



Kingsnakes related to *Lampropeltis mexicana* have had a confusing taxonomic history, with various authorities recognizing anywhere from two to five species. This uncertainty stems from poorly known ranges, relatively few specimens in scientific collections, and extensive color pattern variation. In the following contribution, the authors present new distributional data, review the taxonomic and nomenclatural history of this group, and provide taxonomic recommendations. © Robert W. Hansen



Distribution analysis, taxonomic updates, and conservation status of the *Lampropeltis mexicana* group (Serpentes: Colubridae)

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ABSTRACT: We provide updated distributional information for species of the *Lampropeltis mexicana* group, an assemblage of colorful snakes occurring throughout northern Mexico and the southwestern United States. We generated point locality maps based on 685 records supported by vouchered specimens. The ranges of constituent species are characterized by allopatry, although some species pairs are nearly parapatric. In light of our improved knowledge of the distribution of these taxa, we review the historical taxonomy of the *mexicana* group, provide partial synonymies, and present morphology-based diagnoses for each species. We recognize six species as accurately reflecting biodiversity. The conservation status of each of these species is reviewed in the context of new distributional data and in consideration of our revised taxonomy. We identify range gaps as important targets for future surveys.

Key Words: Snake, *Lampropeltis alterna*, *Lampropeltis greeri*, *Lampropeltis leonis*, *Lampropeltis mexicana*, *Lampropeltis ruthveni*, *Lampropeltis webbi*

RESUMEN: Proporcionamos distribuciones actualizadas de especies del grupo *Lampropeltis mexicana*, un ensamblaje de especies coloridas que se distribuye en el norte de México y el suroeste de Estados Unidos. Generamos mapas con localidades específicas basados en 685 registros de especímenes colectados y depositados. Los rangos de distribución de las especies constituyentes se caracterizan por alopatria, aunque algunos pares de especies son casi parapátricos. A la luz de nuestro conocimiento ampliado de distribución estos taxones, revisamos la taxonomía histórica del grupo *mexicana*, proporcionamos sinonimias parciales y presentamos diagnósticos basados en la morfología para cada especie. Reconocemos que seis especies reflejan efectivamente una biodiversidad. El estatus de conservación de cada especie es revisado en el contexto de nuevos datos de distribución y en consideración de nuestra taxonomía revisada. Identificamos los vacíos en los rangos de distribución como objetivos importantes para el trabajo de campo en el futuro.

Palabras Claves: Culebra, *Lampropeltis alterna*, *Lampropeltis greeri*, *Lampropeltis leonis*, *Lampropeltis mexicana*, *Lampropeltis ruthveni*, *Lampropeltis webbi*

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INTRODUCTION

Snakes of the *Lampropeltis mexicana* group are distributed in northern and central Mexico and the southwestern United States. Collectively, these colorful snakes have attracted a good deal of attention both from herpetologists and amateur naturalists (Garstka, 1982; Tennant, 1984; Hilken and Schlepper, 1998; Dearth, 2002; Merker and Merker, 2005; Greene, 2013). Although treated historically as a monophyletic group or clade (Garstka, 1982; Hilken and Schlepper, 1998), recent molecular studies suggest that some species (e.g., *L. alterna*) may be more closely related to *L. triangulum* (*sensu lato*), or to the *L. pyromelana* and *L. zonata* clades (Bryson et al., 2007; Ruane et al., 2014; Figueroa et al., 2016; Chen et al., 2017). Nonetheless, most researchers have assigned the following four species to the *mexicana* group: *L. alterna* (Brown, 1902), *L. mexicana* (Garman, 1884), *L. ruthveni* Blanchard, 1920, and *L. webbi* Bryson, Dixon, and Lazcano, 2005. Although we refer to the “*mexicana* group” throughout this paper, we acknowledge the strong possibility of its polyphyletic nature.

Our goals were to (1) provide updated distributions for each of the species in this group, as well as to characterize their habitats; (2) review the historical taxonomy; (3) evaluate the conservation status for all species; and (4) recommend directions for future fieldwork.

