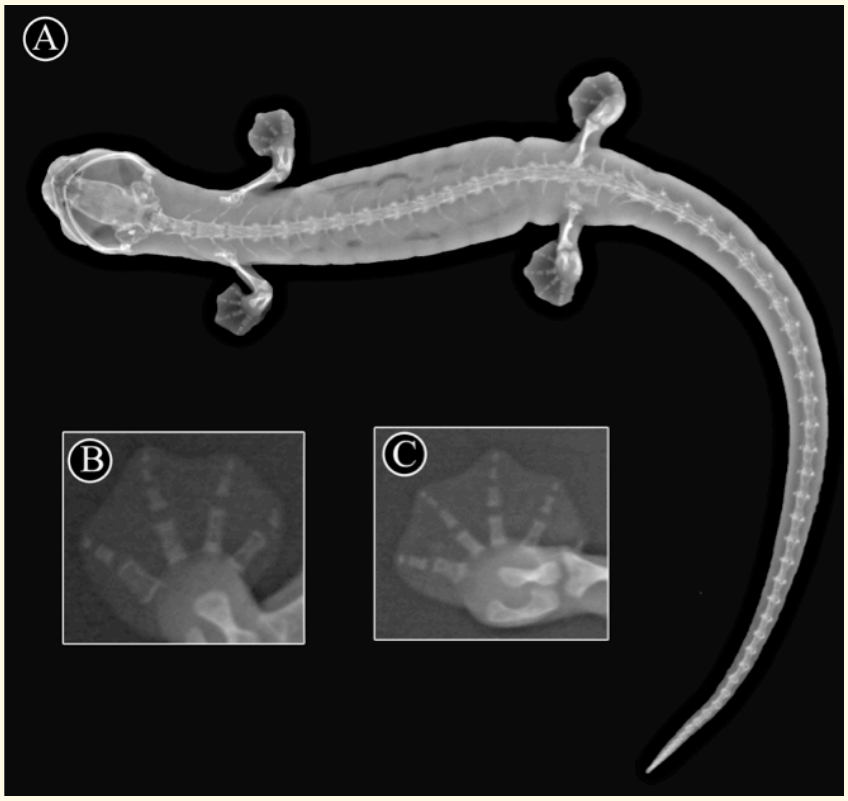

Fig. 4. X–ray images of the holotype of *B. chucantiensis*; A = entire body; B = left hand; and C = left foot.

Fig. 5. *Bolitoglossa* sp. (MHCH 2663), from the Cordillera de Jingurudó.

