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Research article

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Phylogenetic relationships based on morphological data and taxonomy of the genus *Salvadora* Baird & Girard, 1853 (Reptilia, Colubridae)

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Abstract. The genus *Salvadora* has not been subjected to a modern phylogenetic analysis. Described in 1853, its taxonomic history is complex and confusing. In this study, we evaluate the monophyly of the genus and present the first phylogenetic hypothesis based on an analysis of 66 qualitative and quantitative morphological characters of over 1000 specimens representing all described taxa across their entire distribution. Morphological characters were processed in Fast Morphology for subsequent phylogenetic analysis in PAUP under the maximum parsimony criterion. We obtained a single tree in which *Salvadora* appears as a monophyletic group with two clearly defined geographic species groups: a southern *mexicana* group and a northern *grahamiae* group. Based on our phylogenetic hypothesis, we evaluate the taxonomic status of all described taxa. Additionally, we include a diagnosis for all species, distribution maps, and an illustrated dichotomous taxonomic key of the genus.

Keywords. Morphology, phylogeny, patch-nosed snakes.

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Introduction

The taxonomic history of the genus *Salvadora* Baird & Girard, 1853 is rather intricate and convoluted. The genus was described by Baird & Girard (1853), based on the type species *Salvadora grahamiae*.

Jan & Sordelli (1860) described *S. bairdi*, which was placed in the synonymy of *S. grahamiae* by Günther (1863) and Stejneger (1902). Smith (1938) re-evaluated the taxonomic status of *S. grahamiae* and *S. bairdi* and recognized them as two different species.

Cope (1861) proposed that the name of the genus be changed to *Phimothyra* because the name *Salvadora* had already been used by Linnaeus to describe a plant genus, but later withdrew his proposal because the emerging rules of nomenclature no longer required the use of different names for organisms belonging to different kingdoms. Under the name *Phimothyra*, Cope (1866) described *P. hexalepis* as a new species, though he himself later considered it to be a subspecies of *S. grahamiae* (Cope 1875). Stejneger (1902) noted differences between the two taxa and re-elevated *S. hexalepis* to species level. This nomenclature was used until Blanchard (1924) returned it to its previous status as a subspecies of *S. grahamiae*. Schmidt (1940) once again separated them into two separate species.

Günther (1863) recognized the affinity of a snake described as *Zamenis mexicanus* Duméril, Bibron & Duméril, 1854 with *Salvadora* and placed it in the genus *Salvadora*. Later, Stuart (1932) placed the snake *Masticophis pulcherrimus* Cope, 1874 in the genus *Salvadora*.

In a monograph on the genus, Bogert (1939b) concluded that *S. pulcherrima* was limited to Central America and that the Mexican specimens formerly referred to as *S. pulcherrima* should be recognized as *S. lemniscata* (Cope, 1895) because of differences in the scutellation pattern (three preoculars in *S. pulcherrima* vs two in *S. lemniscata*), the color pattern (two longitudinal lines in *S. pulcherrima* vs four in *S. lemniscata*; black and white body color with a green head in *S. pulcherrima*, but olive and brown in *S. lemniscata*), and the number of maxillary teeth (14–15+3 in *S. lemniscata* vs 17+3 in *S. pulcherrima*). Currently, *S. pulcherrima* is considered a synonym of *Leptodrymus pulcherrimus* because Bogert (1947) argued, based on a detailed morphological revision, that there were sufficient differences at the genus level and that *S. pulcherrima* should be included in the genus *Leptodrymus* proposed by Amaral (1927).

Schmidt (1940) described *Salvadora lineata* and a new subspecies of *S. hexalepis*, *S. h. deserticola*. The following year, Smith (1941) described a new species, *S. bogerti*, and two subspecies of existing taxa, *S. intermedia richardi* and *S. hexalepis celeris*.

Bogert (1945) described two new subspecies of *Salvadora hexalepis*, *S. h. klauberi* and *S. h. mojavensis*, in addition to recognizing *S. hexalepis virgultea* and synonymizing *S. h. celeris* with *S. h. deserticola*.

Finally, Hernández-Jiménez *et al.* (2019) described a new species, *Salvadora gymnorhachis*, from the highlands of Central Oaxaca Mexico.

To date, nine species and eight subspecies have been described:

Salvadora Baird & Girard, 1853

S. bairdi Jan in Jan & Sordelli, 1860

S. bogerti Smith, 1941

S. deserticola Schmidt, 1940

S. grahamiae grahamiae Baird & Girard, 1853

S. g. lineata Schmidt, 1940

S. gymnorhachis Hernández-Jiménez, Flores-Villela & Campbell, 2019

S. hexalepis hexalepis (Cope, 1866)

S. h. mojavensis Bogert, 1945

S. h. klauberi Bogert, 1945

S. h. virgultea Bogert, 1935

S. intermedia intermedia Hartweg, 1940

S. i. richardi Smith, 1941

S. lemniscata (Cope, 1895)

S. mexicana (Duméril, Bibron & Duméril, 1854)

Recently, Flores-Villella (1993) and Wallach *et al.* (2014) listed the taxa of this genus without recognizing any subspecies.

In spite of being a fairly abundant and widespread group, the phylogenetic relationships within the genus have not been well studied. Pyron *et al.* (2011, 2013), Figueroa *et al.* (2016), Tonini *et al.* (2016), Zheng & Wiens (2016) and Zaher *et al.* (2019) published molecular phylogenetic trees that include some species of *Salvadora*, but the results reported in those publications differ with regard to the monophyly of the group and the position of *Salvadora* with respect to relationships with other colubrid genera. None of those papers included all of the described taxa.

Recently, Hernández-Jiménez *et al.* (2019) published the description of a new species, *Salvadora gymnorhachis*. In that description, a phylogenetic hypothesis was proposed, based on a single molecular marker but not all described species in the genus were included (7 of 9). However, the hypothesis presented by Hernández-Jiménez *et al.* (2019) represents the most complete phylogenetic tree that has been proposed to date. In this phylogeny, *Salvadora* appears as a monophyletic group (Fig. 1).

There is no phylogenetic hypothesis for the relationships among the species of *Salvadora* based on morphological data and there is no recent analysis of the alpha taxonomy of the genus. While molecular systematics has proven to be a robust tool for the resolution of taxonomic problems, it is also evident that the use of morphological characters in phylogenetic reconstructions has been decreasing. Morphological characters have been shown to be useful in the reconstruction of phylogenetic relationships among many taxa (Jenner 2004; Wiens 2004; Smith & Turner 2005). It is important that phylogenies representing hypotheses about the relationships among terminal taxa in a monophyletic group be supported by different lines of evidence.

Here, we provide an analysis of the alpha taxonomy of the genus and a phylogenetic hypothesis including all taxa described based on an examination of external morphology and dentition, as well as distribution maps and taxonomic keys.

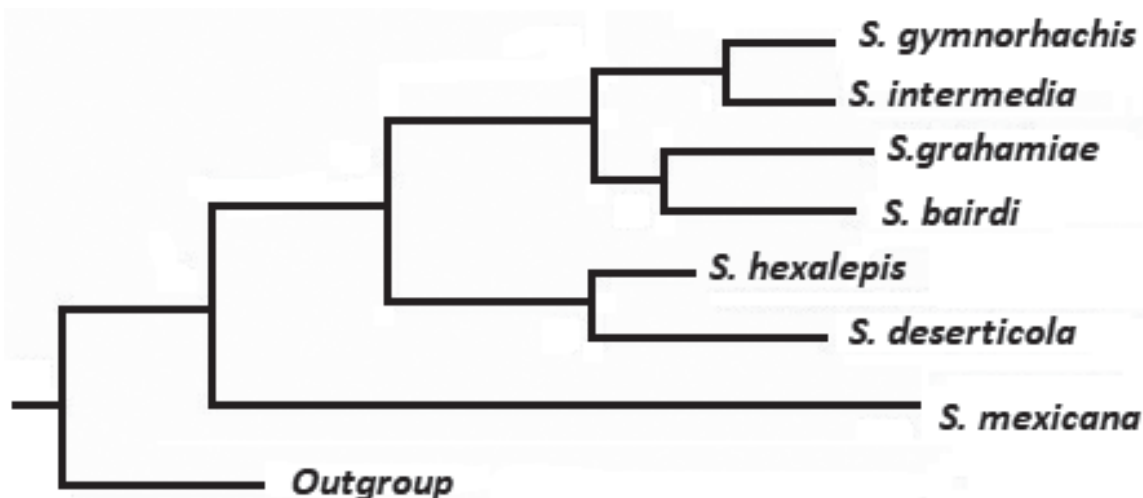


Fig. 1. Molecular phylogenetic tree modified from Hernández-Jiménez *et al.* (2019).

Material and methods

Over 1000 specimens were examined from the following museums: Royal Ontario Museum (ROM), Mayborn Museum Baylor University (MMC), Museum of Vertebrate Zoology (MVZ), Monte L. Bean Life Science Museum, Brigham Young University (BYU), British Museum of Natural History (BMNH), California Academy of Sciences (CAS), Carnegie Museum (CM), University of Colorado Museum (UCM), Field Museum of Natural History (FMNH), Museum of Comparative Zoology, Harvard University (MCZ), University of Kansas, Museum of Natural History (KU), Natural History Museum of Los Angeles (LACM), The Academy of Natural Sciences (ANSP), San Diego Society of Natural History (SDSNH), Texas Cooperative Wildlife Collection (TCWC), National Museum of Natural History, Smithsonian Institution (USNM), Florida Museum of Natural History (UF), University of Illinois, Museum of Natural History (UIMNH), University of Michigan, Museum of Natural History (UMMZ), University of New Mexico, Museum of Southwestern Biology (UNM), University of Texas at El Paso (UTEP), University of Texas at Arlington (UTA), American Museum of Natural History (AMNH), Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC), Escuela de Biología Benemérita Universidad Autónoma de Puebla (EBUAP) and Colección Nacional de Anfibios y Reptiles, Universidad Nacional Autónoma de México (CNAR) (acronyms follow Sabaj-Pérez 2016); collectively representing all taxa throughout the entire distributional range of the genus. The characters we used were similar to those described in previously published studies of the genus *Salvadora* (Bogert 1947) and Hernández-Jiménez *et al.* (2019).

Distribution maps were constructed with all museum records and specimens examined as well as available records in the recent literature, using Quantum GIS ver. 1.7 (QGIS 2012). Revised diagnoses and dichotomous keys were prepared for each taxon.

Three hundred and sixty-one specimens were selected, representing all of the known populations of each taxon (including type or topotypic material for the species and subspecies), since the specimens selected represent all of the variation that we recorded. A detailed analysis of 64 qualitative scale, color pattern and meristic and morphometric characters (Supp. file 1) were used to reconstruct a phylogenetic hypothesis. *Salvadora bogerti* and *Salvadora intermedia richardi* were not included in the reconstruction of the phylogenetic hypothesis because we consider *S. bogerti* to be a synonym of *S. bairdi* and *S. i. richardi* as a junior synonym of *S. intermedia* (see comments in the Results section).

Given that some of the morphological characters analyzed varied within the terminal taxa (polymorphic characters), they were coded as follows: morphometric and meristic characters were coded using the gap-weighting method proposed by Thiele (1993), while for qualitative characters each character state was treated as an independent character and coded as a binary present-absent character (Wilkinson 1995).

The raw data matrix was processed in Fast Morphology ver. 1.0 (Chang & Smith 2001), which transforms the character state into a code that can be used in a parsimony analysis and obtains the frequency of subcharacters using the Generalized Frequency Coding (GFC) technique proposed by Smith & Gutberlet (2001).

The phylogenetic analysis was run in PAUP, ver. 4.0a147 (Swofford 2002), under the maximum parsimony criterion using a heuristic search and the TBR branch exchange algorithm with 1000 replicates adding taxa randomly. A Bootstrap analysis with 1000 pseudoreplicates was then run. As outgroups, the following species of snakes were used: *Masticophis mentovarius* Duméril Bibron & Dumeril, 1854, *Drymarchon melanurus* Duméril Bibron & Dumeril, 1854, *Drymobius margaritiferus* Schlegel, 1837, *Leptophis mexicanus* Duméril Bibron & Dumeril, 1854 and *Leptodrymus pulcherrimus* Cope, 1874, according to previously published studies by Amaral (1927), Bogert (1947), Pyron *et al.* (2011, 2013), and Hernández-Jiménez *et al.* (2019).

