Systematic revision of the Bolitoglossa mexicana species group *(Amphibia: Plethodontidae)* with description of a new species from México

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Running title: Systematics of *Boliotoglossa mexicana* group.

Resumen: Revisión sistemática del grupo de especies de *Bolitoglossa mexicana* (Amphibia: Plethodontidae) con la descripción de una especie nueva de México. - En este trabajo se revisa la taxonomía y sistemática de las salamandras del grupo de *Bolitoglossa mexicana*. La revisión se basa en el análisis filogenético de secuencias de ADN mitocondrial, morfología, y en el examen de series típicas de la mayor parte de las especies. El grupo de *Bolitoglossa mexicana* es un conjunto monofilético de salamandras de gran tamaño, con cola larga, extremedidades grandes, casi completamente palmeadas y que generalmente presentan coloraciones llamativas, con manchas o bandas amarillas, anaranjadas o rojas sobre fondo obscuro. Las especies de este grupo se distribuyen en zonas tropicales de baja altitud, desde San Luis Potosí en el noreste de México, hasta Panamá. En el grupo se incluyen *Bolitoglossa flaviventris*, *Bolitoglossa jacksoni*, *Bolitoglossa lignicolor*, *Bolitoglossa mexicana*, *Bolitoglossa mulleri*, *Bolitoglossa odonnelli*, *Bolitoglossa platydactyla*, *Bolitoglossa salvinii*, *Bolitoglossa striatula*, y *Bolitoglossa yucatana*, a las que hay que añadir *Bolitoglossa mombachoensis*, descrita recientemente, y una especie nueva, *Bolitoglossa alberchi*, que se describe en este trabajo. El nombre *B. mexicana* debe aplicarse en un sentido más restrictivo, ya que algunas poblaciones incluidas con anterioridad en este taxon no forman parte del mismo; mientras que el nombre *B. odonnelli* se aplica en sentido amplio, al incluir bajo esa denominación poblaciones morfológicamente indistinguibles de *B. mexicana*. El análisis filogenético pone de manifiesto la existencia de un problema biológico complicado, ya que los grupos monofiléticos correspondientes a *B. mexicana* y a *B. odonnelli* respectivamente, no constituyen un grupo hermano a pesar de ser morfológicamente indistinguibles entre sí. Este problema no puede resolverse con el análisis exclusivo de marcadores mitocondriales.
Palabras clave: Sistemática, Filogenia, ADN Mitocondrial, Caudata, Plethodontidae, *Bolitoglossa*, grupo *B. mexicana*, Región Neotropical.

Abstract: We revise the systematics and taxonomy of the *Bolitoglossa mexicana* species group, based on analysis of mitochondrial DNA sequences, morphology, and study of typical specimens. The group is a monophyletic assemblage of large-bodied, long-tailed species with large, nearly fully-webbed hands and feet, usually having striking color patterns of tan to bright yellow, orange, or reddish spots, bands and stripes on a dark black background. The species of the group occur mainly in the lowlands, from San Luis Potosí in northeastern México to Panamá. To the taxa previously included in the group, *Bolitoglossa flaviventris*, *Bolitoglossa jacksoni*, *Bolitoglossa lignicolor*, *Bolitoglossa mexicana*, *Bolitoglossa mulleri*, *Bolitoglossa odonnelli*, *Bolitoglossa platydactyla*, *Bolitoglossa salvinii*, *Bolitoglossa striatula*, and *Bolitoglossa yucatana*, we add the recently described *Bolitoglossa mombachoensis*, and a new species described herein, *Bolitoglossa alberchi*. The name *B. mexicana* is applied in a more restrictive sense than formerly, while the name *B. odonnelli* is now used broadly to designate specimens previously assigned to *B. mexicana* on morphological criteria. Well-defined, non-sister, mitochondrial clades corresponding to the morphologically indistinguisable *B. mexicana* and *B. odonnelli* clades pose a complicated biological problem which cannot be solved with the exclusive use of mitochondrial markers.
Key words: Systematics, Phylogeny, Mitochondrial DNA, Caudata, Plethodontidae, *Bolitoglossa*, *B. mexicana* group, Neotropics.

INTRODUCTION

Bolitoglossa is the largest and most widely distributed genus in the Order Caudata and includes about 20% of the recognized salamander species. The genus is currently subdivided in two large informal "alpha" and "beta" sections (WAKE & LYNCH, 1976), each containing a number of species groups (WAKE & ELIAS, 1983). Although discerning phylogenetic structure within the genus has proven to be difficult, because of the extensive homoplasy that characterizes tropical salamanders (WAKE, 1991; WAKE & ELIAS, 1983), a recent study of sequences of two mitochondrial DNA (mtDNA) genes (GARCÍA-PARÍS *et al.*, 2000), provided support for the recognition of a well-defined monophyletic clade corresponding closely to the *Bolitoglossa mexicana* group (sensu TAYLOR, 1952; BRAME AND WAKE, 1963; WAKE AND ELIAS, 1983; GARCÍA-PARÍS *et al.*, 2000).

The *Bolitoglossa mexicana* group is an assemblage of large-bodied, long-tailed species with large, nearly fully-webbed hands and feet, often having striking color patterns of tan to bright yellow, orange, or reddish spots, bands and stripes on a dark blackground color. The species of the group occur mainly in the lowlands from San Luis Potosí in northeastern México to Panamá, except in Chiapas, México where they reach relatively high elevations (approximately 1500 m). They are not commonly encountered (although they were abundant at one time; TAYLOR & SMITH, 1945), and their populations occur usually in low densities; accordingly samples for either detailed morphological or allozyme studies are difficult to obtain. Taxa included in the group are: *Bolitoglossa flaviventris* (Schmidt, 1936), *Bolitoglossa jacksoni* Elias, 1984, *Bolitoglossa lignicolor* (Peters, 1873), *Bolitoglossa mexicana* Duméril, Bibron and Duméril 1854, *Bolitoglossa mulleri* (Brocchi, 1883), *Bolitoglossa odonnelli* (Stuart, 1943), *Bolitoglossa platydactyla* (Gray, 1831), *Bolitoglossa salvinii* (Gray 1868), *Bolitoglossa striatula* (Noble, 1918) and *Bolitoglossa yucatana* (Peters, 1882) (WAKE & ELIAS, 1983; FROST, 1985; GARCÍA-PARÍS *et al.*, 2000), plus the recently described Nicaraguan species *Bolitoglossa mombachoensis* Köhler & McCranie 1999.

Previous phylogenetic studies based on mtDNA sequences (GARCÍA-PARÍS *et al.*, 2000) challenged the monophyly and taxonomic status of the species *B. mexicana* and *B. odonnelli* and proposed that: 1) *B. mexicana* is a non-monophyletic assemblage composed of two or three species, and 2) the morphological distinctiveness of *B. odonnelli* with respect to *B. mexicana* is not correlated with its genetic divergence. Mitochondrial DNA sequences of the *Bolitoglossa mexicana* species complex are phylogenetically placed in three monophyletic clades, some of them more closely related to other species of the group than to each other. Although the overall monophyly of *B. mexicana* plus *B. odonnelli* was not rejected using signed-rank tests (TEMPLETON, 1983), *B. mexicana* remains paraphyletic since *B. odonnelli* is deeply nested within it. These problems added even more confusion to the already complicated taxonomic status of the taxon (SMITH, 1945; MITTLEMAN & SMITH, 1948; THIREAU, 1986).

In this paper we revise the taxonomy and nomenclature of the *B. mexicana* group, including the description of a new species from México. An examination of most of the type material available for the group forces us to introduce some additional nomenclatural changes. We re-analyze the mtDNA data of GARCÍA-PARÍS *et al.* (2000) with the addition of new sequences of the cytochrome b (cyt b) and 16S mtDNA genes for *B. mombachoensis*.

MATERIALS AND METHODS

Phylogenetic analyses of relationships within the *B. mexicana* group and support for its monophyly on molecular grounds have been

presented previously (GARCÍA-PARÍS *et al.*, 2000). Tail tips from two individuals of *B. mombachoensis* and one additional individual of *B. platydactyla* were used to obtain genomic DNA following a protocol modified from MILLER *et al.* (1988). Fragments of 647 base pairs, corresponding to codons 7 (part)-223 (part) of the *Xenopus* cyt b gene (ROE *et al.*, 1985), and of approximately 520 bp of the 16S rDNA corresponding to positions 2510-3059 in the human mitochondrial genome (ANDERSON *et al.*, 1981), were amplified via the polymerase chain reaction (SAIKI *et al.*, 1988) using the primers MVZ 15 and MVZ 18 (MORITZ *et al.*, 1992) for cyt b, and 16Sar and 16Sbr (PALUMBI *et al.*, 1991) for 16S. PCR reactions, DNA sequencing, and sequence alignment were performed as described earlier (GARCÍA-PARÍS *et al.*, 2000).

Phylogenetic inference was based on parsimony (MP) analyses (SWOFFORD, 1997) in combination with various weighting schemes, and on maximum likelihood (ML) analyses (FELSENSTEIN, 1981). Each base position was treated as an unordered character with four alternative states. Positions with gaps were excluded from the analyses or, alternatively, gaps were treated as missing data. Trees were rooted by outgroup comparisons with sequences of *Bolitoglossa adspersa*. Maximum parsimony phylogenies were estimated using the branch and bound algorithm. We searched for the most parsimonious trees with the program PAUP 4.0b5 (D. Swofford, Smithsonian Institution) by using two weighting schemes: assuming equal weights for every codon position, and using a differential transition/transversion weighting scheme (ts/tv = 1/3) and differential weighting of codon positions (3:9:1 for 1st, 2nd and 3rd respectively). We report decay indices (decay) and bootstrap (bs) values in excess of 50% (1000 replicates). Maximum likelihood analyses were performed on the combined (cyt b and 16S) data set. GenBank accession numbers for the sequences of *B. mombachoensis* and *B. platydactyla* as well as previous accession numbers for sequences of this clade are reported in Table 1. A list of specimens used for the mtDNA study and their complete locality data are shown in Appendix 1.

External morphology and coloration were examined in members of the three mitochondrial clades involving samples of the *B. mexicana* complex (GARCÍA-PARÍS *et al.*, 2000). These specimens represent most of the geographic range of the complex from the Atlantic coast of México (Veracruz) to central Honduras. We chose 15 adult specimens from near Palenque (Chiapas, México), part of the type series of *B. moreleti* (Smith, 1945), to represent "Clade 1" of GARCÍA-PARÍS *et al.* (2000), 22 specimens from Playa Escondida near Catemaco (Veracruz, México) to represent "Clade 2", and a series of 12 specimens from Finca El Volcán (Alta Verapaz, Guatemala), the type locality of *B. odonnelli*, to represent "Clade 3" for the morphometric analysis (Appendix 2). We measured 12 highly repeatable dimensions which reflect size and proportional shape of the salamanders (snout-vent length, tail length, snout to gular fold length, head width, axilla-groin length, forelimb length, hind limb length, shoulder width, foot width, head depth, interorbital width and internarial width). Measurements were taken to the nearest 0.01, using vernier calipers. Statistical analyses were run with the program Statistica v. 4.1. We used stepwise discriminant function analyses to ascertain the power of morphological characters to define groups. All measurements were log transformed to meet the assumptions of multivariate normality.

