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A new terrestrial species of *Chiropterotriton* (Caudata: Plethodontidae) from central Mexico

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Abstract

Chiropterotriton is a relatively small genus that comprises 15 species with great morphological and ecological diversity. In previous studies, molecular data provided evidence for a considerable number of species that remain undescribed. In this study, we describe one new species, *Chiropterotriton chico* **sp. nov.** based on molecular and morphological characters. We present mtDNA phylogenetic analyses using Bayesian inference and maximum likelihood that include all described and several undescribed species. Morphometric data from eight recognized species provide evidence for the distinctiveness of the new taxon. Description of this new species adds to the already high salamander diversity of the state of Hidalgo, which is an important area for the diversification of the genus.

Key words: salamanders, bolitogossines, morphology, taxonomy, Hidalgo

Introduction

The tribe Bolitoglossini (Wake 2012) is composed of 305 species (AmphibiaWeb 2017), which represents more than 65% of the known Plethodontid species. It includes 14 genera that show extensive morphological diversification in the Neotropics (Rovito *et al.* 2015). Although this highly diverse group has been studied for many years, molecular tools have shown that the diversity of the group has been underestimated and many species of bolitoglossine salamanders have been recently described based on morphological and molecular data (Townsend *et al.* 2010; Boza-Oviedo *et al.* 2012; Acevedo *et al.* 2013; Rovito & Parra-Olea 2015; Parra-Olea *et al.* 2016).

The genus *Chiropterotriton* currently contains 15 described species, which occur exclusively in Mexico from the northern states of Coahuila, Nuevo León, and Tamaulipas to the south in Oaxaca (AmphibiaWeb 2017). This group shows substantial morphological diversity, including extensive variation in degree of foot webbing and body size. Ecological diversity is also evident in the arboreal, terrestrial, and cave-dwelling habitats of these salamanders. This diversity is largely a product of size change and heterochrony, which is common in plethodontid evolution (Darda 1994; Darda & Wake 2015). The first molecular phylogeny of *Chiropterotriton,* based on allozyme data, was published by Darda (1994) who analyzed samples from 25 populations that included all but two (*C. mosaueri* (Woodall) and *C. multidentatus* (Taylor)) of the then described species. His analysis grouped all species in two geographic assemblages (northern and southern) and suggested the existence of 13 undescribed species. Parra-Olea (2003) presented a mitochondrial phylogeny, which also lacked sequences of *C. mosaueri* and *C. multidentatus,* and included 27 populations. Parra-Olea's phylogeny was in general in agreement with most of the allozyme results and supported seven of Darda's undescribed species. More recently, Campbell *et al.* (2014) described one new species from northern Mexico. Rovito & Parra-Olea (2015) presented a phylogeny based on two mitochondrial genes that included 13 species of *Chiropterotriton,* as well as many undescribed species, and described two more species from northern Mexico. Of these three newly described species, one corresponds to one

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of the 13 undescribed species reported for Darda (1994) while two of them were not included in the phylogenetic analyses of Darda (1994) or Parra-Olea (2003). In general, all published phylogenies agree on the existence of two clades, concordant with the geographic distribution of the species, and support the existence of multiple undescribed species.

In the present paper, we describe a species from El Chico National Park in the state of Hidalgo, which long have been assigned to *Chiropterotriton multidentatus* (Rabb 1958; Wake & Lynch 1976). Only recently has tissue been available from topotypic *C. multidentatus* (Rovito & Parra-Olea 2015), and it has proven crucial in the present study. The description is based on both mtDNA phylogenetic analyses and morphological characters.

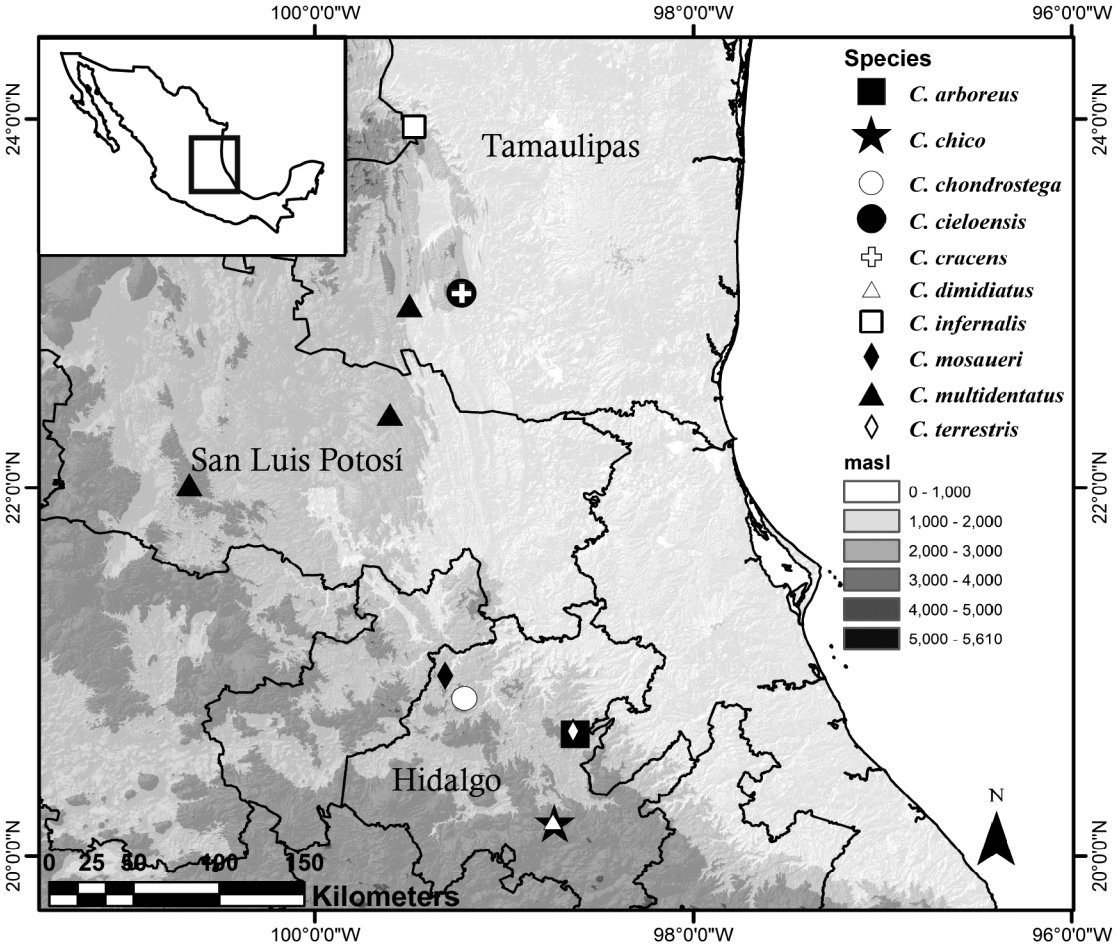

FIGURE 1. Map of *Chiropterotriton* localities in central and northern Mexico used for phylogenetic and morphological comparisons. Distributional ranges for all species of *Chiropterotriton* used in this study are a small area surrounding the locality shown here.

Methods

We analyzed a total of 30 previously published sequences of the large subunit ribosomal RNA (16S) mitochondrial gene (Parra-Olea 2003; Rovito & Parra-Olea 2015). Voucher information and Genbank numbers are given in Table 1. We aligned the sequences with Muscle v.3.8 (Edgar 2004) and used jModelTest2 (Darriba *et al.* 2012) to select the best-fitting nucleotide substitution model substitution model (GTR+I+G). We performed a Bayesian phylogenetic analysis using the program MrBayes 3.2 (Ronquist *et al.* 2012). Two separate runs were done for 20,000,000 generations, with three hot and one cold chains, sampled every 1000 generations, and the first 5000 samples were discarded as burn-in. A maximum likelihood analysis was run in RAxML v.8.0 (Stamatakis 2006). Nodal support was assessed through 1000 bootstrap replicates. *Isthmura boneti* (Alvarez & Martín) and *Thorius*

magnipes Hanken & Wake were used as outgroups in both analyses. Both phylogenetic analyses were run on the CIPRES Science Gateway (Miller *et al.* 2010). Finally, we obtained corrected genetic distances (Kimura two-parameter, K2P) using Mesquite v3.04 (Maddison & Maddison 2015), which are shown in Table 2.

TABLE 1. Voucher information and GenBank numbers for specimens included in phylogenetic analyses from the Museum of Vertebrate Zoology, UC Berkeley (MVZ) and Instituto de Biología, UNAM (IBH). Locality abbreviations: DF: Distrito Federal, Hgo: Hidalgo, NL: Nuevo León, Oax: Oaxaca, Pue: Puebla, SLP: San Luis Potosí, Tamps: Tamaulipas, Ver: Veracruz.