Results

Phylogenetic relationships

A single tree with a length of 584 837 steps was obtained from the heuristic search under the parsimony criterion (Fig. 2). The group made up of all the species and subspecies of the genus appears as a monophyletic group with a Bootstrap value of 100. Within the group, there are two clearly defined clades with high Bootstrap values, one with *S. mexicana* and *S. lemniscata* with a Bootstrap value of 100 (*mexicana* group) and the other with the remaining species and subspecies, also with a Bootstrap

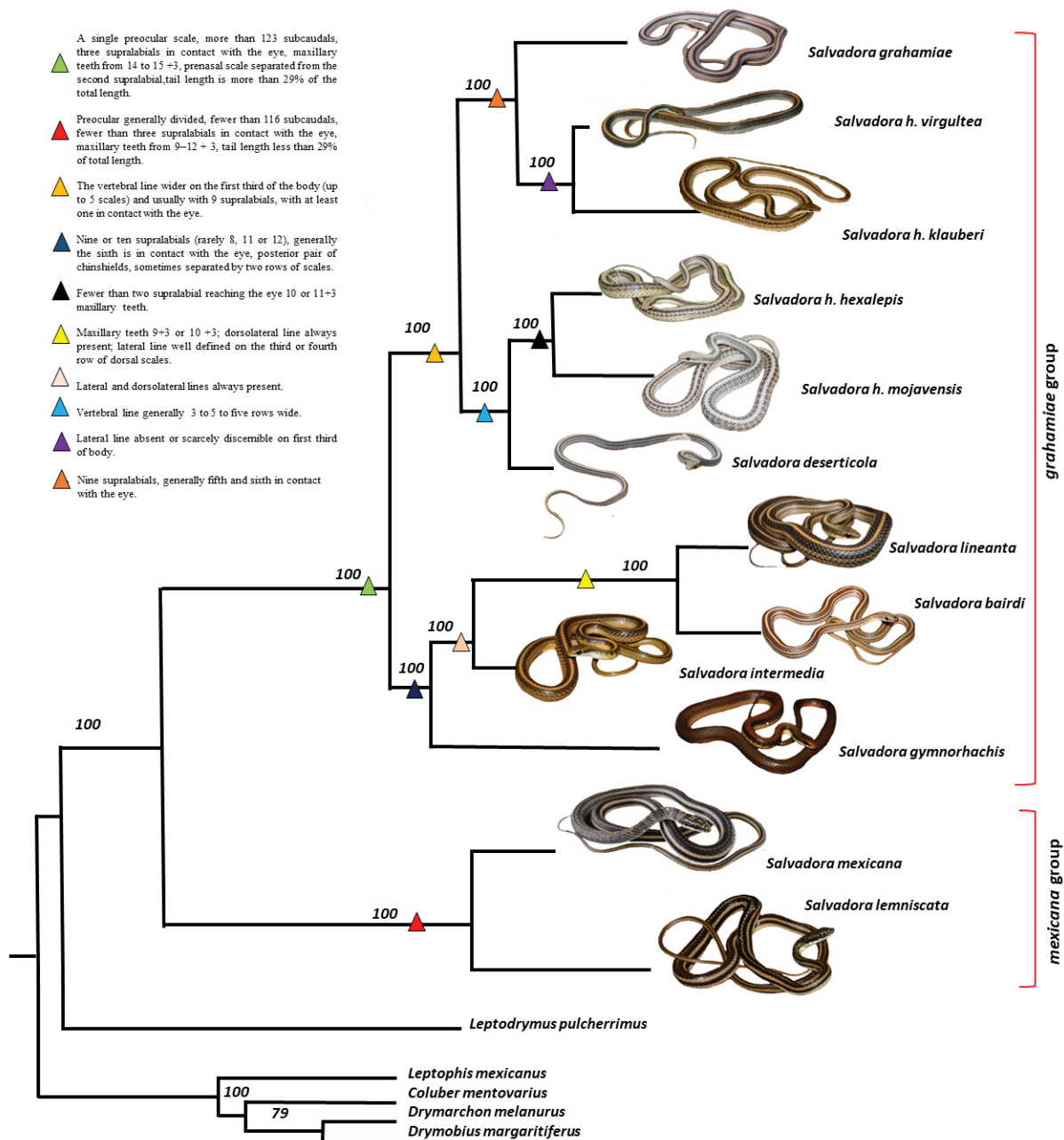


Fig. 2. Tree obtained based on a heuristic search under the parsimony criterion, with a length of 584 837 steps, a consistency index (CI) of 0.8297 and a retention index (RI) of 0.8276; numbers over the nodes represent the Bootstrap values.

value of 100 (*grahamiae* group). Within the second group there are two subgroups. The first contains *Salvadora deserticola*, the four subspecies of *Salvadora hexalepis*, and *Salvadora grahamiae* with high Bootstrap values. The second group contains *Salvadora bairdi* as a sister group to *Salvadora lineata* with a Bootstrap value of 100, also grouped with *Salvadora intermedia* with a Bootstrap value of 100 and includes the most recently described species in the genus, *Salvadora gymnorhachis*.

The monophyly of the genus is supported as all the species have an enlarged rostral scale interceding between the internasals that sometimes has free edges. The two large groups, in which the species and subspecies of *Salvadora* are found, are clearly differentiated by the number of subcaudal scales, the number of maxillary teeth, and the shape of the preocular scale. The *mexicana* group includes the two largest species of the genus *Salvadora*, *S. lemniscata* and *S. mexicana*, while the second group, *grahamiae*, includes all the other species and subspecies of the genus.

Taxonomy

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Family Colubridae Oppel, 1811

Genus *Salvadora* Baird & Girard, 1853

Salvadora Baird & Girard, 1853: 104–105.

Phimothyra Cope, 1861: 566.

Type species

Salvadora grahamiae Baird & Girard, 1853.

Diagnosis

Usually nine-plate supracephalic scaling on the head; enlarged rostral scale that intercedes between the internasals and sometimes has free edges; two nasal scales; preoculars and postoculars present; loreal scale simple or divided; smooth body scales sometimes with two apical pits; 17 rows of scales around the body on the anterior third of body and midbody; cloacal scale divided; subcaudal scales in two series; elongated head; large eyes; round pupil; long tail. Hemipenis simple with spines at the base, replaced midway by calyces that cover half the length of each organ: sulcus simple with a long basal spine. Normally from 9 to 15 maxillary teeth followed by a diastema and three enlarged teeth (9–15+3). Color pattern consisting of two longitudinal, dorsolateral and lateral lines on each side of the body and a pale vertebral line generally present.

Etymology

Derived from the Latin ‘*salvator*’, which means ‘savior’, and ‘*adora*’, which means ‘honor’, an explicit homage to the collector of the type species *S. grahamiae*, Col. J.D. Graham.

Distribution

Southern United States from southern California, western Nevada, Utah, to Arizona, New Mexico, to central Texas; in Mexico, the Baja California Peninsula and Sonora south to the lowlands of Chiapas and Guatemala excluding the Yucatán Peninsula.

Remarks

The phylogenetic hypothesis and the character revision reveal that there are two groups within the genus, as previously suggested by Smith (1938, 1941): *mexicana* and *grahamiae*.

The *mexicana* group

The two species in this group are defined by several synapomorphies: a single preocular scale, more than 123 subcaudal scales, three supralabials in contact with the eye, maxillary teeth from 14 to 15+3, prenasal scale separated from the second supralabial, and the tail length is more than 29% of the total length.

Salvadora lemniscata (Cope, 1895)

Fig. 3

Drymobius lemniscatus Cope, 1895: 203.

Drymobius (Eudryas) pulcherrimus Bocourt 1890: 725–726.

Salvadora lemniscata – Bogert 1939b: 142.

Diagnosis

Rostral slightly elongated and projecting toward the back; 9 supralabials, 3 supralabials in contact with the eye, the fourth, fifth and sixth; generally 12 infralabials, sometimes 11 or 13; single preocular; single loreal; prenasal separated from the second supralabial; a second pair of chinshields larger than the first one in contact with each other or separated by a row of scales; 194–206 ventrals; 128–141 subcaudals; tail is 29 to 34% of total length; 14–15+3 maxillary teeth. Color pattern consists of a pale vertebral line extending from the parietal region, and is three rows wide on the first third of the body and one row wide on the rest of the body, flanked by a pair of dark dorsolateral lines two to four scales wide, interrupted at the neck without touching the head; two dark lateral lines, sometimes slightly interrupted in the neck region or continuing toward the sides of the head, passing by the eyes to the nasal scales.

Differs from the other species in the genus by having more maxillary teeth (14–15+3); a single preocular scale; tail length 29 to 34% of total length; 4 longitudinal lines along the body, dorsolaterals interrupted on the neck region; 194 to 206 ventral scales.

Etymology

The species name comes from the Latin ‘*lemniscatus*’, which means ‘adorned with bands’, doubtless in reference to the stripes along its body.

Type material

MEXICO • “Mexique occidental” [Western Mexico], locality uncertain, probably from Tehuantepec, Oaxaca; F. Sumichrast leg.; MNHN 1891.0260.

Distribution and conservation

From Acapulco in the state of Guerrero southward the Pacific coast, across the Isthmus of Tehuantepec to the coast of Chiapas, the Central Depression of the Grijalva River, and Huehuetenango, Guatemala (Fig. 3).

Within its distribution it occurs in at least two protected natural areas. Mexican legislation has listed this species as subject to Special Protection and the IUCN has it listed as a species of Least Concern.

Remarks

Three additional specimens examined (UTA 45840 Guatemala: Huehuetenango, 2.4 km from Nenton on Road to la Trinidad; UTA 45842 Guatemala: Huehuetenango, 0.3 km S Cuatro caminos, La Democracia-Nenton Road; UTA 45843 Guatemala Nenton, Hacienda Miramar, La Fortuna near Pozo) represent the first records of *Salvadora lemniscata* for Guatemala.

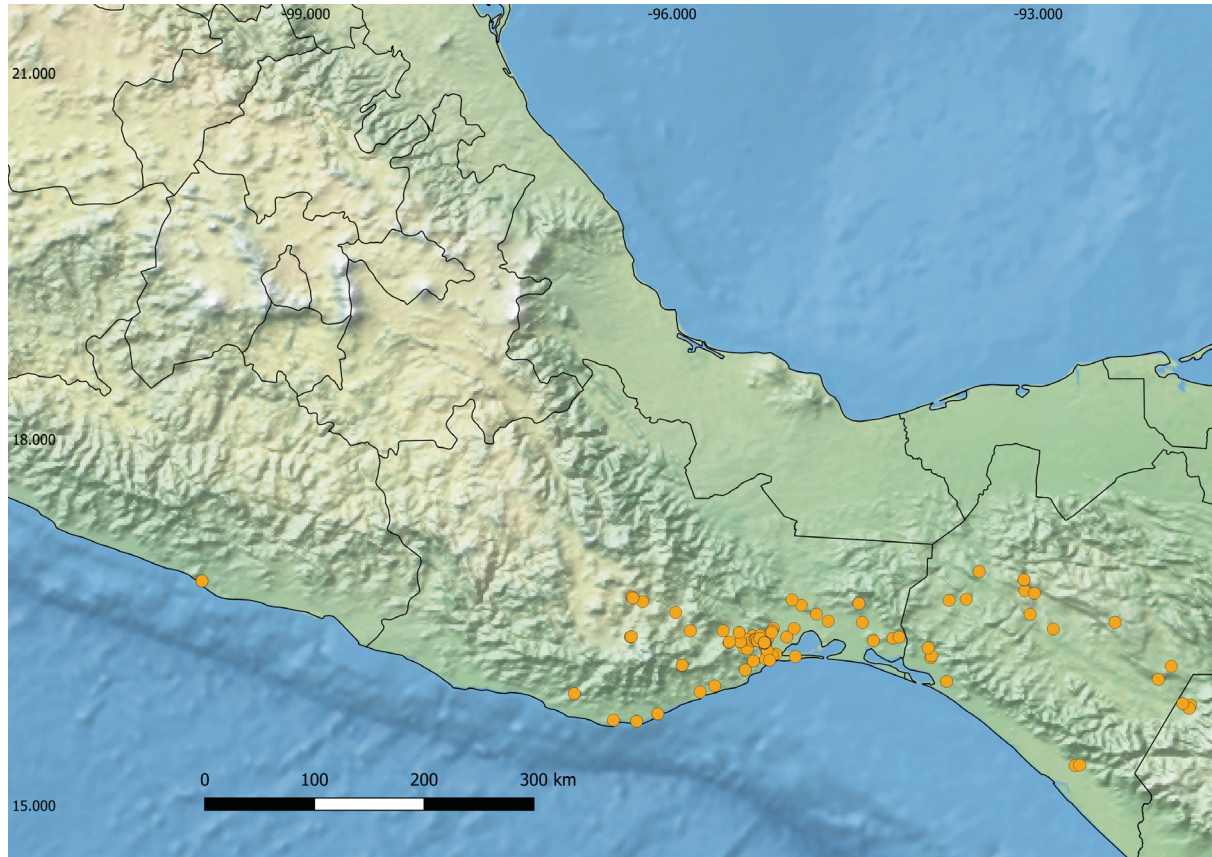


Fig. 3. Locality records of *Salvadora lemniscata* (Cope, 1895).

Salvadora mexicana (Duméril, Bibron & Duméril, 1854)

Fig. 4

Zamenis mexicanus Duméril, Bibron & Duméril, 1854: 695–696.

Salvadora mexicana – Günther 1863: 349.

Diagnosis

Rostral elongated; 9 supralabials, 3 supralabials in contact with the eye, the fourth, fifth and sixth; 10–11 infralabials; a single preocular; a single loreal scale; prenasal in contact with the second supralabial; a second pair of chinshields in contact with each other or separated by a row of scales; 182–197 ventrals; 125–145 subcaudals; tail length is 31 to 42% of total length; 15+3 maxillary teeth. Color pattern on the first third of the body consists of mottled transverse patches becoming transverse bars on the neck; the back of the head is dark with pale longitudinal patch in the center; the rest of the body has pale vertebral line flanked by two dark dorsolateral lines; and two dark lateral lines.

This species differs from its congeners by having a single preocular scale; tail length is approximately one third of the total length (31–42%); and by having four dark longitudinal lines interrupted on the first third of the body where they are replaced by transverse bands or patches.

Etymology

Patronym referring to the country of origin.

Type material

MEXICO • “Cap Corrientes, Mexique” [Jalisco, Cabo Corrientes]; MNHN 3585.

Distribution and conservation

Endemic to Mexico. Occurs from Nayarit southward on the Pacific coast in the states of Nayarit, Jalisco, Colima, Michoacán, Guerrero, and Oaxaca entering the Balsas River Basin, toward central Guerrero, the states of Estado de México, Morelos and southwestern Puebla (Fig. 4).

Within its distribution it is found in at least four protected natural areas. Mexican legislation has listed this species as subject to Special Protection and the IUCN has it listed as a species of Least Concern.