METHODS

We obtained locality data for specimens from institutional collections (listed in the Acknowledgments), published records, and our field records and those of our associates (Appendix 1). We did not include “sight records” that lacked photographic vouchers. We obtained geocoordinates using hand-held GPS units or Google Earth. Unless otherwise indicated, the institutional collection acronyms follow Sabaj (2016). In referring to museum-based records where distances originally were reported in miles (rather than km), we retained the verbatim descriptions to maintain historical accuracy. We use the acronym “DOR” to refer to specimens found dead on road.

In some cases, the georeferenced data we used differed from the coordinates associated with museum records. This situation typically occurred with specimens georeferenced post-collection (in some cases, decades later), usually by a museum worker taking a best estimate of the collection locality. Consequently, some of the georeferenced data associated with museum specimens were highly inaccurate. In instances where we substituted our own coordinates, we did so after examining the original collector’s field notes, personal communication from the collector, or personal knowledge of the collection site. Unless otherwise stated, all coordinates are based on map datum WGS 84. Our distribution maps include point-locality dots as well as outlining to reflect our estimates of overall range based on extrapolation from known records, biogeography, distribution of appropriate habitat, and ground knowledge.

For most localities, we determined habitat information from site photographs. We obtained these from several sources, including publications, field photos, and images downloaded from Google Maps Street View (these were particularly appropriate for specimens obtained on or adjacent to roads).

In describing collection sites, we included the country name (United States or Mexico) with first use of each state name, but not thereafter. We included an accent mark for the state of México but not for the country name Mexico.

MEXICANA GROUP DISTRIBUTION

Collectively, species of the *mexicana* group (Garstka, 1982; Bryson et al., 2007) are known to occur from 19.67°N to 25.03°N, and from 99.19°W to 105.55°W (Fig. 1). Species in this complex have been recorded from 15 states in Mexico and from two in the United States (Table 1), and their distribution spans eight biogeographic formations (Table 2). The species occur in diverse (but rocky) habitats, ranging from arid desert to humid pine-oak forest at elevations from 384 to 2,667 m. These snakes are not commonly observed on the surface, but typically require active searching by turning ground cover, examining rock crevices, or by driving roads and searching rock faces at night. In the accounts that follow, we recognize six species (*alterna*, *greeri*, *leonis*, *mexicana*, *ruthveni*, and *webbi*) and discuss our rationale for this arrangement under Taxonomic Accounts.



Fig. 1. Generalized map of the collective range of the *Lampropeltis mexicana* group in Mexico and the United States.

Table 1. State distribution of species of the <i>Lampropeltis mexicana</i> group.						
	<i>alterna</i>	<i>greeri</i>	<i>leonis</i>	<i>mexicana</i>	<i>ruthveni</i>	<i>webbi</i>
Mexico						
Aguascalientes		X		X		
Coahuila	X		X			
Durango	X	X				X
Guanajuato				X	X	
Hidalgo				X	X	
Jalisco		X			X	
México				X		
Michoacán					X	
Nayarit		X				
Nuevo León	X		X			
Querétaro					X	
San Luis Potosí				X		

Sinaloa						X
Tamaulipas			X	?		
Zacatecas		X				
United States						
New Mexico	X					
Texas	X					

Table 2. Distribution of species of the *Lampropeltis mexicana* group according to Biogeographic Formations delineated by Grünwald et al. (2015). Abbreviations: CD = Chihuahuan Desert; CSMO = Central Sierra Madre Occidental; CP = Central Plateau; WCP = Western Central Plateau; SSMO = Southern Sierra Madre Occidental; NSMO = Northern Sierra Madre Oriental; PSMO = Potosí Sierra Madre Oriental; and ECP = Eastern Central Plateau.

