Descriptions of five new species of the salamander genus *Chiropterotriton* (Caudata: Plethodontidae) from eastern Mexico and the status of three currently recognized taxa

Gabriela Parra Olea [Corresp., 1] , Mirna G. Garcia-Castillo [2, 3] , Sean M. Rovito [4] , Jessie Maisano [5] , James Hanken [6] , David B. Wake [7]

[1] Zoology, Instituto de Biologia UNAM

[2] Zoology, Instituto de Biologia UNAM, Mexico city, Mexico

[3] Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, A.P. 70-153, C.P. 04510, Ciudad de México, México

[4] Unidad de Genómica Avanzada (Langebio), CINVESTAV, Irapuato, Guanajuato, Mexico

[5] Jackson school of Geosciences, University of Texas at Austin, Austin, Texas, United States

[6] Harvard University, Cambridge, Massachussetts, United States

[7] Museum of Vertebrate Zoology, University of California, Berkeley, Berkeley, CA, United States

Corresponding Author: Gabriela Parra Olea
Email address: gparra@ib.unam.mx

The genus *Chiropterotriton* is endemic to Mexico with a geographical distribution along the Sierra Madre Oriental, the Trans Mexican Volcanic Belt and the Sierra de Juárez. The recent use of molecular tools has shown that Mexico's amphibian diversity is highly underestimated, including a large number of cryptic, unnamed species. *Chiropterotriton* has 18 described species including terrestrial, arboreal and cave dwelling species. In previous molecular studies, the presence of multiple undescribed species was evident. We present a phylogenetic hypothesis based on mitochondrial data, which includes all described species and six undescribed taxa. Based on the morphological analyses and, when available, combined with molecular data, we describe five new species of the genus; *Chiropterotriton casasi* sp. nov., *C. ceronorum* sp. nov., *C. melipona* sp. nov., *C. perotensis* sp. nov. and *C. totonacus* sp. nov. In addition, we redescribe two others: *Chiropterotriton chiropterus* and *C. orculus*, and provide a comparable account of one additional sympatric congener. This increases the number of species in the genus to 23, which represent a considerable component of Mexican plethodontid richness.

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G. Parra-Olea[1]*, M. G. García-Castillo[1, 2], S. M. Rovito[3], Jessica A. Maisano[4], J. Hanken[5], and D. B. Wake[6]

[1] Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico
[2] Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, A.P. 70-153, C.P. 04510 Ciudad de México, México
[3] Unidad de Genómica Avanzada (Langebio), CINVESTAV, Irapuato, Guanajuato, Mexico
[4] Jackson school of Geosciences, University of Texas at Austin, Texas, United States
[5] Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States
[6] Department of Integrative Biology and Museum of Vertebrate Zoology, University of California, Berkeley, California, United States

Corresponding author:

Gabriela Parra-Olea

Email address: gparra@ib.unam.mx

26   **ABSTRACT**

28   The genus *Chiropterotriton* is endemic to Mexico with a geographical distribution along the
29   Sierra Madre Oriental, the Trans Mexican Volcanic Belt and the Sierra de Juárez. The recent use
30   of molecular tools has shown that Mexico's amphibian diversity is highly underestimated,
31   including a large number of cryptic, unnamed species. *Chiropterotriton* has 18 described species
32   including terrestrial, arboreal and cave dwelling species. In previous molecular studies, the
33   presence of multiple undescribed species was evident. We present a phylogenetic hypothesis
34   based on mitochondrial data, which includes all described species and six undescribed taxa.
35   Based on the morphological analyses and, when available, combined with molecular data, we
36   describe five new species of the genus; *Chiropterotriton casasi* sp. nov., *C. ceronorum* sp. nov.,
37   *C. melipona* sp. nov., *C. perotensis* sp. nov. and *C. totonacus* sp. nov. In addition, we redescribe
38   two others: *Chiropterotriton chiropterus* and *C. orculus*, and provide a comparable account of
39   one additional sympatric congener. This increases the number of species in the genus to 23,
40   which represent a considerable component of Mexican plethodontid richness.

41   *Key words*: plethodontids, phylogeny, taxonomy, Mexico, bolitoglossines

42   **INTRODUCTION**
43   The genus *Chiropterotriton* Taylor, 1944 has proven to be one of the taxonomically most
44   difficult of all genera of neotropical salamanders. These salamanders vary widely in morphology
45   and ecology from relatively large troglodytic forms to gracile arboreal species. Most species,
46   however, are small to medium sized with a fairly generalized external morphology, representing
47   minor variations on a conserved body plan (Darda and Wake, 2015). This external
48   morphological similarity has complicated recognition of new species and the relationships
49   between them, particularly based on morphological data alone.
50   When Taylor (1944) described the genus, he initially included a number of other Central
51   American salamanders from Nuclear Central America and Costa Rica. These species, which are
52   all relatively small and slender, were recognized as a distinct unit within the genus
53   (*Chiropterotriton* Beta; Wake and Lynch, 1976) and eventually described as several distinct
54   genera (*Cryptotriton*, *Dendrotriton* and *Nototriton*), leaving *Chiropterotriton* endemic to the
55   highlands of Mexico and west of the Isthmus of Tehuantepec. Despite their external similarity,
56   the divergence between each of these genera and *Chiropterotriton* spans the basal node in the
57   Bolitoglossini clade (Rovito et al., 2015). Taxonomy of the Mexican *Chiropterotriton* was
58   complicated not only by their small size and generalized morphology, but also by the fact that
59   two of the earliest species descriptions for the group, *C. chiropterus* (Cope, 1863) and *C. orculus*
60   (Cope, 1865) are very brief and provide imprecise localities, and because the holotype of each
61   species has been lost.
62   Rabb (1958) made a major advance in our understanding of the taxonomy and
63   morphology of the northern species in the group. By examining both topotypic specimens and
64   material from additional localities, he showed that unappreciated diversity existed even within
65   the subset of species from this region based on external morphology and tooth counts. Rabb´s
66   foundational morphological and taxonomic work on the genus was followed by a long period of
67   taxonomic stasis. Following his discovery and description of *Chiropterotriton magnipes* (Rabb,
68   1965), the most morphological distinct species in the genus, no additional species were described
69   for nearly fifty years. Despite the lapse in species descriptions, molecular data made it clear that

70 much diversity lay hidden within already known populations. Darda (1994) derived an allozyme
71 dataset that showed that many populations likely represented distinct species, and his results
72 were largely corroborated by mtDNA sequence data (Parra-Olea, 2003) although there were
73 some discrepancies between the results from the two data sets. Collection of new material from
74 previously known populations for molecular analysis, as well as the discovery of new
75 populations, led to the description of six new species since 2014 (Campbell et al., 2014; Rovito
76 and Parra-Olea, 2015; García-Castillo et al., 2017; García-Castillo et al., 2018). Despite these
77 recent descriptions, many populations from central Mexico have defied assignment to known
78 species and are best recognized as distinct species.
79   The *Chiropterotriton chiropterus* complex has suffered from taxonomic rearrangements,
80 mostly due to imprecise type localities and the lack of adequate samples from those localities.
81 Based on external morphology, Wake and Lynch (1976) defined the *chiropterus* group to include
82 *C. chiropterus, C. chondrostega, C. dimidiatus* and *C. lavae*. Later, on the basis of
83 immunological data, Maxson and Wake (1981) redefined the *chiropterus* group to include only
84 *C. chiropterus* and *C. lavae*. Based on allozyme data, Darda (1994) recognized a group of
85 populations found along the Trans-Mexican Volcanic Belt, which he called the *chiropterus*
86 complex. This group was formed by *C. chiropterus* from La Joya Veracruz, *C. orculus* from
87 Zacualtipan, Hidalgo, and nine additional undescribed species. However, Parra-Olea (2003)
88 concluded that *C. chiropterus* applies exclusively to the low-elevation populations located in or
89 near the city of Huatusco, Veracruz.
90   The *Chiropterotriton orculus* complex is represented by a relatively widespread species
91 of the genus. Based on morphological characters, Cope (1865) described *C. orculus* as *Spelerpes*
92 *orculus* from Mexican Table Land, but four years later he placed this species in synonymy with
93 *C. chiropterus* (Cope, 1869). Darda (1994) allozyme data recognized *C. orculus* as a distinct
94 species, restricting it to two populations. Parra-Olea (2003) added one more population to *C.*
95 *orculus* and emphasized the differentiation levels discordance between allozymes and mtDNA
96 between some populations. Currently, *C. orculus* includes several morphologically uniform
97 populations in central Trans Mexican Volcanic Belt around Mexico City.
98   We focus on populations of *Chiropterotriton* from the eastern Trans Mexican Volcanic
99 Belt and nearby regions of Veracruz and Puebla (Fig. 1). While some of these populations have
100 already been included in allozyme and/or mtDNA analyses, data for others are presented here for
101 the first time. Using a combination of linear morphological measurements, osteological data
102 derived from micro-computed tomography (μCT) scans, and previously published mtDNA and
103 allozyme data we examine the taxonomic status of these populations. We present a phylogenetic
104 hypothesis based on mtDNA which includes all 18 described species plus six undescribed taxa,
105 including populations identified in previous studies as new species within complexes. Based on
106 the molecular data and morphological analyses, we describe five new species. These increase the
107 number of described species from 18 to 23 and still recognize one candidate species not yet
108 described. We redescribe *C. orculus* and *C. chiropterus*, designating neotypes for each, in order
109 to clarify the taxonomic status of nearby populations that resemble one or both of these species
110 in external morphology. Finally, in order to make full comparisons with sympatric taxa for the
111 newly described species, we provide a fuller description of *C. lavae* based on examination of the
112 type series and additional specimens collected subsequently.

113   **MATERIALS AND METHODS**
114 *Amplification and sequencing*

115 Whole genomic DNA was extracted from liver, intestine or tail tissue using DNeasy tissue Kit
116 (Qiagen, Valencia, California, USA). Although a comprehensive molecular analysis of the genus
117 *Chiropterotriton* is beyond the scope of the present work, two mitochondrial fragments of each
118 new species (when available) were sequenced in order to allow comparisons to other members of
119 the genus (Table 1). PCR amplification was done using primers LX12SN1 and LX16S1R for
120 mitochondrial fragment L2; it includes partial sequences from the 12S ribosomal subunit, the
121 tRNA and the large subunit 16S (Zhang et al., 2008). PCR conditions were as follow: 35 cycles
122 at 96º C (2 min), 55ºC (1 min) and 72º C (5 min). We also amplified a fragment of the COI gene
123 using primers dgLCO and dgHCO (Meyer, 2003). PCR conditions were as follows: 35 cycles at
124 94º C (30 s), 50º C (30 s) and 72º C (45 s). We cleaned PCR products with ExoSap-IT (USB
125 Corporation, Cleveland, OH) and sequencing reaction with BigDye Terminator v3.1 cycle kit
126 (Applied Biosystems, Foster City, CA). The products were purified using Sephadex G-50 (GE
127 Heathcare) and run on an ABI 3730 capillary sequencer at the Instituto de Biología, UNAM.

128 *Sequence alignment and phylogenetic analyses*
129 Editing and assembly of sequences were performed in Sequencher 5.0.1 (Gene Codes
130 Corporation). We used Muscle 3.8 (Edgar, 2004) to align L2 and COI sequences. The alignment
131 for the L2 fragment included 36 *Chiropterotriton* samples sequenced in this study, 35 sequences
132 available on GenBank from previous studies (Parra-Olea, 2003; Rovito et al., 2015; García-
133 Castillo et al., 2018) and two additional sequences from *Aquiloeurycea cephalica* and *Thorius* sp.
134 as outgroups. The alignment for COI included seven sequences from this study and 21 from
135 Genbank (García-Castillo et al., 2018). All sequence information is shown in Table 1. We used
136 Mesquite v3.40 (Maddison & Maddison, 2018) to concatenate and review the data matrix. We
137 used PartitionFinder v1.0 (Lanfear et al., 2012) to select substitution model and a partitioning
138 scheme using the Bayesian Information Criterion (BIC). We ran Maximum Likelihood and
139 Bayesian inference through the CIPRES data portal (Miller et al., 2010) for phylogenetic
140 analyses; RAxML v8.2 (Stamatakis, 2014) to generate a Maximum Likelihood tree, with 1000
141 bootstrap replicates as nodal support; and MrBayes v3.2 (Huelsenbeck and Ronquist, 2001) for
142 Bayesian inference, with 20 million generations, sampling every 1000 generations, with four
143 chains to obtain a majority consensus tree. Finally, we used Tracer v.1.7 (Rambaut et al., 2018)
144 to review the convergence and stability of the chains.

145 *Morphological analyses and species descriptions*
146 Species descriptions largely follow the format used by Lynch & Wake (1989) for species of
147 Neotropical plethodontids and include many of the same basic characters and measurements,
148 including coloration and external measurements. We used an electronic vernier calipers to
149 measure 11 characters: snout-vent length (SVL), tail length (TL), axilla-groin distance (AX),
150 forelimb length (FLL), hind limb length (HLL), snout-to-gular-fold distance (head length, HL),
151 head width at angle of jaw (HW), head depth (HD), shoulder width (SW), internarial distance
152 (IN) and right foot width (FW). In order to obtain an index for nostril shape, we used an ocular
153 micrometer to measure the longest and shortest nostril dimensions (nostril length, NL; nostril
154 width, NW) and we calculated a ratio of nostril dimensions (ND = NL/NW). We also counted
155 ankylosed premaxillary (PMT), maxillary (MT) and vomerine teeth (VT). We present counts for
156 PMT and MT together because of the difficulty in distinguishing them in some specimens. We
157 also measured limb interval (LI) as the number of costal folds between adpressed limbs. Positive
158 values equal the number of folds visible between adpressed limbs that don't meet or overlap;
159 negative values denote overlap between limbs. We treat males and females separately to evaluate

160   the extent of sexual dimorphism (Table 2). Finally, 12 additional measurements were obtained
161   for each holotype: anterior rim of orbit to snout, eyelid length, eyelid width, horizontal orbital
162   diameter, interorbital distance, length of third (longest) toe, length of fifth toe, projection of
163   snout beyond mandible, snout to anterior angle of vent, snout to forelimb, tail depth at base, and
164   tail width at base.
165   In addition, µCT scans were used to prepare osteological accounts based primarily on the
166   cranial characters and character states defined by Darda and Wake (2015; Table 3; Fig. 2). Scans
167   made at the University of Texas High Resolution X-Ray CT facility are archived in a digital
168   repository and may be viewed online via the Internet links provided below. The complete scans
169   include the ossified forelimb skeleton as well as the bony skull, but only skulls are illustrated
170   here.
171   We examined 123 individuals from the eight species of principal interest and used
172   published data for comparisons to other species of *Chiropterotriton*. The latter species were
173   chosen for comparison based on either geographic or phylogenetic closeness. All material,
174   including holotypes or neotypes designated below, is deposited at the National Museum of
175   Natural History, Smithsonian Institution, Washington, DC, USA (USNM) and the Museum of
176   Vertebrate Zoology, University of California Berkeley, USA (MVZ) collections (Appendix I).
177   The electronic version of this article in Portable Document Format (PDF) will represent a
178   published work according to the International Commission on Zoological Nomenclature (ICZN),
179   and hence the new names contained in the electronic version are effectively published under that
180   Code from the electronic edition alone. This published work and the nomenclatural acts it
181   contains have been registered in ZooBank, the online registration system for the ICZN. The
182   ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed
183   through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The
184   LSID for this publication is: urn:lsid:zoobank.org:pub:9B4B9DFF-E12B-430D-A541-
185   BA0EBB9B90E6. The online version of this work is archived and available from the following
186   digital repositories: PeerJ, PubMed Central and CLOCKSS.
187
188   **RESULTS**
189   Our phylogenetic reconstruction was based on two mitochondrial fragments, with a final
190   matrix of 2143 bp (gaps included) from 75 individuals that includes all described species of
191   *Chiropterotriton*. Both ML and Bayesian analysis show two main clades in the genus (Fig. 3).
192   The first main clade, with rather low support (BS = 54, not recovered in Bayesian tree), includes
193   12 species that correspond to the north-central distributions: *C. cracens, C, cieloensis, C.*
194   *arboreus, C. multidentatus, C. infernalis, C. mosaueri, C. chondrostega, C. magnipes, C.*
195   *priscus, C. miquihuanus, C. terrestris* and *C. chico.* The second main clade with strong support
196   (Bootstrap, BS = 100 and Posterior Probability, PP = 1.0) also includes 12 species, but with
197   central-southern distributions: *C. dimidiatus, C. totonacus, C. ceronorum, C. lavae, C.*
198   *perotensis, C.* sp. K, *C.* sp. G, *C. orculus, C. melipona, C. aureus, C. nubilus* and *C. chiropterus*.
199   The major clade is the main subject of the following species descriptions and includes four of the
200   five new species that were initially proposed by Darda (1994) as *Chiropterotriton* sp. E, *C.* sp. F,
201   *C.* sp. H and *C.* sp. I. This clade also contains the two redescribed species, *C. orculus* and *C.*
202   *chiropterus*, as well as *C. lavae.* One of the species we describe below, *C. casasi,* has not been
203   found since the collection of the type series in 1969 and no tissue has been available for
204   molecular analyses. Each species is diagnosed by morphological characters through
205   morphometric (Table 2) and osteological comparisons (Figs. 6–8; Table 3).

206 ***Chiropterotriton ceronorum,* new species**
207 Ceron Family Salamander, Salamandra de los Ceron
208 Figures 4A, 5A, 6B, 7B, 8B.
209 *Chiropterotriton chiropterus* (part)—*Gadow, 1905.*
210 *Chiropterotriton* sp. I.—*Darda, 1994 (population 22); Parra-Olea, 2003; Rafaëlli, 2007; Rovito*
211   *& Parra-Olea, 2015; García-Castillo et al., 2017; García-Castillo et al., 2018.*

212 ***Holotype***: USNM 224212, an adult male from ca. 1 km NE Santa Cruz Texmalaquilla (4.7 mi by
213 road NE of Atzitzintla), on south slope of Pico de Orizaba, Puebla, Mexico, 3110 masl, 18.9484º
214 N, 97.2802º W. Collected 3 September 1975 by R. W. McDiarmid.

215 ***Paratypes***: Twenty specimens, all from Puebla, Mexico. Ten males: MVZ 201393, Santa Cruz
216 Texmalaquilla, S side of Mt. Orizaba; USNM 224202, 224207–08, 224211, 224218–20, 224230
217 and 224236, same data as holotype. Ten females: USNM 224240–41, 224247, 224250, 224252–
218 53, 224257, 224259 and 224275–76, same data as holotype.

219 ***Referred specimens***: Two hundred eighty-two specimens, all from Mexico. Santa Cruz
220 Texmalaquilla, Puebla: MVZ 201387–92; USNM 224193–201, 224203–06, 224209–10,
221 224213–17, 224221–29, 224231–35, 224237–39, 224242–46, 224248–49, 224251, 224254–56,
222 224258 and 224260–74. Xometla, Veracruz: CAS 98934–36, 98939, 98953, 98957; KU 106641–
223 65; IBH 30987–88; LACM 117161–230; MVZ 114378–82, 138759, 138761–63, 143910–17,
224 163583–97, 163601–06, 163612, 184830, 195827–30, 198914–17, 198919, 198921, 231345–47,
225 233032–34; and USNM 492145–47.

226 ***Diagnosis*:** This medium-sized species of plethodontid salamander is phylogenetically close to
227 *Chiropterotriton perotensis, C. totonacus* and *C. lavae*; mean SVL 33.9 mm in ten adult males
228 (range 30.6–36.2) and 34.9 mm in ten adult females (range 33.3–38.4). The head is moderately
229 wide; HW averages 15% of SVL in both males and females (range 14–16%). In males, the snout
230 is broad and truncated. Jaw muscles are pronounced and visible as a bulging mass immediately
231 behind the eyes. Eyes are moderately protuberant and extend laterally beyond the jaw margin in
232 ventral view. There are few maxillary teeth in males (mean MT 11.0, range 7–18) but they are
233 more numerous in females (mean MT 47.7, range 36–56). There are few vomerine teeth in males
234 (mean VT 13.0, range 11–17) and females (mean VT 15.9, range 13–22), and they arranged in a
235 curved line that does not extend past the outer margin of the internal choanae. The tail is
236 moderately long; mean TL equals 1.0 of SVL in males (range 0.89–1.12) and 0.97 of SVL in
237 females (range 0.85–1.07). Limbs are moderately long; FLL+HLL averages 54% of SVL in
238 males (range 48–57%) and 50% in females (range 45–54%). Adpressed limbs approach closely
239 or overlap slightly in males (mean LI 0.0, range -0.5–1) but they are separated by as many as two
240 costal folds in females (mean LI 1.5, range 1–2). Digits are slender and expanded distally, with
241 distinct subterminal pads and moderate webbing at the base. All digits are discrete, including the
242 first, which extends beyond the margins of the webbing. The outermost toes are particularly well
243 developed. The smallest male with a mental gland is 30.6 mm SVL. The mental gland is
244 prominent and oval (nearly round) to round. Parotoid glands are not evident.

245 ***Comparisons*:** *Chiropterotriton ceronorum* differs from *C. perotensis* by its larger adult body
246 size size (mean SVL 33.9 mm in male and 34.9 mm in female *C. ceronorum* vs. 29.7 mm in male
247 and 31.7 mm in female *C. perotensis)*, longer limbs (mean LI 0.0 in male and 1.5 in female *C.*

248 *ceronorum* vs. 2.5 in male and 3.3 in female *C. perotensis)*, longer head (mean HL 7.5 mm in
249 male and 7.1 mm in female *C. ceronorum* vs. 6.6 mm in male and 6.7 mm in female *C.*
250 *perotensis*), broader head (mean HW 5.1 mm in both male and female *C. ceronorum* vs. 4.2 mm
251 in male and 4.4 mm in female *C. perotensis*), broader feet (mean FW 3.8 mm in male and 3.5
252 mm in female *C. ceronorum* vs. 2.6 mm in both male and female *C. perotensis*), more maxillary
253 teeth (mean MT 11.0 in male and 47.7 in female *C. ceronorum* vs. 7.2 in male and 27.9 in female
254 *C. perotensis)* and more vomerine teeth (mean VT 13.0 in male and 15.9 in female *C. ceronorum*
255 vs. 9.0 in male and 11.1 in female *C. perotensis)*.
256   *Chiropterotriton ceronorum* differs from *C. totonacus* in its slightly smaller adult body
257 size (mean SVL 33.9 mm in male and 34.9 mm in female *C. ceronorum* vs. 35.7 mm in male and
258 35.5 mm in female *C. totonacus*), shorter tail (mean TL/SVL 1.0 in male and 0.97 in female *C.*
259 *ceronorum* vs. 1.16 in male and 1.20 in female *C. totonacus*), shorter limbs (mean LI 0.0 in male
260 and 1.5 in female *C. ceronorum* vs. -0.6 in male and 0.0 in female *C. totonacus*) and fewer
261 maxillary teeth (mean MT 11.0 in male and 47.7 in female *C. ceronorum* vs. 32.9 in male and
262 52.6 in female *C. totonacus*).
263   *Chiropterotriton ceronorum* differs from *C. melipona* by its larger adult body size (mean
264 SVL 33.9 mm in male and 34.9 mm in female *C. ceronorum* vs. 29.2 mm in male and 28.5 mm
265 in female *C. melipona)*, longer limbs in males (mean LI 0.0 in *C. ceronorum* vs. 2.3 in *C.*
266 *melipona)*, longer head (mean HL 7.5 mm in male and 7.1 mm in female *C. ceronorum* vs. 6.3
267 mm in male and 6.4 mm in female *C. melipona*), broader head (mean HW 5.1 mm in both male
268 and female *C. ceronorum* vs. 4.3 mm in male and 4.2 mm in female *C. melipona*), broader feet
269 (mean FW 3.8 mm in male and 3.5 mm in female *C. ceronorum* vs. 2.4 mm in male and 2.6 mm
270 in female *C. melipona*), more maxillary teeth (mean MT 11.0 in male and 47.7 in female *C.*
271 *ceronorum* vs. 9.5 in male and 31.0 in female *C. melipona)* and more vomerine teeth (mean VT
272 13.0 in male and 15.9 in female *C. ceronorum* vs. 11.0 in male and 13.0 in female *C. melipona*).
273   *Chiropterotriton ceronorum* differs from *C. casasi* in its smaller adult body size (mean
274 SVL 33.9 mm in male and 34.9 mm in female *C. ceronorum* vs. 37.8 mm in male and 40.9 mm
275 in one female *C. casasi*), shorter head (mean HL 7.5 mm in male and 7.1 mm in female *C.*
276 *ceronorum* vs. 8.3 mm in male and 8.6 mm in one female *C. casasi*), narrower head (mean HW
277 5.1 mm in both male and female *C. ceronorum* vs. 5.8 mm in male and 5.9 mm in one female *C.*
278 *casasi*), longer limbs in males (mean LI 0.0 in *C. ceronorum* vs. 0.8 in *C. casasi*), more
279 maxillary teeth (mean MT 11.0 in male and 47.7 in female *C. ceronorum* vs. mean 9.0 in males
280 and 30 in one female *C. casasi*) and more vomerine teeth (mean VT 13.0 in male and 15.9 in
281 female *C. ceronorum* vs. mean 9.0 in males and 13 in one female *C. casasi*).
282   *Chiropterotriton ceronorum* differs from *C. chiropterus* in its smaller adult body size in
283 males (mean SVL 33.9 mm in *C. ceronorum* vs. 37.5 mm in *C. chiropterus*), shorter tail (mean
284 TL/SVL 1.0 in male and 0.97 in female *C. ceronorum* vs. 1.25 in male and 1.19 in female *C.*
285 *chiropterus*), longer limbs (mean LI 0.0 in male and 1.5 in female *C. ceronorum* vs. 0.3 in male
286 and 2.0 in female *C. chiropterus*) and fewer maxillary teeth (mean MT 11.0 in male and 47.7 in
287 female *C. ceronorum* vs. 12.6 in male and 48.0 in female *C. chiropterus*).
288   *Chiropterotriton ceronorum* differs from *C. orculus* in its smaller adult body size (mean
289 SVL 33.9 mm in male and 34.9 in female *C. ceronorum* vs. 35.9 mm in male and 39.0 in female
290 *C. orculus*), longer limbs (mean LI 0.0 in male and 1.5 in female *C. ceronorum* vs. 1.9 in male
291 and 2.9 in female *C. orculus)*, more maxillary teeth (mean MT 11.0 in male and 47.7 in female
292 *C. ceronorum* vs. 8.2 in male and 28.8 mm in female *C. orculus)* and more vomerine teeth (mean
293 VT 13.0 in male and 15.9 in female *C. ceronorum* vs. 8.6 in male and 12.0 in female *C. orculus*).

294   *Chiropterotriton ceronorum* differs from *C. lavae* in being slightly larger (mean SVL
295 33.9 mm in male and 34.9 mm in female *C. ceronorum* vs. 32.4 mm in male and 31.6 mm in
296 female *C. lavae*), a shorter tail (mean TL/SVL 1.0 in male and 0.97 in female *C. ceronorum* vs.
297 1.19 in male and 1.02 in female *C. lavae*), shorter limbs (mean LI 0.0 in male and 1.5 in female
298 *C. ceronorum* vs. -0.6 in male and 0.6 in female *C. lavae*), more maxillary teeth (mean MT 11.0
299 in male and 47.7 in female *C. ceronorum* vs. 7.0 in male and 20.8 in female *C. lavae*), and more
300 vomerine teeth (mean VT 13.0 in male and 15.9 in female *C. ceronorum* vs. 8.9 in male and 11.4
301 in female *C. lavae*).
302   *Chiropterotriton ceronorum* differs from *C. aureus* by its larger adult body size size
303 (mean SVL 33.9 mm in male and 34.9 mm in female *C. ceronorum* vs. 28.5 mm in one male and
304 26.8 mm in female *C. aureus)*, a shorter tail (mean TL/SVL 1.0 in male and 0.97 in female *C.*
305 *ceronorum* vs. 1.28 in one male and 1.16 in female *C. aureus*), longer limbs (mean LI 0.0 in
306 male and 1.5 in female *C. ceronorum* vs. 2.0 in one male and 2.3 in female *C. aureus)*, longer
307 head (mean HL 7.5 mm in male and 7.1 mm in female *C. ceronorum* vs. 6.4 mm in one male and
308 6.0 mm in female *C. aureus*), broader head (mean HW 5.1 mm in both male and female *C.*
309 *ceronorum* vs. 4.0 mm in one male and 3.6 mm in female *C. aureus*), broader feet (mean FW 3.8
310 mm in male and 3.5 mm in female *C. ceronorum* vs. 2.4 mm in one male and 1.8 in female *C.*
311 *aureus*), and more maxillary teeth (mean MT 11.0 in male and 47.7 in female *C. ceronorum* vs.
312 10.0 in one male and 38.3 in female *C. aureus*).
313   *Chiropterotriton ceronorum* differs from *C. nubilus* by its larger adult body size size
314 (mean SVL 33.9 mm in male and 34.9 mm in female *C. ceronorum* vs. 29.4 mm in one male and
315 30.5 mm in female *C. nubilus)*, a shorter tail (mean TL/SVL 1.0 in male and 0.97 in female *C.*
316 *ceronorum* vs. 1.37 in one male and 1.12 in female *C. nubilus*), longer limbs in males (mean LI
317 0.0 in male *C. ceronorum* vs. 2.0 in one male *C. nubilus)*, longer head in males (mean HL 7.5
318 mm in male *C. ceronorum* vs. 6.6 mm in one male *C. nubilus*), broader head (mean HW 5.1 mm
319 in both male and female *C. ceronorum* vs. 4.0 mm in one male and 4.4 mm in female *C.*
320 *nubilus*), and broader feet (mean FW 3.8 mm in male and 3.5 mm in female *C. ceronorum* vs. 2.6
321 mm in male and 2.3 in female *C. nubilus*).

322 ***Description of holotype.*** SVL 36.2 mm, TL 34.3 mm, AX 17.9 mm, SW 3.4 mm, HL 8.1 mm,
323 HW 5.3 mm, HD 2.6 mm, projection of snout beyond mandible 0.8 mm, distance from anterior
324 rim of orbit to snout 2.0 mm, interorbital distance 2.6 mm, eyelid length 1.8 mm, eyelid width
325 1.3 mm, horizontal orbit diameter 1.6 mm, nostril diameter 0.3 mm, FLL 10.0 mm, HLL 10.3
326 mm, snout-to-forelimb length 11.5 mm, snout to anterior angle of vent 35.2 mm, tail width at
327 base 2.4 mm, tail depth at base 2.6 mm, FW 4.6 mm, length of fifth toe 0.7 mm, length of third
328 (longest) toe 1.3 mm, mental gland length 2.0 mm, mental gland width 1.7. Numbers of teeth:
329 premaxillary 3, maxillary 5-4 (right-left) and vomerine 5-6 (right-left). Adpressed limbs are
330 separated by two costal folds.

331 ***Variation***: Specimens of *C. ceronorum* from Xometla are smaller and have a longer tail than
332 those from the type locality: mean SVL 33.9 mm in males and 34.9 mm in females from
333 Texmalaquilla vs. 31.0 mm in males and 32.0 mm in females from Xometla; and mean TL/SVL
334 1.0 in males and 0.97 in females from Texmalaquilla vs. 1.17 in males and 1.08 in females from
335 Xometla.