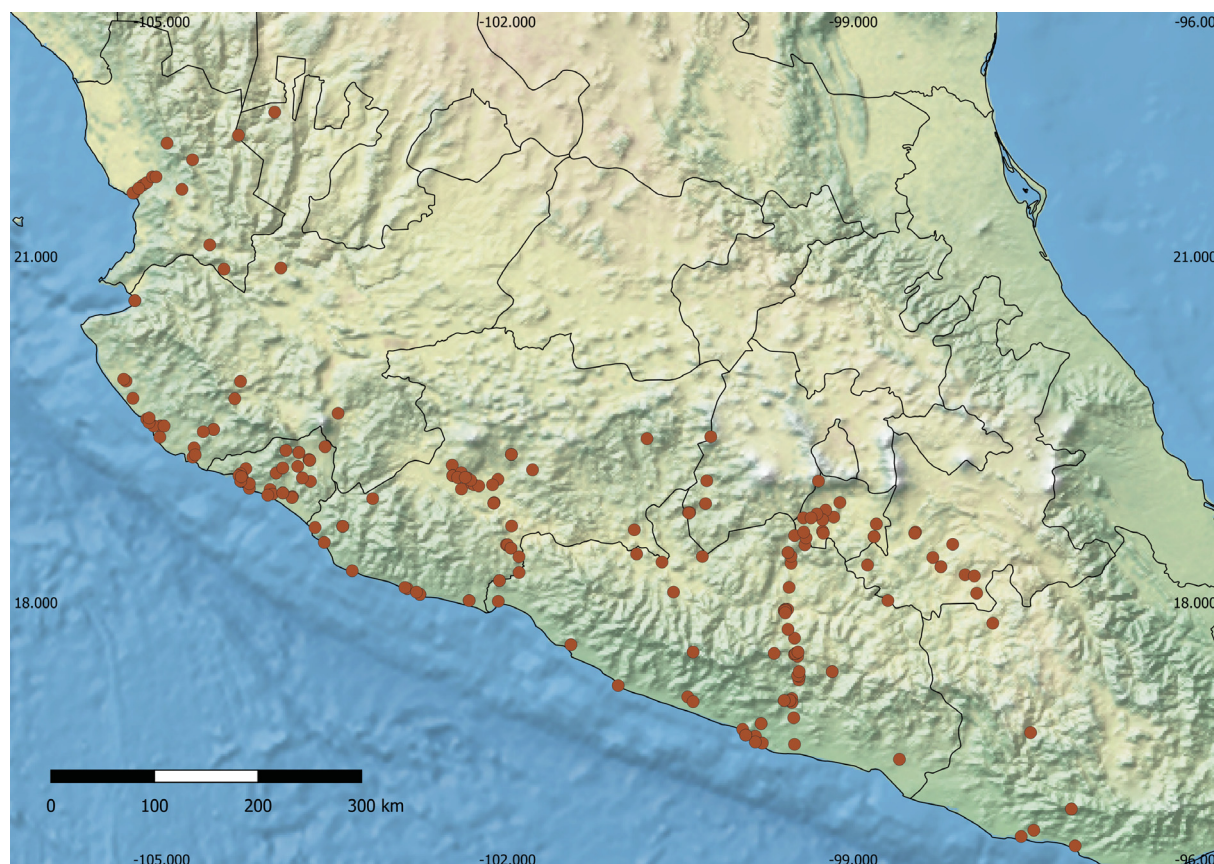


Fig. 4. Locality records of *Salvadora mexicana* (Duméril, Bibron & Duméril, 1854).

The *grahamiae* group

The taxa in this group are defined by several synapomorphies, including preocular generally divided; fewer than 116 subcaudals, normally fewer than three supralabials in contact with the eye, maxillary teeth from 9 to 12+3; tail length less than 29% of total length.

Salvadora bairdi Jan in Jan & Sordelli 1860

Fig. 5

Salvadora bairdi Jan in Jan & Sordelli, 1860: pl. 3 fig. 2.

Salvadora bogerti Smith, 1941: 2–6.

Diagnosis

Rostral without free edges, slightly elongated towards the back interceding between internasals; 8 supralabials, generally fourth and fifth touching the lower edge of the eye; 10 infralabials; preocular divided; a single loreal; prenasal may or may not be in contact with the second supralabial; a second pair of chinshields in contact with each other or sometimes separated by a row of scales; 175–209 ventrals; 82–108 subcaudals; tail length 22 to 29% of the total length; maxillary teeth normally 9+3. Color pattern consists of a pale vertebral line three scales wide that begins on the neck and tapers to one scale wide on the last third of body; two pairs of dark longitudinal lines, dorsolateral lines two to four scales wide not touching the temporal region and connecting on the anterior part, forming a patch that separates them from the parietal region; lateral lines involving the third row of dorsal scales and may or may not be interrupted by an irregular pattern of patches in the posterior region of head.

This species differs from its congeners by having a single loreal, edges of rostral scale not free, maxillary teeth 9+3, and a pale vertebral line that extends to the neck without touching the temporal region.

Etymology

Named in honor of Spencer Fullerton Baird.

Type material

MEXICO • holotype of *Salvadora bogerti*; “Tehuantepec”, locality uncertain; USNM 30296.

MEXICO • holotype of *Salvadora bairdi*; “Méxique” Guanajuato, restricted to Acámbaro, see Smith & Taylor (1950); Museo Civico di Storia Naturale di Milano, Westphal coll.; MSNM (destroyed).

Distribution and conservation

Endemic to Mexico; distributed from Sonora and Chihuahua southward through the states of Sinaloa, Durango, Zacatecas, Nayarit, Jalisco; in central Mexico through the Trans-Mexican Volcanic Belt in the states of Querétaro, Guanajuato, Michoacán, Guerrero, Estado de México, Hidalgo, Morelos, Puebla, and Veracruz (Fig. 5).

Within its distribution, it is found in at least four protected natural areas. Mexican legislation has listed this species as subject to Special Protection and the IUCN has it listed as a species of Least Concern.

Remarks

The holotype of *S. bogerti* is a juvenile purportedly collected by F. Sumichrast in the vicinity of “Tehuantepec”; this locality does not appear to be the usual collecting site of Tehuantepec, Oaxaca, but rather a community in the municipality of San Andrés Tuxtla called Tehuantepec (from the notes of C.M.

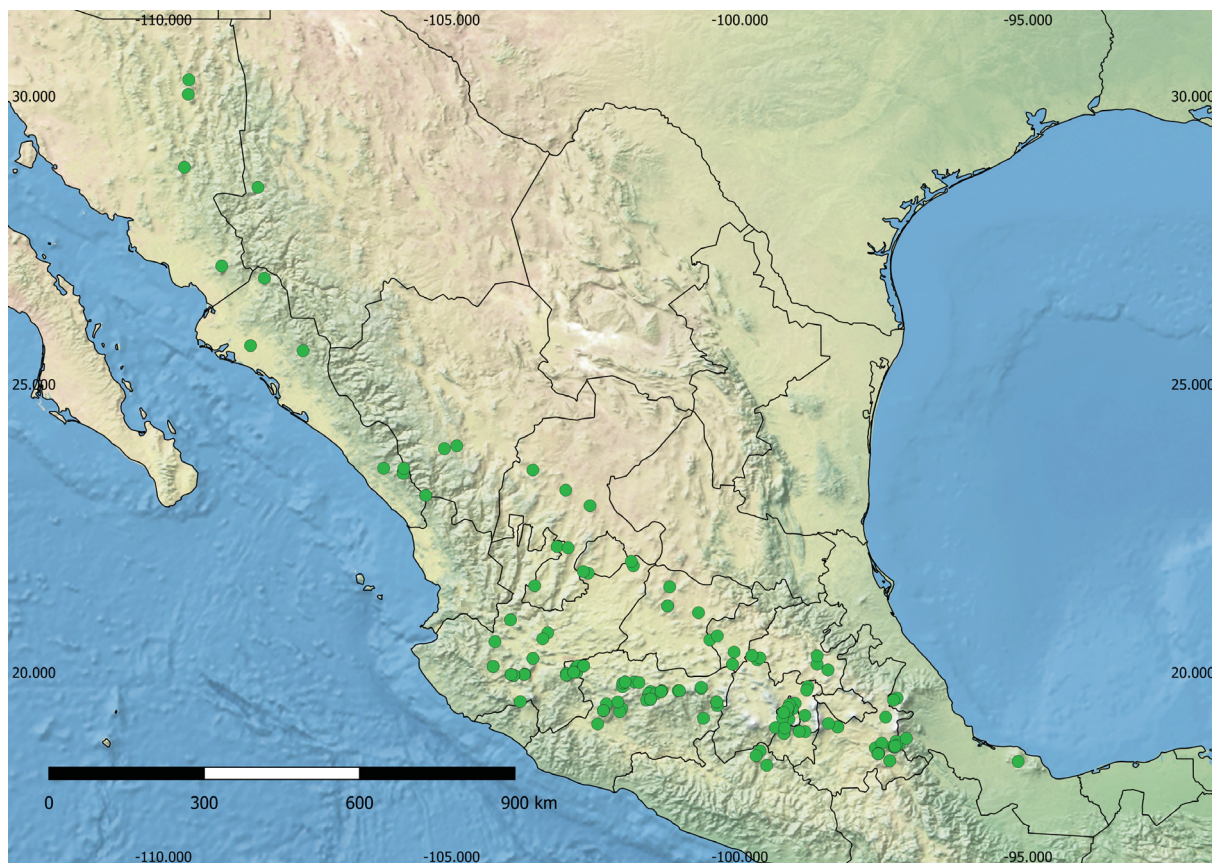


Fig. 5. Locality records of *Salvadora bairdi* Jan & Sordelli, 1860.

Bogert; Pérez-Higareda & Smith 1991). Independently of this, the morphological characteristics of the holotype of *bogerti* correspond with the morphological characteristics of a population of specimens of *Salvadora bairdi* collected in the state of Veracruz, near Cordoba. It is worth mentioning that *Salvadora bairdi* is the species that varies the most in squamation and coloration patterns. After an extensive review of the literature and after many years of collecting (either personal or by other collectors) in the region of Los Tuxtlas, no more specimens have come to light, and it is apparent that the holotype of *S. bogerti* may have been a mislabeled specimen. Pérez-Higareda *et al.* (2007) do not list this species as part of the ophidiofauna of the region; therefore, we conclude that the locality of the type of *Salvadora bogerti* is not from Los Tuxtlas and more likely was collected by Sumichrast near Orizaba; a locality where he lived and made collections.

Some individuals in northern Sinaloa, southern Sonora and Chihuahua have a series of patches or transverse patches on the first third of body; however, in spite of being an isolated population, this character is not constant in the specimens we examined.

***Salvadora deserticola* Schmidt 1940**

Fig. 6

Salvadora hexalepis deserticola Schmidt, 1940: 146, fig. 14.

Salvadora hexalepis celeris Smith, 1941: 9, fig. 6.

Diagnosis

Rostral scale well developed, elongated and with free edges; 9 supralabials, two or rarely three in contact with the eye (generally the fifth and sixth in contact); 11 infralabials; preocular scale divided; a single loreal; prenasal in contact with the second supralabial; a second pair of chinshields separated by two rows of scales; 180–205 ventrals; 66–87 subcaudals; tail is 19 to 23.5% of the total length; maxillary teeth normally 11+3. Color pattern consists of a pale vertebral stripe, five scales wide on the anterior third of the body and three scales wide on the rest of the body, flanked by a pair of dark dorsolateral lines located on the sixth and seventh row and separated from the lateral lines by at least one row of scales; lateral lines begin on the fourth row or on the margins of the third and fourth rows of dorsal scales. Lateral and dorsolateral lines fused on the neck.

Differs from the other species in the genus by having a single loreal, usually not divided; tail shorter (less than 24% of the total length) and fewer subcaudal scales.

Etymology

The species name is derived from the Latin words ‘*desertum*’, which means ‘desert’, and ‘*icola*’, which means ‘inhabitant’, in reference to the habitat at the type locality.

Type material examined

UNITED STATES • ♂, holotype of *Salvadora hexalepis deserticola*; Texas, Brewster County, Government Spring, close to the Chisos Mountains; 6 Oct. 1935; Tom Carney leg.; FMNH 26615.

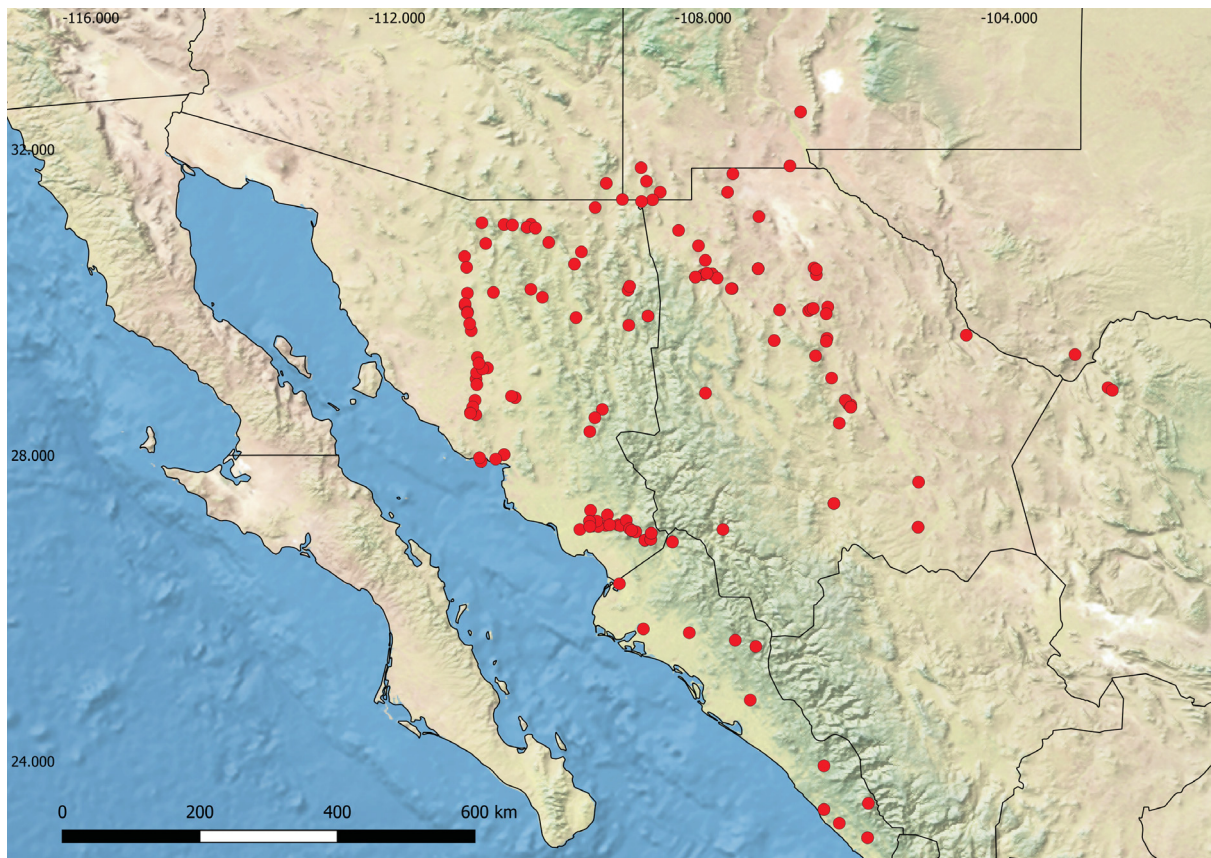


Fig. 6. Locality records of *Salvadora deserticola* Schmidt, 1940.

MEXICO • ♀, holotype of *Salvadora hexalepis celeris*; Sinaloa, San Blas; 28 Mar. 1910; J.N. Rose leg.; USNM 40043.