	CD	CSMO	SSMO	WCP	CP	ECP	NSMO	PSMO
<i>L. alterna</i>	X	X						
<i>L. greeri</i>		X	X		X			
<i>L. leonis</i>							X	
<i>L. mexicana</i>	X				X	X		X
<i>L. ruthveni</i>				X	X			
<i>L. webbi</i>		X						

Lampropeltis alterna

Lampropeltis alterna occurs in New Mexico and Texas in the southwestern United States, and Coahuila, Durango, and Nuevo León in Mexico, at latitudes ranging from 25.03 to 32.11°N. Although suitable habitat is present in the Mexican states of Chihuahua and Zacatecas, the species remains unrecorded there (but see Carabias Lillo et al., 1997). We obtained 469 valid distribution records for *L. alterna* representing 401 unique localities (Fig. 2). A large majority of these (90%) were from the United States, and mostly centered in the eastern part of the species' range in Texas. For example, 174 (41%) of 424 Texas records are from Val Verde County (Table 3). Historically this area has received greater attention from collectors, and *L. alterna* may be more abundant here in the eastern, more humid part of its Texas range. Only 41 records are available for the entirety of Mexico, despite the fact that most of the range of this species likely occurs in that country (Fig. 2).

Published sources of distributional information on *L. alterna*, including discussions of biogeography, are found in the following publications: Smith (1941), Schmidt and Owens (1944), Smith and Buechner (1947), Jameson and Flury (1949), Mecham and Milstead (1949), Flury (1950), Milstead et al. (1950), Smith and Taylor (1950), Axtell (1951), Wright and Wright (1957), Degenhardt and Milstead (1959), Axtell (1959), Gehlbach and Baker (1962), Gehlbach and McCoy (1965), Scudday (1965), Gehlbach (1967), Olson (1973), Worthington and Arvizo (1974), Easterla (1975), Worthington (1976), Morafka (1977), Axtell (1978), Mecham (1978), Miller (1979), Garstka (1982), McCoy (1984), Dixon (1987), Painter et al. (1992), Hakkila (1994), Degenhardt et al. (1996), Carabias Lillo et al. (1997), Hilken and Schlepper (1998), Tennant et al. (1998), Werler and Dixon (2000), Painter et al. (2002), Hibbitts et al. (2003), Salmon et al. (2004), Gadsden et al. (2006), Lemos-Espinal and Smith (2007), Ingrasci et al. (2008), Lazcano et al. (2009), Lavín-Murcio and Lazcano (2010), Lazcano et al. (2010), Couvillon (2011), Castañeda-Gaytán et al. (2012), Lazcano et al. (2012), Price et al. (2012), Rhoads and Salmon (2012), Dixon (2013), Prival and Goode (2014), Ochoa-Ochoa et al. (2014), Lemos-Espinal and Smith (2015b), Lemos-Espinal and Cruz (2015), Lemos-Espinal et al. (2015), Painter and Stuart (2015), Dixon (2015), Contreras-Lozano et al. (2015), Price and Dimler (2015), Heimes (2016), Latella et al. (2016), Nevárez-de los Reyes et al. (2016a), and Nevárez-de los Reyes et al. (2016b). In mapping the Texas range of *alterna*, Dixon (2013) introduced errors not present in the earlier editions (1987, 2000) of his book: Upton County should have been included in the range, while Ward County mistakenly was marked with records of this species. Dixon (2013) also overlooked records for Crane County (Hibbitts et al., 2003) and Kinney County (SBMNH 197; TCWC 26179, mistakenly catalogued as Val Verde County). Dot

Table 3. Locality records for *Lampropeltis alterna* by county or municipality.

	No. of Records	No. of Unique Localities
Mexico (41)		
Coahuila (28)		
Castaños	6	1
Cuatro Ciénegas	9	6
Ramos Arizpe	11	8
Saltillo	1	1
Viesca	1	1
Durango (6)		
Lerdo	1	1
Rodeo	1	1
Santiago Papasquiaro	4	2
Nuevo León (7)		
Bustamante	2	1
García	1	1
Guadalupe	1	1
Hidalgo	1	1
Mina	1	1
Monterrey	1	1
United States (428)		
New Mexico (4)		
Eddy	3	3
Otero	1	1
Texas (424)		
Brewster	71	57
Crane	1	1
Crockett	5	5
Culberson	8	4
Edwards	3	3
El Paso	3	3
Hudspeth	8	5
Jeff Davis	40	38
Kinney	3	2
Pecos	12	11
Presidio	33	31
Reeves	1	1
Sutton	1	1
Terrell	54	41
Upton	7	3
Val Verde	174	164
Totals	469	401