RESULTS

Mitochondrial DNA

We re-analyzed previously published sequences of cyt b and 16S mtDNA genes of samples from the *B. mexicana* group, with the addition of sequences of *B. mombachoensis*

Table 1: Samples used for the DNA analyses, locality, voucher specimen number (or field collector number, where voucher not yet available), and GenBank accession numbers. Cytb accession numbers were inadvertently omitted from Table 1 of García-París et al. (2000).
Tabla 1: Muestras usadas en los análisis de ADN, localidades, número de catálogo del ejemplar (o número de campo, cuando no se posee número de catálogo), y número de entrada de las secuencias en el GenBank ("accession numbers"). Los números de entrada para las secuencias del citocromo-b se omitieron de forma inadvertida de la Tabla 1 de García-París et al. (2000).

Sample no.	Species	Previous designation	Locality and population no.	Museum # no.	Cyt b	16S
1	*B. mexicana*	*B. mexicana*	Belize: Toledo (1)	MVZ 191635	AF212099	AF177588
2	*B. mexicana*	*B. mexicana*	Belize: Toledo (1)	MVZ 191631	–	AF177589
3	*B. mexicana*	*B. mexicana*	Belize: Toledo (1)	MVZ 191632	–	AF218467
4	*B. mexicana*	*B. mexicana*	Honduras: Atlántida (2)	USNM 343451	AF212975	AF218468
5	*B. mexicana*	*B. mexicana*	Honduras: El Paraíso (3)	UTA (ENS 8675)	–	AF218469
6	*B. mexicana*	*B. mexicana*	México: Chiapas (4)	(photo voucher)	AF212976	AF218470
7	*B. odonnelli*	*B. mexicana*	Honduras: Cortés (5)	MVZ 163794	–	AF218471
8	*B. odonnelli*	*B. mexicana*	Honduras: Cortés (5)	MVZ 163795	–	AF218472
9	*B. odonnelli*	*B. mexicana*	Honduras: Cortés (5)	MVZ 163793	–	AF218473
10	*B. odonnelli*	*B. mexicana*	Guatemala: Izabal (6)	UTA (MEA 446)	–	AF218474
11	*B. odonnelli*	*B. mexicana*	Guatemala: Izabal (6)	UTA (ENS7862)	–	AF218475
12	*B. odonnelli*	*B. mexicana*	Honduras: Olancho (7)	MVZ 229068	AF212977	AF218476
13	*B. odonnelli*	*B. mexicana*	Honduras: Copán (8)	MVZ 163797	–	AF218477
14	*B. alberchi*	*B. mexicana*	México: Veracruz (9)	MVZ 163959	AF212978	AF218478
15	*B. alberchi*	*B. mexicana*	México: Veracruz (9)	MVZ 172667	——-	AF218479
16	*B. alberchi*	*B. mexicana*	México: Chiapas (10)	MVZ 194293	AF212979	AF218480
17	*B. alberchi*	*B. mexicana*	México: Chiapas (11)	MVZ 138658	–	AF218481
18	*B. odonnelli*	*B. odonnelli*	Guatemala: Alta Verapaz (12)	MVZ 161046	–	AF218482
19	*B. odonnelli*	*B. odonnelli*	Guatemala: Alta Verapaz (12)	MVZ 161039	–	AF218483
20	*B. lignicolor*	–	Costa Rica: Puntarenas	MVZ (S11132)	–	AF218484
21	*B. yucatana*	–	México: Quintana Roo	MVZ 197507	AF212980	AF218485
22	*B. yucatana*	–	México: Quintana Roo	MVZ 197508	–	AF218486
23	*B. platydactyla*	–	México: Veracruz	MVZ (GP108)	AF212981	AF218487
24	*B. platydactyla*	–	México: Veracruz	MNCN (GP587)	***	***
25	*B. striatula*	–	Costa Rica: Cartago	MVZ 181280	AF212982	AF218488
26	*B. mombachoensis*	–	Nicaragua: Granada	SMF 78718	***	***
27	*B. mombachoensis*	–	Nicaragua: Granada	SMF 78725	***	***
28	*B. flaviventris*	–	México: Chiapas	MVZ 194288	AF212983	AF218489
29	*B. flaviventris*	–	México: Chiapas	MVZ 194287	–	AF218490
30	*B. flaviventris*	–	México: Chiapas	MVZ 163963	–	AF218491
31	*B. adspersa*	–	Colombia: Cundinamarca	MVZ 158485	AF212984	AF218492

and *B. platydactyla* (Table 1). The polytypic *Bolitoglossa mexicana* complex is represented by 19 samples in the analyses. The specimen from Veracruz, México, corresponding to sample 14, was sequenced again for both genes in order to replace the incomplete sequences used in a previous study (GARCÍA-PARÍS *et al.*, 2000). Sequence divergence among taxa is shown in Tables 2 and 3.

Parsimony analysis of the 16S data set produced 60 equally parsimonious trees. We treated gaps as missing data and used the branch and bound algorithm and equal weights for all positions (L = 137 steps; 51 characters were parsimony informative; CI = 0.679; RI = 0.728) (Fig. 1). Samples formerly included in the taxon *B. mexicana* are represented in three clades (samples 1 to 17). A subset of samples from Honduras, Belize, and southern Chiapas (samples 1 to 6) form a clade ("Clade 1") (bs 73%, decay 2). Samples from east-central Veracruz and from western Chiapas form another clade ("Clade 2") (bs 68%, decay 1). Samples from Honduras and Guatemala (samples 7 to13), including typical *B. odonnelli* (samples 18 and 19), form a third clade ("Clade 3") (bs 95%, decay 4). Relationships among these clades are not resolved (Fig. 1), but they collectively do not form a monophyletic group. Analysis of the cyt b data set produced two equally parsimonious trees using the branch and bound algorithm and equal weights for all positions (not shown) in which samples formerly included in *B. mexicana*, are again arranged in three clades.

The combined analysis of the cyt b and 16S data sets produced two equally parsimonious trees using the branch and bound algorithm and equal weights for all positions and treating gaps as missing data (L = 533 steps; 174 characters were parsimony informative; CI = 0. 675; RI = 0. 591) (Fig. 2). The two trees differ in the postion of *B. flaviventris* relative to *B. platydactyla*. The topology of the tree is identical to the topology generated using the cyt b equally weighted data set. Samples formerly included in *B. mexicana* are represented in the same three clades discussed above. A subset of samples from Honduras, Belize, and southern Chiapas form a clade ("Clade 1") (bs 92%, decay 4), with *B. striatula* plus *B. mombachoensis*, forming a basal clade sister to "Clade 1"(bs 84%, decay 3). Samples from east-central Veracruz and western Chiapas form a clade ("Clade 2") (bs 100%, decay 15).

Fig. 1 (la tenemos, pero no podemos abrirla)

Figure 1.- Strict consensus of the 60 equally most parsimonious trees found for sequences of the 16S ribosomal mtDNA. We treated gaps as missing data and used the branch and bound algorithm and equal weights for all positions (L = 137 steps; 51 characters were parsimony informative; CI = 0.679; RI = 0.728). Bootstrap values in excess of 50% are shown above branches. Decay indices are shown below branches. Sample numbers correspond to Table 1.

Figura 1.- Consenso (estricto) de los 60 árboles con número mínimo de pasos generados usando métodos de parsimonia con secuencias de la subunidad 16S del ADN ribosómico mitocondrial. Las posiciones afectadas por inserciones-delecciones se trataron como falta de datos. Se usó el algoritmo "branch and bound" y pesos iguales para todas las posiciones (L = 137 pasos; 51 caracteres informativos; CI = 0.679; RI = 0.728). Se muestran los valores de "bootstrap" superiores al 50%. Los índices de robustez ("decay") se muestran bajo las ramas. Los números de las muestras corresponden a los de la Tabla 1.

Table 2: Matrix of corrected K2P distances for cyt b (above diagonal) and 16S (below diagonal) between samples of the *Bolitoglossa mexicana* species-complex.
Tabla 2: Matriz de distancias corregidas ("K2P") entre secuencias de citocromo b (encima de la diagonal) y de 16S (por debajo de la diagonal) de muestras correspondientes a ejemplares del complejo de *Bolitoglossa mexicana*.

			1	2	3	4	5	6	7	8	9	10
1	*B. mexicana*	1(2,3)	–	0.0094	0.0553	0.1055	0.0999	–	–	0.1126	–	–
2	*B. mexicana*	4(5)	0.0059	–	0.0515	0.1135	0.1039	–	–	0.1167	–	–
3	*B. mexicana*	6	0.0179	0.0240	–	0.1180	0.1094	–	–	0.1175	–	–
4	*B. alberchi*	16(17)	0.0261	0.0323	0.0240	–	0.0286	–	–	0.1105	–	–
5	*B. alberchi*	14(15)	0.0220	0.0281	0.0240	0.0039	–	–	–	0.1171	–	–
6	*B. odonnelli*	7,9,13	0.0386	0.0450	0.0365	0.0200	0.0200	–	–	–	–	–
7	*B. odonnelli*	8	0.0365	0.0428	0.0345	0.0220	0.0220	0.0019	–	–	–	–
8	*B. odonnelli*	12	0.0365	0.0429	0.0343	0.0179	0.0179	0.0039	0.0059	–	–	–
9	*B. odonnelli*	10,11	0.0407	0.0471	0.0387	0.0179	0.0179	0.0019	0.0039	0.0059	–	–
10	*B. odonnelli*	18,19	0.0407	0.0471	0.0387	0.0220	0.0220	0.0019	0.0039	0.0059	0.0039	–

Table 3: Corrected sequence divergence (K2P distances) for cyt b (above diagonal) and 16S (below diagonal) between species of the *Bolitoglossa mexicana* species-group.
Table 3: Divergencia corregida entre secuencias ("K2P") del citocromo b (encima de la diagonal) y del 16S (por debajo de la diagonal) de muestras de especies del grupo de *Bolitoglossa mexicana*.