Species	Locality	Voucher number	Genbank Accessions
C. arboreus	Hgo: 4.3 km E of Hwy 105 junction on road to Tianguistengo	MVZ200622	AY522474
C. chico	Hgo: 3.8 km S Mineral del Chico	MVZ200679	AY522471
C. chiropterus	Ver: Huatusco	MVZ163724	AY522495
C. chondrostega	Hgo: La Venta, 3.6 km NE of jct to hwy Mx 85 on road to La Encarnación	IBH22266	AY523996
C. chondrostega	Hgo: 1.0 km S (by rd) of La Encarnación	IBH28195	KT820673
C. cieloensis	Tamps: 5.6 km (air) NW Gómez Farías	MVZ158570	AY522473
C. cieloensis	Tamps: 5.6 km (air) W Gómez Farías	MVZ173380	AY522459
C. cracens	Tamps: 1.3 km NE (by air) of San José, Reserva de la Biósfera El Cielo	IBH28192	KT820674
C. dimidiatus	Hgo: 4.9 km S Mineral del Chico	IBH22344	AY522463
C. dimidiatus	Hgo: 4.1 km S (by rd) of Mineral del Chico	IBH28196	KT820675
C. infernalis	Tamps: Cueva del Brinco, Conrado Castillo	MVZ269665	KT820694
C. lavae	Ver: La Joya	IBH22342	AY522466
C. lavae	Ver: La Joya	IBH28180	KT820676
C. magnipes	SLP: 1.1 km W Ahuacatlán	MVZ200678	AY522469
C. miquihuanus	NL: 1.8 km S (by rd) of La Encantada on road from La Bolsa to Zaragoza	MVZ269643	KT820697
C. mosaueri	Hgo: 900 m SSE Durango	IBH28179	KT820677
C. multidentatus	SLP: 900 m NE Valle de los Fantasmas	IBH28177	KT820678
C. multidentatus	SLP: 26.2 km E (by rd) of center of Ciudad del Maíz	IBH28194	KT820680
C. multidentatus	Tamps: 22.0 km E (by rd) Tula on road to Ocampo	MVZ269654	KT820681
C. orculus	DF: 8.8 km SW La Venta, Parque Nacional Desierto de los Leones	MVZ138677	AY522444
C. priscus	NL: Cerro Potosí	gp011	AY522476
C. priscus	NL: Cerro Potosí, 30.2 km NW (by rd) of center of Galeana	MVZ269655	KT820682
C. terrestris	Hgo: 4 km NNE Zacualtipán	MVZ172149	AY522455
C. sp. C	Ver: 3.2 km S Puerto del Aire	MVZ163635	AY522453
C. sp. F	Pue: Xicotepec de Juárez	MVZ178707	AY522479
C. sp. G	Pue: 4 km S Chignahuapan	MVZ178703	AY522481
C. sp. H	Ver: 15.9 km S Las Vigas on road to RMO Las Lajas	IBH23066	AY522482
C. sp. I	Pue: Santa Cruz de Texmalaquilla	MVZ201387	AY522488
C. sp. J	Oax: La Esperanza	gp086	AY522489
C. sp. K	Oax: Cerro San Felipe	MVZ173232	AY522491
Isthmura boneti	Oax: Cerro Zempoaltepetl	MVZ163873	AY864714
Thorius magnipes	Pue: Lagunas de San Bernardino	IBH22918	KC884063

TABLE 2. Sequence divergence with Kimura two-parameter distances (upper half) and uncorrected (*p*) distances (lower half).

		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	*C. arboreus*		0.069	0.119	0.115	0.062	0.073	0.122	0.066	0.101	0.124	0.083	0.113
2	*C. chico*	0.065		0.128	0.105	0.075	0.075	0.121	0.062	0.104	0.107	0.088	0.095
3	*C. chiropterus*	0.110	0.117		0.122	0.143	0.119	0.113	0.117	0.083	0.139	0.113	0.127
4	*C. chondrostega*	0.106	0.097	0.112		0.127	0.087	0.118	0.099	0.115	0.110	0.092	0.099
5	*C. cieloensis*	0.059	0.071	0.129	0.116		0.066	0.129	0.069	0.119	0.122	0.092	0.103
6	*C. cracens*	0.068	0.071	0.109	0.082	0.063		0.108	0.068	0.110	0.110	0.074	0.098
7	*C. dimidiatus*	0.112	0.111	0.104	0.108	0.118	0.100		0.123	0.085	0.133	0.102	0.123
8	*C. infernalis*	0.063	0.060	0.108	0.093	0.065	0.065	0.112		0.103	0.120	0.092	0.103
9	*C. lavae*	0.094	0.096	0.078	0.105	0.109	0.101	0.080	0.096		0.127	0.103	0.108
10	*C. magnipes*	0.113	0.098	0.125	0.102	0.111	0.101	0.119	0.110	0.114		0.104	0.109
11	*C. miquihuanus*	0.078	0.083	0.104	0.087	0.086	0.070	0.094	0.086	0.096	0.096		0.094
12	*C. mosaueri*	0.104	0.089	0.116	0.092	0.096	0.092	0.112	0.096	0.099	0.099	0.088	
13	*C. multidentatus*	0.039	0.065	0.116	0.098	0.057	0.065	0.114	0.065	0.104	0.110	0.077	0.114
14	*C. multidentatus*	0.037	0.061	0.111	0.102	0.067	0.066	0.110	0.063	0.092	0.105	0.078	0.112
15	*C. multidentatus*	0.033	0.053	0.105	0.100	0.057	0.059	0.102	0.059	0.086	0.109	0.074	0.110
16	*C. orculus*	0.080	0.087	0.080	0.109	0.096	0.088	0.080	0.090	0.068	0.115	0.086	0.097
17	*C. priscus*	0.094	0.085	0.129	0.102	0.102	0.105	0.108	0.096	0.099	0.109	0.063	0.080
18	*C. terrestris*	0.062	0.028	0.113	0.091	0.067	0.069	0.103	0.056	0.093	0.101	0.080	0.087
19	*C.* sp. C	0.094	0.100	0.070	0.107	0.113	0.105	0.078	0.096	0.014	0.114	0.096	0.101
20	*C.* sp. F	0.119	0.111	0.072	0.114	0.137	0.110	0.104	0.116	0.088	0.125	0.116	0.124
21	*C.* sp. G	0.084	0.095	0.080	0.107	0.105	0.088	0.082	0.092	0.066	0.122	0.082	0.103
22	*C.* sp. H	0.096	0.098	0.082	0.109	0.111	0.107	0.084	0.098	0.012	0.112	0.098	0.099
23	*C.* sp. I	0.090	0.103	0.074	0.110	0.111	0.103	0.080	0.102	0.016	0.115	0.094	0.102
24	*C.* sp. J	0.102	0.112	0.021	0.111	0.121	0.105	0.098	0.104	0.076	0.120	0.098	0.103
25	*C.* sp. K	0.092	0.099	0.072	0.109	0.108	0.088	0.092	0.094	0.062	0.097	0.094	0.100

……continued on the next page

TABLE 2. (Continiued)

		13	14	15	16	17	18	19	20	21	22	23	24	25
1	*C. arboreus*	0.040	0.038	0.034	0.085	0.101	0.065	0.101	0.131	0.089	0.103	0.096	0.110	0.099
2	*C. chico*	0.069	0.064	0.056	0.093	0.090	0.028	0.109	0.121	0.102	0.106	0.111	0.123	0.107
3	*C. chiropterus*	0.127	0.121	0.115	0.085	0.143	0.123	0.074	0.077	0.085	0.087	0.079	0.022	0.077
4	*C. chondrostega*	0.106	0.110	0.108	0.119	0.110	0.098	0.117	0.124	0.117	0.119	0.120	0.121	0.120
5	*C. cieloensis*	0.060	0.071	0.060	0.103	0.110	0.071	0.124	0.153	0.114	0.121	0.122	0.133	0.117
6	*C. cracens*	0.068	0.070	0.062	0.094	0.115	0.073	0.114	0.119	0.094	0.116	0.112	0.114	0.094
7	*C. dimidiatus*	0.125	0.120	0.110	0.085	0.118	0.112	0.083	0.113	0.087	0.090	0.085	0.106	0.099
8	*C. infernalis*	0.069	0.066	0.062	0.096	0.104	0.058	0.103	0.127	0.099	0.105	0.110	0.112	0.101
9	*C. lavae*	0.112	0.098	0.091	0.072	0.108	0.100	0.014	0.094	0.070	0.012	0.016	0.081	0.066
10	*C. magnipes*	0.120	0.115	0.120	0.127	0.120	0.109	0.127	0.139	0.137	0.124	0.127	0.134	0.106
11	*C. miquihuanus*	0.081	0.083	0.079	0.092	0.066	0.084	0.103	0.127	0.087	0.105	0.101	0.106	0.102
12	*C. mosaueri*	0.125	0.122	0.120	0.106	0.085	0.093	0.110	0.137	0.113	0.108	0.111	0.112	0.108
13	*C. multidentatus*		0.028	0.028	0.099	0.108	0.067	0.117	0.129	0.096	0.115	0.115	0.121	0.110
14	*C. multidentatus*	0.027		0.020	0.089	0.115	0.065	0.107	0.129	0.091	0.105	0.103	0.116	0.096
15	*C. multidentatus*	0.027	0.019		0.083	0.108	0.056	0.101	0.122	0.085	0.098	0.098	0.109	0.094
16	*C. orculus*	0.092	0.084	0.078		0.122	0.097	0.070	0.084	0.022	0.076	0.072	0.076	0.047
17	*C. priscus*	0.100	0.105	0.099	0.111		0.102	0.112	0.146	0.114	0.110	0.110	0.135	0.134
18	*C. terrestris*	0.064	0.062	0.054	0.091	0.095		0.104	0.114	0.107	0.102	0.107	0.123	0.105
19	*C.* sp. C	0.108	0.099	0.094	0.066	0.103	0.097		0.087	0.068	0.018	0.006	0.074	0.063
20	*C.* sp. F	0.118	0.117	0.112	0.078	0.131	0.105	0.082		0.083	0.096	0.095	0.072	0.072
21	*C.* sp. G	0.090	0.086	0.080	0.021	0.105	0.099	0.064	0.078		0.070	0.068	0.072	0.044
22	*C.* sp. H	0.106	0.097	0.092	0.072	0.101	0.095	0.017	0.090	0.066		0.020	0.085	0.066
23	*C.* sp. I	0.106	0.096	0.092	0.068	0.101	0.099	0.006	0.088	0.064	0.019		0.074	0.066
24	*C.* sp. J	0.112	0.107	0.101	0.072	0.123	0.113	0.070	0.068	0.068	0.080	0.070		0.068
25	*C.* sp. K	0.102	0.090	0.088	0.045	0.121	0.097	0.060	0.068	0.043	0.062	0.062	0.064	

TABLE 3. Mean ± standard deviation and range of morphological measurements (in mm) and tooth counts for males. Sample size given when different from total number of specimens measured for each species. * Data taken from Rovito & Parra-Olea 2015.

