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A new arboreal *Pseudoeurycea* (Caudata: Plethodontidae) from the Sierra de Zongolica, Veracruz, Mexico

Erasmo Cázares-Hernández[1], H. David Jimeno-Sevilla[1], Sean M. Rovito[2], Marco Antonio López-Luna[3], Luis Canseco-Márquez[4]

1 *Instituto Tecnológico Superior de Zongolica, Colección Científica del ITSZ y Herbario ZON. Km 4 Carretera a la Compañía S/N, Tepetitlanapa CP 95005, Zongolica, Veracruz, México*

2 *Unidad de Genómica Avanzada (LANGEBIO), CINVESTAV, Irapuato, Guanajuato, México*

3 *División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco, Carretera Villahermosa-Cárdenas km 0.5 Villahermosa, Tabasco CP 86039, México*

4 *Laboratorio de Herpetología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Distrito Federal 04510, México*

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Corresponding author: Luis Canseco Márquez (lcanseco@gmail.com)

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Abstract

We describe a new species of plethodontid salamander of the genus *Pseudoeurycea* from the Sierra de Zongolica, Veracruz, Mexico. The new species is distinguished from all other species in the genus by morphological and genetic features and by coloration. Based on a mtDNA phylogeny, the new species belongs to the *Pseudoeurycea juarezi* group and is most closely related to *P. ruficauda* from the Sierra Mazateca in northern Oaxaca. The newly described salamander increases the number of species of plethodontid salamanders from Veracruz to 43 and those recognized from Mexico to 140.

Resumen

Se describe una nueva especie de salamandra pletodóntida del género *Pseudoeurycea* de la Sierra de Zongolica en el Estado de Veracruz. La nueva especie se distingue de todas las especies del género por características morfológicas y genéticas y patrón de coloración. Con base en la filogenia de ADN mitocondrial, la nueva especie pertenece al grupo *P. juarezi* y se encuentra más cercanamente relacionada con *P. ruficauda* de la Sierra Mazateca en el norte de Oaxaca. La descripción de esta nueva salamandra, incrementa el número de especies de salamandras pletodóntidas de Veracruz a 43 y 140 reconocidas para Mexico.

Keywords

Bolitoglossini, *juarezi* group, phylogeny, *Pseudoeurycea jaguar* **sp. nov.**, salamander

Introduction

Mexico has the world's seventh highest diversity of amphibian species (418 species) and is second only to the USA in salamander species diversity (158 species; AmphibiaWeb 2022). The salamanders of the family Plethodontidae are the most diverse group of amphibians in Mexico with 139 species (AmphibiaWeb 2022), representing 33.2% of the amphibians present in the country and including 118 species endemic to Mexico. In Mexico, 16 genera of plethodontids are present, of which 13 (and all but three species) belong to the Neotropical tribe Bolitoglossini (Wake 2012). Bolitoglossines have undergone an adaptive radiation in Mesoamerica, occupying a wide array of habitats, including arboreal habitats in cloud forests (Wake 1987).

Following a taxonomic revision of the Bolitoglossini (Rovito et al. 2015), the genus *Pseudoeurycea* continues to have the highest species diversity of the 16 plethodontid salamander genera present in Mexico, with 40 species distributed from the Trans-Mexican Volcanic Belt south through the highlands of Guerrero and Oaxaca, Mexico to Guatemala (AmphibiaWeb 2022). Of the 40 species in the genus, 36 are endemic to Mexico, three are distributed in Chiapas and Guatemala, and only one (*P. exspectata*) is endemic to Guatemala. Salamanders of the genus *Pseudoeurycea* are small to moderately sized with a generalized morphology, with the exception of three slender, elongate species formerly assigned to the genus *Lineatriton* (Rovito et al. 2015).

With 42 species of plethodontid salamanders (listed by Torres-Hernández et al. 2021), the state of Veracruz ranks second in terms of salamander diversity after Oaxaca with 47 species, surpassing Chiapas and Puebla (24 and 23 species, respectively). Despite having been the focus of herpetological research for decades, new species of salamanders continue to be described from Veracruz (García-Castillo et al. 2018; Sandoval-Comte et al. 2017; García-Bañuelos et al. 2020; Parra-Olea et al. 2020).

In a coniferous forest (*Cupressus*) in the Sierra de Zongolica, we discovered a population of brightly colored salamanders that differed markedly in color pattern and external morphology from all species known from the region. Based on its morphological and molecular distinctiveness, we describe this population as a new species. We consider it to be distinct because it is diagnosable from closely related species based on differences in external morphology and tooth counts, has a distinct color pattern, and represents an independent evolutionary lineage based on phylogenetic analysis that has a similar or greater degree of genetic divergence from described species of the *juarezi* and *leprosa* species groups compared to distances between described species.

Materials and methods

Field work and study site

From September 2015 to July 2016 we conducted 10 sampling sessions (one three-day session per month) in a 1.5 ha portion at the study site. Forty-eight individuals were found, of which 40 were measured and released and eight were collected and preserved (the maximum number allowed by the SEMARNAT collecting permit) and deposited in the Museo de Zoología Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC). We used 10 arboreal traps (cylindrical funnel traps) placed in trees with epiphytic plants, at a height between 2 and 4 m, with a total time of 36 trapping days. We also made random quadrant searches for hand-captures. The study site is a coniferous forest situated in the locality El Mirador, municipality of Texhuacán, Veracruz, at 2,370 m elevation.

Morphological Analysis

The description of the new species follows the format used by Lynch and Wake (1989) for other species in the genus *Pseudoeurycea* and includes the same basic characters and measurements. Larger measurements were taken using dial calipers (to the nearest 0.1 mm); measurements of feet, toes, and some head dimensions (e.g., additional measurements of the holotype), as well as tooth counts, were taken under a stereoscopic microscope. All measurements are in mm and abbreviations are as follows: Distance from snout to posterior angle of vent (snout-vent length, SVL), distance from posterior angle of vent to tip of tail (TL), axilla-groin distance (AX), forelimb length (FLL), hind limb length (HLL), distance from tip of snout to gular fold (head length, HL), width of head at angle of jaw (HW), head depth (HD), interocular distance (IO), distance between external nares (IN), right foot width (RFW), length of longest (third) toe (T3) and length of fifth toe (T5). We also counted maxillary teeth (MT) and premaxillary teeth (PMT) and vomerine teeth (VT) and both sides were summed. Salamanders measured for our morphological analyses are listed in Appendix 1. Color notes are based on living specimens.

We compared the new species with all currently recognized members of the *Pseudoeurycea juarezi* group (i.e., *P. aurantia, P. juarezi, P. ruficauda* and *P. saltator*). Because Neotropical salamanders typically are sexually dimorphic, we separated males and females in the morphological analyses (Tables 1, 2). We calculated mean, standard deviation, and range for all morphological measurements and tooth counts and compared the new species to all species of the *Pseudoeurycea juarezi* group. Teeth were counted by opening jaws with forceps and counting ankylosed teeth (not including spaces where teeth are missing) under a dissecting microscope. For comparisons to other members of the *juarezi* group, tooth counts for maxillary and premaxillary teeth were summed (MT+PMT) because the counts were not available separately for several species.

DNA extraction and sequencing

We extracted DNA from liver tissue using a high salt protocol (Aljanabi and Martinez 1997). We amplified a fragment of the large subunit ribosomal RNA (16S) gene using primers 16Sal and 16Sbr (Palumbi et al. 1991) and a fragment of the cytochrome *b* (cyt *b*) gene using primers MVZ15 and MVZ16 (Moritz et al. 1992). For both loci, PCR conditions consisted of an initial denaturation step at 94°C for 2 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 48°C for 1 min, and extension at 72°C for 1 min, followed by a final extension step at

Table 1. Mean, standard deviation, and range of 13 morphological measurements and tooth counts for males of species of the *Pseudoeurycea juarezi* group. Abbreviations are defined in Materials and methods.