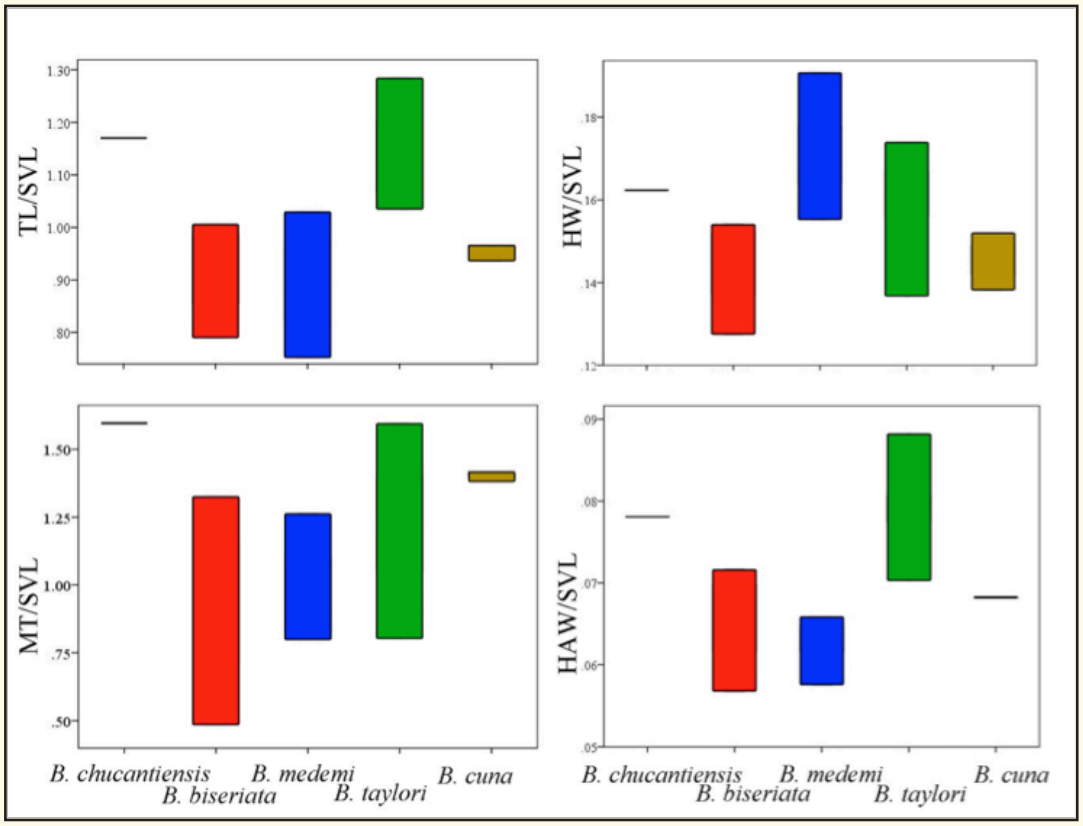

Fig. 6. Morphological diagnostic features showing differences among the species of *Bolitoglossa* from eastern Panama; data for *B. cuna* was taken from the original description (Wake et al., 1973); boxes represent the range of proportions (maximum and minimum values).

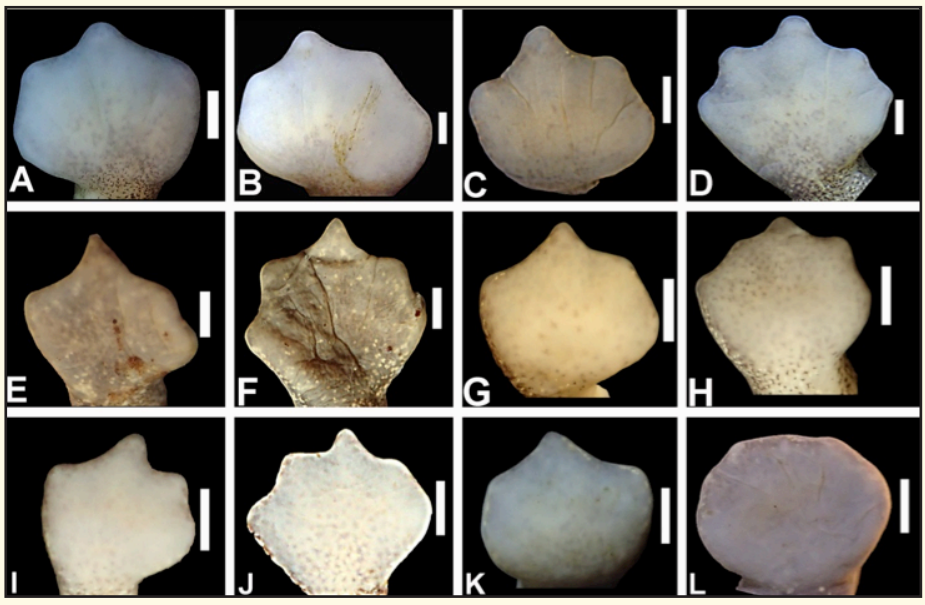

Fig. 7. Shape of the hands and feet in species of *Bolitoglossa* from eastern Panama. A–B = *B. chucantiensis* (holotype) A = left hand, B = right foot; C–D = *B. taylori* (MHCH 2667), C = right hand, D = left foot; E–F = *B. medemi* (MHCH 2662), E = right hand, F = left foot; G–H = *B. biseriata* (SMF 97129, San Blas), G = right hand, H = left foot; I–J = *B. biseriata* (MHCH 2658, Río Tuquesa), I = right hand, J = left foot; and K–L = *B. biseriata* (SMF 97139, Púcuro), K = left hand, L = right foot.