MALES	*C. arboreus* *N* = 9	*C. chondrostega* *N* = 10	*C. cieloensis** *N* = 8	*C. chico* *N* = 15	*C. cracens** *N* = 4	*C. dimidiatus* *N* = 15	*C. infernalis** *N*= *8*	*C. multidentatus** *N* = 7	*C. terrestris* *N* = 15
SVL	33.4±3.62 (27.8–39.5)	23.1±1.07 (21.0–24.6)	32.6±1.96 (30.2–36.1)	38.4±1.99 (36.2–42.6)	25.7±1.98 (23.7–28.0)	24.6±0.97 (23.3–26.7)	36.4±3.84 (31.0–41.6)	33.6±2.92 (29.3–36.7)	24.2±1.33 (21.6–26.9)
TL	41.5±5.91 (32.0–50.4) *N* = 8	25.6±3.91 (19.4–32.4)	38.3±5.25 (32.9–48.1) *N* = 7	45.4±2.81 (40.4–49.5)	30.6±3.65 (26.6–35.4)	22.0±1.71 (18.4–24.1)	44.6±4.72 (38.1–51.9) *N* = 7	37.8±7.52 (30.3–48.9) *N* = 6	25.3±2.26 (19.8–29.2)
AX	16.5±1.74 (13.7–19.7)	11.62±0.47 (11.1–12.4)	16.7±1.27 (15.2–18.9)	19.8±1.19 (17.5–21.7)	13.3±0.99 (12.3–14.7)	13.1±0.74 (11.6–13.9)	18.6±2.25 (15.0–21.1)	17.4±1.72 (15.2–20.0)	12.1±0.76 (10.8–13.3)
FLL	8.2±0.73 (7.2–9.2)	4.9±0.31 (4.5–5.5)	8.6±0.68 (7.7–9.8)	8.4±0.54 (7.2–9.4)	6.1±1.06 (5.1–7.6)	4.5±0.33 (3.7–4.9)	9.8±1.37 (8.0–11.8)	8.8±1.63 (6.8–11.5)	4.7±0.47 (3.9–5.5)
HLL	9.5±0.73 (8.4–10.3)	5.4±0.43 (5.1–6.5)	9.8±0.68 (9.0–10.9)	10.1±0.73 (8.0–10.8)	7.0±1.07 (6.0–8.5)	5.2±0.33 (4.8–5.9)	11.2±1.28 (9.1–12.9)	10.0±2.05 (7.7–13.2)	5.2±0.53 (4.3–6.0)
HL	7.9±0.80 (6.5–9.2)	5.6±0.30 (5.1–6.1)	7.1±0.33 (6.7–7.8)	8.8±0.61 (7.2–9.8)	5.5±0.78 (4.6–6.4)	5.2±0.31 (4.8–5.8)	8.2± 1.07 (6.9–10.1)	7.4±0.87 (6.4–8.9)	5.7±0.33 (5.0–6.1)
HW	5.0±0.49 (4.4–5.7)	3.4±0.19 (3.2–3.8)	4.8±0.30 (4.3–5.4)	5.6±0.24 (5.0–5.9)	3.8±0.52 (3.2–4.4)	3.4±0.20 (2.9–3.7)	5.7± 0.62 (4.6–6.4)	4.9±0.56 (4.1–5.7)	3.5±0.27 (3.2–4.0)
HD	2.5±0.28 (1.9–2.8)	1.8±0.09 (1.68–1.97)	—	2.6±0.20 (2.2–2.9)	—	1.8±0.08 (1.7–1.9)	—	—	1.8±0.21 (1.5–2.3)
SW	4.2±0.52 (3.5–4.9)	3.04±0.19 (2.7–3.4)	—	4.8±0.35 (4.0–5.5)	—	2.9±0.29 (2.3–3.5)	—	—	2.7±0.32 (2.1–3.3)
IN	1.8±0.24 (1.3–2.0)	1.3±0.08 (1.2–1.4)	1.7±0.08 (1.6–1.9)	2.1±0.18 (1.8–2.5)	1.3±0.16 (1.1–1.5)	1.1±0.08 (1.0–1.2)	1.9±0.19 (1.5–2.1)	1.7±0.25 (1.3–2.1)	1.3±0.13 (1.1–1.5)
FW	3.4±0.30 (2.8–3.9)	1.8±0.21 (1.5–2.2)	3.2±0.40 (2.7–3.8)	4.1±0.35 (3.4–4.6)	2.2±0.34 (1.9–2.7)	1.7±0.19 (1.4–2.0)	4.2±0.70 (3.2–5.3)	3.6±0.39 (3.1–4.1)	1.9±0.29 (1.3–2.4)
NL	0.16±0.019 (0.13–0.18)	0.13±0.009 (0.11–0.14)	0.19±0.020 (0.16–0.21) *N* = 4	0.16±0.012 (0.13–0.18)	0.15±0.010 (0.14–0.16)	0.25±0.010 (0.24–0.28)	0.24±0.030 (0.19–0.28) *N* = 4	0.22±0.020 (0.19–0.23) *N* = 4	0.12±0.008 (0.10–0.13)
NW	0.08±0.009 (0.07–0.08)	0.06±0.005 (0.06–0.08)	0.12±0.000 (0.12–0.12) *N* = 4	0.08±0.006 (0.06–0.08)	0.11±0.020 (0.09–0.12)	0.25±0.012 (0.23–0.28)	0.17±0.030 (0.12–0.21) *N* = 4	0.16±0.010 (0.14–0.16) *N* = 4	0.07±0.006 (0.06–0.08)
ND	2.1±0.24 (1.8–2.5)	1.9±0.19 (1.6–2.2)	1.6±0.19 (1.4–1.8) *N* = 4	1.9±0.21 (1.6–2.5)	1.5±0.23 (1.2–1.8)	1.0±0.06 (0.8–1.1)	1.5±0.18 (1.1–1.7) *N* = 4	1.4±0.22 (1.1–1.6) *N* = 4	1.7±0.17 (1.4–2.0)
LI	0.2±0.36 (0–1)	2.0±0.00 (2–2)	-0.2±0.46 (-1–0.5)	0.6±0.30 (0–1)	1.8±0.65 (1–2.5)	3.8±0.35 (3–4)	–0.7± 0.98 (–2–1)	0.1±1.60 (–3–1.5)	1.9±0.32 (1.5–2.5)
PMT+MT	26.5±3.39 (20–30)	22.5±3.71 (18–29)	31.4±3.66 (26–35)	42.3±5.08 (32–54)	36.8±0.96 (36–38)	9.4±2.58 (5–14)	49.3±7.11 (36–56)	40.0±11.06 (26–56)	21.2±3.82 (15–30)
VT	11.2±2.59 (9–17)	7.9±1.52 (6–11)	11.5±2.00 (9–15)	13.6±2.58 (10–19)	12.5±2.08 (10–15)	5.6±1.34 (4–8)	17.6±3.16 (13–22)	13.3±1.70 (11–16)	8.8±1.82 (6–14)

TABLE 4. Mean ± standard deviation and range of morphological measurements (in mm) and tooth counts for females. Sample size given when different from total number of specimens measured for each species. * Data taken from Rovito & Parra-Olea 2015.