	P. aurantia (n=4)	*P. jaguar* sp. nov. (n=2)	*P. juarezi* (n=11)	*P. ruficauda* (n=1)	*P. saltator* (n=2)
SVL	42.5±1.96 (40.2–45.0)	58.3±0.49 (58.0–58.7)	45.5±2.84 (38.5–49.2)	24.2	41.1±1.68 (40.0–42.3)
TL	41.3±4.47 (36.6–47.0)	54.5±18.58 (41.4–67.6)	46.1±6.62 (29.3–52.6)	21.0	43.9±2.87 (41.9–46.0)
AX	21.3±1.44 (19.8–23.2)	29.5±0.11 (29.4–29.6)	22.2±1.57 (19.4–24.6)	11.2	21.0±0.42 (20.7–21.3)
FLL	11.4±1.14 (10.0–12.7)	15.3±4.03 (12.5–18.2)	12.6±0.81 (11.2–13.5)	7.0	11.7±0.26 (11.5–11.9)
HLL	13.2±0.86 (12.4–14.3)	16.6±3.39 (14.2–19)	14.0±0.91 (13.1–15.1)	6.7	13.2±0 (13.2)
HL	10.4±0.57 (9.9–11.2)	14.4±0.98 (13.7–15.1)	11.4±0.79 (9.4–12.5)	6.7	9.9±0.50 (9.5–10.3)
HW	6.6±0.16 (6.5–6.8)	10.0±–0.36 (9.8–10.3)	6.9±0.45 (5.9–7.8)	4.4	6.5±0.24 (6.3–6.7)
HD	3.7±0.18 (3.5–3.9)	4.5±0.28 (4.3–4.7)	3.7±0.45 (3.1–4.6)	—	3.1±0.07 (3.0–3.9)
IO	2.4±0.20(2.2–2.7)	2.9±0 (2.9)	2.4 ±0.22 (2.1–2.7)	—	2.4±0 (2.4)
IN	2.1±0.24 (1.8–2.4)	3.2±0.21 (3.1–3.4)	2.5±0.8 (1.9–2.9)	1.1	2.3±0.21 (2.2–2.5)
RFW	4.7±0.40 (4.2–5.2)	7.8±0.21 (7.7–8.0)	5.1±0.45 (4.3–5.6)	2.1	4.3±0.65 (3.9–4.8)
T3	2.3±0.43 (1.8–2.8)	2.9±0.70 (2.4–3.4)	2.5±0.28 (2.0–2.9)	1.1	2.5±0.23 (2.3–2.6)
T5	1.0±0.12 (0.8–1.1)	1.0±0.07 (1.0–1.1)	1.2±0.20 (0.8–1.5)	0.5	1.1±0.11 (1.1–1.2)
MT + PMT	69±3.16 (66–73)	85.5±13.43 (76–95)	67±10.68 (49–90)	31	67±20.5 (52–81)
VT	23±4.54 (17–27)	30.5±7.77(25–36)	22±2.86 (17–27)	17	26±2.82 (24–28)

Table 2. Mean, standard deviation, and range of 13 morphological measurements and tooth counts for females of species of the *Pseudoeurycea juarezi* group. Abbreviations are definied in Materials and methods.

	P. aurantia (n=2)	*P. jaguar* sp. nov. (n=6)	*P. juarezi* (n=11)	*P. ruficauda* (n=1)	*P. saltator* (n=3)
SVL	42.8±1.84 (41.5—44.1)	59.0±11.85 (42.4–71.0)	47.5 ± 2.53 (44.0—51.3)	38.2	37.6±3.95 (33.4—41.2)
TL	38.0±0.45 (37.7—38.3)	66.1±14.22 (46.4–87.9)	43.9 ± 5.13 (33.1—52.1)	38.2	32.3±2.10 (30.8—33.8) n=2
AX	21.7±1.78 (20.5–23.0)	30.8±6.77 (22.0–39.6)	24.1 ± 1.05 (22.3–25.6)	20.7	20.6±3.06 (17.3–23.3)
FLL	11.1±0.53 (10.7—11.5)	15.1±4.66 (10.1–22.4)	12.0 ± 0.59 (11.5—12.9)	9.4	9.6±1.53 (8.5–11.4)
HLL	12.4±1.08 (11.6—13.2)	15.3±4.68 (9.9–22.3)	13.6 ± 0.71 (12.4—14.7)	9.6	10.3±1.50 (9.4–12.0)
HL	10.5±0.28 (10.3—10.7)	14.6±2.70 (11.0–17.6)	11.4 ± 0.95 (10.0—12.8)	8.5	6.9±2.77 (3.8–9.1)
HW	6.4±0.43 (6.1—6.7)	10.2±1.74 (7.8–12.0)	7.1 ±0.47 (6.2–7.9)	6.1	5.9±0.72 (5.4–6.7)
HD	3.8±0.18 (3.7—3.9)	4.5±0.76 (3.6–5.3)	4.0±0.25 (3.6–4.4)	—	2.7±0.52 (2.3–3.3)
IO	2.0±0 (2.08—2.09)	3.4±0.80 (2.4–4.3)	2.4±0.38 (1.7–3.0)	—	2.0±0.38 (1.8–2.5)
IN	2.0±0.18 (1.9—2.2)	3.2±0.51 (2.7–3.8)	2.1±0.13 (1.9–2.4)	1.2	1.7±0.39 (1.4–2.1)
RFW	4.2±0.18 (4.1—4.3)	7.5±2.10 (4–9.3)	5.0±0.60 (4.0–6.1)	3.9	3.8±0.58 (3.2–4.4)
T3	2.4±0.31 (2.2—2.6)	3.1±0.42 (2.7–3.9)	2.5±0.29 (2.0–3.0)	2	1.8±0.28 (1.6–2.1)
T5	1.0±0.33 (0.8—1.2)	1.0±0.30 (0.7–1.6)	1.1±0.20 (0.9–1.4)	1.3	0.8±0.15 (0.7–1)
MT+PMT	74±9.89 (67–81)	92.6±20.25 (67–116)	73±18.05 (26–96)	—	73±8.71 (67–83)
VT	22±1.41 (21—23)	30.3±7.06 (18–37)	23.2±2.79 (19–26)	—	22±2.64 (19–23)

72°C for 7 min. Amplified fragments were cleaned using 1:5 diluted ExoSAP-IT (USB Corp, Cleveland, OH), cycle sequenced using BigDye v3 terminator chemistry (Applied Biosystems, Foster City, CA) and sequenced on an ABI 3730 capillary sequencer.

Phylogenetic analyses

We obtained 16S and cyt *b* sequences for other species of *Pseudoeurycea* from GenBank; voucher information and GenBank accession numbers for all sequences used in phylogenetic analyses are given in Table 3. *Aquiloeurycea galeanae* was used as the outgroup for all phylogenetic analyses. Sequences for each gene were edited in Geneious V8 (Biomatters, Aukland, NZ), aligned using Muscle v3.8 (Edgar 2004) and concatenated. The final alignment consisted of 1335 bp (526 bp of 16S and 809 bp of cyt *b*). Partition Finder 2.0 (Lanfear et al. 2017) was used to select a partitioning scheme and nucleotide substitution models using the Bayesian Information Criterion (BIC), with data partitioned by gene and cyt *b* data partitioned by codon position. The following partition strategy and substitution models were selected by Partition Finder: 16S + cyt *b* codon position 1—GTR+I+G, cyt *b* codon position 2—HKY+I, and cyt *b* codon position 3—GTR+G.

We used RAxML v8.2 (Stamatakis 2014) to perform maximum likelihood phylogenetic analysis with the partitioning strategy given above and a GTR+G model for all partitions, with 1000 bootstrap replicates to assess nodal support. We used MrBayes 3.2 (Ronquist et al. 2012) to perform Bayesian phylogenetic analysis with three hot and one cold chains run for 20,000,000 generations, sampled every 1000 generations, with the first 5,000 samples discarded as burn-in. Finally, we estimated GTR genetic distances between sequences for each gene using PAUP*

Table 3. Voucher information and GenBank accession numbers for sequences used in phylogenetic analysis.

