



A new species of patch-nosed snake (Colubridae: *Salvadora* Baird and Girard, 1853) from Oaxaca, Mexico

CARLOS ALBERTO HERNÁNDEZ-JIMÉNEZ^{1,2,4,5}, OSCAR FLORES-VILLELA^{2,3} & JONATHAN ATWOOD CAMPBELL³

¹Facultad de Ciencias Biológicas, Benemérita Universidad Autónoma de Puebla. Ave. San Claudio s/n Edif. 112 Ciudad C. P 72570 Puebla. Pue. México.

²Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, A. P. 70–399, México, D.F. 04510

³Department of Biology, The University of Texas at Arlington, Arlington, Texas 76019.

⁴Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México México, Ciudad de México, 04510

⁵Corresponding author. E-mail: acaltetepon22@gmail.com

Abstract

A new species of snake of the genus *Salvadora* from Oaxaca, Mexico, is described. This taxon was confused with *S. intermedia* in previous taxonomic descriptions. It is characterized by lacking a pale vertebral stripe and by having incomplete dorsolateral stripes that do not reach the posterior part of the body, which is typical of congeners; by having both dorsolateral stripes separated each other by five to six scale rows on anterior part of body; and other scalation characters as well as the number maxillary teeth. The importance of this snake and its conservation is discussed.

Key words: Taxonomy, Description, Colubridae

Introduction

Snakes of the genus *Salvadora* are members of the most diverse and phylogenetically complex snake clade in the world, the Colubridae, in which the genera *Coluber* and *Drymarchon*, *Phyllorhynchus*, *Tantilla*, *Trimorphodon* and *Masticophis* are postulated like sister taxa to be closed related (Figueroa *et al.* 2016; Pyron *et al.* 2011; 2013; Tonini *et al.* 2016; Zheng & Wiens, 2016). Species of *Salvadora* are medium-sized, diurnal snakes, inhabiting a variety of environments from sea level to over 2,500 m. They occur from the southwestern United States through Mexico to the Grijalvan Depression of Chiapas (Bogert 1939a) and extreme western Guatemala (JAC-pers. obs.). According to Bogert (1939a), the genus *Salvadora* is characterized by having an enlarged rostral scale with free edges; a color pattern consisting of lateral and dorsolateral stripes, and usually a distinct vertebral stripe; and 17 rows of dorsal scales on the anterior and middle part of the body, which are reduced to 13 posteriorly (Bogert 1939a).

Smith (1938, 1941) suggested that two groups exist within the genus *Salvadora*. These groups are differentiated by the number of caudal scales, number of maxillary teeth, and cephalic scutellation. The *mexicana* group includes the two largest species of the genus *Salvadora*: *S. lemniscata* and *S. mexicana*, while the second group, *grahamiae*, includes all other species.

The taxonomic history of the genus *Salvadora* is relatively convoluted. Since the generic description by Baird & Girard (1853), there have been a number of taxonomic and nomenclatural changes, which have created problems in recognizing the validity of certain taxa (Stejneger 1902, Blanchard 1924, Amaral 1927, Stuart 1932, Bogert 1939b, 1945, 1947, Schmidt 1940, Smith 1941, Cope 1860, Günther 1863). Currently, seven species and six subspecies are recognized (Smith & Smith 1976; Flores-Villela 1993, Wallach *et al.* 2014).

During the course of revising species in the genus *Salvadora*, we conducted extensive fieldwork in Mexico to

collect representative specimens and tissue samples. Our survey of Oaxacan material revealed an undescribed species of *Salvadora* identified as *S. intermedia* in other collections. The population of *Salvadora* **sp. nov.** from Central Oaxaca and *S. intermedia* are similar in scalation, maxillary teeth and in relative geographical proximity (although not sympatric with *S. intermedia* or any other *Salvadora* species).

Material and methods

We examined 361 specimens representing all known species of the genus *Salvadora* (Appendix 1) and a total of six specimens from Oaxaca representing the new species, all of which are deposited in museum collections. The holotype was collected during surveys conducted during August 2014 and was photographed prior to euthanasia. Liver and heart tissues were stored in 96% ethanol, and the specimen was fixed in 10% formalin and subsequently transferred to 70% ethanol. Museum abbreviations follow Sabaj-Perez (2013). Nomenclature of scales and the format for the diagnosis follow that of previously published species of *Salvadora* (Bogert 1945). Most morphometric and meristic data were taken under a dissecting microscope, head measurements by using a digital caliper to the nearest 0.1 mm, and body measurements using a ruler to the nearest 1.0 mm. Data taken were: snout-vent length (SVL = measured from tip of snout to vent); tail length (TaL = measured from vent to tip of tail); total length TL; proportional tail length (TaL/ SVL); dorsal scale rows at neck (DSN = number of scale rows one head length behind head); scale rows at mid-body (MSR = number of scale rows at mid-body); dorsal scale rows anterior to the vent (DSV = number of dorsal scale rows head length prior to vent); dorsal scale rows (DSR = general scale formula = DSN–MSR–DSV); ventral scales (VS = number of scales from first ventral scale posterior to preventrals (sensu Dowling 1951) to vent, excluding cloacal scute); subcaudal scales (SCS = number of paired caudal scales excluding the terminal spine); maxillary teeth (MT = number of maxillary teeth); lateral stripe (LS); dorsolateral stripe (DS); vertebral stripe (VST). Color descriptions follow Smithe (1975). Recognition of this species is based on the phylogenetic species concept proposed by Frost & Hillis (1990).

Additionally we performed a molecular phylogenetic analysis to evaluate the divergence of *Salvadora* **sp. nov.** with *S. intermedia* and five of seven species described in the genus. DNA extraction was taken from fresh tissues and stored in 95% ethanol. Genomic DNA was extracted from tissues using DNAeasy Blood and Tissue Kit (Quiagen) using standard protocol. We amplified a fragment of 770bp containing part of NADH dehydrogenase subunit 4 (ND4) including complete rRNA and partial tRNA. Using the primers NDF (CAC CTA TGA CTA CCA AAA CCT CAT GT) and LeuR (CAT TAC TTT TAC TTG GAT TTG CAC CA) modified from previous studies (Arevalo *et al.* 1994; Harvey *et al.* 2000). We used polymerase chain reaction under the following conditions: initial denaturation at 94°C for 3 min, then 35 cycles of denaturation for 30 s at 94°C, annealing for 45 s at 55°C, and extension for 90 s at 72°C, followed by a final extension at 72°C for 10 min.

Products were sent to the High-Throughput Genomics Center, University of Washington, to obtain sequences, using the same set of primers as used for the PCR. Overlapping sequence (forward and reverse) were assembled using Staden Package Software (Bonfield, *et al.* 1995) and then aligned using MUSCLE (Edgar, 2004) in MEGA software (Tamura *et al.* 2011).

For the Phylogenetic analyses, sequences available in GenBank for *Masticophis flagellum* (AF138747.1), *Tantilla vermiformis* (KR814714.1), *Drymarchon corais* (DQ902314.1), and *Mastigodryas dorsalis* (KR814714.1) were included as outgroups.

Maximum likelihood phylogenetic reconstruction was implemented in MEGA (Tamura *et al.* 2011) with 100 independent searches using the GTRGAMMA (GTR+G) model that was determined by model selection using the Bayesian Information criterion in MEGA (Tamura *et al.* 2011). Nodal support for the best scoring ML tree was bootstrap proportions from 1000 pseudoreplicates

Results

Salvadora gymnorhachis, sp. nov.