336   ***Coloration in life*:** These notes are based on study of a series of diapositives taken by Gabriela
337   Parra-Olea from near Xometla and by James Hanken and Roy W. McDiarmid from the vicinity
338   of Santa Cruz Texmalaquilla. Colors are from Köhler (2012).
339   The single Xometla specimen is generally dark brown and lacks a dorsal stripe or band.
340   Dorsal and lateral coloration reddish brown (Mahogany Red, 34) anteriorly becoming brown
341   (Brussels Brown, 33) medially and posteriorly. Lateral and ventral surfaces grayish (Smoke
342   Gray, 266). Face and cheeks as well as limbs bright gray-brown (Smoke Gray, 267, to Light
343   Drab, 269). Snout Ground Cinnamon (270) to True Cinnamon (28) to Vinaceous (247) at its tip.
344   Upper eyelid Cream Yellow (82) at rim. Iris Cream Yellow (82) to bright Trogon Yellow (81)
345   dorsally but much darker and brownish ventrally. Manus and pes bright light gray (Pale Neutral
346   Gray, 296) but essentially colorless at the digit tips, which are transparent and show underlying
347   reddish blood vessels.
348   The Texmalaquilla specimens (nine) all have dark to very dark basic ground color
349   dorsally and laterally (venter not visible). Usually a dorsal band or stripe is present that extends
350   from the posterior surface of the head (over the anterior extension of the epaxial muscles) to the
351   tail tip. The band is almost uninterrupted in some specimens but is discontinuous or contains
352   numerous spots or flecks of darker color in others. The stripe can be very bright and can be rich
353   reddish (Pratt's Rufous, 72), orange-brown (Flesh Ocher, 57, to Orange Rufous, 56) to Salmon
354   Color (58) and Dark Salmon Color (59). In others it is Clay Color (18, 20).

355   ***Coloration in preservative*:** The holotype is a uniform dark tannish brown dorsally, becoming
356   paler laterally and very pale cream color ventrally. The dark tannish brown extends to the tip of
357   the tail. Limbs are yellowish. Mental gland is beige. Nine paratypes are uniform dorsally,
358   ranging from golden tan to very dark grey; in some, the tail is slightly paler than the dorsum.
359   These nine paratypes have lateral surfaces paler than dorsal, and ventral surfaces are much
360   lighter than lateral surfaces. The remaining eleven paratypes have a stripe of some sort. The
361   stripe is always paler than immediately adjacent lateral parts, but it can be very obscure and seen
362   mainly in the tail or it can extend all the way from the nape to the tip of the tail. The stripe is
363   bright yellow in some individuals but typically is darker; in some specimens there is a suffusion
364   of black in the middle of the stripe. All individuals are paler ventrally, but in some very dark
365   animals the venter is dark gray and only the gular area is pale. The mental gland is usually pale.

366   ***Osteology*:** This account is based on examination of a μCT scan of the anterior skeleton of
367   USNM 224212, an adult male, 36.2 mm SVL (Figs. 6–7; Table 3). The skull is robust in its
368   degree of ossification, although many roofing bones are extremely thin. Paired frontals and
369   parietals are for the most part well-articulated with one another; there is only a narrow but
370   elongate frontoparietal fontanelle, mostly along the midline. Anteriorly, the frontals articulate
371   with the nasal and prefrontal bones, as well as with the ascending processes of the single
372   premaxilla. The ascending processes never contact one another but gradually widen as they
373   establish an articulation with the frontals, thereby enclosing the internasal fontanelle. The palatal
374   shelf of the premaxilla is very narrow and barely evident. Paired septomaxillary bones are
375   present but small. The nasal bone is triangular but very thin, and somewhat larger than the
376   prefrontal, which is more rectangular in shape. Both bones are overlapped by the facial process
377   of the maxilla, but where the three bones meet the foramen for the nasolacrimal duct has eroded
378   the facial process and the prefrontal but not the adjacent nasal. The anterior, toothed portion of
379   the maxilla comprises only around 40% of the length of the bone; the remaining 60% is
380   edentulous and saber-shaped. In dorsal view, the posterior tip of each maxilla doesn't bow out

381 laterally as they do in some congeners (e.g., *C. orculus*). There are five maxillary teeth on the
382 right side and seven on the left. There is but a single, short premaxillary tooth. The
383 orbitosphenoid, while relatively large, is only weakly articulated to the parasphenoid and frontal
384 and mostly separated from the parietal.
385   The otic capsule bears a distinct crest that extends anteriorly from the midpoint of the
386 lateral semicircular canal to about the anterior third of the anterior semicircular canal. A narrow,
387 spine-like tab is reflected ventromedially from the posterolateral margin of the parietal, ending at
388 about the middle of the vertical extent of the orbitosphenoid. The squamosal is robust and
389 expanded anteroventrally. The quadrate is stout. A stubby, thick-based stylus is present on the
390 operculum. Paired vomers are well developed but barely articulate at the midline posterior to the
391 internasal fontanelle. The preorbital process of each vomer is elongate, twisted and somewhat
392 expanded laterally. Each side bears six vomerine teeth, which are deployed medially and do not
393 extend onto the preorbital process. The median parasphenoid bone is triangular, but its caudal
394 end is slightly bowed posteriorly. Paired parasphenoid tooth patches are separate at the midline;
395 each bears approximately 60 teeth. The mandible is relatively stout. The articular bone is well
396 ossified. The prearticular bone is well developed and bluntly rounded anteriorly, with a high
397 coronoid process. There are 15 or 16 teeth on each dentary bone.
398   Digital formulae are 1-2-3-2 on each side. The terminal phalanx is barely expanded on
399 each finger. Mesopodial cartilages are not mineralized.

400 ***Distribution and ecology***: *Chiropterotriton ceronorum* occurs on the southern slopes of Pico de
401 Orizaba in the states of Puebla and Veracruz at elevations that range from 2600 to approximately
402 3100 masl. Specimens have been found in arboreal bromeliads as well as under terrestrial cover
403 objects.

404 ***Remarks***: *Chiropterotriton ceronorum* is found in sympatry with *Pseudoeurycea gadovii*, *P.
405 leprosa*, *Thorius spilogaster* and *T. lunaris*. Much of the natural habitat has been destroyed in
406 recent years, making the species difficult to find. This species occurs at higher elevations than
407 the nearby (to the NE) *Chiropterotriton chiropterus*.

408 ***Conservation status***: *Chiropterotriton ceronorum* was very common during the 1970s, but is
409 now very difficult to find, probably because of extensive habitat modification. On two visits to
410 the area in 2015, no individuals of this species were seen while all the species with which it is
411 known to co-occur were found. The remaining forest in the area where it lives is severely
412 fragmented with ongoing degradation. We recommend that it be designated as Critically
413 Endangered (CR) based on criterion B1ab(iii) (extent of occurrence < 100 km^2, severely
414 fragmented range and continuing decline in area, extent, and quality of habitat).

415 ***Etymology***: The species name honors the Ceron family of Cuautlalpan, Veracruz, who have
416 assisted generations of herpetologists in collecting salamanders in the general region of Pico de
417 Orizaba.

418

419 ***Chiropterotriton perotensis, new species***
420 Valle Alegre Salamander, Salamandra de Valle Alegre
421 Figures 4B, 5B, 6F, 7F, 8F.

422 *Chiropterotriton chiropterus* (part).—*Smith and Taylor, 1948; Wake et al., 1992.*
423 *Chiropterotriton* sp. H.—*Darda, 1994; Parra-Olea, 2003; Rafaëlli, 2007; Rovito & Parra-Olea,*
424   *2015; García-Castillo et al., 2017; García-Castillo et al., 2018.*
425 *Chiropterotriton* sp.—*Rovito et al., 2015.*
426

427 **Holotype:** MVZ 200693, an adult female from 14.4 km S (by road surfaced with rocks) Las
428 Vigas de Ramírez at Microwave Station, Valle Alegre, Veracruz, Mexico, 3020 masl,
429 19.56917ºN, 97.09528ºW (EPE = max. error distance 1.142 km). Collected 26 August 1982 by
430 D. M. Darda and S. Sessions.

431 **Paratypes:** Nineteen specimens, all from Veracruz, Mexico. Twelve males: MVZ 114356 and
432 114359, road from Las Vigas de Ramírez to microwave station on N Flank Cofre de Perote, 11.6
433 km S (by road) Las Vigas; MVZ 173428–29, Las Vigas de Ramírez, microondas road; MVZ
434 178661 and 178663–65, 8–15.5 km S (via microondas road) Las Vigas de Ramírez; MVZ
435 200681–83 and 200698, 14.4 km S (by Rock Rd.) Las Vigas de Ramírez at microwave station.
436 Seven females: MVZ 173438–39, Las Vigas de Ramírez, microondas road; MVZ 186711, road
437 to microwave station, 15 km S (by road) Las Vigas de Ramírez; MVZ 200691, 200694–95 and
438 200702, 14.4 km S (by Rock Rd.) Las Vigas de Ramírez at microwave station.

439 **Referred specimens:** Seventy-one specimens, all from Veracruz, Mexico. IBH 16778–82, 22384,
440 22391, 22395, 23062, 23066, 23072, 29853, 29857, 29863–64, 29866, 29872, 30840–41, 30844,
441 30847, 31032–39 and 31055–62; KU 100747–54; MVZ 114351, 114355, 114357, 114358,
442 173440–41, 178659–60, 178662, 178666–68, 200684–86, 200688–90, 200692, 200695–97,
443 200699–701 and 200703.

444 **Diagnosis:** This is a small but stout species of plethodontid salamander that is phylogenetically
445 related to *Chiropterotriton lavae*, *C. ceronorum* and *C. totonacus*; mean SVL 29.7 mm in 12
446 adult males (range 26.5–32.8) and 31.7 mm in eight adult females (range 27.4–34.3). The head is
447 moderately wide; HW averages 14% of SVL in both males and females (range 13–15%). The
448 snout is short. Eyes are small and typically do not protrude laterally beyond the jaw margin in
449 ventral view; they are less prominent than in most other species of *Chiropterotriton*. Jaw muscles
450 caudal to the eyes are variably developed but generally pronounced. There are few maxillary
451 teeth in males (mean MT 7.2, range 2–17) and moderate numbers in females (mean MT 27.9,
452 range 19–36). There are few vomerine teeth in both males (mean VT 9.0, range 7–12) and
453 females (mean MT 11.1, range 10–13), which are arranged in a curved line that does not extend
454 lateral to the outer margin of the internal choana. The tail is moderately sized; mean TL equals
455 1.03 of SVL in males (range 0.92–1.16) and 1.0 of SVL in females (range 0.79–1.11). Limbs are
456 short; FLL+HLL averages 47% of SVL in males (range 44–50%) and 43% of SVL in females
457 (range 41–46%). Adpressed limbs are widely separated—they never overlap—in both males
458 (mean LI 2.5, range 1–3) and females (mean LI 3.3, range 2–4). Manus and pes are relatively
459 small for the genus. Digital webbing ranges from absent to slight; when present, it is limited to
460 the metatarsal region. The first digit is small and usually included within the webbing, although a
461 small portion of it may be free at the tip. The outermost digit is less prominent than in other
462 species; digit 5 (pes) is distinctly shorter than digits 2–4. Subterminal pads are present but not
463 prominent. An oval-shaped mental gland present in males but is not particularly prominent. The

464   smallest male with a mental gland is 29.3 mm SVL. Paratoid glands are present in many
465   individuals and prominent in some.

466   **Comparisons:** *Chiropterotriton perotensis* differs from *C. ceronorum* in its smaller adult body
467   size (mean SVL 29.7 mm in male and 31.7 mm in female *C. perotensis* vs. 33.9 mm in male and
468   34.9 mm in female *C. ceronorum*), shorter limbs (mean LI 2.5 in male and 3.3 in female *C.*
469   *perotensis* vs. 0.0 in male and 1.5 in female *C. ceronorum*), shorter head (mean HL 6.6 mm in
470   male and 6.7 mm in female *C. perotensis* vs. 7.5 mm in male and 7.1 mm in female C.
471   *ceronorum*), narrower head (mean HW 4.2 mm in male and 4.4 mm in female *C. perotensis* vs.
472   5.1 mm in both male and female *C. ceronorum*), narrower feet (mean FW 2.6 mm in both male
473   and female *C. perotensis* vs. 3.8 mm in male and 3.5 mm in female *C. ceronorum*)*, fewer
474   maxillary teeth (mean MT 7.2 in male and 27.8 in female *C. perotensis* vs. 11.0 in male and 47.7
475   in female *C. ceronorum*) and fewer vomerine teeth (VT 9.0 in male and 11.1 in female *C.*
476   *perotensis* vs. 13.0 in male and 15.9 in female *C. ceronorum*).
477   *Chiropterotriton perotensis* differs from *C. totonacus* in its smaller adult body size (mean
478   SVL 29.7 mm in male and 31.7 mm in female *C. perotensis* vs. 35.7 mm in male and 35.5 mm in
479   female *C. totonacus*), shorter tail (mean TL/SVL 1.0 in both male and female *C. perotensis* vs.
480   1.16 in male and 1.20 in female *C. totonacus*), shorter limbs (mean LI 2.5 in male and 3.3 in
481   female *C. perotensis* vs. -0.6 in male and 0.0 in female *C. totonacus*), shorter head (mean HL 6.6
482   mm in male and 6.7 mm in female *C. perotensis* vs. 8.5 mm in male and 7.6 mm in female *C.*
483   *totonacus*), narrower head (mean HW 4.2 mm in male and 4.4 mm in female *C. perotensis* vs.
484   5.2 mm in both male and female *C. totonacus*), narrower feet (mean FW 2.6 mm in both male
485   and female *C. perotensis* vs. 4.2 mm in male and 4.0 mm in female *C. totonacus*), fewer
486   maxillary teeth (mean MT 7.2 in male and 27.9 in female *C. perotensis* vs. 32.9 in male and 52.6
487   in female *C. totonacus*) and fewer vomerine teeth (mean VT 9.0 in male and 11.1 in female *C.*
488   *perotensis* vs. 11.6 in male and 13.7 in female *C. totonacus*).
489   *Chiropterotriton perotensis,* while very similar in morphological proportions to *C.*
490   *melipona,* differs by its shorter limbs in females (mean LI 3.3 in *C. perotensis* vs. 1.8 in *C.*
491   *melipona*), fewer maxillary teeth (mean MT 7.2 in male and 27.9 in female *C. perotensis* vs. 9.5
492   in male and 31.0 in female *C. melipona*) and fewer vomerine teeth (mean VT 9.0 in male and
493   11.1 in female *C. perotensis* vs. 11.0 in male and 13.0 in female *C. melipona*).
494   *Chiropterotriton perotensis* differs from *C. casasi* in its smaller adult body size (mean
495   SVL 29.7 mm in male and 31.7 mm in female *C. perotensis* vs. 37.8 mm in male and 40.9 mm in
496   one female *C. casasi*), shorter limbs (mean LI 2.5 in male and 3.3 in female *C. perotensis* vs.
497   0.80 in male and 1.0 in one female *C. casasi*), shorter head (mean HL 6.6 mm in male and 6.7
498   mm in female *C. perotensis* vs. 8.3 mm in male and 8.6 mm in one female *C. casasi*), narrower
499   head (mean HW 4.2 mm in male and 4.4 mm in female *C. perotensis* vs. 5.8 mm in male and 5.9
500   mm in one female *C. casasi*), narrower feet (mean FW 2.6 mm in both male and female *C.*
501   *perotensis* vs. 3.7 mm in both male and one female *C. casasi*), fewer maxillary teeth (mean MT
502   7.2 in male and 27.9 in female *C. perotensis* vs. 9.0 in male and 30.0 in one female *C. casasi*)
503   and fewer vomerine teeth in females (11.1 in *C. perotensis* vs.13.0 in one *C. casasi*).
504   *Chiropterotriton perotensis* differs from *C. chiropterus* by its smaller adult body size
505   (mean SVL 29.7 mm in male and 31.7 mm in female *C. perotensis* vs. 37.5 mm in male and 33.5
506   mm in female *C. chiropterus*), shorter tail (mean TL/SVL 1.0 in both male and female *C.*
507   *perotensis* vs. 1.25 in male and 1.19 in female *C. chiropterus*), shorter limbs (mean LI 2.5 in
508   male and 3.3 in female *C. perotensis* vs. 0.30 in male and 2.0 in female *C. chiropterus*), shorter
509   head (mean HL 6.6 mm in male and 6.7 mm in female *C. perotensis* vs. 8.1 mm in male and 7.3

510 mm in female *C. chiropterus*), narrower head (mean HW 4.2 mm in male and 4.4 mm in female
511 *C. perotensis* vs. 5.6 mm in male and 4.8 mm in female *C. chiropterus*), narrower feet (mean FW
512 2.6 mm in both male and female *C. perotensis* vs. 3.7 mm in male and 3.1 mm in female *C.*
513 *chiropterus*), fewer maxillary teeth (mean MT 7.2 in male and 27.9 in female *C. perotensis* vs.
514 12.6 in male and 48.0 in female *C. chiropterus*) and fewer vomerine teeth (mean VT 9.0 in male
515 and 11.1 in female *C. perotensis* vs. 10.6 in male and 12.5 in female *C. chiropterus*).
516   *Chiropterotriton perotensis* differs from *C. orculus* in its smaller adult body size (mean
517 SVL 29.7 mm in male and 31.7 mm in female *C. perotensis* vs. 35.9 mm in male and 39.0 mm in
518 female *C. orculus*), slightly shorter limbs (mean LI 2.5 in male and 3.3 in female *C. perotensis*
519 vs. 1.9 in male and 2.9 in female *C. orculus*), shorter head (mean HL 6.6 mm in male and 6.7
520 mm in female *C. perotensis* vs. 7.4 mm in male and 8.0 mm in female *C. orculus*), narrower head
521 (mean HW 4.2 mm in male and 4.4 mm in female *C. perotensis* vs. 5.0 mm in male and 5.2 mm
522 in female *C. orculus*), narrower feet (mean FW 2.6 mm in both male and female *C. perotensis* vs.
523 3.2 mm in male and 3.4 mm in female *C. orculus*) and fewer maxillary teeth (mean MT 7.2 in
524 male and 27.9 in female *C. perotensis* vs. 8.2 in male and 28.8 in female *C. orculus*).
525   *Chiropterotriton perotensis* differs from *C. lavae* in having a smaller adult body size in
526 males (mean SVL 29.7 mm in *C. perotensis* vs. 32.4 mm in *C. lavae*), shorter limbs (mean LI 2.5
527 in male and 3.3 in female *C. perotensis* vs. -0.6 in male and 0.6 in female *C. lavae*), a slightly
528 narrower head (mean HW 4.2 in male and 4.4 in female *C. perotensis* vs. 4.9 in male and 4.7 in
529 female *C. lavae*), a shorter head (mean HL 6.6 mm in male and 6.7 mm in female *C. perotensis*
530 vs. 7.5 mm in male and 7.0 mm in female *C. lavae*), narrower feet (FW 2.6 mm in both male and
531 female *C. perotensis* vs. 3.7 mm in male and 3.3 mm in female *C. lavae*) and more maxillary
532 teeth in females (mean MT 27.9 in *C. perotensis* vs. 20.8 in *C. lavae*).
533   *Chiropterotriton perotensis* differs from *C. aureus* in its smaller adult body size (mean
534 SVL 29.7 mm in male and 31.7 mm in female *C. perotensis* vs. 28.5 mm in male and 26.8 mm in
535 female *C. aureus*), shorter tail in males (mean TL/SVL 1.0 in both male and female *C. perotensis*
536 vs. 1.28 in male and 1.16 in female *C. aureus*), broader head (mean HW 4.2 mm in male and 4.4
537 mm in female *C. perotensis* vs. 4.0 mm in male and 3.6 mm in female *C. aureus*), broader feet in
538 females (mean FW 2.6 mm in female *C. perotensis* vs. 1.8 mm in female *C. aureus*), fewer
539 maxillary teeth in females (mean MT 27.9 in female *C. perotensis* vs. 38.3 in female *C. aureus*)
540 and fewer vomerine teeth in males (mean VT 9.0 in male *C. perotensis* vs. 15.0 in male *C.*
541 *aureus*).
542   *Chiropterotriton perotensis* differs from *C. nubilus* in having a shorter tail (mean
543 TL/SVL 1.0 in both male and female *C. perotensis* vs. 1.37 in male and 1.12 in female *C.*
544 *nubilus*), shorter limbs (mean LI 2.5 in male and 3.3 in female *C. perotensis* vs. 2.0 in male and
545 1.5 in female *C. nubilus*), and fewer maxillary teeth (mean MT 7.2 in male and 27.9 in female *C.*
546 *perotensis* vs. 13.0 in male and 41.5 in female *C. nubilus*)

547 ***Description of holotype***: SVL 31.1 mm, TL 30.7 mm, AX 16.4 mm, SW 3.1 mm, HL 6.8 mm,
548 HW 4.2 mm, HD 2.0 mm, projection of snout beyond mandible 0.4 mm, distance from anterior
549 rim of orbit to snout 1.7 mm, interorbital distance 1.8 mm, eyelid length 2.2 mm, eyelid width
550 0.8 mm, horizontal orbit diameter 1.4 mm, FLL 6.5 mm, HLL 6.7 mm, snout-to-forelimb length
551 8.8 mm, snout to anterior angle of vent 29.5 mm, tail width at base 2.1 mm, tail depth at base 2.6
552 mm, FW 2.5 mm, length of fifth toe 0.5 mm, length of third (longest) toe 1.2 mm. Numbers of
553 teeth: premaxillary 6, maxillary 15-16 (right-left) and vomerine 7-6 (right-left). Adpressed limbs
554 are separated by 4 costal folds.

555 ***Coloration in life*:** Color notes in life are not available for specimens in the type series, but notes
556 were recorded for the following referred specimens. IBH 29853, 29857, 29863, 29864, 29866
557 and 29872, 15 km S of Las Vigas on road to Valle Alegre: General coloration dark with a dark
558 reddish brown dorsal stripe in some and obscure brown to grayish brown stripe in others. The
559 reddish stripe is brightest laterally with darker pigment medially. Small guanophores are
560 abundantly distributed over the mainly very dark pigment dorsally. The iris is golden brown to
561 dark brown. The venter is dark to very dark. In one adult there is a complete melanophore
562 network; in another, dense punctuations. Some white guanophores are prominent in the darker
563 individual. IBH 22384, 22395, 23062, 23066 and 23072, 15.9 km on microondas road, Las
564 Vigas: Adults are very dark dorsally--almost black--with a fine speckling of obscure white
565 overlying the ground color. Fine background mottling of dark brown on black. Limbs are black
566 with some paler highlights medially, but become brown distally. The iris is dark brownish black.
567 The venter is dark, dense mainly punctate melanophores, with a very fine superficial sprinkling
568 of white ventrolaterally. The gular area is slightly paler. Juveniles have an indistinct brown
569 stripe, which is less apparent in larger animals.

570 ***Coloration in preservative*:** The holotype is a uniform dark brown dorsally and laterally,
571 becoming blackish brown on the tail. The venter is much paler than the dorsum, becoming dark
572 brown under the tail. Limbs are dark brown. There is no other distinguishing color. Two of the
573 paratypes have a hint of a dorsal stripe, which is slightly paler than surrounding areas. The
574 manus and pes are paler, but in general are brown to blackish brown.

575 ***Osteology*:** This account is based on examination of a μCT scan of the anterior skeleton of MVZ
576 200693, an adult female, 31.1 mm SVL (Figs. 6–8; Table 3). The skull is compact. Individual
577 cranial roofing bones are for the most part well developed, although there is a marked
578 frontoparietal fontanelle that begins at the frontal-parietal border and extends posteriorly along
579 the midline. The frontal is fairly robust. Anteriorly, it is solidly articulated with the ascending
580 processes of the single premaxilla, which arise separately and remain distinct along their entire
581 length. The processes expand laterally where they articulate with the frontal bones. The
582 premaxilla lacks a palatal shelf and there are no septomaxillary bones. The nasal bone is
583 triangular but very thin. It is considerably larger than the rectangular prefrontal, which is distinct
584 but small. A foramen for the nasolacrimal duct has eroded the anteroventral margin of the
585 prefrontal, the posteroventral margin of the nasal, and the dorsal edge of the facial process of the
586 maxilla. The anterior, toothed portion of the maxilla comprises approximately 75–80% of the
587 length of the bone; the remaining edentulous portion is thinner and cleaver-like. The facial
588 process of the maxilla extends rostrally. There are 16 maxillary teeth on the left side and 17 on
589 the right. There are seven premaxillary teeth. The orbitosphenoid is moderately well developed
590 and relatively large, but it is only weakly articulated to the parasphenoid and frontal and
591 separated from the parietal.
592 The otic capsule bears a modest dorsal crest above the anterior semicircular canal but
593 there is no distinct otic process. A well-developed tab extends ventromedially from the
594 posterolateral surface of the parietal. It is relatively long and spine-like and extends through
595 about two-thirds of the vertical extent of the orbitosphenoid. The squamosal bone is relatively
596 stout, roughly triangular, and abuts the otic capsule along a broad front that subtends the lateral
597 semicircular canal. The quadrate bone is relatively small and inconspicuous. The columella bears
598 a distinct stylus. Bodies of the vomer are well ossified but also well separated at the midline.
599 Each preorbital process is short, ending at the lateral edge of the internal naris. There are nine

600 vomerine teeth on the right side and six on the left; a few are deployed on the preorbital process.
601 The parasphenoid is fairly broad anteriorly; its posterior border is straighter (less rounded) than
602 in some other species. Paired parasphenoid tooth patches meet at the midline both anteriorly and
603 posteriorly, but not in between. There are approximately 105 fully developed teeth on each side
604 and smaller, less-developed teeth along each lateral margin. The mandible is robust. The articular
605 is only partly ossified. The prearticular is relatively small and has a low coronoid process. Teeth
606 are small and very numerous on each dentary bone, but a reliable count cannot be made from the
607 CT scan.
608   Digital formulae are 1-2-3-2 on each side. The distal tip of the terminal phalanx is
609 slightly expanded on each finger. Mesopodial cartilages are not mineralized.

610 **_Distribution and ecology_:** *Chiropterotriton perotensis* is found in Cofre de Perote, Veracruz,
611 Mexico, both in pine-and-fir forest and from the tree line to the summit. Elevations range from
612 2950 to 4015 m. Specimens have been found under terrestrial objects and active on road banks
613 and boulders at night. The species occurs in sympatry with *Aquiloeurycea cephalica*, *Isthmura*
614 *naucampatepetl*, *Pseudoeurycea leprosa* and *P. melanomolga*.

615 **_Remarks_:** Allozymes of this species were studied by Darda (his unnamed species H) (1994),
616 who also reported a sympatric species (his species D). These two were separated by four fixed
617 differences (out of 17 proteins studied). Parra-Olea (2003) was unable to obtain mtDNA
618 sequence from his remaining (ground and degraded) tissue samples and did not find additional
619 specimens. We consider the dissected carcasses to be inadequate for preparation of a formal
620 description, but we note the presence of a likely additional species of *Chiropterotriton* at the Las
621 Lajas locality. Like *C perotensis,* this unnamed species is small, but apparently more slender and
622 lighter in coloration. The two are not sister-taxa.
623   We think that the specimens reported as *Chiropterotriton chiropterus* from 11,000 feet on
624 Cofre de Perote by Smith and Taylor (1948) belong to *C. perotensis.*

625 **_Conservation status_:** We recommend that the species be designated as Endangered based on
626 criterion B1ab(iii) (extent of occurrence < 5000 km^2, habitat severely fragmented with
627 continuing decline in area, extent, and quality of habitat; IUCN, 2012).

628 **_Etymology_:** The species name is a noun in the genitive case. It refers to the Cofre de Perote
629 volcano, where the species is found.

630
631
632 **_Chiropterotriton totonacus_, new species**
633 Cruz Blanca Salamander, Salamandra de Cruz Blanca
634 Figures 4C, 5C, 6G, 7G, 8G.
635 *Chiropterotriton* sp. E.—*Darda, 1994.*
636 *Chiropterotriton chiropterus* (part).—*Taylor and Smith, 1945*; *Smith and Taylor, 1948; Wake et*
637 *al., 1992.*

638 **_Holotype_:** MVZ 163945, an adult female from 6 km W Las Vigas de Ramírez, Veracruz,
639 Mexico, 2420 masl, 19.635º N, 97.159166º W (EPE = max. error distance 5.71 km). Collected
640 25 July 1979 by D. B. Wake.

N

Paratypes: Nineteen specimens, all from Veracruz, Mexico. Ten males: MVZ 163947–49, 163989–90, 163993, 171903, 171905, 171907 and 171909, 6 km W Las Vigas de Ramírez. Nine females: MVZ 136981–82, 136986, pine forest along Mexican Hwy. 140, 4 km W Las Vigas de Ramírez; MVZ 138703–04, 138716 and 138765, Mexican Hwy. 140, 4.5 km W (by road) Las Vigas de Ramírez; MVZ 163943 and 171910, 6 km W Las Vigas de Ramírez.

Referred specimens: Fifty-two specimens, all from Veracruz, Mexico. IBH 00122 and 31030–31031; MVZ 136983–85, 137029, 138702, 138705–15, 138717–19, 163942, 163944, 163946, 163991–92, 163994, 171904, 171906, 171908 and 171911–31.

Diagnosis: This medium-sized species of plethodontid salamander is phylogenetically close to *Chiropterotriton lavae*, *C. perotensis* and *C. ceronorum*; mean SVL 35.7 mm in ten adult males (range 32.0–38.6) and 35.5 mm in ten adult females (range 31.8–38.3). The head is moderately wide; HW averages 15% of SVL in both sexes (range 14–16). Jaw muscles are prominent in both sexes. Adult males have a broad, blunt snout with pronounced nasolabial protuberances that extend below the lip. Eyes are large and prominent and extend laterally beyond the jaw margin in ventral view. There are numerous maxillary teeth in males (mean MT 32.9, range 18–48) and even more teeth in females (mean MT 52.6, range 45–60). There are few vomerine teeth in both males (mean VT 11.6, range 10–15) and females (mean MT 13.7, range 9–17), which are arranged in a curved line that does not extend past the lateral margin of the internal choana. The tail is long and slender and typically exceeds SVL; mean TL equals 1.16 of SVL in males (range 0.92–1.24) and 1.20 in females (range 1.06–1.38). Limbs are moderately long; FLL+HLL averages 59% of SVL in males (range 55–64%) and 57% in females (range 53–62%). Adpressed limbs closely approach or overlap in males (mean LI -0.6, range -1–1) and females (mean LI 0.0, range -1–1). The manus and pes are relatively wide; digital tips are somewhat expanded and there are distinct subterminal pads. Digital webbing extends to the base of the terminal phalanx. The first (innermost) digit, while distinct, is included in the web except at its tip. Mental glands are large, oval-shaped and relatively prominent in males. The smallest male with a mental gland is 32.0 mm SVL. Parotoid glands are well marked in some individuals but less evident in others.

Comparisons: *Chiropterotriton totonacus* differs from *C. ceronorum* in its larger adult body size (mean SVL 35.7 mm in male and 35.5 mm in female *C. totonacus* vs. 33.9 mm in male and 34.9 mm in female *C. ceronorum*), longer tail (mean TL/SVL 1.16 in male and 1.20 in female *C. totonacus* vs. 1.0 in male and 0.97 in female *C. ceronorum*), longer limbs (mean LI -0.6 in male and 0.0 in female *C. totonacus* vs. 0.0 in male and 1.5 in female *C. ceronorum*), longer head (mean HL 8.5 mm in male and 7.6 mm in female C. *totonacus* vs. 7.5 mm in male and 7.1 mm in female *C. ceronorum*), slightly larger feet (mean FW 4.2 mm in male and 4.0 mm in female *C. totonacus* vs. 3.8 mm in male and 3.5 mm in female *C. ceronorum*), more maxillary teeth (mean MT 32.9 in male and 52.6 in female *C. totonacus* vs. 11.0 in male and 47.7 in female *C. ceronorum*) and fewer vomerine teeth (mean VT 11.6 in male and 13.7 in female *C. totonacus* vs. 13.0 in male and 15.9 in female *C. ceronorum*).

    Chiropterotriton totonacus differs from *C. perotensis* in its larger adult body size (mean SVL 35.7 mm in male and 35.5 mm in female *C. totonacus* vs. 29.7 mm in male and 31.7 mm in female *C. perotensis*), longer tail (mean TL/SVL 1.16 in male and 1.20 in female *C. totonacus* vs. 1.0 in both male and female *C. perotensis*), longer limbs (mean LI -0.60 in male and 0.0 in female *C. totonacus* vs. 2.5 in male and 3.3 in female *C. perotensis*), longer head (mean HL 8.5 mm in male and 7.6 mm in female C. *totonacus* vs. 6.6 mm in male and 6.7 mm in female *C.*

685   *perotensis*), broader head (mean HW 5.2 mm in both male and female *C. totonacus* vs. 4.2 mm
686   in male and 4.4 mm in female *C. perotensis*), larger feet (mean FW 4.2 mm in male and 4.0 mm
687   in female *C. totonacus* vs. 2.6 mm in both male and female *C. perotensis*), more maxillary teeth
688   (mean MT 32.9 in male and 52.6 in female *C. totonacus* vs. 7.2 in male and 27.9 in female *C.*
689   *perotensis*) and more vomerine teeth (mean VT 11.6 in male and 13.7 in female *C. totonacus* vs.
690   9.0 in male and 11.1 in female *C. perotensis*).