Species	Voucher number	GenBank 16S	GenBank cyt *b*
P. ahuitzotl	IBH 30211	MT303858	MT295473
P. altamontana	IBH 22220	KP886861	KP900064
P. anitae	MVZ 137939	AF451227	—
P. aurantia	IBH 20370	KP886844	KP900048
P. brunnata	MVZ 137947	AF451232	—
P. cochranae	IBH 23064	KP886864	KP900067
P. conanti	MVZ 146786	AF451241	—
P. exspectata	MVZ 160919	AF451234	—
P. firscheini	IBH 30995	MT303859	MT295469
P. jaguar **sp. nov.**	MZFC-HE 35855	OP605487	OP617200
P. gadovii	IBH 22982	KP886846	KP900050
P. goebeli	CRVA1017	MT303860	MT295472
P. juarezi	IBH 29718	KP886848	KP900052
P. leprosa	IBH 22406	KP886866	KP900069
P. lineola	IBH 29719	KP886867	KP900070
P. longicauda	IBH 22247	KP886849	KP900053
P. lynchi	GP160	AF451225	AF451204
P. melanomolga	IBH 22784	KP886868	KP900071
P. mixcoatl	IBH 14194	KP886869	KP900072
P. mixteca	GP0289	AF380829	AF380790
P. mystax	GP372	AF380795	AF380756
P. nigromaculata	MVZ 185977	AF451238	—
P. obesa	MVZ 241574	KP886870	KP900073
P. orchileucos	IBH 22562	KP886858	KP900062
P. orchimelas	IBH 22999	KP886860	KP900063
P. papenfussi	IBH 14198	KP886850	KP900054
P. rex	MVZ 263590	KP886852	KP900056
P. robertsi	IBH 22232	KP886853	KP900057
P. ruficauda	IBH 21646	KP886871	KP900074
P. saltator	IBH 22895	KP886854	KP900058
P. smithi	IBH 29720	KP886855	KP900059
P. tenchalli	IBH 29721	KP886856	KP900060
P. tlahcuiloh	IBH 30233	MT303865	MT295474
P. unguidentis	MVZ 117432	MT303866	—
P. werleri	IBH 22294	KP886872	KP900075
Ixalotriton niger	IBH 29715	KP886874	KP900077
I. parvus	AMA2534	KP886873	KP900076
Aquiloeurycea galeanae	IBH 24595	KP886847	KP900051

v4 (Swofford 2002). All analyses were run on the Cipres Science Gateway (Miller et al. 2010).

Results

Systematics

Pseudoeurycea jaguar sp. nov.

http://zoobank.org/4A693A70-A098-4E24-B02E-B602B6B10321

Figs 1, 2, 3, 4

Chresonymy. *Pseudoeurycea* sp. – Cázares-Hernández et al. 2021.

Suggested English name: Jaguar Salamander.

Suggested Spanish name: Tlaconete jaguar.

Holotype. MZFC-HE 28694. An adult male from El Mirador, Texhuacan Municipality, Veracruz, Mexico (18°38′04.8″N, 97°03′35.0″W, 2,367 m elevation, WGS84 datum), collected by Erasmo Cázares Hernández on 5 September 2015.

Paratypes. Seven. One male: MZFC-HE 35855 (10 September 2015); six females: MZFC-HE 35859 (10 September 2015), MZFC-HE 28686 (11 September 2015), MZFC-HE 35856–57 (14 September 2015), MZFC-HE 35858, 28685 (10 October 2015). Same locality as the holotype.

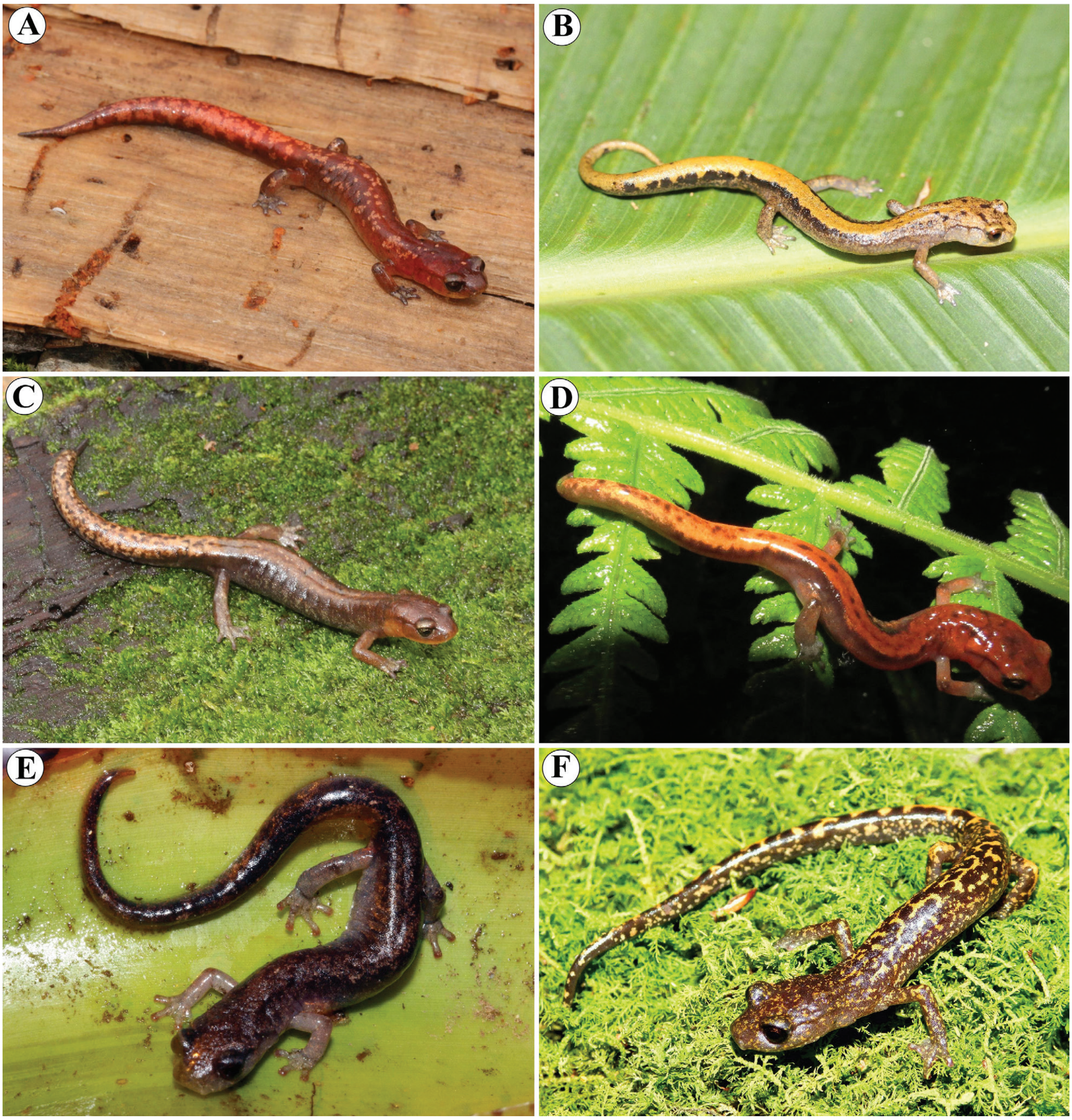

Figure 1. Live specimens of all members of the *P. juarezi* group. **A** *P. aurantia* (Peña Verde, Oaxaca), Photo by Sean Rovito; **B** *P. saltator* (Sierra de Juárez, Oaxaca), Photo by Sean Rovito; **C**, **D** *P. juarezi* (Cerro Pelón, Sierra de Juárez, Oaxaca), Photos by Sean Rovito and Luis Canseco, respectively; **E** *P. ruficauda* (near Plan de Guadalupe, Oaxaca), Photo by Sean Rovito; **F** Holotype of *P. jaguar* **sp. nov.** from the type locality, Photo by Erasmo Cázares.