FEMALES	*C. arboreus* *N = 5*	*C. chondrostega* *N = 11*	*C. cieloensis** *N = 4*	*C. chico* *N = 15*	*C. cracens** *N = 15*	*C. dimidiatus* *N = 15*	*C. infernalis** *N = 1*	*C. multidentatus** *N = 9*	*C. terrestris* *N = 15*
SVL	32.2±3.47 (29.3–38.0)	25.4±1.73 (23.5–28.2)	31.1±2.73 (28.3–34.4)	39.3±2.59 (35.9–44.3)	27.4±3.30 (23.2–34.0)	25.8±1.55 (23.0–29.0)	29.7	34.0±6.27 (24.5–41.9)	23.0±1.92 (21.6–27.6)
TL	37.4±5.82 (33.7–47.6)	24.2±3.70 (17.6–31.0)	31.9±5.32 (24.5–36.0)	44.1±3.65 (37.0–49.0)	28.8±6.17 (17.2–38.4)	22.4±1.84 (19.8–25.1)	34.5	34.9±5.81 (26.5–43.6)	22.4±1.89 (21.0–28.5)
AX	16.7±1.55 (15.3–19.2)	13.4±0.89 (12.5–14.9)	16.8±1.98 (14.1–18.9)	21.8±1.64 (19.0–23.9)	14.5±1.99 (11.5–18.5)	14.7±1.23 (12.5–17.2)	14.2	17.5±3.59 (11.5–22.5)	12.0±1.22 (11.2–15.3)
FLL	7.4±0.93 (6.8–9.0)	5.0±0.30 (4.3–5.3)	8.1±0.98 (7.1–9.4)	8.2±0.59 (7.2–9.0)	6.4±1.53 (4.4–8.8)	4.3±0.43 (3.7–5.1)	7.2	8.6±2.12 (5.9–11.7)	4.3±0.36 (3.9–5.4)
HLL	8.9±0.61 (8.3–9.6)	5.5±0.42 (4.9–6.1)	9.4±0.95 (8.8–10.8)	9.6±0.84 (8.4–11.1)	7.3±1.46 (5.5–9.7)	4.9±0.47 (4.3–6.1)	8.9	9.8±2.29 (6.7–13.5)	4.8±0.44 (4.3–5.8)
HL	7.6±0.87 (6.9–9.0)	5.7±0.33 (5.4–6.5)	6.9±0.65 (6.3–7.7)	8.7±0.62 (7.9–9.9)	5.8±0.84 (4.8–7.1)	5.0±0.33 (4.4–5.6)	6.2	7.4±1.37 (5.2–9.2)	5.2±0.35 (5.1–6.1)
HW	4.9±0.51 (4.5–5.7)	3.7±0.19 (3.4–4.0)	4.9±0.59 (4.5–5.8)	5.7±0.41 (5.1–6.7)	4.1±0.62 (3.2–5.1)	3.5±0.24 (3.1–3.9)	4.3	5.1±0.89 (3.7–6.2)	3.3±0.48 (2.2–4.2)
HD	2.1±0.24 (1.8–2.4)	1.9±0.09 (1.7–2.0)	—	2.8±0.28 (2.4–3.4)	—	2.0±0.20 (1.7–2.2)	—	—	1.8±0.20 (1.6–2.3)
SW	4.0±0.42 (3.6–4.7)	3.13±0.26 (2.8–3.8)	—	5.1±0.36 (4.6–5.8)	—	3.1±0.26 (2.7–3.5)	—	—	2.8±0.29 (2.6–3.6)
IN	1.8±0.06 (1.7–1.8)	1.2±0.11 (1.1–1.4)	1.6±0.13 (1.5–1.8)	2.1±0.13 (1.9–2.3)	1.3±0.19 (1.0–1.6)	1.2±0.14 (1.0–1.6)	1.4	1.6±0.23 (1.3–2.0)	1.2±0.14 (1.1–1.5)
FW	3.5±0.62 (2.9–4.4)	1.8±0.18 (1.5–2.2)	3.1±0.55 (2.3–3.6)	4.2±0.58 (3.4–5.5)	2.5±0.67 (1.8–3.5)	1.7±0.25 (1.2–2.2)	2.8	3.5±0.80 (2.3–4.6)	1.7±0.25 (1.4–2.2)
NL	0.16±0.009 (0.15–0.17)	0.12±0.010 (0.11–0.14)	0.21±0.020 (0.19– 0.23) N = 3	0.15±0.008 (0.14–0.16)	0.19±0.030 (0.14–0.23) N = 14	0.21±0.026 (0.19–0.26)	0.20	0.21±0.020 (0.19–0.23) N = 5	0.11±0.009 (0.10–0.13)
NW	0.08±0.007 (0.07–0.08)	0.06±0.007 (0.04–0.08)	0.12±0 (0.12–0.12) N = 3	0.08±0.015 (0.06–0.11)	0.12±0.030 (0.09–0.19) N = 14	0.24±0.020 (0.19–0.28)	0.19	0.14±0.020 (0.12–0.16) N = 5	0.07±0.009 (0.07–0.08)
ND	2.00±0.19 (1.8–2.2)	1.97±0.21 (1.6–2.3)	1.80±0.20 (1.6–2.0) N = 3	1.95±0.27 (1.4–2.2)	1.60±0.27 (1.2–2.0) N = 14	0.89±0.10 (0.8–1.0)	1.13	1.5±0.18 (1.3–1.8) N = 5	1.5±0.22 (1.2–2.0)
LI	1.0±0 (1–1)	3.0± 0.0 (3–3)	0.1±0.85 (-1–1)	2.1±0.39 (1.5–3.0)	2.1±0.89 (0.5–3.5)	4.9±0.25 (4.0–5.0)	–0.5	1.0±0.97 (0.5–2)	2.6±0.28 (2–3)
PMT +MT	33.4±3.43 (28–36)	40.9±5.33 (33–48)	46.8±6.40 (42–56)	56.5±4.79 (48–67)	49.5±11.07 (32–74)	34.4±4.11 (27–41)	53	47.8±11.24 (34–66)	38.1±7.04 (27–53)
VT	12.4±2.41 (9–15)	9.54±2.29 (6–14)	12.8±1.71 (11–15)	15.6±1.79 (13–19)	12.0±2.48 (7–16)	8.33±1.34 (6–11)	15	13.1±3.02 (10–19)	9.9±1.92 (8–14)

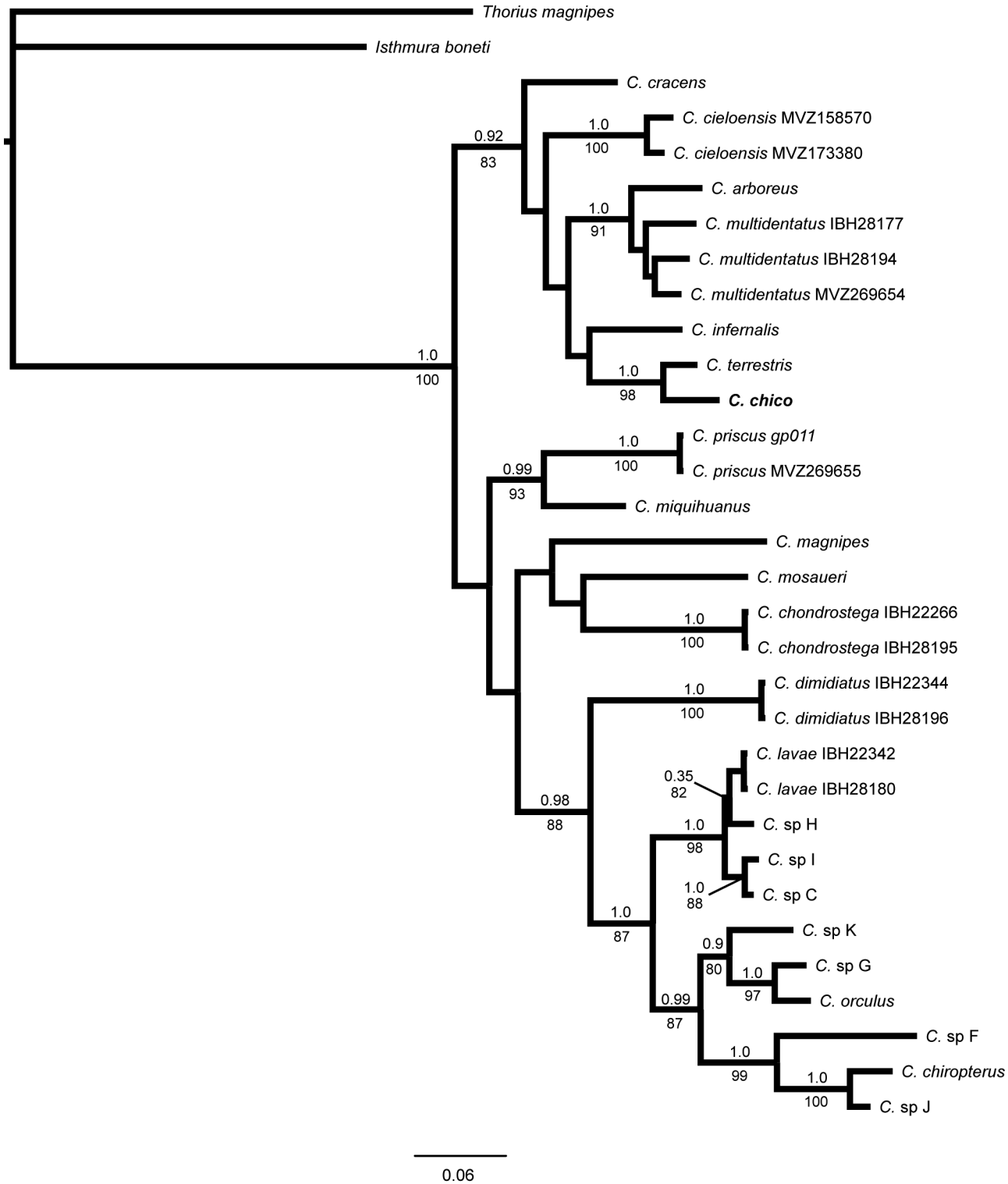

FIGURE 2. Mitochondrial DNA gene tree of *Chiropterotriton* from Bayesian analysis of 16S sequences. Numbers above branches represent posterior probabilities and numbers below branches are boostrap values from maximum likelihood phylogenetic analysis.

Species descriptions follow the format used by Lynch and Wake (1989) for species of Neotropical plethodontids and include the same basic characters and measurements. The comparisons for the new species were made with the other five members of its clade from our phylogenetic analyses (see Results) as well as with other geographically proximate species. We examined specimens of other species that occur in Hidalgo, *Chiropterotriton*

arboreus (Taylor), *C. chondrostega* (Taylor), *C. dimidiatus* (Taylor) and *C. terrestris* (Taylor) (Appendix 1), and we used the published measurements of *C. mosaueri* (Woodall 1941; Rabb 1958; Rovito & Parra-Olea 2015), *C. cracens* Rabb, *C. cieloensis* Rovito & Parra-Olea, *C. infernalis* Rovito & Parra-Olea, and *C. multidentatus* (Rovito & Parra-Olea 2015) that occur in Hidalgo, Tamaulipas and San Luis Potosí.

We compared measurements of 181 specimens (91 males and 90 females) from nine species of *Chiropterotriton* from central and northern Mexico (Fig. 1, Tables 3 and 4, Appendix 1). We took measurements of 11 characters to the nearest 0.1 mm with a Vernier calipers: snout-vent length (SVL), tail length (TL), axilla-groin distance (AX), forelimb length (FLL), hind limb length (HLL), snout to gular fold distance (head length, HL), head width at angle of jaw (HW), head depth (HD), shoulder width (SW), internarial distance (IN), and right foot width (FW). We also measured the widest and narrowest nostril dimensions (nostril length, NL, and nostril width, NW) using an ocular micrometer and calculated a ratio of nostril dimensions (ND = NL/NW) as an index of nostril shape. We counted maxillary (MT), premaxillary (PMT), and vomerine teeth (VT) and we present counts for PMT and MT together because of the difficulty in distinguishing them in some specimens. We also measured limb interval (LI) as the number of costal folds between adpressed limbs, with positive values meaning grooves between limbs and negative values meaning overlap between limbs. We separated males and females in order to account for sexual dimorphism in the statistics. Twelve additional measurements were obtained for the holotype: anterior rim of orbit to snout, eyelid length, eyelid width, horizontal orbital diameter, interorbital distance, length of third (longest) toe, length of fifth toe, projection of snout beyond mandible, snout to anterior angle of vent, snout to forelimb, tail depth at base, and tail width at base.