			1	2	3	4	5	6	7	8	9	10
1	*B. mexicana*	4	–	0.1039	0.1167	–	0.0957	0.1339	0.1336	0.1007	0.0743	0.1577
2	*B. alberchi*	14	0.0281	–	0.1171	–	0.1229	0.1344	0.1262	0.1417	0.1126	0.1506
3	*B. odonnelli*	12	0.0429	0.0179	–	–	0.1136	0.1463	0.1350	0.1216	0.1212	0.1506
4	*B. lignicolor*	20	0.0447	0.0280	0.0300	–	–	–	–	–	–	–
5	*B. yucatana*	21	0.0386	0.0302	0.0365	0.0384	–	0.1392	0.1312	0.1122	0.1027	0.1480
6	*B. platydactyla*	23	0.0553	0.0362	0.0403	0.0382	0.0363	–	0.0299	0.1904	0.1568	0.1296
7	*B. platydactyla*	24	0.0552	0.0403	0.0446	0.0423	0.0404	0.0098	–	0.1712	0.1449	0.1288
8	*B. striatula*	25	0.0302	0.0220	0.0281	0.0343	0.0282	0.0468	0.0510	–	0.0293	0.1716
9	*B. mombachoensis*	26	0.0323	0.0240	0.0343	0.0280	0.0302	0.0446	0.0489	0.0059	–	0.1717
10	*B. flaviventris*	28	0.0667	0.0470	0.0512	0.0618	0.0492	0.0531	0.0533	0.0579	0.0622	–

Fig. 2 (la tenemos, pero no podemos abrirla)

Figure 2.- Strict consensus of the 2 equally most parsimonious trees obtained for the combined cyt b and 16S sequence data set (1166 bp). We treated gaps as missing data and used the branch and bound algorithm and equal weights for all positions (L = 533 steps; 174 characters were parsimony informative; CI = 0.675; RI = 0.591). Bootstrap values in excess of 50% are shown above branches. Decay indices are shown below branches. Maximum likelihood analyses differ in the presence of a monophyletic *B. platydactyla - B. flaviventris* assemblage (-ln L = 4016.957). Sample numbers correspond to Table 1.

Figura 2.- Consenso (estricto) de los 2 árboles con número mínimo de pasos generados usando métodos de parsimonia con una combinación de secuencias mitocondriales de la subunidad 16S del ADN ribosómico y del gen del citocromo b (1166 bp). Las posiciones afectadas por inserciones-delecciones se trataron como falta de datos. Se usó el algoritmo "branch and bound" y pesos iguales para todas las posiciones (L = 533 pasos; 174 caracteres informativos; CI = 0.675; RI = 0.591). Se muestran los valores de "bootstrap" superiores al 50%. Los índices de robustez ("decay") se muestran bajo las ramas. Los análisis basados en "maximum likelihood" difieren en que *B. platydactyla* y *B. flaviventris* forman un grupo monofilético (-ln L = 4016.957). Los números de las muestras corresponden a los de la Tabla 1.

The sample from Honduras is basal ("Clade 3") to these two subclades within the large, main clade (bs 94%, decay 7). Relationships among these clades are resolved although the support for a sister taxon relationship between Clade 2 and the remainder of the terminal clade is low (bs 69%, decay 4) (Fig. 2). Analysis of the combined data set using ML resulted in a tree (-ln L = 4016.957) with a topology identical to the MP tree except in that *B. platydactyla* and *B. flaviventris* form a monophyletic group.

All analyses of the cytb and 16S data sets, independent and combined, support the inclusion of *B. mombachoensis* within the *B. mexicana* species group. In all analyses it is the sister taxon of *B. striatula* (bs 88 to 100%), with which it shares a similar general morphology (KÖHLER & MCCRANIE, 1999). Genetic divergence between *B. mombachoensis* and *B. striatula* is low (K2p 2.9% for cyt b, and 0.6% for 16S; KIMURA, 1980), ranging within the level of intraspecific variation generally found within species of this clade (Tables 2 and 3).

What has been called *B. mexicana* (samples 1 to 17) is consistently paraphyletic in the mtDNA analyses. All analyses recognize three well supported clades that include *B. mexicana* samples (Figs. 1 and 2): Clade 1 includes samples from eastern Chiapas, Honduras, and Belize (samples 1 to 6); Clade 2 includes all samples from east-central Veracruz and western Chiapas (samples 14 to 17); and Clade 3 includes samples from eastern Guatemala and Honduras (7 to 13), among which typical *B. odonnelli* is nested (samples 18 and 19). Except for the basal split within Clade 1, samples from Clades 1 and 3 are apparently not structured geographically, but include representatives from both coastal and inland Honduras. Clade 2 is restricted to the northern and eastern range of the complex in México. By contrast with comparisons between currently recognized species, K2p distances between the three clades are relatively large (Tables 2 and 3). These distances range from 10.0-11.8 % for cyt b and 1.8-4.7 % for 16S.

External morphology

Morphometrics

Mean and standard deviation of all measurements for members of each mtDNA clade are shown in Table 4. A stepwise discriminant function analysis was conducted on a series of adults using 11 log transformed external measurements (tail length was excluded). The resulting classification matrix, including classification probabilities proportional to group size, placed 93.7% of the specimens in their correct populations (Table 5). All 21 specimens of Clade 2 were correctly classified. One of 15 specimens from Palenque (Clade 1) was classified as belonging to Clade 3, and two of 12 specimens from Finca El Volcán, Guatemala, (Clade 3) were classified as belonging to Clade 1 (Fig. 3). Variables that contribute the most to the discrimination of groups are head width, snout-vent length, fore limb length, snout-gular fold length, shoulder width and head depth (Table 5). To remove the effect of size, a second stepwise discriminant analysis was performed using the residuals of the regression of each variable versus snout-vent length. The percentage of correct group classification was lower (81.2%), but variables contributing the most to discrimination were also head width, shoulder width, snout-gular fold length and fore limb length.

Fig. 3 (la tenemos, pero no podemos abrirla)

Figure 3.- Scatterplot of canonical scores (root 1 vs root 2) resulting from the discriminant function analysis. Open squares correspond to *Bolitoglossa mexicana*, circles to *B. alberchi sp. nov.* and triangles to *B. odonnelli*. The classification matrix is shown in Table 5. See text for details and measurements included. Specimens used are listed in Appendix 2.

Figura 3.- Diagrama con los valores canónicos ("root 1 vs root 2") resultantes del análisis discriminante. Los cuadrados vacíos corresponden a *Bolitoglossa mexicana*, los círculos a *B. alberchi sp. nov.* y los triángulos a *B. odonnelli*. La matriz de clasificación se muestra en la Tabla 5. En el texto se especifican detalles del análisis y la lista de variables incluidas. Los ejemplares utilizados se reseñan en el Apéndice 2.

Coloration

The color pattern of specimens sequenced included in Clade 1 is heterogeneous. Most individuals are characterized by a dorsal pattern that we informally designate as "three banded" and which corresponds to the following description, based on MVZ 191632 from Belize. The dorsum has a general chocolate-brown continuous background, which extends to most of the ventral region, the dorsal region of the tail and limbs, the sides of the head, and the flanks. This background coloration is broken along the dorsal region of the head and trunk by two series of cream-yellow irregular spots, more or less fused from one to the next, which run from the anterior edge of the eyes to the base of the tail (including the upper eyelid), forming two irregular broken lines. These irregular series are separated on the head by an irregular broad zone of dark background coloration, in the form of an inverted triangle, often with yellow spots that are denser anteriorly. This dark zone is abruptly replaced at the posterior end of the head by a broad and continuous, mid-dorsal yellow band. This band fades and terminates at the base of the tail, and it is not in contact with the thin light

Table 4: Mean, standard deviation and rank of external measurements for members of each mtDNA clade . *Bolitoglossa alberchi* (Clade 2), *B. mexicana* (Clade 1), and *B. odonnelli* (Clade 3). Snout-vent length (SVL), snout to gular fold length (SGFL), head width (HW), axilla-groin length (AGL), forelimb length (FL), hind limb length (HL), shoulder width (SW), foot width (FW), head depth (HD), interorbital width (IOW), internarial width (INW), and limb interval (LIV).

Table 4: Media, desviación estandar y rango de medidas externas obtenidas de ejemplares correspondientes a cada uno de los diferentes clados obtenidos en los análisis de ADN mitocondrial. *Bolitoglossa alberchi* (Clado 2), *B. mexicana* (Clado 1) y *B. odonnelli* (Clado 3). Longitud hocico-cloaca (SVL), longitud hocico-pliegue gular (SGFL), anchura de la cabeza (HW), longitud desde la axila hasta la ingle (AGL), longitud de la pata anterior (FL), longitud de la pata posterior (HL), anchura a nivel escapular (SW), anchura del pié (FW), altura de la cabeza (HD), distancia interorbital (IOW), distancia entre narinas (INW) y longitud entre patas (LIV).

		SVL	SGFL	HW	AGL	FL	HL	SW	FW	HD	IOW	INW	LIV
B. alberchi	**x**	68,23	15,11	10,20	38,58	14,79	16,19	7,86	7,28	5,17	5,91	3,61	1,79
Clade 2	**sd**	10,8	1,9	1,4	7,2	2,0	2,2	1,6	1,3	1,1	0,8	0,6	0,8
	min	45,1	10,7	7,5	24,1	9,5	10,0	4,6	4,3	3,9	3,9	2,3	0,0
	max	97,1	20,2	13,8	60,3	19,0	19,7	11,9	10,2	8,5	7,5	4,6	3,0
	n	22	22	22	22	21	21	21	21	21	21	21	21
B. mexicana	**x**	59,76	13,41	8,38	34,14	12,08	13,21	6,79	6,11	4,53	5,03	2,95	3,07
Clade 1	**sd**	7,1	1,2	0,8	4,2	1,2	1,5	1,0	0,8	0,9	0,4	0,3	0,6
	min	47,0	11,1	6,6	27,3	10,3	10,6	5,5	4,7	3,7	4,3	2,4	2,0
	max	78,6	16,5	10,3	45,7	14,9	17,4	9,4	7,8	7,1	6,1	3,5	4,0
	n	15	15	15	15	15	15	15	15	15	15	15	15
B. odonnelli	**x**	60,41	12,82	8,40	34,69	12,92	13,91	6,38	6,38	4,24	4,98	2,98	2,54
Clade 3	**sd**	4,4	0,7	0,5	3,2	0,7	0,8	0,7	0,5	0,3	0,2	0,3	0,6
	min	54,5	11,8	7,6	31,0	11,5	12,8	5,5	5,8	3,7	4,6	2,5	2,0
	max	67,4	13,9	9,3	39,9	14,0	15,6	8,0	7,3	4,8	5,5	3,5	3,5
	n	12	12	12	12	12	12	12	12	12	12	12	12

Table 5. A: Classification matrix (observed vs predicted clasifications) obtained using stepwise discriminant function analysis. A priori classification probabilities are proportional to group size. B.- List of variables retained in the stepwise analyses. F-remove, p-level and tolerancy are indicated for each variable. Snout-vent length (SVL), snout to gular fold length (SGFL), head width (HW), forelimb length (FL), shoulder width (SW), head depth (HD) were retained.