Distribution and conservation

Southwestern Texas, southwestern New Mexico, and southeastern Arizona, southward on each flank of the Sierra Madre Occidental in Mexico in the states of Sonora, Chihuahua, Coahuila and Sinaloa (Fig. 6).

It is found in at least two protected natural areas in Sonora. Mexican legislation has not listed this species and the IUCN has it listed as a species of Least Concern.

Salvadora grahamiae Baird & Girard, 1853

Fig. 7

Salvadora grahamiae Baird & Girard, 1853: 104–105.

Phimothyra grahamiae – Cope 1861: 566.

Diagnosis

Well-developed rostral scale, elongated and with free edges; 8 or 9 supralabials, fourth and fifth or fifth and sixth supralabial in contact with the eye; normally 10 infralabials; a single loreal scale; preocular divided; prenasal scale in contact with the second supralabial; a second pair of chinshields separated by a row of scales; 178–200 ventral scales and 89–106 subcaudals; maxillary teeth normally 10+3. Color pattern consists of a pale vertebral line extending to the top of the head, three to five rows of scales wide on the first third of the body reduced to only three on posteriorly; head bordered by a pair of continuous dorsolateral lines from the loreal region throughout the body, with dark line on the sixth and seventh lines of dorsal scales; Sometimes with an inconspicuous lateral line at third row of dorsal scales.

Salvadora grahamiae differs from *S. lineata* by having inconspicuous or absent lateral lines, and differs from other congeners by having the tail approximately one quarter of the total length (22–29%); loreal scale not divided, posterior chinshields separated by a two row of scales; and the vertebral line up to five scales wide on anterior of body.

Etymology

Dedicated to the collector of the taxon, J.D. Graham.

Type material examined

UNITED STATES • ♂; Arizona, Cochise County, Huachuca Mountains, limited to Sonora (Bogert 1939a); J.D. Graham leg.; USNM 2081.

Distribution and conservation

From western Texas, northern Coahuila, Chihuahua, and Sonora to northern Arizona and New Mexico (Fig. 7). It occurs in several protected natural areas in Mexico and the United States. Mexico and the United States have not listed this species in any protection category, and it is on the IUCN red list as a species of Least Concern.

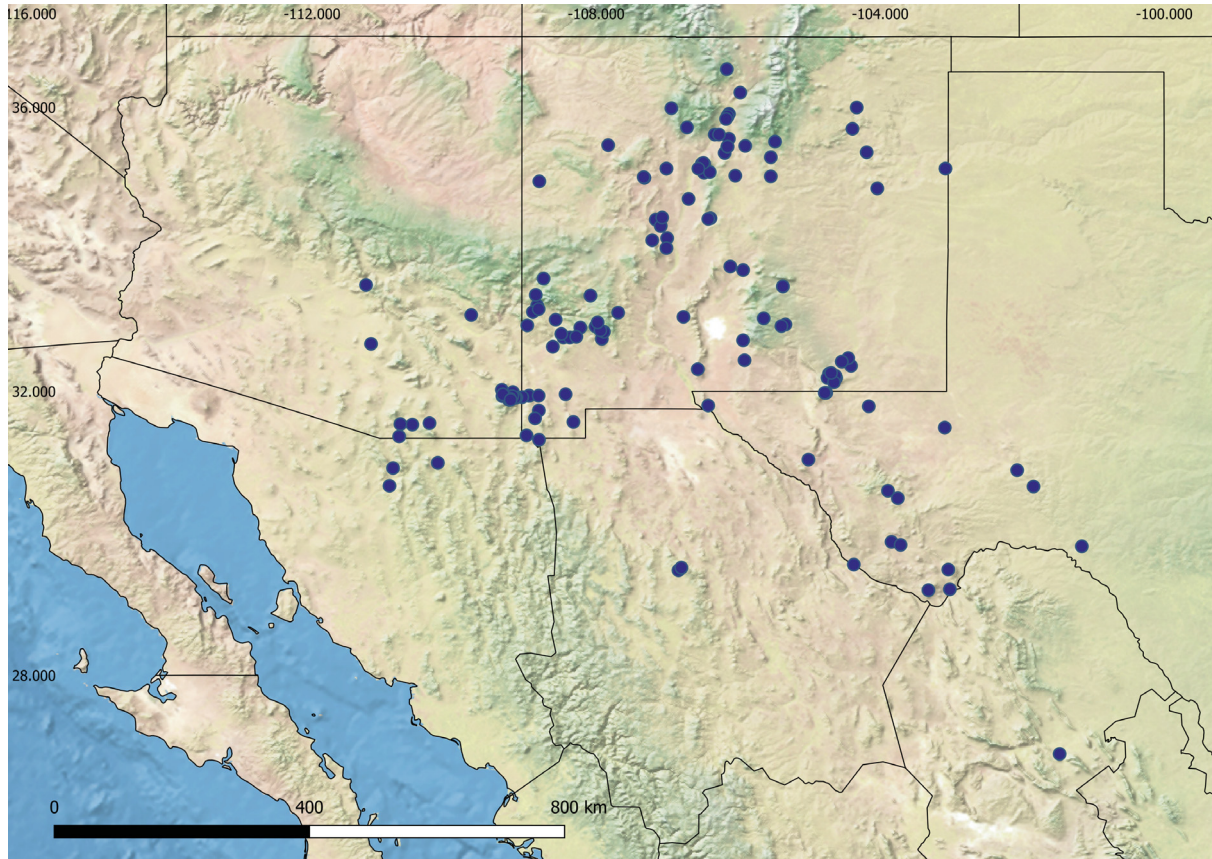


Fig. 7. Locality records of *Salvadora grahamiae* Baird & Girard, 1853.

Salvadora lineata Schmidt, 1940

Fig. 8

Salvadora lineata Schmidt, 1940: 143–150.

Salvadora grahamiae lineata Hartweg, 1940: 259.

Diagnosis

Well-developed rostral scale, elongated and with free edges; 8 or 9 supralabials, fourth and fifth in contact with the eye; 9 to 11 infralabials; preocular divided; a single loreal scale; prenasal scale in contact with or separated from the second supralabial; a second pair of chinshields in contact with each other or separated by a row of scales; 179–202 ventral scales; 81–107 subcaudal scales; maxillary teeth normally 10+3. Color pattern consists of a pale vertebral line reaching the top of the head, three to five rows of scales wide on the first third of the body and only three posteriorly; head bordered by a pair of continuous dorsolateral lines from the loreal region across the body, dark line on the sixth and seventh dorsal scales; lateral line paler than the well-developed dorsolateral line on the third row of dorsal scales.

Differs from *S. grahamiae* by having a pair of well-defined lateral lines on the third row of the dorsal scales, extending from the first third of the body and to the cloaca.

Etymology

Derived from the Latin ‘*linea*’, meaning ‘line’, in reference to the conspicuous lateral line.

Type material examined

UNITED STATES • ♀; Texas, Kleberg County, Kingsville; 1938; J.C. Cross; FMNH 28605.

Distribution and conservation

United States from eastern Texas southward through northwestern Mexico in the states of Chihuahua, Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas, San Luis Potosí, Guanajuato Querétaro, Michoacán, Hidalgo, Puebla and northern Veracruz (Fig. 8).

This species occurs in several protected natural areas in Mexico and the United States. Mexico and the United States have not listed this species in any protection category, but it is on the IUCN red list as a species of Least Concern.

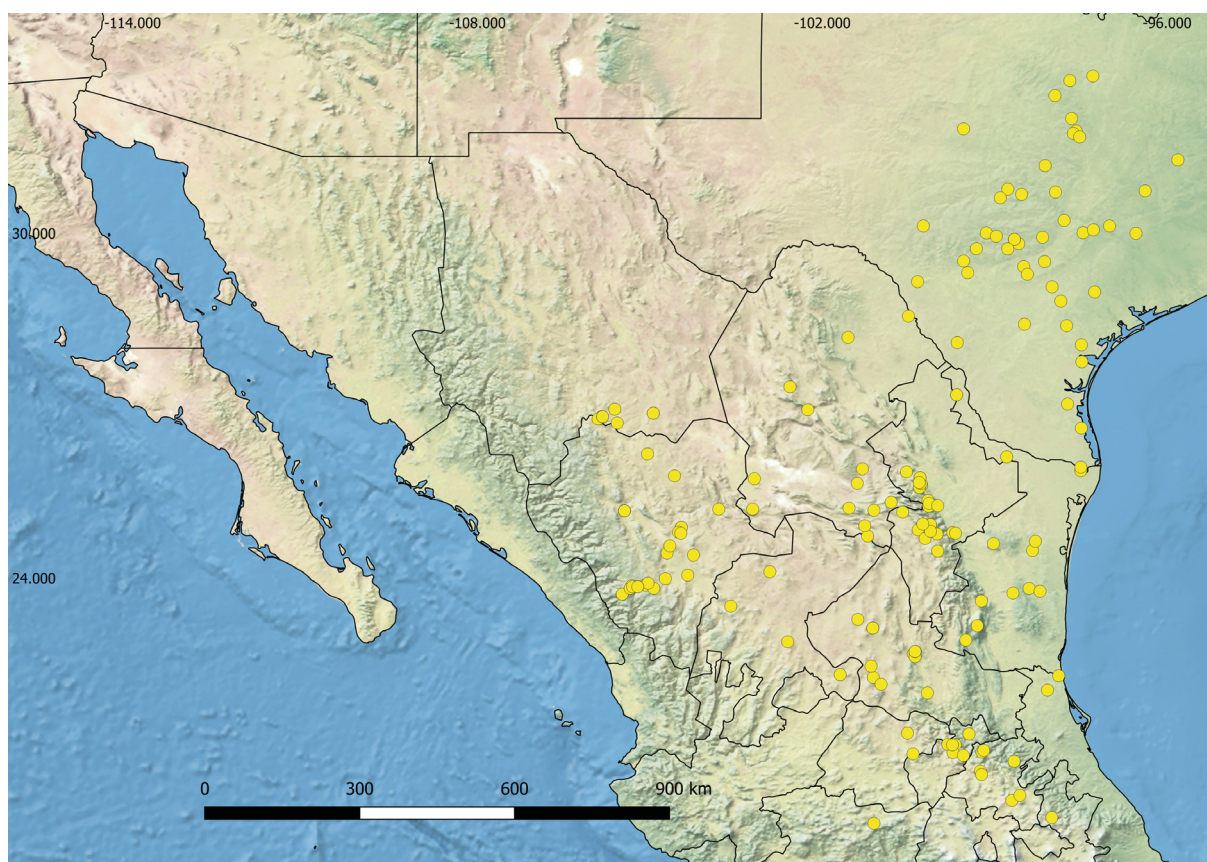


Fig. 8. Locality records of *Salvadora lineata* Schmidt, 1940.

Salvadora hexalepis (Cope, 1866)

Fig. 9

Phimothyra hexalepis Cope, 1866: 304.

Subspecies included

S. hexalepis hexalepis

S. hexalepis virgultea

S. hexalepis mojavesis

S. hexalepis klauberi

Diagnosis

Well-developed rostral scale with free lateral edges; normally 9 supralabials, or occasionally 8 or 10; supralabials in contact with the eye, usually only sixth is in contact; 10–11 infralabials; preocular divided; loreal scale normally divided; prenasal scale separated from the second supralabial; a second pair of chinshields separated by two rows of scales; ventral scales 180–213; subcaudal scales vary from 75 to 103; maxillary teeth 10–12+3. With the exception of *S. hexalepis virgultea*, the dark dorsolateral lines are normally separated from the lateral lines at the level of the third and fourth rows of dorsal scales; tail length is 20 to 26% of the total body length.

Salvadora hexalepis differs at the species level from the other species in the *grahamiae* group by having a divided preocular, fewer than 113 subcaudals, and a tail length less than 29% of the total length. It differs from *S. grahamiae*, *S. intermedia*, *S. gymnorhachis* and *S. bairdi* by having 9 to 10 supralabials, the sixth in contact with the eye versus 8 supralabials present in the other species in the *grahamiae* group. It differs from *S. deserticola* by having a divided loreal and 75–103 subcaudals.

Type material examined

UNITED STATES • Arizona, Fort Whipple; USNM 7894.

Distribution and conservation

This species occurs in the southwestern United States from Nevada, southern Utah, southward through California, Arizona, the Baja California Peninsula and Sonora including Tiburón, San José, and Espiritu Santo Islands in the Gulf of California. (Fig. 9).

Within its distribution, *S. hexalepis* has been recorded in several protected natural areas in Mexico and the United States. Mexico and the United States do not extend legal protection to this species. It is listed by the IUCN as a species of Least Concern.

Salvadora hexalepis hexalepis (Cope, 1866)

Fig. 9

Diagnosis

Nine supralabials; sixth supralabial in contact with the eye; 10 infralabials; a single subocular sometimes present; 186–213 ventrals; 75–98 subcaudals; tail 20 to 25 % of total length; 10+3 maxillary teeth; a pale vertebral line contacting the parietal region, three to five scale rows wide on the first third of the body, three rows wide posteriorly, bordered by a pair of dorsolateral lines up to four scale rows wide, extending from the temporal region to the tip of the tail, halfway along the body the dorsolateral lines are divided giving rise to another lateral line distinguishable to the tip of tail.

This taxon differs from *S. h. klauberi* by having a single supralabial in contact with the eye, whereas *S. h. klauberi* has two supralabials (the fifth and sixth) in contact; in *S. h. mojavesis* the supralabials and the lower edge of the eyes are separated by two or more suboculars; *S. h. hexalepis* is similar to *S. h. virgultea* in that many individuals have a single supralabial in contact with the eye; however, these subspecies differ in coloration pattern, with the head of *S. h. virgultea* being brown and the lateral line becoming faded and indistinguishable at about the middle of the body (in *S. h. hexalepis* the head is gray, the vertebral line is up to five rows of scales wide, and in the middle of the body the lateral line is completely separated from the dorsolateral line).

Etymology

From the Latin ‘*hexa*’ for ‘six’ and ‘*lepis*’ for ‘scale’, which can be interpreted as six-sided scales.

Distribution

It occurs from the southeast of California, United States, southward to northeastern Baja California, central Arizona southward through the northeast portion of the Sonoran Desert, including Tiburón Island (Fig. 9).

Salvadora hexalepis virgultea (Bogert, 1935)

Fig. 9

Salvadora grahamiae virgultea Bogert, 1935: 89.