Diagnosis. Assigned to the genus *Pseudoeurycea* based on the presence of a sublingual fold, comparatively short fifth toe compared to the fourth, limited foot webbing, relatively large size, and mitochondrial DNA sequences.

Morphologically, we distinguish the new species from the other salamanders that occur in the region and from the others of the genus *Pseudoeurycea* based on size of the body and tail, limb length, digit shape, shape and size of the head, and especially by external coloration (dorsal and ventral coloration of head, body and tail). *Pseudoeurycea jaguar* is easily distinguished from the other species of the genus *Pseudoeurycea* by its unique color pattern (Figs 1, 4).

Based on mtDNA, this new species is closely related to members of the *P. juarezi* group (*sensu* Canseco-Márquez and Parra-Olea 2003; Parra-Olea et al. 2004). It is distinguished from species of the *P. juarezi* group by its larger body size (SVL males: *P. aurantia* SVL 40.2–45.0, *P. jaguar* **sp. nov.** 58.0–58.7 mm, *P. juarezi* 44.0–51.3 mm, *P. ruficauda* 24.2 mm, *P. saltator* 40.0–42.3 mm; females: *P. aurantia* 41.5–44.1 mm, *P. jaguar* **sp. nov.** 42.4–71.0 mm, *P. juarezi* 38.5–48.0 mm, *P. ruficauda* 38.2 mm, *P. saltator* 33.4–41.2 mm; Tables 1 and 2) and wider head (HW males: *P. aurantia* 9.9–11.2 mm, *P. jaguar* **sp. nov.** 13.7–15.1 mm, *P. juarezi* 10.0–12.6 mm, *P. ruficauda* 6.7 mm, *P. saltator* 9.5–10.3 mm; females: *P. auran-*

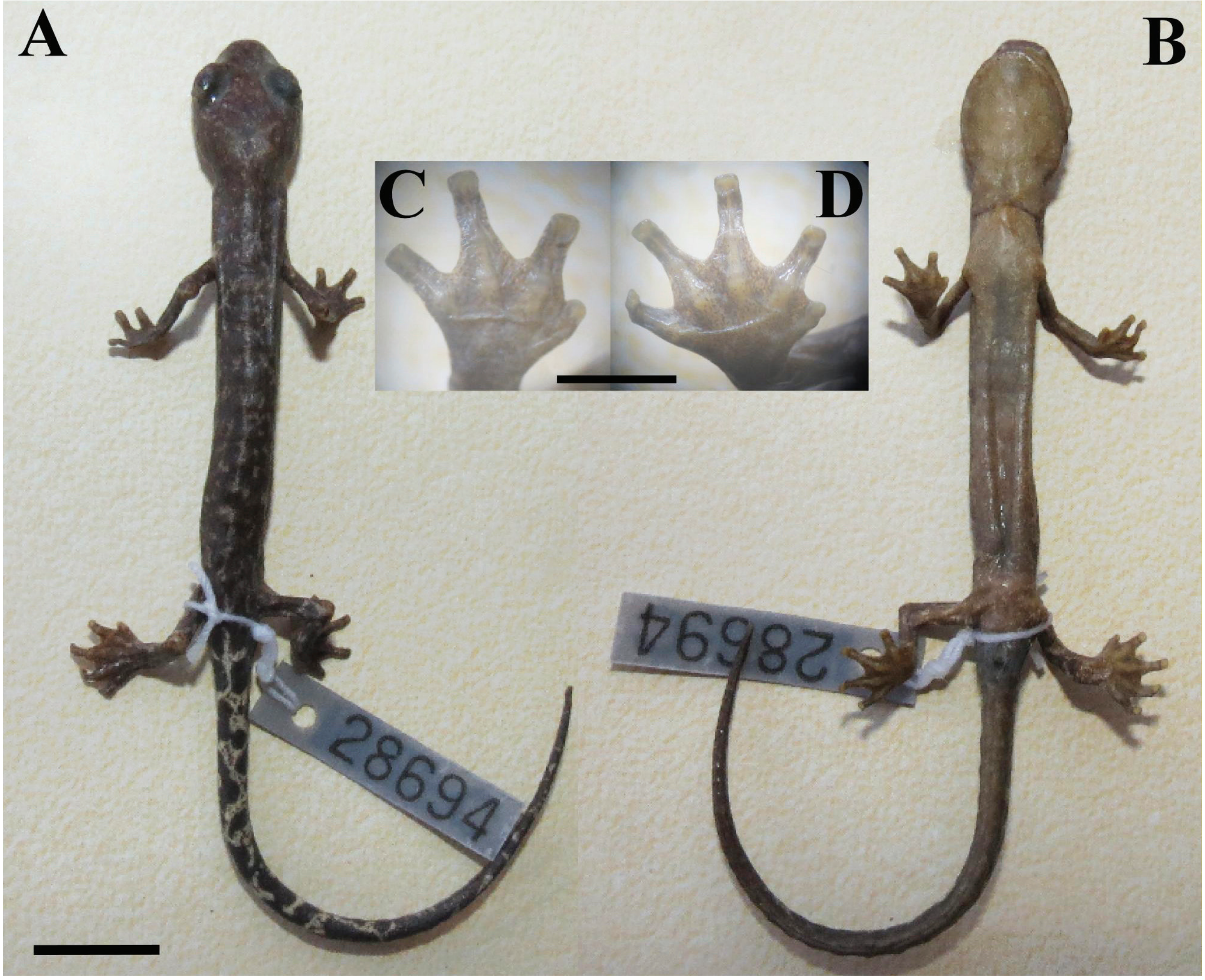

Figure 2. **A** Dorsal and **B** ventral view of the holotype of *Pseudoeurycea jaguar* sp. nov (MZFC-HE 28694), scale bar = 10 mm. **C** Ventral view of right hand and **D** right foot. Scale bar = 3 mm.

tia 10.3–10.7 mm, *P. jaguar* **sp. nov.** 11.0–17.6 mm, *P. juarezi* 9.4–12.5 mm, *P. ruficauda* 8.5 mm, *P. saltator* 3.8–9.1 mm. Females have a relatively longer tail (TL/SVL females: *P. aurantia* 0.86–0.90, *P. jaguar* **sp. nov.** 0.93–1.25, *P. juarezi* 0.70–1.12, *P. ruficauda* 0.99, *P. saltator* 0.88–0.92). *Pseudoeurycea jaguar* **sp. nov.** has more maxillary and premaxillary teeth (mean MT + PMT males: *P. aurantia* 69, *P. jaguar* **sp. nov.** 85.5, *P. juarezi* 73, *P. ruficauda* 31, *P. saltator* 67; females; *P. aurantia* 74, *P. jaguar* **sp. nov.** 92.6, *P. juarezi* 67, *P. saltator* 73) and vomerine teeth (mean VT males: *P. aurantia* 25, *P. jaguar* **sp. nov.** 30.5, *P. juarezi* 23.3, *P. ruficauda* 17, *P. saltator* 26; females; *P. aurantia* 22, *P. jaguar* **sp. nov.** 30.3, *P. juarezi* 22, *P. saltator* 22). The head of *P. jaguar* is longer and wider than that of other species (HL males: *P. aurantia* 9.9–11.2, *P. jaguar* **sp. nov.** 13.7–15.1 mm, *P. juarezi* 10.0–12.6 mm, *P. ruficauda* 6.7 mm, *P. saltator* 9.5–10.3 mm; females: *P. aurantia* 10.3–10.7 mm, *P. jaguar* **sp. nov.** 11.0–17.6 mm, *P. juarezi* 9.4–12.5 mm, *P. ruficauda* 8.5 mm, *P. saltator* 3.8–9.1 mm; HW males: *P. aurantia* 6.3–6.8, *P. jaguar* **sp. nov.** 9.8–10.3 mm, *P. juarezi* 6.2–7.9 mm, *P. ruficauda* 4.4 mm, *P. saltator* 6.3–6.7 mm; females: *P. aurantia* 6.1–6.7 mm, *P. jaguar* **sp. nov.** 7.8–12.0 mm, *P. juarezi* 5.9–7.8 mm, *P. ruficauda* 6.1 mm, *P. saltator* 5.4–6.7 mm). No other species of *Pseudoeurycea* from Veracruz or Puebla has such large, extensively webbed feet and long limbs.