maps in Lemos-Espinal and Smith (2007) and Lemos-Espinal et al. (2015) indicate a record for Municipio de Ocampo in northern Coahuila (corresponding to UF 24750 [J. Lemos-Espinal, pers. comm.]; 3.5 mi S of San Miguel, elev. 5,000 ft.). This specimen, however, actually was obtained ~380 km to the southeast in Municipio de Ramos Arizpe. The confusion derives from the fact that there are two towns named San Miguel in Coahuila. An examination of the collector's field notes on file at the Florida Museum of Natural History confirms the southern locality in Ramos Arizpe as the correct one. Additionally, a recent report of a first state record for Zacatecas is in error (Campos-Rodríguez et al., 2017).

The northernmost record of *L. alterna* is 2.2 mi. (by air) N of El Paso Gap, Guadalupe Mountains, Eddy County, New Mexico, United States (UTEP 18600; approximately 32.11817°N, 104.83617°W). The eastern range-margin populations include Cerro de la Silla, near Monterrey, Nuevo León, Mexico (UANL 5018; Salmon et al., 2004; 25.61520°N, 100.26348°W), Sierra Gomas W of Bustamante, Nuevo León (UANL 7672; 26.50245°N, 100.52622°W; Nevárez-de los Reyes et al., 2016b), Sierra El Fraile y San Miguel, Nuevo León (TNHC 100686; 25.94963°N, 100.47659°W; Nevárez-de los Reyes et al., 2016b), and Dunbar Cave, Edwards County, Texas (UMMZ 122688; Gehlbach and Baker, 1962; approximately 29.93955°N, 100.54049°W). The western range-margin records include the vicinity of Hueco Tanks, Hueco Mountains, El Paso County, Texas (UTEP 18912; 31.90779°N, 106.04831°W) and the eastern slope Sierra Madre Occidental northwest of Santiago Papasquiaro, Municipio de Santiago Papasquiaro, Durango (UTADC 1096; Ingrasci et al., 2008; approximately 25.087°N, 105.542°W). The southernmost record is from 5 mi. S of San Antonio, Durango (TCWC 36892; 25.03386°N, 104.47901°W; Garstka, 1982).

Lampropeltis alterna is closely associated with rocky terrain within the Chihuahuan Desert (Miller, 1979) and adjacent uplands, which include the Chisos, Davis, and Guadalupe mountains of Texas and New Mexico, the Sierra Madre Occidental of Durango, and northern outliers of the Sierra Madre Oriental of Nuevo León. Chihuahuan Desert collection sites in Texas are characterized by limestone or volcanic substrates and plant communities dominated by *Larrea tridentata* (Creosote),

Prosopis glandulosa (Honey Mesquite), *Agave lechuguilla* (Lechuguilla), Sotol (*Dasyllirion texanum*), and other spiny succulents (Merker and Merker, 2005; T. D. Hibbitts, pers. comm.). At higher elevations within Texas and New Mexico, collection sites are characterized by *Quercus* spp. (oaks), *Juniperus pinchotii* (Redberry Juniper), *Pinus remota* (Texas Pinyon Pine), and species of *Agave* (Merker and Merker, 2005) (Fig. 3).