691   *Chiropterotriton totonacus* differs from *C. melipona* in its larger adult body size (mean
692   SVL 35.7 mm in male and 35.5 mm in female *C. totonacus* vs. 29.2 mm in male and 28.5 mm in
693   female *C. melipona*), longer tail in females (mean TL/SVL 1.20 in *C. totonacus* vs. 1.11 in *C.*
694   *melipona*), longer limbs (mean LI -0.60 in male and 0.0 in female *C. totonacus* vs. 2.3 in male
695   and 1.8 in female *C. melipona*), longer head (mean HL 8.5 mm in male and 7.6 mm in female C.
696   *totonacus* vs. 6.3 mm in male and 6.4 mm in female *C. melipona*), broader head (mean HW 5.2
697   mm in both male and female *C. totonacus* vs. 4.3 mm in male and 4.2 mm in female *C.*
698   *melipona*), larger feet (mean FW 4.2 mm in male and 4.0 mm in female *C. totonacus* vs. 2.4 mm
699   in male and 2.6 mm in female *C. melipona*) and more maxillary teeth (mean MT 32.9 in male
700   and 52.6 in female *C. totonacus* vs. 9.5 in male and 31.0 in female *C. melipona*).

701   *Chiropterotriton totonacus* differs from *C. casasi* in its smaller adult body size (mean
702   SVL 35.7 mm in male and 35.5 mm in female *C. totonacus* vs. 37.8 mm in male and 40.9 mm in
703   one female *C. casasi*), longer limbs (mean LI -0.6 in male and 0.0 in female *C. totonacus* vs.
704   0.80 in male and 1.0 in one female *C. casasi*), narrower head (mean HW 5.2 in both male and
705   female *C. totonacus* vs. 5.8 in male and 5.9 in one female *C. casasi*), larger feet (mean FW 4.2 in
706   male and 4.0 in female *C. totonacus* vs. 3.7 in both male and one female *C. casasi*) and fewer
707   maxillary teeth (mean MT 32.9 in male and 52.6 in female *C. totonacus* vs. 9.0 in male and 30 in
708   one female *C. casasi*).

709   *Chiropterotriton totonacus* differs from *C. chiropterus* in its smaller adult body size in
710   males (mean SVL 35.7 mm in *C. totonacus* vs. 37.5 mm in *C. chiropterus*), shorter tail (mean
711   TL/SVL 1.16 in male and 1.20 in female *C. totonacus* vs. 1.25 in male and 1.19 in female *C.*
712   *chiropterus*), longer limbs (mean LI -0.60 in male and 0.0 in female *C. totonacus* vs. 0.3 in male
713   and 2.0 in female *C. chiropterus*), longer head (mean HL 8.5 mm in male and 7.6 mm in female
714   C. *totonacus* vs. 8.1 mm in male and 7.3 mm in female *C. chiropterus*), larger feet in males
715   (mean FW 4.2 mm in *C. totonacus* vs. 3.7 mm in *C. chiropterus*), more maxillary teeth (mean
716   MT 32.9 in male and 52.6 in female *C. totonacus* vs. 12.6 in male and 48.0 in female *C.*
717   *chiropterus*) and more vomerine teeth (mean VT 11.6 in male and 13.7 in female *C. totonacus*
718   vs. 10.6 in male and 12.5 in female *C. chiropterus*).

719   *Chiropterotriton totonacus* differs from *C. orculus* in its smaller adult body size in
720   females (mean SVL 35.5 mm in *C. totonacus* vs. 39.0 mm in *C. orculus*), longer tail (mean
721   TL/SVL 1.16 in male and 1.20 in female *C. totonacus* vs. 1.0 in both male and female *C.*
722   *orculus*), longer limbs (mean LI -0.60 in male and 0.0 in female *C. totonacus* vs. 1.9 in male and
723   2.9 in female *C. orculus*), longer head in males (mean HL 8.5 mm in C. *totonacus* vs. 7.4 mm in
724   *C. orculus*), larger feet (mean FW 4.2 mm in male and 4.0 mm in female *C. totonacus* vs. 3.2
725   mm in male and 3.4 mm in female *C. orculus*), more maxillary teeth (mean MT 32.9 in male and
726   52.6 in female *C. totonacus* vs. 8.2 in male and 28.8 in female *C. orculus*) and more vomerine
727   teeth (mean VT 11.6 in male and 13.7 in female *C. totonacus* vs. 8.6 in male and 12.0 in female
728   *C. orculus*).

729   *Chiropterotriton totonacus* differs from *C. lavae* in its larger adult body size (mean SVL
730   35.7 mm in male and 35.5 mm in female *C. totonacus* vs. 32.4 mm in male and 31.6 mm in

731 female *C. lavae*), longer tail in females (mean TL/SVL 1.20 in *C. totonacus* vs. 1.02 in *C. lavae*),
732 longer limbs in females (mean LI 0.0 in *C. totonacus* vs. 0.6 in *C. lavae*), longer head (mean HL
733 8.5 mm in male and 7.6 mm in female C. *totonacus* vs. 7.5 mm in male and 7.0 mm in female *C.*
734 *lavae*), slightly broader head (mean HW 5.2 mm in both male and female *C. totonacus* vs. 4.9
735 mm in male and 4.7 mm in female *C. lavae*), larger feet (mean FW 4.2 mm in male and 4.0 mm
736 in female *C. totonacus* vs. 3.7 mm in male and 3.3 mm in female *C. lavae*), more maxillary teeth
737 (mean MT 32.9 in male and 52.6 in female *C. totonacus* vs. 7.0 in male and 20.8 in female *C.*
738 *lavae*) and more vomerine teeth (mean VT 11.6 in male and 13.7 in female *C. totonacus* vs. 8.9
739 in male and 11.4 in female *C. lavae*).
740   *Chiropterotriton totonacus* differs from *C. aureus* in its larger adult body size (mean SVL
741 35.7 mm in male and 35.5 mm in female *C. totonacus* vs. 28.5 mm in one male and 26.8 mm in
742 female *C. aureus*), longer limbs (mean LI -0.6 in male and 0.0 in female *C. totonacus* vs. 2.0 in
743 one male and 2.3 in female *C. aureus*), longer head (mean HL 8.5 mm in male and 7.6 mm in
744 female *C. totonacus* vs. 6.4 mm in one male and 6.0 mm in female *C. aureus*), larger feet (mean
745 FW 4.2 mm in male and 4.0 mm in female *C. totonacus* vs. 2.4 mm in one male and 1.8 mm in
746 female *C. aureus*), more maxillary teeth (mean MT 32.9 in male and 52.6 in female *C. totonacus*
747 vs. 10.0 in one male and 38.3 in female *C. aureus*) and fewer vomerine teeth (mean VT 11.6 in
748 male and 13.7 in female *C. totonacus* vs. 15.0 in one male and 12.3 in female *C. aureus*).
749   *Chiropterotriton totonacus* differs from *C. nubilus* in its larger adult body size (mean
750 SVL 35.7 mm in male and 35.5 mm in female *C. totonacus* vs. 29.4 mm in one male and 30.5
751 mm in female *C. nubilus*), longer limbs (mean LI -0.6 in male and 0.0 in female *C. totonacus* vs.
752 2.0 in one male and 1.5 in female *C. nubilus*), larger feet (mean FW 4.2 mm in male and 4.0 mm
753 in female *C. totonacus* vs. 2.6 mm in one male and 2.3 mm in female *C. nubilus*), and more
754 maxillary teeth (mean MT 32.9 in male and 52.6 in female *C. totonacus* vs. 13.0 in one male and
755 41.5 in female *C. nubilus*).

756 ***Description of holotype***: SVL 35.8 mm, TL 49.2 mm, AX 18.3 mm, SW 3.7 mm, HL 7.7 mm,
757 HW 5.3 mm, HD 2.4 mm, projection of snout beyond mandible 0.7 mm, distance from anterior
758 rim of orbit to snout 2.2 mm, interorbital distance 2.0 mm, eyelid length 2.2 mm, eyelid width
759 1.2 mm, nostril diameter 0.2 mm, FLL 9.9 mm, HLL 11.5 mm, snout-to-forelimb length 12.4
760 mm, snout to anterior angle of vent 33.5 mm, tail width at base 3.0 mm, tail depth at base 2.7
761 mm, FW 4.6 mm, length of fifth toe 0.8 mm, length of third (longest) toe 1.8 mm. Numbers of
762 teeth: premaxillary 6, maxillary 27-23 (right-left) and vomerine 7-7 (right-left). Tips of
763 adpressed limbs meet.

764 ***Coloration in life***: No color information is available for the type series in life; description based
765 on photos of three recently collected specimens (IBH 31030, 31031, IBH 30998). Dorsal
766 background very dark brownish grey. Broad, reddish-brown dorsal band with background color
767 showing only along midline (IBH 31030), broken and irregular (IBH 30998), or completely
768 absent (IBH 31031). Small, pale grey specks present in some specimens. Dorsal surface of tail
769 similar to dorsal coloration on body. IBH 30998 has two orangish-brown blotches at base of tail.
770 Head dark grey with brown blotches or grey specks, similar to dorsal coloration. Paratoid region
771 brownish in specimens with a regular or irregular dorsal band present, grey in IBH 31031 Flanks
772 and upper surface of limbs medium grey with small pale grey and brown flecks, numerous in
773 some specimens while nearly absent in others; toe tips reddish. Gular region pale grey; ventral
774 surface of body, tail, and limbs medium grey. Iris dark golden-brown.

775 ***Coloration in preservative*:** The holotype is medium brown with an obscure dorsal stripe, darker
776 brown along the margin and more reddish brown on the stipe with a narrow darker median line.
777 The head is medium brown with a light bar extending between the eyes and snout mottled with
778 dark cream and brown. Limbs mottled with light brown upper limbs especially near the body,
779 darker lower limbs with light tan digits. The venter is mainly pale with some mottled darker
780 brown. The gular region is mottled with dark cream and brown. Undersides of the tail are paler
781 than its lateral surfaces. One specimen (MVZ 193943) has a distinct yellowish stripe bordered
782 laterally by a very dark band of pigment, with the stripe extending to the tip of the tail. Most
783 others are uniformly pale brown to tan dorsally with some darker brown. One individual (MVZ
784 1639547) is generally paler gray brown.

785 ***Osteology*:** This account is based on examination of a µCT scan of the anterior skeleton of MVZ
786 163945, an adult female, 35.8 mm SVL (Figs. 6–8; Table 3). The skull is relatively broad and
787 somewhat ovoid in dorsal and ventral views. Many of the dermal investing bones are thin and
788 weakly ossified, especially anteriorly. Paired frontal bones extend anterolaterally, but they are
789 largely eroded anteromedially except for a pair of anteriorly directed spikes along the midline
790 (one per side). Each frontal has a posterolateral tab that overlaps the adjacent parietal, but
791 otherwise these bones only weakly articulate with one another, leaving a moderately sized
792 frontoparietal fontanelle. The single premaxilla is delicate and lacks a palatal shelf. Ascending
793 processes initially approach one another but then diverge posterodorsally until they articulate
794 with the weak anterior end of the frontal bone. They enclose a huge internasal fontanelle, but
795 unlike in many congeners they are not expanded posteriorly. There are no septomaxillary bones.
796 The nasal bone is triangular but irregular in outline. It barely articulates with the facial process of
797 the maxilla and with the frontal but is separate from the prefrontal, which is relatively small—
798 smaller than the nasal. The foramen of the nasolacrimal duct has eroded the anteroventral margin
799 of the prefrontal, the posterior margin of the nasal and the dorsal margin of the facial process of
800 the maxilla. Teeth are deployed along nearly the entire length of the maxillary bone, leaving only
801 a small edentulous portion at its posterior tip. There are 21 maxillary teeth on each side and six
802 premaxillary teeth. The orbitosphenoid is shortened anteroposteriorly and rather thin. It is only
803 weakly articulated to the parasphenoid and is mostly separated from both the frontal and the
804 parietal.
805 Otic capsules lack crests except for a slight projection along the anterolateral margin of
806 each lateral semicircular canal. However, the anteromedial edge of each capsule is overlapped by
807 a bony shelf that extends from the posterolateral portion of the adjacent parietal bone. A
808 relatively large, triangular tab descends from the posterolateral margin of the parietal. The tab is
809 sharply reflected ventromedially and ends in a rounded point at about the midpoint of the vertical
810 extent of the orbitosphenoid. The roughly triangular squamosal articulates with the otic capsule
811 dorsally. The quadrate bone is relatively small and incompletely ossified. The columella bears a
812 pronounced stylus. Paired vomers are relatively large, but the body of each bone is very weakly
813 ossified anteriorly. They do not articulate at the midline. Preorbital processes are very long.
814 There are six teeth on the left side and five on the right; one or two are deployed at the base of
815 each preorbital process. The parasphenoid bone is triangular. Paired parasphenoid tooth patches
816 progressively broaden posteriorly and then round off caudally. There are 80–85 teeth in each
817 patch. The mandible is relatively weak. The articular bone is poorly ossified. The prearticular
818 bone is small, with a relatively low coronoid process. Each dentary bone bears 24 teeth.
819 Digital formulae are 1-2-3-2 right and 1-2-2-2 left. The distal tip of the terminal phalanx
820 is slightly expanded on each finger. Mesopodial cartilages are not mineralized.

821 ***Distribution and ecology*:** *Chiropterotriton totonacus* is known from Veracruz, Mexico, along
822 the ridge between Cruz Blanca and Las Vigas at elevations between 2200 and 2450 masl, and
823 from La Joya at 2000 masl. It occurs in mossy pine forest and is terrestrial. Recently collected
824 specimens were found under logs in disturbed pine forest.

825 ***Remarks:*** This species occurs in sympatry at the upper end of its range above Las Vigas with *P.*
826 *leprosa* and *Thorius munificus*, and at the lower end of its range near La Joya with
827 *Chiropterotriton lavae, Pseudoeurycea lynchi, Thorius minydemas, and Isthmura gigantea*, and
828 throughout is range with *Aquiloeurycea cephalica*. We think this is Darda's (1994) species E (his
829 population 7), which he assigned to *C. chiropterus*. It differs from *C. lavae* by two fixed
830 allozymic differences and a Nei D value of 0.148, but we have no samples of a second species
831 (in addition to *C. lavae*) from La Joya so our assignment of Darda's material must be viewed as
832 tentative. He had no specimens from the area west of Las Vigas or Cruz Blanca. If we assume
833 that Darda's species E is assignable to *C. totonacus*, it is surprising that it is so distinct from *C.*
834 *perotensis* (seven fixed differences, Nei D = 0.725). It is closer to Darda's species C from Puerto
835 del Aire (3 fixed differences) and I from regions to the south of Pico de Orizaba (5 fixed
836 differences), the latter here named *C. ceronorum*. We are not yet prepared to deal with species C
837 at this time.
838   *Chiropterotriton totonacus* has long been known from the Las Vigas-Cruz Blanca area,
839 and from Toxtlacoaya, above La Joya (Taylor and Smith, 1945; Smith and Taylor, 1948). The
840 species was reported to occur under clumps of dead grass, under and in rotten logs, under loose
841 bark, and in stump holes that had filled with pine needles and loose earth.

842 ***Conservation status*:** Most of the pine forest around Las Vigas de Ramírez has been cut down or
843 fragmented into very small patches. Recently, we found three specimens (one in 2016 and two in
844 2017) in a secondary pine forest near the type locality at Cruz Blanca . This secondary forest,
845 which is highly disturbed and has few logs or cover objects where salamanders could be found,
846 is the only place where the species is currently known to occur given that nearly all forest from
847 the type locality has been logged. The largest extent of remaining forest in the area is in the
848 "Bosque Estatal San Juan del Monte", but *C. totonacus* has not been found there despite survey
849 efforts. Based on its scarcity and very limited geographic range, we recommend that this species
850 be designated as Critically Endangered under IUCN Red List criterion B1ab(iii) (extent of
851 occurrence < 100 km^2, distribution severely fragmented with continuing decline in area, extent,
852 and quality of habitat; IUCN, 2012).

853 **Etymology:** The specific epithet refers to the native Totonac culture of the central region of
854 Veracruz where *Chiropterotriton totonacus* is found.
855
856
857 ***Chiropterotriton melipona*, new species**
858 Xicotepec Salamander, Salamandra de Xicotepec
859 Figures 4D, 5D, 6D, 7D, 8D.
860
861 *Chiropterotriton* sp. F.—*Darda, 1994; Parra-Olea, 2003; Rafaëlli, 2007; Rovito & Parra-Olea,*
862   *2015; García-Castillo et al., 2017; García-Castillo et al., 2018.*

863 **Holotype**: MVZ 200726, an adult male from Xicotepec de Juárez, 3.3 km S of Hotel Mi
864 Ranchito on Mexican Hwy. 130, 2.1 km E on road to La Unión, Puebla, México, 1080 masl,
865 20.227755º N, 97.953269º W (EPE = max. error distance 1.0 km). Collected 8 December 1983
866 by D. M. Darda and P. A. Garvey.

867 **Paratypes**: Seven specimens, all from Puebla, Mexico. Four males: MVZ 178706 and 178708,
868 3.9 km S of Xicotepec de Juárez on Mexican Hwy. 130; MVZ 200723–24, Xicotepec de Juárez,
869 Mexican Hwy. 130, 21 km E on road to La Unión. Three females: MVZ 178707, 3.9 km S of
870 Xicotepec de Juarez on Mexican Hwy. 130; MVZ 185972, 2.2 km on road to Patla from junction
871 with Mexican Hwy. 130 SW out of Xicotepec de Juárez; MVZ 200725, Xicotepec de Juárez,
872 Mexican Hwy. 130, 21 km E on road to La Unión.

873 **Referred specimens**: Two specimens: IBH 30112 and MVZ 133019, Cuetzalan, Puebla, Mexico.

874 **Diagnosis**: This is a small species of plethodontid salamander phylogenetically related to
875 *Chiropterotriton chiropterus*; mean SVL 29.2 mm in four adult males (range 26.4–31.4) and
876 28.5 mm in three adult females (range 27.1–29.8). The head is moderately wide; HW averages
877 15% of SVL in both males and females (range 14–15%). Adults have a broad, bluntly rounded
878 snout and adult males have moderately developed nasolabial protuberances. Eyes are large and
879 prominent and extend laterally beyond the jaw margin in ventral view. There are few maxillary
880 teeth in males (mean MT 9.5, range 7–12) and moderate numbers of teeth in females (mean MT
881 31.0, range 25–34). There are few vomerine teeth in both males (mean VT 11.0, range 8–15) and
882 females (mean VT 13.0, range 9–19), which are arranged in a row that does not extend lateral to
883 the outer margin of the internal choana. The tail is long and slender and exceeds SVL in all
884 adults with complete tails; mean TL/SVL 1.16 in males (range 1.10–1.22) and 1.11 in females
885 (range 1.03–1.18). Limbs are short; FLL+HLL averages 46% of SVL in males (range 39–50) and
886 49% in females (range 46–52). Adpressed limbs are widely separated and never overlap in males
887 (mean LI 2.3, range 2–2.5) and females (mean LI 1.8, range 1.0–2.5). Manus and pes are
888 relatively small; digits are slender and their tips only slightly expanded. Digital webbing ranges
889 from slight to absent and is limited to the metatarsal region. The first digit is distinct but largely
890 included in the webbing. Subterminal pads are small but well developed. A relatively small,
891 rounded to oval-shaped mental gland present in most adult males. The smallest adult male
892 (pigmented testes) is 26.4 mm SVL; the smallest male with a mental gland is 28.5 mm SVL.
893 Parotoid glands are not evident.

894 **Comparisons**: *Chiropterotriton melipona* differs from *C. ceronorum* in its smaller adult body
895 size (mean SVL 29.2 mm in male and 28.5 mm in female *C. melipona* vs. 33.9 mm in male and
896 34.9 mm in female *C. ceronorum*), shorter tail (mean TL/SVL 1.16 in male and 1.11 in female *C.*
897 *melipona* vs. 1.0 in male and 0.97 in female *C. ceronorum*), shorter head (mean HL 6.3 mm in
898 male and 6.4 mm in female *C. melipona* vs. 7.5 mm in male and 7.1 mm in female *C.*
899 *ceronorum*), narrower head (mean HW 4.3 mm in male and 4.2 mm in female *C. melipona* vs.
900 5.1 mm in both male and female *C. ceronorum*), shorter limbs in males (mean LI 2.3 in *C.*
901 *melipona* vs. 0.0 in *C. ceronorum*), narrower feet (mean FW 2.4 mm in male and 2.6 mm in
902 female *C. melipona* vs. 3.8 mm in male and 3.5 mm in female *C. ceronorum*), fewer maxillary
903 teeth (mean MT 9.5 in male and 31.0 in female *C. melipona* vs. 11.0 in male and 47.7 in female
904 *C. ceronorum*) and fewer vomerine teeth (mean VT 11.0 in male and 13.0 in female *C. melipona*
905 vs. 13.0 in male and 15.9 in female *C. ceronorum*).

906   *Chiropterotriton melipona* differs from *C. perotensis* in its slightly smaller adult body
907   size (mean SVL 29.2 mm in male and 28.5 mm in female *C. melipona* vs. 29.7 mm in male and
908   31.7 mm in female *C. perotensis*), shorter tail (mean TL/SVL 1.16 in male and 1.11 in female *C.*
909   *melipona* vs. 1.0 in both male and female *C. perotensis*), shorter head (mean HL 6.3 mm in male
910   and 6.4 mm in female *C. melipona* vs. 6.6 mm in male and 6.7 mm in female *C. perotensis*),
911   more maxillary teeth (mean MT 9.5 in male and 31.0 in female *C. melipona* vs. 7.2 in male and
912   27.9 in female *C. perotensis*) and fewer vomerine teeth (mean VT 11.0 in male and 13.0 in
913   female *C. melipona* vs. 9.0 in male and 11.1 in female *C. perotensis*).
914   *Chiropterotriton melipona* differs from *C. totonacus* in its smaller adult body size (mean
915   SVL 29.2 mm in male and 28.5 mm in female *C. melipona* vs. 35.7 mm in male and 35.5 mm in
916   female *C. totonacus*), shorter head (mean HL 6.3 mm in male and 6.4 mm in female *C. melipona*
917   vs. 8.5 mm in male and 7.6 mm in female *C. totonacus*), narrower head (mean HW 4.3 mm in
918   male and 4.2 mm in female *C. melipona* vs. 5.2 mm in both male and female *C. totonacus*),
919   shorter limbs (mean LI 2.3 in male and 1.8 in female *C. melipona* vs. -0.6 in male and 0.0 in
920   female *C. totonacus*), narrower feet (mean FW 2.4 mm in male and 2.6 mm in female *C.*
921   *melipona* vs. 4.2 mm in male and 4.0 mm in female *C. totonacus*) and more maxillary teeth
922   (mean MT 9.5 in male and 31.0 in female *C. melipona* vs. 32.9 in male and 52.6 in female *C.*
923   *totonacus*).
924   *Chiropterotriton melipona* differs from *C. casasi* in its smaller adult body size (mean
925   SVL 29.2 mm in male and 28.5 mm in female *C. melipona* vs. 37.8 mm in male and 40.9 mm in
926   one female *C. casasi*), shorter tail in males (mean TL/SVL 1.16 in *C. melipona* vs. 1.0 in *C.*
927   *casasi*), shorter head (mean HL 6.3 mm in male and 6.4 mm in female *C. melipona* vs. 8.3 mm in
928   male and 8.6 mm in one female *C. casasi*), narrower head (mean HW 4.3 mm in male and 4.2
929   mm in female *C. melipona* vs. 5.8 mm in male and 5.9 mm in one female *C. casasi*), shorter
930   limbs (mean LI 2.3 in male and 1.8 in female *C. melipona* vs. 0.8 in male and 1.0 in one female
931   *C. casasi*) and narrower feet (mean FW 2.4 mm in male and 2.6 mm in female *C. melipona* vs.
932   mean 3.7 mm in both male and one female *C. casasi*).
933   *Chiropterotriton melipona* differs from *C. chiropterus* in its smaller adult body size
934   (mean SVL 29.2 mm in male and 28.5 mm in female *C. melipona* vs. 37.5 mm in male and 33.5
935   mm in female *C. chiropterus*), shorter tail in males (mean TL/SVL 1.16 in *C. melipona* vs. 1.25
936   in *C. chiropterus*), shorter head (mean HL 6.3 mm in male and 6.4 mm in female *C. melipona* vs.
937   8.1 mm in male and 7.3 mm in female *C. chiropterus*), narrower head (mean HW 4.3 mm in
938   male and 4.2 mm in female *C. melipona* vs. 5.6 mm in male and 4.8 mm in female *C.*
939   *chiropterus*), shorter limbs in males (mean LI 2.3 in *C. melipona* vs. 0.3 in *C. chiropterus*),
940   narrower feet (mean FW 2.4 mm in male and 2.6 mm in female *C. melipona* vs. 3.7 mm in male
941   and 3.1 mm in female *C. chiropterus*) and fewer maxillary teeth (mean MT 9.5 in male and 31.0
942   in female *C. melipona* vs. 12.6 in male and 48.0 in female *C. chiropterus*).
943   *Chiropterotriton melipona* differs from *C. orculus* in its smaller adult body size (mean
944   SVL 29.2 mm in male and 28.5 mm in female *C. melipona* vs. 35.9 mm in male and 39.0 mm in
945   female *C. orculus*), shorter tail (mean TL/SVL 1.16 in male and 1.11 in female *C. melipona* vs.
946   1.02 in both male and female *C. orculus*), shorter head (mean HL 6.3 mm in male and 6.4 mm in
947   female *C. melipona* vs. 7.4 mm in male and 8.0 mm in female *C. orculus*), narrower head (mean
948   HW 4.3 mm in male and 4.2 mm in female *C. melipona* vs. 5.0 mm in male and 5.2 mm in
949   female *C. orculus*), shorter limbs in males (mean LI 2.3 in *C. melipona* vs. 1.9 in *C. orculus*),
950   narrower feet (mean FW 2.4 mm in male and 2.6 mm in female *C. melipona* vs. 3.2 mm in male
951   and 3.4 mm in female *C. orculus*), more maxillary teeth (mean MT 9.5 in male and 31.0 in

952 female *C. melipona* vs. 8.2 in male and 28.8 in female *C. orculus*) and more vomerine teeth
953 (mean VT 11.0 in male and 13.0 in female *C. melipona* vs. 8.6 in male and 12.0 in female *C.*
954 *orculus*).
955   *Chiropterotriton melipona* differs from *C. lavae* in its smaller adult body size (mean SVL
956 29.2 mm in male and 28.5 mm in female *C. melipona* vs. 32.4 mm in male and 31.6 mm in
957 female *C. lavae*), shorter head (mean HL 6.3 mm in male and 6.4 mm in female *C. melipona* vs.
958 7.5 mm in male and 7.0 mm in female *C. lavae*), narrower head (mean HW 4.3 mm in male and
959 4.2 mm in female *C. melipona* vs. 4.9 mm in male and 4.7 mm in female *C. lavae*), shorter limbs
960 (mean LI 2.3 in male and 1.8 in female *C. melipona* vs. -0.6 in male and 0.6 in female *C. lavae*),
961 narrower feet (mean FW 2.4 mm in male and 2.6 mm in female *C. melipona* vs. 3.7 mm in male
962 and 3.3 mm in female *C. lavae*), more maxillary teeth (mean MT 9.5 in male and 31.0 in female
963 *C. melipona* vs. 7.0 in male and 20.8 in female *C. lavae*) and more vomerine teeth (mean VT
964 11.0 in male and 13.0 in female *C. melipona* vs. 8.9 in male and 11.4 in female *C. lavae*).
965   *Chiropterotriton melipona* differs from *C. aureus* in its larger adult body size (mean SVL
966 29.2 mm in male and 28.5 mm in female *C. melipona* vs. 28.5 mm in one male and 26.8 mm in
967 female *C. aureus*), shorter tail in females(mean TL/SVL 1.11 in female *C. melipona* vs. 1.16 in
968 female *C. aureus*), wider head (mean HW 4.3 mm in male and 4.2 mm in female *C. melipona* vs.
969 4.0 mm in one male and 3.6 mm in female *C. aureus*), longer limbs in females (mean LI 1.8 in
970 female *C. melipona* vs. 2.3 in female *C. aureus*), and wider feet in females (mean FW 2.6 mm in
971 female *C. melipona* vs. 1.8 mm in female *C. aureus*).
972   *Chiropterotriton melipona* differs from *C. nubilus* in having a shorter head (mean HL 6.3
973 mm in male and 6.4 mm in female *C. melipona* vs. 6.6 mm in one male and 7.4 mm in female *C.*
974 *nubilus*), and less maxillary teeth (mean MT 9.5 in male and 31.0 in female *C. melipona* vs. 13 in
975 one male and 41.5 in female *C. nubilus*).

976 **Description of holotype**: SVL 28.5 mm, TL 31.4 mm, AX 15.5 mm, SW 3.3 mm, HL 6.3 mm,
977 HW 4.1 mm, HD 2.1 mm, projection of snout beyond mandible 0.7 mm, distance from anterior
978 rim of orbit to snout 1.5 mm, interorbital distance 1.4 mm, distance between corners of eyes 2.2
979 mm, interorbital width 1.3 mm, eyelid length 1.7 mm, eyelid width 0.9 mm, nostril diameter 0.2
980 mm, FLL 5.1 mm, HLL 6.1 mm, snout-to-forelimb length 8.4 mm, distance from snout to
981 anterior angle of vent 24.4 mm, snout to gular fold distance 6.3 mm, tail depth at base 2.7 mm
982 and FW 2.2 mm. Numbers of teeth: premaxillary 3, maxillary 4-4 (right-left) and vomerine 7-8
983 (right-left). Adpressed limbs are separated by 2.5 costal folds.

984 **Coloration in life**: Color notes in life are not available for the type series of this species, thus we
985 describe coloration from a photo of one of the referred specimens (IBH 30112). The head is dark
986 brown with numerous pale grey specks on the rostrum, sides of head, interocular region, and
987 eyelids. This brown coloration with grey specks extends from behind each eye in an inverted
988 triangle to the nuchal region. Both sides of this triangle in parotoid region are orangish-brown.
989 Orange-brown coloration extends in a band along dorsum and along the dorsal side of tail, where
990 it is more yellowish along midline and orangish-brown along edges. Flanks are dark brown with
991 numerous pale gray specks. Limbs Grey-brown with some pale yellow-brown specks; manus and
992 pes greyish. Sides of tail dark brown. Iris coppery.

993 **Coloration in preservative**: The holotype, while faded, is generally bright yellow to yellowish
994 tan. The snout is pale yellow with scattered brown pigment. A broad, bright yellow dorsal stripe
995 extends from the eyes to the tip of the tail. It is bordered by a dark stripe that arises at the eye and

996 extends posteriorly onto the tail. This dark stripe, in turn, is bordered by a pale brown stripe that
997 becomes paler ventrolaterally. The venter is very pale, almost pigmentless. The tail has some
998 light brown pigment along its lateral margins. Paratypes all faded but yellowish tan with a pale
999 yellowish tan dorsal stripe evident in all individuals to some degree.Dorsal stripe always
1000 bordered by a thin dorsal lateral light brown stripe. Venter very pale. Manus and pes are pale.