Figs. 1, 2

urn:lsid:zoobank.org:act:FA3E5069-814D-4890-BC45-489F9AF4133B

Holotype. An adult female (MZFC 28775) from near San Pedro y San Pablo Ayutla, Distrito Mixe, Oaxaca, Mexico (17.00159° N, -96.08443° W; datum = WGS84), 2100 m above sea level, collected in pine-oak forest on August 22, 2014 (Fig. 3).



FIGURE 1. Differences in the length of the dorsolateral stripes of *Salvadora*. Top, holotype of *Salvadora gymnorhachis* sp. nov. (MZFC 28775) from San Pedro y San Pablo Ayutla, Sierra Mixe. Oaxaca, Mexico. Bottom, *Salvadora intermedia* from Chilpancingo, Guerrero, Mexico. Notice the, see text for details.

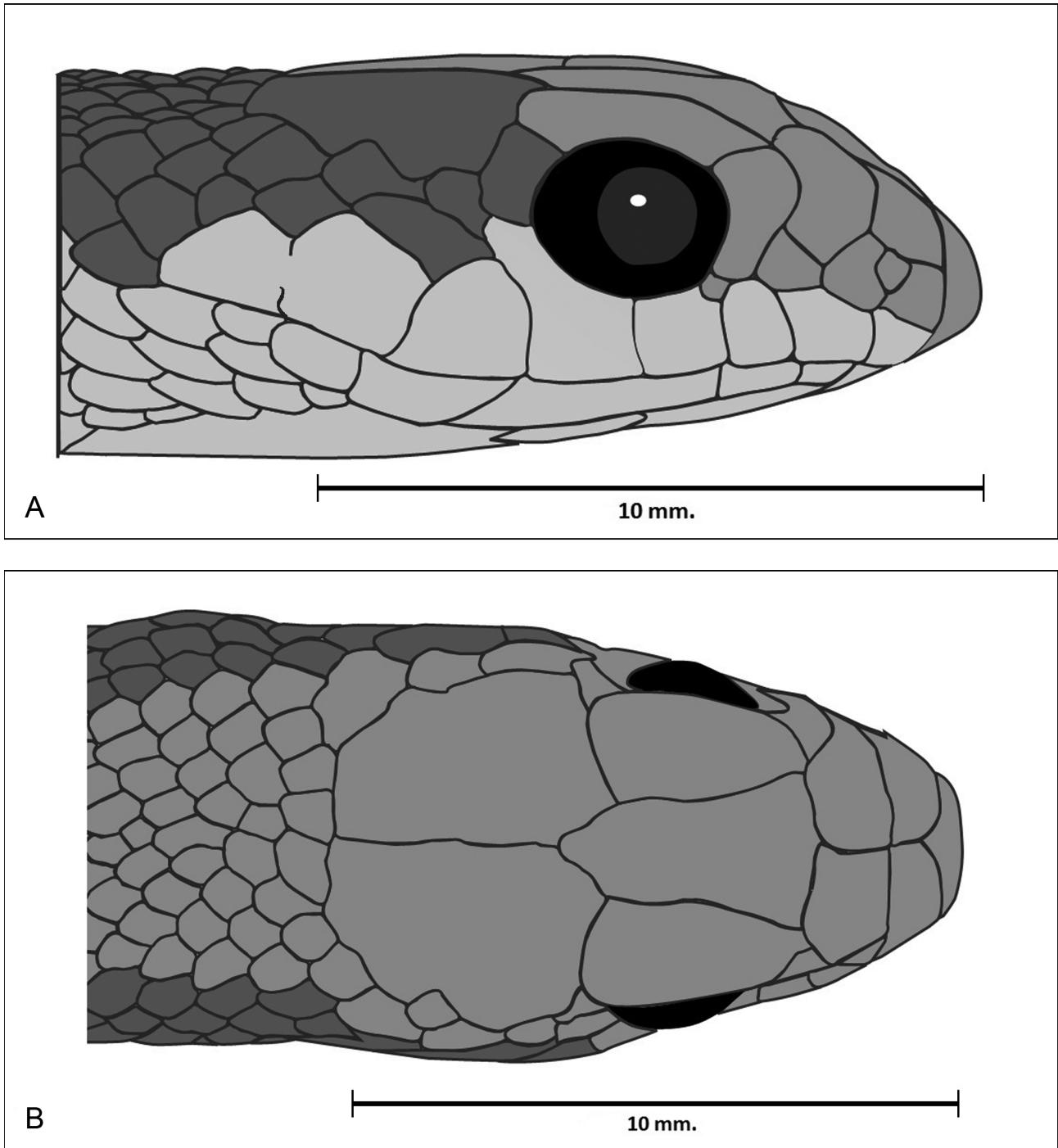


FIGURE 2. Head of holotype of *Salvadora gymnorhachis* sp. nov. (MZFC 28775). A, lateral view. B, dorsal view. Drawing based on a photograph taken of preserved specimen.

Paratypes. Five, all from the state of Oaxaca, Mexico. A juvenile female (AMNH 84992) from San Pablo Mitla, 1900 m; an adult male (AMNH 91090) from 8.3 km north of Mitla, 2100 m; and an adult female (AMNH 100910) from 2 km west of San Lorenzo Albarradas, 2000 m; all three from Distrito de Tlacolula. An adult female (AMNH 100909) from 12 km (via road) southwest of San Pedro y San Pablo Ayutla, 1760 m, Distrito de Mixe; and an adult female (UIMNH 56849), near Santa Catalina Quierí, 2364 m, Distrito de Yautepec.

Diagnosis. *Salvadora gymnorhachis* differs from all its congeners by lacking a pale vertebral line, and dorsolateral stripes extending only to about the middle of the body (vs other species in which these stripes extend by throughout whole length of the body) (Table 1); *Salvadora gymnorhachis* also differs from *S. grahamiae*, *S. bairdi*, *S. mexicana*, and *S. lemniscata* by having 11 maxillary teeth followed by a diastema and three enlarged teeth

(9–10+3 in *S. grahamiae* and *S. bairdi*; 14–15+3 in *S. mexicana* and *S. lemniscata*); it further differs from *S. mexicana* and *S. lemniscata* by having fewer than 105 subcaudals (vs more than 124), a divided preocular (vs single in *S. mexicana* and *S. lemniscata*); from *S. deserticola* and *S. hexalepis* by having second and third supralabials in contact with loreal (vs third, fourth, and sometimes fifth contacting loreal); and from *S. intermedia* by having six and five scale rows separating dorsolateral stripes on anterior and middle part of body, respectively (vs 3 and 1-2 scale rows separating stripes on anterior and middle part of body, respectively).

TABLE 1. Comparisons of several characters among species of *Salvadora*. MT = Maxillary teeth, VS = ventral scales, CS = caudal scales, %TL–TaL = % of tail length in respect to total length, PS = preocular scale (Unique or Divided), TS = transversal stripes on first third of body (Absent or Present), VST = vertebral stripe along length of body, bordered by dorsolateral stripes, DS = dorsolateral stripes (Present or Absent), LS = lateral stripes (Present or Absent), PCHS = posterior pair of genials clearly separated (Present or Absent), L = loreal scale (Simple or Divided), S = supralabials, I = infralabials.