Table 5. A: Matriz de clasificación (clasificación de los casos observados frente a los asignados) obtenida utilizando la función discriminante generada en el análisis por pasos "stepwise discriminant analysis". Las probabilidades de clasificación "a priori" son proporcionales al tamaño muestral del grupo. B.- Lista de las variables mantenidas en el análisis por pasos. Se indica la F de eliminación, la probablilidad y la tolerancia para cada variable. Se mantuvieron en los análisis: Longitud hocico-cloaca (SVL), longitud hocico-pliegue gular (SGFL), anchura de la cabeza (HW), longitud de la pata anterior (FL), anchura a nivel escapular (SW) y altura de la cabeza (HD).

		B. alberchi	***B. mexicana***	***B. odonnelli***
		p = 0.437	p = 0.312	p = 0.250
B. alberchi	100%	21	0	0
B. mexicana	93,3%	0	14	1
B. odonnelli	83,3%	0	2	10

Table 5.B

	F-remove	**p-level**	**tolerance**
HW	29,504	0,0000	0,0656
SVL	31,542	0,0000	0,0323
FL	17,603	0,0000	0,1149
SGFL	8,677	0,0007	0,1047
SW	5,947	0,0055	0,1848
HD	3,545	0,0413	0,3131

lateral irregular broken series of light marks except at the posterior end of the head.

This generalized "three banded" coloration pattern occurs, in addition to the individuals for which sequences are available, in most specimens examined from Belize, northern Guatemala, and north-eastern Chiapas (Figs. 4 A-B and Fig. 5 B), and corresponds to what is generally considered to be the typical *B. mexicana* coloration pattern. A large series of specimens examined from Honduras and Guatemala show the following variants of this pattern: a) dark areas between the yellow bands more or less linear and continuous from the posterior end of the head to the base of the tail, where they are broken: Sierra de Caral, Guatemala: UTAVC A45509; Sierra de las Minas, Guatemala: UTAVC A29689; Peña Blanca, Honduras: MVZ 163792, MVZ 163794-95, MVZ 163799-800. b) dark lateral bands continuous only on the anterior half of the body; the upper side of the tail is almost yellow except for a few dots: Sierra de Caral: UTAVC A48593; Sierra de las Minas: UTAVC A29684; Santa Rosa de Copán, Honduras: MVZ 163797, MVZ 171077. c) dark lateral bands discontinuous but still distinctive. The dorsum is almost entirely yellow. Sierra de Caral: UTAVC A48198; Izabal: UTAVC A21442; Peña Blanca: MVZ 187203-04; El Paraíso, Honduras: MVZ 128579-80. An example of this pattern from Guatemala is presented by

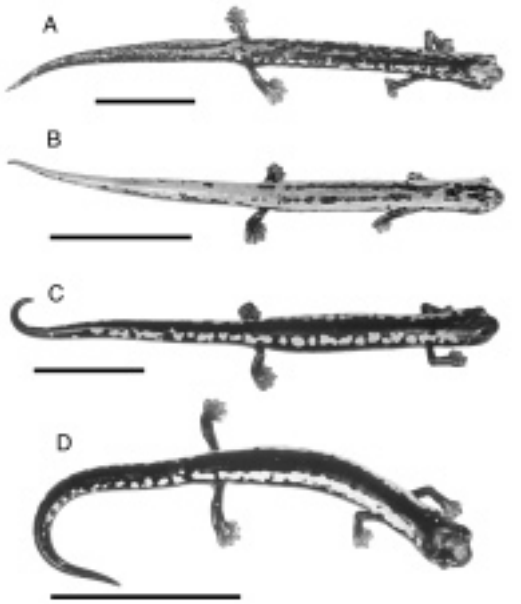

Figure 4. A-B.- Dorsal pattern of *Bolitoglossa mexicana* from Chiapas, México: a) Lagos de Montebello, MVZ uncatalogued; b) Amparo Agua Tinta, MVZ161071. C-D. Habitus of typical *Bolitoglossa odonnelli* from Finca El Volcán, in Alta Verapaz, Guatemala: c) MVZ 161034; d) MVZ 161041.
Figura 4. A-B.- Diseño dorsal de ejemplares de *Bolitoglossa mexicana* de Chiapas, México: a) Lagos de Montebello, MVZ sin catalogar; b) Amparo Agua Tinta, MVZ161071. C-D. Aspecto dorsal de ejemplares típicos de *Bolitoglossa odonnelli* procedentes de Finca El Volcán, en Alta Verapaz, Guatemala: c) MVZ 161034; d) MVZ 161041.

Stuart (1948, pl. 2, Fig. 2). An extreme case is represented by a juvenile specimen from Las Marías, Honduras (MVZ 229069), in which the dark bands are reduced to a narrow strip of dark spots, so reduced that contact among the central and lateral light bands is discernible based on the difference in coloration among them. d) a heterogeneous assemblage of three banded animals, with yellow bands almost always bordered by white, that are either continuous or interrupted (Montañas del Mico, Guatemala): UTAVC A42824, UTAVC A42828).

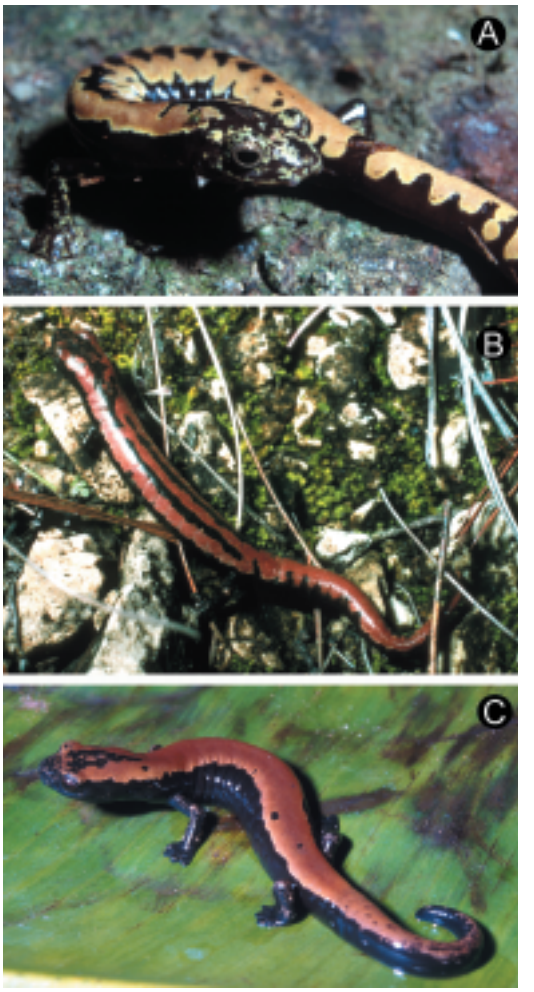

Figure 5.- Representative specimens of the *B. mexicana* species group: a) *Bolitoglossa alberchi*, from near Los Tuxtlas - Monte Pío (Veracruz, México); b) *Bolitoglossa mexicana*, from Lagos de Montebello (Chiapas, México) (mtDNA sequences from this specimen are included in Clade 1, see Figs. 1 and 2); c) *Bolitoglossa platydactyla*, from near Cuautlapan (Veracruz, México) (GP108).
Figura 5.- Especímenes representativos del grupo de especies de *B. mexicana*: a) *Bolitoglossa alberchi*, de los alrededores de Los Tuxtlas - Monte Pío (Veracruz, México); b) *Bolitoglossa mexicana*, de los Lagos de Montebello (Chiapas, México) (las secuencias de ADN mitocondrial de este ejemplar se incluyen en el Clado 1, ver Figs. 1 y 2); c) *Bolitoglossa platydactyla*, de los alrededores de Cuautlapan (Veracruz, México) (GP108).

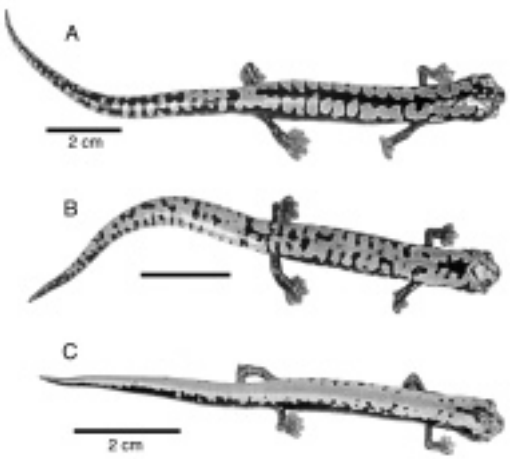

Fig. 6. A-C.- Aspecto dorsal de ejemplares de *Bolitoglossa alberchi* procedentes de Veracruz, México: a) Playa Escondida,14 km (por carretera) al NE de Sontecomapan, MVZ163961, paratipo; b) Playa Escondida, 14 km (por carretera) al NE de Sontecomapan, MVZ 138658; c) Ejemplar juvenil, Coyame, MVZ sin catalogar.

Fig. 6. A-C.- FALTA TRAD. INGLES Aspecto dorsal de ejemplares de *Bolitoglossa alberchi* procedentes de Veracruz, México: a) Playa Escondida,14 km (por carretera) al NE de Sontecomapan, MVZ163961, paratipo; b) Playa Escondida, 14 km (por carretera) al NE de Sontecomapan, MVZ 138658; c) Ejemplar juvenil, Coyame, MVZ sin catalogar.

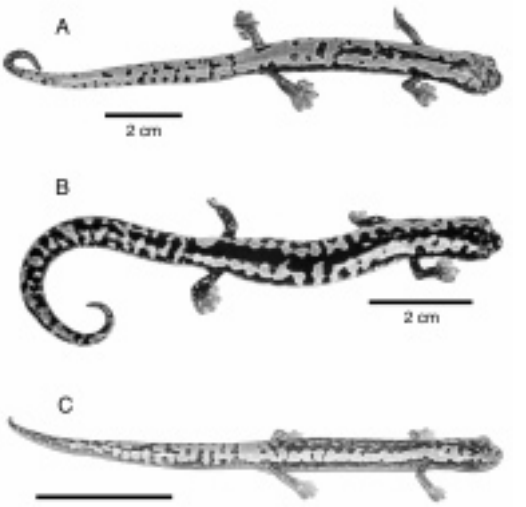

Figure 7. A-C.- Dorsal pattern of *Bolitoglossa alberchi* from Chiapas, México: a) 26.5 km N Ocozocuautla, MVZ194293; b) Belisario Domínguez, near Palenque, MVZ 176838; c) 4.0 mi N Tapilula, MVZ 171338**.**

Figura 7. A-C.- Diseño dorsal de *Bolitoglossa alberchi* de Chiapas, México: a) 26.5 km al N de Ocozocuautla, MVZ194293; b) Belisario Domínguez, cerca de Palenque, MVZ 176838; c) 4.0 mi al N de Tapilula, MVZ 171338**.**

Individuals from Chiapas show the typical dorsal coloration described as "three banded", although the band pattern tends to be more obscured with dark dots that are not clearly aligned (Fig. 4 A). A few specimens (MVZ 118994-96) are characterized by large size and the presence of a marked ventral speckling similar to that shown by specimens of Clade 2 (see below).