The new species is further distinguished from all members of the *juarezi* group, as well as from all other species of *Pseudoeurycea* and all salamander species from central Veracruz, by color pattern. *Pseudoeurycea jaguar* has irregular yellow mottling on the dorsum on a brown or nearly black background. In *P. aurantia* the ground color is reddish brown with bright orange blotches or mottling present on the dorsum; these blotches coalesce on the tail (Fig. 1A), and some individuals have small dark spots on the tail and dorsum. *Pseudoeurycea saltator* has a uniformly dark gray-brown dorsal ground color that is invariably overlain by a paler yellow or golden mid-dorsal stripe (Fig. 1B). *Pseudoeurycea juarezi* typically has yellow-brown dorsal coloration on the head and forming a dorsal band to the tip of the tail, with scattered black spots on the dorsum and tail (Fig. 1C); the color pattern in this species can be variable, some specimens have small dark spots on a yellowish background (Fig. 1D) while others are darker brown or reddish-brown dorsally with yellow or golden mottling on the tail. Dorsal coloration in *P. ruficauda* is orange-tan with coppery-gold highlights that

Figure 3. A Ventral view of male paratype of *Pseudoeurycea jaguar* **sp. nov.** (MZFC-HE 35855) showing the mental gland. **B** Ventral view of right hand and **C** right foot of a female paratype (MZFC-HE 28685). **D** Male paratype male showing overlapping digits when appressed to the side of the body (MZFC-HE 35855). Scale bar = 2 mm.

are mixed with black (Fig. 1E). The ventral part of the tail of *P. jaguar* is paler than the dorsal part (lead gray), darkening towards the tip, with very small and clear flecks evenly distributed along the median portion of the venter. Both *P. melanomolga* and *P. gadovii* have some version of yellowish spots on a dark background, but the spots in these species are arranged in regular rows unlike the mottling seen in *P. jaguar. Pseudoeurycea lynchi* has greenish, rather than yellow, blotches and mottling and tends to show less background color compared to *P. jaguar. Pseudoeurycea nigromaculata* also typically shows less background color and often is primarily yellowish on the tail, and *P. granitum* has irregular blotches and a pale interorbital bar that are lacking in *P. jaguar*.

Description of the holotype. A relatively large adult male (58.7 SVL), body slender, head relatively long and broad (HW/SVL = 0.17), wider than body, neck region well defined (Fig. 2A, B). Snout slightly truncate in dorsal view and rounded in lateral view, eyes moderate in size, slightly protruding, not exceeding margin of jaw in dorsal view. Nostrils small, oval. Nearly round and relatively prominent mental gland (2.4 mm wide) (Fig. 2B). Costal folds 13, counting one each in axilla and groin. Tail longer than body (TL/SVL = 1.15), tapering gradually along length, slender posteriorly ending in a point. Limbs long, overlap by 2 costal folds when appressed to side of body (Fig. 3D). Hands and feet broad, digits long and relatively slender, blunt with distinct subterminal pads. Hands and feet highly webbed compared to most other members of the genus (although only moderately webbed compared with species of *Bolitoglossa* or some *Chiropterotriton*), with webbing extending to the middle of the penultimate phalanx on third toe of foot. First toe short, fifth toe short compared to fourth long, 2.1 times larger than the first finger. Digits in order of decreasing length: III–II–IV–I on hands; III–IV–II–V–I on feet. Phalangeal formulae 1–2–3–2 for hands and 1–2–3–3–2 for feet (Fig. 2C, D). Teeth numerous: maxillary teeth 92 (45/47); premaxillary teeth 3, enlarged compared to maxillary teeth; vomerine teeth 36, arranged in two arcs (18/18) extending beyond the choanae. Nasolabial protuberances well developed.

Measurements of the holotype (in mm). Snout to posterior angle of vent (SVL) 58.7; head width 10.3; head length 14.8; head depth at angle of jaw 4.7; eyelid length 3.9; eyelid width 3.0; anterior rim of orbit to snout 4.9; eye diameter 4.4; interorbital distance 3.5; snout to forelimb 21.0; internarial distance 3.1; intercanthal distance 4.1; nostril diameter 0.4; snout projection beyond mandible 1.1; snout to anterior angle of vent 55.4; axilla to groin 29.4; tail length 67.6; tail width at base 4.3; tail depth at base 4.7; forelimb length 18.2; hind limb length 19; hand width 5.1; foot width 8.0; length of the longest (third) toe 2.5; length of fifth toe 0.8; mental gland width 2.4; mental gland length 2.3. Tooth counts: premaxillary 3; maxillary 45/47; vomerine 18/18.

Variation and sexual dimorphism. The type series includes eight specimens, two males and six females. There

Figure 4. Color pattern of *Pseudoeurycea jaguar* **sp. nov.** Adults: **A** Male holotype (MZFC-HE 28694); **B**, **C**, **D** Female paratypes (MZFC-HE 35856-57, 28685, respectively; and released male (**E**) and female (**F**). Juveniles (all released). **G** A specimen < 22 mm SVL; **H** a specimen measuring 30 mm SVL; **I**, **J** specimens measuring 33 mm SVL. Photos by Erasmo Cázares.

is marked sexual dimorphism; adult females reach a larger size than males (SVL 42.4–71.0 mm in females vs. 58.0–58.7 mm in males), head relatively broad (9.8–12.0 mm in females and 9.8–10.3 mm in males) and have a more robust body compared to males (shoulder width 7.6–10.8 in females vs 7.2–7.3 mm in males). Adult males have a well-developed, nearly round mental gland (width 2.8 mm) (Fig. 3A) and few premaxillary teeth (3–4 vs.13–20 in females). Hands and feet are broader in females (foot width 7.7–8 mm in males and 8.3–9.3 in females) (Fig. 3B, C).

Coloration of the holotype in life (Fig. 4A). Dorsum and dorsal surface of head solid dark chocolate brown with extensive yellow speckling or mottling; yellow specks small on head, becoming larger and mottled on the dorsum and even larger and more continuous on tail. Sides of head brown with yellow speckling, with the same proportion of yellow toward back of the head, mouth and dorsal surface of the head. Dorsal surface of tail same color as dorsum, with the yellow mottling more continuous, but reduced at tip. Sides of body dark brown above midline, with yellow flecks (small flecks combined with larger and elongated flecks) and slightly paler brown with limited yellow mottling below midline. Dorsal surface of limbs brown chocolate (same color as dorsal surface of head, body and tail) with yellow specks, which are larger and elongated on the hind limbs; dorsal surface of feet brown with small yellow specks. Ventral surface of body, limbs, gular region and tail pale brown with small yellow flecks. Iris dark brown with yellow specks around the pupil.

Coloration of the holotype in preservative (Fig. 2A, B). Dorsum nearly uniformly dark gray, including head and tail, hands, and feet. All irregular spots on body and specks on head cream. Ventral surface of body, limbs and gular region pale gray with numerous cream specks.

Color variation in adult and juvenile specimens (Fig. 4). The color pattern is similar in most adult specimens. Irregular blotches on the body can vary in size and shape and can be yellow or orange, forming elongated or rounded patterns; they are smaller on the head and become larger along the dorsum and even larger on the tail, but their size varies from specimen to specimen (Fig. 4). Regardless of the size of the blotches on the dorsum, most specimens have a mottled pattern. There were two adult specimens, one female (MZFC-HE 35857, Fig. 4C) and one male, that were almost completely dark with small yellow blotches. There appears to be ontogenetic variation in color pattern. In juveniles, the dorsum is almost entirely dark brown or black, without the yellow mottling or blotches as in adults. Some of the smallest specimens (22 mm SVL) are almost totally black, with little or no yellow dorsal coloration (Fig. 4G, H). Slightly larger juveniles (30–40 mm SVL), show more yellow dorsal coloration (Fig. 4I, J).