Fig. 8. Color variation in *B. biseriata*. A = Burbayar field station; B = San Blas ridge (SMF 97129); C = San Blas ridge (SMF 97127); D = San Blas ridge (SMF 97641); E = Río Pucuro (SMF 97139); F = Río Tuquesa (MHCH 2658); G = Donoso, Colón; and H = Río Tuquesa (MHCH 2659).

Fig. 9. Color variation in *B. medemi*. A–B = San Blas ridge (SMF 97130); C–D = San Blas ridge (SMF 97131); and E–F = Río Tuquesa (SMF 97132).

Fig. 10. Color variation in *B. taylori*. A = SMF 97136; B = SMF 97135; C = SMF 97133; D = SMF 97138; E = MHCH 2666; F = MHCH2669; G = left foot (SMF 97137); and H = left hand (SMF 97137).

Key to the genus *Bolitoglossa* in eastern Panama

1a. Tail length equal to SVL or distinctly longer, (TL/SVL = 1.04–1.28); tail cylindrical; dorsum mainly red or dark brown, uniform or with cream to yellow blotches or patches with speckles 2

1b. Tail shorter than SVL (TL/SVL = 0.75–1.03); tail cylindrical or laterally compressed; dorsal coloration uniform, bicolored, black, red, or brown 3

2a. Dorsum brown with large patches with yellowish speckling; feet completely webbed, with a slight indentation between tips of toes and fingers . . . . . *Bolitoglossa chucantiensis*

2b. Dorsum brown, black, cream, or red, without patches of yellow speckling; extensive webbing on feet, evident indentation between tips of toes and fingers . . . . . *Bolitoglossa taylori*

3a. Tail laterally compressed, tip of 3rd toe and 3rd finger sharply pointed, abruptly protruding the hand and foot . . . . . *Bolitoglossa medemi*

3b. Tail cylindrical; tip of 3rd toe and 3rd finger not abruptly protruding the hand or foot 4

4a. More than 66 maxillary teet . . . . . *Bolitoglossa cuna*

4b. Fewer than 61 maxillary teeth . . . . . *Bolitoglossa biseriata*

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Appendix 1. Supplementary table of specimens used in phylogenetic analyses, with their corresponding GenBank accession number of 16S and COI mtDNA.

Species	16S	COI	Country
B. adspersa MVZ 158485	AF218492 (4)		Colombia: Cundinamarca
B. alberchi MVZ 194293	AF218480 (4)		Mexico: Chiapas
B. alberchi MVZ 163959	AF218478 (4)		Mexico: Veracruz
B. alvaradoi MVZ 215735	AY526157		Costa Rica: Heredia: El Plástico
B. aureogularis UCR 19858	JQ899151		Costa Rica
B. aureogularis UCR 19859	JQ899152		Costa Rica
B. aureogularis UCR 19892	JQ899153		Costa Rica
B. aureogularis UCR 19893	JQ899154		Costa Rica
B. biseriata S13236	AY526118		Panamá: Nusagandi: Kuna Yala
B. bramei UCR 20483	JQ899159		Costa Rica
B. bramei UCR 20484	JQ899160		Costa Rica
B. bramei UCR 20851	JQ899142		Costa Rica
B. bramei MVZ 225893	—		
B. carri USNM 523276	AY526138		Honduras: Cerro Cantagallo
B. carri USNM 523277	AY526139		Honduras: Cerro Cantagallo
B. celaque SMF 78087	AY526140		Honduras: Lempira
B. celaque SMF 78088	AY526141		Honduras: Lempira
B. cerroensis MVZ 233516	AF199233		