Clade 2 is represented by populations of large, strikingly colored salamanders that are black, with two broad dorsal series of grayish-green to yellow chevrons aligned in two stripes, occasionally joined across the midline in a complicated pattern (Figs. 5 C, 6 and 7). They also differ from specimens from the other clades in having broad heads and long limbs; we describe this clade as a new species later in this paper.

Coloration patterns of the individuals assigned to Clade 3 can be grouped in two main categories, one that corresponds to typical *B. odonnelli*, and a second basically indistinguishable from the "three banded" pattern of specimens from Clade 1. The coloration pattern of *B. odonnelli* is relatively homogeneous (Fig. 4 C-D), consisting of a general chocolate-brown continuous ground color which includes most of the ventral region, the dorsolateral region of the trunk, tail and limbs, the sides of the head, and the flanks. This background coloration is broken along the dorsolateral region of the trunk by two series of cream-yellow irregular spots, more or less fused from one to the next. These partially fused spots form two irregular broken lines, exten-

ding from the posterior edge of the head to the second third of the length of the tail. These lines continue onto the dorso-lateral region of the head as series of small spots or dots that are sometimes joined in a thin line. Spots occasionally appear on the upper eyelids, and along the complete length of the tail. These two lines are broadly separated by the dorsal dark background coloration. In some specimens the light lines tend to be confluent at the posterior end of the head or along the tail, and some other individuals display a few isolated mid-dorsal yellow spots, but there is never either a mid-dorsal band or a dense reticulate pattern as shown in Clade 2, except on the anterior third of the tail (MVZ 161084). Juveniles show the same pattern as the adults. This coloration pattern is constant in the area of Finca El Volcán, Alta Verapaz, Guatemala (MVZ 161029-46, 161081-90, 200426-27) (Fig. 4 C-D), the type locality of *B. odonnelli*. We have examined some specimens from Honduras and Guatemala with a color pattern little differentiated from typical *B. odonnelli*; their general ground color is dark brown, including most of the dorsal portions of the head. There are two broad dorso-lateral yellow bands that are longitudinally continuous. These bands extend from the level of the anterior margin of the eye to the base of the tail, where they become discontinuous. The tail has two discontinuous dorso-lateral bands formed by yellow blotches that are more or less fused; these light bands tend to be broken until reduced to a series of thin comma-shaped marks, more or less fused together (Sierra de Caral: UTAVC A45496, UTAVC A45506; Montañas del Mico: UTAVC A32880; Peña Blanca: MVZ 163793). Specimens are found from Honduras that are intermediate between this pattern and that described from Clade 1. These individuals are characterized by a broad central dark band that is split medially by a yellow series of blotches that become fused, forming a narrow band near the posterior end of the trunk (MVZ 163798).

The only specimens from Honduras that we can attribute with certainty to Clade 1 or 3 are those for which molecular data exist. An example of the dilemma is a specimen from Río Catacamas, near Catacamas, Olancho (MVZ 229068) that is a member of Clade 3. The color pattern is three banded, similar to that described for Clade 1, but the width of the yellow bands is greater. The two dorso-lateral bands are continuous and are lighter in coloration than the mid-dorsal region. The dorsolateral bands fuse at the base of the tail and the posterior end of the head. Scattered yellow marks are present on the upper surface of the limbs, and a few on the under surface.

We examined large series of specimens from various localities in Honduras and Guatemala which cannot be sorted into any of the main color morphs described. Often these specimens have yellow dorsolateral bands irregularly drawn, usually broken and thin. Three modal patterns are distinguishable, but there are intermediates:

a) mid-dorsal yellow line well developed and uninterrupted, but laterals are thin and often broken (Izabal, Guatemala: UTAVC A21444-45; San Francisco: MVZ 194028).
b) mid-dorsal yellow line reduced to a thin line that is often broken by the broad dark lateral bands (Montañas del Mico: UTAVC A51494, UTAVC A33630).
c) mid dorsal yellow line is obliterated or non-distinct, because broken lateral bands disrupt the pattern (Montañas del Mico: UTAVC A33629, UTAVC A33633).

Some individuals from Honduras have intermediate combinations of traits and defy categorization (Montañas del Mico: UTAVC A42829, UTAVC A21430, UTAVC A32882, UTAVC A33634; Sierra de Caral UTAVC A455505; Olancho: UTAVC A19826.

DISCUSSION

Phylogenetic relationships of the B. mexicana complex

In agreement with previous analyses (GARCÍA-PARÍS *et al.*, 2000), genetic divergence among the three clades previously included in *B. mexicana* is great, and the clades do not form a monophyletic group (Figs. 1 and 2). Clade 1 is the sister of *B. striatula* plus *B. mombachoensis*, and *B. yucatana*. Clades 2 and 3 are sister to each other, but they differ markedly in morphological grounds. Clade 3 includes representatives of *B. odonnelli* nested among samples of putative *B. mexicana*. As we have shown, analyses of coloration and external morphology only partly resolves identification problems.

The possibility of reticulation among Clades 1 and 3 cannot be disregarded considering our limited sampling. The biological problem posed by these clades is still far from resolution and the addition of nuclear markers (protein or DNA) will be necessary to clarify the taxonomic and morphological puzzle that they represent. It is conceivable that Clade 1 are 3 are conspecific and that we recovered a paraphyletic gene tree. However, genetic distances among Clades are great (Tables 2 and 3) and based on the relative level of intra- and inter-clade divergence in mtDNA, reciprocal monophyly is expected also for nuclear markers. Additionally, given the conservative nature of evolution in the 16S gene, we think it is unlikely that Clade 1 are 3 represent a single taxonomic unit, and therefore we favor the assignation of an operational name for each of these Clades.

Providing a name for each of these three clades is not a trivial matter given the apparent lack of congruence between coloration and mitochondrial DNA sequence data. The problem is further complicated by the taxonomy of the group, which has been subjected to multiple interpretations and changes through time, and is far from stable. Only the taxon represented by Clade 2 is clearly diagnosable on both morphological and genetic grounds, and there is no available name which can be applied to it. Its description is presented in the following paragraphs. The availability of names for Clades 1 and 3 depends on the taxonomic criteria followed and requires a discussion on type specimen assignation and associated nomenclatural problems discussed later in this paper.

Description of a new species from México

Bolitoglossa alberchi New Species

Holotype: MVZ 163962, an adult male collected near Playa Escondida, approximately 14 km (road) NE Sontecomapan, Veracruz, México, 18° 56' N, 95° 05' W, at ca. 50 m elevation on 17-20 July , 1979, by T. J. Papenfuss, S. K. Sessions, D. B. Wake, and T. A. Wake.

Paratypes: MVZ 163959-163961, 163783-163791, same data as holotype (Fig. 6 A). UTAVC 7788, 7804, 7811, 7852, 7854-55, 7857, 7901, 7903, 7909, 7.7 mi (by road) NW Sontecomapan, 18°53' N, 95°07' W, Veracruz, México

Referred Specimens: MVZ 183658, 9.5 mi N Berriozábal, Chiapas, México; MVZ 194293, cafetal 26.5 km N Ocozocoautla, on road to Apic Pac, Chiapas, México (775 m) (Fig. 7 A); MVZ 172665-172667, 193155, 200568, 208378, Playa Escondida, Veracruz, México; UTAVC 2048, W slope volcan Santa Marta, Veracruz, México; UTAVC 2154, 2156, 2210, Los Tuxtlas, 5.6 mi ESE Tebanca, Veracruz, México; UTAVC 2212-2219, 2234, 2236-40, 2243 (2.1 mi NW Sontecomapan); UTVAC 2212-19, 2234, 2236-40, 2243, 2.3 mi NW Sontecompan, 18° 53' N, 95° 05' W, Veracruz, México; UTVAC 7778-87, 7789-7803, 7805-10, 7812-51, 7853, 7856, 7858-60, 7873, 7875, 7877-78, 7880-85, 7887, 7892, 7894-7900; 7902, 7904-08, 7910-11, 7.7 mi (by road) NW Sontecomapan, 18° 53' N, 95° 07' W, Veracruz, México; UTAVC 7797-7799, 1.8 miles S Juan Diaz Covarrubias, Veracruz, México.

Diagnosis: A large (adults to about 100 mm svl), long tailed, member of the *Bolitoglossa mexicana* complex with broad, fully webbed hands and feet distinguished from other members of the complex by its broad head, long limbs, and differences in mitochondrial DNA sequences (cyt b, 16S).

Description: *Bolitoglossa alberchi* is a large, robust species (SVL 59.4-69.6, x = 65.9 [SD 3.4] in 12 males; 45.1-97.1, x = 71.0 [SD 15.5] in 10 females) with a broad, relatively flat head that is well demarcated from the body (Fig. 6). The eyes are large and moderately protuberant. Nostrils are small, and there are small nasolabial protuberances that are most evident in males. Mental glands in males are large and oval, broader than long. Grooving patterns of the head and neck region are typical of the genus. Vomerine teeth are in long rows, or patched rows, and are relatively numerous (17-32, x = 23.5 in 11 males; 19-35, x = 31.2 in 11 females). Small maxillary teeth are present, usually in long series, but occasional nearly toothless individuals are encountered (4-55, x = 27.2 in 11 males; 1-66, x = 37.2 in 11 females). Premaxillary teeth are frequently absent and when present are small and inconspicuous, even in males, where they are advanced in position and protrude through the upper lip (0-5, x = 3.0 in 11 males; 0-2, x = 0.5 in 11 females). Limbs are long, and may nearly overlap in males (limb interval 0-2, x = 1.3 in 12 males; 1.5-3, x = 2.3 in 11 females).

Measurements of the Holotype (in millimeters): Head width 10.1; snout to gular fold (head length) 15.8; head depth at posterior angle of jaw 5.9; eyelid length 4.2; eyelid width 2.4; anterior rim of orbit to snout 4.1; horizontal orbital diameter 2.6; interorbital distance 5.1; distance between vomerine teeth and parasphenoid teeth 1.6; snout to forelimb 20.6; distance separating internal nares 1.2; distance separating external nares 3.4; nostril diameter 0.33; snout projection beyond mandible 1.3; snout to posterior angle of vent (SL) 68.0; snout to anterior angle of vent 61.0; axilla to groin 37.1; tail length 69.9; tail width at base 4.6; tail depth at base 5.2; forelimb length (to tip of longest digit) 14.8; hind limb length 15.9; width of right hand 5.1; width of right foot 7.7.

Tooth Counts: premaxillary teeth 2, maxillary teeth 31, vomerine teeth 23.