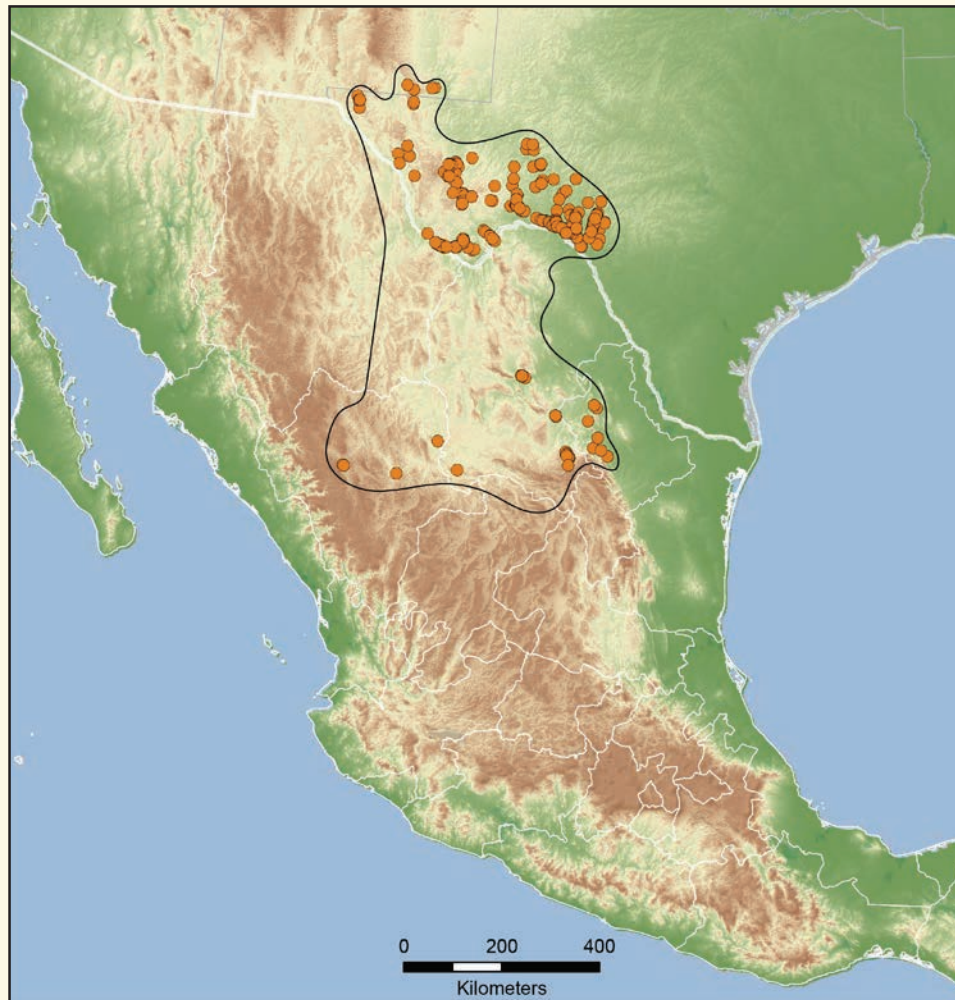


Fig. 2. Distribution map of *Lampropeltis alterna*.

In Mexico, *L. alterna* occurs in diverse rocky habitats ranging from arid *Larrea*-dominated landscapes in the Cuatro Ciénegas basin of Coahuila to a mix of Chihuahuan Desert and Tamaulipan Scrub at easternmost localities (e.g., vicinity of Monterrey, Nuevo León) (Fig. 4a–g). On the eastern flank of the Sierra Madre Occidental in western Durango, several specimens have come from rugged Madrean pine-oak woodland at high elevation (Ingrasci et al., 2008), perhaps the most unusual area occupied by this species (Fig. 4h). In the Sierra Gomas (a northeastern outlier of the Sierra Madre Oriental, Nuevo León), the habitat consists of steep, rocky, and heavily vegetated slopes; characteristic plant species here include *Populus nigra*, *Salix* sp., *Prosopis glandulosa*, *Acacia farnesiana*, *A. rigida*, *Fraxinus greggii*, and *Helietta parvifolia* (Nevárez-de los Reyes et al., 2016b) (Fig. 4d).