Results

Our phylogenetic hypothesis based on mtDNA (Fig. 2) shows that the populations from Hidalgo are not close relatives of topotypic *C. multidentatus*, but instead are the sister species of the much smaller *C. terrestris*, from farther north in Hidalgo. Such a relationship was suggested by studies of allozymes and mtDNA in previous studies (Darda 1994; Parra-Olea 2003; Rovito & Parra-Olea 2015), but topotypic samples of *C. multidentatus* were lacking in the former two studies. In our analysis *C. chico* is well supported as the sister species of *C. terrestris* (Posterior probability = 1.0, bootstrap = 97) and both are placed in a clade that contains five species (*C. arboreus*, *C. cieloensis*, *C. cracens*, *C. infernalis,* and *C. multidentatus*), which range across the states of Hidalgo, San Luis Potosí, and Tamaulipas. Genetic divergence between *C. chico* and its sister species *C. terrestris* is 2.8% for both K2P distance and uncorrected (*p*) distance (Table 2).

Taxonomy

Amphibia

Caudata

Plethodontidae

***Chiropterotriton chico* sp. nov.**
El Chico Salamander
Salamandra de El Chico
(Figures 3A and 4A)

Chiropterotriton multidentata (part)*:* Taylor, 1944.
Chiropterotriton cf multidentatus (part)*:* Rabb, 1958; Darda, 1994.
Chiropterotriton sp. 15: Parra-Olea, 2003; Rovito & Parra-Olea, 2015

Holotype. MVZ 118888, an adult male from El Chico National Park, Hidalgo, Mexico, 2950–3050 m, 20.184154º N, 98.734437º W (maximum error distance 5477 m). Collected 31 July 1972 by James Lynch and Lynne D. Houck.

Paratypes. Twenty-nine specimens, all from Hidalgo, Mexico. Fifteen males: MVZ 118752, 118804, 118811, 118821, 118827, 118842, 118869, 118900, 119053, 119057, 119078, 119166, 119212, 119216, El Chico National Park; MVZ 138852, road to El Chico National Park, 1.0 km N (by road) junction Hwy. 105. Fourteen females: MVZ 114436, El Chico National Park, 4 km S (by road) Mineral del Chico; MVZ 118740, 118791, 118793, 118798, 118800, 118816, 118901, 118905, 119016, 119034, 119062, 119179, 119193, El Chico National Park.

Referred specimens. CAS 13112–13113; ENCB 139-142; IBH 23105; LACM 68955–69037, 69066–69071, 124057–124087, 168383–168388; MCZ A-25605–25606, A-93296 –93297; MVZ 46909, 97959, 98956–99022, 103938–103960, 106596–106655, 114292–114297, 114420–114435, 114437–114489, 118047–118739, 118741–118751, 118753–118790, 118792, 118794–118797, 118799, 118801–118803, 118805–118810, 118812–118815, 118817–118820, 118822–118826, 118828–118841, 118843–118868, 118870–118887, 118889–118899, 118902–118904, 118906–119015, 119017–119033, 119035–119052, 119054–119056, 119058–119061, 119063–119077, 119079–119165, 119167–119178, 119180–119192, 119194–119211, 119213–119215, 119217–119220, 128972–128977, 138853–138866, 143864–143893, 163620–163629, 172142–172147, 183645–183654, 195833–195835, 199175–199190, 200679, 219569–219571; UCM 41242–41252; UMMZ 151186–151192; USNM 116324–116338, 134284–134286, 201055-201057, 204910–204913, 249001-249004; UTEP 657–658.

Diagnosis. A plethodontid salamander assigned to *Chiropterotriton* because of small size, presence of sublingual fold, and distinctive shape of the digits of the hand and foot (with a relatively long outer digit; Wake & Elias 1983), as well as on the basis of analyses of mtDNA sequence data. Phylogenetically most closely related to *C. terrestris*, also from the state of Hidalgo. Morphological differences between *C. chico* and its sister taxon *C. terrestris* are much larger size (mean SVL 38.4 in males and 39.3 in females of *C. chico* vs. 24.1 in males, 23.0 in females of *C. terrestris*), relatively longer tail (mean TL/SVL 1.18 in males and 1.12 in females of *C. chico* vs. 1.05 in males and 0.97 in females of *C. terrestris*), longer limbs (mean LI 0.6 costal folds in males and 2.1 in females of *C. chico* vs. 1.9 in males, 2.6 in females of *C. terrestris*), longer head (mean HL 8.8 in males and 8.7 in females of *C. chico* vs. 5.7 in males and 5.2 in females of *C. terrestris*), broader head (mean HW 5.6 in males and 5.7 in females of *C. chico* vs. 3.5 in males and 3.3 in females of *C. terrestris*), broader feet (mean FW 4.1 in males and 4.2 in females of *C. chico* vs. 1.9 in males and 1.6 in females of *C. terrestris*), more maxillary and premaxillary teeth (mean MT+PMT 42.3 for males and 56.5 for females of *C. chico* vs. 21.2 for males and 38.2 for females of *C. terrestris)*, and more vomerine teeth (mean VT 13.6 in males and 15.6 in females of *C. chico* vs. 8.8 in males and 9.9 in females of *C. terrestris)*.

Chiropterotriton chico differs from *C. arboreus* in the following characteristics: larger size (mean SVL 38.4 in males, 39.3 in females of *C. chico* vs. 33.4 in males, 32.2 in females of *C. arboreus*), relatively longer tail (mean TL/SVL 1.18 in males, and 1.12 in females of *C. chico* vs. 0.83 in males and 0.87 in females of *C. arboreus*), shorter limbs (mean LI 0.6 in males, 2.1 in females of *C. chico* vs. 0.2 in males, 1.0 in females of *C. arboreus*), longer head (mean HL 8.8 in males and 8.7 in females of *C. chico* vs. 7.9 in males and 7.5 in females of *C. arboreus*), broader head (mean HW 5.6 in males and 5.7 in females of *C. chico* vs. 5.0 in males and 4.8 in females of *C. arboreus*), broader feet (mean FW 4.1 in males and 4.2 in females of *C. chico* vs. 3.4 in males and 3.5 in females of *C. arboreus*), more maxillary and premaxillary teeth (mean MT+PMT 42.3 for males and 56.5 for females of *C. chico* vs. 26.5 for males and 33.4 for females of *C. arboreus*) and more vomerine teeth (mean VT 13.6 in males and 15.6 in females of *C. chico* vs. 11.2 in males, and 12.4 in females of *C. arboreus*).

Chiropterotriton chico differs from *C. chondrostega* in the following characteristics: larger size (mean SVL 38.4 in males, 39.3 in females of *C. chico* vs. 23.0 in males, 25.4 in females of *C. chondrostega*), longer tail (mean TL/SVL 1.18 in males and 1.12 in females of *C. chico* vs. 0.92 in males and 1.07 in females of *C. chondrostega*), longer limbs (mean LI 0.6 in males and 2.1 in females of *C. chico* vs. 2.0 in males, 3.0 in females of *C. chondrostega*), longer head (mean HL 8.8 in males and 8.7 in females *C. chico* vs. 5.5 in males and 5.7 in females of *C. chondrostega*), broader head (mean HW 5.6 in males and 5.7 in females of *C. chico* vs. 3.4 in males and 3.7 in females of *C. chondrostega*), broader feet (mean FW 4.1 in males and 4.2 in females of *C. chico* vs. 1.8 in males and females of *C. chondrostega*), more maxillary teeth (mean MT+PMT 42.3 for males and 56.5 for females of *C. chico* vs. 22.5 for males and 40.9 for females of *C. chondrostega*), and more vomerine teeth (mean VT 13.6 in males and 15.6 in females of *C. chico* vs. 8 in males and 10 in females of *C. chondrostega*).

Chiropterotriton chico differs from *C. mosaueri* by its relatively shorter tail (mean TL/SVL 1.18 in males and 1.12 in females of *C. chico* vs. 1.31 in males and 1.39 in a female of *C. mosaueri*), narrower head (mean HW 5.6 in males and 5.7 in females of *C. chico* vs. 6.8 in males and 7.0 in a female of *C. mosaueri*), fewer maxillary and

premaxillary teeth (mean MT+PMT 42.3 for males and 56.5 for females of *C. chico* vs. mean MT 69.0 for males and 70 for a female of *C. mosaueri*), and fewer vomerine teeth (mean VT 13.6 in males and 15.6 in females of *C. chico* vs. 28 in males and 20 in a female of *C. mosaueri*) (Woodall 1941; Rabb 1958; Rovito & Parra-Olea 2015).

Chiropterotriton chico differs from *C. multidentatus,* by its larger size (mean SVL 38.4 in males, 39.3 in females of *C. chico* vs. 33.6 in males, 34.0 in females of *C. multidentatus*), slightly longer tail (mean TL/SVL 1.18 in males, and 1.12 in females of *C. chico* vs. 1.13 in males and 1.03 in females of *C. multidentatus*), shorter limbs (mean LI 0.6 in males, 2.1 in females of *C. chico* vs. 0.1 in males, 1.0 in females of *C. multidentatus)*, longer head (mean HL 8.8 in males and 8.7 in females *C. chico* vs. 7.4 in both males and females of *C. multidentatus*), broader head (mean HW 5.6 in males and 5.7 in females of *C. chico* vs. 4.9 in males and 5.1 in females of *C. multidentatus*), broader feet (mean FW 4.1 in males and 4.2 in females of *C. chico* vs. 3.6 in males and 3.5 in females of *C. multidentatus*), and fewer maxillary and premaxillary teeth (mean MT+PMT 26.0 for males and 36.0 for females of *C. chico* vs. 40.0 for males and 49.0 for females of *C. multidentatus*).