1001 ***Osteology*:** This account is based on examination of a µCT scan of the anterior skeleton of MVZ
1002 178706, an adult male, 28.5 mm SVL, which may be sexually immature and not representative
1003 of the adult condition (Figs. 6–8; Table 3). The skull is weakly developed and delicate, both in
1004 general and relative to other members of the genus such as *C. chiropterus*, and even *C. casasi*.
1005 Cranial roofing bones are very thin. Frontals are weakly articulated with each other and with the
1006 paired parietals, leaving a relatively large frontoparietal fontanelle that extends both
1007 anteroposteriorly (in the midline) and transversely (at the frontal-parietal interface). Paired
1008 ascending processes of the single premaxilla begin diverging immediately dorsal to the dental
1009 process. They continue to diverge posterolaterally and ultimately articulate in grooves on the
1010 anterior part of the paired frontals, enclosing a large internasal fontanelle. Unlike in many other
1011 congeners, they remain thin and are not expanded at their dorsal ends. A palatal shelf is barely
1012 evident on the premaxillary; it's virtually absent. Tiny paired septomaxillae lie approximately at
1013 the level of the articulation between premaxilla and maxilla. Nasal bones are expansive but
1014 otherwise weakly developed, with indistinct borders anteriorly and weak articulations with
1015 adjacent bones, including both the prefrontal and the maxilla. The prefrontal is well articulated
1016 with the facial process of the maxilla ventrally and overlaps the frontal dorsally. A foramen for
1017 the passage of the nasolacrimal duct is framed by the anterior margin of the prefrontal, the
1018 posterolateral margin of the nasal, and the dorsal midportion of the facial process of the maxilla.
1019 There are five large teeth on the anterior portion of each maxilla. The posterior half of the bone
1020 lacks teeth and resembles a shallow cleaver. There are three premaxillary teeth. The
1021 orbitosphenoid is fairly well developed, although not well articulated with the parietal. In
1022 general, the braincase is moderately well developed.
1023   There is a nascent bony crest on the otic capsule above the anterior semicircular canal
1024 where it abuts a bony shelf that extends posterolaterally from the parietal. The parietal also bears
1025 a moderately developed, posterolateral tab that is sharply directed ventomedially. The tab is
1026 triangular and ends in a rounded point at a level about halfway through the vertical extent of the
1027 orbitosphenoid. The squamosal is a roughly triangular bone that articulates dorsally with the otic
1028 capsule opposite the lateral semicircular canal. In lateral view, its ventral portion appears to
1029 buttress the otic capsule ventral to the lateral semicircular canal, but when viewed from different
1030 angles these bones can be seen to be well separated. The quadrate bone is relatively small and
1031 inconspicuous. The columellar stylus is distinct, cylindrical and long. Paired vomers are
1032 relatively robust; they barely articulate in the midline posterior to the internasal fontanelle.
1033 Preorbital processes are very long. There are four-to-six vomerine teeth on each side; two or
1034 three of these are deployed at the base of each preorbital process. The parasphenoid bone is
1035 broadly triangular. Paired parasphenoid tooth patches are well separated from each other and
1036 from the vomerine teeth anteriorly. Each patch bears approximately 75 teeth. The mandible is
1037 unremarkable. The articular bone is poorly ossified. The prearticular bone has a coronoid process
1038 of moderate height. There are seven teeth on the right dentary bone and eight on the left.
1039   Digital formula is 1-2-3-2 on each side. There is a slightly expanded knob at the tip of the
1040 terminal phalanx on the two longest fingers of each hand (digits 3 and 4). Mesopodial cartilages
1041 are not mineralized.

1042   *Distribution and ecology*: *Chiropterotriton melipona* is known from the Sierra Norte in the
1043   northernmost part of Puebla near Cuetzalan, Xocoyolo and Xicotepec de Juarez at elevations
1044   between 690 and 1420 masl. It likely occurs between known localities near Cuetzalan and
1045   Xicotepec. This range includes the lowest elevational record of any known species of the genus.
1046   The species is arboreal and has been collected from banana plants and bromeliads and has been
1047   found in sympatry with *Aquiloeurycea quetzalanensis.*

1048   *Remarks:* This species was included in Darda's (1994) electrophoretic study as population 19,
1049   new species F. It was most similar to populations 12 (*C. lavae*; three fixed differences, Nei D =
1050   0.22) and 19 (new species F, sympatric with *C. lavae*; three fixed differences, Nei D = 0.23).

1051   *Conservation status*: Most mature forest at known localities for this species has been cut down,
1052   and the species has recently been found in small patches of forest and secondary vegetation, as
1053   well as cafetales. Because of the highly fragmented nature and decreasing quality of forest
1054   habitat within its range, we recommend that the species be designated as Endangered based on
1055   IUCN criterion B1ab(iii) (extent of occurrence < 5000 km^2, distribution severely fragmented
1056   continuing decline in extent, and quality of habitat; IUCN, 2012).

1057   **Etymology.** Xicotepec, the name of the type locality, comes from the Nahuatl language and
1058   means "place of the jicotes." Jicotes are stingless bees of the genus *Melipona*. The name used for
1059   this species is a noun in apposition referring to the genus *Melipona*.

1060
1061   *Chiropterotriton casasi*, **new species**
1062   Tlapacoyan Salamander, Salamandra de Tlapacoyan
1063   Figures 2, 4E, 5E, 6A, 7A, 8A.
1064

1065   *Holotype*: MVZ 92874, an adult male from 13 mi SW Tlapacoyan, Veracruz, Mexico,
1066   19.868483º N, 97.301500º W (EPE = max. error distance 2 km). Collected 26 December 1969 by
1067   R. Altig.

1068   *Paratypes*: Four males, MVZ 92875 and 92877–79, and one female, MVZ 92876, all from the
1069   type locality.

1070   *Diagnosis*: This is a relatively large species of *Chiropterotriton* that stands out from other
1071   species considered here in being relatively stout and long legged, and being morphologically
1072   distinct; mean SVL 37.8 mm in four adult males (range 34.5–42.0). Only one female has been
1073   collected, SVL 40.9 mm. The head is moderately wide; HW averages 16% of SVL in males
1074   (range 13–17%) and 14% in the female. In males, the snout is broad and truncated. Jaw muscles
1075   are pronounced and visible as a bulging mass immediately caudal to the eyes. Eyes are
1076   moderately protuberant and extend laterally beyond the jaw margin in ventral view. There are
1077   few maxillary teeth in males (mean MT 9.0, range 6–13) but they are more numerous in the
1078   female (MT 30). There are few vomerine teeth in males (mean VT 9.0, range 8–11) and the
1079   female (VT 13), which are arranged in a row that extends to, or just lateral to, the inner margin of
1080   the internal choana. The tail is moderately long; mean TL equals 1.0 of SVL in males (range
1081   0.90–1.15). Limbs are short and slender; FLL+HLL averages 57% of SVL in males (range 55–

1082   60) and 55% in the female. Adpressed limbs approach closely in males (mean LI 0.8, range 0.0–
1083   1) and are separated by one costal fold in the female. Digits are long and slender with blunt tips,
1084   distinct subterminal pads, and moderate webbing that extends onto the penultimate phalanx of
1085   the third toe. Digits II–V are discrete, while digit I is very short and does not extend beyond the
1086   webbing. The outermost toes are particularly well developed. The mental gland is oval-shaped in
1087   adult males. The smallest male with a mental gland is 37.2 mm SVL. Parotoid glands are not
1088   evident.

1089   **Comparisons**: *Chiropterotriton casasi* differs from *C. ceronorum* in its larger adult body size
1090   (mean SVL 37.8 mm in male and 40.9 mm in one female *C. casasi* vs. 33.9 mm in male and 34.9
1091   mm in female *C. ceronorum*), longer head (mean HL 8.3 mm in male and 8.6 mm in one female
1092   *C. casasi* vs. 7.5 mm in male and 7.1 mm in female *C. ceronorum*), broader head (mean HW 5.8
1093   mm in male and 5.9 mm in one female *C. casasi* vs. 5.1 mm in both male and female *C.*
1094   *ceronorum*) and shorter limbs in males (mean LI 0.8 in *C. casasi* vs. 0.0 in *C. ceronorum*).
1095   *Chiropterotriton casasi* differs from *C. perotensis* in its larger adult body size (mean SVL
1096   37.8 mm in male and 40.9 mm in one female *C. casasi* vs. 29.7 mm in male and 31.7 mm in
1097   female *C. perotensis*), longer head (mean HL 8.3 mm in male and 8.6 mm in one female *C.*
1098   *casasi* vs. 6.6 mm in male and 6.7 mm in female *C. perotensis*), broader head (mean HW 5.8 mm
1099   in male and 5.9 mm in one female *C. casasi* vs. 4.2 mm in male and 4.4 mm in female *C.*
1100   *perotensis*), longer limbs (mean LI 0.8 in male and 1.0 in one female *C. casasi* vs. 2.5 in male
1101   and 3.3 in female *C. perotensis*), larger feet (mean FW 3.7 mm in both male and one female *C.*
1102   *casasi* vs. 2.6 mm in both male and female *C. perotensis*).
1103   *Chiropterotriton casasi* differs from *C. totonacus* in its larger adult body size (mean SVL
1104   37.8 mm in male and 40.9 mm in one female *C. casasi* vs. 35.7 mm in male and 35.5 mm in
1105   female *C. totonacus*), shorter tail (mean TL/SVL 1.0 in male *C. casasi* vs. 1.16 in male *C.*
1106   *totonacus;* the only female specimen of *C. casasi* has a broken tail), longer head in females
1107   (mean HL 8.6 mm in one *C. casasi* vs. 7.6 mm in *C. totonacus*), broader head in females (mean
1108   HW 5.9 mm in one *C. casasi* vs. 5.2 mm in *C. totonacus*), shorter limbs (mean LI 0.8 in male
1109   and 1.0 in one female *C. casasi* vs. -0.6 in male and 0.0 in female *C. totonacus*), narrower feet
1110   (mean FW 3.7 mm in both male and one female *C. casasi* vs. 4.2 mm in male and 4.0 mm in
1111   female *C. totonacus*) and fewer maxillary teeth (mean MT 9.0 in male and 30 in one female *C.*
1112   *casasi* vs. 32.9 in male and 52.6 in female *C. totonacus*).
1113   *Chiropterotriton casasi* differs from *C. melipona* in its larger adult body size (mean SVL
1114   37.8 mm in male and 40.9 mm in one female *C. casasi* vs. 29.2 mm in male and 28.5 mm in
1115   female *C. melipona*), shorter tail (mean TL/SVL 1.04 in male *C. casasi* vs. 1.16 in male *C.*
1116   *melipona;* the only female specimen of *C. casasi* has a broken tail), longer head (mean HL 8.3
1117   mm in male and 8.6 mm in one female *C. casasi* vs. 6.3 mm in male and 6.4 mm in female *C.*
1118   *melipona*), broader head (mean HW 5.8 mm in male and 5.9 mm in one female *C. casasi* vs. 4.3
1119   mm in male and 4.2 mm in female *C. melipona*), longer limbs (mean LI 0.8 in male and 1.0 in
1120   one female *C. casasi* vs. 2.3 in male and 1.8 in female *C. melipona*) and broader feet (mean FW
1121   3.7 mm in both male and one female *C. casasi* vs. 2.4 mm in male and 2.6 mm in female *C.*
1122   *melipona*).
1123   *Chiropterotriton casasi* differs from *C. chiropterus* in its larger adult body size in females
1124   (mean SVL 40.9 mm in one *C. casasi* vs. 33.5 mm in *C. chiropterus*), shorter tail (mean TL/SVL
1125   1.04 in male *C. casasi* vs. 1.25 in male *C. chiropterus;* the only female specimen of *C. casasi* has
1126   a broken tail), longer head (mean HL 8.3 mm in male and 8.6 mm in one female *C. casasi* vs. 8.1
1127   mm in male and 7.3 mm in female *C. chiropterus*), narrower head (mean HW 5.8 mm in male

1128 and 5.9 mm in one female *C. casasi* vs. 5.6 mm in male and 4.8 mm in female *C. chiropterus*),
1129 shorter limbs in males (mean LI 0.8 in *C. casasi* vs. 0.3 in *C. chiropterus*) and fewer maxillary
1130 teeth (mean MT 9.0 in male and 30 in one female *C. casasi* vs. 12.6 in male and 48.0 in female
1131 *C. chiropterus*).
1132   *Chiropterotriton casasi* differs from *C. orculus* in its larger adult body size (mean SVL
1133 37.8 mm in male and 40.9 mm in one female *C. casasi* vs. 35.9 mm in male and 39.0 mm in
1134 female *C. orculus*), longer head (mean HL 8.3 mm in male and 8.6 mm in one female *C. casasi*
1135 vs. 7.4 mm in male and 8.0 mm in female *C. orculus*), broader head (mean HW 5.8 mm in male
1136 and 5.9 mm in one female *C. casasi* vs. 5.0 mm in male and 5.2 mm in female *C. orculus*) and
1137 longer limbs (mean LI 0.8 in male and 1.0 in one female *C. casasi* vs. 1.9 in male and 2.9 in
1138 female *C. orculus*).
1139   *Chiropterotriton casasi* differs from *C. lavae* in its larger adult body size (mean SVL
1140 37.8 mm in male and 40.9 mm in one female *C. casasi* vs. 32.4 in male and 31.6 in female *C.*
1141 *lavae*), shorter tail in males (mean TL/SVL 1.04 in *C. casasi* vs. 1.19 in *C. lavae*), longer head
1142 (mean HL 8.3 mm in male and 8.6 mm in one female *C. casasi* vs. 7.5 mm in male and 7.0 mm
1143 in female *C. lavae*), broader head (mean HW 5.8 mm in male and 5.9 mm in one female *C.*
1144 *casasi* vs. 4.9 mm in male and 4.7 mm in female *C. lavae*), shorter limbs (mean LI 0.8 in male
1145 and 2.0 in one female *C. casasi* vs. -0.6 in male and 0.6 in female *C. lavae*) and more maxillary
1146 teeth in females (mean MT 30 in one *C. casasi* vs. 20.8 in *C. lavae*).
1147   *Chiropterotriton casasi* differs from *C. aureus* in its larger adult body size (mean SVL
1148 37.8 mm in male and 40.9 mm in one female *C. casasi* vs. 28.5 mm in one male and 26.8 mm in
1149 female *C. aureus*), shorter tail (mean TL/SVL 1.0 in male *C. casasi* vs. 1.28 in one male *C.*
1150 *aureus;* the only female specimen of *C. casasi* has a broken tail), longer head (mean HL 8.3 mm
1151 in male and 8.6 in one female *C. casasi* vs. 6.4 mm in one male and 6.0 in female *C. aureus*),
1152 broader head (mean HW 5.8 mm in male and 5.9 in one female *C. casasi* vs. 4.0 mm in one male
1153 and 3.6 in female *C. aureus*), longer limbs (mean LI 0.8 in male and 1.0 in one female *C. casasi*
1154 vs. 2.0 in one male and 2.3 in female *C. aureus*), and wider feet (mean FW 3.7 mm in both male
1155 and one female *C. casasi* vs. 2.4 mm in one male and 1.8 mm in female *C. aureus*).
1156   *Chiropterotriton casasi* differs from *C. nubilus* in its larger adult body size (mean SVL
1157 37.8 mm in male and 40.9 mm in one female *C. casasi* vs. 29.4 mm in one male and 30.5 mm in
1158 female *C. nubilus*), shorter tail (mean TL/SVL 1.0 in male *C. casasi* vs. 1.37 in one male *C.*
1159 *nubilus;* the only female specimen of *C. casasi* has a broken tail), longer head (mean HL 8.3 mm
1160 in male and 8.6 mm in one female *C. casasi* vs. 6.6 mm in one male and 7.4 in female *C. nubilus*),
1161 broader head (mean HW 5.8 mm in male and 5.9 mm in one female *C. casasi* vs. 4.0 mm in one male
1162 and 4.4 in female *C. nubilus*), longer limbs (mean LI 0.8 in male and 1.0 in one female *C. casasi*
1163 vs. 2.0 in one male and 1.5 in female *C. nubilus*), wider feet (mean FW 3.7 mm in both male and
1164 one female *C. casasi* vs. 2.6 mm in one male and 2.3 mm in female *C. nubilus*) and less
1165 maximally teeth in females (mean MT 30.0 in female *C. casasi* vs 41.5 in female *C. nubilus*).

1166 ***Description of holotype:*** SVL 42.0 mm, TL 37.6 mm, AX 20.4 mm, SW 3.8 mm, HL 8.8 mm,
1167 HW 5.6 mm, HD 2.8 mm, projection of snout beyond mandible 0.2 mm, distance from anterior
1168 rim of orbit to snout 1.7 mm, interorbital distance 2.4 mm, eyelid length 2.1 mm, eyelid width
1169 1.1 mm, horizontal orbit diameter 2.1 mm, nostril diameter 0.4 mm, FLL 10.7 mm, HLL 12.6
1170 mm, snout-to-forelimb length 11.4 mm, distance from snout to anterior angle of vent 36.6 mm,
1171 tail width at base 3.3 mm, tail depth at base 3.9 mm, FW 4.0 mm, length of fifth toe 0.8 mm,
1172 length of longest (third) toe 1.2 mm, mental gland length 1.3 mm, mental gland width 1.3.

1173   Numbers of teeth: premaxillary 4, maxillary 4-4 (right-left) and vomerine 4-4 (right-left).
1174   Adpressed limbs are separated by 0 costal folds.

1175   ***Coloration in life***: No data.

1176   ***Coloration in preservative***: Faded brown, dorsally and laterally. No sign of dorsal stripe. Limbs
1177   mottled. Head is uniform pale brown with some mottling on the snout. The paratypes present
1178   some variation. The entire body of MVZ 92876 is mottled with faded pale and dark brown. A
1179   pale band extends between the anterior part of the eyes; the snout is very mottled. Posteriorly, the
1180   body is strongly mottled; the anterior part of the tail has an irregularly bordered light dorsal
1181   stripe. MVZ 92875 is less boldly mottled but has some mottling. All of them have a paler venter
1182   than dorsum. MVZ 92877 also has a pale bar that extends between the eyes.

1183   ***Osteology***: This account is based on examination of a μCT scan of the anterior skeleton of MVZ
1184   92874, an adult male, 42.0 mm SVL (Figs. 6–8; Table 3). The skull is robust and well developed.
1185   Notable features include the complete articulation of the paired frontals and parietals—there is
1186   no frontoparietal fontanelle—and a robust premaxillary bone with paired ascending processes
1187   that broaden laterally as each approaches a solid articulation with the frontal bone on the same
1188   side. A distinct, albeit narrow palatal shelf is present on the premaxilla, and the two ascending
1189   processes enclose a distinct fontanelle. Tiny paired septomaxillae bones are well separated from
1190   all other bones. The triangular nasal is weakly developed anteriorly, where the bone is very thin
1191   and has an irregular edge. It is partially overlapped laterally by the facial process of the maxilla.
1192   A large prefrontal articulates anteriorly with the nasal bone, its ventral portion is overlapped by
1193   the facial process of the maxilla, and it bears an ascending, pointed tab that overlaps the frontal
1194   extensively. The anteroventral margin of the prefrontal and the adjacent portion of the facial
1195   process of the maxilla are eroded by a foramen that allows passage of the nasolacrimal duct.
1196   Otherwise, the facial process of the maxillary bone is broad and robust and solidly articulated
1197   with adjacent bones. The maxillary bone resembles that in *Aneides* (Wake, 1963); the toothed
1198   portion is confined to the anterior 45–50% of the bone, whereas posteriorly the bone is cleaver-
1199   shaped with an extended posterior tip. There is a distinct, relatively broad palatal shelf on the
1200   lingual side. There are few maxillary teeth—five on each side—but they are large, sharp and
1201   recurved, with highly reduced anterior cusps. There are three premaxillary teeth. They appear
1202   unicuspid and sharp but are shorter than the maxillary teeth. The well-developed orbitosphenoid
1203   is solidly articulated with neighboring bones, forming a relatively stout braincase.
1204   A prominent bony crest overlies the anterior semicircular canal dorsally. It is derived
1205   from the posterolateral portion of the parietal and the anteromedial portion of the otic capsule.
1206   An additional, crest-like spur emerges at right angles from this crest and is directed
1207   posterolaterally. A second, smaller crest similarly overlies the posterior semicircular canal. The
1208   parietal bears a very large and well-developed posterolateral tab that is sharply reflected
1209   ventromedially, extending nearly two-thirds down the vertical extent of the orbitosphenoid. The
1210   very robust squamosal articulates dorsally with the otic capsule opposite the lateral semicircular
1211   canal. As in other species, the shape of its curved anterior margin conforms closely with, but is
1212   nevertheless separate from, the lateral face of the otic capsule. The quadrate is small and
1213   inconspicuous, but appears to be well developed. There is a short, stout stylus on the columella,
1214   which otherwise is just a rounded ossicle. Bodies of the paired vomers articulate tightly at the
1215   midline posterior to the internasal fontanelle. Preorbital processes are long. There are four
1216   vomerine teeth on the right side and five on the left; one or two teeth are deployed at the base of

1217   each preorbital process. The unpaired parasphenoid bone is robust. It is narrow anteriorly but
1218   gradually widens posteriorly until very near the caudal end where it reaches its maximum width.
1219   Paired parasphenoid tooth patches are well separated from one another medially and from the
1220   vomerine teeth rostrally. There are approximately 95–100 teeth in each patch. The mandible is
1221   robust. The articular is fully ossified and appears to be fused to the prearticular bone. The height
1222   of the large coronoid process on the prearticular exceeds that of the dentary bone ventral to it.
1223   There are six sharply recurved and somewhat enlarged teeth on each dentary bone.
1224   Only the distal portion of each forelimb is visible in the CT scan. Digital formulae are 1-
1225   2-3-2 on each side. Mesopodial cartilages are not mineralized.

1226   ***Distribution and ecology***: *Chiropterotriton casasi* is known only from the type locality.
1227   Vegetation at this locality now consists of secondary forest and thicket, but was likely cloud
1228   forest in the past. The species could occur somewhat more widely, but little intact forest remains
1229   in the vicinity of the type locality.

1230   ***Remarks***: The phylogenetic position of *Chiropterotriton casasi* relative to congeners is unknown
1231   due to the lack of tissue samples for genetic analyses. Geographically associated species include
1232   *C. chiropterus, C. melipona, C. perotensis, C. totonacus, C. ceronorum* and *C. lavae*. We have
1233   searched repeatedly in the vicinity of the type locality and have found another, unnamed, species
1234   of *Chiropterotriton,* but not this species.

1235   ***Conservation status***: *Chiropterotriton casasi* has not been seen since the original collection in
1236   1969, and nearly all of the primary forest at the type locality has been cut down. Efforts to find
1237   this species at the type locality in recent years have not been successful. We recommend that it
1238   be designated as Critically Endangered based on criterion B1ab(iii) (extent of occurrence < 100
1239   km^2, distribution severely fragmented and known from only one locality, continuing decline in
1240   extent and quality of habitat; IUCN, 2012). Concerted efforts should be made to extant
1241   populations of this species in remaining habitat patches near the type locality.

1242   ***Etymology***: The species name honors Gustavo Casas Andreu, a Mexican herpetologist who has
1243   dedicated his career to describe the biodiversity of Mexican amphibians and reptiles.

1244   **REDESCRIPTIONS**
1245   Original descriptions of *Chiropterotriton chiropterus* (Cope, 1863) and *C. orculus* (Cope, 1865)
1246   were extremely brief and contained relatively little information about the species' morphology.
1247   We provide more detailed redescriptions of both of these species, including the designation of a
1248   neotype for each. Common names declared for these species are from Liner and Casas-Andreu
1249   (2008).
1250

1251   ***Chiropterotriton chiropterus*** *Cope, 1863*
1252   Common Flat-footed Salamander, Salamandra de Pie Plana Común
1253   Figures 4G, 5G, 6E, 7E, 8E.
1254   *Chiropterotriton* sp. J.—*Darda, 1994 (population 23, 24)*
1255   *Chiropterotriton* sp.—*Wake, 1987; Papenfuss and Wake, 1987; Lynch and Wake, 1989;*
1256   *Wake et al., 1992*

1257   *Neotype*: MVZ 85590, an adult male from 1.4 mi southwest by road southwest edge of Huatusco
1258   de Chicuellar, Veracruz, Mexico, 19.141388ºN, 96.98083ºW (EPE = max. error distance 1.202
1259   mi). Collected 16 January 1969 by R. W. McDiarmid and R. D. Worthington.

1260   *Additional specimens examined*: Twelve specimens, all from 1.4 mi southwest by road
1261   southwest edge of Huatusco de Chicuellar, Veracruz, Mexico. Eight males: MVZ 85588–89,
1262   85591–92, 85594, 85599, 85613, and 85602; and four females: MVZ 85597–98, 85605 and
1263   85632.

1264   *Diagnosis*: This is a medium-sized species of plethodontid salamander phylogenetically related
1265   to *C. melipona*; mean SVL 37.5 mm in eight adult males (range 36.1–38.8) and 33.5 mm in four
1266   adult females (range 30.7–36.7). The head is of moderately wide; HW averages 15% of SVL in
1267   both males and females (range 14–16). The snout is broad and bluntly rounded in males. Jaw
1268   muscles are relatively pronounced. Eyes are moderately protuberant and extend laterally beyond
1269   the jaw margin in ventral view. There are few maxillary teeth in males (mean MT 12.6, range 9–
1270   17) but many in females (mean MT 48.0, range 42–57). There are few vomerine teeth in both
1271   males (mean VT 10.6, range 9–12) and females (mean VT 12.5, 10–15), which are arranged in a
1272   row that does not reach or barely reaches the inner margin of the internal choana. The tail is long
1273   and slender and exceeds SVL by a considerable amount in nearly all specimens; mean TL equals
1274   1.25 of SVL in males (range 1.13–1.38) and 1.19 in females (1.01–1.26). Limbs are short to
1275   moderate length; FLL+HLL averages 52% of SVL in males (range 48–54%) and 50% in females
1276   (range 47–53%). Adpressed limbs closely approach or overlap slightly in males (mean LI 0.3,
1277   range -0.5–1) but are more widely separated in females (mean LI 2.0, range 1.5–2.5). Manus and
1278   pes are relatively small, digits are slender. Subterminal pads are small but well developed.
1279   Digital webbing ranges from slight to absent and is limited to the metatarsal region. The first
1280   digit is distinct but largely included in the webbing. Digital tips are only slightly expanded. The
1281   mental gland is oval-shaped and not especially prominent in males. The smallest mature male
1282   (pigmented testes) is 36.1 mm SVL; the smallest male with a mental gland is 33.3 mm SVL.
1283   Parotoid glands are not evident.

1284   *Comparisons*: *Chiropterotriton chiropterus* differs from *C. ceronorum* in its larger adult body
1285   size in males (mean SVL 37.5 mm in *C. chiropterus* vs. 33.9 mm in *C. ceronorum*), longer tail
1286   (mean TL/SVL 1.25 in male and 1.19 in female *C. chiropterus* vs. 1.0 in male and 0.97 in female
1287   *C. ceronorum*), shorter limbs (mean LI 0.3 in male and 2.0 in female *C. chiropterus* vs. 0.0 in
1288   male and 1.5 in female *C. ceronorum*), longer head (mean HL 8.1 mm in male and 7.3 mm in
1289   female *C. chiropterus* vs. 7.5 mm in male and 7.1 mm in female *C. ceronorum*), broader head in
1290   males (mean HW 5.6 mm in *C. chiropterus* vs. 5.1 mm in *C. ceronorum*) and fewer vomerine
1291   teeth (mean VT 10.6 in male and 12.5 in female *C. chiropterus* vs. 13.0 in male and 15.9 in
1292   female *C. ceronorum*).
            Chiropterotriton chiropterus differs from *C. perotensis* in its larger adult body size (mean
1293   SVL 37.5 mm in male and 33.5 mm in female *C. chiropterus* vs. 29.7 mm in male and 31.7 mm
1294   in female *C. perotensis*), longer tail (mean TL/SVL 1.25 in male and 1.19 in female *C.
1295   chiropterus* vs. 1.0 in both male and female *C. perotensis*), longer limbs (mean LI 0.3 in male
1296   and 2.0 in female *C. chiropterus* vs. 2.5 in male and 3.3 in female *C. perotensis*), longer head
1297   (mean HL 8.1 mm in male and 7.3 mm in female *C. chiropterus* vs. 6.6 mm in male and 6.7 mm
1298   in female *C. perotensis*), broader head (mean HW 5.6 mm in male and 4.8 mm in female *C.
1299   chiropterus* vs. 4.2 mm in male and 4.4 mm in female *C. perotensis*), broader feet (mean FW 3.7
1300

1301 mm in male and 3.1 mm in female *C. chiropterus* vs. 2.6 mm in both male and female *C.*
1302 *perotensis*), fewer maxillary teeth (mean MT 12.6 in male and 48.0 in female *C. chiropterus* vs.
1303 7.2 in male and 27.9 in female *C. perotensis*) and more vomerine teeth (mean VT 10.6 in male
1304 and 12.5 in female *C. chiropterus* vs. 9.0 in male and 11.1 in female *C. perotensis*).
1305   *Chiropterotriton chiropterus* differs from *C. totonacus* in its larger adult body size in
1306 males (mean SVL 37.5 mm in *C. chiropterus* vs. 35.7 mm in *C. totonacus*), longer tail (mean
1307 TL/SVL 1.25 in male and 1.19 in female *C. chiropterus* vs. 1.16 in male and 1.20 in female *C.*
1308 *totonacus)*, shorter limbs (mean LI 0.3 in male and 2.0 in female *C. chiropterus* vs. -0.60 in male
1309 and 0.0 in female *C. totonacus*), shorter head (mean HL 8.1 mm in male and 7.3 mm in female
1310 *C. chiropterus* vs. 8.5 mm in male and 7.6 mm in female C. *totonacus*), narrower feet in males
1311 (mean FW 3.7 mm in *C. chiropterus* vs. 4.2 mm in *C. totonacus*), fewer maxillary teeth (mean
1312 MT 12.6 in male and 48.0 in female *C. chiropterus* vs. 32.9 in male and 52.6 in female *C.*
1313 *totonacus*) and fewer vomerine teeth (mean VT 10.6 in male and 12.5 in female *C. chiropterus*
1314 vs. 11.6 in male and 13.7 in female *C. totonacus*).
1315   *Chiropterotriton chiropterus* differs from *C. melipona* in its larger adult body size (mean
1316 SVL 37.5 mm in male and 33.5 mm in female *C. chiropterus* vs. 29.2 mm in male and 28.5 mm
1317 in female *C. melipona*), longer tail (mean TL/SVL 1.25 in male and 1.19 in female *C.*
1318 *chiropterus* vs. 1.16 in male and 1.11 in female *C. melipona*), longer head (mean HL 8.1 mm in
1319 male and 7.3 mm in female *C. chiropterus* vs. 6.3 mm in male and 6.4 mm in female *C.*
1320 *melipona*), wider head (mean HW 5.6 mm in male and 4.8 mm in female *C. chiropterus* vs. 4.3
1321 mm in male and 4.2 mm in female *C. melipona*), longer limbs in males (mean LI 0.3 in *C.*
1322 *chiropterus* vs. 2.3 in *C. melipona*), wider feet (mean FW 3.7 mm in male and 3.1 mm in female
1323 *C. chiropterus* vs. 2.4 mm in male and 2.6 mm in female *C. melipona*) and more maxillary teeth
1324 (mean MT 12.6 in male and 48.0 in female *C. chiropterus* vs. 9.5 in male and 31.0 in female *C.*
1325 *melipona*).
1326   *Chiropterotriton chiropterus* differs from *C. casasi* in its smaller adult body size in
1327 females (mean SVL 33.5 mm in *C. chiropterus* vs. 40.9 mm in one *C. casasi*), longer tail in
1328 males (mean TL/SVL 1.25 in *C. chiropterus* vs. 1.04 in *C. casasi*), shorter head (mean HL 8.1
1329 mm in male and 7.3 mm in female *C. chiropterus* vs. 8.3 mm in male and 8.6 mm in one female
1330 *C. casasi*), broader head (mean HW 5.6 mm in male and 4.8 mm in female *C. chiropterus* vs. 5.8
1331 mm in male and 5.9 mm in one female *C. casasi*), longer limbs in males (mean LI 0.3 in *C.*
1332 *chiropterus* vs. 0.8 in *C. casasi*) and more maxillary teeth (mean MT 12.6 in male and 48.0 in
1333 female *C. chiropterus* vs. 9.0 in male and 30 in one female *C. casasi*).
1334   *Chiropterotriton chiropterus* differs from *C. orculus* in its longer tail (mean TL/SVL 1.25
1335 in male and 1.19 in female *C. chiropterus* vs. 1.02 in both male and female *C. orculus*), longer
1336 head in males (mean HL 8.1 mm in *C. chiropterus* vs. 7.4 mm in *C. orculus*), wider head in
1337 males (mean HW 5.6 mm in *C. chiropterus* vs. 5.0 mm in *C. orculus*), longer limbs (mean LI 0.3
1338 in male and 2.0 in female *C. chiropterus* vs. 1.9 in male and 2.9 in female *C. orculus*), wider feet
1339 in males (mean FW 3.7 mm in *C. chiropterus* vs. 3.2 mm in *C. orculus*) and more maxillary teeth
1340 (mean MT 12.6 in male and 48.0 in female *C. chiropterus* vs. 8.2 in male and 28.8 in female *C.*
1341 *orculus*).
1342   *Chiropterotriton chiropterus* differs from *C. lavae* in its larger adult body size (mean
1343 SVL 37.5 mm in male and 33.5 mm in female *C. chiropterus* vs. 32.4 mm in male and 31.6 mm
1344 in female *C. lavae*), longer tail (mean TL/SVL 1.25 in male and 1.19 in female *C. chiropterus* vs.
1345 1.19 in male and 1.02 in female *C. lavae*), shorter limbs (mean LI 0.3 in male and 2.0 in female
1346 *C. chiropterus* vs. -0.6 in male and 0.6 in female *C. lavae*), longer head (mean HL 8.1 mm in

1347 male and 7.3 mm in female *C. chiropterus* vs. 7.5 mm in male and 7.0 mm in female *C. lavae*),
1348 broader head (mean HW 5.6 mm in male and 4.8 mm in female *C. chiropterus* vs. 4.9 mm in
1349 male and 4.7 mm in female *C. lavae*), more maxillary teeth (mean MT 12.6 in male and 48.0 in
1350 female *C. chiropterus* vs. 7.0 in male and 20.8 in female *C. lavae*) and more vomerine teeth
1351 (mean VT 10.6 in male and 12.5 in female *C. chiropterus* vs. 8.9 in male and 11.4 in female *C.*
1352 *lavae*).
1353   *Chiropterotriton chiropterus* differs from *C. aureus* in its larger adult body size (mean
1354 SVL 37.5 mm in male and 33.5 mm in female *C. chiropterus* vs. 28.5 mm in one male, mean
1355 26.8 mm in females *C. aureus*), relatively longer limbs in males (mean LI 0.3 in male *C.*
1356 *chiropterus* vs. 2.0 in one male *C. aureus*), longer head (mean HL 8.1 mm in male and 7.3 mm in
1357 female *C. chiropterus* vs. 6.4 mm in one male, mean 6.0 mm in female *C. aureus*), broader head
1358 (mean HW 5.6 mm in male and 4.8 mm in female *C. chiropterus* vs. 4.0 mm in one male, 3.6
1359 mm in female *C. aureus*), and larger feet (mean FW 3.7 mm in male and 3.1 in female *C.*
1360 *chiropterus* vs. 2.4 mm in one male, 1.8 in females of *C. aureus*).
1361   *Chiropterotriton chiropterus* differs from *C. nubilus* in its larger adult body size (mean
1362 SVL 37.5 mm in male and 33.5 mm in female *C. chiropterus* vs. 29.4 mm in one male, mean
1363 30.5 mm in females *C. nubilus*), relatively longer limbs in males (mean LI 0.3 in male *C.*
1364 *chiropterus* vs. 2.0 in one male *C. nubilus*), longer head in males (mean HL 8.1 mm in *C.*
1365 *chiropterus* vs. 6.6 mm in one male *C. nubilus*), broader head (mean HW 5.6 mm in male and 4.8
1366 mm in female *C. chiropterus* vs. 4.0 mm in one male, 4.4 mm in female *C. nubilus*), and larger
1367 feet (mean FW 3.7 mm in male and 3.1 in female *C. chiropterus* vs. 2.6 mm in one male, 2.3 in
1368 females of *C. nubilus*).