B. cerroensis DBW5123	AF199233 (2)	Costa Rica: San José: Cuericí, 5 km E Villa Mills
B. colonnea No voucher	AY526119	Panamá: Chiriquí: Reserva Forestal Fortuna
B. colonnea SMF 94461	JX434645	Panama
B. colonnea SMF 94460	JX434644	Panama
B. colonnea CHP 6526	FJ766578	Panama
B. compacta UCR 20532	JQ899163	Costa Rica
B. conanti MVZ 225843	AY526142	Honduras: Cortés: El Cusuco
B. decora USNM 497533	AY526143	Honduras: Olancho: Monte Escondido
B. diaphora MVZ 225847	AY526144	Honduras: Cortés: El Cusuco
B. dofleini MVZ 161607	AF218497 (4)	Guatemala: Alta Verapaz
B. dunni USNM 523280	AY526145	Honduras: Cortés: San Pedro Sula
B. engelhardti MVZ 167789	AF218496 (4)	Guatemala: San Marcos
B. epimela MVZ 181260	AY526120	
B. epimela MVZ 181260	AY526120	Costa Rica: Cartago: Turrialba
B. epimela MVZ 181260	AY526120	
B. flavimembris MVZ 143698	AY526146	Guatemala: San Marcos
B. flaviventris MVZ 194288	AF218489 (4)	Mexico: Chiapas
B. franklini MVZ 185991	AY526147	Mexico: Chiapas: Volcán Tacaná
B. gomezi UCR 20399	JQ899155	Costa Rica
B. gomezi UCR 20413	—	Costa Rica
B. gomezi UCR 20414	JQ899156	Costa Rica
B. gomezi UCR 20415	JQ899157	Costa Rica
B. gomezi UCR 20417	JQ899158	Costa Rica
B. gomezi UCR 20843	JQ899140	Costa Rica
B. gomezi UCR 20844	JQ899147	Costa Rica
B. gomezi UCR 20845	JQ899148	Costa Rica
B. gomezi UCR 20846	JQ899149	Costa Rica
B. gomezi UCR 20847	—	Costa Rica
B. gomezi UCR 20848	JQ899139	Costa Rica
B. gomezi UCR 20849	JQ899141	Costa Rica
B. gomezi UCR 20850	JQ899146	Costa Rica
B. gracilis MVZ 229171	AY526122	Costa Rica
B. gracilis MVZ 229170	AY526121	Costa Rica: Cartago: Reserva Tapantí
B. gracilis MVZ 229171	AY526122	Costa Rica: Cartago: Reserva Tapantí
B. hartwegi MVZ (DBW945)	AF218494 (4)	Mexico: Chiapas
B. hermosa MVZ 163690	AF416686 (5)	Mexico: Guerrero: 11.3 mi NE Atoyac
B. jugivagans SMF 94467	KC428634	Panama
B. kamuk UCR 20852	JQ899143	Costa Rica
B. kamuk UCR 20853	JQ899144	Costa Rica
B. kamuk UCR 20854	JQ899145	Costa Rica
B. lignicolor SMF 91996	JX434643.1	Panama
B. lignicolor SMF 89803	JX434642.1	Panama
B. lignicolor SMF 91994	JX434641.1	Panama
B. lignicolor SMF 91997	JX434640.1	Panama
B. lignicolor SMF 94459	JX434639.1	Panama
B. lignicolor AH 431	JX434638.1	Panama
B. lincolni MVZ 143564	AY526148	Guatemala: San Marcos

