A New Species of *Cryptotriton* (Caudata: Plethodontidae) from Eastern Guatemala

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A new species of lungless salamander (Plethodontidae) is described from the mountains of eastern Guatemala. The new species is distinguished from all other members of its genus by its yellow ventral coloration. It is geographically closest to its sister taxon, *Cryptotriton veraepacis*, from which it differs in several osteological features as well as nostril size and shape. Molecular analyses with allozyme loci and mitochondrial DNA also support its distinctiveness from *C. veraepacis*. This miniaturized species inhabits cloud forest habitats and has been found most commonly in bromeliads.

Se describe una nueva especie de la familia Pletodontidae de las montañas del este de Guatemala. *Cryptotriton sierraminensis* se distingue de todos los otros miembros de su género por su coloración del vientre amarillo. Ésta especie está más cerca geográficamente a su especie hermana, *Cryptotriton veraepacis*, de la que se distingue por varios aspectos osteológicos y por el tamaño y forma de los orificios nasales. Análisis moleculares con allozimas y ADN mitocondrial apoyan sus diferencias con *C. veraepacis*. Esta especie miniaturizada vive en los bosques nubosos y ha sido encontrada con mayor frecuencia en bromelias.

As currently understood, the Neotropical salamander genus *Cryptotriton* (Caudata: Plethodontidae) contains six described species. One is restricted to Honduras (*C. nasalis*), two to Mexico (*C. adelos* in Oaxaca and *C. alvarezdeltoroi* in Chiapas), and the remaining three occur in eastern Guatemala (*C. monzoni*, *C. veraepacis*, and *C. wakei* [Fig. 1]). Prior to García-París and Wake (2000), all six species were included in the genus *Nototriton*. Good and Wake (1993) conducted a phylogenetic analysis of the Costa Rican species of *Nototriton* using allozymes and found them to form a clade. As outgroups for their analysis, Good and Wake used 11 species of *Oedipina* (a probable sister taxon to *Nototriton* [Wake and Elias, 1983; Wiens et al., 2007]) and two populations of *N. veraepacis* (now *C. veraepacis*). An unexpected finding was that the population of *C. veraepacis* from the Purulhá region (the type locality of the species) differed greatly from the population from the Sierra de las Minas in allozymes (11 fixed allele differences among 23 allozyme loci) despite their geographic proximity (55 km). An F_{ST} value (0.935; Wright, 1951) based on those differences suggests complete genetic separation (the maximum F_{ST} value is 1.000).

García-París and Wake (2000) sequenced the first portion of the cytochrome *b* gene (385 bp) and the large (16S) ribosomal subunit gene (rDNA) for four species of *Cryptotriton*: *C. alvarezdeltoroi*, *C. nasalis*, *C. veraepacis*, and an undescribed species (*Cryptotriton* sp. A). They performed a maximum parsimony analysis in PAUP (Swofford, 2000) and estimated sequence divergence values using the Kimura 2-parameter (K2p) distance (Kimura, 1980). They found pairwise sequence divergence (K2p) between *C. veraepacis* and *Cryptotriton* sp. A was 0.0448 for the 16S gene and 0.0870–0.0932 for the cytochrome *b* gene. Such a level of sequence divergence is comparable to, or greater than, that between many pairs of sister species of *Nototriton* (García-París and Wake, 2000). Analyses of allozymes, mtDNA, color pattern, and morphometrics suggest that the samples from the Sierra de las Minas, Department of Zacapa represent a new species described below.

MATERIALS AND METHODS

Allozymes.—Nine specimens of *C. veraepacis* (single locality) and six specimens of *Cryptotriton* from the Sierra de las Minas (two localities, $n = 5$ and $n = 1$, respectively) were examined for variation in 23 proteins (see table 2 of Good and Wake [1993] for identifications, abbreviations, and buffer systems for proteins). Liver and intestine samples were collected from freshly killed specimens and stored at −76°C. Ground tissues from each specimen were combined with deionized water and then subjected to horizontal starch gel electrophoresis using standard techniques (Selander et al., 1971; Harris and Hopkinson, 1976). Similarity measures were calculated by hand or using BIOSYS-1 version 1.7 (Swofford and Selander, 1989).