1369 ***Description of Neotype:*** SVL 38.8 mm, TL 46.0 mm, AX 20.8 mm, SW 4.1 mm, HL 8.0 mm,
1370 HW 5.4 mm, HD 2.8 mm, projection of snout beyond mandible 0.4 mm, distance from anterior
1371 rim of orbit to snout 1.8 mm, interorbital distance 2.4 mm, eyelid length 2.7 mm, eyelid width
1372 1.2 mm, horizontal orbit diameter 1.7 mm, nostril diameter 0.4 mm, FLL 9.5 mm, HLL 10.8 mm,
1373 snout-to-forelimb length 10.2 mm, distance from snout to anterior angle of vent 36.7 mm, tail
1374 width at base 2.8 mm, tail depth at base 2.7 mm, FW 3.6 mm, length of fifth toe 0.9 mm, length
1375 of longest (third) toe 1.5 mm, mental gland length 1.3 mm, mental gland width 1.3. Numbers of
1376 teeth: premaxillary 5, maxillary 6-10 (right-left) and vomerine 5-5 (right-left). Adpressed limbs
1377 are separated by 0 costal folds.

1378 ***Coloration in life***: Data have been derived from diapositives of seven specimens from Huatusco
1379 taken by Roy W. McDiarmid. This is a generally brightly colored species in which yellowish
1380 colors predominate. It is generally pale laterally and ventrally. A dorsal light band is generally
1381 present that extends onto the tail, sometimes to the tip, but there are some darker specimens that
1382 lack an obvious stripe. Coloration varies extensively from one specimen to the next with respect
1383 to the nature of the dorsal band and its coloration. In one large adult, the color is a relatively
1384 intense Orange Rufous (5) at the origin of the band, behind the eyes, but it becomes lighter and
1385 yellower posteriorly and on the sides of the head and neck, from Tawny Olive (17) to Pale Horn
1386 Color (11), then Yellow Ochre (14). Over the shoulder and more posteriorly, yellowish-to-cream
1387 spots (Light Buff, 2) form in a dorsolateral ragged line, with the dorsomedial stripe becoming
1388 Light Neutral Gray (297) grading into Pale Neutral Gray (296) and extending onto the tail as
1389 Pale Mauve (204) with speckles of Cinnamon Drab (50). The limbs are yellowish (Chamois, 84).
1390 The iris is dark ventrally but has a yellow-gold highlight. The dorsal eyelid is pale and colorless.
1391 A faint light cream bar extends between the eyes.

1392   Another specimen is more colorful dorsally. The head is complexly colored with a bright
1393 snout (Salmon Color, 82) to the midpoint between the eyes. A dark bar extends between the
1394 eyes, beginning on the eyelid, and an inverted triangular dark area extends posteriorly to the
1395 anterior boundary of the epaxial muscles. The temporal region of the head back over the
1396 shoulders is light in coloration (Chamois, 84) and there is a lateral excursion of the color over the
1397 shoulder region. The base of the tail becomes brighter and rich reddish brown (Carmine, 64). The
1398 limbs are a bright mottling of gray and yellow (Cream Yellow, 82, to Chamois 84).
1399   Some animals are darker than the above but most have a light, bright dorsal coloration in
1400 the tan-to-yellow range with some brighter orange on the snout. In some the dorsal coloration is
1401 pale to very pale. There is usually a bar between the eyes and a ventrolateral excursion of the
1402 dorsal band in front of and over the shoulders.

1403 ***Coloration in preservative*:** The dorsum is a relatively pale brown, either uniform or with an
1404 indistinct, broad brown dorsal stripe bordered by thin, darker-brown dorsolateral lines that
1405 extend from the nape to the base of the tail. The dorsal surface of the tail is a relatively pale
1406 brown with some darker mottling; the head sometimes has a small amount of darker mottling.
1407 The venter and gular region are a uniform pale tan; the ventral side of the tail is a uniform,
1408 slightly darker brown.

1409 ***Osteology*:** This account is based primarily on examination of a μCT scan of the skull of MVZ
1410 85602, an adult male, 38.9 mm SVL (Figs. 6–8; Table 3). In addition, four cleared-and-stained
1411 specimens were scored for osteological characters evaluated by Darda & Wake (2015). The skull
1412 is well developed. The cranial roof is complete: paired frontals and parietals articulate across the
1413 midline—there is no frontoparietal fontanelle—although tabs that extend posteriorly from the
1414 frontals to overlap the parietals, which are present in some congeners, are absent. Rostral bones
1415 articulate firmly with one another, including many overlapping articulations, such as the
1416 prefrontal and nasal by the maxilla. Ascending processes of the single premaxilla are separate
1417 along their entire length and broaden laterally as they approach their articulation with the
1418 frontals. A very small septomaxilla is present on each side. The nasal is large, including an
1419 anteromedial protrusion that forms a medial wall to the external naris and nearly contacts the
1420 premaxilla at its rostral articulation with the maxilla. The prefrontal is robust; dorsally, it
1421 overlaps the frontal bone whereas ventrally it is overlapped by the facial process of the maxilla.
1422 The foramen for the nasolacrimal duct has eroded abutting portions of the facial process of the
1423 maxilla, the nasal and the prefrontal. The five teeth on the left maxilla and six on the right are
1424 confined to the anterior 50% of each bone. The remaining (edentulous) portion of each maxilla is
1425 cleaver-like. There are four premaxillary teeth. The orbitosphenoid is fully articulated with the
1426 frontal and parietal dorsally and the parasphenoid ventrally, thus forming a solid braincase.
1427   There are two large (elevated) crests on each otic capsule. One arises dorsal to the
1428 anterior semicircular canal. The other emerges at right angles from the midpoint of the first crest
1429 and extends posterolaterally towards the lateral semicircular canal. A moderately sized tab
1430 emerges from the posterolateral edge of the parietal and is sharply reflected ventromedially,
1431 extending at least halfway down the vertical extent of the orbitosphenoid. The squamosal, while
1432 typical for *Chiropterotriton*, bears a distinctive longitudinal ridge on its lateral face. The
1433 quadrate, while robust, is nevertheless small and inconspicuous. The columellar stylus is well
1434 developed for *Chiropterotriton*; it comprises a short but distinct rod that is directed towards but
1435 does not contact the squamosal. Paired vomers articulate medially both anteriorly and
1436 posteriorly, partially obliterating the internasal fontanelle in ventral view. Preorbital processes of

1437 the vomer are spine-like—elongate and pointed—and completely lack teeth. There are five
1438 vomerine teeth on the right side and six on the left. The parasphenoid bone is relatively narrow
1439 posteriorly. Paired parasphenoid tooth patches are separated across midline; each bears 45–50
1440 teeth. The mandible is robust. The articular bone is robust and solidly articulated with the
1441 prearticular and the dentary. The prearticular is well developed; the coronoid process is very
1442 high. There are 10 teeth on the right dentary bone and 11 on the left.
1443   Digital formulae are 1-2-3-2 on each side. The distal tip of the terminal phalanx is greatly
1444 expanded on each finger except the first. Mesopodial cartilages are not mineralized.

1445 **Distribution and ecology**: *Chiropterotriton chiropterus* is found from the vicinity of the type
1446 locality near Huatusco, Veracruz, south to the Sierra de Juárez, Oaxaca. Geographically
1447 associated species include *C. orculus*, *C. perotensis*, *C. ceronorum* and *C. lavae*.

1448 **Remarks**: Populations from the Sierra de Juárez, Oaxaca, were previously considered to
1449 represent an undescribed species (*Chiropterotriton* sp. J) based on allozyme data (Darda, 1994),
1450 but that study lacked specimens of topotypic *C. chiropterus*. Mitochondrial DNA sequenced data
1451 showed that *Chiropterotriton* sp. J is most closely related to *C. chiropterus*. Based on
1452 examination of a series of specimens from the north slope of Cerro Pelón, Oaxaca, we are unable
1453 to find any discrete morphological differences between these populations that would support the
1454 recognition of *C.* sp. J as a distinct species. We therefore assign populations from Oaxaca
1455 previously referred to *Chiropterotriton* sp. J to *C. chiropterus*.

1456 **Conservation status**: *Chiropterotrition chiropterus* is designated as Critically Endangered by the
1457 most recent IUCN Red List of Threatened Species (Parra-Olea et al., 2008).

1458

1459 ***Chiropterotriton orculus* Cope, 1865**
1460 Cope's Flat-footed Salamander, Salamandra de Pie Plano de Cope
1461 Figures 4G, 5G, 6E, 7E, 8E.
1462 **Spelerpes orculus**—Cope, 1865: 196. Syntypes: USNM or ANSP, not now present in
1463   either collection. Type locality: "Mexican Table Land" (Frost, 2019).
1464 **Spelerpes chiropterus** (part)—*Cope, 1869: 106; Taylor and Smith, 1945; Smith and*
1465   *Taylor, 1948.*
1466 **Chiropterotriton orculus**—*Darda, 1994.*

1467 **Neotype**: MVZ 138783, an adult male from the ridge between Popocatepetl and
1468 Iztaccihuatl, along Mexican Hwy. 196, 16.2 km by road east jct Mexican Hwy. 115,
1469 Mexico, Mexico, 3300 masl, 19.0973ºN, 98.6829º W. Collected 26 July 1976 by J. F.
1470 Lynch, D. B. Wake and M. E. Feder.

1471 **Additional specimens examined**: Nineteen specimens, all from the ridge between
1472 Popocatepetl and Iztaccihuatl, México, Mexico. Nine males: MVZ 76161, 138694,
1473 138696–97, 138700, 138778, 138784, 138804 and 200630; and ten females: MVZ 138686,
1474 138688, 138776–77, 138779, 138781, 138793, 138796–97 and 200629.

1475 **Diagnosis**: This is a medium-sized species of *Chiropterotriton*; mean SVL 35.9 mm in ten
1476 adult males (range 33.6–38.9) and 39.0 mm in ten adult females (range 34.9–43.0). The

1477 head is moderately wide; HW averages 14% of SVL in males (range 13–15) and 13% in
1478 females (range 12–14). Jaw muscles are prominent in both males and females. Adult males
1479 have a broad, bluntly rounded snout with broad and moderately developed nasolabial
1480 protuberances. Eyes are large and relatively prominent and extend slightly beyond the jaw
1481 margin in ventral view. There are few maxillary teeth in males (mean MT 8.2, range 5-11)
1482 and moderate numbers in females (mean MT 28.8, range 23–35). There are few vomerine
1483 teeth in both males (mean VT 8.6, 5–11) and females (mean VT 12.0, range 9–15), which
1484 are arranged in a curved row that does not extend lateral to the outer margin of the internal
1485 choana. The tail is moderately long and slightly exceeds snout-vent length in most
1486 specimens; mean TL/SVL equals 1.02 in both males (range 0.86–1.15) and females (range
1487 0.87–1.12). Limbs are short to moderately long in both females and males; FLL+HLL
1488 averages 51% of SVL in males (range 43–56) and 47% in females (range 44–50).
1489 Adpressed limbs approach closely in males (mean LI 1.9, range 0.0–3.0) but are widely
1490 separated in females (mean LI 2.9, range 2.0–3.0). The manus and pes are relatively small,
1491 digits are broad. Subterminal pads are well developed. Digital webbing ranges from slight
1492 to moderate, extending to the base of the penultimate phalanx on the third toe. The first
1493 digit is distinct but barely emerges from the webbing. Digital tips are only slightly
1494 expanded. The mental gland is prominent, relatively large and oval (nearly round) in males.
1495 The smallest mature male is 33.6 mm SVL.

1496 ***Comparisons***: *Chiropterotriton orculus* differs from *C. ceronorum* in its larger adult body
1497 size (mean SVL 35.9 mm in male and 39.0 mm in female *C. orculus* vs. 33.9 mm in male
1498 and 34.9 mm in female *C. ceronorum*), shorter limbs (mean LI 1.9 in male and 2.9 in
1499 female *C. orculus* vs. 0.0 in male and 1.5 in female *C. ceronorum)*, fewer maxillary teeth
1500 (mean MT 8.2 in male and 28.8 in female *C. orculus* vs. 11.0 in male and 47.7 in female *C.*
1501 *ceronorum)* and fewer vomerine teeth (mean VT 8.6 in male and 12.0 in female *C. orculus*
1502 vs. 13.0 in male and 15.9 in female *C. ceronorum*).
1503   *Chiropterotriton orculus* differs from *C. perotensis* in its larger adult body size
1504 (mean SVL 35.9 mm in male and 39.0 mm in female *C. orculus* vs. 29.7 mm in male and
1505 31.7 mm in female *C. perotensis*), slightly longer limbs (mean LI 1.9 in male and 2.9 in
1506 female *C. orculus* vs. 2.5 in male and 3.3 in female *C. perotensis*), longer head (mean HL
1507 7.4 mm in male and 8.0 mm in female *C. orculus* vs. 6.6 mm in male and 6.7 mm in female
1508 *C. perotensis*), broader head (mean HW 5.0 mm in male and 5.2 mm in female *C. orculus*
1509 vs. 4.2 mm in male and 4.4 mm in female *C. perotensis*), larger feet (mean FW 3.2 mm in
1510 male and 3.4 mm in female *C. orculus* vs. 2.6 mm in both male and female *C. perotensis*)
1511 and more maxillary teeth (mean MT 8.2 in male and 28.8 in female *C. orculus* vs. 7.2 in
1512 male and 27.9 in female *C. perotensis*).
1513   *Chiropterotriton orculus* differs from *C. totonacus* in its larger adult body size in
1514 females (mean SVL 39.0 mm in *C. orculus* vs. 35.5 mm in *C. totonacus*), shorter tail (mean
1515 TL/SVL 1.02 in both male and female *C. orculus* vs. 1.16 in male and 1.20 in female *C.*
1516 *totonacus*), shorter limbs (mean LI 1.9 in male and 2.9 in female *C. orculus* vs. -0.60 in
1517 male and 0.0 in female *C. totonacus)*, shorter head in males (mean HL 7.4 mm in *C.*
1518 *orculus* vs. 8.5 mm in C. *totonacus*), narrower feet (mean FW 3.2 mm in male and 3.4 mm
1519 in female *C. orculus* vs. 4.2 mm in male and 4.0 mm in female *C. totonacus)*, fewer
1520 maxillary teeth (mean MT 8.2 in male and 28.8 in female *C. orculus* vs. 32.9 in male and
1521 52.6 in female *C. totonacus*) and fewer vomerine teeth (mean VT 8.6 in male and 12.0 in
1522 female *C. orculus* vs. 11.6 in male and 13.7 in female *C. totonacus*).

1523   *Chiropterotriton orculus* differs from *C. melipona* in its larger adult body size
1524   (mean SVL 35.9 mm in male and 39.0 mm in female *C. orculus* vs. 29.2 mm in male and
1525   28.5 mm in female *C. melipona*), shorter tail (mean TL/SVL 1.02 in both male and female
1526   *C. orculus* vs. 1.16 in male and 1.11 in female *C. melipona*), longer head (mean HL 7.4 mm
1527   in male and 8.0 mm in female *C. orculus* vs. 6.3 mm in male and 6.4 mm in female *C.*
1528   *melipona*), broader head (mean HW 5.0 mm in male and 5.2 mm in female *C. orculus* vs.
1529   4.3 mm in male and 4.2 mm in female *C. melipona*) and broader feet (mean FW 3.2 mm in
1530   male and 3.4 mm in female *C. orculus* vs. 2.4 mm in male and 2.6 mm in female *C.*
1531   *melipona*).
1532   *Chiropterotriton orculus* differs from *C. casasi* in its smaller adult body size (mean
1533   SVL 35.9 mm in male and 39.0 mm in female *C. orculus* vs. 37.8 mm in male and 40.9 mm
1534   in one female *C. casasi*), shorter head (mean HL 7.4 mm in male and 8.0 mm in female *C.*
1535   *orculus* vs. 8.3 mm in male and 8.6 mm in one female *C. casasi*), narrower head (mean HW
1536   5.0 mm in male and 5.2 mm in female *C. orculus* vs. 5.8 mm in male and 5.9 mm in one
1537   female *C. casasi*) and shorter limbs (mean LI 1.9 in male and 2.9 in female *C. orculus* vs.
1538   0.8 in male and 1.0 in one female *C. casasi*).
1539   *Chiropterotriton orculus* differs from *C. chiropterus* in its shorter tail (mean
1540   TL/SVL 1.02 in both male and female *C. orculus* vs. 1.25 in male and 1.19 in female *C.*
1541   *chiropterus*), shorter head in males (mean HL 7.4 mm in *C. orculus* vs. 8.1 mm in *C.*
1542   *chiropterus*), narrower head in males (mean HW 5.0 mm in *C. orculus* vs. 5.6 mm in *C.*
1543   *chiropterus*), shorter limbs (mean LI 1.9 in male and 2.9 in female *C. orculus* vs. 0.3 in
1544   male and 2.0 in female *C. chiropterus*), narrower feet in males (mean FW 3.2 mm in *C.*
1545   *orculus* vs. 3.7 mm in *C. chiropterus*) and fewer maxillary teeth (mean MT 8.2 in male and
1546   28.8 in female *C. orculus* vs. 12.6 in male and 48.0 in female *C. chiropterus*).
1547   *Chiropterotriton orculus* differs from *C. lavae* in its larger adult body size (mean
1548   SVL 35.9 mm in male and 39.0 mm in female *C. orculus* vs. 32.4 mm in male and 31.6 mm
1549   in female *C. lavae*), shorter tail in males (mean TL/SVL 1.02 in *C. orculus* vs. 1.19 in *C.*
1550   *lavae*), shorter limbs (mean LI 1.9 in male and 2.9 in female *C. orculus* vs. -0.60 in male
1551   and 0.6 in female *C. lavae*) and more maxillary teeth (mean MT 8.2 in male and 28.8 in
1552   female *C. orculus* vs. 7.0 in male and 20.8 in female *C. lavae*).
1553   *Chiropterotriton orculus* differs from *C. dimidiatus* in its larger adult body size
1554   (mean SVL 35.9 mm in male and 39.0 mm in female *C. orculus* vs. 24.6 mm in male and
1555   25.8 mm in female *C. dimidiatus*), longer tail (mean TL/SVL 1.02 in both male and female
1556   *C. orculus* vs. 0.89 in male and 0.87 in female *C. dimidiatus*), longer limbs (mean LI 1.90
1557   in male and 2.90 in female *C. orculus* vs. 3.8 in male and 4.9 in female *C. dimidiatus*),
1558   longer head (mean HL 7.4 mm in male and 8.0 mm in female *C. orculus* vs. 5.2 mm in
1559   male and 5.0 mm in female *C. dimidiatus*), broader head (mean HW 5.0 mm in male and
1560   5.2 mm in female *C. orculus* vs. 3.4 mm in male and 3.5 mm in female *C. dimidiatus*),
1561   broader feet (mean FW 3.2 mm in male and 3.4 mm in female *C. orculus* vs. 1.7 mm in
1562   both male and female *C. dimidiatus*), more maxillary teeth (mean MT 8.2 in male and 28.8
1563   in female *C. orculus* vs. 3.8 in male and 17.0 in female *C. dimidiatus*) and more vomerine
1564   teeth (mean VT 8.6 in male and 12.0 in female *C. orculus* vs. 5.6 in male and 8.3 in female
1565   *C. dimidiatus*).
1566   *Chiropterotriton orculus* differs from *C. chico* in its smaller adult body size in
1567   males (mean SVL 35.9 mm in *C. orculus* vs. 38.4 mm in *C. chico*), shorter tail (mean
1568   TL/SVL 1.02 in both male and female *C. orculus* vs. 1.18 in male and 1.12 in female *C.*

1569   *chico*), shorter limbs (mean LI 1.90 in male and 2.90 in female *C. orculus* vs. 0.6 in male
1570   and 2.1 in female *C. chico*), shorter head (mean HL 7.4 mm in male and 8.0 mm in female
1571   *C. orculus* vs. 8.8 mm in male and 8.7 mm in female *C. chico*), narrower head (mean HW
1572   5.0 mm in male and 5.2 mm in female *C. orculus* vs. 5.6 mm in male and 5.7 mm in female
1573   *C. chico*), narrower feet (mean FW 3.2 mm in male and 3.4 mm in female *C. orculus* vs.
1574   4.1 mm in male and 4.2 mm in female *C. chico*) and fewer vomerine teeth (mean VT 8.6 in
1575   male and 12.0 in female *C. orculus* vs. 13.6 in male and 15.6 in female *C. chico*).
1576   *Chiropterotriton orculus* differs from *C. arboreus* in its larger adult body size
1577   (mean SVL 35.9 mm in male and 39.0 mm in female *C. orculus* vs. 33.4 mm in male and
1578   32.2 mm in female *C. arboreus*), longer tail (mean TL/SVL 1.02 in both male and female
1579   *C. orculus* vs. 0.83 in male and 0.87 in female *C. arboreus*) and shorter limbs (mean LI
1580   1.90 in male and 2.90 in female *C. orculus* vs. 0.20 in male and 1.0 in female *C. arboreus*).
1581   *Chiropterotriton orculus* differs from *C. terrestris* in its larger adult body size
1582   (mean SVL 35.9 mm in male and 39.0 mm in female *C. orculus* vs. 24.2 mm in male and
1583   23.0 mm in female *C. terrestris*), longer head (mean HL 7.4 mm in male and 8.0 mm in
1584   female *C. orculus* vs. 5.7 mm in male and 5.2 mm in female *C. terrestris*), broader head
1585   (mean HW 5.0 mm in male and 5.2 mm in female *C. orculus* vs. 3.5 mm in male and 3.3
1586   mm in female *C. terrestris*) and broader feet (mean FW 3.2 mm in male and 3.4 mm in
1587   female *C. orculus* vs. 1.9 mm in male and 1.7 mm in female *C. terrestris*).
1588   *Chiropterotriton orculus* differs from *C. aureus* by being larger (mean SVL 35.9
1589   mm in male and 39.0 mm in female *C. orculus* vs. 28.5 mm in one male, mean 26.8 mm in
1590   female *C. aureus*), shorter tail (mean TL/SVL 1.02 in both male and female *C. orculus* vs.
1591   1.28 in one male, mean 1.16 in female *C. aureus*), relatively shorter limbs in females (mean
1592   LI 2.9 in female *C. orculus* vs. 2.3 in female *C. aureus*), larger head (mean HL 7.4 mm in
1593   male and 8.0 mm in female *C. orculus* vs. 6.4 mm in one male, mean 6.0 mm in female *C.*
1594   *aureus*)*,* broader head (mean HW 5.0 mm in male and 5.2 mm in female *C. orculus* vs. 4.0
1595   mm in one male, 3.6 mm in female *C. aureus*), and broader feet (mean FW 3.2 mm in male
1596   and 3.4 mm in female *C. orculus* vs. 2.4 mm in one male, mean 1.8 mm in female *C.*
1597   *aureus*).
1598   *Chiropterotriton orculus* differs from *C. nubilus* in larger shorter (mean SVL 35.9 mm in
1599   male and 39.0 mm in female *C. orculus* vs. 29.4 mm in one male, mean 30.5 mm in female *C.*
1600   *nubilus*), shorter tail (mean TL/SVL 1.02 in both male and female *C. orculus* vs. 1.37 in one
1601   male, mean 1.12 in female *C. nubilus*), relatively shorter limbs in females (mean LI 2.9 in female
1602   *C. orculus* vs. 1.5 in female *C. nubilus*), longer head (mean HL 7.4 mm in male and 8.0 mm in
1603   female *C. orculus* vs. 6.6 mm in one male, mean 7.4 mm in female *C. nubilus*), broader head
1604   (mean HW 5.0 mm in male and 5.2 mm in female *C. orculus* vs. 4.0 mm in one male, mean 4.4
1605   mm in female *C. nubilus*), and broader feet (mean FW 3.2 mm in male and 3.4 mm in female *C.*
1606   *orculus* vs. 2.6 mm in one male, mean 2.3 mm in female *C. nubilus*).

1607   ***Description of neotype:*** SVL 38.9 mm, TL 33.6 mm, AX 20.5 mm, SW 4.0 mm, HL 8.1
1608   mm, HW 5.5 mm, HD 2.4 mm, projection of snout beyond mandible 0.6 mm, distance from
1609   anterior rim of orbit to snout 2.3 mm, interorbital distance 2.3 mm, eyelid length 3.5 mm,
1610   eyelid width 1.6 mm, horizontal orbit diameter 1.8 mm, nostril diameter 0.3 mm, FLL 9.3
1611   mm, HLL 9.6 mm, snout-to-forelimb length 9.5 mm, distance from snout to anterior angle
1612   of vent 33.8 mm, tail width at base 3.1 mm, tail depth at base 3.2 mm, FW 3.5 mm, length
1613   of fifth toe 0.5 mm, length of longest (third) toe 1.2 mm, mental gland length 1.3 mm,

1614   mental gland width 1.3. Numbers of teeth: premaxillary 4, maxillary 4-5 (right-left) and
1615   vomerine 5-4 (right-left). Adpressed limbs are separated by 2 costal folds.

1616   ***Coloration in life***: No information is available for the neotype or topotypic individuals; this
1617   description is based on photos of specimens from Lagunas de Zempoala. The background
1618   dorsal color is very dark grey. A broad dorsal band is typically present, varying in color
1619   from reddish brown to tan or nearly golden brown; the background color is visible only
1620   along midline. This coloration continues onto the tail, although the band is less regular and
1621   somewhat broken up in many individuals. The head is very dark brown, with splotches of
1622   brown similar in coloration to those on the dorsum. Small, pale-grey specks often present
1623   on both head and tail. The dorsal band is bordered by very dark grey. Some individuals lack
1624   a dorsal band and are very dark-brownish-grey dorsally with pale flecks throughout. Flanks
1625   are dark grey with pale grey specks, which are numerous on the body with some on the
1626   sides of the head and few to none on the sides of the tail. Upper side of limbs either similar
1627   in coloration to flanks or slightly paler. The iris is coppery.

1628   ***Coloration in preservative***: The dorsum, head and tail are a uniform medium brown. The
1629   upper side of the limbs and feet are paler brown. The venter, gular region and underside of
1630   the forelimbs are tan to pale brown; the underside of the hind limbs and tail are slightly
1631   darker brown.