Distribution and natural history. *Pseudoeurycea jaguar* **sp. nov.** is known only from Sierra de Zongolica (Fig. 5A). It is found in a mature coniferous forest (Fig. 5B, C) at 2,360–2,367 m, which is dominated by *Cupressus benthamii*, *Pinus patula*, *Alnus acuminata*, and *Saurauria leucocarpa* with an understory of *Fuchsia microphyla*, *Rubus* sp., *Licianthes synanthera*; and herbaceus plants including *Didymaea alsinoides*, *Chusquea mulleri* and *Begonia oaxacana*. There is an abundant presence of epiphytes, including *Tillandsia imperialis* and *Elaphoglossum paleaceum*, with extensive growth of mosses.

Pseudoeurycea jaguar **sp. nov.** is mainly an arboreal species with nocturnal habits. The species was observed active at night on trees, shrubs, rocks, herbaceous plants, and moss and was also observed moving on the ground. Most of the trees where *P. jaguar* was observed contained layers of moss and bromeliads. By day, we found *P. jaguar* **sp. nov.** hidden behind or within the layers of moss that cover the trunks of the trees, in particular two species of moss (*Ptychomitrium* sp. and *Anacolia menziesii*).

Other species of plethodontids that share habitat with *P. jaguar* **sp. nov.** in the study site are *Aquiloeurycea cafetalera*, *Chiropterotriton* sp., *Isthmura gigantea*, *Parvimolge townsendi*, *Thorius* sp. and *T. troglodytes*.

Intraspecific antagonistic behavior. Antagonistic behavior between individuals in a population has been described in several species of plethodontid salamanders (Jaeger and Forester 1993; Staub 1993; Lynn et al. 2019). However, this behavior has been little studied or observed in Mexican plethodontids. During our population study, we only found one individual of *P. jaguar* in each trap or tree studied. Initially, we collected some individuals, transported them to the laboratory, and took morphological measurements for mark-recapture studies. On the first sampling trip, we kept three containers with more than one individual, considering that each container represented a particular section of the study area. In the first one, we kept five immature individuals with a large adult, in the second container a pair of adult individuals, and in the third container two large adult individuals with a young adult. In all the containers there were signs of serious aggression. In the first, three of the five juvenile individuals disappeared; in the second, the female and male adults mutilated each other, leaving the male blind and the female with serious injuries to the body; in the third container, the youngest individual was killed. Some individuals of the population studied have regenerated or regenerating tails, indicating some level of predation or possibly agonistic interaction between them.

Etymology. The specific epithet *jaguar* is a noun in apposition and refers to the similarity between the dorsal color pattern of the salamander and that of the jaguar (*Panthera onca*). In the last three years the presence of this endangered feline has been recorded in some places in the Sierra de Zongolica and it seems appropriate to honor this emblematic species in the region.

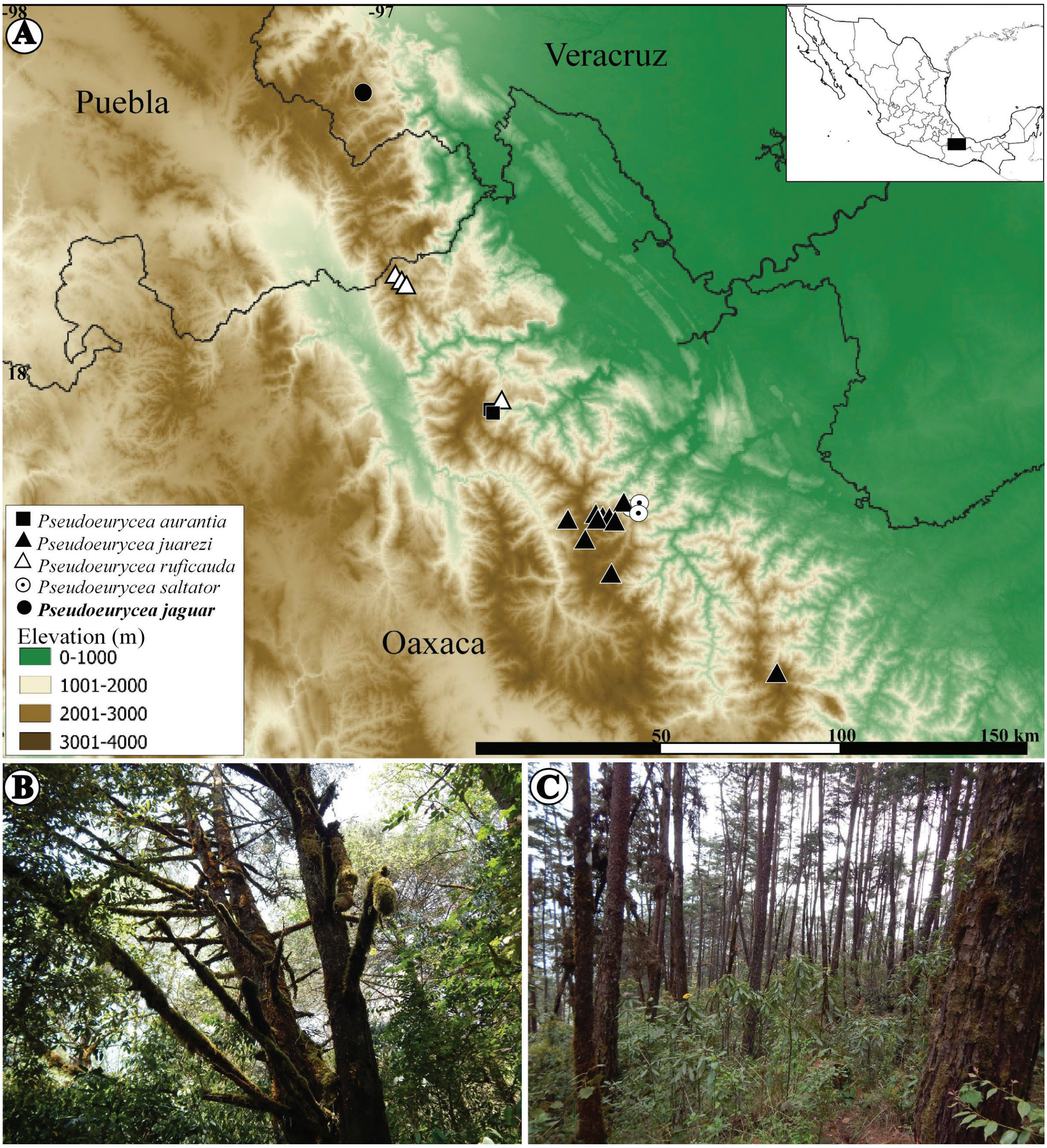

Figure 5. **A** Geographic distribution of members of the *P. juarezi* group. **B**, **C** Habitat at the type locality of *Pseudoeurycea jaguar* **sp. nov.** *Cupressus* forest, roots, trunk and branches of the trees have moss of the genera *Ptychomitrium* sp. and *Anacolia*.

Molecular systematics

The results of our mtDNA phylogenetic analysis (Fig. 6) showed that *Pseudoeurycea jaguar* **sp. nov.** belongs to the *Pseudoeurycea juarezi* group and is the sister taxon of *Pseudoeurycea ruficauda* with strong support (Bootstrap proportion [BS] = 74, Posterior Probability [PP] = 0.98). These two species were part of a strongly supported clade (BS = 83, PP = 1.0) with three additional species from northern Oaxaca: *P. aurantia, P. juarezi,* and *P. saltator.* GTR genetic distances between *P. jaguar* and *P. ruficauda* were 0.030 (16S) and 0.096 (cyt *b*). These distances were comparable to those between sister species in the *leprosa* group and larger than those between other species in the *juarezi* group (Table 4). The 16S GTR distance between *P. juarezi* and *P. saltator* is 0.0, and the distance of *P. aurantia* to both of these species is 0.006; the largest distance for 16S between sister species in these two groups is 0.034 between *P. conanti* and *P. mystax*. For cyt *b*, GTR distances range from a minimum of 0.037 between *P. juarezi* and *P. saltator* to a maximum of 0.113 between *P. obesa* and *P. werleri*.