Morphology.—Twenty-five specimens of *C. veraepacis* and 53 specimens of *Cryptotriton* from the Sierra de las Minas were compared to detect differences in body proportions between the two species. All of the specimens used for allozyme analysis were also used in the morphometric analysis. The 78 specimens were measured for the following 17 mensural characters: snout–vent length (SL), tail length (TL), axilla–groin length (AG), trunk width (TW), snout–gular length (SG), head width (HW), nostril length (NL), nostril width (NW), inter-nostril distance (IN), eye–nostril distance (EN), inter-eye distance (IE), eye width (EW), forelimb length (FLL), hind limb length (HLL), foot width (FW), toe III length (T3), and toe V length (T5). A Principle Component Analysis (PCA) was conducted on the covariance matrix of log transformations of all 17 measurements (SAS PRINCOMP procedure [SAS Language, version 6. First edition. SAS

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Submitted: 8 May 2008. Accepted: 24 November 2008. Associate Editor: D. Kizirian.
 DOI: 10.1643/CH-08-086

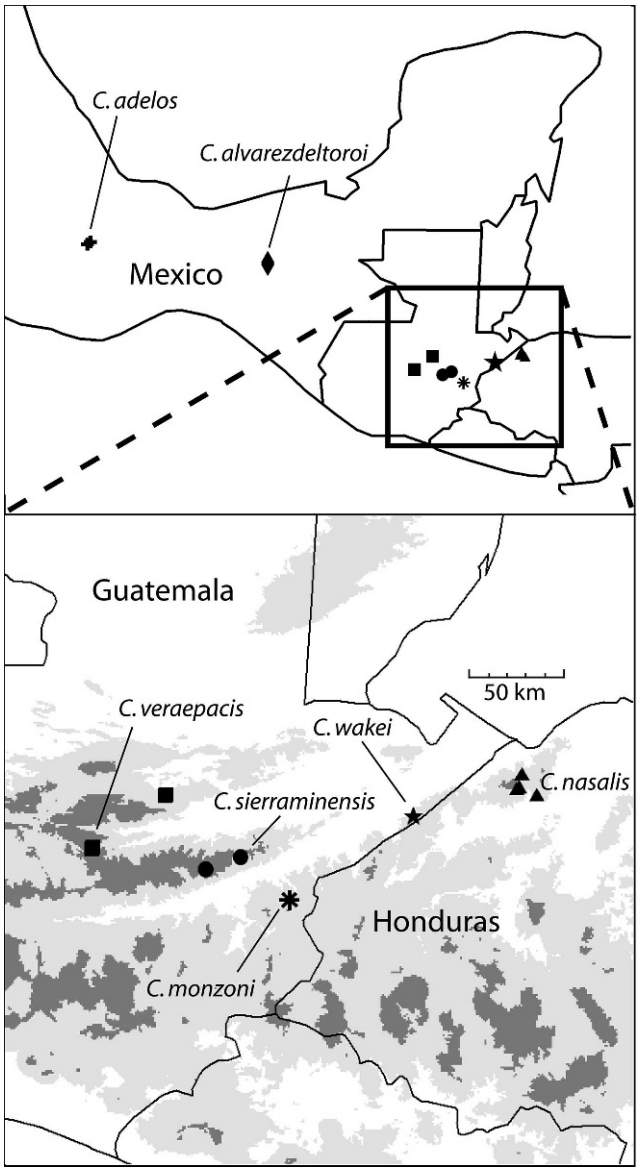

Fig. 1. Map of known localities for *Cryptotriton adelos* (crosses), *C. alvarezdeltoroi* (diamonds) in Mexico, *C. veraepacis* (squares), *C. sierraminensis* (circles), *C. monzoni* (asterisk), and *C. wakei* (star) in Guatemala, and *C. nasalis* (triangles) in Honduras. Light gray shading represents areas between 500 m and 1500 m elevation, and dark gray shading represents areas above 1500 m elevation.

Institute Inc., Cary, NC, 1990]). Discriminant Function Analysis (DFA; SAS DISCRIM procedure [SAS Institute, 1990]) was performed on the same covariance matrix to determine if specimens were correctly identified to species based on morphology. Institutional abbreviations for specimens used in morphometric analysis are as listed at http://www.asih.org/codons.pdf. Four cleared-and-stained specimens of *C. sierraminensis* (MVZ 150913, 150920, paratypes MVZ 160905 and MVZ 160899) and one of *C. veraepacis* (MVZ 112492, a paratype) were used for osteological examination.