Within the United States, the elevation ranges from 384 m near Del Rio, Kinney County, Texas (TCWC 26179) to 1,860 m in the Davis Mountains, Jeff Davis County, Texas (TNHC 100777). Most elevations are higher in Mexico, ranging from 521 m in the Sierra Gomas, Nuevo León (UANL 7662) and 786 m at Cuatro Ciénegas, Coahuila (TNHC 100776) to 2,311 m in the Sierra Madre Occidental, Durango (TNHC 100778).

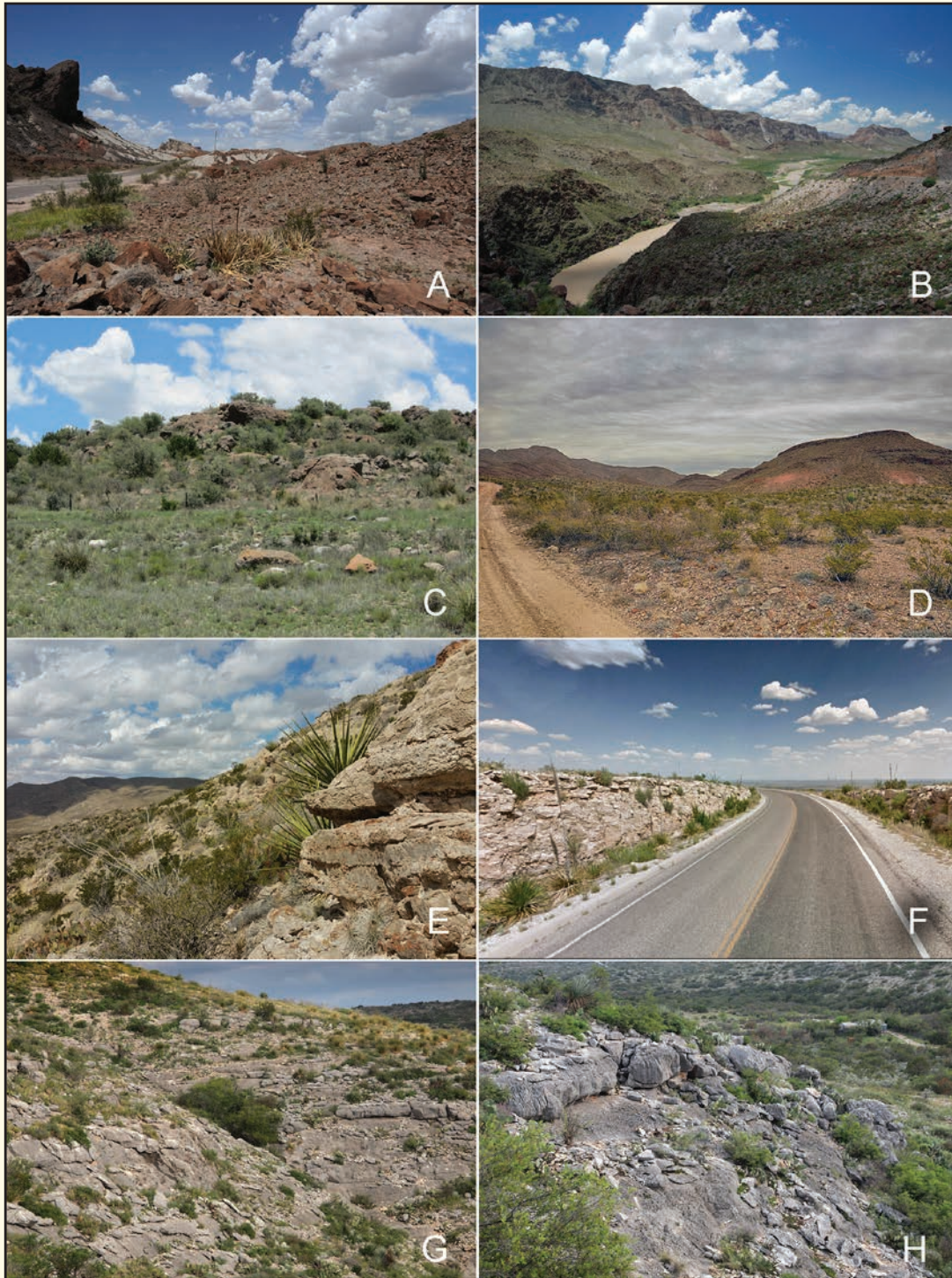


Fig. 3. Habitat of *Lampropeltis alterna* in Texas and New Mexico, United States. (A) Castolon Peak area, Big Bend National Park, Brewster County, Texas, elev. ~660 m, July of 2012; (B) Rio Grande (= Rio Bravo), from