B. longissima USNM 523285	AY526149	Honduras: Olancho: Pico La Picucha
B. macrinii GP 384	AF416689 (5)	Mexico: Oaxaca: San Gabriel Mixtepec
B. marmorea MVZ 210286	AF218493	
B. marmorea MVZ 210286	AF218493 (4)	Panamá: Chiriquí
B. medemi S13237	AY526123	Panamá: Nusagandi: Kuna Yala
B. mexicana MVZ 176838	GU725457	
B. mexicana MVZ 191635	AF177588 (4)	Belize: Toledo: Blue Creek
B. mexicana USNM 343451	AF218468 (4)	Honduras: Atlántida
B. mexicana (photo voucher Bo71)	AF218470 (4)	Mexico: Chiapas
B. minutula MVZ 225870	AY526124	
B. minutula MVZ 225870	AY526124	Costa Rica: Puntarenas: Las Tablas, Cerro Pando
B. mombachoensis SMF 78718	AY133488 (6)	Nicaragua: Granada
B. mombachoensis SMF 78725	AY133489 (6)	Nicaragua: Granada
B. morio MVZ 143677	AF218495 (4)	Guatemala: San Marcos
B. morio MVZ 232970	AY526150	Guatemala: San Marcos
B. nigrescens UCR 20539	JQ899164	Costa Rica
B. oaxacensis IBH 13374	AF416690 (5)	Mexico: Oaxaca: 40 km N San Gabriel Mixtepec
B. occidentalis MVZ 194254	AY526115	Mexico: Chiapas: Berriozabal
B. odonnelli MVZ 229068	AF218476 (4)	Honduras: Olancho
B. palmata KU 217422	AY526125	Ecuador: Napo: Cordillera de Guacamayos a 31 km de Baeza
B. palmata KU 217423	AY526126	Ecuador: Napo: Cordillera de Guacamayos a 31 km de Baeza
B. paraensis INPA 3098	AY526127	Brazil: Amazonas: Rio Juruá
B. paraensis LSUMZ H-3086	AY526128	Brazil: Amazonas: Rio Ituxi at the Madeireira Scheffer
B. paraensis LSUMZ H-13735	AY526129	Brazil: Acre: 5 km N Porto Walter
B. peruviana LSUMZ H-12838	AY526130	Ecuador: Sucumbios: Estación Científica University Católica, Cuyabeno
B. peruviana KU 217421	AY526131	Ecuador: Napo: Jatún Sacha
B. pesrubra UCR 12068	AY526132	Costa Rica
B. pesrubra MVZ 210360	EU448105	Costa Rica
B. pesrubra MVZ 190923	EU448104	Costa Rica
B. pesrubra MVZ210361	—	Costa Rica
B. platydactyla GP 108	AF218487 (4)	Mexico: Veracruz
B. platydactyla GP 587	AY133487 (6)	Mexico: Veracruz
B. porrasorum MVZ 225852	AY526151	Honduras: Atlántida: Cerro Búfalo
B. riletti MVZ 194328	AF416696 (5)	Mexico: Oaxaca: 20.9 km NE Putla
B. robinsoni UCR 20489	JQ899161	Costa Rica
B. robusta MVZ190830	EU448109	Costa Rica
B. rostrata MVZ 163683	AY526152	Guatemala: Huehuetenango
B. rostrata MVZ 163930	AY526153	Guatemala: Huehuetenango
B. rufescens MVZ 194333	AY526116	Belize: Toledo: Blue Creek National Park
B. schizodactyla No voucher	AY526133	Panamá: Coclé: Parque Nacional El Copé
B. sima MVZ 163575	AY526134	Colombia: Valle del Cauca
B. sombra CH 7478	JQ899165	Panama
B. sombra UCR 225871	AY526136	Costa Rica
B. soyoorum MVZ 190847	EU448108	Costa Rica
B. sp. 1 MVZ 167947	AY526135	Colombia: Cundinamarca: El Soche