RESULTS

Allozymes.—A total of 35 alleles was detected among 23 protein loci scored. Eleven loci (ACOH, ADH, EST-1, GDH, HCDH, IDH-1, IDH-2, LDH, MDH-2, MPI, and PK) showed identical alleles in both species, and 11 (AAT, ACOH-2, ADA, EST-2, G6PDH, GPI, NADH-DH, PGDH, PEP-1, PEP-2, and PGM) showed fixed differences between them. At MDH-1, *C. veraepacis* was fixed for an allele that was present at a frequency of 0.75 in the *Cryptotriton* from the Sierra de las Minas. These allele distributions yield the following genetic distances: Nei (1978) = 0.654; Rogers (1972) = 0.485; Cavalli-Sforza and Edwards (1967) chord = 0.626; Cavalli-Sforza and Edwards (1967) arc = 0.695. Wright's (1951) F_{ST} including all populations of both species averaged over all loci is 0.935. Including only the two populations of from the Sierra de las Minas, F_{ST} is 0.099.

Morphology.—No clear separation of the *C. veraepacis* and the Sierra de las Minas samples was observed in PCA. However, DFA correctly classified *C. veraepacis* specimens 90.9% of the time and the Sierra de las Minas specimens 77.8% of the time.

Sixteen of the morphometric characters also were analyzed individually to determine if any significant differences exist between *C. veraepacis* and the Sierra de las Minas populations. Each of the measurements was divided by SL to adjust for overall specimen size. Because the resulting ratios are not necessarily normally distributed, they were subjected to nonparametric Mann-Whitney U tests in order to identify significant differences. *Cryptotriton* from the Sierra de las Minas have significantly shorter tails (TL, $P = 0.018$), broader trunks (TW, $P = 0.015$), longer hind legs (HLL, $P = 0.005$), and wider feet (FW, $P = 0.003$). In addition, *C. veraepacis* has more elongate nostrils (measured by nostril length [NL] divided by nostril width [NW], $P = 0.015$). Despite these significant differences, overlap occurs in all measurements.

In delimiting species, we follow the Evolutionary Species Concept (Simpson, 1961:153; Wiley, 1978). A high degree of genetic differentiation, shown by both allozyme analysis and mitochondrial DNA sequence results, and internal and external morphological differences between *Cryptotriton veraepacis* and populations in the Sierra de las Minas indicate that these populations represent independent, historically isolated lineages on separate evolutionary trajectories.

Cryptotriton sierraminensis, new species

Sierra de las Minas Hidden Salamander
Figure 2A, 2B

Cryptotriton sp. A García-París and Wake, 2000.

Holotype.—MVZ 257801, male, Guatemala, Departamento de Zacapa, Sierra de las Minas, Municipio Rio Hondo, Finca Planada de Margot, 18.7 km (by road) from CA-9 at Aldea Las Pozas (km 143.5), 15°10′12″N, 89°30′52″W (WGS84 datum), 1720 m, 3 May 2007, S. M. Rovito, C. Vásquez-Almazán, T. Papenfuss, and E. G. Ruano.

Paratypes.—(n = 20), MVZ 160898–160914, Guatemala, Depto. Zacapa, Sierra de las Minas, 10.5 km N. Hwy. CA-9 at Santa Cruz (km 126), 2020 m, 21 July 1978, D. B. Wake, E. J. Koford, P. Elias, and T. A. Wake (MVZ 160899 and 160905 cleared and stained); USAC 1118, Guatemala, Depto. Zacapa, Sierra de las Minas, Volcán de los Monos, 6.1 km west (by road) from San Lorenzo Marble Mine, 15°6′44″N, 89°40′40″W (WGS84 datum), 2200 m, same general locality as previously listed specimens, 6 September 2006, S. M. Rovito, C. Vásquez-Almazán, and T. Papenfuss; USAC 1124, Guatemala, Depto. Zacapa, Sierra de las Minas, Finca