the United States side of the border with Coahuila, Mexico, along FM 170, Presidio County, Texas, elev. 865 m, June of 2009; (C) vicinity of Paisano Gap west of Alpine, Presidio County, Texas, elev. ~1,510 m, June of 2009; (D) Indio Mountains, Hudspeth County, Texas, elev. 1,224 m, December of 2015; (E) Hueco Mountains, Hudspeth County, Texas, elev. 1,316 m, March of 2015; (F) Carlsbad Caverns National Park, Eddy County, New Mexico, elev. 1,335 m, August of 2015; and (G, H) Devil's River drainage, Val Verde County, Texas, elev. 530 m, September of 2016.

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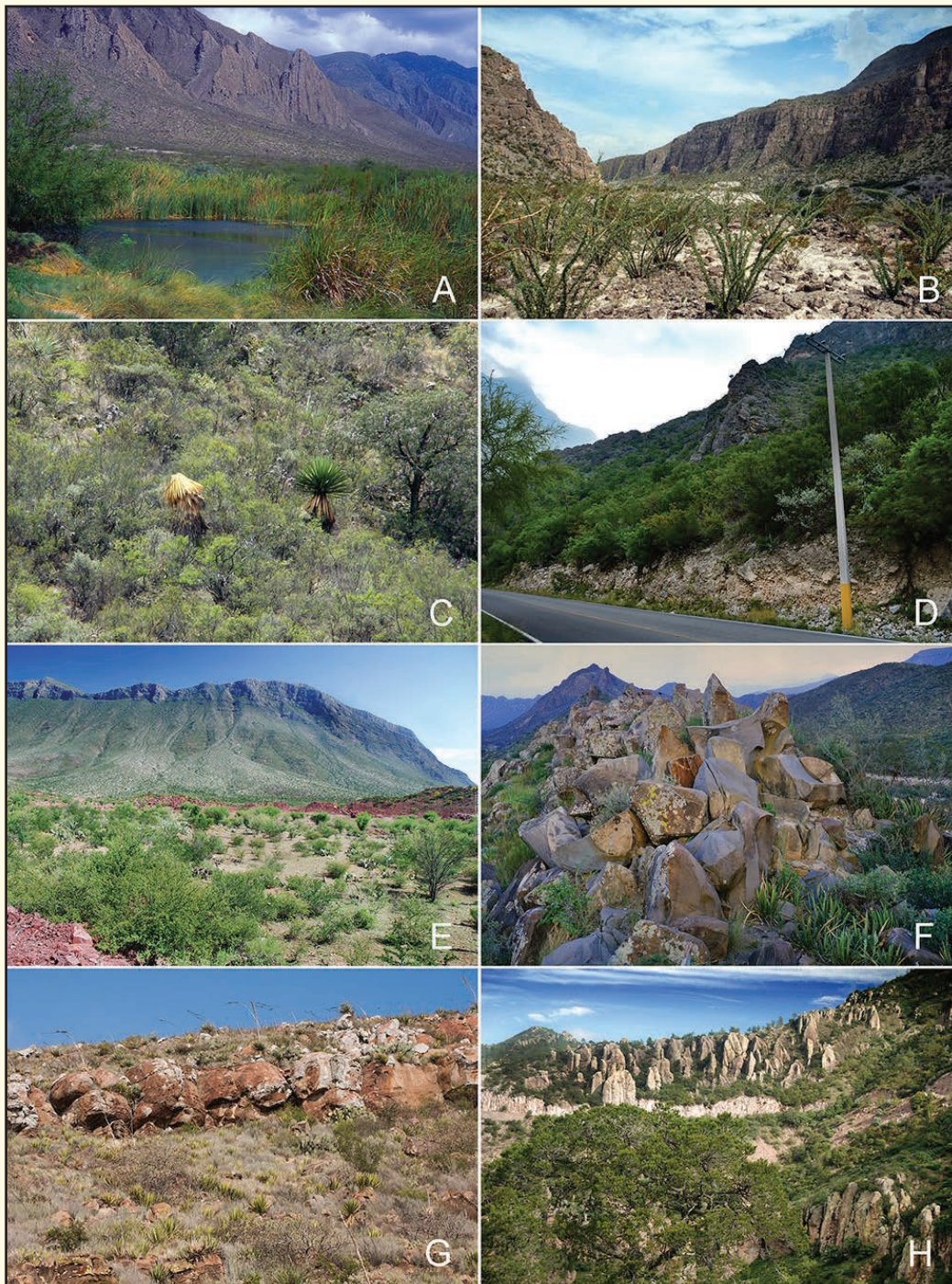