1632   ***Osteology***: This account is based on examination of a µCT scan of the anterior skeleton of
1633   the neotype: MVZ 138783, an adult male, 38.9 mm SL (Figs. 6–8; Table 3). The skull is
1634   compact and robust, especially anteriorly. The snout is blunt in lateral view. Cranial roofing
1635   bones are moderately well ossified. Paired frontals articulate across the midline anteriorly
1636   for about two thirds of their length but then separate to participate in a relatively large
1637   frontoparietal fontanelle, which includes about three fourths of the length of the parietals.
1638   Posteriorly extending tabs of the frontals overlap the parietals anteriorly. Ascending
1639   processes of the single premaxilla approach one another medially but remain separate for
1640   their entire length. They twist and broaden greatly as they ascend before establishing a firm
1641   articulation with the frontal. The dental process of the premaxilla is deep (high) but no
1642   palatal shelf is evident. Septomaxillae are present on both sides; they are very small but
1643   nevertheless well developed for *Chiropterotriton*. The nasal bone is broadly triangular, but
1644   also thin and less well-developed anteromedially. It barely abuts the premaxilla medially
1645   and the maxilla laterally; is separated from the prefrontal posterolaterally; and slightly
1646   overlaps the frontal posteriorly. The prefrontal is broad, compact and almost quadrangular.
1647   The foramen for the nasolacrimal duct has eroded the ventral margin of the prefrontal and
1648   the dorsal margin of the facial process of the maxilla, but the nasal is not involved. The
1649   maxilla is edentulous posteriorly for about 55% of its length. Its posterior tips flare laterally
1650   beyond the margin of the lower jaw in dorsal view. There are five large maxillary teeth on
1651   each side and four premaxillary teeth. The orbitosphenoid, while moderately well-
1652   developed, is articulated solidly to the parasphenoid, weakly to the frontal, and not at all to
1653   the parietal. The oculomotor foramen is absent on the right side.
1654   There are no prominent crests on the dorsal surface of either otic capsule. The
1655   posterolateral tab of the parietal is well-developed but relatively short and triangular; it is
1656   reflected ventromedially and ends in a rounded point about halfway down the vertical
1657   extent of the orbitosphenoid. The squamosal bone is more elongate and less triangular than

1658 in other *Chiropterotriton*; its dorsal tip articulates with a small portion of the otic capsule
1659 opposite the lateral semicircular canal. The quadrate is small and inconspicuous. The stylus
1660 on the columella is short and stout. Paired bodies of the vomer are reasonably well
1661 developed but they barely articulate medially posterior to the internasal fontanelle.
1662 Postorbital processes of are long, thin and slightly curved. There are six vomerine teeth on
1663 the right side and six on the left; one or two teeth are deployed at the base of each preorbital
1664 process. The parasphenoid expands posteriorly but truncates abruptly at its caudal border.
1665 Each lateral edge is sculpted by a shallow notch opposite the jaw articulation, and by an
1666 erosion of bone (and teeth) opposite the ventromedially directed parietal tab. It has an
1667 unusual shape along the lateral margin. Paired parasphenoid tooth patches are separated
1668 across the midline; each bears 50–52 fully developed teeth, but there are many additional
1669 developing teeth along the lateral margin. The mandible is solid. The articular bone is well
1670 developed and may be at least partly fused to the pre articular on each side. The prearticular
1671 has a relatively high coronoid process. There are approximately 12 teeth on each dentary
1672 bone.
1673 Digital formulae are 1-2-3-2 on each side. There is a tiny expanded knob at the tip
1674 of each terminal phalanx. Mesopodial cartilages are not mineralized.

1675 ***Distribution and ecology***: *Chiropterotriton orculus* is restricted to the central and eastern
1676 portion of the Trans Mexican Volcanic Belt (La Marquesa, Desierto de los Leones, Ajusco,
1677 Lagunas de Zempoala, Iztaccihuatl, Popocatépetl, Rio Frio and La Malinche). It occurs in
1678 pine and fir forest and is terrestrial; it is typically found under the bark of logs or inside
1679 rotting logs.

1680 ***Remarks***: This species was raised from synonymy with *C. chiropterus* by Darda (his
1681 species G, population 20). While it is relatively widespread, we are unsure of its
1682 northeastern limits.

1683 ***Conservation status***: *Chiropterotriton orculus* is designated as Vulnerable by the most
1684 recent IUCN Red List of Threatened Species (Parra-Olea & Wake, 2008). The species
1685 remains relatively common near Lagunas de Zempoala.

1686
1687 **OTHER SPECIES OF *CHIROPTEROTRITON* FROM CENTRAL VERACRUZ**
1688 In addition to the recently described *C. aureum* and *C. nubilum*, *C. lavae* also occurs in the
1689 mountains of central Veracruz. While Taylor's (1942) original description of this species was
1690 relatively thorough, we provide a brief overview of this species for comparative purposes using
1691 additional specimens collected since the type series. We also examined the holotype and several
1692 paratypes of this species to provide additional information not contained in Taylor's description.
1693
1694 ***Chiropterotriton lavae*** *(Taylor, 1942)*
1695 *Bolitoglossa lavae—Taylor, 1942. Holotype:* EHT-HMS 28937, now FMNH 100118. *Type*
1696 *locality:* "2 miles west of La Joya-Veracruz", Mexico.
1697 Pigmy Flat-footed Salamander, Salamandra de pie plano pigmea
1698 Figures 4H, 5H, 6C, 7C, 8C.

1699   ***Specimens examined***: Nineteen specimens, all from La Joya, Veracruz, Mexico. Ten males:
1700   MVZ 163912–13, 163915, 171873–74, 173394–95, 173398, 178685 and 192789; and nine
1701   females: MVZ 106537, 106548, 171876, 171881, 171885, 171901, 192788, 197788 and 200638.

1702   ***Diagnosis***: This is a medium-sized species of plethodontid salamander phylogenetically
1703   related to *Chiropterotriton totonacus, C. perotensis* and *C. ceronorum*; mean SVL 32.4 mm
1704   in ten adult males (range 31.1–33.8) and 31.6 mm in nine adult females (range 27.9–34.9).
1705   The head is moderately wide; HW averages 15% of SVL in males (range 14–17) and 15%
1706   in females (range 14–16). Jaw muscles are prominent in both males and females. Adult
1707   males and females have a bluntly rounded snout with moderately developed nasolabial
1708   protuberances. Eyes are large and prominent and extend laterally well beyond the jaw
1709   margin in ventral view. There are few maxillary teeth in males (mean MT 7.0, range 1–10)
1710   and moderate numbers in females (mean MT 20.8, range 13–36). There are few vomerine
1711   teeth in both males (mean VT 8.9, 7–10) and females (mean VT 11.4, range 8–15), which
1712   are arranged in a short row that does not reach or barely reaches the inner margin of the
1713   internal choana. The tail is moderately long and slightly exceeds SVL in most specimens;
1714   mean TL/SVL equals 1.19 in males (range 1.11–1.27) and 1.02 in females (range 0.85–
1715   1.15). Limbs are moderately to very long in both females and males; FLL+HLL averages
1716   59% of SVL in males (range 53–65) and 54% in females (range 50–59). Adpressed limbs
1717   closely approach or overlap in males (mean LI -0.60, range -1.0–0.0) but are more
1718   separated in females (mean LI 0.6, range 0.0–2.0). The manus and pes are moderate in size.
1719   Subterminal pads are well developed. Digital webbing is modest, reaching only to the base
1720   of the penultimate phalanx on the third toe. The first digit is included entirely in webbing.
1721   Digital tips are slightly expanded. The mental gland is oval (nearly round), somewhat
1722   prominent and moderately sized in males. The smallest male with a mental gland is 31.2
1723   mm SVL.

1724   ***Comparisons***: *Chiropterotriton lavae* differs from *C. ceronorum* in its slightly smaller adult
1725   body size (mean SVL 32.4 mm in male and 31.6 mm in female *C. lavae* vs. 33.9 mm in male and
1726   34.9 mm in female *C. ceronorum*), longer tail (mean TL/SVL 1.19 in male and 1.02 in female *C.*
1727   *lavae* vs. 1.0 in male and 0.97 in female *C. ceronorum*), longer limbs (mean LI -0.6 in male and
1728   0.6 in female *C. lavae* vs. 0.0 in male and 1.5 in female *C. ceronorum*), fewer maxillary teeth
1729   (mean MT 7.0 in male and 20.8 in female *C. lavae* vs. 11.0 in male and 47.7 in female *C.*
1730   *ceronorum*) and fewer vomerine teeth (mean VT 8.9 in male and 11.4 in female *C. lavae* vs. 13.0
1731   in male and 15.9 in female *C. ceronorum*).
1732   *Chiropterotriton lavae* differs from *C. perotensis* in its larger adult body size in males
1733   (mean SVL 32.4 mm in *C. lavae* vs. 29.7 mm in *C. perotensis*), longer limbs (mean LI -0.6 in
1734   male and 0.6 in female *C. lavae* vs. 2.5 in male and 3.3 in female *C. perotensis*), slightly wider
1735   head (mean HW 4.9 in male and 4.7 in female *C. lavae* vs. 4.2 in male and 4.4 in female *C.*
1736   *perotensis*), longer head (mean HL 7.5 mm in male and 7.0 mm in female *C. lavae* vs. 6.6 mm in
1737   male and 6.7 mm in female *C. perotensis*), wider feet (FW 3.7 mm in male and 3.3 mm in female
1738   *C. lavae* vs. 2.6 mm in both male and female *C. perotensis*) and slightly fewer maxillary teeth in
1739   females (mean MT 20.8 in *C. lavae* vs. 27.9 in *C. perotensis*).
1740   *Chiropterotriton lavae* differs from *C. totonacus* in its smaller adult body size (mean
1741   SVL 32.4 mm in male and 31.6 mm in female *C. lavae* vs. 35.7 mm in male and 35.5 mm in
1742   female *C. totonacus*), shorter tail in females (mean TL/SVL 1.02 in *C. lavae* vs. 1.20 in *C.*
1743   *totonacus*), shorter limbs in females (mean LI 0.6 in *C. lavae* vs. 0.0 in *C. totonacus*), shorter

1744 head (mean HL 7.5 mm in male and 7.0 mm in female *C. lavae* vs. 8.5 mm in male and 7.6 mm
1745 in female C. *totonacus*), slightly narrower head (mean HW 4.9 mm in male and 4.7 mm in
1746 female *C. lavae* vs. 5.2 mm in both male and female *C. totonacus*), narrower feet (mean FW 3.7
1747 mm in male and 3.3 mm in female *C. lavae* vs. 4.2 mm in male and 4.0 mm in female *C.*
1748 *totonacus)*, fewer maxillary teeth (mean MT 7.0 in male and 20.8 in female *C. lavae* vs. 32.9 in
1749 male and 52.6 in female *C. totonacus*) and fewer vomerine teeth (mean VT 8.9 in male and 11.4
1750 in female *C. lavae* vs. 11.6 in male and 13.7 in female *C. totonacus*).
1751   *Chiropterotriton lavae* differs from *C. melipona* in its larger adult body size (mean SVL
1752 32.4 mm in male and 31.6 mm in female *C. lavae* vs. 29.2 mm in male and 28.5 mm in female *C.*
1753 *melipona*), longer head (mean HL 7.5 mm in male and 7.0 mm in female *C. lavae* vs. 6.3 mm in
1754 male and 6.4 mm in female *C. melipona*), broader head (mean HW 4.9 mm in male and 4.7 mm
1755 in female *C. lavae* vs. 4.3 mm in male and 4.2 mm in female *C. melipona*), longer limbs (mean
1756 LI -0.6 in male and 0.6 in female *C. lavae* vs. 2.3 in male and 1.8 in female *C. melipona*),
1757 broader feet (mean FW 3.7 mm in male and 3.3 mm in female *C. lavae* vs. 2.4 mm in male and
1758 2.6 mm in female *C. melipona*), fewer maxillary teeth (mean MT 7.0 in male and 20.8 in female
1759 *C. lavae* vs. 9.5 in male and 31.0 in female *C. melipona*) and fewer vomerine teeth (mean VT 8.9
1760 in male and 11.4 in female *C. lavae* vs. 11.0 in male and 13.0 in female *C. melipona*).
1761   *Chiropterotriton lavae* differs from *C. casasi* in its smaller adult body size (mean SVL
1762 32.4 mm in male and 31.6 mm in female *C. lavae* vs. 37.8 mm in male and 40.9 mm in one
1763 female *C. casasi*), longer tail in males (mean TL/SVL 1.19 in *C. lavae* vs. 1.04 in *C. casasi*),
1764 shorter head (mean HL 7.5 mm in male and 7.0 mm in female *C. lavae* vs. 8.3 mm in male and
1765 8.6 mm in one female *C. casasi*), narrower head (mean HW 4.9 mm in male and 4.7 mm in
1766 female *C. lavae* vs. 5.8 mm in male and 5.9 mm in one female *C. casasi*), longer limbs (mean LI
1767 -0.6 in male and 0.6 in female *C. lavae* vs. 0.8 in male and 1.0 in one female *C. casasi*) and
1768 fewer maxillary teeth in females (mean MT 20.8 in *C. lavae* vs. 30 in *C. casasi*).
1769   *Chiropterotriton lavae* differs from *C. chiropterus* in its smaller adult body size (mean
1770 SVL 32.4 mm in male and 31.6 mm in female *C. lavae* vs. 37.5 mm in male and 33.5 mm in
1771 female *C. chiropterus*), shorter tail (mean TL/SVL 1.19 in male and 1.02 in female *C. lavae* vs.
1772 1.25 in male and 1.19 in female *C. chiropterus)*, longer limbs (mean LI -0.6 in male and 0.6 in
1773 female *C. lavae* vs. 0.3 in male and 2.0 in female *C. chiropterus*), shorter head (mean HL 7.5
1774 mm in male and 7.0 mm in female *C. lavae* vs. 8.1 mm in male and 7.3 mm in female *C.*
1775 *chiropterus*), narrower head (mean HW 4.9 mm in male and 4.7 mm in female *C. lavae* vs. 5.6
1776 mm in male and 4.8 mm in female *C. chiropterus*), fewer maxillary teeth (mean MT 7.0 in male
1777 and 20.8 in female *C. lavae* vs. 12.6 in male and 48.0 in female *C. chiropterus*) and fewer
1778 vomerine teeth (mean VT 8.9 in male and 11.4 in female *C. lavae* vs. 10.6 in male and 12.5 in
1779 female *C. chiropterus*).
1780   *Chiropterotriton lavae* differs from *C. orculus* in its smaller adult body size (mean SVL
1781 32.4 mm in male and 31.6 mm in female *C. lavae* vs. 35.9 mm in male and 39.0 mm in female *C.*
1782 *orculus*), longer tail in males (mean TL/SVL 1.19 in *C. lavae* vs. 1.02 in *C. orculus*) and longer
1783 limbs (mean LI -0.6 in male and 0.6 in female *C. lavae* vs. 1.9 in male and 2.9 in female *C.*
1784 *orculus*).
1785   *Chiropterotriton lavae* differs from *C. aureus* in its larger adult body size (mean SVL
1786 32.4 mm in male and 31.6 mm in female *C. lavae* vs. 28.5 mm in one male, mean 26.8 mm in
1787 female *C. aureus*), larger head (mean HL 7.5 mm in male and 7.0 mm in female *C. lavae* vs. 6.4
1788 mm in one male, mean 6.0 mm in female *C. aureus)*, broader head (mean HW 4.9 mm in male
1789 and 4.7 mm in female *C. lavae* vs 4.0 mm in one male, 3.6 mm in female *C. aureus*), longer

1790   limbs (mean LI -0.6 in male and 0.6 in female *C. lavae* vs. 2.0 in one male, mean 2.3 in female
1791   *C. aureus*), and broader feet (mean FW 3.7 mm in male and 3.3 mm in female *C. lavae* vs. 2.4
1792   mm in one male, mean 1.8 mm in female *C. aureus*).
1793   *Chiropterotriton lavae* differs from *C. nubilus* in its larger adult body size in males
1794   (mean SVL 32.4 mm in *lavae* vs. 29.4 mm in one male *C. nubilus*), shorter tail (mean TL/SVL
1795   1.19 in male and 1.02 in female *C. lavae* vs. 1.37 in one male, mean 1.12 in female *C. nubilus*),
1796   broader head (mean HW 4.9 mm in male and 4.7 mm in female *C. lavae* vs. 4.0 mm in one male,
1797   mean 4.4 mm in female *C. nubilus*), relatively longer limbs (mean LI -0.6 in male and 0.6 in
1798   female *C. lavae* vs. 2.0 in one male, mean 1.5 in female *C. nubilus*), and broader feet (mean FW
1799   3.7 mm in male and 3.3 mm in female *C. lavae* vs 2.6 mm in one male, mean 2.3 mm in female
1800   *C. nubilus*).

1801   ***Measurements of holotype:*** Adult female, SVL 33.5 mm, TL 40.7 mm, AX 18.1 mm, SW
1802   4.8 mm, HL 7.7 mm, HW 5.6 mm, HD 2.9 mm, projection of snout beyond mandible ,
1803   interorbital distance 2.1 mm, eyelid length 1.3 mm, FLL 9.2 mm, HLL 9.7 mm, snout-to-
1804   forelimb length 10.2 mm, snout to anterior angle of vent 33 mm, length of fifth toe 0.9 mm,
1805   distance from eye to nostril 1.2, internarial distance 2.0, FW 4.0, length of longest (third)
1806   toe 1.6 mm. Numbers of teeth: premaxillary 6, maxillary 16-14 (right-left) and vomerine 6-
1807   6 (right-left). Taylor (1942) listed 28 maxillary and premaxillary teeth on each side but
1808   counted missing teeth, while we count only ankylosed teeth that are present. Adpressed
1809   limbs touch.

1810   ***Coloration in life***: Dorsal coloration highly variable. Background dorsal color dark brown; some
1811   individuals have a broad, continuous dorsal band of yellow, reddish-brown or orangish-brown to
1812   pale brown stretching from posterior portion of head to tip of tail, while in other individuals this
1813   dorsal band is either irregular, reduced to paler brown or golden-brown blotches or streaks, or
1814   absent. Head dark brown, often with golden-brown specks, especially between eyes and snout.
1815   Flanks, sides of tail, and dorsal side of limbs and feet dark brown, typically uniform along dorsal
1816   edge but often with paler brown or golden-brown flecks or tan streaks below; toe tips reddish.
1817   Venter dark grey to paler grey, with some white speckling in some individuals. Iris golden-
1818   brown.

1819   ***Coloration in preservative***: The dorsum, tail and head are relatively pale to dark brown, often
1820   with a paler, broad dorsal band that is bordered by darker brown coloration. The paler
1821   background color is often faintly mottled with darker brown. The venter is a uniform tan to pale
1822   brown; the underside of the tail and limbs are a slightly darker brown. The gular region is tan to
1823   pale brown, sometimes with a small amount of mottling.

1824   ***Osteology***: This account is based on examination of a μCT scan of the anterior skeleton of MVZ
1825   163912, an adult male, 33.8 mm SVL (Figs. 6–8). The skull is well developed. The cranial roof
1826   is for the most part complete and solidly articulated. There is no frontoparietal fontanelle,
1827   although there are slight gaps medially between the paired frontals and paired parietals.
1828   Ascending processes of the single premaxillary bone remain separate along their entire length;
1829   each broadens laterally as it approaches its dorsal articulation with the adjacent frontal. A very
1830   narrow palatal shelf is present on each side of the premaxilla but absent medially. There are no
1831   septomaxillary bones. The nasal bone is large and triangular, but also very thin and poorly
1832   ossified. The prefrontal bone is rectangular and robust; its ventral portion is overlapped

1833   extensively by the facial process of the maxilla. The foramen of the nasolacrimal duct has eroded
1834   the prefrontal along its anteroventral margin and the dorsal margin of the facial process of the
1835   maxilla; the nasal abuts the foramen but is eroded minimally, if at all. The maxillary bone is
1836   saber-like in lateral view, not cleaver-like as in many other *Chiropterotriton*. Its posterior,
1837   edentulous portion comprises about 60% of the length of the bone. There are four maxillary teeth
1838   on each side and two premaxillary teeth. The teeth are thin and poorly developed. The
1839   orbitosphenoid is very thin and delicate. It is solidly articulated to the parasphenoid but weakly
1840   articulated to the frontal and parietal.
1841   A prominent bony ridge overlies the anterior semicircular canal dorsally. It is derived
1842   from the posterolateral portion of the parietal bone and the anteromedial portion of the otic
1843   capsule. An additional, crest-like spur emerges at right angles from this crest and is directed
1844   posterolaterally. A second ridge similarly overlies the posterior semicircular canal. The
1845   squamosal bone is robust and roughly triangular. A well-developed, spine-like tab on the
1846   ventrolateral margin of each parietal is sharply reflected ventromedially and extends nearly the
1847   full vertical extent of the orbitosphenoid. The quadrate is small and inconspicuous and
1848   incompletely ossified. There is a stubby, stout stylus on the columella, with a limited free
1849   portion. Paired vomers are weakly ossified; they approach one another across the midline
1850   posterior to the internasal fontanelle but do not articulate. Preorbital processes are needle-like—
1851   thin and elongate. There are four vomerine teeth on each side; one tooth is deployed at the base
1852   of the preorbital process, but only on the left side. The parasphenoid bone is relatively wide
1853   anteriorly. Each lateral edge is sculpted by a deep notch opposite the jaw articulation. Paired
1854   parasphenoid tooth patches are widely separated across the midline; each contains approximately
1855   50 teeth. The mandible is stout. The articular is well ossified. The prearticular is very thin in its
1856   central portion but has a moderately high coronoid process. There are eight teeth on each dentary
1857   bone. The posterior teeth are sharply recurved and needle-like.
1858   Digital formulae are 1-2-3-2 on each side. Phalanges appear to be slightly thinner than in
1859   other *Chiropterotriton*. There is a slightly expanded knob at the tip of each terminal phalanx of
1860   digits 2–4. Mesopodial cartilages are not mineralized.

1861   ***Distribution and ecology***: *Chiropterotriton lavae* is known only from forested areas between the
1862   towns of Toxtlacoaya and La Joya, along the road from Perote to Xalapa, Veracruz, Mexico. It
1863   occurs in bromeliads in the cloud forest and has been found in somewhat disturbed habitat in and
1864   around La Joya.

1865   ***Remarks***: As part of the redescription of this species, we examined the holotype and part of the
1866   series of paratypes at the Field Museum of Natural History. The portion of the type series
1867   examined corresponds closely in morphology to the specimens that we examined.
1868   There has long been a suspicion that two species of *Chiropterotriton* occur in the vicinity
1869   of La Joya. For example, Smith and Taylor (1948) report *Chiropterotriton chiropterus* (almost
1870   certainly not that species) from Toxtlacoaya, and they also report *C. lavae* from that site. This
1871   small village is at the western edge of La Joya. Darda (1994) also reports two species from La
1872   Joya, *C. lavae* and his new species E (which we tentatively assign to *C. totonacus* in this paper).
1873   We have only found one species in the La Joya region.

1874   ***Conservation Status***: *Chiropterotriton lavae* is designated as Critically Endangered by the most
1875   recent IUCN Red List of Threatened Species (IUCN SSC Amphibian Specialist Group, 2016).

1876 Much of the habitat where it occurs is highly disturbed or has been converted to pasture, but this
1877 species remains relatively common even in disturbed forest where there are bromeliads.

1878   **DISCUSSION**
1879   Despite the passage of nearly fifty years between the description of *C. magnipes* and *C.*
1880 *miquihuanus*, it has long been known based on both morphological and molecular evidence that
1881 a great deal of additional diversity exists within the genus (Rabb, 1958; Darda, 1994; Parra-Olea,
1882 2003). The recent descriptions of three species identified as distinct in previous morphological or
1883 molecular analyses (*C. chico, C. cieloensis* and *C. infernalis*) went some way towards
1884 formalizing the known but undescribed diversity of *Chiropterotriton*, while the descriptions of
1885 three species more not included in previous analyses (*C. aureus, C. miquihuanus,* and *C. nubilus*)
1886 showed that there is still previously undocumented diversity left to discover. Of the five species
1887 we describe here, four were previously identified as distinct, while the fifth (*C. casasi*) has not
1888 been included in any previous analysis. These five species add to the already high diversity of
1889 the eastern portion of the Trans-Mexican Volcanic Belt (TMVB).
1890   Using allozyme data, Darda (1994) provided the first in-depth taxonomic study of the
1891 genus *Chiropterotriton* that included molecular data. Darda's *C. chiropterus* complex (the
1892 southern clade) was formed by *C. chiropterus* (represented in his study by sp. E from La Joya,
1893 Veracruz) and *C. orculus* (represented by sp. G from Chignahuapan, Puebla), plus nine
1894 undescribed taxa: *C.* sp A, *C.* sp B, and *C.* sp F, from Puebla; *C.* sp C, *C.* sp D, *C.* sp H, and *C.*
1895 sp I from Veracruz; and *C.* sp. J and *C.* sp. K from Oaxaca. Once sequences of mitochondrial
1896 genes became available, Parra-Olea (2003) defined the type localities for *C. chiropterus* and *C.*
1897 *orculus*. Parra-Olea (2003) assigned the name *C. chiropterus* to populations from Huatusco,
1898 Veracruz leaving Darda's sp. E as an undescribed species. She also assigned the name *C. orculus*
1899 to populations from the central region of the Trans Mexican Volcanic belt including Darda's sp.
1900 A and sp. B, indicating that sp. G from Chignahuapan might represent an undescribed taxon. No
1901 further taxonomic work was performed on this complex until now. Based on our analyses
1902 including molecular and morphological data, here, we describe four of these taxa: *C. totonacus*
1903 (sp. E from La Joya Veracruz), *C. melipona* (sp. F from Xicotepec, Veracruz), *C. perotensis* (sp.
1904 H and sp. D from Las Vigas, Veracruz) and *C. ceronorum* (sp. I from Santa Cruz Texmalaquilla,
1905 Puebla). We assign *C.* sp J from La Esperanza, Oaxaca as part of *C. chiropterus*.
1906   Phylogenetic evidence, based first on allozyme data (Darda, 1994) and continuing with
1907 mtDNA data from the work of Parra-Olea (2003) to the present study has been indispensable to
1908 working out species limits within the genus. One of the most problematic taxonomic issues with
1909 the genus *Chiroperotriton* was the status of *C. chiropterus*. The fact that the original description
1910 contained little morphological information, combined with an imprecise type locality and lost
1911 holotype, made assignment of populations to this species difficult. At different times, this name
1912 has been applied to populations ranging from Tamaulipas south through San Luis Potosí,
1913 Querétaro, Hidalgo, and Veracruz. Furthermore, the species is relatively generalized in
1914 morphology, resembling a number of other small to medium-sized members of the genus. Our
1915 designation of a neotype formalized the assignment of the name *C. chiropterus* for populations
1916 from the region of Huatusco, Veracruz, following Parra-Olea (2003). Inclusion of samples from
1917 Huatusco in both phylogenetic and morphological analyses allowed us to distinguish several of
1918 the new species from the eastern edge of the TMVB. Furthermore, while Parra-Olea (2003)
1919 restricted *C. chiropterus* to the vicinity of Huatusco, we now understand that it ranges south to
1920 northern Oaxaca. Rather than being microendemic, it now has one of the largest ranges of any
1921 *Chiropterotriton*. Similarly, while Darda (1994) restricted *C. orculus* to a single population

1922 based on allozyme data, while our results support the status of *C. orculus* as a more widely
1923 ranging species throughout the eastern TMVB.
1924   Of the species identified as undescribed in previous analyses (Darda, 1994; Parra-Olea,
1925 2003), only *Chiropterotriton* sp. C, sp. G, and sp. K have not been either described or assigned to
1926 an existing species. We believe that *C.* sp. C (from Puerto del Aire, Veracruz) likely represents a
1927 distinct species but currently lack sufficient material to describe it. Major declines in salamander
1928 abundance have occurred at this site (Rovito et al., 2009) and no *Chiropterotriton* have been
1929 found in recent years. *Chiropterotriton* sp. G is similar to *C. orculus* in external morphology and
1930 was assigned that species by Darda (1994), but Parra-Olea (2003) reversed this decision and
1931 applied the name *C. orculus* to populations around Mexico City. Additional morphological
1932 analyses are necessary to determine if *C.* sp. G represents a distinct species or can be assigned to
1933 the wider-ranging *C. orculus.* The case of *C. sp.* K, however, is more difficult. This species,
1934 collected only once in 1980, has not been seen over the course of many visits to Cerro San
1935 Felipe, Oaxaca. While it is possible that the locality is in error, many other species at this site
1936 have undergone catastrophic declines (Parra-Olea et al., 1999; Rovito et al., 2009).
1937 *Chiropterotriton* sp. K may be present on Cerro San Felipe at greatly diminished abundance, or it
1938 may simply exist on a part of the mountain that has not been checked on subsequent visits; the
1939 locality of the known specimens is not specific enough to determine exactly where they were
1940 collected. Concerted field efforts covering different parts of Cerro San Felipe are needed to
1941 confirm that *C.* sp. K does indeed exist at the locality. While the descriptions of *C. perotensis*
1942 (sp. D and sp. H), *C. totonacus* (sp. E), *C. ceronorum* (sp. I) and *C. melipona* (sp. F), together
1943 with the assignment of *C.* sp. J to *C. chiropterus*, nearly deal with all the identified but
1944 undescribed diversity within the genus, we continue to discover populations that likely represent
1945 additional, undescribed species of *Chiropterotriton* from eastern portions of the TMVB.
1946   These five new species increase the content of *Chiropterotriton* from 18 to 23. This
1947 represents a considerable increase to the somewhat slow but steady rise in species descriptions
1948 trajectory that began in the 1980s when molecular data became readily available. With the use of
1949 protein electrophoresis data, 19 new species of salamanders were described from Mexico
1950 (Hanken and Wake, 1994, 1998, 2001; Hanken et al., 1999) and with the use of mitochondrial
1951 markers 31 new species have been described from Mexico since 2001 (Parra-Olea et al., 2001,
1952 2002, 2004, 2004b, 2005, 2005b, 2010, 2016; Brodie et al., 2002; Canseco-Márquez & Parra-
1953 Olea, 2003; Canseco-Márquez & Gutiérrez-Mayen, 2005; Rovito et al., 2012, 2015b; Rovito &
1954 Parra-Olea, 2015; García-Castillo et al., 2017, 2018; Sandoval-Comte et al., 2017). Thus, almost
1955 40% of Mexican bolitoglossines have been described using molecular characters in combination
1956 with morphological and ecological traits. The number of described species in *Chiropterotriton*
1957 alone has nearly doubled over the course of five years, and we expect that additional fieldwork in
1958 the TMVB and Sierra Madre Oriental will reveal additional species.

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Gabriela Parra-Olea conceived and designed the experiments, contributed reagents/materials/analysis tools, obtained molecular and morphological data, wrote the paper, and authored drafts of the paper.
- Mirna G. García-Castillo conceived and designed the experiments, performed the experiments, obtained molecular and morphological data, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Sean Rovito conceived and designed the experiments, performed the experiments, contributed materials, obtained morphological data, wrote the paper, and authored drafts of the paper.
- Jessie Masianocontributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper, digital movies of CT scans.
- James Hanken conceived and designed the experiments, performed the experiments,.analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- David Wake conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Animal Ethics

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2009

2010 Collection permits were provided by the Secretaría del Medio Ambiente y Recursos Naturales
2011 (SEMARNAT): SGPA/DGVS/00947/16, SGPA/DGVS/03038/17 and FAUT-0303, issued to
2012 Gabriela Parra-Olea.

2013

2014 **Data Deposition**
2015 The following information was supplied regarding data availability:
2016 The sequences of *Chiropterotriton* are accessible at GenBank: XXXXX–XXXXX. (GenBank
2017 numbers to be added upon acceptance).

2018 The raw data of skull from CT scanning is available at: (data to become available upon
2019 acceptance).
2020
2021 *Chiropterotriton casasi*

2022 *Chiropterotriton ceronorum*

2023 *Chiropterotriton chiropterus*

2024 *Chiropterotriton lavae*

2025 *Chiropterotriton melipona*

2026 *Chiropterotriton orculus*

2027 *Chiropterotriton perotensis*

2028 *Chiropterotriton totonacus*
2029
2030 **New Species Registration**
2031 The following information was supplied regarding the registration of a newly described species:
2032
2033
2034
2035 *Chiropterotriton ceronorum*
2036 urn:lsid:zoobank.org:act:5BE9F6D2-CACD-41F7-8E1C-09C5E0FE140A
2037 *Chiropterotriton perotensis*
2038 urn:lsid:zoobank.org:act:54AB015C-5CCD-46C7-B260-8BACA8D02C68
2039 *Chiropterotriton totonacus*
2040 urn:lsid:zoobank.org:act:831CB0EF-5D91-4DEC-A4B1-76714D9C21AD
2041 *Chiropterotriton melipona*
2042 urn:lsid:zoobank.org:act:ED19C47F-B804-4FFB-A004-A258625E3E25
2043 *Chiropterotriton casasi*

2044   urn:lsid:zoobank.org:act:248D1A23-66B7-4672-8AA3-44C4058D4F4F
2045   Publication
2046   urn:lsid:zoobank.org:pub:9B4B9DFF-E12B-430D-A541-BA0EBB9B90E6

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2213

Figure 1

Geographic distribution of *Chiropterotriton* in Mexico

Geographic distribution of *Chiropterotriton* in Mexico. Numbers correspond to the following species: (1) *C. priscus*; (2) *C. miquihuanus*; (3) *C. infernalis*; (4) *C. cieloensis*; (5) *C. cracens*; (6) *C. multidentatus* (Cd. Maíz); (7) *C. multidentatus* (Rancho Borbotón); (8) *C. multidentatus* (Sierra de Álvarez); (9) *C. magnipes*; (10) *C. mosaueri*; (11) *C. chondrostega*; (12) *C. terrestris*; (13) *C. arboreus* (Zacualtipán); (14) *C. arboreus* (Zilacatipan); (15) *C. dimidiatus*; (16) *C. chico*; (17) *C. melipona* (Xicotepec); (18) *C. melipona* (Cuetzalan); (19) *C. sp. G*; (20) *C. casasi*; (21) *C. aureus*; (22) *C. totonacus*; (23) *C. lavae*; (24) *C. nubilus* (Tlalnehuayocan); (25) *C. nubilus* (Coxmatla); (26) *C. perotensis* (Las Lajas); (27) *C. perotensis* (Llanillo redondo); (28) *C. perotensis* (Conejo); (29) *C. chiropterus* (Huatusco); (30) *C. ceronorum* (Xometla); (31) *C. ceronorum* (Texmalaquilla); (32) *C. orculus* (Amecameca); (33) *C. orculus* (Amecameca); (34) *C. orculus* (Ciudad de México); (35) *C. orculus* (Bosque de Tlalpan); (36) *C. orculus* (Desierto de los Leones); (37) *C. orculus* (Ajusco); (38) *C. orculus* (Lagunas de Zempoala); (39) *C. chiropterus* (La Esperanza); (40) *C. chiropterus* (Yolox) and (41) *C. sp. K*.