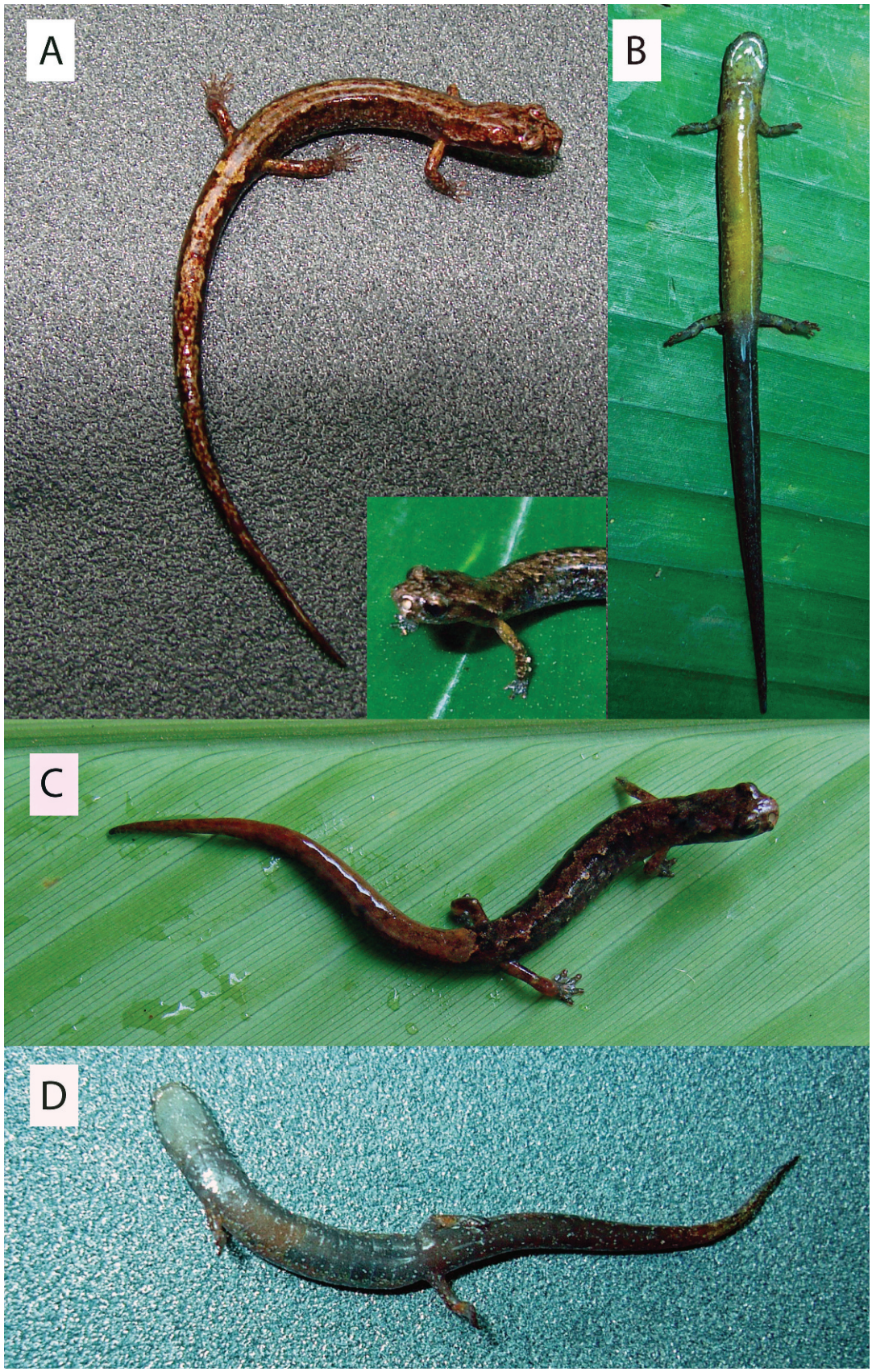

Fig. 2. (A) Dorsal view of the holotype of *C. sierraminensis*, with inset showing view of head. (B) Ventral view of a paratype (USAC 1118), showing characteristic yellow coloration. (C) Dorsal and (D) ventral views of a specimen of *C. veraepacis* (CRVA1112).

Planada de Margot, 18.7 km (by road) from CA-9 at Aldea Las Pozas (km 143.5), 1850 m, 3 May 2007, C. Vásquez-Almazán, S. M. Rovito, T. Papenfuss, and E. G. Ruano; USAC 1125, Guatemala, Depto. Zacapa, Sierra de las Minas, approx. 2 km from Finca Planada de Margot, 16.7 km (by road) from CA-9 at Aldea Las Pozas (km 143.5), 15°9′41″N, 89°30′58″W (WGS84 datum), 1720 m, 4 May 2007, C. Vásquez-Almazán and E. G. Ruano.

Diagnosis.—Average sized for genus (SL 16.08–35.43 mm, mean 26.74 mm). Nostrils large (*C. sierraminensis* nostril width/SL 0.214–0.307, mean 0.258 vs. *C. veraepacis* 0.169–0268, mean 0.222); more ovoid in shape (nostril width/nostril height 1.154–1.952, mean 1.451) than those of *C. veraepacis* (nostril width/nostril height 1.034–1.321, mean 1.152). Assigned to *Cryptotriton* based on García-París and Wake (2000). Distinguished unambiguously from all other *Cryptotriton* species by yellow ventral color in life (vs. dark uniform gray in *C. veraepacis*) and pale mottling on gular region (Fig. 2). Dark line from eye toward forelimb insertion usually present in *C. sierraminensis*, but usually lacking in *C. veraepacis*.