B. sp. 2 MVZ 225871	AY526136		Costa Rica: Puntarenas
B. sp. 3 MVZ 233028	AY526154		El Salvador: Santa Ana: Metapán
B. sp. 3 MVZ 200535	AY526155		El Salvador: Santa Ana: Metapán
B. sp. 4 UCR 12066	AY526137		Costa Rica: Cartago: Macho Gaff
B. splendida UCR 19835	JQ899150		Costa Rica
B. striatula MVZ 181280	AF218488 (4)		Costa Rica: Cartago
B. subpalmata MVZ 194828	AF212091		Costa Rica
B. subpalmata MVZ 229172	AF416697 (5)		Costa Rica: Puntarenas: Monteverde Cloud Forest Preserve
B. synoria SMF 78084	AY526156		Honduras: Ocotepeque: Cerro El Pital
B. tica UCR 12065	AY526137		Costa Rica
B. tica UCR 20514	JQ899162		Costa Rica
B. tica MPG 2008	EU448106		Costa Rica
B. yucatana MVZ 197507	AF218485 (4)		Mexico: Quintana Roo
B. zapoteca IBH 13375	AF416698 (5)		Mexico: Oaxaca: Santa María Ecatepec
B. zapoteca IBH 13376	AF416699 (5)		Mexico: Oaxaca: Santa María Ecatepec
B. altamazonica KU 222111	AY526117		Perú: Loreto: 1.5 km N Teniente López
Nototriton matama UCR 20215	JQ899166		Costa Rica
Nototriton picadoi MVZ 225899	AF199144		Costa Rica
Oedipina alleni MVZ 190857	AF199207		Costa Rica
B. nicefori Clone 001	KC257105.1		Colombia
B. leandrae PAT 240	KC257104.1		Colombia
B. leandrae PAT236	KC257103.1		Colombia
B. leandrae PAT 237	KC257102.1		Colombia
B. tamaense PAT 431	KC257101.1		Colombia
B. tamaense PAT 451	KC257100.1		Colombia
B. tamaense PAT 363	KC257099.1		Colombia
B. tamaense PAT 387	KC257098.1		Colombia
B. biseriata MHCH 2658	KM527322	KM527307	Chiriquí, Panama
B. biseriata MHCH 2668	KM527334	KM527317	Darién Panama
B. chucantiensis **sp. nov.** MHCH 2665	KM527324	KM527308	Darién Panama
B. colonnea SMF 97136	KM527326	KM527310	Darién Panama
B. medemi MHCH 2660	KM527325	KM527309	Darién Panama
B. medemi SMF 97131	KM527327	KM527311	Darién Panama
B. medemi SMF 97133	KM527328	KM527312	Darién Panama
Bolitoglossa sp. SMF 97138	KM527329	KM527313	Darién Panama
B. taylori MHCH 2663	KM527331	KM527314	Darién Panama
B. taylori MHCH 2664	KM527333	KM527316	Darién Panama
B. taylori MHCH 2666	KM527340	KM527321	Darién Panama
B. taylori SMF 97128	KM527336	KM527319	Darién Panama
B. taylori SMF 97130	KM527337	KM527320	Darién Panama
B. taylori SMF 97139	KM527332	KM527315	Darién Panama
B. taylori SMF 97141	KM527335	KM527318	Darién Panama
B. biseriata SMF 97135	KM527339		Darién Panama
B. taylori SMF 97140	KM527323		Darién Panama
B. schyzodactyla SMF 97127	KM527338		Darién Panama
B. biseriata MHCH 2659	KM527330		Darién Panama

Appendix 2. Supplementary table of specimens and their respective localities, used for morphological comparisons.