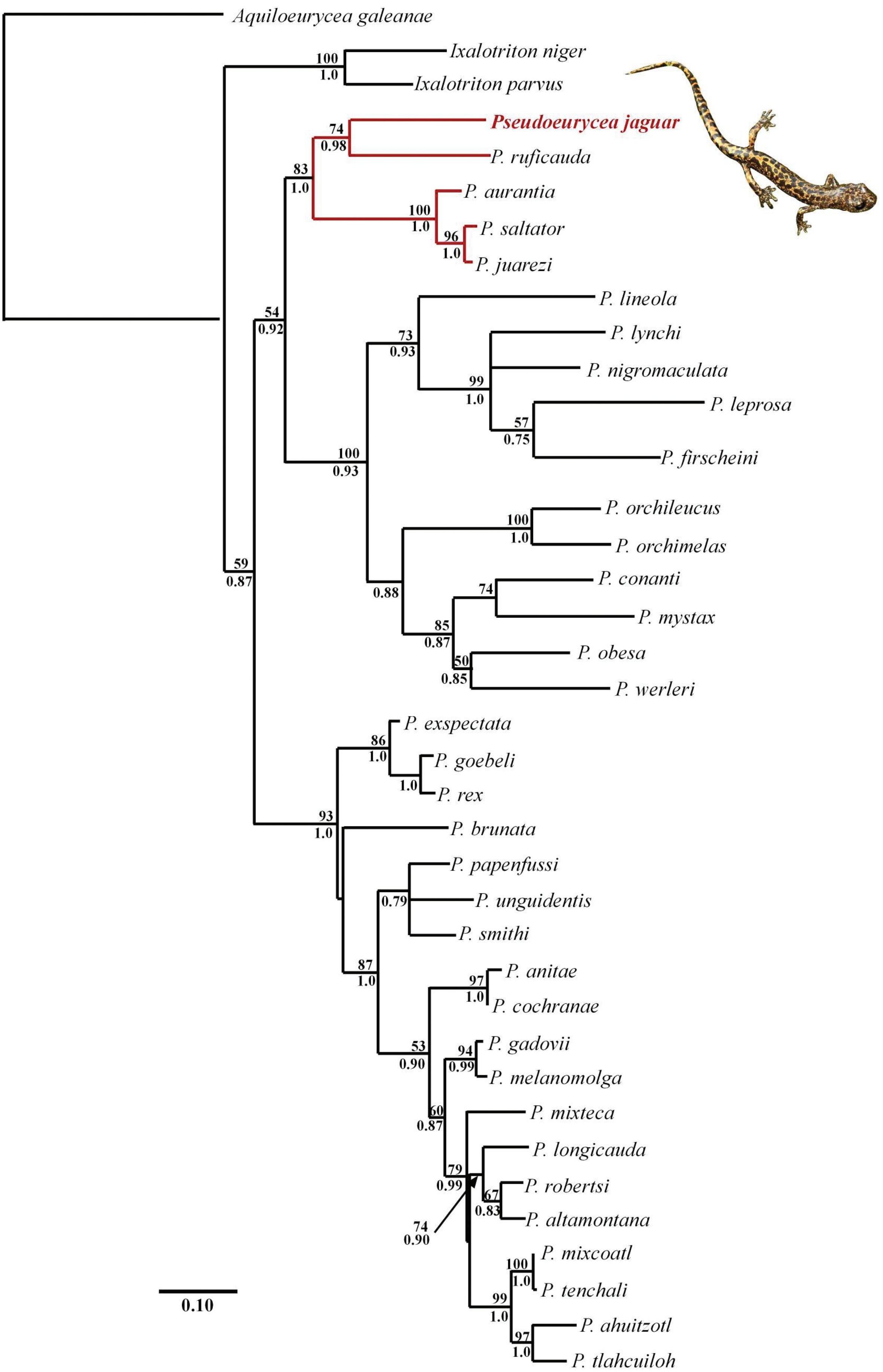

Figure 6. Phylogeny estimated from maximum likelihood analysis of 16S and cyt *b* mtDNA sequence data. Numbers above branches are bootstrap proportions from RAxML analysis and numbers below branches are posterior probabilities from Bayesian analysis. Bootstrap proportions below 50 and posterior probabilities below 50 are not shown. The *P. juarezi* group is indicated in red.

Table 4. Generalized time-reversible (GTR) distances between species of the *juarezi* and *leprosa* groups of *Pseudoeurycea*. 16S distances are given above the diagonal and cyt *b* distances below the diagonal. Distances between *P. jaguar* and other species are shown in bold.

	P. mystax	**P. lynchi**	**P. nigro-maculata**	**P. firscheini**	**P. leprosa**	**P. rufi-cauda**	**P. jaguar**	**P. aurantia**	**P. juarezi**	**P. saltator**	**P. obesa**	**P. werleri**	**P. lineola**	**P. orchi-leucos**	**P. orchi-melas**
P. conanti	0.034	0.043	0.049	0.047	0.043	0.056	**0.047**	0.043	0.041	0.041	0.043	0.041	0.043	0.038	0.043
P. mystax	—	0.036	0.045	0.052	0.043	0.047	**0.047**	0.048	0.050	0.050	0.038	0.038	0.038	0.034	0.034
P. lynchi	0.172	—	0.023	0.030	0.023	0.036	**0.028**	0.034	0.037	0.037	0.041	0.039	0.036	0.032	0.038
P. nigromaculata	—	—	—	0.032	0.030	0.043	**0.036**	0.038	0.041	0.041	0.047	0.050	0.047	0.039	0.052
P. firscheini	0.201	0.137	—	—	0.023	0.050	**0.043**	0.045	0.048	0.048	0.059	0.061	0.052	0.050	0.052
P. leprosa	0.199	0.100	—	0.090	—	0.038	**0.041**	0.039	0.041	0.041	0.045	0.048	0.045	0.041	0.050
P. ruficauda	0.180	0.191	—	0.192	0.204	—	**0.030**	0.025	0.028	0.028	0.050	0.057	0.052	0.043	0.061
P. ***jaguar***	**0.161**	**0.158**	**—**	**0.177**	**0.177**	**0.096**	—	**0.023**	**0.026**	**0.026**	**0.040**	**0.048**	**0.045**	**0.025**	**0.045**
P. aurantia	0.150	0.175	—	0.166	0.154	0.165	**0.164**	—	0.006	0.006	0.050	0.050	0.047	0.036	0.047
P. juarezi	0.158	0.182	—	0.159	0.160	0.146	**0.161**	0.037	—	0.000	0.043	0.050	0.045	0.034	0.045
P. saltator	0.161	0.193	—	0.166	0.171	0.162	**0.168**	0.043	0.037	—	0.043	0.050	0.045	0.034	0.045
P. obesa	0.113	0.187	—	0.204	0.188	0.171	**0.174**	0.158	0.174	0.185	—	0.032	0.036	0.027	0.038
P. werleri	0.117	0.172	—	0.201	0.199	0.180	**0.161**	0.150	0.158	0.161	0.113	—	0.045	0.030	0.038
P. lineola	0.193	0.156	—	0.153	0.167	0.173	**0.174**	0.184	0.179	0.184	0.175	0.193	—	0.030	0.034
P. orchileucos	0.165	0.193	—	0.169	0.186	0.135	**0.172**	0.176	0.173	0.176	0.180	0.165	0.170	—	0.021
P. orchimelas	0.157	0.168	—	0.166	0.162	0.161	**0.172**	0.189	0.193	0.195	0.171	0.157	0.175	0.083	—

Discussion

Based on mtDNA, *Pseudoeurycea jaguar* **sp. nov.** belongs to the *P. juarezi* group. Except for the new species, which is endemic to the Sierra de Zongolica of Veracruz, all the species belonging to the *P. juarezi* group are distributed in cloud forest in the highlands of northern Oaxaca, in the Sierra de Juárez, Sierra Mazateca and Sierra Mixe. There is geographical congruence in this clade (Figs 5, 6). *Pseudoeurycea jaguar* **sp. nov.** has the northernmost distribution of this subclade; it is most closely related to another arboreal species *P. ruficauda* from the cloud forest from Sierra Mazateca and Sierra de Juárez in northern Oaxaca, to which it is closest geographically. These two species are the sister group of the other subclade, which is composed of the terrestrial salamanders *P. aurantia,* from cloud forest of Peña Verde, Oaxaca (south of the Sierra Mazateca), and *P. juarezi,* from cloud forest of the Sierra de Juárez and Sierra Mixe, and the arboreal *P. saltator* from Sierra Juárez (south of Peña Verde).