Description of holotype.—Head not large; paratoid glands not in evidence. Eyes of moderate size and moderately protuberant, extending slightly beyond margin of jaw. Limbs of moderate length; well-developed hands and feet; fully differentiated, unwebbed digits. Long, tapering tail. Posteriorly-flattened oval-shaped mental hedonic gland present.

Measurements of the holotype (in millimeters).—Head width 3.8; snout to gular fold (head length) 5.6; head depth at posterior angle of jaw 2.4; eyelid length 1.7; eyelid width 0.8; anterior rim of orbit to snout 1.4; horizontal orbit diameter 1.0; interorbital distance 1.2; snout to forelimb 7.9; distance separating external nares 0.8; snout projection beyond mandible 0.4; snout to posterior angle of vent (SL) 27.5; snout to anterior angle of vent 25.2; axilla to groin 15.9; tail length 35.5; tail width at base 2.1; tail depth at base 2.3; forelimb length 6.0; hind limb length 6.7; width of right manus 1.8; width of right pes 2.5; length of longest toe 1.0; length of shortest toe 0.3; maximum nostril diameter 0.8; shoulder width 2.8.

Coloration of the holotype in life.—The dorsum is a medium reddish brown with numerous golden brown to tan patches, as well as some darker chocolate brown patches. The golden brown and tan patches continue onto the dorsal surface of the tail, forming an irregular jagged stripe that extends posteriorly for most of the length of the tail. The sides of the body are covered with pale flecks on the brown background from the insertion of the forelimb to just behind the insertion of the hind limb. The ventral surface of the tail is brown-gray with numerous pale flecks. The venter is a striking bright yellow in the center, and gray with pale flecks surrounding the yellow areas (Fig. 2). This coloration extends onto the gular region, with less extensive small yellow blotches on a gray background with pale flecks. The yellow coloration also extends onto the ventral surface of the limbs to about halfway down the limb, and the underside of the feet is a pale gray. The dorsal surface of the limbs is similar in color to the body, with the pale brown patches extending onto the limbs, while the ventral surface is a paler yellow with some brown mottling. The forelimbs are a pale tan-yellow color near the point of insertion, and the feet are a paler brown.

Coloration of the holotype in alcohol.—The dorsum of the holotype is solid dark brown with very little paler brown mottling. The flanks are somewhat paler, grading to some extent into the much paler venter. The venter is pale beige in the center with substantial gray mottling, especially in the gular region. The head and limbs are generally similar to the body in color pattern, being brown above and pale beneath; the limbs differ in that their dorsal surfaces are pale near the limb insertions and have pale mottling all the way to the feet, and the head differs in that there is a faint dark stripe running posteriorly from the eye to the forelimb insertions. The dorsal surface of the tail also is similar to the trunk in color, but has a faint irregular stripe of a paler brown starting at its insertion and becoming indistinct about two-thirds of the way to the tail tip. The ventral surface is a medium solid brown and is paler than the dorsal surface. There are two pale spots flanking the midline on the dorsal surface of the tail at its insertion (i.e., just posterior to the hind limbs).

Variation in color pattern.—All aspects of color pattern vary. Although the venter is usually heavily mottled, gular mottling is limited in several specimens; the venter is always substantially paler than the dorsum. The dark stripes posterior to the eyes are very distinct in some specimens and extend all the way to the forelimb insertions, while in others they are obscure, though always present. A few specimens have some yellow-tan mottling on the tail, and the two basal tail spots sometimes are obscure.

Osteology.—*Cryptotriton veraepacis* and *C. sierraminensis* are similar in most osteological features (see detailed osteological description of *C. veraepacis* in Lynch and Wake, 1978). The prefrontal is pierced by the nasolacrimal foramen in *C. veraepacis*, while it is strongly evacuated along the anterior edge in three of four specimens of *C. sierraminensis* examined (Fig. 3) and pierced in the fourth specimen (MVZ 150913). The evacuated condition of the prefrontal is shared with *C. nasalis* and *C. alvarezdeltoroi* (Papenfuss and Wake, 1987), but, based on the four specimens examined, the pierced prefrontal is not unique to *C. veraepacis* (and seems to occur in *C. adelos*, based on radiographs; Papenfuss and Wake, 1987). The septomaxillary bone is absent in all five specimens examined, as in other species of *Cryptotriton*. The frontal processes of the premaxillary bone are fused at their origin and then separate distally in *C. sierraminensis*, and are somewhat flared at the end. In *C. veraepacis*, the preorbital process of the vomer is absent, while there is a very short preorbital process in *C. sierraminensis* with approximately two vomerine teeth on it (Fig. 3). This condition also differentiates *C. sierraminensis* from all other species of *Cryptotriton* (Papenfuss and Wake, 1978). A tibial spur is present in both *C. veraepacis* and *C. sierraminensis*, distinguishing these two species from *C. nasalis*, which has only a rudimentary tibial spur (Lynch and Wake, 1978). The foot morphology of *C. sierraminensis* resembles that of *C. veraepacis* and other species of *Cryptotriton* (Fig. 4).