Voucher	Species	Locality	Country	Coordinates		Elev. (m)
				N	W	
SMF97127	*B. biseriata*	Serranía de San Blas	Panama	9.0602	–77.9827	463
SMF97641	*B. biseriata*	Serranía de San Blas	Panama	9.0602	–77.9827	463
MHCH2663	*B.* sp.	Filo entre río Sambú and quebrada Aldo, Serranía de Jingurudó.	Panama	7.6802	–78.0387	958
SMF97141	*B. chucantiensis*	Cerro Chucantí, Serranía de Majé	Panama	8.8034	–78.4601	1,424
SMF97128	*B. colonnea*	Camino Cable Car, Reserva Forestal Fortuna, Chiriquí	Panama	8.7185	–82.2331	1,217
MHCH2658	*B. cuna*	Bajo pequeño, Río Tuquesa, camp2 Cerro Pechito parado, Serranía de Darién	Panama	8.4755	–77.5488	472
MHCH2659	*B. cuna*	Bajo pequeño, Río Tuquesa, camp2 Cerro Pechito parado, Serranía de Darién	Panama	8.4791	–77.5280	718
SMF97129	*B. cuna*	Serranía de San Blas	Panama	9.0602	–77.9827	463
MHCH2660	*B. medemi*	Bajo pequeño, Río Tuquesa, camp3 Cerro Pechito parado, Serranía de Darién	Panama	8.4800	–77.5194	859
MHCH2661	*B. medemi*	Bajo pequeño, Río Tuquesa, camp3 Cerro Pechito parado, Serranía de Darién	Panama	8.4791	–77.5280	718
MHCH2662	*B. medemi*	Bajo pequeño, Río Tuquesa, camp3 Cerro Pechito parado, Serranía de Darién	Panama	8.4791	–77.5280	718
SMF97130	*B. medemi*	Serranía de San Blas	Panama	9.0614	–77.9796	344
SMF97131	*B. medemi*	Serranía de San Blas	Panama	9.0611	–77.9797	340
SMF97132	*B. medemi*	Bajo pequeño, Río Tuquesa, camp2 Cerro Pechito parado, Serranía de Darién	Panama	8.4791	–77.5280	718
SMF97140	*B. schizodactyla*	Cerro Narices, Parque Nacional Santa Fé, Provincia de Veraguas	Panama	8.5632	–81.0524	841
MHCH2664	*B.* sp.	Cerro Chucantí, Serranía de Majé	Panama	8.8034	–78.4601	1,424
SMF97139	*B. biseriata*	Río Púcuro river, Serranía de Darien	Panama	8.0410	–77.3613	306
MHCH2665	*B. taylori*	Serranía de Pirre	Panama	7.9791	–77.7085	1,124
MHCH2666	*B. taylori*	Serranía de Pirre	Panama	7.9769	–77.7085	1,104
MHCH2667	*B. taylori*	Serranía de Pirre	Panama	7.9615	–77.7037	1,310
MHCH2668	*B. taylori*	Serranía de Pirre	Panama	7.9615	–77.7037	1,310
MHCH2669	*B. taylori*	Serranía de Pirre	Panama	7.9474	–77.7042	1,317
SMF97133	*B. taylori*	Serranía de Pirre	Panama	7.9880	–77.7076	1,135
SMF97134	*B. taylori*	Serranía de Pirre	Panama	7.9779	–77.7085	1,112
SMF97135	*B. taylori*	Serranía de Pirre	Panama	7.9786	–77.7085	1,112
SMF97136	*B. taylori*	Serranía de Pirre	Panama	7.9789	–77.7085	1,129
SMF97137	*B. taylori*	Serranía de Pirre	Panama	7.9632	–77.7043	1,267
SMF97138	*B. taylori*	Serranía de Pirre	Panama	7.9474	–77.7042	1,317
UMNH3847	*B. biseriata*	Río Paya	Panama	7.9041	–77.4755	100
KUH116520	*B. biseriata*	Campamento Sasardi, Serranía de San Blas	Panama	8.8888	–77.7229	12
KUH116521	*B. biseriata*	Campamento Summit, Serranía de San Blas	Panama	8.8558	–77.7472	358
KUH116523	*B. biseriata*	Boca de Río Concepcion	Panama	8.8320	–80.9794	10
KU116519	*B. cuna*	Campamento Sasardi, San Blas	Panama	8.8888	–77.7229	12
USNM150036	*B. cuna*	Armila, San Blas	Panama	8.6624	–77.4646	10
S13237	*B. medemi*	Nusagandi, San Blas	Panama	9.3300	–78.9667	356
KU116530	*B. medemi*	Jaque–Imamado, Cordillera de Jurado	Panama	7.3805	–77.9550	800
KU116534	*B. medemi*	Río Imamado	Panama	7.4270	–77.9647	50