Taxon/(No.of specimens)	MT	VS	CS	%TL–TaL	PS
<i>Salvadora bairdi</i> (36)	9–10+3	172–205	82–105	≤ 28%	D
<i>Salvadora deserticola</i> (28)	11+3	180–201	66–86	≤ 28%	D
<i>Salvadora gymnorhachis</i> (6)	11+3	176–186	92–103	≤ 28%	D
<i>Salvadora grahamiae</i> (97)	10+3	177–202	81–107	≤ 28%	D
<i>Salvadora hexalepis</i> (88)	11–13+3	180–213	75–103	≤ 28%	D
<i>Salvadora intermedia</i> (37)	11+3	173–190	84–114	≤ 28%	D
<i>Salvadora lemniscata</i> (25)	14+3	194–205	128–141	≥ 29%	U
<i>Salvadora mexicana</i> (44)	15+3	182–197	124–145	≥ 29%	U

continued.

Taxon/(No.of specimens)	TS	VST	DS	LS	PCHS	L	S	I
<i>Salvadora bairdi</i> (36)	A	P	P	P	A	S	7–8	9
<i>Salvadora deserticola</i> (28)	A	P	P	P	P	S	9–10	10–12
<i>Salvadora gymnorhachis</i> (6)	A	A	A	A	P	S	8–9	8–10
<i>Salvadora grahamiae</i> (97)	A	P	P	P/A	A	S	7–9	9–12
<i>Salvadora hexalepis</i> (88)	A	P	P	P	P	D	10–12	8–11
<i>Salvadora intermedia</i> (37)	A	P	P	P	P	S	8–10	9–12
<i>Salvadora lemniscata</i> (25)	A	P	P	P	A	S	9–10	11–13
<i>Salvadora mexicana</i> (44)	P	P	P	P	A	S	9	11–12

Description of holotype. Rostral with free lateral edges, extending slightly between internasal suture; plates behind rostral on top of head including prefrontals, supraoculars, frontal and paired parietals; on side of head prenasal separated from second supralabial; loreal situated above second and third supralabials; two preoculars, upper larger, contacting prefrontal and supraocular; lower preocular small, situated above third and fourth supralabials; two postoculars at left side, lower contacting fifth and sixth supralabials; one postocular at right side touching the large fifth supralabial; temporals 2 + 2, lower contacting fifth, sixth, and seventh supralabials (Fig. 2A); 8/8 supralabials; fourth and fifth touching eye; 8/8 infralabials, first pair meeting at midventral line behind small mental, first four pairs reaching anterior genials; fourth infralabial enlarged more than length of anterior genials; posterior genials smaller than anterior genials, separated by single row of two median scales; dorsal scales in 19 rows immediately behind head at level of ventral 3, 17 rows at level of ventral scale 13; 16 rows at midbody at level of ventral scale 90, and 13 scale rows anterior to vent at level of ventral scale 170; 182 ventrals; cloacal scute divided, bordered laterally by small scales; tail incomplete, 80+ subcaudals; 11 maxillary teeth, increasing in size posteriorly, followed by diastema and three enlarged teeth (11+3).

Measurements. Total length 612 mm; SVL 471 mm; TaL 141 mm (tip missing), comprising about 23 % of total length.

Coloration. Pattern consisting of a pair of dark dorsolateral stripes (89 Jet black; Smithe, 1975) beginning at level

of postoculars, extending to middle of body where stripes grade into ground color; dorsolateral stripes occupying upper half of second dorsal scale row and covering four scale rows on anterior part of body, reduced to three scales wide just before becoming inconspicuous at about mid-body; field between dorsolateral stripes brown (223B Verona brown), six rows wide at anterior part of body, five at middle of body where stripes begin to fade; posterior part of body gray (45 Smoke gray); ventral surface of body whitish (92 Pale horn) except for salmon color (6 Salmon) on lateral portion of ventrals of posterior part of body and venter of tail; lateral edges of ventral scales black.

Variation of Paratypes. Except for minor differences in scutellation, paratypes closely resemble holotype (Table 2); ventrals in females 176–184, single male with 186 ventrals; subcaudals 92–103 in females, tail incomplete in single male; supralabials 8/8 in most specimens, except in female from near Municipality of San Lorenzo Albarradas, Oaxaca with 9 on one side; third and fourth supralabial reaching second (lower) postocular on individuals from District of Tlacolula, Oaxaca, whereas female from Municipality of Santa Catalina Quieri, Oaxaca (UIMNH 56849) and female from Municipality of San Pedro y San Pablo Ayutla, Oaxaca (AMNH R–100909) with only fifth supralabial touching postocular; anterior nasal in contact with second supralabial in all specimens, except the one from Municipality of Mitla (AMNH 91090), Oaxaca, in which anterior nasal slightly separated from second supralabials; two supralabials, reaching loreal in all specimens except for one female (AMNH 100910) with three on left side; body length 852 to 975 mm, male being largest in series and female holotype smallest (Table 2).

TABLE 2. Variation between holotype and paratypes of *Salvadora gymnorhachis* in selected morphological characters. MT = maxillary teeth, VS = ventral scales, CS = caudal scales, SVL = snout vent length; TaL = tail length; S = supralabials, I = infralabials; P2S = prenasal in contact with 2nd supralabial (Contact or Separated); SCL = supralabial in contact with loreal left/right; PR = preoculars; P = postoculars; S2P = supralabials in contact with 2nd postocular; PCH = posterior pair of genials clearly separated (Present or Absent); SCE = 4th and 5th supralabials in contact with eye (Present or Absent); DSD = dorsolateral stripes disappear on the middle of the body (Present or Absent); PSF = preocular separated from frontal (Present or Absent); VST = vertebral stripe along body bordered by dorsolateral stripes (Present or Absent).

	MT	VS	CS	SVL (mm)	TaL (mm)	S	I	P2S
MZFC 28775 (Holotype)	11+3	182	82+	612	141	8/8	8	S
AMNH R–84992	11+3	177	101	237	80	8/8	10	C
AMNH R–91090	11+3	186	80+	782	140	8/8	10	S
AMNH R–100910	11+3	180	103	933	218	9/8	10	C
AMNH R–100909	11+3	176	92	852	228	8/8	10	S
UIMNH –56849	11+3	184	96			8/8		C

continued.

	SCL	PR	P	S2P	PCH	SCE	DSD	PSF	VST
MZFC 28775 (Holotype)	2/2	2	2/1	2	P	P	P	P	A
AMNH R–84992	2/2	2	2/2	2	P	P	P	P	A
AMNH R–91090	2/2	2	2/2	2	P	P	P	P	A
AMNH R–100910	3/2	2	2/2	2	P	P	P	P	A
AMNH R–100909	2/2	2	2/2	1	P	P	P	P	A
UIMNH –56849	2/2	2	2/2	1	P	P	P	P	A

Male closely resembling females, including holotype, in lacking vertebral stripe; male paler, however, with little more than vestiges of dorsolateral stripes; prior to preservation lips and throat white, in contrast to yellow venter of anterior portion of trunk and two lowermost rows of scales (Bogert, unpublished notes); posteriorly yellow color of the venter grading into salmon color extending to underside of tail; basal portions of lower dorsal scales on the posterior of trunk appreciably darker than margins; individual having brownish body flanked with yellow anteriorly gradually becoming gray speckled with black posteriorly; dorsolateral stripes obsolescent in preserved specimen, more conspicuous in live snake.