Life history and ecology.—*Cryptotriton sierraminensis* is an arboreal, bromeliad-dwelling specialist, as are several other members of its genus (*C. veraepacis* and *C. nasalis*: Wake, 1987; *C. adelos*: Papenfuss and Wake, 1987). The salamanders were all collected from inside arboreal bromeliads, as were two clutches of unattended eggs (n = 50 and n = 9,

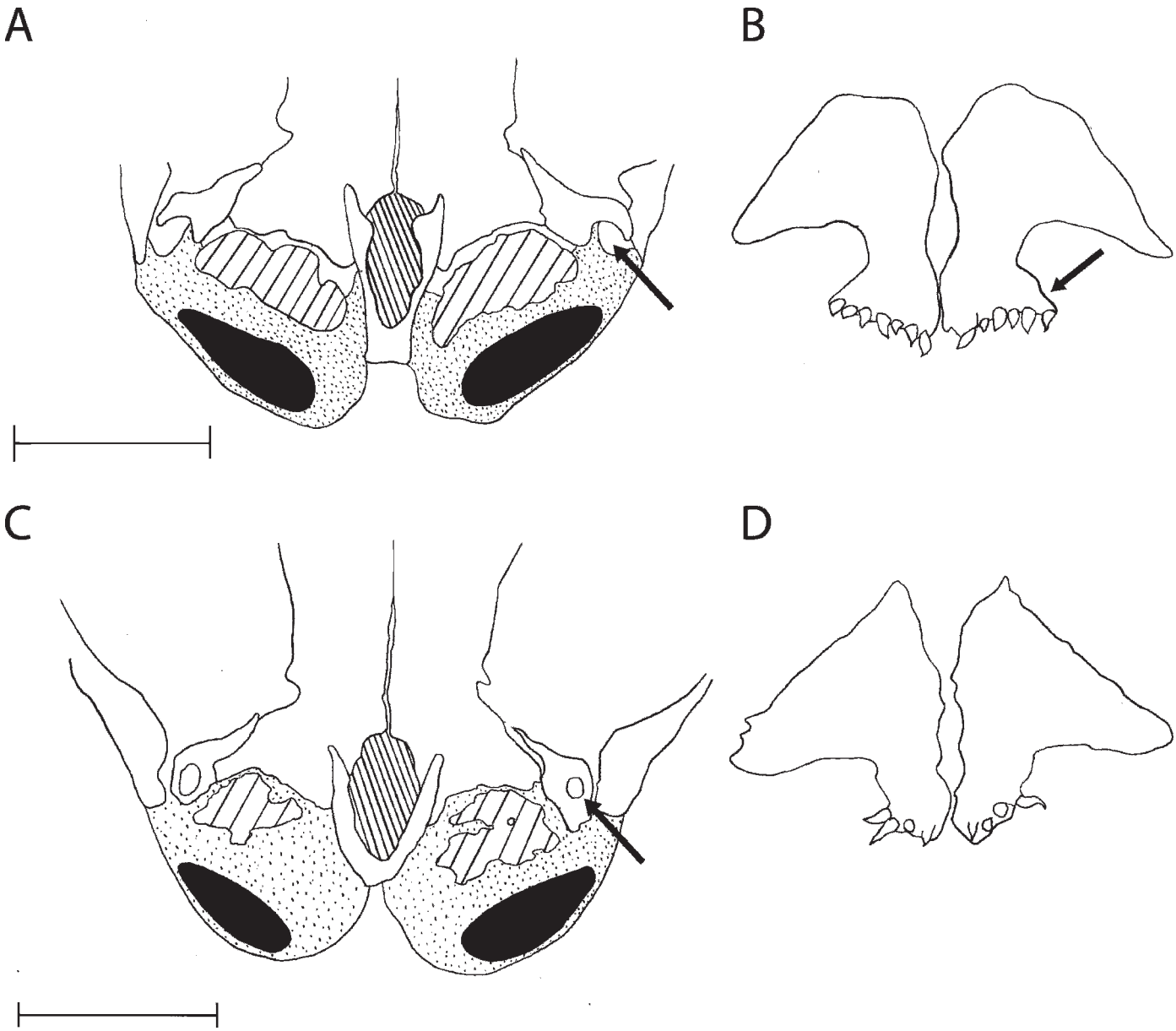

Fig. 3. (A) Dorsal view of nasal capsule region of *C. sierraminensis* (MVZ 160905), with arrow pointing to evacuated region of prefrontal where nasolacrimal duct passes through ventrally into nasal capsule. Heavy lines, nasal bone; fine lines, internasal fontanelle; stipple, cartilaginous nasal capsule; blackened area, opening in nasal capsule for external nares. Scale bar represents 1 mm. (B) Vomer of *C. sierraminensis* (MVZ 150920). Arrow points to rudimentary preorbital vomerine process. (C) Nasal capsule region of *C. veraepacis* (MVZ 112492). Arrow points to pierced area where nasolacrimal duct passes ventrally into nasal capsule. Scale bar represents 1 mm. (D) Vomer of *C. veraepacis* (MVZ 112492), lacking preorbital process.

respectively). The number of unattended eggs in the larger clutch suggests communal egg-laying without brooding by adults. This behavior, unusual for tropical plethodontids, has been observed in *Nototriton barbouri* (McCranie and Wilson, 1992). Unattended egg clutches have also been reported in *Nototriton picadoi* (Good and Wake, 1993; Bruce, 1998), *Nototriton guanacaste* (Good and Wake, 1993), and *Oedipina maritima* (García-París and Wake, 