KU116544	*B. taylori*	Filo sur, Cerro Cituro, Serranía de Pirre	Panama			1,100
GML6077	*B. taylori*	Filo sur, Cerro Cituro, Serranía de Pirre	Panama			1,100
KU116540	*B. taylori*	Filo sur, Cerro Cituro, Serranía de Pirre	Panama			1,100
KU116542	*B. taylori*	Filo sur, Cerro Cituro, Serranía de Pirre	Panama			1,100
KU116535	*B. taylori*	Vertiente sureste de Cerro Pirre	Panama			1,440
KU116543	*B. taylori*	Filo sur, Cerro Cituro, Serranía de Pirre	Panama			1,100
KU116545	*B. taylori*	Filo sur, Cerro Cituro, Serranía de Pirre	Panama			1100
KU116539	*B. taylori*	Filo norte, Cerro Cituro, Serranía de Pirre	Panama			900–1,000
KU116538	*B. taylori*	Filo norte, Cerro Cituro, Serranía de Pirre	Panama			960
BM 97.11.12.22	*B. phalarosoma*	Medellín, Antioquia	Panama			1,538
BM 97.11.12.21	*B. phalarosoma*	Medellín, Antioquia	Panama			1,538
KU116533	*B. medemi*	Río Jaqué, Darien	Panama	7.4167	–77.9486	50
LAMC42276	*B. medemi*	Finca Chibiguí, Río Arquía, Antioquia	Colombia	6.2499	–76.4999	300
LAMC42278	*B. medemi*	Finca Chibiguí, Río Arquía, Antioquia	Colombia			
LAMC42279	*B. medemi*	Río Opogodó at Serranía de Baudo	Colombia	6.8334	–77.2999	80
LAMC42280	*B. medemi*	Camino entre Río Opogodó y Río Napipí	Colombia	6.7167	–77.1663	60
LAMC70565	*B. medemi*	Alto de Buey, Chocó	Colombia			400
LAMC70566	*B. medemi*	Camino de Yupe, Chocó	Colombia			605
LAMC70567	*B. medemi*	Camino de Yupe, Chocó	Colombia			400–500
LAMC70568	*B. medemi*	Camino de Yupe, Chocó	Colombia			605
LAMC72067	*B. medemi*	Finca Chibiguí, Río Arquía, Antioquia	Colombia			
ICN–MHN 54440	*B. guaneae*	Río Fonce, vereda La Chapa, flanco oeste de la Cordillera Oriental	Colombia	6.1351	–73.0991	1,836

Abel Batista is a Panamanian who received a Masters degree in Biological Sciences at the Universidad de los Andes in Bogotá, Colombia, and currently is a Ph.D. student at Senckenberg Research Institute, Frankfurt am Main, Germany. Abel is specializing in the study of amphibians and reptiles from eastern Panama, and his research focuses on barcoding, biogeography, conservation, taxonomy, and bioacoustics.

Gunther Köhler received a degree in Veterinary Medicine (Staatsexamen) at the University Gießen, Germany in 1993 and a doctoral degree at Goethe University Frankfurt am Main, Germany in 1995; since that time he has been the Curator of Herpetology at the Senckenberg Research Institute, Frankfurt am Main, Germany. His research focuses on the Neotropical herpetofauna, primarily that of Central America and Mexico. To date, Gunther has authored 26 books and 165 research papers on amphibians and reptiles.

Konrad Mebert is an independent researcher and international project coordinator based in Switzerland, who focuses on reptiles. After completing a Master's degree on geographic variation and the effects of inbreeding on the Dice Snake at the University of Zürich, Switzerland, and a doctoral degree on hybrid zones in North American water snakes at Old Dominion University, Virgina, he currently is associated with the University of Basel in Switzerland. To date, Konrad has authored more than 80 professional and popular publications and two books on such topics as evolution, ecology, biodiversity, and conservation. His passion for photography and love of travel have led him to all continents except Australia, but his preference is the Neotropics where he has developed a special affection for Panama.

Milan Vesely is a biologist (Ph.D.) who is vice-president of Czech Herpetological Society. An assistant professor in the Department of Zoology at Palacky University in Olomouc, Czech Republic, for almost two decades Milan has focused his research interests on the herpetofauna of Central America. During his career, Milan has authored numerous popular and scientific papers on amphibian and reptile taxonomy, ecology, and parasites, and also is co-author (with Gunther Köhler and Eli Greenbaum) of a book entitled *The Amphibians and Reptiles of El Salvador*.