Diagnosis

Nine supralabials, the sixth or the fifth and sixth in contact with the eye; 10–11 infralabials; suboculars absent; 188–200 ventral scales; 84–103 subcaudal scales; tail 21 to 26% of the total length; maxillary teeth 10+3. A pale vertebral line three rows of scales wide is in contact with the parietal region, bordered by a pair of dorsolateral lines brown in color, five rows of scales wide extending from the temporal region to the tip of the tail. At about midbody the lateral line gives rise to a thinner lateral line that is one row of scales wide.

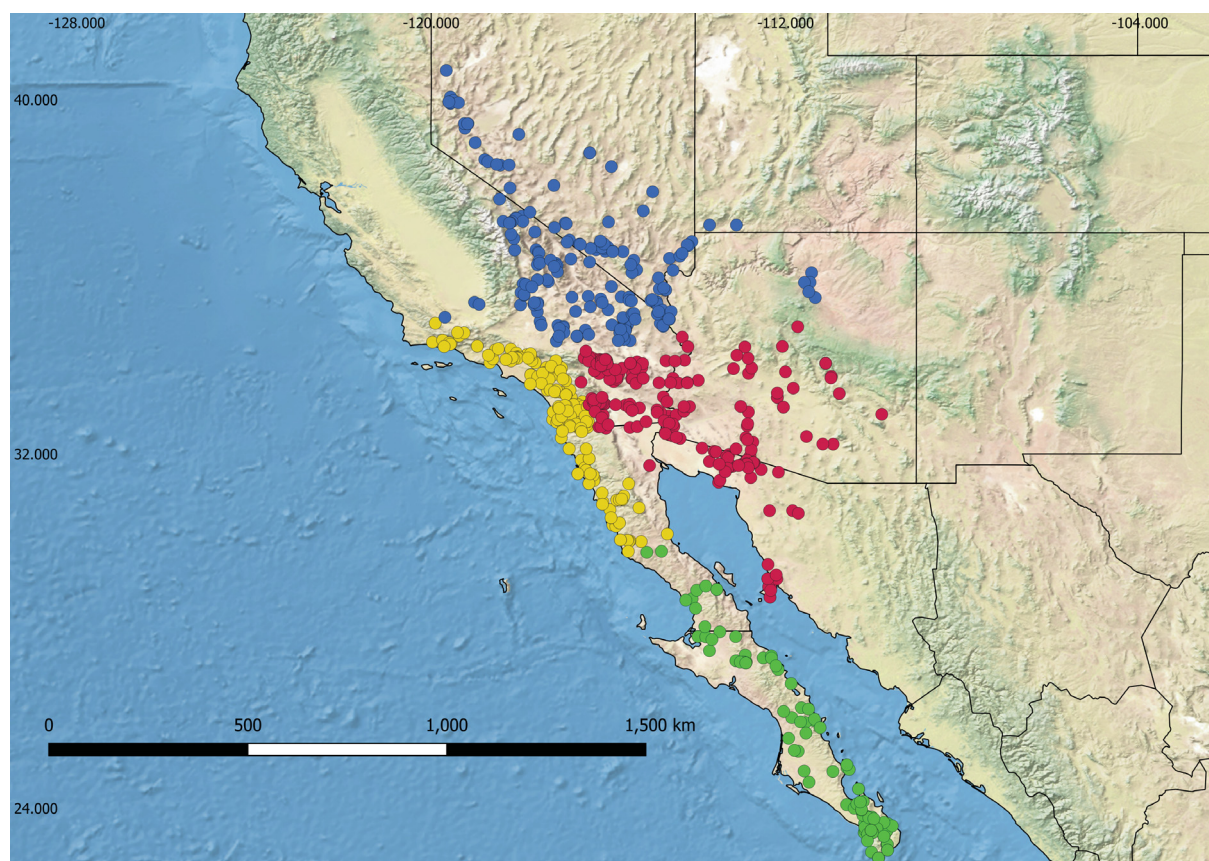


Fig. 9. Locality records of *Salvadora hexalepis* (Cope, 1866) and its subspecies. Blue dots represent *S. h. mojaviensis* Bogert, 1945; yellow dots *S. h. virgultea* Bogert, 1935; red dots *S. h. hexalepis* (Cope, 1866) and green dots *S. h. klauberi* Bogert, 1945.

Salvadora h. klauberi differs in having 12+3 maxillary teeth; in *S. h. mojavenis* suboculars separate the supralabials from the lower edge of the eye; *S. h. hexalepis* sometimes also lacks suboculars and has a single supralabial in contact with the eye similar to *S. h. virgultea*, but it differs in its color pattern (in *S. h. virgultea* the vertebral line involves three scale rows; the head is brown, and a lateral line is not distinguishable). In *S. h. hexalepis* the vertebral line is up to five scale rows wide; the head is gray; and the lateral line at midbody is completely separated from the dorsolateral line.

Etymology

From the Latin ‘*virgultus*’, meaning ‘covered with scrub’, for the habitat in which the taxon occurs.

Type material examined

UNITED STATES • ♂; California, San Diego County; 32.67778° N, 116.72709° W; 29 Jun. 1929; Deerhorn Flat leg.; SDSNH 12025.

Distribution

Regions adjacent to the Pacific coast and adjacent foothills in southwestern California, southward to the southern portion of Baja California, where is it parapatric with *S. h. klauberi* (Fig. 9).

Salvadora hexalepis mojavenis Bogert, 1935

Fig. 9

Salvadora hexalepis mojavenis Bogert, 1945: 14.

Diagnosis

Nine supralabials, no supralabial in contact with the eye or only sixth in contact; 10–11 infralabials; from two to three suboculars; 190–207 ventral scales; 82–96 subcaudal scales; tail 20 to 25% of total length; 11+3 maxillary teeth; a pale vertebral line that does not reach the parietal region, bordered by a pair of dorsolateral lines and a pair of somewhat inconspicuous lateral lines and irregular bars along the body that interrupt the dorsolateral and lateral lines.

Differs from all conspecific subspecies by having two or three suboculars present.

Etymology

Toponym alluding to its distribution that is concentrated in the Mojave Desert.

Type material examined

UNITED STATES • ♂; California, San Bernardino County, Deadman Point, 11.5 miles SE of Victorville, at the south end of the Granite Mountains; 19 Jun. 1935; C.M. Bogert leg.; AMNH 63000.

Distribution

Endemic to the United States. Distributed south of the San Joaquín Valley and the Mojave Desert, east and north of the foothills of the San Gabriel and San Bernardino mountains, to Pyramid Lake in western Nevada, the Virgin River Basin in southern to western Utah, and portions of the Painted Desert in northern Arizona near the Grand Canyon and the canyon of the small Colorado River (Fig. 9).

Salvadora hexalepis klauberi Bogert, 1945

Fig. 9

Salvadora hexalepis klauberi Bogert, 1945: 14.

Diagnosis

Nine supralabials, generally fifth and sixth in contact with the eye; 10–11 infralabials; suboculars normally absent; 180–203 ventral scales; 78–99 subcaudal scales; tail 21 to 26% of total length; 12+3 maxillary teeth; a pale vertebral line three to five rows wide contacting the parietal region, bordered by a pair of dark dorsolateral lines up to four rows wide extending from the temporal region to the margins between the fifth and fourth rows of scales, lateral lines one or two scales wide fused with the dorsolateral lines on first third of the body.

Differs from *S. h. mojavenensis* by lacking suboculars, differs from *S. h. hexalepis* by having fifth and sixth supralabials bordering the eye and differs from *S. h. virgultea* by having 12+3 maxillary teeth.

Etymology

Dedicated to Laurence Monroe Klauber.

Type material

MEXICO • ♂; Baja California Sur, Cape San Lucas; 6 Aug. 1933; Fred Lewis leg.; Collection of L.M. Klauber No. 20912.

Distribution

Endemic to Mexico, present from northern Baja California southward through Baja California Sur, including the San José and Espiritu Santo Islands (Fig. 9).

Salvadora intermedia Hartweg, 1940

Fig. 10

Salvadora intermedia Hartweg, 1940: 256–259.

Salvadora intermedia richardi Smith, 1941: 6–9.

Salvadora intermedia intermedia – Smith, 1941: 7.

Diagnosis

Rostral scale elongated; generally 8 supralabials (occasionally 9), the fourth and fifth normally in contact with the eye; 10–11 infralabials; preocular scale divided; a single loreal scale; prenasal scale in contact with or separated from the second supralabial; chinshields in contact or separated by two small scales; ventral scales 172 to 190; subcaudal scales 84 to 114; tail is 23 to 30% of the total length; 11+3 maxillary teeth. Color pattern formed by a vertebral line three scales rows wide, yellowish in color and in contact with the parietal region; a pair of lateral lines is fused with the dorsolateral lines on first third of body, separated at second third of the body to tail; dorsolateral lines wide and dark, diverging at the neck, passing through the temporal region to eye.

Salvadora intermedia differs from its congeners by having a divided preocular scale; fewer than 116 subcaudal scales; 8 supralabials, the fourth and fifth in contact with the eye; the second pair of chinshields in contact with each other or separated by a row of scales; and two dark dorsolateral lines that diverge at the neck, passing through the temporal to eye.

Type material examined

MEXICO • ♂, holotype of *Salvadora intermedia intermedia*; Guerrero, vicinity of Chilpancingo; W.W. Brown leg.; UMMZ 85733.

MEXICO • ♂, holotype of *Salvadora intermedia richardi*; Puebla, 1 mile N of Tehuacán; 8 Aug. 1940; R.C. Taylor leg.; Collection E.H. Taylor and H.M. Smith No. 23470; UIMNH 25071.

Distribution and conservation

Endemic to Mexico. Distributed in central-southern Mexico from the vicinity of Chilpancingo, Guerrero, eastward through central Oaxaca and northward to southwestern Puebla (Fig. 10).

Within its distribution it is found in at least two protected natural areas. Mexican legislation has listed this species as subject to Special Protection and the IUCN has it listed as a species of Least Concern.

Remarks

Salvadora intermedia richardi was described by Smith (1941), who based his description on a single specimen collected one mile from Tehuacán, Puebla (UIMNH 25071). Smith (1941) thought this specimen represented a disjunct population of the populations of *S. intermedia* at Guerrero. Smith (1941) defined *S. intermedia richardi* as having the prenasal scale separated from the second supralabial and by its number of ventral scales. However, we examined 37 individuals of *S. intermedia* along what appears to be a continuous distribution from Guerrero and through Oaxaca to southern Puebla, and found that only seven of these specimens had the condition of the prenasal scale separated from the second supralabial described by Smith (1941): three from Oaxaca (MZFC 04059, MZFC 23857, MZFC 23871), three from Guerrero (MCZ 33642, MZFC 02878, FMNH 109866), one from Puebla (MZFC 14384). Additionally, the number of ventral scales of these specimens falls within the range previously described for *S. intermedia*. Based on these findings, we conclude that these characters are part of the

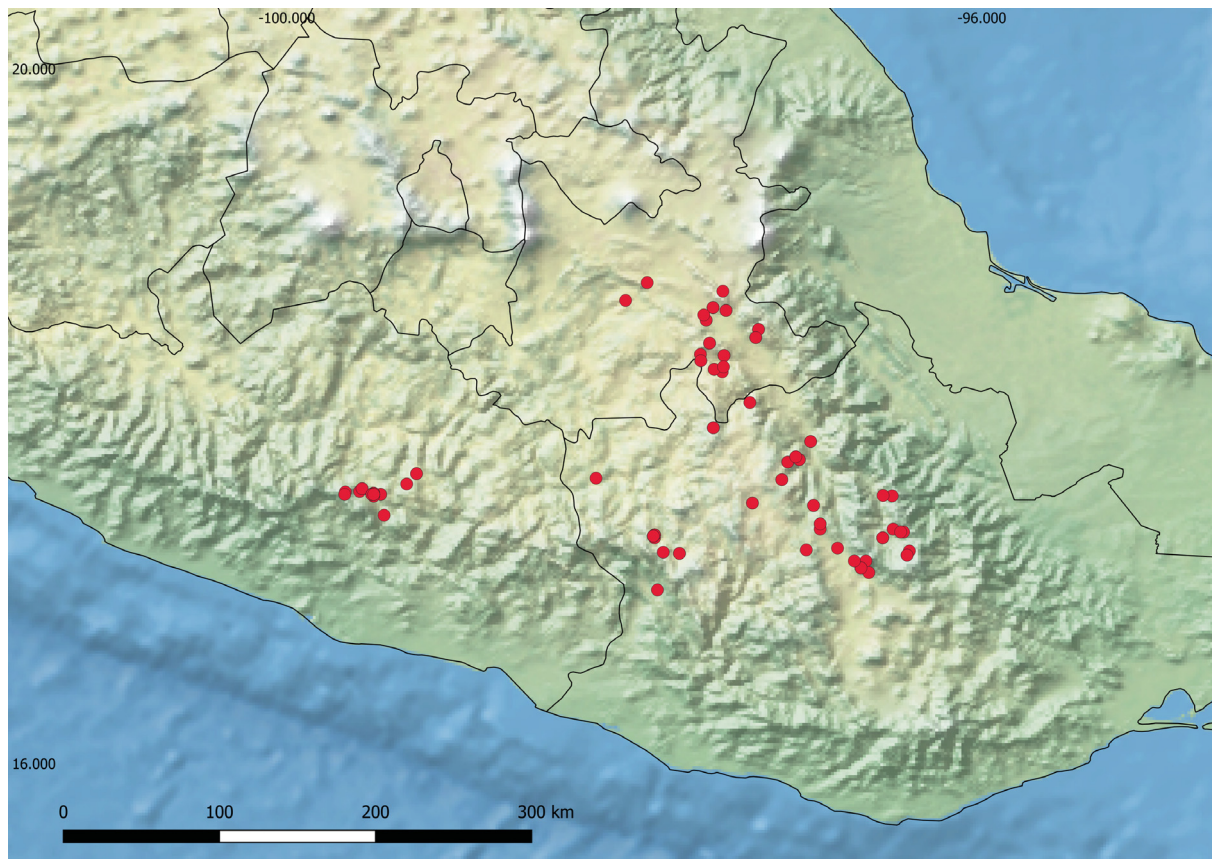


Fig. 10. Locality records of *Salvadora intermedia* Hartweg, 1940.

intrapopulational variation of *S. intermedia* and that *S. i. richardi* should be considered a junior synonym of *S. intermedia* as previously suggested by Davis & Dixon (1957).