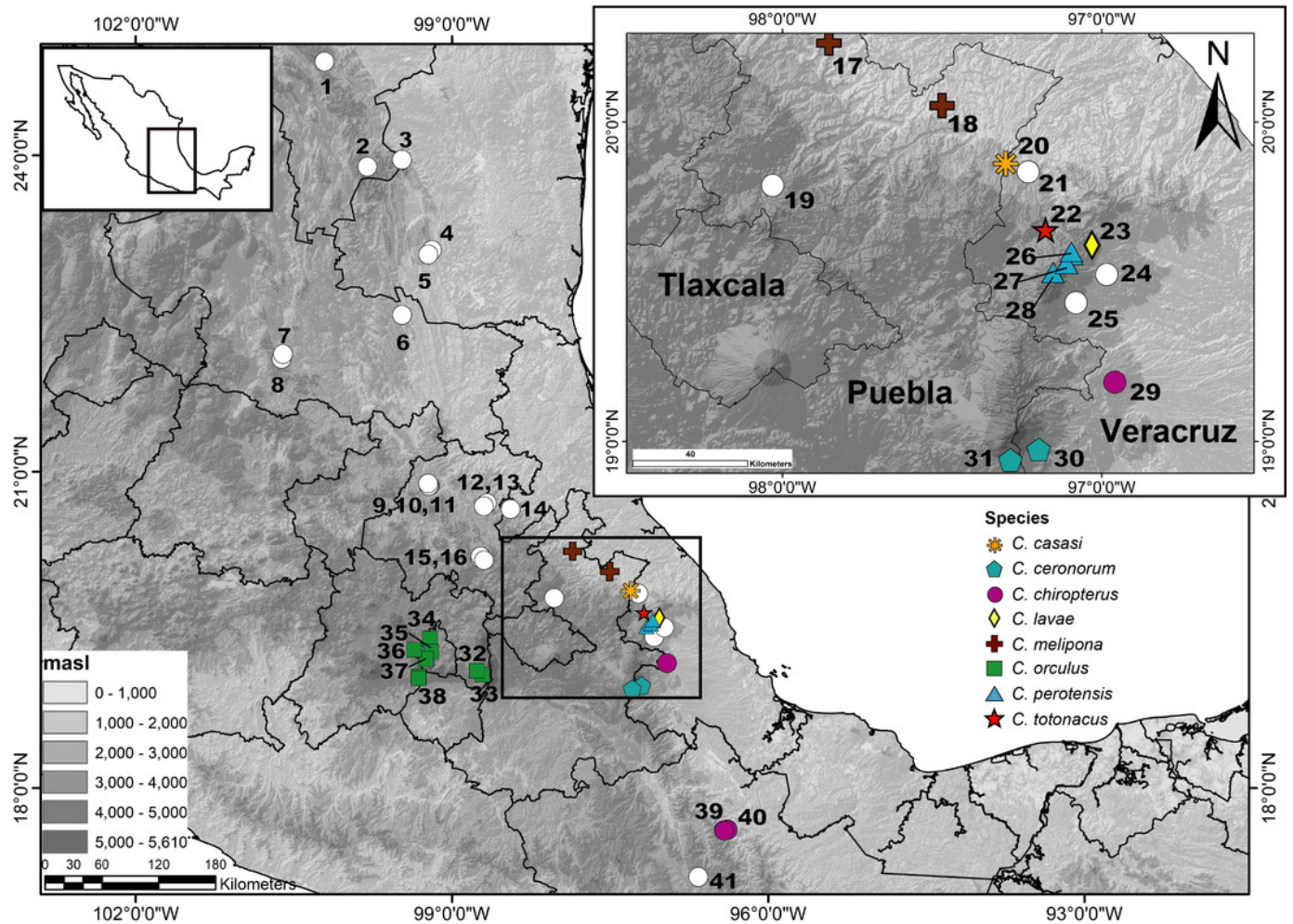



Figure 2

Skull of the holotype of *Chiropterotriton casasi* seen in dorsal, ventral and lateral views

Figure 2: Skull of the holotype of *Chiropterotriton casasi* seen in dorsal, ventral and lateral views. Images are derived from a µCT scan of MVZ 92874, an adult male. Arrows point to the septomaxillary bone. Abbreviations: AP, ascending process of the premaxilla; CO, columella; CP, coronoid process of the prearticular; DE, dentary; FP, facial process of the maxilla; FR, frontal; MX, maxilla; NA, nasal; NL, foramen of the nasolacrimal duct; OC, otic capsule; OR, orbitosphenoid; PA, parietal; PF, prefrontal; PM, premaxilla; PO, preorbital process of the vomer; PR, prearticular; PS, parasphenoid; QU, quadrate; SQ, squamosal; VO, vomer. Scale bar, 1 mm.

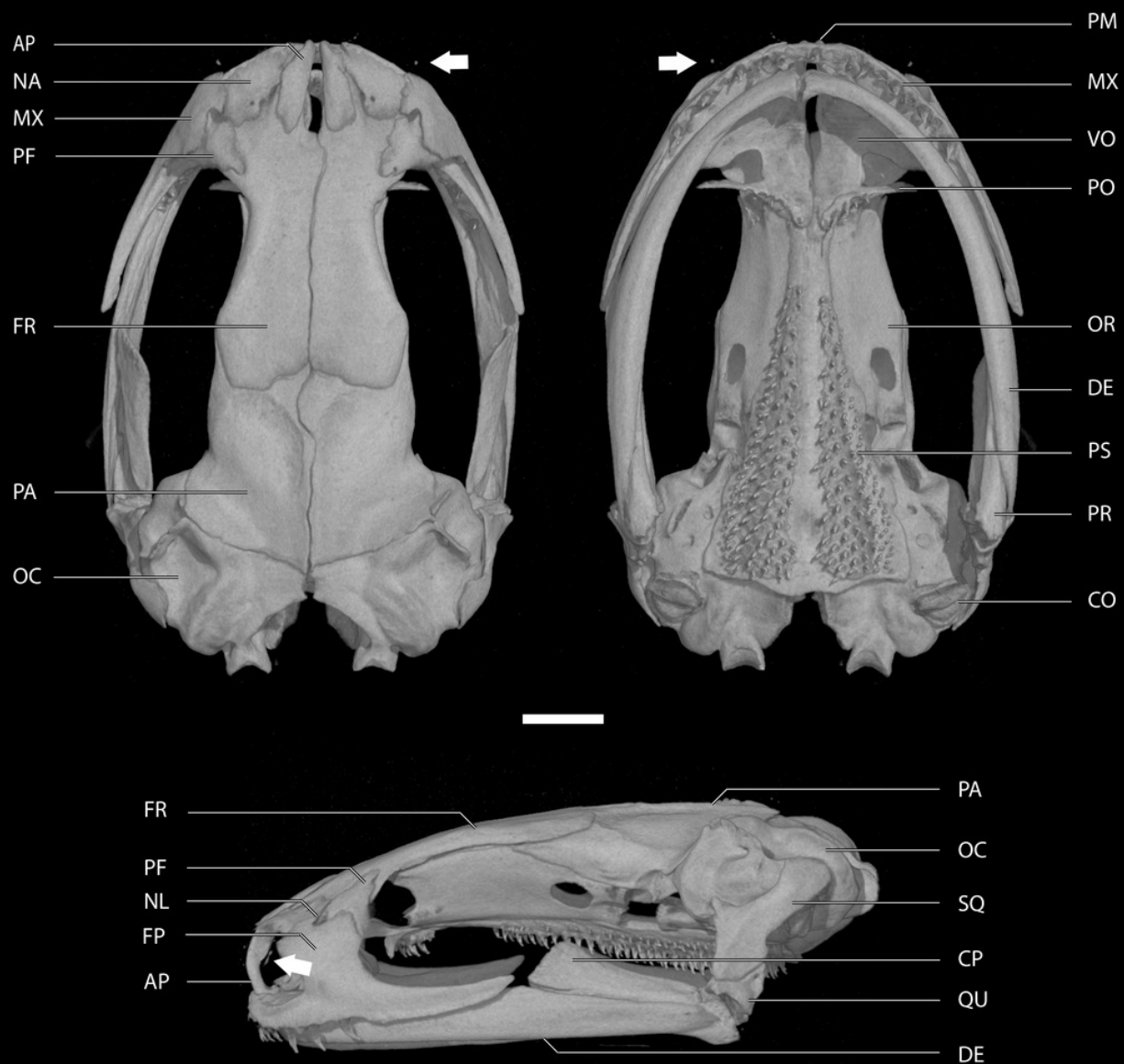



Figure 3

Maximum likelihood (ML) phylogeny of the genus *Chiropterotriton* based on two mitochondrial markers

Maximum likelihood (ML) phylogeny of the genus *Chiropterotriton* based on two mitochondrial markers. Both ML and Bayesian measures of nodal support are indicated by bootstrap proportions (BS; above) and posterior probabilities (PP; below), respectively. Asterisks indicate statistically significant support in both analyses (PP > 0.95, BS > 70). Numbers in parentheses refer to localities from Figure 1.

Thorius sp. GP1650
Aquiloeurycea cephalica IBH30253
C. cracens IBH28192 (5)
* C. cieloensis IBH28190 (4)
C. cieloensis IBH28181 (4)
* C.arboreus IBH28191 (13)
C.arboreus IBH22847 (14)
* C. multidentatus IBH28193 (6)
* C. multidentatus IBH30104 (6)
C. multidentatus IBH28194 (6)
* C. multidentatus IBH28177 (8)
* C. multidentatus IBH30102 (8)
C. multidentatus IBH23111 (7)
* C. infernalis MVZ269665 (3)
C. infernalis IBH29575 (3)
C. mosaueri IBH28179 (10)
* C. chondrostega IBH28195 (11)
C. chondrostega IBH30098 (11)
* C. magnipes IBH30093 (9)
C. magnipes IBH28176 (9)
C. priscus IBH22367 (1)
* C. miquihuanus IBH30330 (2)
C. miquihuanus IBH30329 (2)
* C. terrestris GP215 (12)
C. chico MVZ200679 (16)
* C. dimidiatus IBH22344 (15)
C. dimidiatus IBH28196 (15)
* C. totonacus IBH31030 (22)
C. totonacus IBH31031 (22)
C. ceronorum IBH30987 (30)
C. ceronorum IBH30988 (30)
C. ceronorum MVZ201387 (31)
C. ceronorum MVZ201389 (31)
* C. lavae IBH22360 (23)
C. lavae IBH22369 (23)
C. lavae IBH22349 (23)
C. lavae IBH22351 (23)
C. perotensis IBH31033 (28)
C. perotensis IBH31032 (28)
C. perotensis IBH31036 (28)
C. perotensis IBH31034 (28)
C. perotensis IBH31035 (28)
* C. perotensis IBH31037 (27)
C. perotensis IBH22568 (26)
C. perotensis IBH22395 (26)
C. perotensis IBH23066 (26)
C. perotensis IBH31038 (27)
C. perotensis IBH31039 (27)
C. sp. K MVZ173231(41)
* C. sp. G MVZ178700 (19)
C. sp. G MVZ178703 (19)
* C. orculus IBH26478 (37)
C. orculus IBH30765 (33)
C. orculus IBH22866 (32)
C. orculus IBH30746 (32)
C. orculus IBH30943 (33)
C. orculus IBH22210 (34)
C. orculus IBH29851 (38)
C. orculus MVZ138672 (36)
C. orculus AMH300 (36)
C. orculus IBH31023 (38)
C. orculus EPR (35)
C. melipona IBH30112 (18)
* C. melipona MVZ178706 (17)
C. melipona MVZ178707 (17)
C. melipona MVZ200723 (17)
* C. aureus IBH31042 (21)
C. aureus IBH31044 (21)
* C. nubilus CARIE0740 (24)
C. nubilus IBH31048 (25)
* C. chiropterus CARIE0777 (29)
C. chiropterus CARIE0719 (29)
C. chiropterus IBH30099 (40)
C. chiropterus IBH30088 (40)
C. chiropterus IBH22736 (40)
C. chiropterus GP088 (39)
C. chiropterus IBH22550 (39)

32
0.8
28
0.81
33
46
0.73
12
61
0.81
62
0.68
81
0.84
73
0.95
75
0.83
70
0.88
58
0.96

0.04

Figure 4

Photographs of heads, hands and feet of preserved specimens of eight species of *Chiropterotriton*

Photographs of heads, hands and feet of preserved specimens of eight species of *Chiropterotriton*. (A) *C. ceronorum,* holotype, USNM 224212; (B) *C. perotensis,* paratype, MVZ 186711; (C) *C. totonacus,* holotype, MVZ 163945; (D) *C. melipona,* paratype, MVZ 178706; (E) *C. casasi,* holotype, MVZ 92874; (F) *C. chiropterus,* neotype, MVZ 85590; (G) *C. orculus,* MVZ 138776; (H) *C. lavae,* MVZ 106436. Right hands and feet are seen in dorsal view.

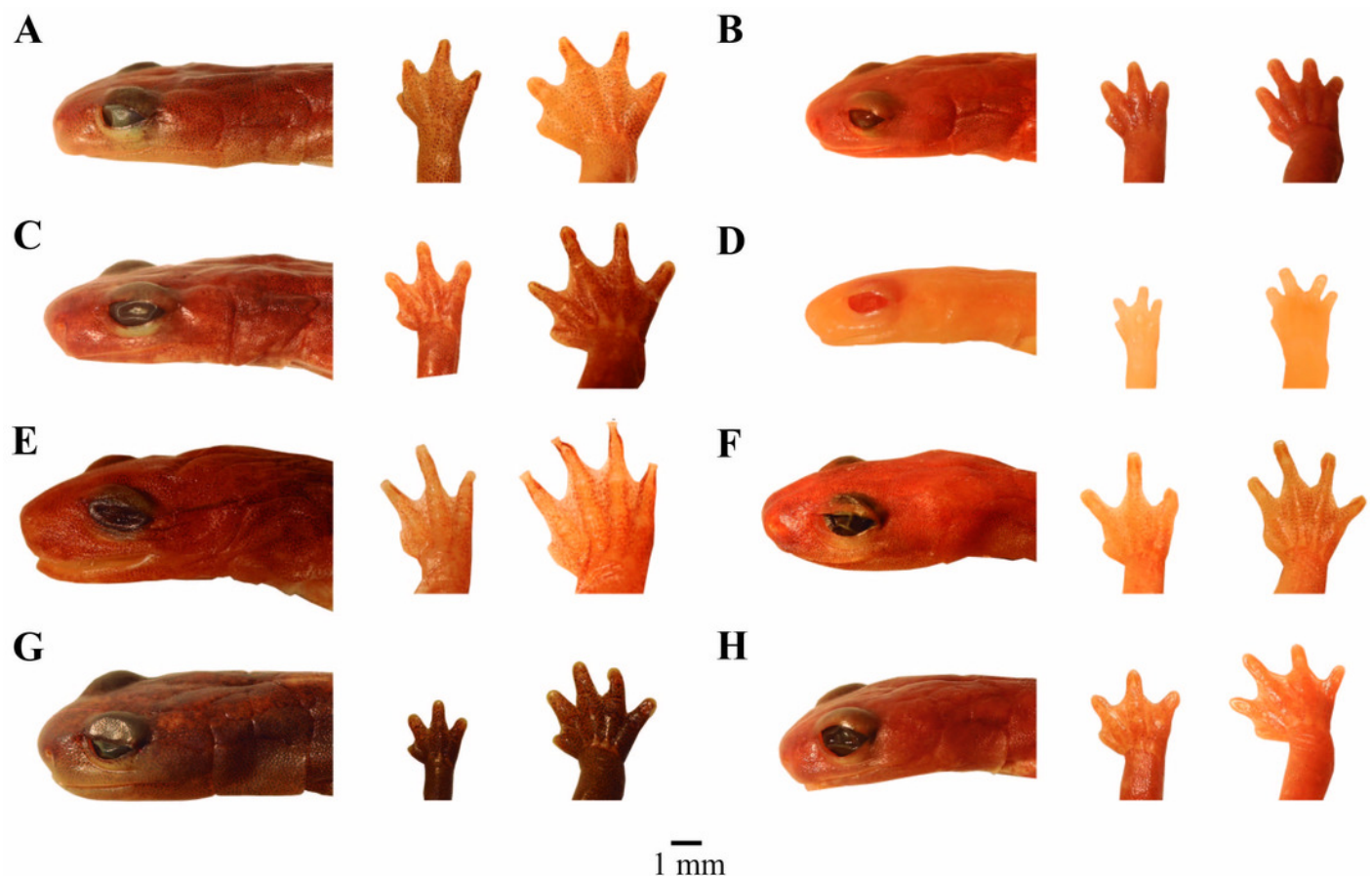



Figure 5

Photographs of live and preserved specimens of eight species of *Chiropterotriton*.

Photographs of live and preserved specimens of eight species of *Chiropterotriton*.

(A) *C. ceronorum*, IBH 30988; (B) *C. perotensis*, IBH 30745; (C) *C. totonacus*, IBH 31031; (D) *C. melipona*, IBH 30112; (E) *C. casasi*, paratype, MVZ 92876; (F) *C. chiropterus*, CARIE 0719; (G) *C. orculus*, IBH 30997; (H) *C. lavae*, IBH 22365.

Figure 6

Skulls of eight *Chiropterotriton* species seen in dorsal view

Skulls of eight *Chiropterotriton* species seen in dorsal view. A: *C. casasi*—holotype, MVZ 92874, an adult male; B: *C. ceronorum*—holotype, USNM 224212, an adult male; C: *C. lavae*—neotype, MVZ 163912, an adult male; D: *C. melipona*—paratype, MVZ 178706, an adult male; E: *C. orculus*—neotype, MVZ 138783, an adult male; F: *C. perotensis*—paratype, MVZ 200693, an adult male; G: *C. totonacus*—holotype, MVZ 163945, an adult female; H: *C. chiropterus*—MVZ 85602, an adult male. Arrows point to the prominent frontoparietal fontanelle in the cranial roof in D and F, to the unusually narrow ascending processes of the premaxillary bone at the rostral end of the skull in D and G, and to the tiny septomaxillary bones adjacent to the external nares in E and H. All skulls are depicted at the same length; scale bar, 1 mm. Anterior is at the top. Images are derived from μCT scans.

A casasi ―

B ceronorum ―

C lavae ―

D melipona ―

E orculus ―

F perotensis ―

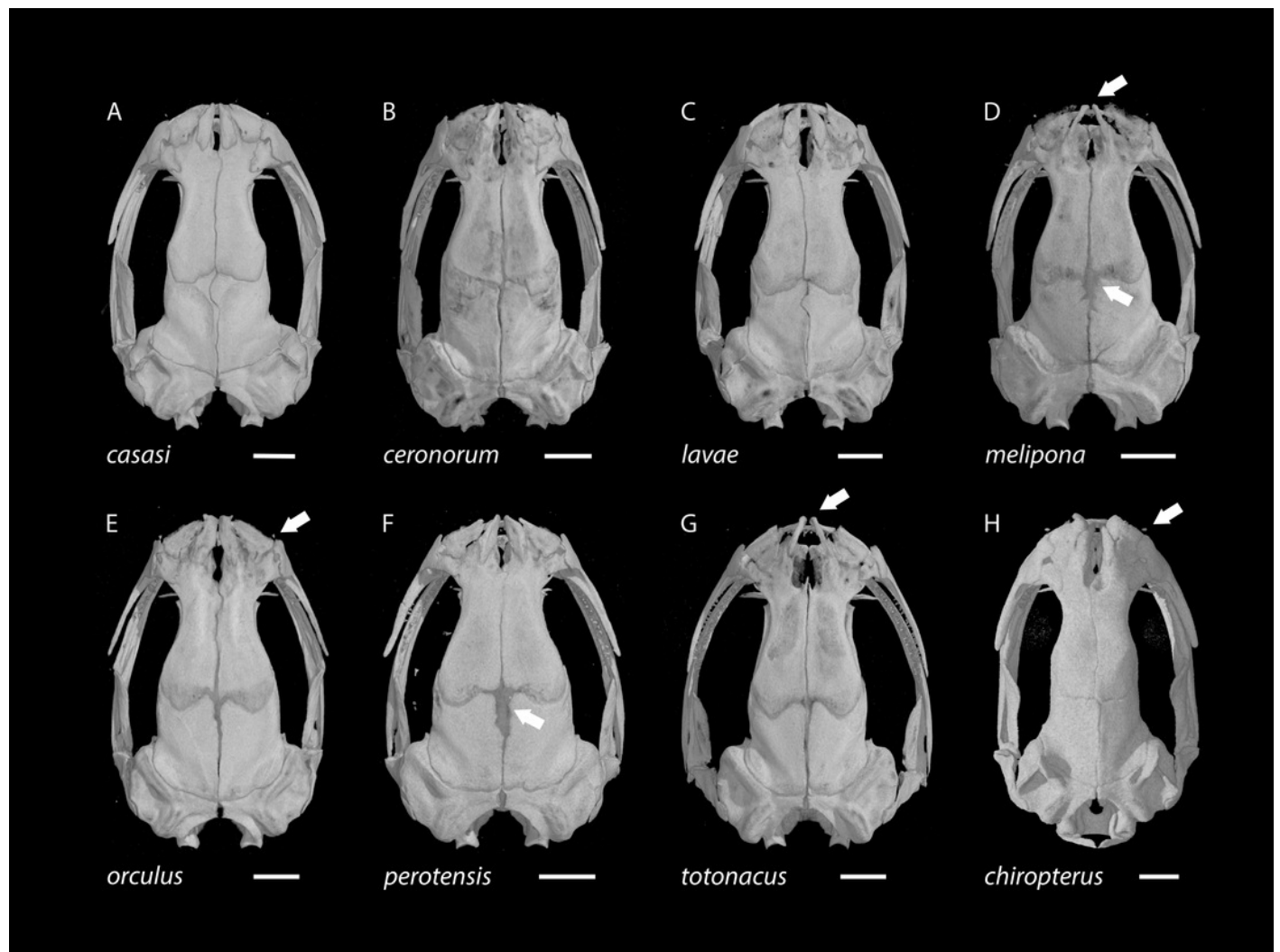
G totonacus ―

H chiropterus ―

Figure 7

Skulls of eight *Chiropterotriton* species seen in ventral view.

Skulls of eight *Chiropterotriton* species seen in ventral view. A: *C. casasi*—holotype, MVZ 92874, an adult male; B: *C. ceronorum*—holotype, USNM 224212, an adult male; C: *C. lavae*—neotype, MVZ 163912, an adult male; D: *C. melipona*—paratype, MVZ 178706, an adult male; E: *C. orculus*—neotype, MVZ 138783, an adult male; F: *C. perotensis*—paratype, MVZ 200693, an adult male; G: *C. totonacus*—holotype, MVZ 163945, an adult female; H: *C. chiropterus*—MVZ 85602, an adult male. Arrows point to the long versus short preorbital process of the vomer in A and F, respectively; and to the unusually small parasphenoid tooth patch in C versus the much larger patch in F. All skulls are depicted at the same length; scale bar, 1 mm. Anterior is at the top. Images are derived from µCT scans.

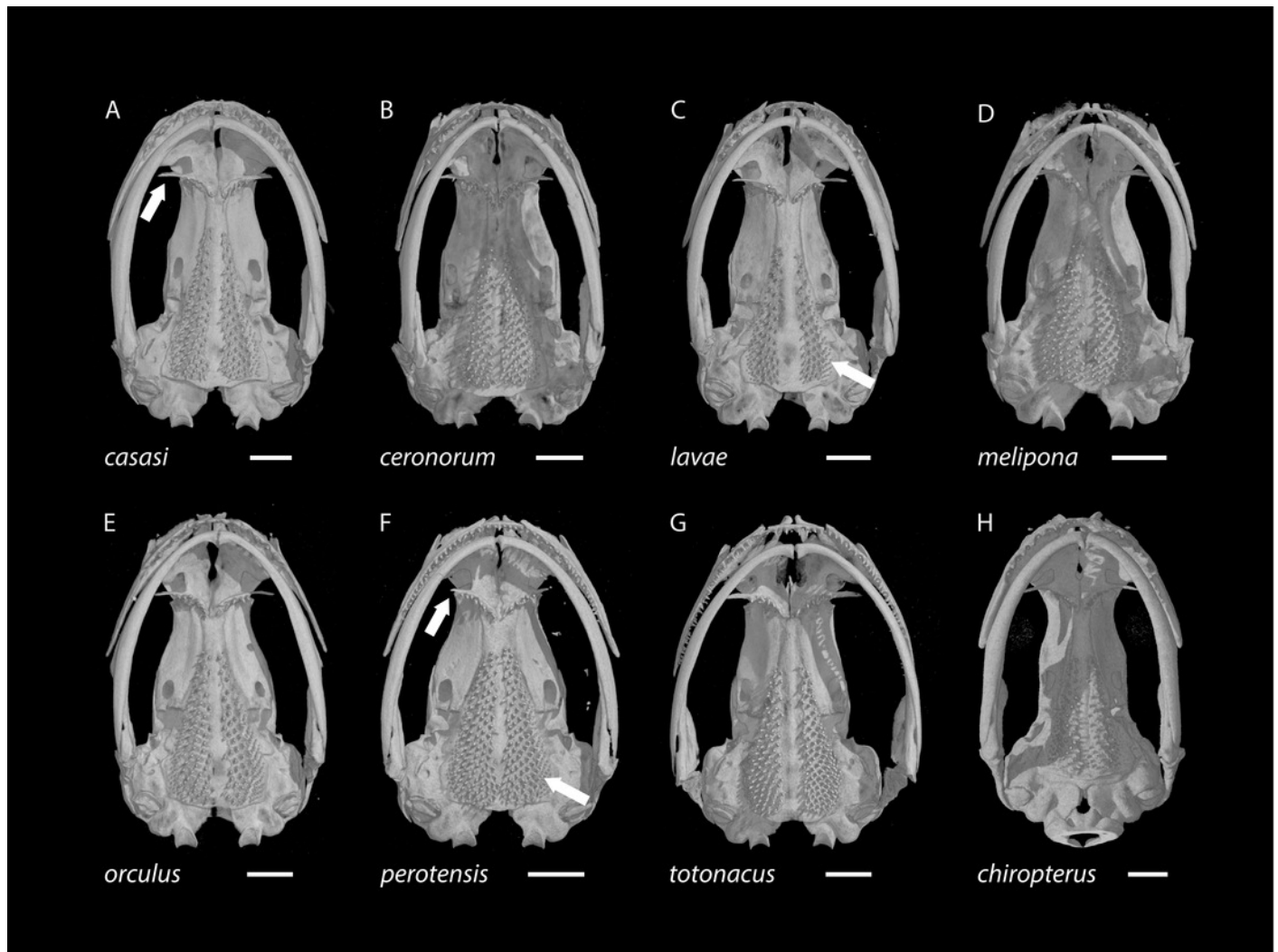
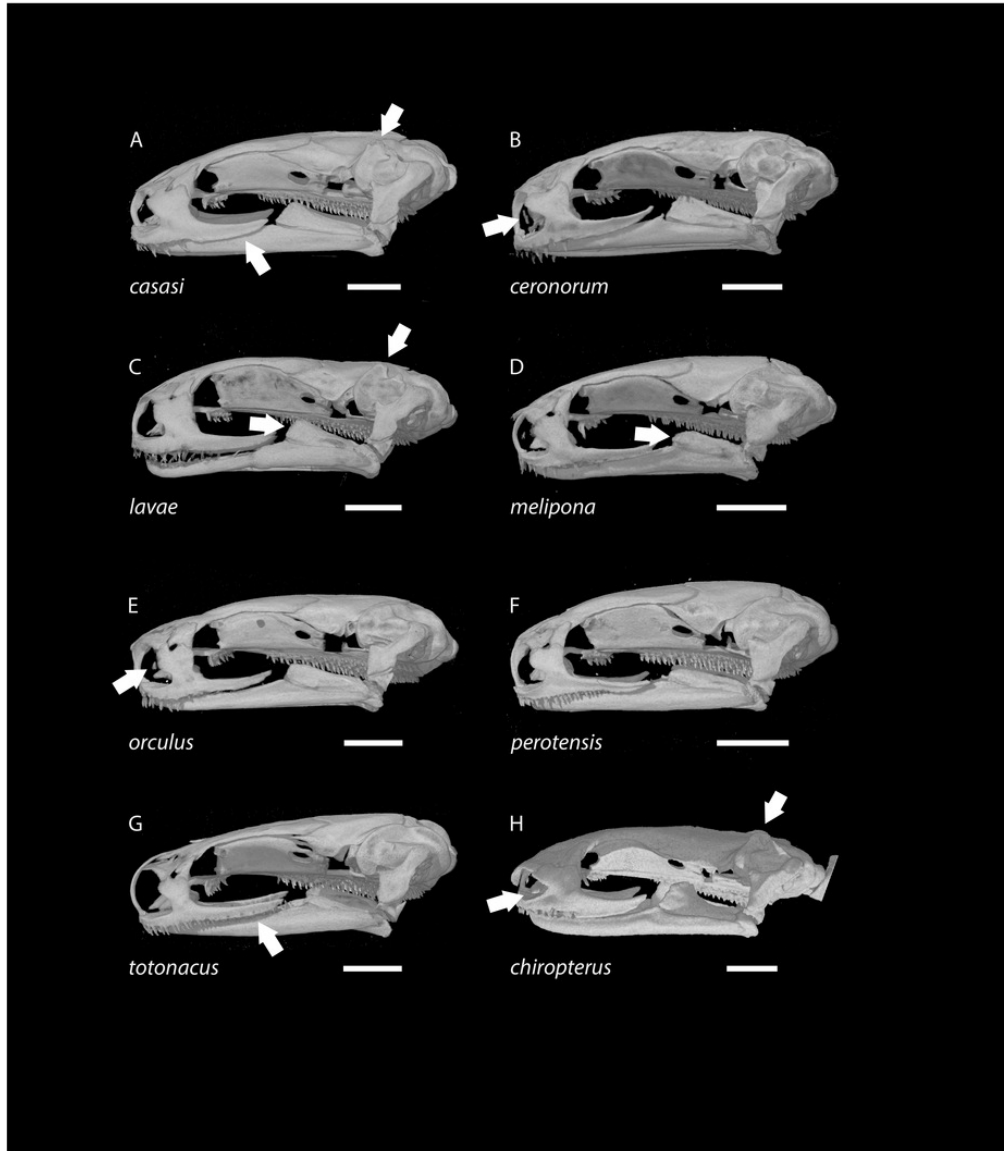



Figure 8

Skulls of eight *Chiropterotriton* species seen in lateral view

Skulls of eight *Chiropterotriton* species seen in lateral view. A: *C. casasi*—holotype, MVZ 92874, an adult male; B: *C. ceronorum*—holotype, USNM 224212, an adult male; C: *C. lavae*—neotype, MVZ 163912, an adult male; D: *C. melipona*—paratype, MVZ 178706, an adult male; E: *C. orculus*—neotype, MVZ 138783, an adult male; F: *C. perotensis*—paratype, MVZ 200693, an adult male; G: *C. totonacus*—holotype, MVZ 163945, an adult female; H: *C. chiropterus*—MVZ 85602, an adult male. Arrows point to prominent dorsal crests on the otic capsule in A, C and H; to the high versus low coronoid process on the prearticular bone of the lower jaw in C and D, respectively; to the tiny septomaxillary bones in B, E and H; and to the posterior portion of the maxillary bone, which typically is dorsoventrally expanded and edentulous in males (A) versus narrow and toothed in females (G). All skulls are depicted at the same length; scale bar, 1 mm. Anterior is to the left. Images are derived from μCT scans.