FIGURE 3. Habitat of *Salvadora gymnorhachis* sp. nov. A, type locality, pine-oak vegetation at 2060 m elevation. B, general view of the area at the type locality with habitat degradation (deforested areas, corn field and road), San Pedro y San Pablo Ayutla, Distrito Mixe, Oaxaca.

Etymology. The specific epithet comes from the Greek “*gymnós*”, meaning “naked”, and “*ráchī*” dorsum, in reference that this is the only species of *Salvadora* that does not have dorsal vertebral stripes and has incomplete dorsolateral ones.

Habitat and Conservation. The holotype was found beneath a rock in a transitional area between a crop field and pine-oak forest (Fig. 3A). The distribution of this species undoubtedly has been greatly modified by anthropogenic activities, which has increased the rate of deforestation at the type locality (Fig. 3B). None of the collection sites are located in protected areas. Despite intensive fieldwork in Oaxaca, only six specimens of this species have been collected, all between 1960 and 2014.

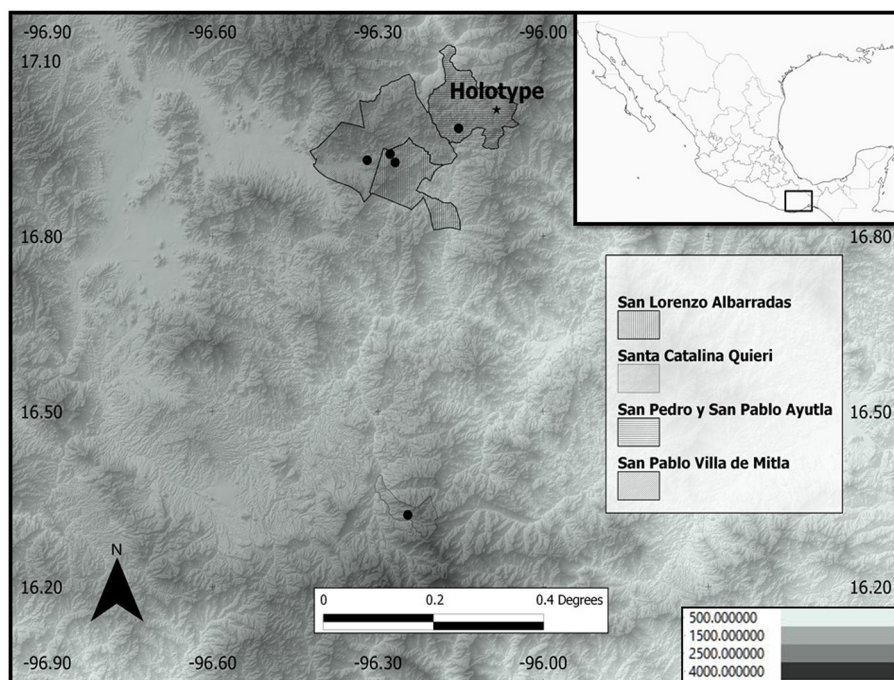


FIGURE 4. Geographic distribution of *Salvadora gymnorhachis* sp. nov. The star indicates the type locality, circles localities for paratypes.

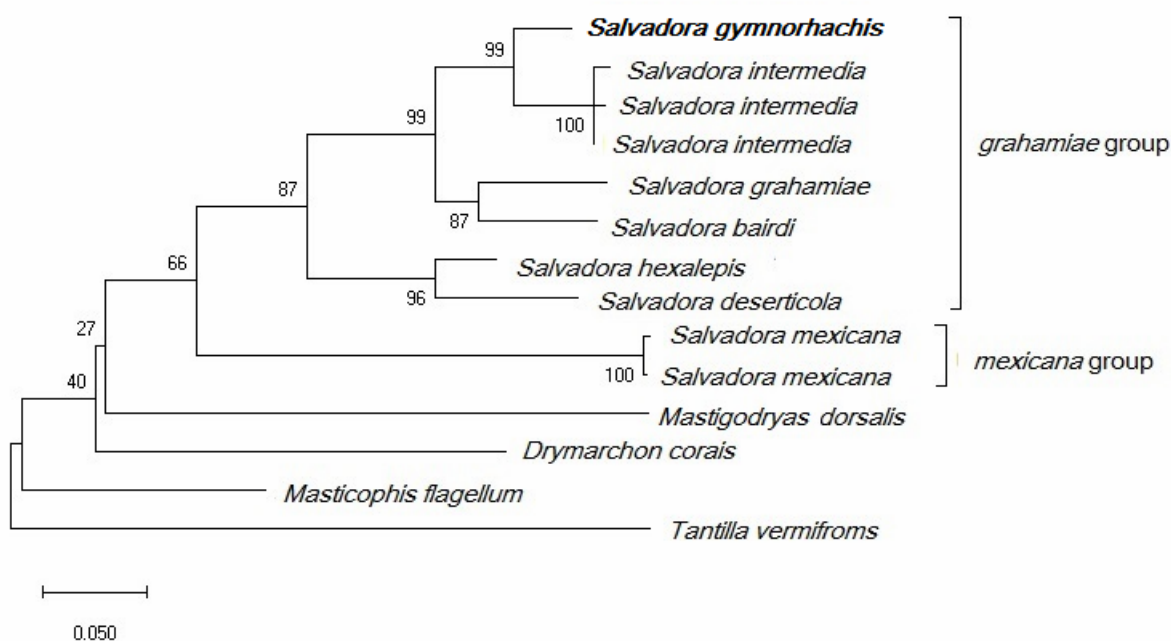


FIGURE 5. Molecular phylogenetic relationships of the genus *Salvadora*, based on ND4 mitochondrial gene, under the criterion of Maximum Likelihood (HKY+G model). Numbers under the nodes represent Maximum likelihood bootstrap support values.

Distribution. Most individuals have been collected in central Oaxaca along the unnumbered State secondary road between Mitla and Ayutla in the Distritos de Tlacolula and Mixe at elevations of 1760 to 2364 m. The species is also known in the south near Santa Catalina Quierí in Distrito de Yautepec at elevations exceeding 1600 m. The entire range of this species is drained by the upper tributaries of the Río Tehuantepec (Fig. 4). Most of the river valleys of the region contain fingers of upper tropical deciduous forest extending from lower coastal regions and the higher slopes and ridges are covered with pine-oak forest.

The phylogenetic analysis performed gave one phylogenetic tree (Fig. 5) with maximum likelihood value of -2709.59. The genus *Salvadora* is retrieved as monophyletic, with sampled species forming two strongly supported clades (*mexicana* group and *grahamiae* group). *Salvadora gymnorhachis* is nested within the *grahamiae* group as the sister taxon of *Salvadora intermedia*.