Salvadora gymnorhachis Hernández, Flores & Campbell, 2019

Fig. 11

Diagnosis

Eight–9 supralabials, two supralabials, fourth and fifth in contact with the eye; 8–10 infralabials; preocular scale divided; a single loreal scale; prenasal in contact or separated from the second supralabial; a second pair of chinshields in contact or separated by a row of scales; 176–186 ventral scales; 92–103 subcaudal scales; tail is 18 to 21% of the total length; 11 + 3 maxillary teeth. Color pattern consists of a pair of dark dorsolateral lines that begin behind the eyes and fade before reaching the middle of the body, without a well-defined vertebral line and lacking lateral lines.

This species differs clearly from the other species by lacking dorsolateral lines on about the posterior two-thirds of the body and by lacking vertebral and lateral lines across the body.

Etymology

The name is derived from the Greek prefixes ‘*gymnós*’, which means ‘naked’ and ‘*ráchi*’ which means ‘back’.

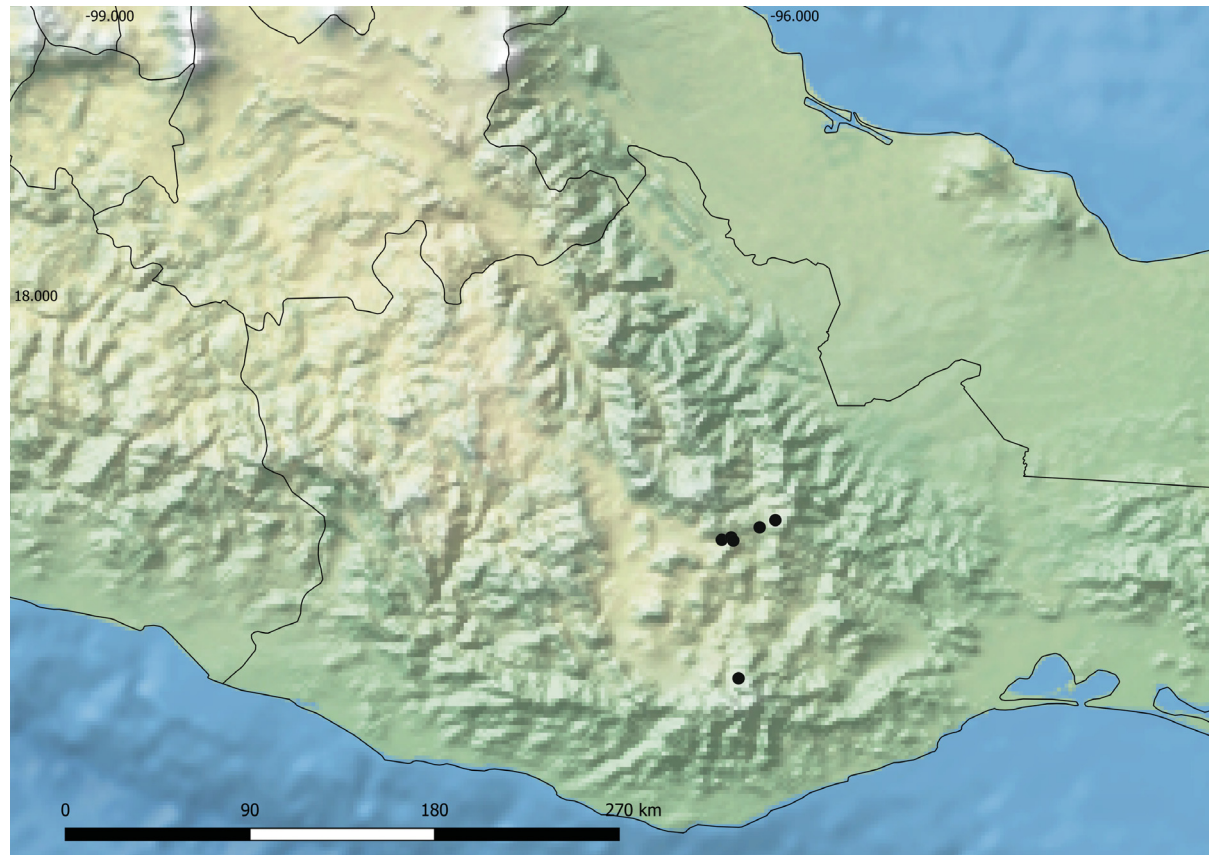


Fig. 11. Locality records of *Salvadora gymnorhachis* Hernández-Jiménez, Flores-Villela & Campbell, 2019.

Type material examined

MEXICO • ♀; Oaxaca, Distrito Mixe, San Pedro and San Pedro Ayutla; 17.00159° N, 96.08443° W; 24 Aug. 2014; MZFC 28775.

Distribution and conservation

Mountains of central Oaxaca, Mexico (Fig.11).

This is a recently described taxon and one of limited distribution that is not known to inhabit any protected natural areas. This species is not included in Mexican legislation and is not in the IUCN’s red list.

Dichotomous key for the species and subspecies of the genus *Salvadora*

- 1. A single preocular (Fig. 12A); more than 123 subcaudals; three supralabials in contact with the eye; maxillary teeth 14+3 to 15+3; tail length more than 29% of total body length (*mexicana* group). 2
- Preocular generally divided (Fig. 12B); fewer than 116 subcaudals; normally fewer than three supralabials in contact with the eye; maxillary teeth from 9+3 to 12+3; tail length generally less than 29% of total body length (*grahamiae* group)..... 3

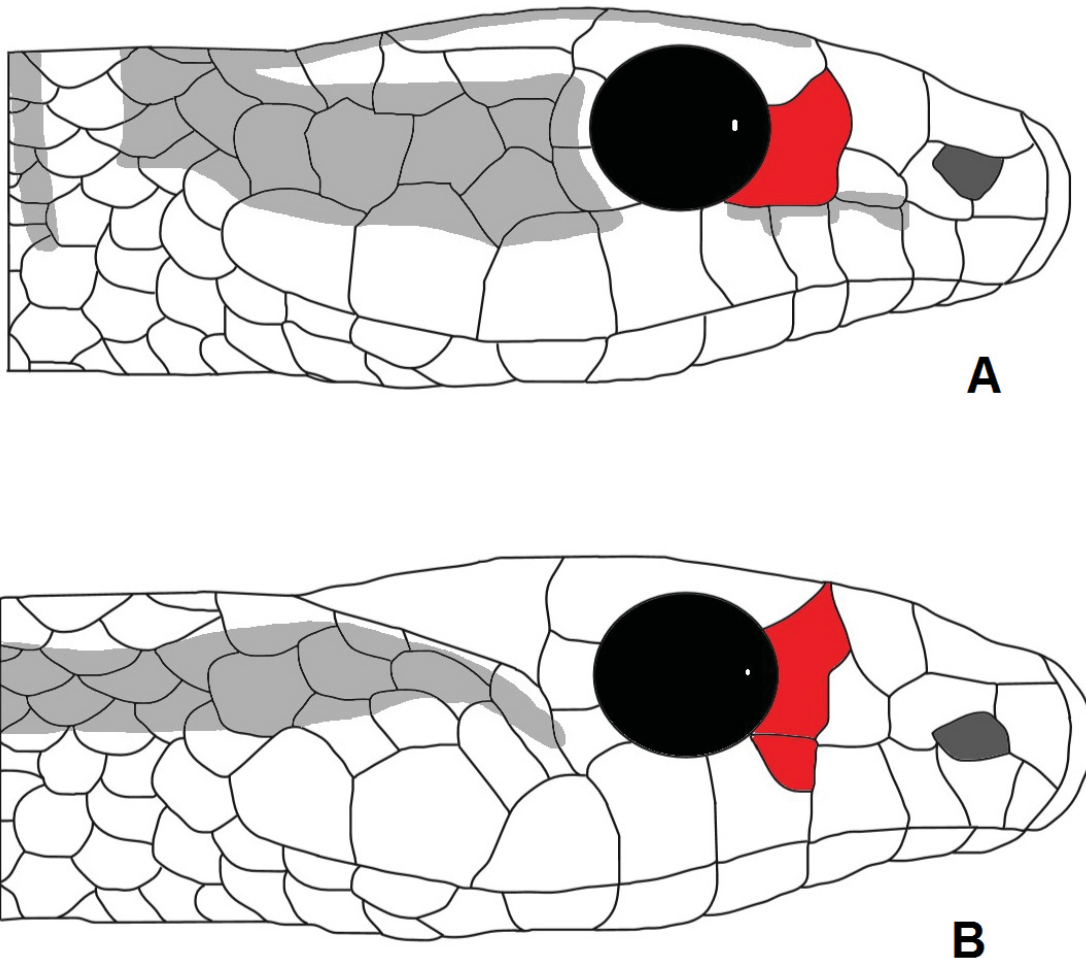


Fig. 12. A. Single preocular. B. Preocular generally divided.

2. Four longitudinal lines on the posterior part of the body that are interrupted in the first third of the body by transverse patches or crossbars (Fig. 13A); 182–197 ventral scales; tail length 31% to 42% of total length; maxillary teeth 15+3*S. mexicana* (Duméril, Bibron & Duméril, 1854)
- Four well-defined longitudinal lines extending along the body without transverse patches or crossbars on the first third of body (Fig. 13B); 194 to 205 ventral scales; tail length between 29% and 33% of total length; maxillary teeth 14+3*S. lemniscate* (Cope, 1895)

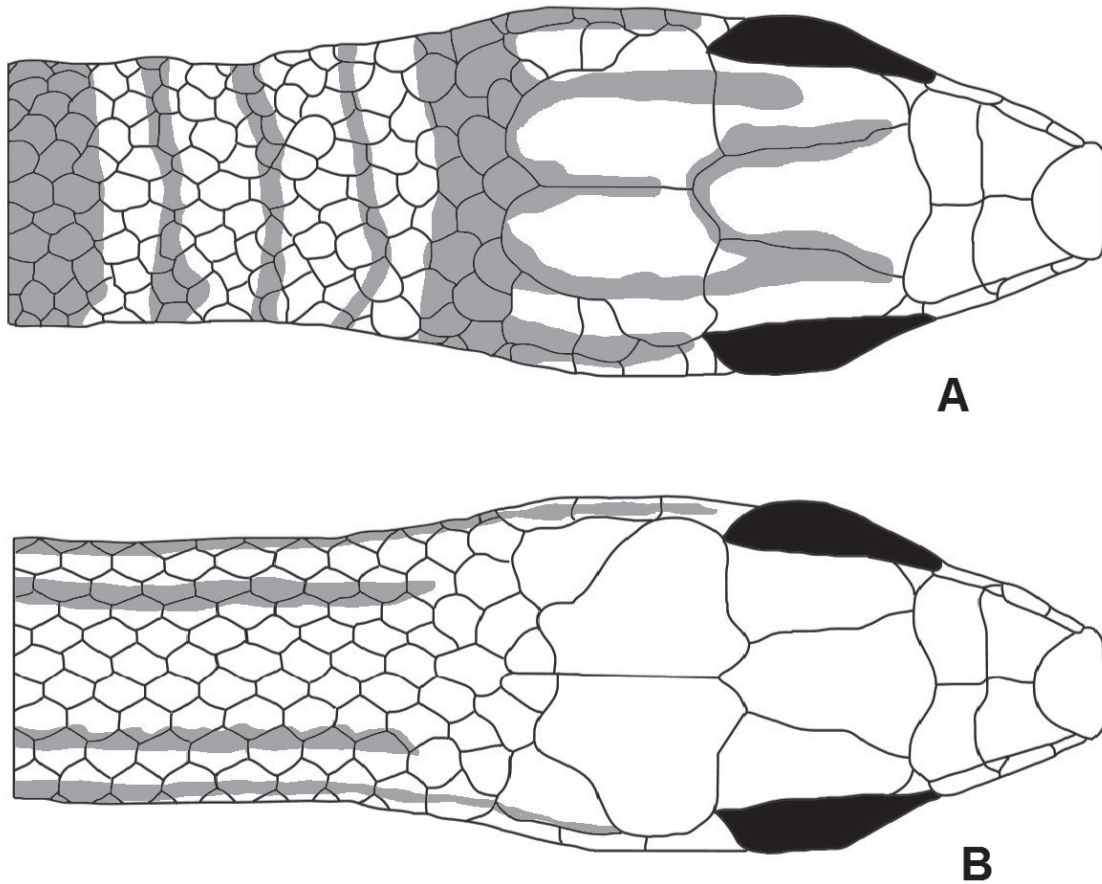


Fig. 13. **A.** Longitudinal lines interrupted in the first third of the body. **B.** Longitudinal lines extending along the body.

3. Supralabials normally eight (rarely 7 or 9), fourth and fifth in contact with the eye (Fig. 14A); a second pair of chinshields in contact with each other or separated by one row of scales (Fig. 15A) 4
- Nine or ten supralabials (rarely 11 or 12), generally the sixth is in contact with the eye (Fig. 14B); posterior pair of chinshields sometimes separated by two rows of scales (Fig. 15B) 8
4. Maxillary teeth 11+3; dorsolateral lines normally present along the body or incomplete present only in the first third of body, lateral line normally present on third or fourth row of dorsal scales, or absent when the dorsolateral line is incomplete (populations from Guerrero, Oaxaca or south of Puebla) 5

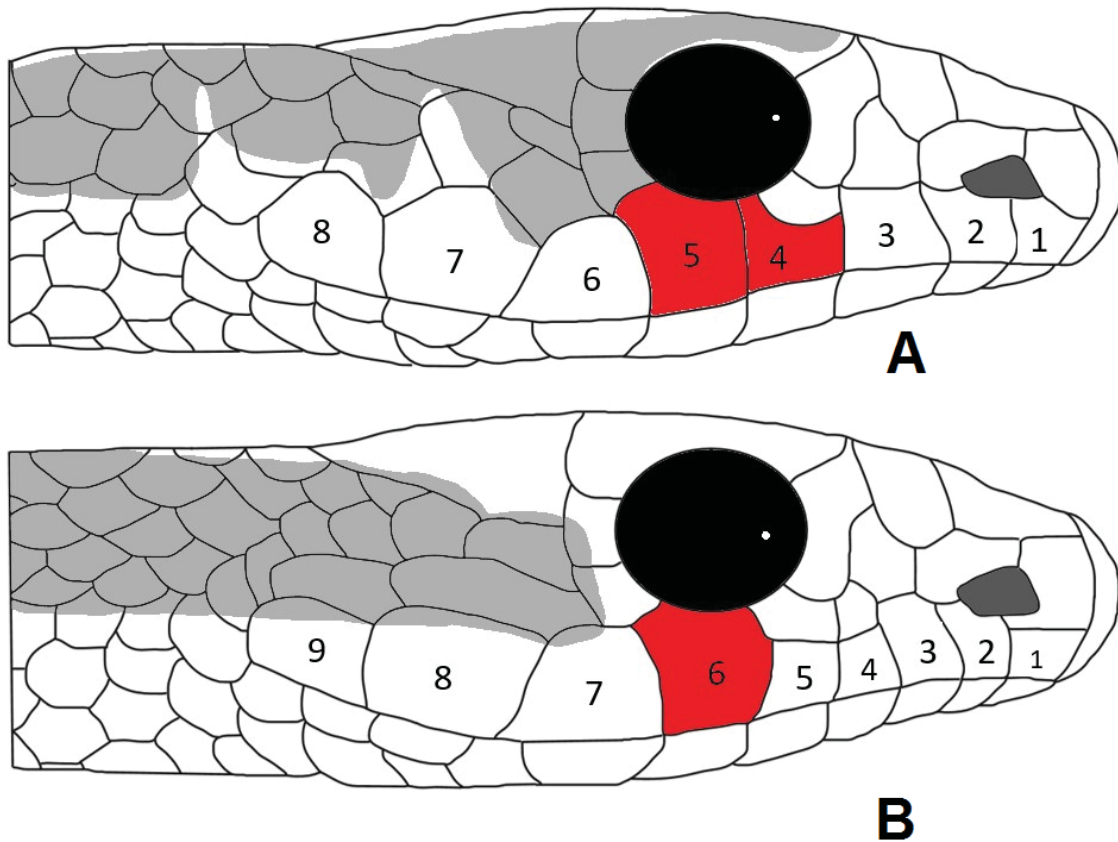


Fig. 14. A. Supralabials fourth and fifth in contact with the eye. B. Sixth supralabial in contact with the eye.