Voucher information and Genbank numbers

Voucher information and Genbank numbers for specimens used for phylogenetic analyses from Colección Nacional de Anfibios y Reptiles, Instituto de Biología, UNAM (IBH), Museum of Vertebrate Zoology (MVZ) and Colección de Referencia de Anfibios y Reptiles del Instituto de Ecología, A. C. Numbers in parentheses correspond to geographic location shown in Figure 1

1 Table 1. Voucher information and Genbank numbers for specimens used for phylogenetic
2 analyses from Colección Nacional de Anfibios y Reptiles, Instituto de Biología, UNAM (IBH),
3 Museum of Vertebrate Zoology (MVZ) and Colección de Referencia de Anfibios y Reptiles del
4 Instituto de Ecología, A. C. Numbers in parentheses correspond to geographic location shown in
5 Figure 1.

Species	Voucher Number	Locality	16S Genbank	COI Genbank
C. arboreus	IBH 28191	Hidalgo: 6.8 km SW (by rd) of Zacualtipán on road to Tianguistengo (13)	MK 335386	MK 335232
C. arboreus	IBH 22847	Veracruz: 3.2 km S Zilacatipan (14)		–
C. aureus	IBH 31042	Veracruz: 6.5 km (by air) N from Atzalan, ejido de desarrollo urbano Quetzalcoatl (21)	MK 335396	MK 335242
C. aureus	IBH 31044	Veracruz: 6.5 km (by air) N from Atzalan, ejido de desarrollo urbano Quetzalcoatl (21)	MK 335397	MK 335243
C. ceronorum	IBH 30987	Veracruz: 1.1 km N Xometla (30)		
C. ceronorum	IBH 30988	Veracruz: 1.1 km N Xometla (30)		
C. ceronorum	MVZ 201387	Puebla: Santa Cruz de Texmalaquilla (31)	AY 522488	–
C. ceronorum	MVZ 201389	Puebla: Santa Cruz de Texmalaquilla (31)	AY 522487	–
C. chico	MVZ 200679	Hidalgo: 3.8 km S Mineral del Chico (16)	AY 522471	–
C. chiropterus	CARIE 0777	Veracruz: Huatusco (29)	MK 335407	MK 335253
C. chiropterus	CARIE 0719	Veracruz: Huatusco (29)	MK 335408	–
C. chiropterus	IBH 30099	Oaxaca: San Bernardo, 4.8 km SW (by rd) of La Esperanza on MX 177 (40)	MK 335409	MK 335254
C. chiropterus	IBH 22736	Oaxaca: San Bernardo, ca. 5 km SW (by rd) of La Esperanza on MX 175 (40)		–
C. chiropterus	IBH 30088	Oaxaca: ca. 400 m from MX 175 on road to San Isidro Yolox (40)		–
C. chiropterus	IBH 22550	Oaxaca: La Galera, 11.0 km SW (by rd) of La Esperanza on MX175 (39)		–
C. chiropterus	GP 088	Oaxaca: 67 Km N Guelatao, trail to San Isidro, La Esperanza (39)	AY 522490	–
C. chondrostega	IBH 28195	Hidalgo: 1.0 km S (by rd) of La Encarnación on road to MX 85, Parque Nacional los Marmoles (11)		–
C. chondrostega	IBH 30098	Hidalgo: 1.0 km S (by rd) of La Encarnación on road to MX 85, Parque Nacional los Marmoles (11)	MK 335383	MK 335229
C. cieloensis	IBH 28181	Tamaulipas: 0.2 km E (by air) of Rancho El Cielo, 6.9 km NNW (by air) of center of Gómez Farías, Reserva de la Biosfera El Cielo (4)	MK 335385	MK 335231
C. cieloensis	IBH 28190	Tamaulipas: 0.2 km E (by air) of Rancho El Cielo, 6.9 km NNW (by air) of center of Gómez Farías, Reserva de la Biosfera El Cielo (4)		–

C. cracens	IBH 28192	Tamaulipas: Road from Alta Cima to San Jose, 1.3 km NE (by air) of San Jose, Reserva de la Biosfera El Cielo (5)	MK 335384	MK 335230
C. dimidiatus	IBH 22344	Hidalgo: 4.3 km N Hwy 105 at Mineral del Monte (15)		–
C. dimidiatus	IBH 28196	Hidalgo: 4.1km S (by rd) of Mineral del Chico on road to Pachuca, Parque Nacional El Chico (15)	MK 335390	MK 335236
C. infernalis	MVZ 269665	Tamps: Cueva del Brinco, Conrado Castillo, ca. 43.5 km SW (by rd) of Ejido Guayabas (3)	MK 335382	MK 335228
C. infernalis	IBH 29575	Tamaulipas: Conrado Castillo, ca. 43.5 km SW (by rd) of Ejido Guayabas (3)		
C. lavae	IBH 22349	Veracruz: 200 m N Hwy 140 at La Joya (23)		–
C. lavae	IBH 22351	Veracruz: 200 m N Hwy 140 at La Joya (23)		–
C. lavae	IBH 22360	Veracruz: 200 m N Hwy 140 at La Joya (23)		–
C. lavae	IBH 22369	Veracruz: 200 m N Hwy 140 at La Joya (23)	MK 335393	MK 335239
C. magnipes	IBH 28176	Hidalgo: "El Coní", 900 m SSE of center of Durango, Municipio Zimapan, Parque Nacional los Marmoles (9)	MK 335387	MK 335233
C. magnipes	IBH 30093	Hidalgo: "El Coní", 900 m SSE of center of Durango, Municipio Zimapan, Parque Nacional los Marmoles (9)		–
C. melipona	IBH 30112	Puebla: 7.1 km N (by rd) of center of Cuetzalan on road to Yohualichán (18)	MK 335410	MK 335255
C. melipona	MVZ 178706	Puebla: 3.9 km S Xicotepec de Juárez (17)	AY 522477	–
C. melipona	MVZ 200723	Puebla: Xicotepec de Juárez (17)	AY 522478	–
C. melipona	MVZ 178707	Puebla: Xicotepec de Juárez (17)	AY 522479	–
C. miquihuanus	IBH 30329	Nuevo León: 1.8 km S (by rd) of La Encantada on road from La Bolsa to Zaragoza (2)	MK 335381	MK 335227
C. miquihuanus	IBH 30330	Nuevo León: 22.6 km N (by rd) of La Bolsa on road to Zaragoza (2)		–
C. mosaueri	IBH 28179	Hidalgo: "El Coní", 900 m SSE of center of Durango, Municipio Zimapan, Parque Nacional los Marmoles (10)	MK 335388	MK 335234
C. multidentatus	IBH 28177	San Luis Potosí: Cueva el Madroño, 900 m NW (by air) of entrance to Valle de los Fantasmas on MX 70, Sierra de Alvarez (8)	MK 335416	–
C. multidentatus	IBH 30102	San Luis Potosí: Cueva el Madroño, 900 m NW (by air) of entrance to Valle de los Fantasmas on MX 70, Sierra de Alvarez (8)	MK 335417	–
C. multidentatus	IBH 28193	San Luis Potosí: 26.2 km E (by rd) of center of Ciudad del Maíz on MX 80, at turnoff to RMO Las Antenas San Luis Potosí (6)	MK 335412	–
C. multidentatus	IBH 30104	San Luis Potosí: 26.2 km E (by rd) of center of Ciudad del Maíz on MX 80, at turnoff to RMO Las Antenas San Luis Potosí (6)	MK 335414	–

C. multidentatus	IBH 28194	San Luis Potosí: 26.2 km E (by rd) of center of Ciudad del Maíz on MX 80, at turnoff to RMO Las Antenas San Luis Potosí (6)	MK 335413	–
C. multidentatus	IBH 23111	San Luis Potosí: Rancho Borbortón (7)	MK 335415	–
C. nubilus	IBH 31048	Veracruz: 8.2 km W from Xico, Coxmatla (25)	MK 335402	MK 335248
C. nubilus	CARIE 0740	Veracruz: Bosque Rancho Viejo, Tlalnehuayocan (24)	MK 335406	MK 335252
C. orculus	IBH 30765	Estado de México: Amecameca, road to Popocatepetl volcano (33)	MK 335391	MK 335237
C. orculus	IBH 30746	Estado de México: Amecameca, road to Popocatepetl volcano (32)	MK 335392	MK 335238
C. orculus	IBH 30943	Estado de México: Amecameca, road to Popocatepetl volcano (33)		–
C. orculus	IBH 22866	Estado de México: Amecameca, road to Popocatepetl volcano (32)		–
C. orculus	IBH 22210	Ciudad de Mexico: Colonia Prolongación Miguel Hidalgo (34)		–
C. orculus	AMH 300	Ciudad de Mexico: Desierto de los Leones (36)		–
C. orculus	EPR	Ciudad de Mexico: Bosque de Tlalpan (35)		–
C. orculus	IBH 29851	Morelos: Parque Nacional Lagunas de Zempoala (38)		–
C. orculus	IBH 31023	Morelos: Parque Nacional Lagunas de Zempoala (38)		–
C. orculus	IBH 26478	Ciudad de Mexico: El Ajusco, km 29.4 from Picacho-Ajusco road (37)		–
C. orculus	MVZ 138672	Ciudad de Mexico: Desierto de Los Leones National Park, 8.8 km [rd.] SW La Venta by Mexico Hwy. 15 (36)	AY 522442	–
C. perotensis	IBH 22395	Veracruz: 15.9 km on microondas road, Las Vigas (26)		–
C. perotensis	IBH 22568	Veracruz: Microondas las Lajas (26)	KP 886893	–
C. perotensis	IBH 23066	Veracruz: 15.9 km on microondas road, Las Vigas (26)		–
C. perotensis	IBH 31032	Veracruz: Conejo, road to the peak of Cofre de Perote (28)		–
C. perotensis	IBH 31033	Veracruz: Conejo, road to the peak of Cofre de Perote (28)		–
C. perotensis	IBH 31034	Veracruz: Conejo, road to the peak of Cofre de Perote (28)		–
C. perotensis	IBH 31035	Veracruz: Conejo, road to the peak of Cofre de Perote (28)		
C. perotensis	IBH 31036	Veracruz: Conejo, road to the peak of Cofre de Perote (28)		–
C. perotensis	IBH 31037	Veracruz: 2 km (by air) al NE de Llanillo redondo camino a Valle Alegre (27)		–

C. perotensis	IBH 31038	Veracruz: 2 km (by air) al NE de Llanillo redondo camino a Valle Alegre (27)		–
C. perotensis	IBH 31039	Veracruz: 2 km (by air) al NE de Llanillo redondo camino a Valle Alegre (27)		
C. priscus	IBH 22367	Nuevo León: 19.4 km W 18 de Marzo, Cerro Potosí (1)	MK 335380	MK 335226
C. terrestris	GP 215	Hidalgo: 5.3 km N Hwy 105 at Zacualtipan (12)	MK 335389	MK 335235
C. totonacus	IBH 31030	Veracruz: El Polvorín, 5 km SW of Villa Aldama (22)		
C. totonacus	IBH 31031	Veracruz: El Polvorín, 5 km SW of Villa Aldama (22)		
C. sp. G	MVZ 178700	Puebla: 4 km S Chignahuapan (19)	AY 522480	–
C. sp. G	MVZ 178703	Puebla: 4 km S Chignahuapan (19)	AY 522481	–
C. sp. K	MVZ 173231	Oaxaca: Cerro San Felipe (41)	AY 522493	–
Aquiloeurycea cephalica	IBH 30253	Hidalgo: 1.0 km S (by rd) of La Encarnación on road to MX 85, Parque Nacional los Mármoles	MK 335378	–
Thorius sp.	IBH 30942	Oaxaca: Santa María Chilchotla, Sierra Mazateca.		–

Mean ± standard deviation (above) and range (below) of morphometric variables

Mean ± standard deviation (above) and range (below) of morphometric variables from males and females of *C. aureus*, *C. nubilus*, *C. ceronorum*, *C. perotensis*, *C. totonacus*, C. *melipona*, *C. casasi*, *C. chiropterus*, *C. orculus* and *C. lavae*. Measurements are given in millimeters (mm), except TL/SLV (proportional value), LI (limb interval), and tooth counts.

males	C. aureus N = 1	C. nubilus N = 1	C. ceronorum N = 10	C. perotensis N = 12	C. totonacus N = 10	C. melipona N = 4	C. casasi N = 4	C. chiropterus N = 8	C. orculus N = 10	C. lavae N = 10
SVL	28.5	29.4	33.9±1.54 (30.6–36.2)	29.7±1.92 (26.5–32.8)	35.7±1.96 (32.0–38.6)	29.2±2.25 (26.4–31.4)	37.8±3.10 (34.5–42.0)	37.5±0.98 (36.1–38.8)	35.9±1.36 (33.6–38.9)	32.4±0.92 (31.-33.8)
TL	36.5	40.2	33.9±1.99 (30.4–37.7)	30.9±3.06 (26.0–35.2) N = 8	41.1±3.20 (34.3–44.9) N = 9	33.9±3.37 (31.0–38.2)	39.1±3.29 (36.8–42.9) N = 3	47.3±3.24 (42.6–52.3) N = 7	36.6±2.87 (33.3–41.0) N = 9	38.5±2.11 (36.2–42.3)
TL/SVL	1.28	1.37	1.00±0.06 (0.89–1.12)	1.03±0.08 (0.92–1.16) N = 8	1.16±0.10 (0.92–1.24) N = 9	1.16±0.05 (1.10–1.22)	1.04±0.13 (0.90–1.15) N = 3	1.25±0.08 (1.13–1.38) N = 7	1.02±0.08 (0.86–1.15) N = 9	1.19±0.06 (1.11–1.27)
AX	15.5	15.9	16.9±0.70 (15.5–17.9)	15.5±0.93 (14.2–17.0)	18.3±1.30 (16.7–20.4)	15.7±1.30 (14.0–17.0)	19.8±0.46 (19.4–20.4)	19.6±0.59 (18.7–20.8)	18.6±1.04 (17.1–20.5)	16.2±0.87 (14.7–17.4)
FLL	5.9	6.4	8.9±0.69 (7.2–10.0)	6.8±0.59 (5.5–7.8)	10.0±0.72 (8.9–10.9)	6.3±0.86 (5.1–7.0)	9.9±0.59 (9.4–10.7)	9.1±0.44 (8.2–9.5)	8.9±0.65 (7.4–9.6)	9.3±0.59 (8.4–10.2)
HLL	7.5	7.1	9.4±0.83 (7.5–10.3)	7.2±0.61 (6.1–8.2)	11.0±1.00 (9.4–12.2)	7.2±0.83 (6.1–7.9)	11.5±0.74 (11.1–12.6)	10.3±0.47 (9.5–10.8)	9.3±0.64 (8.2–10.4) N = 9	9.9±0.72 (8.5–11.0)
HL	6.4	6.6	7.5±0.55 (6.3–8.2)	6.6±0.33 (6.1–7.1)	8.5±0.64 (7.7–9.5)	6.3±0.52 (5.5–6.6)	8.3±0.60 (7.5–8.8)	8.1±0.41 (7.7–8.9)	7.4±0.47 (6.7–8.1)	7.5±0.33 (7.2–8.1)
HW	4.0	4.0	5.1±0.35 (4.3–5.5)	4.2±0.18 (3.9–4.5)	5.2±0.29 (4.8–5.7)	4.3±0.33 (3.9–4.6)	5.8±0.45 (5.3–6.3)	5.6±0.22 (5.4–6.0)	5.0±0.35 (4.5–5.5)	4.9±0.31 (4.5–5.6)
HD	1.8	2.0	2.5±0.17 (2.1–2.7)	2.0±0.18 (1.7–2.3)	2.4±0.34 (2.1–3.3)	2.3±0.22 (2.1–2.6)	2.5±0.28 (2.2–2.8)	2.7±0.07 (2.6–2.8)	2.4±0.13 (2.2–2.7)	2.5±0.19 (2.3–2.9)
SW	3.4	3.4	3.6±0.29 (3.0–3.9)	2.7±0.28 (2.3–3.4)	3.6±0.28 (3.2–4.0)	3.3±0.26 (3.1–3.7)	3.5±0.37 (3.1–3.8)	4.0±0.35 (3.2–4.4)	3.4±0.30 (3.1–4.0)	3.1±0.30 (2.6–3.5)
IN	1.0	1.2	2.3±0.18 (2.0–2.6)	1.7±0.26 (1.1–2.0)	2.4±0.23 (1.9–2.7)	1.4±0.13 (1.3–1.6)	2.1±0.30 (1.7–2.4)	1.9±0.13 (1.7–2.1)	2.2±0.19 (1.9–2.5)	2.3±0.20 (1.9–2.5)
FW	2.4	2.6	3.8±0.44 (2.9–4.6)	2.6±0.33 (2.1–3.1)	4.2±0.45 (3.5–4.9)	2.4±0.27 (2.2–2.8)	3.7±0.19 (3.6–4.0)	3.7±0.33 (3.3–4.4)	3.2±0.22 (2.8–3.5)	3.7±0.39 (3.1–4.2)

LI	2.0	2.0	0.0±0.41 (-0.5–1.0)	2.5±0.67 (1.0–3.0)	-0.6±0.70 (-1.0–1.0)	2.3±0.29 (2.0–2.5)	0.8±0.50 (0.0–1.0)	0.3±0.53 (-0.5–1.0)	1.9±0.88 (0.0–3.0)	-0.6±0.52 (-1.0–0.0)
PMT	4.0	7.0	3.4±0.97 (3.0–6.0)	2.8±0.97 (0.0–4.0)	4.8±0.63 (4.0–6.0)	2.3±1.50 (1.0–4.0)	3.5±1.29 (2.0–5.0)	3.6±1.30 (2.0–5.0)	2.7±0.82 (2.0–4.0)	3.3±2.00 (0.0–6.0)
MT	10.0	13.0	11.0±3.30 (7.0–18.0)	7.2±4.73 (2.0–17.0)	32.9±7.80 (18.0–48.0)	9.5±2.38 (7.0–12.0)	9.0±2.94 (6.0–13.0)	12.6±3.46 (9.0–17.0)	8.2±2.25 (5.0–11.0)	7.0±2.71 (1.0–10.0)
VT	15.0	10.0	13.0±2.05 (11.0–17.0)	9.0±1.65 (7.0–12.0)	11.6±1.90 (10.0–15.0)	11.0±2.94 (8.0–15.0)	9.0±1.41 (8.0–11.0)	10.6±1.06 (9.0–12.0)	8.6±1.90 (5.0–11.0)	8.9±1.10 (7.0–10.0)

females	*C. aureus* N = 3	*C. nubilus* N = 2	*C. ceronorum* N = 10	*C. perotensis* N = 8	*C. totonacus* N = 10	*C. melipona* N = 3	*C. casasi* N = 1	*C. chiropterus* N = 4	*C. orculus* N = 10	*C. lavae* N = 9
SVL	26.8±0.86 (26.0–27.7)	30.5±3.89 (27.7–33.2)	34.9±1.53 (33.3–38.4)	31.7±2.19 (27.4–34.3)	35.5±1.90 (31.8–38.3)	28.5±1.36 (27.1–29.8)	40.9	33.5±2.55 (30.7–36.7)	39.0±2.70 (34.9–43.0)	31.6±2.46 (27.9–34.9)
TL	31.1±1.41 (30.1–32.1)	34.3±5.16 (30.6–37.9)	33.9±2.82 (28.5–38.2)	31.5±3.31 (27.0–37.3) N = 7	42.6±5.08 (36.3–49.2) N = 6	32.3±2.26 (30.7–33.9) N = 2	34.0 br	39.5±2.35 (37.0–42.6)	39.2±3.64 (34.7–44.7) N = 9	32.5±4.89 (25.7–40.1)
TL/SVL	1.16±0.00 (1.16–1.16)	1.12±0.03 (1.10–1.14)	0.97±0.07 (0.85–1.07)	1.00±0.11 (0.79–1.11) N = 7	1.20±0.13 (1.06–1.38) N = 6	1.11±0.11 (1.03–1.18) N = 2	–	1.19±0.12 (1.01–1.26)	1.02±0.08 (0.87–1.12) N=9	1.02±0.10 (0.85–1.15)
AX	15.0±0.49 (14.7–15.6)	16.4±2.69 (14.5–18.3)	18.5±0.95 (17.1–20.0)	16.6±1.58 (13.6–19.2)	18.7±0.95 (17.3–20.1)	15.8±0.59 (15.4–16.5)	20.3	18.5±2.27 (15.4–20.7)	21.2±1.58 (18.6–23.2)	16.3±1.68 (13.9–18.5)
FLL	5.3±0.42 (4.8–5.6)	6.5±0.28 (6.3–6.7)	8.6±0.38 (8.1–9.3)	6.7±0.61 (5.9–7.5)	9.7±0.85 (8.7–11.3)	6.5±0.72 (6.0–7.3)	10.6	7.8±0.48 (7.1–8.2)	8.9±0.63 (7.6–10.0)	8.2±0.72 (7.1–9.5)
HLL	6.7±0.35 (6.4–7.1)	7.2±0.14 (7.1–7.3)	8.9±0.70 (7.3–9.9)	7.1±0.66 (6.1–8.2)	10.8±0.93 (9.3–12.5)	7.4±0.58 (7.1–8.1)	12.0	8.9±0.31 (8.4–9.1)	9.5±0.57 (8.6–10.4)	8.8±0.73 (7.5–9.8)
HL	6.0±0.31 (5.7–6.3)	7.4±0.99 (6.7–8.1)	7.1±0.29 (6.6–7.6)	6.7±0.31 (6.2–7.2)	7.6±0.38 (7.0–8.1)	6.4±0.60 (5.8–7.0)	8.6	7.3±0.56 (6.5–7.8)	8.0±0.52 (7.4–8.9)	7.0±0.42 (6.3–7.6)
HW	3.6±0.10 (3.5–3.7)	4.4±0.14 (4.3–4.5)	5.1±0.21 (4.7–5.3)	4.4±0.21 (4.1–4.6)	5.2±0.22 (5.0–5.6)	4.2±0.25 (4.0–4.5)	5.9	4.8±0.21 (4.5–5.0)	5.2±0.29 (4.7–5.6)	4.7±0.30 (4.1–5.0)
HD	1.8±0.02 (1.8–1.8)	2.0±0.07 (1.9–2.0)	2.4±0.12 (2.3–2.6)	2.2±0.17 (2.0–2.5)	2.3±0.17 (2.0–2.6)	2.4±0.12 (2.3–2.5)	2.6	2.5±0.14 (2.3–2.6)	2.6±0.32 (2.3–3.4)	2.3±0.18 (2.1–2.7)

SW	3.1±0.17 (3.0–3.3)	3.3±0.28 (3.1–3.5)	3.7±0.24 (3.3–4.1)	3.1±0.22 (2.6–3.3)	3.6±0.17 (3.4–3.9)	3.2±0.15 (3.1–3.4)	3.3	3.6±0.38 (3.3–4.1)	3.9±0.46 (3.4–4.8)	3.3±0.33 (2.8–3.8)
IN	1.1±0.06 (1.0–1.1)	1.2±0.02 (1.2–1.2)	1.9±0.15 (1.5–2.1)	1.8±0.14 (1.6–2.0)	2.2±0.19 (2.0–2.5)	1.4±0.06 (1.4–1.5)	2.3	1.7±0.38 (1.4–2.1)	2.1±0.25 (1.7–2.5)	1.8±0.13 (1.6–2.0)
FW	1.8±0.21 (1.6–2.0)	2.3±0.57 (1.9–2.7)	3.5±0.40 (2.8–3.9)	2.6±0.24 (2.2–3.0)	4.0±0.52 (3.3–4.8)	2.6±0.38 (2.3–3.0)	3.7	3.1±0.37 (2.6–3.5)	3.4±0.37 (2.6–3.9)	3.3±0.27 (3.0–3.7)
LI	2.3±0.58 (2.0–3.0)	1.5±0.71 (1.0–2.0)	1.5±0.41 (1.0–2.0)	3.3±0.71 (2.0–4.0)	0.0±0.67 (-1.0–1.0)	1.8±0.76 (1.0–2.5)	1.0	2.0±0.41 (1.5–2.5)	2.9±0.32 (2.0–3.0)	0.6±0.73 (0.0–2.0)
PMT	6.3±0.58 (6.0–7.0)	6.5±0.71 (6.0–7.0)	7.4±0.97 (6.0–9.0)	6.1±2.17 (4.0–11.0)	7.0±1.05 (6.0–9.0)	7.0±1.73 (6.0–9.0)	6.0	6.3±1.26 (5.0–8.0)	7.1±0.88 (6.0–8.0)	7.2±1.99 (4.0–10.0)
MT	38.3±1.53 (37.0–40.0)	41.5±2.12 (40.0–43.0)	47.7±7.26 (36.0–56.0)	27.9±5.03 (19.0–36.0)	52.6±4.50 (45.0–60.0)	31.0±5.20 (25.0–34.0)	30.0	48.0±7.94 (42.0–57.0) N = 3	28.8±4.05 (23.0–35.0)	20.8±6.69 (13.0–36.0)
VT	12.3±1.53 (11.0–14.0)	13.5±0.71 (13.0–14.0)	15.9±2.69 (13.0–22.0)	11.1±1.13 (10.0–13.0)	13.7±2.11 (9.0–17.0)	13.0±5.29 (9.0–19.0)	13.0	12.5±2.38 (10.0–15.0)	12.0±1.94 (9.0–15.0)	11.4±2.30 (8.0–15.0)

Cranial osteological variation among Chiropterotriton species based on characters and character states defined by Darda & Wake (2015).

Cranial osteological variation among Chiropterotriton species based on characters and character states defined by Darda & Wake (2015). Each species is represented by a single μCT-scanned specimen except C. chiropterus, for which there are an additional four cleared-and-stained (c&s) specimens. States that are not observed in these specimens are omitted, e.g., character 6, state c. All specimens show the same state for characters 11 (squamosal process absent) and 12 (vomer preorbital process present). Each species name is followed by the specimen's museum catalog number, sex (F, female; M, male) and snout-vent length. Instances in which two states are listed for a given character (*) represent right-left asymmetry in that specimen.

Table 3. Cranial osteological variation among *Chiropterotriton* species based on characters and character states defined by Darda & Wake (2015). and-stained (c&s) specimens. States that are not observed in these specimens are omitted, e.g., character 6, state c. All specimens show the same specimen's museum catalog number, sex (F, female; M, male) and snout-vent length. Instances in which two states are listed for a given character

Species	1. Septomaxilla development a) absent	b) present	2. Nasal-premaxilla articulation a) separate	b) abut	c) overlap	3. Nasal-maxilla articulation a) separate	b) abut	c) overlap	4. Nasal-prefrontal articulation a) separate	b) abut	c) overlap	5. Nasal-frontal articulation a) separate	b) overlap
*C. ceronorum,*sp. nov. USNM 224212, M, 36.2 mm		X	-	X		-		X	-	X		-	X
			-			-			-			-	
*C. perotensis,*sp. nov. MVZ 200693, F, 31.1 mm	X		X					X	X*	X*			X
*C. totonacus,*sp. nov. MVZ 163945, F, 35.8 mm	X		X			X			X			X	
*C. melipona,*sp. nov. MVZ 178706, M, 28.5 mm		X	X				X			X		X	
*C. casasi,*sp. nov. MVZ 92874, M, 42.0		X			X			X		X			X

	A	B	C	D	E	F	G	H	I	J	K
mm											
C. chiropterus MVZ 85602, M, 38.9 mm		X			X		X		X		X
C. chiropterus,c&s MVZ 85596, M, 40.0 mm		X		X			X			X	X
C. chiropterus,c&s MVZ 85632, F, 34 mm		X	X				X		X		X
C. chiropterus,c&s MVZ 85594, M, 36 mm		X			X		X			X	X
C. chiropterus,c&s MVZ 85613, M, 37.7 mm		X		X			X			X	X
C. orculus MVZ 138783, M, 38.9 mm		X		X		X		X			X
C. lavae MVZ 163912, M, 33.8 mm	X			X			X	X			X

Appendix

Specimens examined for morphological comparison

1   **APPENDIX 1**. Specimens examined for morphological comparisons.

3   *Chiropterotriton casasi:* Mexico, Veracruz: MVZ 92874–78, 13 mi SW

4   Tlapacoyan.

5   *Chiropterotriton ceronorum:* Mexico, Puebla: USNM 224202, 224207–08,

6   224211–12, 224218–20, 224230, 224236, 224240–41, 224247, 224250, 224252–

7   53, 224257, 224259, 224275–76, Santa Cruz Texmalaquilla (4.7 mi by road NE of

8   Atzitzintla), ca. 1 km NE of, on south slope of Pico de Orizaba.

9   *Chiropterotriton chiropterus:* Mexico, Veracruz: MVZ 85588–92, 85594,

10   85597–99, 85605, 85613, 85632, 1.4 mi SW (by road) SW edge of Huatusco de

11   Chicuellar.

12   *Chiropterotriton lavae:* Mexico, Veracruz: MVZ 106537, 106548, W edge

13   of La Joya, along Hwy. 140; MVZ 163912–13, 163915, 171873–74, 171876,

14   171881, 171885, 171901, 173394–95, 173398, 192788–89, 197788, La Joya;

15   178685, La Joya, Mexico Hwy. 140; MVZ 200638 forest W of La Joya.

16   *Chiropterotriton melipona:* Mexico, Puebla: MVZ 178706–08, 3.9 km S

17   Xicotepec de Juárez on Hwy. 130; MVZ 185972, 2.2 km on road to Patla from

18   junction with Hwy. 120 SW out of Xicotepec de Juárez; MVZ 200724–26, 3.3 km

19   S of Hotel M Ranchito on Mexico Hwy. 130, 2.1 km E on road to La Unión,

20   Xicotepec de Juárez.

21   *Chiropterotriton orculus:* Mexico, Estado de México: MVZ 76161, 138686,

22   138688, 138694, 138696–97, 138700, 138776–79, 138781, 138783–84, 138793,

23   138796–97, 138804, 200629–30, ridge between Volcanoes Popocatepetl and

24   Iztaccihuatl, along Mexico Hwy. 196, 16.2 km E (by road) Hwy. 115.

25   *Chiropterotriton perotensis:* Mexico, Veracruz: MVZ 114356, 114359, road

26   from Las Vigas de Ramírez to Microwave Station on N Flank Cofre de Perote,

27   11.6 km S (by road) Las Vigas; MVZ 173428–29, 173438–39, Las Vigas de

28 Ramírez, Microondas road; MVZ 178661, 178663–65, 8–15.5 km S (via

29 Microondas Rd.) Las Vigas de Ramírez; MVZ 186711, road to Microwave Station,

30 15 km S (by road) Las Vigas de Ramírez; MVZ 200681–83, 200691, 200693–95,

31 200698, 200702 14.4 km S (by Rock Rd.) Las Vigas de Ramírez at Microwave

32 Station.

33 ***Chiropterotriton totonacus:*** MVZ 136981–82, 136986, pine forest along

34 Mexico Hwy. 140, 4 km W Las Vigas de Ramírez; MVZ 138703–04, 138716,

35 138765, Mexico Hwy. 140, 4.5 km W (by road) Las Vigas de Ramírez; MVZ

36 163943, 163945, 163947–49, 163989–90, 163993, 171903, 171905, 171907,

37 171909–10, 6 km W Las Vigas de Ramírez.