Coloration: This is a strikingly patterned species. The type series was black in life, generally with two dorsal series of grayish-green to yellow chevrons aligned in two stripes occasionally joined across the midline in a complicated pattern (Figs. 5 C, 6 and 7). The dorsal stripes frequently nearly fuse to form a band that is interrupted by black spots and blotches. The holotype has a band that starts on the back of the head as a series of two broken stripes, but on the body the broken fragments join across the midline to form a series of irregular bars separated by black ground color and small spots of light color in two series. In several specimens the two dorsal stripes are broken into a long series of chevrons, while in another there is a broken dorsal band with the two stripes evident only on the head and neck. In some large adults the dorsal marks are reduced to a series of thin transverse bands which give a barred appearance to the animal. The flanks are marked by large, longitudinally-oriented patches (marks) of a soft yellowish color. There are also greenish-yellow spots and marks on the limbs, hands and feet. The snout and nostril region is covered by a dense speckling of yellowish green fine dots and flecks, similar to those on the throat. The tail is boldly marked with the same color as the stripes, and frequently the tail appears to be ringed. The regenerated tail is dark with a fine speckling dispersed over its entire surface, very different from the typical color of non-regenerated tails. In some individuals the dorsal color is less greenish, being sandy-tan to yellow. When present, the greenish-yellow color is most prominent on the head and anterior trunk. The dorsum of the head is

boldly marked with contrasting light and black color. The iris is tan to grayish-tan. Ventral coloration is dark-brown with white-yellowish flecks, dispersed over the entire ventral surface. Density and size of this flecks is largely variable. One specimen from Belisario Domínguez, near Palenque (MVZ 1768359), and another from near Tapilula (MVZ 171338, Fig. 7 C), both in Chiapas, show a slightly divergent color pattern characterized by the presence of a distinct series of isolated mid-dorsal light spots which tend to form a dorsal line, placed between the typical *B. alberchi* chevron-like marks.

Juvenile specimens show a less contrasting pattern, with a broader extension of the yellow dorsal marks that appear almost completely fused in almost all the specimens studied (Fig. 6 C). A few juveniles have the yellow marks restricted to the sides. The yellowish flecks of the ventral coloration are usually extended and cover most of the ventral region in the juveniles

Behavior: The type series consists of adults and juveniles that were found on vegetation shortly after nightfall. They are lively, active animals with long tails that coil and twitch. Several specimens were found on vegetation in the late afternoon, active during daylight hours on vegetation from a few cm to a m above ground. These individuals had very warm body temperatures (28- 28.4 C) (FEDER *et al*., 1982). At night salamanders moved easily through a kind of leaf "canopy" between 20 cm and 1 m above ground (air temperature 28.2 C, D. B. Wake field notes). During the rainy season individuals are frequently found on vertical tree trunks, head down, with their body parallel to the main axis of the tree, presumably ambushing prey (Fig. 8; and M. A. López-Luna com. pers.).

Habitat: The type series was collected in a rain forest remnant just above the beach along the Gulf of México.

Range: The species is known from two disjunct regions, along the ocean-facing slopes of the mountain range known as Los Tuxtlas, northeast of Catemaco in east-central Veracruz, México, and in the mesic low mountains (as high as 1080 m) of western Chiapas, México.

Figure 8.- Nocturnal behaviour of *Bolitoglossa alberchi* near Los Tuxtlas - Monte Pío (Veracruz, México).
Figura 8.- Comportamiento nocturno de *Bolitoglossa alberchi* cerca de Los Tuxtlas - Monte Pío (Veracruz, México).

Etymology: The species is named in memory of Pere Alberch, who conducted outstanding morphological studies of members of this species complex and whose early death deprived us of a brilliant contributor to salamander biology.

Comparisons: For morphological comparisons with members of the *B. mexicana* complex we selected adult specimens from the type series of *B. moreleti* to represent "Clade

1", and from a series of *B. odonnelli* from Finca El Volcán, Alta Verapaz, Guatemala, to represent "Clade 3". Members of the three clades are apparently similar in size and in degree of webbing of the hands and feet as well as in many proportions, but *B. alberchi* has a much broader head and longer limbs (Fig. 9) than the other two, and has slightly larger hands and feet.

A discriminant function analysis was conducted on a series of adults using external measurements. The resulting classification matrix indicates that all 21 specimens of *B. alberchi* were correctly classified (Table 5). The characters that contribute the most to the discrimination of groups are head width, and shoulder width.

Comments: *Bolitoglossa alberchi* was illustrated in GUNTHER (1885-1902: Tab. 75c) (BMNH 1857.7.31.31, identified as *Oedipus variegatus*) and in the frontispiece of WAKE & LYNCH (1976) (MVZ 138658, identified as *B. mexicana*). MUÑOZ-ALONSO & LAZCANO-BARRERO (1992) reported that *B. mexicana* and *B. platydactyla* occur in sympatry in Reserva Ecológica el Ocote, extreme western Chiapas. Through their courtesy we have examined the specimens assigned to *B. mexicana,* and on morphological grounds we assign them to *B. alberchi*.

Falta fig. 9 (no está)

Figure 9.- Scattergrams showing relationship of head width to snout - posterior angle of vent length (svl) (top), and of hind limb length to svl (bottom) for three samples representing *Bolitoglossa alberchi* (open circles), *B. odonnelli* (triangles), and *B. mexicana* (open squares).

Figura 9.- Diagramas que muestran la relación entre la anchura de la cabeza y la longitud hocico - margen posterior de la cloaca ("svl") (parte superior), y entre la longitud de la pata posterior y "svl" (parte inferior) en tres muestras representativas de *Bolitoglossa alberchi* (círculos), *B. odonnelli* (triángulos), y *B. mexicana* (cuadrados).

Taxonomy and nomenclature of the B. mexicana complex

The genus *Bolitoglossa* was created by DUMÉRIL, BIBRON & DUMÉRIL (1854), with *Bolitoglossa mexicana* as its type species (TAYLOR, 1944). The taxon known as *B. mexicana* is considered a taxonomic nightmare (SMITH, 1945; MITTLEMAN & SMITH, 1948; THIREAU, 1986). Most of the taxonomic and nomenclatural problems within the group are derived from the fact that the type series of several species often contained individuals from more than a single species. Subsequent determinations led to errors in the identification and designation of lectotypes and restrictions of type localities. We summarize here the information available and when necessary we designate lectotypes for the taxa involved, with the aim of preserving as far as possible the current names for the species involved.

GRAY (1831) described *Salamandra variegata* Gray 1831 (nec Bory 1828) on the basis

Figure 10.- Type series of *Salamandra variegata* Gray, 1831 (nec Bory, 1828), and of *Salamandra platydactyla* Gray, 1831. Lectotype: BMNH 1848.8.16.24 (above), and paralectotype BMNH 1.111.11.1a (below). The paralectotype is an individual of *Bolitoglossa mexicana*.

Figura 10.- Serie típica de *Salamandra variegata* Gray, 1831 (nec Bory, 1828), y de *Salamandra platydactyla* Gray, 1831. Lectotipo: BMNH 1848.8.16.24 (parte superior), and paralectotipo BMNH 1.111.11.1a (parte inferior). El paralectotipo es un ejemplar de *Bolitoglossa mexicana*.

of two individuals, currently BMNH 1848. 8.16.24 and BMNH 1.111.11.1a (Fig. 10). The study of these specimens reveals that the specimen BMNH 1.111.11.1a fits Gray's description (Wake in THIREAU, 1986), which corresponds to the usual conception of *B. mexicana*. The first specimen (BMNH 1848. 8.16.24) corresponds to our generalized understanding of *B. platydactyla* (Wake in THIREAU, 1986).

Salamandra variegata Gray, 1831 is a homonym of *Salamandra variegata* Bory, 1828 (a junior synonym of *Triturus marmoratus*), for which subsequently GRAY (1831) applied the substitute name: *Salamandra platydactylus* Gray, 1831. The type series of *S. platydactylus* consists of the type series of *S. variegata* Gray, 1831. No formal lectotype designation has been proposed, and in order to stabilize the name *B. platydactyla* for taxonomic purposes we designate here specimen BMNH 1848.8.16.24 as the lectotype of *Salamandra variegata* (Fig. 10). The type locality of *S. variegata* is "Mexico" (GRAY, 1831). We designate the specimen BMNH 1.111.11.1a paralectotype of *Salamandra variegata.* Therefore the type series of *S. platydactylus* consists of: the above designated lectotype (BMNH 1848.8.16.24) corresponding to *B. platydactyla* , and the paralectotype (BMNH 1.111.11.1a), which is assignable to *B. mexicana*. COPE (1860) described *Oedipus carbonarius* from specimens of Jalapa (Veracruz, México). This name was subsequently synonymized with *Salamandra variegata* by FOWLER & DUNN (1917). Cope's description fits the lectotype of *S. variegata*, and since the name *B. platydactyla* replaces *S. variegata* , the name *O. carbonarius* should be treated as a junior synonym of *B. platydactyla*.

DUMÉRIL *et al.* (1854) proposed the name *Bolitoglossa mexicana* for a heterogeneous series of salamanders, including among others two specimens collected by Morelet in "Dolorès peten (Guatemala)" (sic) (Fig. 11). BOULENGER (1882), and later MITTLEMAN & SMITH (1948), and THIREAU (1986), discussed the restriction of the type series of *B. mexicana* to those two specimens from Petén. SMITH (1945) concluded that the type of *B. mexicana* was the individual figured by BROCCHI (1883: pl. 18 bis, fig. 3). The provenance of that particular individual was erroneously indicated in Brocchi's plate as "Vera Cruz" (see below), and that drove SMITH (1945) to consider *B. mexicana* to be a synonym of *B. platydactyla*. MITTLEMAN & SMITH (1948) rectified the origin of the specimen illustrated by BROCCHI (op. cit.), based on Brocchi's own text, and concluded that the specimen was one of the individuals collected by Morelet in Petén. This restriction is in agreement with SCHMIDT (1936), who used the name *B. mexicana* exclusively for the Petén salamanders. Later, SMITH (1966) designated as "lectoholotype" for *B. mexicana* the specimen figured by BROCCHI (1883: pl. 18 bis, fig. 3). This specimen was identified as MNHP 4747A by SMITH (1966), when in fact the correct number is MNHP 4747 (THIREAU, 1986). THIREAU (1986) considered the action of SMITH (1966) invalid and treated MNHP 4747 and 4747A as syntypes. However, a lec-

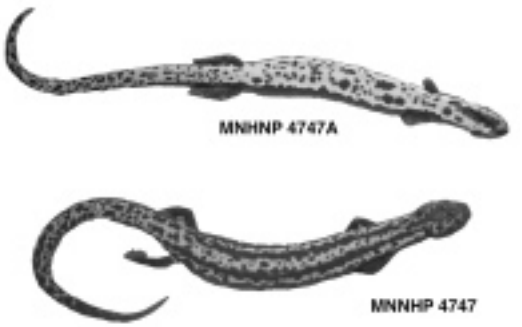

Figure 11.- Lectotype, MNHP 4747 (below) and paralectotype, MNHP 4747A (above) of *Bolitoglossa mexicana* Duméril, Bibron and Duméril, 1854.
Figura 11.- Lectotipo, MNHP 4747 (parte inferior) and paralectotipo, MNHP 4747A (parte superior) de *Bolitoglossa mexicana* Duméril, Bibron and Duméril, 1854.

totype designation is not necessary since SMITH (1966) already designated as lectotype ofb *B. mexicana* the specimen figured by BROCCHI (1883: pl. 18 bis, fig. 3), which is MNHP 4747 (Fig. 11). The type locality of *B. mexicana* is therefore Dolores in Petén (Guatemala)(THIREAU, 1986), which stabilizes the name *B. mexicana*, solving most of the problems concerning that name.