2000). Bruce (1998) suggested that the small size of *Nototriton* may prevent them from effectively defending clutches from predators and that egg desiccation may not be a problem for these cloud forest inhabitants. McCranie and Wilson (1992) also state that, as *N. barbouri* eggs develop during the wet season, parental care to prevent desiccation may not be necessary. The same may be true in *C. veraepacis*, as the clutches of eggs were found in July, during the wet season in the Sierra de las Minas. Communal laying of unguarded eggs is also reported in *Batrachoseps* (Jockusch and Mahoney, 1997) and some *Hemidactylium* (Harris and Gill, 1980).

All specimens have been found at elevations of 1700–2200 m. The habitat is composed of cloud forest in the lower montane moist forest life zone (Holdridge, 1967) with a mixture of large broadleaf and pine trees, as well as tree ferns. Trees are covered in a dense growth of epiphytes and mosses. On Volcán de los Monos, *Bolitoglossa helmrichi* was found in bromeliads and at Finca Planada de Margot; both *B. helmrichi* and a second, undescribed species of *Bolitoglossa* (Larson, 1983; Rovito and Vásquez-Almazán, unpubl.) were found along with *C. veraepacis* in bromeliads. *Bolitoglossa meliana* was found under ground cover objects at both sites

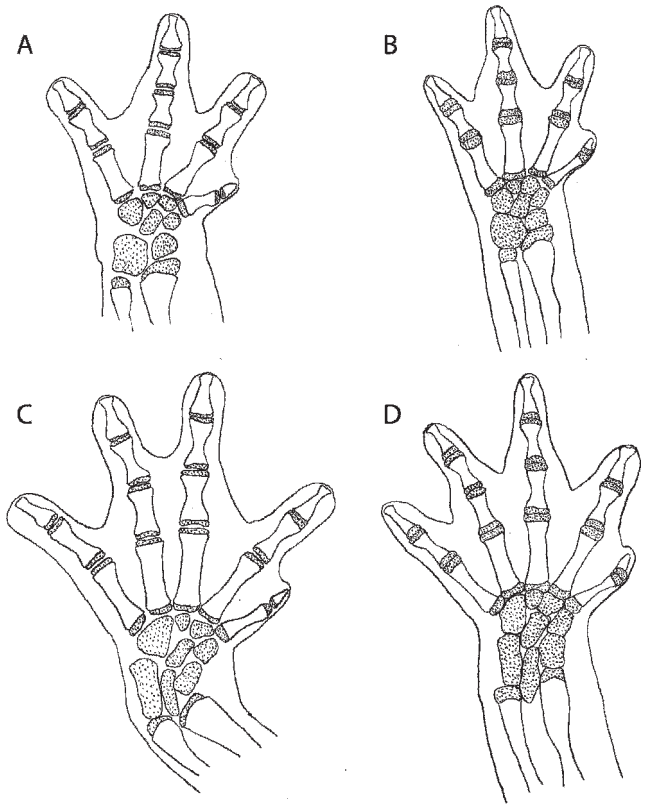

Fig. 4. (A) Left hand of *C. sierraminensis* (MVZ 150920) and (B) *C. veraepacis* (MVZ 112492). (C) Left foot of *C. sierraminensis* (MVZ 150920) and (D) *C. veraepacis* (MVZ 112492).

in the 1970s, but has not been seen on recent visits to either site.