Because of its arboreal habits, *P. jaguar* is likely vulnerable to logging and most of the trees it occupies are species of economic value. Logging is occurring in the Sierra de Zongolica, including the forest where *P. jaguar* **sp. nov.** occurs. Logging in the forests of the Sierra de Zongolica is not properly regulated and in many places it is carried out clandestinely. There is no follow-up to timber harvesting programs intended to mitigate the impacts on the flora and fauna found in the forests under management. Further studies are required to determine the distribution and population status of *P. jaguar* **sp. nov.** This would allow us to obtain more information about its natural history, as well as its relationship with the forest environments it inhabits. Based on the circumstances of the habitat, population ecology and observed behavior, we apply the evaluation criteria of the IUCN Red List (IUCN 2012), and the Risk Assessment Manual (MER for its acronym in Spanish) of the Secretaría de Medio Ambiente y Recursos Naturales (Sánchez-Salas et al. 2013), and we propose that *P. jaguar* **sp. nov.** should be considered as a species at risk.

Based on our direct observations and with the best available evidence on salamander communities in the region, we can affirm that *P. jaguar* is a vulnerable taxon and that it may face risk of extinction in the wild. The species is currently known from only one locality, within a potential distribution range of less than 20,000 km^2 (following MER criteria, Sánchez et al. 2007) and restricted to a single known type of vegetation. These populations appear to be strongly fragmented and we infer that because of the decrease in habitat quality due to changes in land use and logging of forests, there is a continuous long-term reduction (more than 10 years) in population size (estimated in fewer than 10,000 adult individuals currently).

These changes may not be reversible in the long term due to the effects of human activity, climate change affecting its habitat, and/or chance events (for example, disease outbreaks) that could put the species at greater risk. With this information, we suggest a provisional assessment of *P. jaguar* as "Vulnerable" using the Red List criteria (VU 4a, c; B1ab (iii); C1; D2) (IUCN 2012) and Threatened (A) by the MER (Sánchez et al. 2007).

The species diversity of the Sierra de Zongolica is high, and it is important to continue exploring other areas, since several records and new species have recently been discovered (Canseco-Márquez et al. 2016; De La Torre-Loranca et al. 2020; García-Vázquez et al. 2022). This region is topographically complex, which generates a diversity of microclimates and a great variety of ecosystems, including Evergreen Tropical Forest, Cloud Forest, Coniferous Forest and Pine-Oak forests (Rzedowski 2006; Miranda and Hernández 1963). The northern and southwestern parts of the Sierra contain pine-oak forest, coniferous forest, cloud forest; the central and southeast portions have elements of cloud forest, tropical forest-cloud forest ecotones, evergreen tropical forest and tropical lowland vegetation; the elevations generally go from 100 to 2500 m. The Sierra de Zongolica is very important for its high number of plethodontid salamanders (14 species; Cázares-Hernández et al. 2021): *Bolitoglossa platydactyla* (in cloud forest and evergreen tropical forest), *B. rufescens* (in evergreen tropical forest), *Aquiloeurycea cafetalera, Isthmura gigantea* (in cloud forest and pine-oak forest), *Parvimolge townsendi*, *Pseudoeurycea firscheini, P. granitum, P. nigromaculata*, *P. lineola*, *P. jaguar, P. werleri, Thorius pennatulus, T. troglodytes* and *Chiropterotriton* sp. (in cloud forest, evergreen tropical forest and *Cupressus* forest). Additional fieldwork in the Sierra de Zongolica and adjacent regions of Puebla could reveal additional salamander species or expand the known distribution of *P. jaguar,* highlighting the need for continued herpetological exploration in the region.

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Appendix

Specimens examined:

Institutional abbreviations for museums and collections follow Sabaj (2022). Museum of Vertebrate Zoology, UC Berkeley (MVZ), Instituto de Biología, UNAM (IBH), Museo de Zoología, Facultad de Ciencias, UNAM (MZFC) and Escuela de Biología, Benemérita Universidad Autónoma de Puebla (EBUAP).

***Pseudoeurycea aurantia* (n=5)**. MEXICO: OAXACA: 11.8 km E (by air) Concepción Pápalo, Sierra de Juárez (MVZ 270127─28, 270132, 270134–35). 4 km W Peña Verde (EBUAP 2051, Holotype).

***Pseudoeurycea jaguar* sp nov.** (n=9) MEXICO: VERACRUZ: Texhuacan Municipality: El Mirador (MZFC-HE 28694 holotype, MZFC-HE 28685–86, 35855–59, paratypes, MZFC-HE 35860)

Pseudoeurycea juarezi. (n=21) MEXICO: OAXACA: 52 km W Guelatao along Mexico Hwy. 175 (MVZ 112192, 147186, 162121); N slope of Cerro Pelón along Mexico Hwy. 175, 52–54 km N (by road) Guelatao (MVZ 131031, 131037, 131039); 0.7 mi E (by road) Cerro Pelón from point where road crosses top (MVZ 86053); 0.7 mi E (by road) or NE Cerro Pelón (MVZ 86072); 1.1 km N (by rd) of Cerro Pelón mirador on MX Hwy 175 (IBH 32420); Cerro Pelón, near Mexico Hwy. 175, 108.9 km N (by road) Oaxaca de Juárez from junction Pan American Hwy. (MVZ 114386–87); 52 km W Guelatao along Mexico Hwy. 175 (MVZ 112196, 147198); Mexico Hwy. 175, 57 km N (by road) Guelatao (MVZ 131044); 1.5 km NE (by road) Cuajimoloyas, Distrito Ixtlán (MVZ 131097); 18.7 km E (by road) Cuajimoloyas along road to Cajones (MVZ 194309); 5.8 km NW (by rd) of junction with road to Zacatepec on MX Hwy 179 to Totontepec Villa de Morelos (IBH 32365); 11.1 mi SW (by road) Totontepec [=Totontepec Villa de Morelos] (MVZ 163769); 19 km SW (by road) Totontepec [=Totontepec Villa de Morelos] (MVZ 164662–63, 164665); Cerro Zempoaltepec (MVZ 163874);

Pseudoeurycea ruficauda. (n=2) MEXICO: OAXACA: 4.0 km NE (by rd) of Peña Verde on road to Tlalixtac Viejo, Sierra de Juárez (IBH 22610); 2 km NW Puerto de Soledad (MVZ 236762).

Pseudoeurycea saltator. (n=5) MEXICO: OAXACA: San Pedro Yolox Municipality: La Galera, 11.0 km SW (by rd) of La Esperanza on MX Hwy 175 (IBH 32193, 32402); 65 km NE of Guelatao, by Mexico Hwy. 175 (MVZ 112230, 147263); forest along Mexico Hwy. 175, 129.9 km N (by road) Oaxaca de Juárez Ctr., junction Panam Hwy (MVZ 114398).