Discussion

Snakes of the genus *Salvadora* are characterized by an enlarged rostral and a dorsal color pattern of a pale vertebral stripe bordered by darker dorsolateral stripes and, in some species, a pair of usually narrower, dark lateral stripes. This color pattern is characteristic of all previously known species except *S. mexicana*, which has a mottled pattern with transverse bands on the anterior portion of the body. The species described here exhibits a somewhat different color pattern. There is only one reference to an aberrant color pattern that, according to Bogert (1945), occurs in *S. hexalepis mojavensis* from southwestern Utah and northern Arizona. This pattern consists of dark cross bars on the body reaching the lower scale rows and sometimes the ventrals that obscure the vertebral stripe. *Salvadora gymnorhachis* consistently lacks the dorsal stripe typical of all congeners. Also, *S. gymnorhachis* lacks the lateral stripes that occasionally are not present in *S. grahamiae*, a species that is not sympatric with *S. gymnorhachis*. The conspicuous characteristics of color pattern, including the lack of a vertebral stripe and the incomplete dorsolateral stripes, were overlooked on the few individuals examined by previous workers. Based on the number of preoculars, maxillary teeth, number of subcaudals and proportion of TaL/SVL, there appear to be two species groups in the genus. The *mexicana* group (*S. mexicana* + *S. lemniscata*) is defined by having a single preocular; 14-15+3 maxillary teeth; more subcaudals; and longer tail size in proportion to body size (> 29%). While the second group *S. grahamiae* (*S. grahamiae* + *S. bairdi* + *S. intermedia* + *S. deserticola* + *S. hexalepis*) is defined by having a divided preocular; < 13+3 maxillary teeth; less caudals; and shorter tail size in proportion to body size (< 29%). *Salvadora gymnorhachis* belongs to the second group. These two groups as defined by Smith (1938, 1941) were recovered in the molecular phylogeny (Fig. 5). It is clear the position of *Salvadora gymnorhachis* is with the *grahamiae* group and *Salvadora intermedia* is sister taxon, as we predicted.

This new species of *Salvadora* further augments the endemic herpetofauna of the state of Oaxaca, which is considered richest in the overall biodiversity of Mexico (Flores-Villela & Gerez 1994, García-Mendoza *et al.* 2004). There are many areas where there has been little biological exploration that will no doubt further increase the diversity known from this state. Recent reviews of specimens in collections and field expeditions to some areas of Oaxaca have revealed the presence of undescribed species of plants (López-Ferrari & Espejo-Serna 2009, 2014, López-Ferrari *et al.* 2011), invertebrates (Morón & Nogueira 2012, Woller *et al.* 2014) and herpetozoans (Canseco-Márquez *et al.* 2008, Köhler *et al.* 2014, Campbell 2015, Campbell *et al.* 2016). In this regard, Oaxaca easily outranks all other Mexican states in diversity of amphibians and reptiles (Ochoa-Ochoa & Flores-Villela 2006, Caviedes-Solis *et al.* 2015, Mata-Silva *et al.* 2015). The complex physiography and diversity of habitats created by elevational gradients and differences in vegetation, provides an intricate backdrop for evolution scarcely rivaled elsewhere in Mexico. Oaxaca not only harbors great herpetofaunal diversity, but endemism is extremely high (Flores-Villela & Gerez 1994), remarkably so for reptiles (Mata-Silva *et al.* 2015). *Salvadora gymnorhachis* is found in the areas of endemism of Tehuacán-Morelos in central Oaxaca identified by Ochoa-Ochoa & Flores-Villela (2006), distinct in its faunal composition from other endemic areas on the Gulf of Mexico Coast of this state (northern Oaxaca) and Veracruz.

This snake is restricted to the mountains of north-central Oaxaca, while other members of the genus *Salvadora* have a more extensive distribution. *Salvadora gymnorhachis* appears to be an uncommon snake and has mostly avoided the hands of collectors. We think its conservation status should be carefully considered, because the species is not present in any protected area.

Acknowledgments

We are grateful to O. Olivares, M. Vargas and A. Aguilar for their valuable help in the field. We would like to especially thank the late C. M. Bogert for his contributions to the understanding of the genus of *Salvadora* and for his legacy to Mexican herpetology. Prior to his death, he gave JAC copious unpublished notes on the genus *Salvadora* in which he had already noticed differences in coloration of certain Oaxacan specimens. CONACYT provided a scholarship to CAHJ (Scholarship No. 175,623) as a Graduate Student of Posgrado en Ciencias Biológicas UNAM; this publication is part of his doctoral dissertation. OFV thanks the support of DGAPA, UNAM during a sabbatical year at UT, Arlington. We thank the AMNH and D. Frost, for their support; to the Theodore Roosevelt Memorial Grant awarded to CHJ to help fund fieldwork in Oaxaca, and to D. Kizirian, L. Vonnahme, C. Franklin and E. Smith for their help in review of this taxon. We are grateful to the following collections and their curators for the loan of specimens ANSP, BMNH, BYU, CAS, CM, FMNH, LACM, KU, MCZ, MSB, MVZ, ROM, SDSNH, TCWC, UCM, UF, UIMNH, UMMZ, UNM, UTA, UTEP. J. A. Hernández-Gómez, O. Olivares and I. Bautista helped with the figures. To M. Rosete for the help in the lab work. Collecting permits in Mexico were issued by SEMARNAT to OFV permit FAUT-0015. We followed all proper guidelines for collecting and preserving specimens recommended by Beaupre (2004).

References

- Amaral, A.D. (1927) Studies of neotropical ophidia VI. A new genus of snakes from Honduras. *Bulletin of the Antivenin Institute of America*, 1, 28–29.
- Arevalo, E., Davis, S.K. & Sites, J.W.J. (1994) Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology*, 43, 387–418.
<https://doi.org/10.1093/sysbio/43.3.387>
- Baird, S.F. & Girard, C. (1853) *Catalogue of North American Reptiles in the Museum of the Smithsonian Institution*. Part 1 Serpents, Smithsonian Institution, 172 pp.
- Beaupre, S.J. (2004) *Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research*, 2nd edition. American Society of Ichthyologists and Herpetologists, 43 pp.
- Blanchard, F.N. (1924) A key to the snakes of the United States, Canada and Lower California. *Papers of the Michigan Academy of Science, Arts and Letters*, 4, 1–115.
- Bogert, C.M. (1939a) A Study of the Genus *Salvadora*, the Patch-nosed Snakes. *Publication of the University of California at Los Angeles in Biological Sciences*, 1, 177–236.
- Bogert, C.M. (1939b) Notes on snakes of the genus *Salvadora* with a redescription of a neglected Mexican species. *Copeia*, 1939, 140–147.
<https://doi.org/10.2307/1436808>
- Bogert, C.M. (1945) Two Additional Races of the Patch-nosed Snake, *Salvadora hexalepis*. *American Museum Novitates*, 1285, 1–14.
- Bogert, C.M. (1947) The status of the genus *Leptodrymus* Amaral, with comments on modifications of colubrid pre-maxillae. *American Museum Novitates*, 1352, 1–14.
- Bonfield, J.K., Smith, K.F. & Staden, R. (1995) A new DNA sequence assembly program. *Nucleic Acids Res*, 23, 4992–4999.
<https://doi.org/10.1093/nar/23.24.4992>
- Campbell, J.A. (2015) A new species of *Rhadinella* (Serpentes: Colubridae) from the Pacific versant of Oaxaca, Mexico. *Zootaxa*, 3918 (3), 397–405.
<https://doi.org/10.11646/zootaxa.3918.3.3>
- Campbell, J.A., Solano-Zavaleta, I., Flores-Villela, O., Caviades-Solis, I.W. & Frost, D.R. (2016) A New Species of *Abronia* (Squamata: Anguidae) from the Sierra Madre del Sur of Oaxaca, México. *Journal of Herpetology*, 50 (1), 149–156.
<https://doi.org/10.1670/14-162>
- Canseco-Márquez, L., Gutiérrez-Mayén, M.G. & Mendoza-Hernández, A.A. (2008) A new species of night lizard of *Lepidophyma* (Squamata: Xantusiidae) from Cuicatlán Valley, Oaxaca, México. *Zootaxa*, 1750, 59–67.
- Caviades-Solis, I.W., Vázquez-Vega, L.F., Solano-Zavaleta, I., Pérez-Ramos, E., Rovito, S.M., Devitt, T.J., Heimes, P., Flores-Villela, O.A., Campbell, J.A. & Nieto Montes de Oca, A. (2015) Everything is not lost: recent records, rediscoveries, and range extensions of Mexican frogs. *Mesoamerican Herpetology*, 2, 230–241.
- Cope, E.D. (1860), Catalogue of the Colubridae in the Museum of the Academy of Natural Sciences of Philadelphia. Part 3. *Proceedings of the Academy Natural Sciences Philadelphia*, 12, 553–566.
- Dowling, H.G. (1951) A proposed standard system of counting ventrals in snakes. *British Journal Herpetology*, 1, 97–99.
- Edgar, R.C. (2004) Muscle: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32,

1792–1797.