Chiropterotriton chico differs from *C. cieloensis* by its larger size (mean SVL 38.4 in males, 39.3 in females of *C. chico* vs. 32.6 in males, 31.1 in females of *C. cieloensis*), shorter limbs (mean LI 0.6 in males, 2.1 in females of *C. chico* vs. -0.2 in males, 0.1 in females of *C. cieloensis)*, longer head (mean HL 8.8 in males and 8.7 in females of *C. chico* vs. 7.1 in males and 6.9 in females of *C. cieloensis*), broader head (mean HW 5.6 in males and 5.7 in females of *C. chico* vs. 4.8 in males and 4.9 in females of *C. cieloensis*), broader feet (mean FW 4.1 in males and 4.2 in females of *C. chico* vs. 3.2 in males and 3.1 in females of *C. cieloensis*); more maxillary and premaxillary teeth (mean MT+PMT 42.3 for males and 56.5 for females of *C. chico* vs. 31.0 for males and 47.0 for females of *C. cieloensis*), and more vomerine teeth (mean VT 13.6 in males and 15.6 in females of *C. chico* vs. 11.5 in males, and 12.8 in females of *C. cieloensis*).

Chiropterotriton chico differs from *C. infernalis* by its larger size (mean SVL 38.4 in males, 39.3 in females of *C. chico* vs. 36.4 in males, 29.7 in a female of *C. infernalis*), shorter limbs (mean LI 0.6 in males, 2.1 in females of *C. chico* vs. -0.7 in males, -0.5 in a female of *C. infernalis)*, less extensive feet webbing (moderate webbing that extends just onto penultimate phalanx in *C. chico* vs. extensive foot webbing onto penultimate phalange in *C. infernalis*; Fig. 3A, I), and slightly longer head (mean HL 8.8 in males and 8.7 in females *C. chico* vs. 8.2 in males and 6.2 in a female of *C. infernalis*).

Chiropterotriton chico differs from *C. cracens* in body size (mean SVL 38.4 in males, 39.3 in females of *C. chico* vs. 25.7 in males, 27.4 in females of *C. cracens*) and by having shorter limbs in males (mean LI 0.6 of *C. chico* vs. 1.8 of *C. cracens*), a longer head (mean HL 8.8 in males and 8.7 in females *C. chico* vs. 5.5 in males and 5.8 in females of *C. cracens*), broader head (mean HW 5.6 in males and 5.7 in females of *C. chico* vs. 3.8 in males and 4.1 in females of *C. cracens*), broader feet (mean FW 4.1 in males and 4.2 in females of *C. chico* vs. 2.2 in males and 2.5 in females of *C. cracens*), and more maxillary and premaxillary teeth (mean MT+PMT 42.3 for males and 56.5 for females of *C. chico* vs. 36.8 for males and 49.5 for females of *C. cracens*).

Chiropterotriton chico differs from its sympatric species *C. dimidiatus* by its larger size (mean SVL 38.4 in males, 39.3 in females of *C. chico* vs. 24.6 in males, 25.8 in females of *C. dimidiatus*), relatively longer tail (mean TL/SVL 1.18 in males, and 1.12 in females vs. 0.89 in males, and 0.86 in females of *C. dimidiatus*), longer limbs (mean LI 0.6 in males, 2.1 in females of *C. chico* vs. 3.8 in males, 4.9 in females of *C. dimidiatus*), longer head (mean HL 8.8 in males and 8.7 in females of *C. chico* vs. 5.2 in males and 5.0 in females of *C. dimidiatus*), broader head (mean HW 5.6 in males and 5.7 in females of *C. chico* vs. 3.4 in males and 3.5 in females of *C. dimidiatus*), broader feet (mean FW 4.1 in males and 4.2 in females of *C. chico* vs. 1.7 in both males and females of *C. dimidiatus*), more numerous maxillary and premaxillary teeth (mean MT+PMT 42.3 for males and 56.5 for females of *C. chico* vs. 9.4 for males and 34.4 for females of *C. dimidiatus*), and vomerine teeth (mean VT 13.6 in males and 15.6 in females of *C. chico* vs. 5.6 in males, and 8.3 in females of *C. dimidiatus*). Moreover, *C. chico* is easily distinguished for relative narrow nostril size (mean NW/HW 0.01 in both males and females of *C. chico* vs. 0.07 in both males and females of *C. dimidiatus*), this character is evident even in very small individuals.

Chiropterotriton chico differs from most of the remaining species of the genus, in having relatively large size (mean SVL 38.4 males, 39.3 females). Exceptions are the much stouter and somewhat larger *C. priscus* Rabb (mean SVL 38.5 males, 41.8 females; Rovito & Parra-Olea 2015) and *C. magnipes* Rabb (range SVL 40–53 males, 51–60 females; Campbell *et al.* 2014). *C. chico* has more maxillary teeth than most other species of this genus (mean MT+PMT 42.3 for males and 56.5 for females), except for *C. multidentatus* (mean MT+PMT 40.0 for males and 47.8 for females; Rovito & Parra-Olea 2015) and *C. infernalis* (mean MT+PMT 42.3 for males and 56.5 for

females; Rovito & Parra-Olea 2015) which have similar numbers of teeth, and *C. magnipes* (males average 79; Campbell *et al.* 2014) and *C. mosaueri* (range in males 56–69; Campbell *et al.* 2014), which have more maxillary teeth.

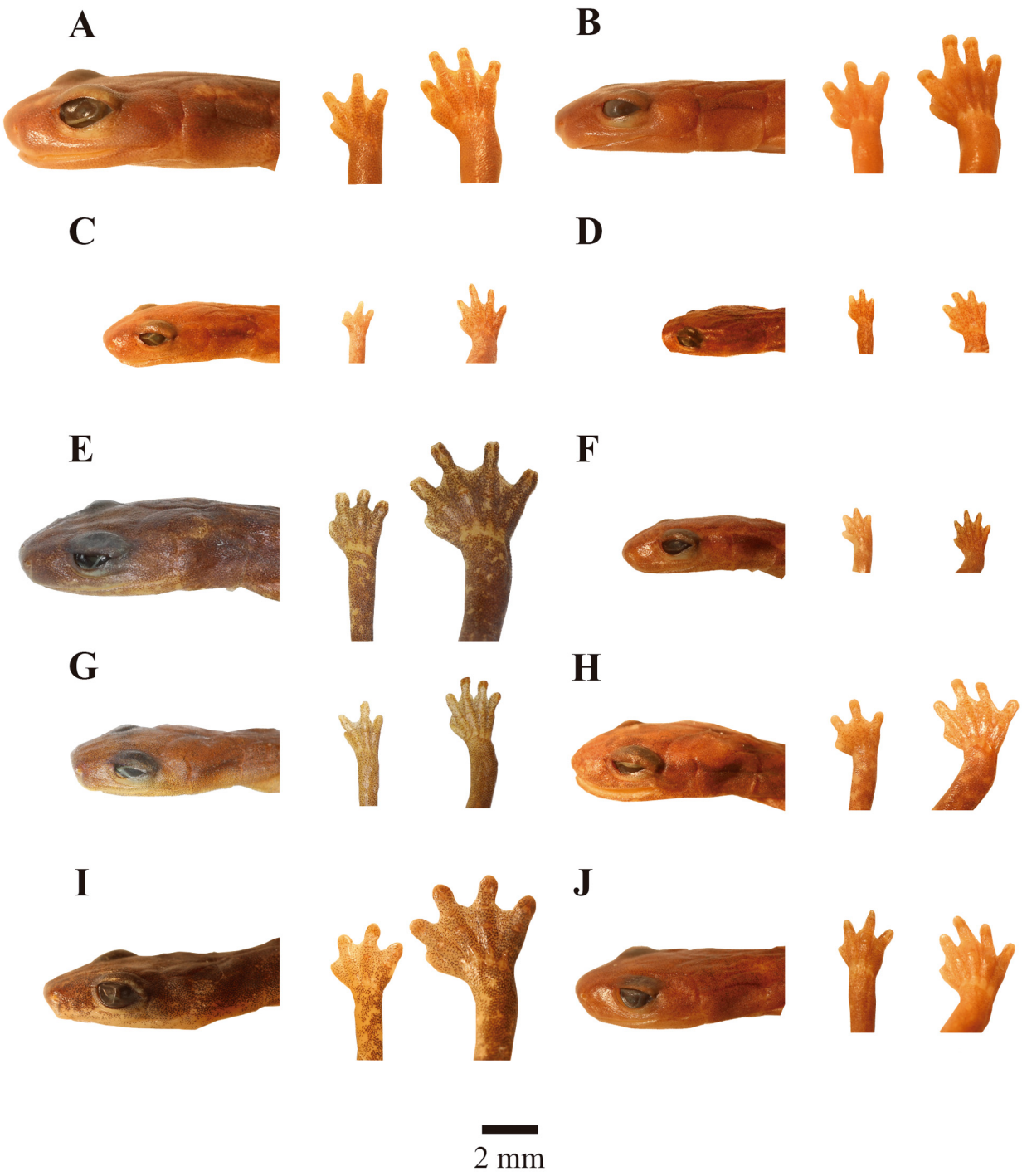

FIGURE 3. Head, hand and foot morphology of *Chiropterotriton* specimens from Hidalgo **A)** *C. chico,* holotype MVZ 118888, **B)** *C. arboreus,* MVZ 172159, **C)** *C. chondrostega* MVZ 106660, **D)** *C. dimidiatus* MVZ 178671, **E)** *C. mosaueri* IBH 28179, **F)** *C. terrestris,* MVZ 106700, and Tamaulipas and San Luis Potosí **G)** *C. cieloensis,* holotype IBH 29561, **H)** *C. cracens* MVZ 129005, **I)** *C. infernalis,* holotype MVZ 269665, **J)** *C. multidentatus* MVZ 163908. Scale bar corresponds to 2 mm.