- Maxillary teeth 9+3 or 10+3; dorsolateral line always present; lateral line well defined on the third or fourth row of dorsal scales, or vestigial or absent..... 6
- 5. Dorsolateral lines present along the entire body; a light, yellowish vertebral line; lateral lines always present; tail length 23 to 30 % of total body length*S. intermedia* Hartweg, 1940
- Dorsolateral lines absent on the second and last third of the body; no lateral lines on body; tail length is 19 to 21 % of total length.....
..... *S. gymnorhachis* Hernández-Jiménez, Flores-Villela & Campbell, 2019
- 6. Maxillary teeth 9+3; vertebral line normally separated from the parietal region by a patch formed by the fusion of the dorsolateral lines (Fig. 16A); dorsolateral lines do not reach the temporal region; vertebral line three scale rows wide on the first and second third of the body (sometimes interrupted by dark blotches), and one row wide on the last third; lateral line well defined and separated from the dorsolateral line the entire length of the body *S. bairdi* Jan & Sordelli, 1860
- Maxillary teeth 10+3; vertebral line reaching the parietal region (Fig. 16B); dorsolateral lines pass through the temporal region to the eye; vertebral line from three to five rows wide on the first third of the body, and three rows wide on the second and last third of the body; lateral line present, vestigial or barely discernible, or may be absent in some specimens 7

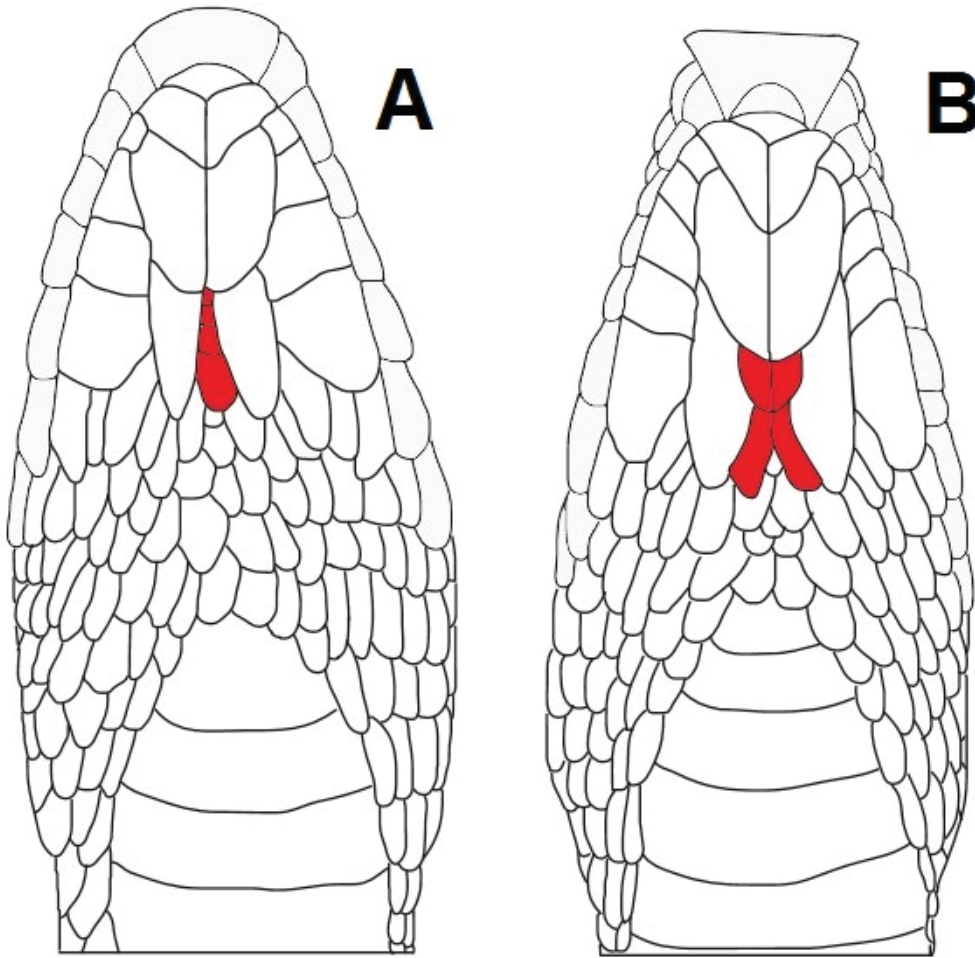


Fig. 15. **A.** Second pair of chinshields separated by one row of scales. **B.** Second pair of chinshields separated by two rows of scales.

7. Lateral line absent, vestigial, or scarcely discernible (Fig. 17A)
*S. grahamiae* Baird & Girard, 1853
 – Lateral line always present and well defined (Fig. 17B)*S. lineata* Schmidt, 1940
8. Loreal scale normally single (Fig. 18A); vertebral line five rows wide on the first third of body; lateral line well defined, largely restricted to adjoining margins of scales in third and fourth rows, clearly separated from the dorsolateral line on the second and last thirds of body; 68 to 86 subcaudals.....*S. deserticola* Schmidt, 1940
 – Loreal normally divided (Fig. 18B); vertebral line generally 3 rows wide, sometimes more; lateral line ill-defined or well-defined but fused or feebly separated from the dorsolateral lines; 75 to 103 subcaudals..... 9
9. Vertebral line yellowish in color, no more than three scale rows in width along the entire body; dorsolateral lines brown fused with the lateral lines in the anterior part of body but feebly separated posteriorly, generally without subocular scales, overall appearance brown.....
 *S. h. virgultea* Bogert, 1935

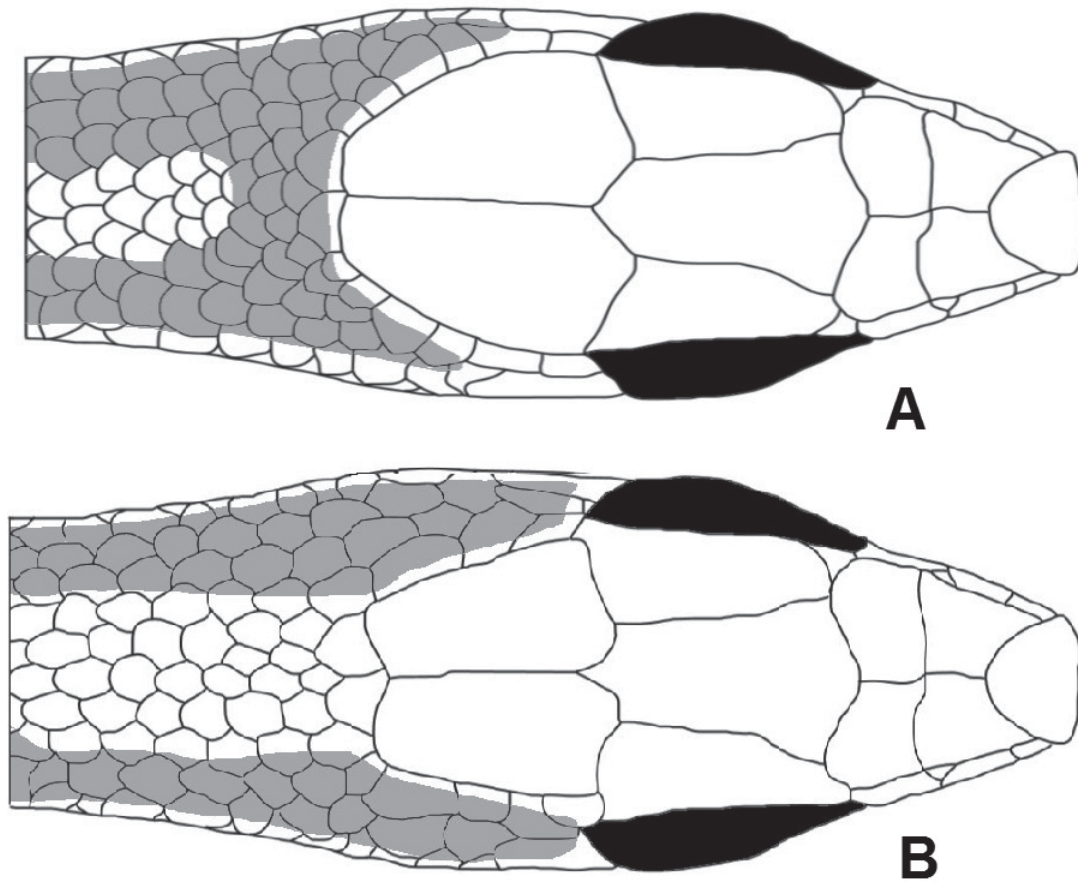


Fig. 16. A. Vertebral line normally separated from the parietal region. B. Vertebral line reaching the parietal region.

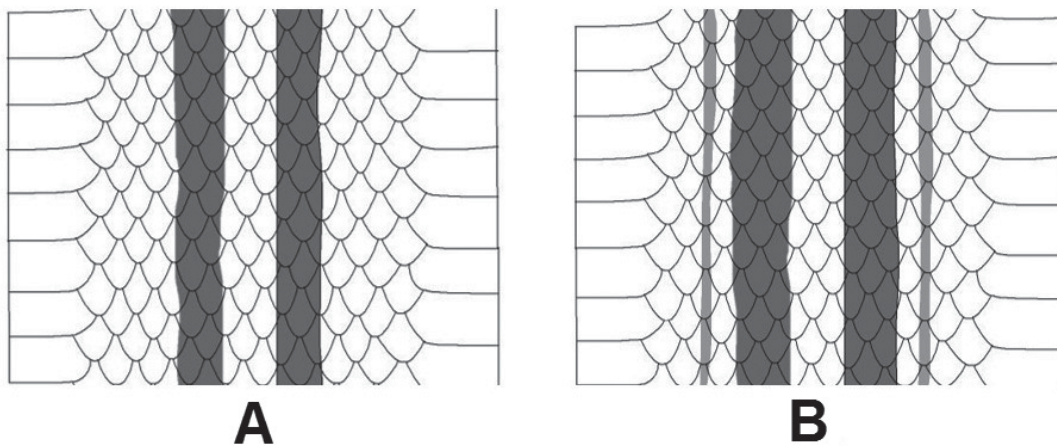


Fig. 17. A. Lateral line absent. B. Lateral line always present and well defined.

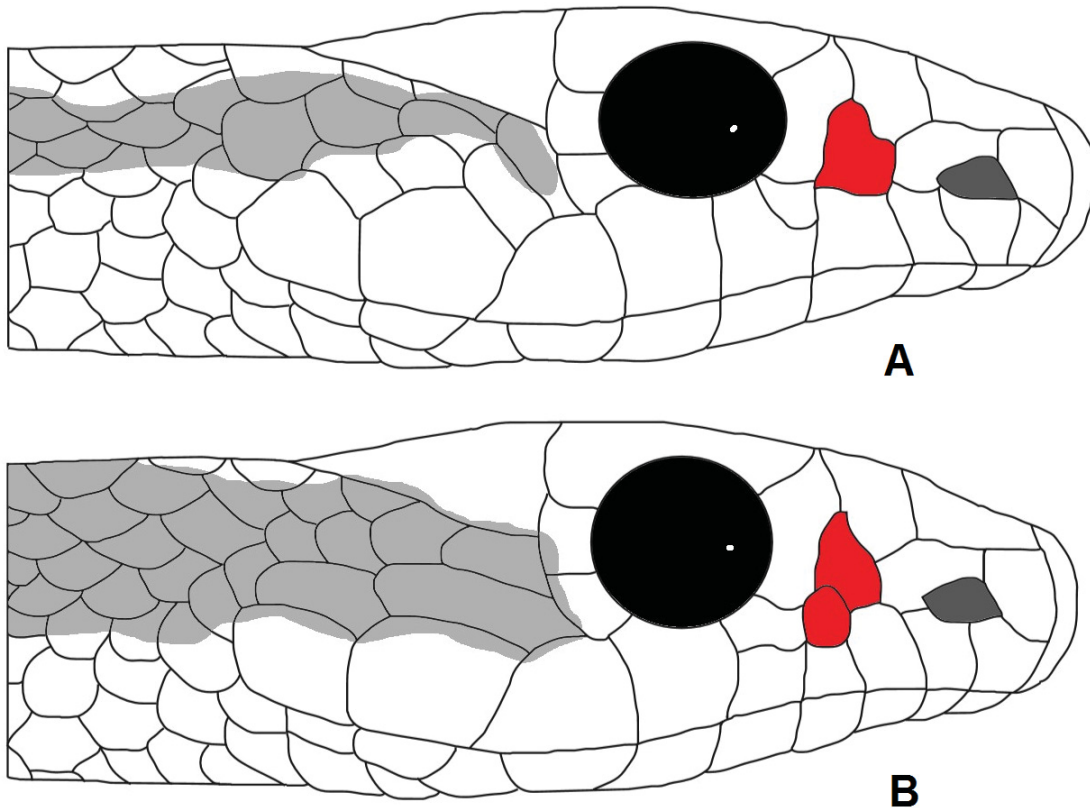


Fig. 18. **A.** Loreal scale single. **B.** Loreal normally divided.