The lectotype of *B. mexicana* from Petén is a "three banded" specimen (Fig. 11). Our mtDNA data set indicates the existence of two well defined clades (Clade 1 and Clade 3), either of which on grounds of color pattern could bear the name *B. mexicana*.

We were unable to obtain specimens from the type locality of *B. mexicana* (Dolores, Petén) for the molecular studies, and therefore the name *B. mexicana* might be attributed to either Clade 1 or 3. It is not possible to reject its inclusion in Clade 1 or 3 based solely on geographical proximity since both clades seem to be widely distributed. In order to preserve the name *B. odonnelli*, we apply the name *B. mexicana* for the specimens included in the mtDNA Clade 1. However if subsequent molecular studies based on nuclear genes demonstrate the identity at the species level of the specimens from Guatemala, Honduras, and Belize from Clades 1 and 3, the name *B. odonnelli* will lack biological meaning and will then be considered a junior synonym of *B. mexicana*, a name that will apply to both clades. Specimens from Clade 3, with the exception of the Alta Verapaz individuals (see comments about *B. odonnelli* below), are indistinguishable from the type specimens of *B. mexicana*.

SMITH (1945) described *Bolitoglossa moreleti* because he considered *B. mexicana* to be a synonym of *B. platydactyla*. SMITH's (1945) proposal of synonymizing *B. mexicana* with *B. platydactyla* was based on the problems concerning the restriction of the type series of *B. mexicana* already discussed. Accordingly, SMITH (op. cit.) proposed a new name for what was then considered to be *B. mexicana*. However, SMITH (1945) did not propose a simple name replacement, but rather described a new species, *B. moreleti* Smith, 1945, using material collected near Palenque (Chiapas, México), relatively far from the type locality of *B. mexicana* (Petén, Guatemala). The type series of *B. moreleti* is astonishingly heterogeneous in coloration (TAYLOR AND SMITH, 1945), and it includes specimens which can be attributed to either Clades 1, 2 and 3 based in color pattern. The series, from near Palenque (Chiapas), likely includes a possible contact zone among clades in Chiapas. However, the holotype of *B. moreleti* (USNM116079) is figured in TAYLOR & SMITH (1945: fig. 58 c), and it shows a coloration pattern similar to the lectotype of *B. mexicana* (Fig. 11). We lack samples for the molecular study from the area of Palenque, the type locality of *B. moreleti*, but specimens of Clade 1 from southeastern Chiapas (which are geographically close to Palenque) are genetically divergent from other populations included in either Clades 1 or 3 of the *B. mexicana* complex (Table 2). There are also some minor differences in color pattern between the samples of Chiapas and the remaining sam-

ples of Clade 1, although they are not sufficient to allow for a consistent identification of these specimens (Figs. 4 A-B and 5 B). Based on the genetic divergence of the representatives of Clade 1 from Chiapas with respect to the remaining samples of the *B. mexicana* complex, it is conceivable that they represent a differentiated taxon, which should take the name *B. moreleti*. However, given that the molecular sampling is limited in Chiapas, and that in practical terms, the samples of Clade 1 from Chiapas cannot be distinguished morphologically from other samples of either Clade 1 or 3, we follow a more conservative taxonomic approach, and consider *B. moreleti* as a junior synonym of *B. mexicana*.

Bolitoglossa odonnelli Stuart, 1943, was described from Finca El Volcán, in the Departamento de Alta Verapaz in Guatemala. The coloration of *B. odonnelli* is constant around the type locality (see above) (Fig. 4 C-D). However, mtDNA from topotypic material of *B. odonnelli* is basically identical to mtDNA from other populations of Clade 3 from Guatemala and Honduras (Table 2), which show a markedly different habitus, typical of *B. mexicana* (similar to the specimen shown in Fig. 4 B). The diagnosis of *B. odonnelli* is perfectly valid (STUART, 1948), and the name could be retained for the entire Clade 3, losing however, its diagnosability on morphological grounds, since individuals with typical *B. mexicana* habitus are also present in Clade 3. Individuals with a color pattern similar to that of typical *B. odonnelli* have been found scattered among specimens with typical *B. mexicana* coloration in other localities, and therefore the color pattern of typical *B. odonnelli* can be considered a simple local variation. Both Clades 1 and 3, representing *B. mexicana* and *B. odonnelli*, occur in Honduras and we cannot separate them either by coloration or morphology. For the present time, following GARCÍA-PARÍS *et al.* (2000), we recommend that populations from Honduras be referred as the *B. mexicana* complex.

BROCCHI (1883) described three additional species assignable to this complex: *Spelerpes mulleri*, *Spelerpes punctatum* and *Spelerpes attitlanensis*. The holotype of *Spelerpes punctatum*, MNHP 6392 (Fig. 12), corresponds to *B. lignicolor* and thus *S. punctatum* is a junior synonym of *B. lignicolor* (Wake in THIREAU, 1986).

The type series of *Spelerpes mulleri* consists of at least four individuals, MNHNP 6395, 6395A, 6395B and 6395C, collected from three possible localities "les bords du Rio Polochie", "Rio de la Pasion" and "Les montagnes qui dominent Coban". STUART (1943) restricted the type locality of *S. mulleri* to "Les montagnes qui dominent Coban" without lectotype designation, but the specimens illustrated by Brocchi correspond to two species. BROCCHI's (1883) pl. 20, figs. 4 and 5, correspond to our current understanding of *B. mulleri*, while the individual figured in BROCCHI's (1883) pl. 20, fig. 3, which corresponds to Brocchi's description of specimens from "les bords du Rio Polochie", is according to STUART (1943), an intergrade between *B. mexicana* and *B. odonnelli.* In order to preserve the name *B. mulleri* for taxonomic purposes, we designate here as lectotype of *Spelerpes mulleri* the specimen MNHNP 6395, which might correspond either to Brocchi's pl. 20, fig. 4, or fig. 5, from the locality "Les montagnes qui dominent Coban". The specimens of

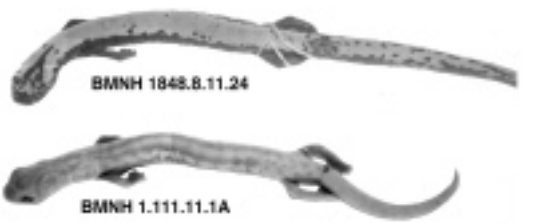

Figure 12.- Holotype of *Spelerpes punctatum* Brocchi, 1883 (MNHP 6392), a specimen of *Bolitoglossa lignicolor*.

Figura 12.- Holotipo de *Spelerpes punctatum* Brocchi, 1883 (MNHP 6392), que corresponde a un ejemplar de *Bolitoglossa lignicolor*.

the type series are in bad condition and cannot be exactly attributed to the figure of Brocchi (THIREAU, 1986).

The coloration pattern in alcohol of *B. mulleri* from Alta Verapaz and Huehuetenango varies substantially among individuals from a single population. Some individuals completely lack a dorsal yellow stripe, in some others it is reduced to a thin line, and others show a distinct mid-dorsal thin line over a dark dorsal band, which is flanked by a paler band (MVZ 149331). This latter pattern might correspond to the pattern of the individual figured by BROCCHI (1883: pl. 20, fig. 3), if the flanking bands of the drawing were over-represented by the artist. Unfortunately the poor condition of the type series does not allow us to confirm this assumption. In a few specimens the yellow band extends onto the head, where it bifurcates and breaks into small spots that reach the posterior end of the eyelids. Occasional yellow spots, more or less joined, are evident on the tail of some specimens.

The type series of *Spelerpes attitlanensis* Brocchi, 1883, consists of the holotype and one paratype (THIREAU, 1986). The holotype (MNHNP 6398) (Fig. 13 A) is actually an individual corresponding to *B. salvinii*, and the paratype (MNHNP 6399) (Fig. 13 B) corresponds to *B. flaviventris* (Schmidt, 1936). *Spelerpes attitlanensis* is therefore a junior synonym of *B. salvinii* (SCHMIDT, 1936; Wake in THIREAU, 1986). The holotype of *Oedipus salvinii* Gray, 1868 (BMNH 1865.6.10.19H) is shown in Fig. 13 C.

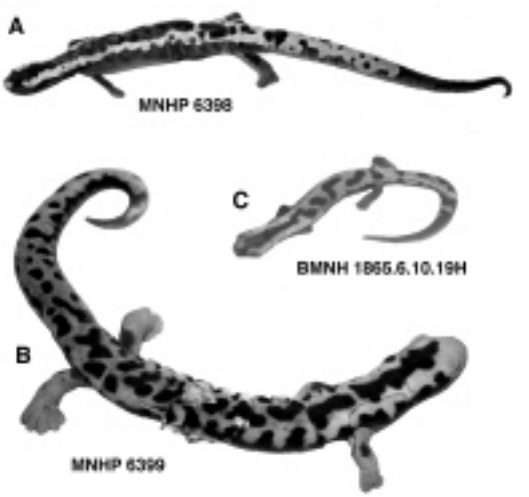

Figure 13.- Type specimens associated to *Bolitoglossa salvinii*. A: Holotype of *Spelerpes attitlanensis* Brocchi, 1883 (MNHP 6398), which corresponds to *B. salvinii* (Gray, 1868). B: Paratype of *Spelerpes attitlanensis* Brocchi, 1883 (MNHP 6399), which corresponds to *Bolitoglossa flaviventris* (Schmidt, 1936). C: Holotype of *Oedipus salvinii* Gray, 1868 (BMNH 1865.6.10.19H).

Figura 13.- Ejemplares tipo asociados a *Bolitoglossa salvinii*. A: Holotipo de *Spelerpes attitlanensis* Brocchi, 1883 (MNHP 6398), que corresponde a *B. salvinii* (Gray, 1868). B: Paratipo de *Spelerpes attitlanensis* Brocchi, 1883 (MNHP 6399), que corresponde a *Bolitoglossa flaviventris* (Schmidt, 1936). C: Holotipo de *Oedipus salvinii* Gray, 1868 (BMNH 1865.6.10.19H).

Taxonomic catalogue of the Bolitoglossa mexicana group

The nomenclatural status of the species of the *B. mexicana* group is summarized in the following catalogue. We are not including obvious misidentifications, misapplications of a name to a different species, nor first citations for a published name in the following list of synonyms. Differences in names spelling corresponding to gender changes ("-a" vs "-us" and "-um"), some proper name modifications ("u" vs "ue" and "ü"; "y" vs "j"), and "-i" vs "-ii" endings are not included.