FIGURE 4. Photos in life of *Chiropterotriton.* **A)** *Chiropterotriton chico,* DBW (Jan 1974) **B)** *C. arboreus,* DBW, **C)** *C. chondrostega,* SMR (IBH 28195), **D)** *C. dimidiatus,* DBW 1342-45, **E)** *C. mosaueri* SMR (IBH 28179), **F)** *C. terrestris,* DBW, **G)** *C. cieloensis,* SMR holotype (IBH 29561), **H)** *C. cracens,* SMR (IBH 28192), **I)** *C. infernalis,* SMR holotype (MVZ 269665), **J)** *C. multidentatus* SMR (IBH 29571).

Description. This is a medium sized species of *Chiropterotriton*; mean SVL 38.4 in fifteen adult males (range 36.2–42.6) and 39.3 in fifteen adult females (range 35.9–44.3). The head is relatively narrow and moderately long (Fig. 3), HW averages 14% of SVL in both males and females (range 11–16). In males, the snout is broad and truncated. Jaw muscles are pronounced and visible as a bulging mass immediately behind the eyes. Eyes are moderately protuberant and extend laterally beyond the jaw margin in ventral view. There are a moderate number of maxillary and premaxillary teeth in males (mean MT+PMT 42.3, range 32–52) and more in females (mean MT+PMT 56.5, range 48–67). There are few vomerine teeth in males (mean 13.6, range 10–19) and females (mean 15.6, range 13–19). The tail is long; mean TL equals 1.18 of SVL in males (range 0.96–1.27) and 1.12 of SVL in females (range 0.98–1.24). Limbs are moderate and slender; (FLL+ HLL)/SVL average 0.48 in males (range 0.82–1.11) and 0.98 in females (range 0.87–1.13). Adpressed limbs approach closely on males (mean LI 0.6, range 0–1)

but they are separated by as many as two costal folds in females (mean 2.1, range 1.5–3.0). Digits are slender and expanded distally, with distinct subterminal pads and moderate webbing at the base. All digits are discrete, however the first barely extends beyond the margins of the webbing and it extends just onto penultimate phalanx of the longest toe (Fig. 3). The outermost toes are particularly well developed. The smallest male with a mental gland is 36.2 SVL. Parotoid glands not evident. Prominent oval-shaped mental gland is present in all adult males. Vomerine teeth arranged in a well-defined line extending to outer margin of choanae. Digits in order of increasing length: hand I-IV-II-III, foot I-V-II-IV-III. Phalangeal formulae: hand 1-2-3-2, foot 1-2-3-3-2.

Coloration of the holotype in alcohol. Holotype uniform dark tannish brown dorsally becoming paler laterally and very pale cream ventrally. There is a central reddish brown stripe flanked by yellow lines. The stripe extends from to the postocular region, where it has yellow spots, to the base of the tail where it also leaves two yellow spots. The entire tail is a slightly darker brown than the body. Limbs are lighter in color than dorsum but still dark brown. Snout is mottled with dark and light brown. Dorsal surface of hands and feet only slightly lighter than body.

Measurements of the holotype (in mm), tooth counts and limb interval.— SVL 42.2, TL 46.1, AX 22.4, SW 5.2, HL 9.8, HW 6.3, HD 3.1, projection of snout beyond mandible 1.4, anterior rim of orbit to snout 2.7, interorbital distance 2.6, eyelid length 2.2, eyelid width 1.4, horizontal orbit diameter 2.7, NL 0.14, NW 0.06, FLL 8.5, HLL 10.7, snout to forelimb 12.8, snout to anterior angle of vent 42.1, tail width at base 3.1, tail depth at base 3.2, FW 4.0, length of fifth toe 0.7, length of third (longest) toe 1.2. MT+PMT 60, VT 6-7 (right-left sides). Adpressed limbs separated by two costal folds.

Habitat and range. This species is only known from Parque Nacional El Chico in Hidalgo, Mexico at an elevation between 2400 and 3050 m, in pine-oak forest. It is unlikely to occur more widely, because surrounding areas have been extensively surveyed.

Etymology. The species name *chico* is in reference to the national park where the species occurs. Parque Nacional El Chico in Hidalgo, Mexico has been a protected area since 1922. The species name is used as an invariable noun in apposition to the generic name.

Remarks. This species was previously considered as conspecific with *C. multidentatus* and occurs in sympatry with *C. dimidiatus* and *Aquiloeurycea cephalica*. Likewise, *Isthmura bellii* has been collected very near sites where *C. chico* was once common (MVZ 118953, 118954, 128978), but it is unknown if the two species occur in syntopy.

Discussion

Molecular tools have been of great help in uncovering a large diversity of species that were missed using only traditional (morphological) approaches because of the outward similarity of species. For Mexican salamanders, there has been a steady pace of species description leading to an increase of about 55% in the known diversity in the last 24 years (Flores-Villela & Canseco-Marquez 2004; AmphibiaWeb 2017). This study contributes with the description of one species, increasing the number of *Chiropterotriton* species from 15 to 16. Historically, this genus has been considered to represent a relatively small number of species despite the multiple undescribed taxa proposed in previous studies (Rabb 1958; Wake & Lynch 1976; Darda 1994; Parra-Olea 2003). Recently, three new species have been described with morphological comparisons (Campbell *et al.* 2014) and also molecular phylogenetic analyses (Rovito & Parra-Olea 2015), but at least seven undescribed taxa remain: *C.* sp. C, *C.* sp. H, and *C.* sp. I from Veracruz; *C.* sp. F and *C.* sp. G from Puebla; and *C.* sp. J and *C.* sp. K from Oaxaca.

Chiropterotriton chico was first referenced by Taylor (1938) who listed specimens from El Chico, Hidalgo as paratypes of *Oedipus multidentata.* Later, they were assigned to *C. multidentatus* by Taylor (1944) as its southernmost population. Rabb (1958) noted morphological differences between this population and those from Tamaulipas. Allozyme evidence (Darda 1994) identified the El Chico population as a new species (*C.* sp. 15, population 15) and Parra-Olea (2003) agreed, based on her mtDNA phylogeny (*C.* sp. 15, population 12). Although *C. chico* is the sister species of *C. terrestris,* they are easily differentiated by morphological characters. The body size of *C. chico* makes it one of the largest species of this genus; only *C. magnipes, C. mosaueri* and *C. priscus* are larger.

From the 1950s into the 1970s, *Chiropterotriton chico* was incredibly abundant locally. D. Wake visited the park in August 1971 (field notes, Museum of Vertebrate Zoology), and recorded a very high density of

salamanders. At high elevation (3000 m) salamanders were found under roadside rocks on barren soil. A salamander was found under every 10th to 12th rock and more than 75 *C. chico* were seen (as well as 10 *C. dimidiatus*). At lower elevation (estimated from topographic maps as 2400 m), in oak forest, Wake wrote: "I have never seen anything like the density of salamanders encountered here! I'm sure we could have collected thousands if we had wished". Any shelter had salamanders, and it was a rare log than had none. Only five bromeliads were opened but one contained a *C. chico*. Many cover objects housed multiple specimens: seven under a log 1.2 m (four feet) long, twelve under a log 3.0 m (ten feet) long, ten under a flat piece of wood (0.3x0.6 m in dimensions), etc. Yet, at another site less than 4 km away, no salamanders were found.

High numbers were encountered on other trips, but by the mid-1970s salamanders became uncommon and then rare. Apparently, the decline of *C. chico* is not related to habitat loss or disturbance. Parra-Olea *et al.* (1999) did not report important changes in habitat quality or availability in El Chico National Park, however, they found a lower density of salamanders than observed in the 1970s. Parra-Olea found one individual of *C. chico* and two of *C. dimidiatus* in 2002 while S. Rovito found one of *C. chico* and several for C. *dimidiatus* in 2016. While these declines are not well understood, one suggested factor is the arrival of the pathogenic chytrid fungus *Batrachochytrium dendrobatidis*. The fungus was absent in a sample of 30 individuals sampled in 1972, but present in a sample of 40 from 1974 (Cheng *et al*. 2011).

Given the standard criteria used by the International Union for the Conservation of Nature for its assessment of species to be added to the Red List of Threatened Species (IUCN 2017), we think that a listing of Critically Endangered is warranted for *C. chico* according to criterion B1 ab(v), where B1 corresponds to the geographic range that is estimated to be less than 100 km^2, at only a single location (a) and continuing decline (b) for number of mature individuals (v). The species has declined severely in abundance, with declines exceeding 80% based on the number of individuals seen in field surveys, in the limited area from which it is known. Extensive exploration has taken place in the immediate vicinity of the park and throughout much of the state of Hidalgo, but no additional populations have been found.

Hidalgo includes an unusual region where two of the main mountain complexes of Mexico meet: the Trans-Mexican Volcanic Belt (TMVB) and Sierra Madre Oriental (SMO). These ranges are known to have a high degree of topographic, geologic and climatic variability than has promoted a high biodiversity (Luna *et al.* 2004; Luna *et al.* 2007). This is especially true for the herpetofauna from Hidalgo (Lemos-Espinal & Smith 2015), which is the state with the highest number of species of *Chiropterotriton* (6), representing 37.5% of the described species of this genus.