- Vertebral line light grey in color, more than three rows wide (3 to 7) on the first third of the body; dorsolateral lines brown or grey in color, and four rows wide on the first third of the body, three rows wide in the second and one row wide on the last third of the body, and regularly separated or slightly separated from the lateral lines, with or without subocular scales 10
- 10. Normally two supralabials reaching the eye (Fig. 19A); 12+3 maxillary teeth *S. h. klauberi* Bogert, 1945
- Fewer than two supralabial reaching the eye (Fig. 19B); 10 or 11+3 maxillary teeth 11
- 11. Supralabials normally separated from the eye by the presence of two or more subocular scales (Fig. 20A); 10–11 infralabial scales; 11+3 maxillary teeth; sometimes with an irregular pattern of bars running the length of the body that interrupt the dorsolateral and lateral lines *S. h. mojavenis* Bogert, 1945
- One supralabial in contact with the eye (Fig. 20B); normally without suboculars or when present there is only one; normally 10 infralabials; 10+3 maxillary teeth; vertebral line three scales in width; dorsolateral line nearly gray, often irregularly pigmented, and obscurely separated from lateral line anteriorly, over-all appearance gray *S. h. hexalepis* (Cope, 1866)

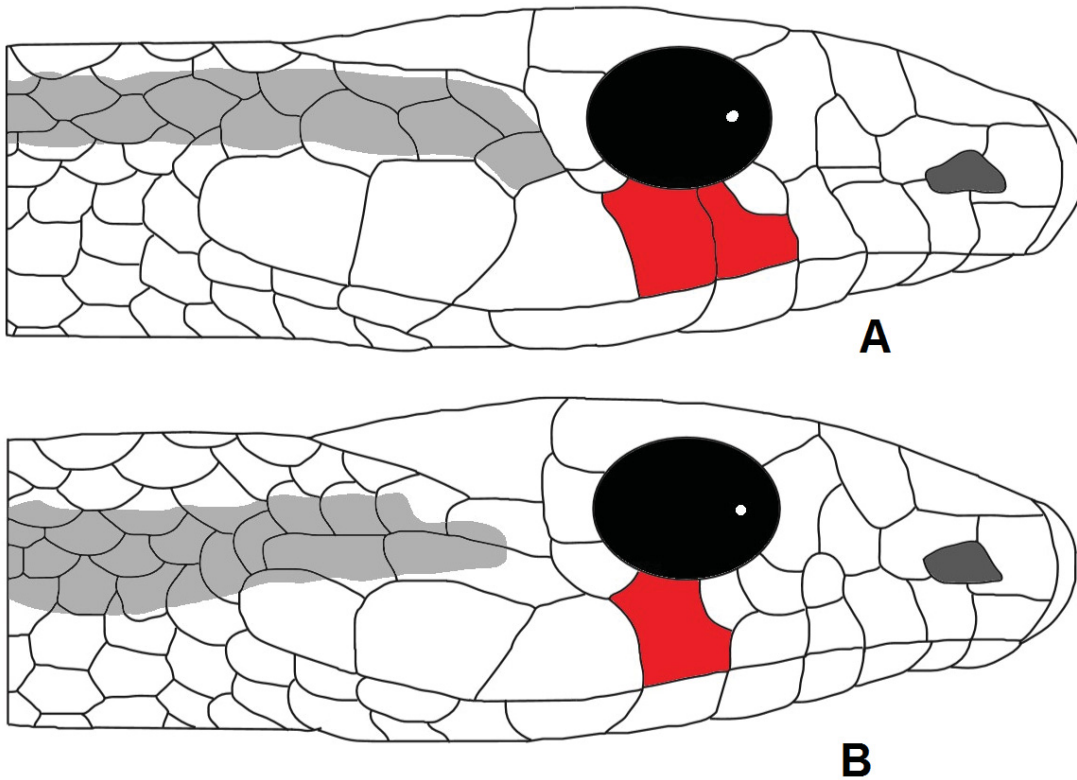


Fig. 19. A. Two supralabials reaching the eye. B. Fewer than two supralabials reaching the eye.

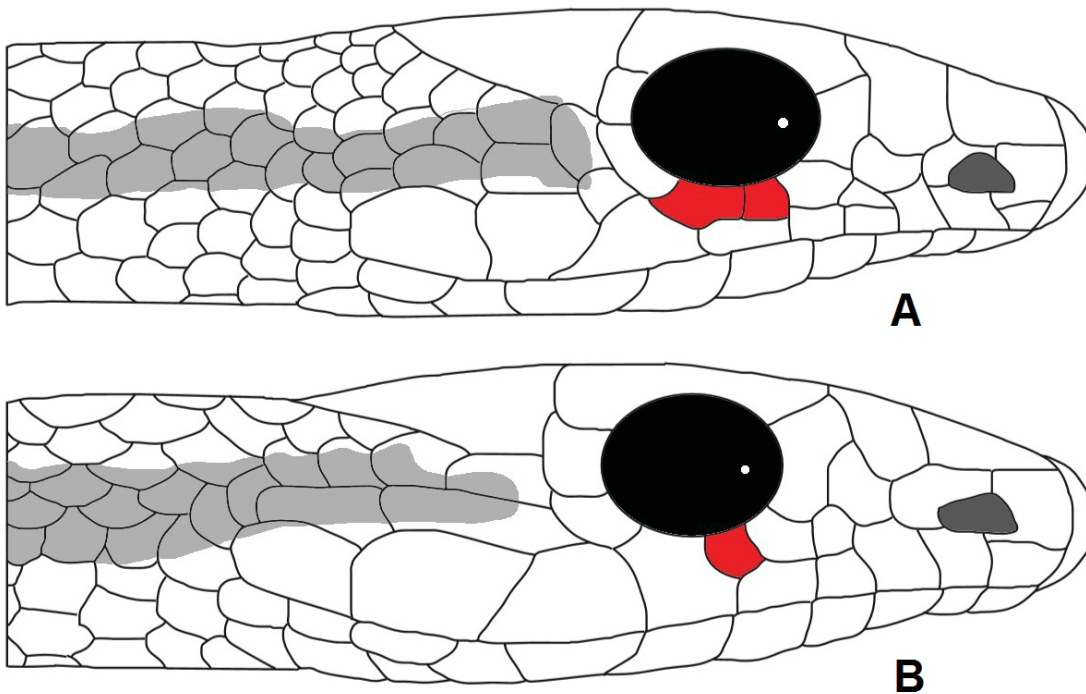


Fig. 20. A. Two or more subocular scales. B. One supralabial in contact with the eye.

Discussion

The genus *Salvadora* is a monophyletic group supported by several morphological synapomorphies, including enlarged rostral (usually with free edges), partially intervening between internasals; dorsal scales 17-17-13; and dorsolateral lines on at least one-third of body. Lannutti (2000) in an unpublished thesis reported a monophyletic *Salvadora*, including the genus *Leptodrymus*. Lannutti (2000) used a different set of morphological characters and in his analyses used gap weighing as proposed by Thiele (1993). We also use the method of Thiele, but polymorphic characters were subjected to splitting into bins, as suggested by Wiens (1995). We used Fast Morphology (Smith & Gutberlet 2001), which incorporates as much variation as possible in polymorphic characters and analyzed them in a way to allow a parsimony algorithm to improve the results giving a workable hypothesis of relationships. Our results agree with those of the molecular hypothesis proposed by Hernández-Jiménez *et al.* (2019), which recovered *Salvadora* as monophyletic. However, in the molecular based phylogenies of Figueroa *et al.* (2016) and Tonini *et al.* (2016), *Salvadora* does not appear as a monophyletic group, though their phylogenies did not include all the species of the group.

The phylogeny presented here found *Leptodrymus* to be a sister taxon to *Salvadora*, placed at the base of the monophyletic *Salvadora*. Our preliminary molecular data show *Leptodrymus* in a separate clade from that of *Salvadora* in agreement with the phylogenetic hypothesis of Tonini *et al.* (2016). Bogert (1947) proposed *Salvadora* and *Leptodrymus* as separate genera in his investigation of the relationships of *Leptodrymus* with other colubrid genera. Based on our analysis, we maintain *L. pulcherrimus* separate from *Salvadora*. Some of the characters that place *Leptodrymus* close to *Salvadora* may be convergent, such as the enlarged rostral and the pattern of longitudinal lines on the dorsum. Even with these characters, *Leptodrymus* does not fall in the ingroup with *Salvadora*, as occurred in the analysis of Lannutti (2000).

Our morphological cladogram supports the two groups that Smith (1938, 1941) suggested exist within the genus. These were also corroborated in the molecular phylogeny by Hernández-Jiménez *et al.* (2019) placed *S. mexicana* at the base of the phylogeny, being the sister taxon of *grahamiae* group taxa. The *S. mexicana* group is defined by a single preocular; three supralabials contacting eye (4th, 5th and 6th); maxillary teeth 14 to 15+3; between 120 and 150 subcaudals; tail size in proportion to body size (>29%); vertebral line at midbody one scale wide; and dorsolateral lines wider in the second third of body (3 scales wide). Our hypothesis of relationships among taxa within the *mexicana* and *grahamiae* groups differs from that proposed by Smith (1938, 1941).

Species in the *S. grahamiae* group share the following characters: divided preocular; supralabials, when contacting the eye, no more than two, or separate from the eye by suboculars (*S. hexalepis* subsp.); maxillary teeth < 13+3; less than 120 subcaudals; tail size in proportion to body size (<29%); vertebral line at midbody three scale wide, very rarely narrow in some specimens of *S. intermedia*; and dorsolateral lines narrow along body (2 or less scales wide).

The polytypic taxon *Salvadora hexalepis*, with four subspecies, was not recovered as a monophyletic clade. In our phylogeny, *S. h. klauberi* and *S. h. virgultea* are sister taxa, and *S. grahamiae* is sister to these two subspecies. Both subspecies of *S. hexalepis* are distributed in the westernmost part of the distributional range of the genus. *Salvadora h. mojaviensis* is a sister taxon of *S. h. hexalepis* and both are sister taxa with *S. deserticola*, all of which are distributed in southeastern California, southern Nevada and southwestern Arizona. Both clades mentioned above are parapatric, one in the extreme west, and the other more inland to the east. The previous molecular phylogeny by Hernández-Jiménez *et al.* (2019) did not include all the subspecies of *S. hexalepis*, therefore it is not possible to compare our results at this level. Nevertheless, the *S. hexalepis* group is the sister group of *S. deserticola* under both hypotheses.

Hartweg (1940) was curious about the relationship between *S. intermedia* and *S. bairdi*, as well as the relationship of these two species with *S. lineata*. In our phylogeny, these three taxa form a monophyletic sister group to *S. gymnorhachis*, though in the previous molecular phylogeny (Hernández-Jiménez *et al.* 2019), *S. gymnorhachis* is the sister taxon of *S. intermedia*, and *S. bairdi* appears as a sister taxon of *S. grahamiae*.

Smith (1938) suggested that *S. bairdi* and *S. grahamiae* are closely related, if considering several characters of cephalic squamation. Our results show these two taxa in different clades of the *S. grahamiae* group. Nevertheless, *S. bairdi* is more closely related to *S. lineata* as suggested by Schmidt (1940).

The clade formed by *S. grahamiae* and the subspecies of *S. hexalepis* and *S. deserticola* is characterized by taxa that have the vertebral line wider on the first third of the body (up to 5 scales) and usually with 9 supralabials, with at least one in contact with the eye. Schmidt (1940) proposed that the population of *S. grahamiae* from western Texas was most closely related to *S. h. hexalepis* from Arizona and may represent an undescribed taxon. We examined specimens from both regions and found no significant differences between them.

We conclude that the genus *Salvadora* is composed of 9 species, one of them polytypic (*S. hexalepis* with four subspecies). We support the suggestion of Davis & Dixon (1957) that *S. i. richardi* is not a valid taxon and, therefore, no subspecies are recognized for this taxon.

Owing to the lack of diagnostic characters, and the confusion regarding the type locality, we conclude that *S. bogerti* (Smith 1941) is a junior synonym of *S. bairdi*. Due to morphological differences (see above under *S. grahamiae*) and the phylogenetic position of the two subspecies of *S. grahamiae* (see Fig. 2), we elevate these subspecies to the status of species, a conclusion that is supported by our preliminary molecular data and an unpublished thesis by Lannutti (2000).

Regarding *Salvadora hexalepis* and its subspecies, our morphological data indicate this taxon is non-monophyletic; however, our preliminary molecular data and the placement of these taxa in Fig. 1 do not agree. We will refrain from suggesting any taxonomic change until more evidence has been published.

This is the first phylogenetic study of the snake genus *Salvadora* that includes all described taxa. We confirm the existence of two subclades corresponding with the two groups within the genus, a southern *mexicana* group and a northern *grahamiae* group. The monophyly of *Salvadora* is supported by several morphological synapomorphies. This genus is part of the Old Northern biogeographic element of Savage (1982), having its southern distribution limit in western Guatemala, but its greatest diversification is associated with the North American deserts. The majority of the taxa are part of the *S. grahamiae* group or the northern clade of *Salvadora*. Clarification of the relationship of *Salvadora* with the genus *Leptodymus* will require additional molecular information.

Prior to our study, there were other incomplete molecular phylogenies that did not include all the taxa described, at the level of species and subspecies or employ the widespread geographic sampling of each taxon. The phylogeny and revision of the alpha taxonomy of the group, that we present here, represents the first hypothesis that includes all the taxa described in the group and a detailed revision of its alpha taxonomy throughout its entire distributional range, and provides an extra line of evidence for understanding the taxonomic situation of the genus *Salvadora*. The evidence from morphological phylogeny analyses corroborates most of the clades in our hypothesis based on previously published molecular data. We think that it is necessary to complement this information at the molecular level with a more extensive sampling that includes several populations and all the taxa described in the group.

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The authors declare that they have no potential conflicts of interest.

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Supp. file 1. Specimens and character matrix used for phylogenetic reconstruction.

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