<https://doi.org/10.1093/nar/gkh340>

- Figuroa, A., McKelvy, A.D., Grismer, L.L., Bell, C.D. & Lailvaux, S.P. (2016) A species level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PLoS ONE*, (9), 11, 1–31.
<https://doi.org/10.1371/journal.pone.0161070>
- Flores-Villela, O. (1993) Herpetofauna Mexicana. *Special Publication Carnegie Museum of Natural History*, 17, 1–73.
- Flores-Villela, O. & Gerez, P. (1994) *Conservación en México, vertebrados, vegetación y uso del suelo* 2nd ed. CONABIO-UNAM, Mexico, 439 pp.
- Frost, D.R. & Hillis, D.M. (1990) Species in concept and practice: herpetological applications. *Herpetologica*, 46, 87–104.
- García-Mendoza, A.J., Ordoñez-Díaz, M.J. & Briones-Salas, M. (2004) *Biodiversidad de Oaxaca*. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza and World Wildlife Found. Mexico, 605 pp.
- Günther, A. (1863) Third account of the snakes in the collection of the British Museum. *Annals and Magazine of Natural History*, (3), 12, 348–365.
<https://doi.org/10.1080/00222936308681536>
- Harvey, M.B., Barker, D.G., Ammerman, L.K. & Chippindale, P.T. (2000) Systematics of the pythons of the *Morelia amethistina* complex (Serpentes: Boidae) with the description of three new species. *Herpetological Monographs*, 2000, 139–185.
<https://doi.org/10.2307/1467047>
- Köhler, G., Gómez-Trejo-Pérez, R., Petersen, C.B.P. & Méndez de la Cruz, F. (2014) A new species of pine anole from the Sierra Madre del Sur in Oaxaca, Mexico (Reptilia: Squamata: Dactyloidae: *Anolis*). *Zootaxa*, 3753, 453–468.
<https://doi.org/10.11646/zootaxa.3753.5.4>
- López-Ferrari, A.R. & Espejo-Serna, A. (2009) Nuevas combinaciones en monocotiledóneas mexicanas IV (Bromeliaceae, Orchidaceae). *Acta Botanica Mexicana*, 89, 43–46.
- López-Ferrari, A.R. & Espejo-Serna, A. (2014) *Hechtia rubicunda* (Bromeliaceae; Hechtioideae), una nueva especie de Oaxaca, México. *Acta Botanica Mexicana*, 107, 153–164.
<https://doi.org/10.21829/abm107.2014.205>
- López-Ferrari, A.R., Espejo-Serna, A., Ceja-Romero J. & Mendoza-Ruiz, A. (2011) *Aechmea enigmatica* (Bromeliaceae; Bromelioideae) una nueva especie del estado de Oaxaca, México. *Acta Botanica Mexicana*, 95, 1–9.
<https://doi.org/10.21829/abm95.2011.262>
- Mata-Silva, V., Johnson, J.D., Wilson, L.D. & García-Padilla, E. (2015) The herpetofauna of Oaxaca, Mexico: composition, physiographic distribution and conservation status. *Mesoamerican Herpetology*, 2, 6–62.
- Morón, M.A. & Nogueira, G. (2012) *Phyllophaga (Phyllophaga) josepalaciosi* (Coleoptera: Melolonthidae: Melolonthinae) nueva especie del sur de Oaxaca, México. *Dugesiana*, 19, 69–72.
- Ochoa-Ochoa, L. & Flores-Villela, O. (2006) *Áreas de diversidad y endemismo de la herpetofauna Mexicana*. UNAM-CONABIO, Mexico, 211 pp.
- Pyron, R.A., Burbrink, F.T., Colli, G.R., Nieto-Montes de Oca, A., Vitt, L.J., Kuczynski, C.A. & Wiens, J.J. (2011) The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics Evolution*, 58, 329–34.
<https://doi.org/10.1016/j.ympev.2010.11.006>
- Pyron, R.A., Burbrink, F.T. & Wiens, J.J. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13, 1–93.
<https://doi.org/10.1186/1471-2148-13-93>
- Sabaj-Perez, M.H. (2013) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: An online reference (v4.0). American Society of Ichthyologists and Herpetologists, Washington, DC. Available from: <http://www.asih.org/resources>. (accessed 31 August 2015)
- Schmidt, K.P. (1940) Notes on Texan snakes of the genus *Salvadora*. Zoological Series. *Field Museum of Natural History Zoological Series*, 24, 143–150.
- Smith H.M. (1938) Notes of the snakes of the genus *Salvadora*. *The University of Kansas Science Bulletin*, 25, 229–237.
<https://doi.org/10.5962/bhl.part.1701>
- Smith, H.M. (1941) Further Notes on Mexican Snakes of the Genus *Salvadora*. *Smithsonian Miscellaneous Collections*, 99, 1–12.
- Smith, H.M. & Smith, R.B. (1976) *Synopsis of the herpetofauna of Mexico, Vol. III*. Source analysis and index for Mexican reptiles. John Johnson, 997 pp.
- Smithe, F.B. (1975) *Naturalist Color Guide*. American Museum of Natural History, New York, 229 pp.
- Stejneger, L. (1902) The reptiles of the Huachuca Mountains, Arizona. *Proceedings of the United States National Museum*, 25, 149–158.
<https://doi.org/10.5479/si.00963801.1282.149>
- Stuart, L.C. (1932) Studies on neotropical Colubrinae. I. The taxonomic status of the genus *Drymobius* Fitzinger. *Occasional Papers Museum of Zoology University Of Michigan*, 236, 1–16.
- Tamura, K., Peterson, D., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular evolutionary genetics analysis using likelihood, evolutionary distance and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739.

<https://doi.org/10.1093/molbev/msr121>

- Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W. & Pyron, R.A. (2016) Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, 204, 23-31.
<https://doi.org/10.1016/j.biocon.2016.03.039>
- Wallach, V., Williams, K.L. & Boundy, J. (2014) Snakes of the world, a catalogue of living and extinct species. CRC Press, Boca Raton, Florida, 1209 pp.
<https://doi.org/10.1201/b16901>
- Woller, D.A., Fontana, P., Marino-Perez, R. & Song, H. (2014) Studies in Mexican Grasshoppers: *Liladownsia fraile*, a new genus and species of Dactyloptini (Acrididae: Melanoplineae) and an updated molecular phylogeny of Melanoplineae. *Zootaxa*, 3793 (4), 475–495.
<https://doi.org/10.11646/zootaxa.3793.4.6>
- Zheng, Y. & Wiens, J.J. (2016) Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular phylogenetics and evolution*, 94, 537–547.
<https://doi.org/10.1016/j.ympev.2015.10.009>

APPENDIX 1. Material examined.