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References

Acevedo, A.A., Wake, D.B., Marquez, R. & Silva, K. (2013). Two new species of salamanders, genus *Bolitoglossa* (Amphibia: Plethodontidae). *Zootaxa*, 3609 (1), 69–84. https://doi.org/10.11646/zootaxa.3609.1.5

AmphibiaWeb (2017) Berkeley, California: AmphibiaWeb: Information on Amphibian Biology and Conservation [web application]. Available from: http://www.amphibiaweb.org (accessed 18 February 2017)

Boza-Oviedo, E., Rovito, S.M., Chaves, G., Garcia-Rodriguez, A., Artavia, L.G., Bolanos, F. & Wake, D.B. (2012) Salamanders from the eastern Cordillera de Talamanca, Costa Rica, with descriptions of five new species (Plethodontidae: *Bolitoglossa*, *Nototriton*, and *Oedipina*) and natural history notes from recent expeditions. *Zootaxa*, 3309, 36–61.

Campbell, J.A., Streicher, J.W., Cox, C.L. & Brodie, E.D. Jr. (2014) A new salamander of the genus *Chiropterotriton* (Caudata: Plethodontidae) from the Sierra Madre Oriental of Tamaulipas, Mexico. *South American Journal of Herpetology*, 9, 228–234.
https://doi.org/10.2994/SAJH-D-14-00042.1

Cheng, T.L., Rovito, S.M., Wake, D.B. & Vredenburg, V.T. (2011) Coincident mass extirpation of neotropical amphibians with the emergence of the infectious fungal pathogen *Batrachochytrium dendrobatidis*. *Proceedings of the National Academy Sciences, USA*, 108, 9502–9507.
https://doi.org/10.1073/pnas.1105538108

Darda, D.M. (1994) Allozyme variation and morphological evolution among Mexican salamanders of the genus *Chiropterotriton* (Caudata: Plethodontidae). *Herpetologica*, 50, 164–187.

Darda, D.M. & Wake, D.B. (2015) Osteological variation among extreme morphological forms in the Mexican salamander genus *Chiropterotriton* (Amphibia: Plethodontidae): Morphological evolution and homoplasy. *PLoS ONE*, 10 (6), 1–34.
https://doi.org/10.1371/journal.pone.0127248

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9 (8), 772.
https://doi.org/10.1038/nmeth.2109

Edgar, R.C. (2004) MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics*, 5, 1–19.
https://doi.org/10.1186/1471-2105-5-113

Flores-Villela, O. & Canseco-Márquez, L. (2004) Nuevas especies y cambios taxonómicos para la herpetofauna de México. *Acta Zoológica Mexicana*, New Series, 2, 115–144.

IUCN (2017) The IUCN Red List of Threatened Species. Version 2017-1. Available from: http://www.iucnredlist.org (accessed 7 August 2017)

Lemos-Espinal, J.A. & Smith, G.R. (2015) Amphibians and reptiles of the state of Hidalgo, Mexico. *Checklist*, 11, 1–11.
https://doi.org/10.15560/11.3.1642

Luna, I., Morrone, J. & Espinosa, D. (2004) Biodiversidad de la Sierra Madre Oriental. Universidad Nacional Autónoma de México. México, D.F., 527 pp.

Luna, I., Morrone, J. & Espinosa, D. (2007) *Biodiversidad de la Faja Volcánica Transmexicana. Universidad Nacional Autónoma de México*. Universidad Nacional Autónoma de México, Facultad de Estudios Superiores Zaragoza e Instituto de Biología, México, D.F., 514 pp.

Lynch, J.F. & Wake, D.B. (1989) Two new species of *Pseudoeurycea* (Amphibia: Caudata) from Oaxaca, Mexico. *Contributions in Science, Natural History Museum of Los Angeles County*, 411, 11–22.

Maddison, W.P & Maddison, D.R (2015) Mesquite: a modular system for evolutionary analysis. Version 3.04. Available from: http://mesquiteproject.org (accessed 22 August 2017)

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 2010, 1–8.
https://doi.org/10.1109/GCE.2010.5676129

Parra-Olea, G. (2003) Phylogenetic relationships of the genus *Chiropterotriton* (Caudata: Plethodontidae) based on 16S ribosomal mtDNA. *Canadian Journal of Zoology*, 81, 2048–2060.
https://doi.org/10.1139/z03-155

Parra-Olea, G., García-París, M. & Wake, D.B. (1999) Status of some populations of Mexican salamanders (Amphibia: Plethodontidae). *Revista de Biología Tropical. San José*, 47, 217–223.

Parra-Olea, G., Rovito, S. M., García-París, M., Maisano, J.A., Wake, D.B. & Hanken, J. (2016) Biology of tiny animals: three new species of minute salamanders (Plethodontidae: *Thorius*) from Oaxaca, Mexico. *PeerJ*, 4, e2694.
https://doi.org/10.7717/peerj.2694

Rabb, G.B. (1958) On certain Mexican salamanders of the plethodontid genus *Chiropterotriton*. *Occasional Papers of the Museum of Zoology, University of Michigan*, 587, 1–37.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
https://doi.org/10.1093/sysbio/sys029

Rovito, S.M. & Parra-Olea, G. (2015) Two new species of *Chiropterotriton* (Caudata: Plethodontidae) from northern Mexico. *Zootaxa*, 4048 (1), 57–74.
https://doi.org/10.11646/zootaxa.4048.1.3

Rovito, S.M., Parra-Olea, G., Recuero, E. & Wake, D.B. (2015) Diversification and biogeographical history of Neotropical plethodontid salamanders. *Zoological Journal of the Linnean Society*, 175, 167–188.
https://doi.org/10.1111/zoj.12271

Stamatakis, A. (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed

models. *Bioinformatics*, 22, 2688–2690.
https://doi.org/10.1093/bioinformatics/btl446
Taylor, E.H. (1938) Concerning Mexican salamanders. *The University of Kansas Science Bulletin*, 25, 259–313.
https://doi.org/10.5962/bhl.part.1703
Taylor, E.H. (1944) The genera of plethodont salamanders in Mexico. *The University of Kansas Science Bulletin*, 12, 189–232.
https://doi.org/10.5962/bhl.part.6508
Townsend, J.H., Butler, J.M., Wilson, L.D. & Austin, J.D. (2010) A distinctive new species of moss salamander (Caudata: Plethodontidae: *Nototriton*) from an imperiled Honduran endemism hotspot. *Zootaxa,* 2434, 1–16.
Wake, D.B. (2012) Taxonomy of salamanders of the family Plethodontidae (Amphibia: Caudata). *Zootaxa*, 3484, 75–82.
Wake, D.B. & Elias, P. (1983) New genera and a new species of Central American salamanders, with a review of tropical genera (Amphibia, Caudata, Plethodontidae). *Contributions in Science, Natural History Museum of Los Angeles County*, 345, 1–19.
Wake, D.B. & Lynch, J.F. (1976) The distribution, ecology and evolutionary history of plethodontid salamanders in tropical America. *Bulletin of the Natural History Museum of Los Angeles County*, 25, 1–65.
Woodall, H.T. (1941) A new Mexican salamander of the genus *Oedipus*. *Occasional Papers of the Museum of Zoology, University of Michigan*, 444, 1–4.

APPENDIX 1. Specimens examined for morphological analysis.

Chiropterotriton arboreus: Mexico, Hidalgo: MVZ 106381, 11 km S Tianguistengo (1 km N Zacualtipán); MVZ 114333–114335, 2.4 km SSW (by road) Tianguistengo along road to Zacualtipán; MVZ 163917, 163919, 172159, 172160, 172162–172163, 3.4 km S Tianguistengo; MVZ 200621, 200623–200625, 4.3 km E of junction of Mexico Hwy. 105 and Old Hwy. to Tianguistengo.

Chiropterotriton chico: Mexico, Hidalgo: MVZ 114436, El Chico Parque Nacional, 4 km S (by road) Mineral del Chico; MVZ 118740, 118752, 118791, 118793, 118798, 118800, 118804, 118811, 118816, 118821, 118827, 118842, 118869, 118888, 118900–118901, 118905, 119016, 119034, 119053, 119057, 119062, 119078, 119166, 119179, 119193, 119212, 119216, El Chico Parque Nacional; MVZ 138852, road to El Chico National Park, 1.0 km N (by road) junction Hwy. 105. *Chiropterotriton chondrostega*: Mexico, Hidalgo: MVZ 106656–106657, 106659–106666, 11 km S Tianguistengo, ca. 1 km N Zacualtipán; MVZ 163987–163988, 172148–172154, 172156–172157, 4 km NNE Zacaultipan.

Chiropterotriton dimidiatus: Mexico, Hidalgo: MVZ 98939, 98942, 98947, El Chico Parque Nacional, 9.7 mi (by winding road) from Hwy. 105 and 5.5 mi (by winding road) from Park Custodian house; MVZ 103961–103963, 103968, El Chico Parque Nacional, N slope along Rd. between summit and town of El Chico; MVZ 106460, 106465, 106468, 106471, 106474, 106493, 106495, 106514–106515, El Chico Parque Nacional, 4 km S Mineral del Chico; MVZ 114248, 114251, 114261, 114265, 114268, 114274, 114291–114292, El Chico Parque Nacional, between Park Headquarters and Mineral del Chico; MVZ 118727, 118729, 118732, 118735, 185962, 195832, El Chico Parque Nacional.

Chiropterotriton terrestris: Mexico, Hidalgo: MVZ 106668–106669, 106672, 106677–106678, 106681, 106683, 106685, 106690–106692, 106694–106695, 106700, 106705–106706, 106712–106713, 106718–106720, 106722, 106724, 11 km S Tianguistengo, ca. 1 km N Zacualtipán; MVZ 114302, 114304, 114316, 114339, 114343, 114345, 12.8 km SSW (by road) Tianguistengo (along road to Zacaultipan); MVZ 200636, 4.3 km E of junction of Mexico Hwy. 105 and Old Hwy. to Tianguistengo.