Bolitoglossa alberchi García-París, Parra-Olea, Brame and Wake, h.o.

Bolitoglossa alberchi García-París, Parra-Olea, Brame and Wake, (this paper). Type locality: Playa Escondida, approximately 14 km (road) NE Sontecomapan, Veracruz, México, at ca. 50 m of elevation, 18° 56' N, 95° 05' W.

Bolitoglossa flaviventris (Schmidt, 1936)

Oedipus flaviventris Schmidt, 1936: 148. Type locality: "Chicharras, Chiapas".

Bolitoglossa flaviventris (Schmidt, 1936): Taylor and Smith, 1945: 547.

Bolitoglossa jacksoni Elias, 1984

Bolitoglossa jacksoni Elias, 1984: 7. Type locality: "Las Nubes sector of Finca Chiblac, approximately 12 km NNE of Santa Cruz Barillas, Depto. Huehuetenango, Guatemala, at about 1,400 m elevation"

Bolitoglossa lignicolor (Peters, 1873)

Spelerpes (*Oedipus*) *lignicolor* Peters, 1873: 617. Type locality: "Chiriqui"; the label on the jar accompanying the type indicates "Camaron, Provinz Chiriqui" (Bauer *et al.*, 1993).

Spelerpes punctatum Brocchi, 1883: 115. Type Locality: "Mexique"; corrected to "Veragua (Panama)" by Thireau (1986).

Oedipus ahli Unterstein, 1930: 272. Type locality**:** "Val del Pilatan, Cordilleren".

Oedipus lignicolor (Peters, 1873): Dunn, 1924: 99.

Bolitoglossa lignicolor (Peters, 1873): Taylor, 1944: 219.

Bolitoglossa ahli (Unterstein, 1930): Taylor, 1944: 219.

Bolitoglossa palustris Taylor, 1949: 283. Type Locality: "San Isidro el General".

Bolitoglossa mexicana Duméril, Bibron and Duméril, 1854

Bolitoglossa mexicana Duméril, Bibron and Duméril, 1854: 93. Type locality: "Dolorès, peten (Guatemala)".

Salamandra togata Valenciennes *In* Duméril, Bibron, and Duméril, 1854: 94. *Nomen nudum*.

Salamandra mexicana Cuvier *In* Duméril, Bibron, and Duméril, 1854: 94. *Nomen nudum*.

Spelerpes mexicana (Duméril, Bibron, and Duméril, 1854): Hallowell, 1856: 11.

Geotriton mexicana (Duméril, Bibron, and Duméril, 1854): Garman, 1884: 40.

Oedipus mexicanus (Duméril, Bibron, and Duméril, 1854): Schmidt, 1936: 146.

Bolitoglossa moreleti Smith, 1945: 17. Type locality: "vicinity of Palenque, Chiapas".

Bolitoglossa mombachoensis Köhler and McCranie, 1999

Bolitoglossa mombachoensis Köhler and McCranie, 1999: 90. Type locality: "Volcán Mombacho (11° 49.99' N, 85° 58.77' W), 1100 m elevation, Departamento de Granada, Nicaragua".

Bolitoglossa mulleri (Brocchi, 1883)

Spelerpes mulleri Brocchi, 1883: 116. Type locality: "haute Vera Paz: Les montagnes qui dominent Coban".

Spelerpes copei Brocchi, 1883: 113. *Nomen nudum*.

Oedipus mülleri (Brocchi, 1883): Schmidt, 1936: 150.

Bolitoglossa mulleri (Brocchi, 1883): Taylor, 1944: 219.

Oedipus mexicanus mulleri (Brocchi, 1883): Stuart, 1948: 19.

Bolitoglossa moreleti muelleri (Brocchi, 1883): Duellman, 1963: 220.

Bolitoglossa mexicana muelleri (Brocchi, 1883): Wake and Brame, 1963: 386.

Bolitoglossa odonnelli (Stuart, 1943)

Oedipus odonnelli Stuart, 1943: 10. Type locality: "Cafetal just east of the hacienda at Finca Volcán, Alta Verapaz, Guatemala. Altitude, 1200 meters"

Oedipus mexicanus odonnelli Stuart, 1943: Stuart, 1948: 19.

Bolitoglossa mexicana odonnelli (Stuart, 1943): Wake and Brame, 1963: 386.

Bolitoglossa odonnelli (Stuart, 1943): Wake and Elias, 1983: 10.

Bolitoglossa platydactyla (Gray, 1831)

Salamandra variegata Gray, 1831 (nec Bory, 1828), *In* Griffith and Pidgeon: 107. Type locality: "Mexico".

Salamandra platydactylus Gray, 1831, *In* Griffith and Pidgeon: 107. Replacement name for *S. variegata* Gray, 1831.

Oedipus platydactylus (Gray, 1831): Tschudi, 1838: 58.

Oedipus variegatus (Gray, 1831): Gray, 1850: 48.

Geotriton carbonarius Cope, 1860: 373. Type Locality: Not stated in the original publication. The types are from "Jalapa, Mexico" (Fowler and Dunn, 1917; Dunn, 1926).

Oedipus carbonarius (Cope, 1860): Cope, 1869: 103.

Spelerpes variegatus (Gray, 1831): Strauch, 1870: 84.

Geotriton variegata (Gray, 1831): Garman, 1884: 39.

Bolitoglossa platydactyla (Gray, 1831): Taylor, 1944: 219.

Bolitoglossa salvinii (Gray, 1868)

Oedipus salvinii Gray, 1868: 297. Type locality: Guatemala, Pacific Coast.

Spelerpes attitlanensis Brocchi, 1883: 115. Type Locality: "volcan d'Attitlan".

Spelerpes salvinii (Gray, 1868): Müller, 1878: 579.

Oedipus carbonarius salvinii Gray, 1868: Cope, 1879: 267.

Oedipus variegatus salvinii Gray, 1868: Cope, 1887: 8.

Oedipus attitlanensis (Brocchi, 1883): Dunn, 1924: 99.

Bolitoglossa salvinii (Gray, 1868): Taylor, 1944: 219.

Bolitoglossa striatula (Noble, 1918)

Oedipus striatulus Noble, 1918: 344. Type locality: "Cukra, Eastern Nicaragua".

Oedipus striatulus (Noble, 1918): Dunn, 1926: 416.

Bolitoglossa striatula (Noble, 1918): Taylor, 1944: 219.

Bolitoglossa yucatana (Peters, 1882)

Spelerpes (*Oedipus*) *yucatanus* Peters, 1882: 137. Type locality: "Yucatan"

Spelerpes yucatanicus Boulenger, 1882: 72. Type Locality: "Yucatan".

Oedipus jucatanicus (Boulenger, 1882): Cope, 1887: 8.

Oedipus yucatanus (Peters, 1882): Dunn, 1924: 99.

Bolitoglossa yucatana (Peters, 1882): Taylor, 1944: 219.

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Appendix I

List of material included in the DNA study (MVZ: Museum of Vertebrate Zoology, University of California at Berkeley; SMF: Senckenberg Museum und Forschinstitut; UTAVC: University of Texas at Arlington; GP: G. Parra-Olea field number; LDW: L. D. Wilson field number; MGP: M. García-París photographic collection):

B. adspersa: **Colombia**: Cundinamarca: Ubate, MVZ 158485.

B. alberchi: **México**: Chiapas: Cafetal, 26.5 km N Ocozocuautla on road to Apic Pac, MVZ 194293; 7.5 mi N of Berriozabal, MVZ 138658; Veracruz: Playa Escondida, E of Catemaco (30 km NNE), MVZ 163959; Playa Escondida, N of Catemaco, MVZ 172667.

B. flaviventris: **México**: Chiapas: 2.0 - 6.5 mi N Tapachula on road to Nueva Alemania, MVZ 194287-194288; Finca La Esperanza, 5 km (by road) E Acocoyagua, MVZ 163963.

***B. lignicolor*: Costa Rica:** Puntarenas: Finca La Dibujada, Buenos Aires - Osa, MVZ (s 11132).

B. mexicana: **Belize**: Toledo: vicinity of Indian Village of Blue Creek, MVZ 191631, 191632, 191635.

Honduras: El Paraíso: Las Manos, 13° 48' N - 86° 34' W, UTA (ENS 8675); Atlántida: Quebrada de Oro, 15 38 N 86 47 W, 600 m elev., USNM 343451. **México**: Chiapas: Lagos de Montebello, (MGP photographic voucher).

***B. mombachoensis*: Nicaragua**: Granada: Volcán Mombacho, near lower antenna (11°49.99'N, 85°58.77'W), 1100 m, SMF 78718, SMF 78725.

B. odonnelli: **Guatemala**: Alta Verapaz: Finca El Volcán, 875m, 25 km (road) NW Senahú, MVZ 161039, 161046; Izabal: Morales: Sierra de Caral: Finca la Firmeza, UTA (MEA 446); Morales: Sierra de Caral: Camino Finca Quebradas - Cerro Pozo de Agua, UTA (ENS 7862).

Honduras: Copán: 2 km N Santa Rosa de Copán, MVZ 163797; Cortés: Cafetal, 8 km (road) W Peña Blanca, MVZ 163794, 163795; 3.1 km (by road) S Peña Blanca, MVZ 163793; Olancho: Río Catacamas, near Catacamas, 480 m elev., MVZ 229068.

***B. platydactyla*: México:** Veracruz: vic. of Cuautlapan, GP 108; Hotel Playa Azul vic. of Catemaco, GP 587.

***B. striatula*: Costa Rica**: Cartago: I.I.C.A., 4.5 km ESE Turrialba, MVZ 181280.

***B. yucatana*: México**: Quintana Roo: 13-19 km (road) Cobá, MVZ 197507, 197508.

Appendix II

List of material included in the morphometric study (MVZ: Museum of Vertebrate Zoology, University of California at Berkeley; UTAVC: University of Texas at Arlington):

Bolitoglossa alberchi: México: Veracruz: Playa Escondida, approximately 14 km (road) NE Sontecomapan (n = 22) (MVZ 163959-62, MVZ 172665-67, MVZ 163782, MVZ 163791, MVZ 193155, MVZ 200568, MVZ 208378, UTAVC 7788, UTAVC 7803-04, UTAVC 7811, UTAVC 7852, UTAVC 7854-55, UTAVC 7857, UTAVC 7901, UTAVC 7909)

Bolitoglossa mexicana: México: Chiapas: San Juanito, nearPalenque (n = 15) (USNM 116071-79, USNM 116090-91, USNM 116095-98).

Bolitoglossa odonnelli: Guatemala: Alta Verapaz: Finca El Volcán (n = 12) (MVZ 161030-36, MVZ 161038, MVZ 161040, MVZ 161045-46, MVZ 161081).