Salvadora bairdi: MEXICO: GUANAJUATO: Guanajuato City: CAS 4413; HIDALGO: Huichapan: AMNH 88826; Tulancingo: MMC R16522; JALISCO: La Mesa Maria Leon: KU 102972; Magdalena: FMNH 114529; Mazamitla: KU 29510; San Clemente: TCWC 54524; Sayula: MMC R16525; Sierra de Cuale: KU 73632; Tapala 1.5 mi NW, ca. 40.0 mi NW Ciudad Guzman: UTA 4380; Tapala, 2.4 km NW: UTA 4382; MICHOACAN : Carapan, 4 mi S: UTA 4563; Cojumatlan: FMNH 114531; Entre Zitacuaro y Rio Tuxpan: FMNH 114533; Jiquilpan 12 mi W: UTA 6046; Tacicuaro: FMNH 114535, FMNH 37051, FMNH 114538; Tuzantla, Zitacuaro 45.8 mi W on Hwy 15 Michoacan: CM 67072; Uruapan: FMNH 114527; PUEBLA: Cacaloapan: FMNH 114530; Cacaloapan 1.01 mi W: UTA R 4903; Cholula: AMNH 19629; Tlacotepec 7 mi SE: UMMZ 126543; QUERÉTARO: Amealco: TCWC 53064; SINALOA: Choix: KU 68753; Plomosas 1.0 mi E: KU 5966; Santa Lucia Via Hwy: KU 78917, KU 78918; Sierra Surutata: CAS 159227; Villa Unión: AMNH 103126; VERACRUZ: Acultzingo: UIMNH 18744, FMNH 114526, UMMZ 88707; Cumbres: MMC R 16516; ZACATECAS: NO DETERMINADO : Ummz 118446;

Salvadora deserticola: MEXICO: CHIHUAHUA: 14 miles N of Colonia Dublan: BYU 13978; 2 miles N of Colonia Juarez: BYU 13351; 5 mi N Cerro Campana: MVZ 71001; Ahumada: CM 60072, CM 60073; Belleza: AMNH 68954; Camargo: UTEP 1318; Chihuahua: AMNH 68436; El Sueco: CAS 169814; Gallegos 24 mi (By road) S: UTEP 7782; Rio Santa Clara: MVZ 75877; Villa Ahumada: UTEP 7781; SINALOA: Culiacan: MVZ 70273; El Coyote: MVZ 136784; Los Mochis: MMC R 16349; Mazatlán: MVZ 059287; Rosario: KU 73626; Vaca: KU 83411; SONORA: Alamos: AMNH 64151, AMNH 64152; Guaymas: AMNH 75894, MVZ 56520, MVZ 72427; Guirocoba: AMNH 63725; Vicinity of Navojoa: BYU 41125; Nuevo Casa Grandes: UIMNH 46017; UNITED STATES: NEW MEXICO: Doña Ana: UTEP 16021; TEXAS: Chisos Mountains 5 mi E Government Spring: FMNH 26615;

Salvadora grahamiae: MEXICO: CHIHUAHUA: Arroyo El Mesteño: MVZ 71002, MVZ 73015; Cañón del arroyo Del Alamo: MVZ 68872; Sierra del Nido Arroyo Mesteño: UTA R17802; Santa Bárbara: AMNH 68199; COAHUILA: 8 mi S Fuentes on road 10 May 1938: FMNH 28793; General Cepeda: KU 35058; Jaral: FMNH 1539; La Gacha: KU 33585; Pico de Jimuelo: KU35059; Saltillo: MMC R 16348; DURANGO: El Salto: AMNH 68362; Llano Grande: KU 182703; Rodio: AMNH 85260; Villa de Madera: KU 37790; HIDALGO: 5 mi S Jacala: TCW 4121; E Pachuca on Hwy 105, 2.4 mi (winding Rd.) from Rd. N to El Chico Nat. Pk.: LACM 68954; San Miguel: MCZ 11433; MICHOACAN: Morelia: AMNH 62276; NUEVO LEÓN: Galeana: AMNH 85259; Real: UF 7617; QUERETARO: Pena Blanca: TCW 54836; Pinal Amoles: UTA R 16138; San Joaquín: TCW 41019, TCW 41018; SONORA: Canyon N of Cano Diablo, Sierra San Luis: UTA R 17803; TAMAULIPAS: Nuevo Laredo: AMNH 69944; Rancho Carricitos: TCW 49937; ZACATECAS: Juan Aldama: UTEP 7789; Morelos: AMNH 118018; Saltillo (Coahuila) 51 mi S Hwy 54: CM 60076; UNITED STATES: ARIZONA: Cave Creek Canyon: AMNH 107359; Graham: AMNH 126739; Painted Canyon Chiricahua: AMNH 75120; Pinal Co: ANSP 28079; NEW MEXICO: Bernalillo: UNM 43356; Catron Co: UTEP 2535; Chaves: UNM 72019; Cibola: UNM 61195; Doña Ana: LACM 2679; Eddy: UNM 48567; Grant: UTA R54090; Grant Co: UTEP 2034; Harding: UNM 61480; Lincon: UNM 151; Otero Country: UTEP 6270, MVZ 139385; Rio Arriba: UNM 30876; San Miguel: UNM 4147; Sandoval: UNM 48784; Santa Fe: UNM 61455; Sierra: UTEP 18940; Torrance: UNM 60991; TEXAS: Aransa Rockport: KU 61119; Atascosa: SDSNH 30736; Austin: LACM 67030; Bastrop: TCW 14066; Beeville: MVZ 52384, UTA R59352; Bell: TCW 27455; Bexar: ROM 4191; Brady: AMNH 64405; Brewster: ROM 9958, UTA 10288; Burleson: TCW 52080; Caldwell: TCW 20274; Cameron: UTA 54066; Corpus: FMNH 45789; Coryell: FMNH 37211; Crockett: UTEP 15636; Culberson: UTEP 12337; Edwards: KU 83167; Frio: TCW 64017; Gillespie: KU 63887, TCW 64017; Hamilton: KU 221254; Hays: TCW 18309; Hidalgo: TCW 33951; Hood: UNM 33524; Hudspeth: UTEP 33524; Hueco Gas Road, El paso Country: UTEP 968; Jeff Davis Co Davis Mountans, Mt Locke: FMNH 29497; Kendall: TCW 42873; Kenedy: AMNH 160238; Kleberg Kingsville: FMNH 28605; Loyosa: ROM 4196; Pecos: TCW 66893; Presidio: TCW 52084; Schleicher: KU 83166; Somervell: TCW 57008; Starr: KU 145920, UTEP 13896; Tal Verde: TCW 38886; Terrell: TCW 623, UTEP 9052; Travis: UTEP 18346; Weatherford Parker: MVZ 12706.