Distribution.—*Cryptotriton sierraminensis* is known from only two localities in Municipio Rio Hondo, Department of Zacapa, Guatemala, which are separated by 18.7 km (by air). Both known localities are on the south side of the Sierra de las Minas, between 1700 m and 2200 m. While the locality on Volcán de los Monos is inside the Sierra de las Minas Biosphere reserve, the type locality is outside the reserve and has no formal protection at present. The species likely occurs at other sites on the southern side of the Sierra de las Minas.

Remarks.—*Cryptotriton veraepacis* and *C. sierraminensis* (as *C.* sp. A) are sister taxa (García-París and Wake, 2000). García-París and Wake (2000) deposited nucleotide sequences in GenBank (cyt *b*: AF199122–199127 for *C. veraepacis* and AF199128–199129 for *C. sierraminensis* [as *C.* sp. A]; 16S: AF199197 for *C. veraepacis* and AF199198 for *C. sierraminensis* [as *C.* sp. A]).

Etymology.—The specific epithet is an adjective that makes reference to the Sierra de las Minas, Guatemala, where the species occurs.

MATERIAL EXAMINED

Morphometric analysis.—*Cryptotriton veraepacis* (*n* = 25). Guatemala, Depto. Baja Verapaz: MVZ 172708–09, UTA 7454, 2.5 mi SE Purulhá on CA-14; UTA 7455, 2.0 mi S Purulhá; UTA 7456, 2.4 km S Purulhá; MVZ 167773–75, 167783–87, 167967–72, 167991, 167993–96, 215913, 6.5 mi ESE Purulhá.

Cryptotriton sierraminensis (*n* = 53). Guatemala, Depto. Zacapa: MVZ 150882–87, 150889–91, 150893–99, Volcán de los Monos, 11 km N Santa Cruz; MVZ 150900–12, 150914–19, 150921–22, 167992, Finca Planada de Margot, 15 km NNE Río Hondo; MVZ 160897–98, 160900–04, 160906–14, Sierra de las Minas, 10.5 km N CA-9 at Santa Cruz (km 126).

Osteology.—*Cryptotriton veraepacis*. Guatemala, Depto. Baja Verapaz: MVZ 112492, 4.2 km S (by road) Purulhá on CA-14.

Cryptotriton sierraminensis. Guatemala, Depto. Zacapa: MVZ 150913, 150920, Finca Planada de Margot, 15 km NNE Río Hondo; MVZ 160905, 160899, 10.5 km N CA-9 at Santa Cruz (km 126), Sierra de las Minas.

Allozyme analysis.—*Cryptotriton veraepacis* (*n* = 9). Guatemala, Depto. Baja Verapaz: MVZ 167773, 167785–87, 167991, 167993–96, 6.5 mi ESE Purulhá.

Cryptotriton sierraminensis (*n* = 6). Guatemala, Depto. Zacapa: MVZ 160898–902, 10.5 km N CA-9 at Santa Cruz (km 126), Sierra de las Minas; MVZ 167992, Finca Planada de Margot, 15 km NNE Río Hondo.

ACKNOWLEDGMENTS

This work would not have been possible without the help of J. Vargas, who generously provided access, lodging, and field help at Finca Planada de Margot, the type locality for this species. E. Koford, T. Wake, and P. Elias provided important help in the field. T. Papenfuss provided critical help in obtaining all recently collected specimens of this species. Collecting permits for fieldwork in Guatemala were provided by the Consejo Nacional de Areas Protegidas (CONAP), permit #00269-A to C. Vásquez-Almazán and S. Rovito. Animal use was approved by the University of California–Berkeley protocol #R278 for S. Rovito and protocol #R093 for D. Wake. This material is based upon work supported by a grant from the University of California Institute for Mexico and the United States (UC MEXUS) and the Consejo Nacional de Ciencia y Tecnología de México (CONACYT), and was also supported by the National Science Foundation (current grant EF-0334939, D.B.W.).

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