Salvadora hexalepis: MEXICO: BAJA CALIFORNIA: Bahía de los Ángeles: MVZ 161558; Bahía de los Ángeles Beach Flats: MVZ 161434; Catarina: MVZ 45397; Ensenada: CM 6123; La Paz: LACM 51850; Rosario: MVZ 161435; San Luis: CAS 84140; San Matías: FMNH 1164; Sierra San Pedro: MVZ 140866; Tijuana: SDSNH 29111; BAJA CALIFORNIA NORTE: 31 mi Se Rancho Santa Ynez NR Santa María Mission: CAS 135199; 36 mi Sur Tijuana: CAS 16298; Arroyo San Telmo: CAS 182411; Bahía de los Ángeles: ROM 13548; El Rosario: ROM 13519, SDSNH 45955; Ensenada: SDSNH 18938; Mina Onix San Quintín: SDSNH 1068; Punta Cabras: SDSNH 19694; Punta de San Quitín: CAS 182410; Rancho San José Tecate: SDSNH 58575; Rosario: SDSNH 42805; San Antonio: SDSNH 8855; San Jose: SDSNH 5131; San Quitín: SDSNH 32622; Santa Catarina: SDSNH 18166; Santo Tomas: SDSNH 16713, SDSNH 42946, SDSNH 52921; Sierra San Pedro: CAS 1723; BAJA CALIFORNIA SUR: 17 M W Santa Rosalía: LACM 103090; 29 Mi SW Santiago City Hall on Mexico Hwy 1: LACM 21537; Bahía Asunción: FMNH 130668; Espíritu Santo: CAS 146563; La Paz: AMNH 87610, MCZ 37228; Loreto: SDSNH 30387; Mulege: KU 185655; Rancho El Rodeo: CAS 147705; San Antonio: KU 78919; San Ignacio: KU 185656, ROM 13663, SDSNH 3827; San Isidro: SDSNH 6232; San José del Cabo: CAS 182413; San Pedro La Presa: CAS 147726; Todos Santos: KU 185654, CAS 45957; GOLFO DE CALIFORNIA: Isla San Jose: CAS 14016; Isla Tiburón: CAS 53246; SONORA: Desemboque: AMNH 74723; Isla Tiburón: SDSNH 52913; UNITED STATES: ARIZONA: Coconino: SDSNH 34439; Coconino Country: MVZ 193329; La Paz 4 mi S Quartzite: MVZ 71995; Maricopa: SDSNH 39081, LACM 115913; Mohave: LACM 126009, MVZ 180263; No Determinado: ROM 23325, UTA R 50703, UTA R 51340, UTA R 51341, UTA R 44903; Pima: ROM 23351; Yuma: SDSNH 13734, MVZ 59288, Yuna: CAS 33810; CALIFORNIA: Bernardino Country: MVZ 64120; Dixon Johnson Inyo: MVZ 6689; Inyo: LACM 103009; Kem Country: MVZ 175842; La Arroyo Seco Canyon: MVZ 794; Riverside: LACM 21523; Riverside Pinto Basin: MVZ 43028; San Bernardino: ROM 19755; San Diego: MVZ 27018; San Diego Tecate: SDSNH 23483; NEVADA: Clark: CM 66186; Clark Country: MVZ 52444; Esmeralda Country: MVZ 182612, MVZ 228582; Lincoln Pahrnagat Valley: MVZ 111401; Lyon Country: MVZ 42088; Mineral Country, Walter Lake: MVZ 20396; Nevada: UTA R 45163, UTA R50716; Rock Valley: MVZ 97087.

Salvadora intermedia: MÉXICO: GUERRERO: 2.5 mi S Almolonga: TCW 11597; Chilpancingo: FMNH 103531, FMNH 38305, FMNH 3807, MCZ 3363, MCZ 33642, FMNH 109866; Chilpancingo de los Bravos: MZFC 23201, MZFC 02878, MVZ 45190, MVZ 45191; Mazatlan Cuahutemoc Chilpancingo: KU 61121; Omiltemi Chilpancingo de los Bravos: MZFC 02876; OAXACA: 3.8 mi (By Mex HWY 190) Puebla Oaxaca Border: BYW 41315; Cerro San Felipe: UCM 44519, UIMNH 56849, UIMNH 62412; Chicahuaxtla: MZFC 04059; El Moral: AMNH 94693; El Tejocote: MZFC 07483, MZFC 21280, MZFC 08577; La Carbonera: AMNH 97843; San Juan Bautista: MZFC 08578; Santa Maria Yavesia: MZFC 23865, MZFC 23857, MZFC 23871; Santiago Comaltepec: MZFC 06523; Santiago Tamazola: MZFC 18272; El Tejocote Estación de Microondas, km 141: MZFC 06011; Tejocotes: AMNH 106969, UTA(CV) 6621, UTA R 25837; PUEBLA: NO DETERMINADO : UTA R52602; Tepanco de López: MZFC 25258, MZFC 14384; Zapotitlán: MZFC 00819.

Salvadora lemniscata: MÉXICO: CHIAPAS: 11.8 mi SW Las Cruces: LACM 59035; 2.5mi SE Arriaga: LACM 38202, Amiaga: TCWC 21545; Cintalapa: CAS 163495, TCWC 21544; Escuintla: FMNH 102681; N side of Tuxtla Gutierrez: UF 117789; Trinitana: TCWC 21910; Tuxtla Gutierrez: UMMZ 12153, UMMZ 121532; GUERRERO: Acapulco: AMNH 19627; OAXACA: Huatulco: AMNH 61755; NW Ciudad de Oaxaca: TCWC 56841; NW Totoloapan: UCM 49244; Tehuantepec: AMNH 65142; NW Zanatepec: UCM 41196; Pozo Rio: AMNH 66806; Puente de Vaca: KU 95783; Quiengola: AMNH 66814; Rincon Barba: UIMNH 18731; UIMNH 18732; San Jose Lachanguini Miahuatlan: UCM 41195; Tapanatepec, 20 mi W on Mex Hwy 190: LACM 103698; Tehuantepec: AMNH 64588; Ventosa: CAS 114078,

Salvadora mexicana: MEXICO: COLIMA: Colima: AMNH 126418; Manzanillo: CAS 132121; Paso del Rio: AMNH 12782; GUERRERO: 1 mi SW Tierra Colorada: TCWC 7491; ; 2 mi S of Mexcala 1500 ft: UMMZ 114428; Acahuizotla: TCWC 11596, TCWC 11633; Acapulco: SDSNH 36280, SDSNH 36288; Agua de Obispo: KU 87465; Chilpancingo: UMMZ 84762, AMNH 72509, FMNH 38295; Chilpancingo de los Bravos: MVZ 45034; Mexcala: TCWC 11627, TCWC 11628 Omilteme: MCZ 42664; Petacalco: TCWC 55530; Tierra Colorada: KU 67715; JALISCO: Melanque: KU 95784; Puerto Vallarta: UIMNH 41441, CAS 132119; Union de Tula 5 mi SW: KU 67716; MICHOACAN: 12 mi SW of La Placita sea level: UMMZ 101474; Apatzingan: FMNH 39021, FMNH 39023; Capirio 600 ft: UMMZ 119449; El Sabino: FMNH 102864; El Sabino Uruapan: FMNH 102858; La Puerta de la Playa: UMMZ 105157; Santa Ana 2000 ft: UMMZ 119448; Trail El Tequiz to Ojos de Agua de San Telmo 10 mi S of Coahuayana 100 ft: UMMZ 101473; MORELOS: 12 Km NW Axochiapan: TCWC 7318, TCWC 7320; 2 Km S Jonacatepec: TCWC 7319; Laguna El Rodeo: TCWC 4120; NAYARIT: San Blas: UIMNH 84203, UIMNH 84204, UIMNH 84202; PUEBLA: Acatlan: MVZ 164372; Matamoros: KU 39560, KU 050674; Tehuiztango: AMNH 93347.