Fig. 4. Habitat of *Lampropeltis alterna* in Coahuila, Durango, and Nuevo León, Mexico. (A) Cuatro Ciénegas, Municipio de Cuatro Ciénegas, Coahuila, elev. ~810 m, July of 1996; (B) Cuatro Ciénegas, Municipio de Cuatro Ciénegas, Coahuila, elev. ~810 m, July of 2007; (C) Sierra de Jimulco, Municipio de Viesca, Coahuila, elev. 1,809 m, July of 2009; (D) Cañon de Bustamante, Sierra Gomas, Municipio de Bustamante, Nuevo León, elev. 521 m, May of 2016; (E) Sierra La Gavia, Municipio de Castaños, Coahuila, elev. ~1,300 m, July of 2008; (F) northwest of Ramos Arizpe, Municipio de Ramos Arizpe, Coahuila, elev. 1,200 m, September of 1985; (G) Sierra Pedernales, Municipio de Mina, Nuevo León, elev. 785 m, October of 2007; and (H) Sierra Madre Occidental northwest of Santiago Papasquiaro, Municipio de Santiago Papasquiaro, Durango, elev. 2,311 m, August of 2007.

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Lampropeltis greeri

Lampropeltis greeri is endemic to the southeastern versant of the Sierra Madre Occidental of Mexico, where it has been recorded from the states of Aguascalientes, Durango, Jalisco, Nayarit, and Zacatecas. We obtained 64 valid distribution records corresponding to 41 discrete localities for *L. greeri* (Fig. 5). Most records are from a small area of Durango, reflecting repeated field visits to the type locality (Webb, 1961) and the surrounding areas by herpetologists during the last four decades. More recent exploration has expanded the known range into the states of Aguascalientes (Quintero-Díaz et al., 2001), Jalisco (Hansen and Bryson, 2009), and Nayarit (Hansen et al., 2011). Chávez-Avila et al. (2015) erroneously removed this taxon (reported as *L. mexicana*) from the list of species occurring in Jalisco, apparently overlooking the report by Hansen and Bryson (2009). Published sources of distributional information concerning *L. greeri*, including discussions of biogeography, include Webb (1961), Gehlbach and Baker (1962), Gehlbach and McCoy (1965), Liner and Dundee (1977), Wilson and McCranie (1979), Garstka (1982), Webb (1984), McCranie and Wilson (1987), Liner (1996), Hilken and Schlepper (1998), Quintero-Díaz et al. (2001), McCranie and Wilson (2001), Hubbs (2004), Vázquez-Díaz and Quintero-Díaz (2005), Hansen and Bryson (2009), Savage and Hansen (2009), Ahumada-Carrillo et al. (2011), Hansen et al. (2011), Carbajal-Márquez and Quintero-Díaz (2014), Ahumada-Carrillo et al. (2014), Woolrich-Piña et al. (2016), Campos-Rodríguez et al. (2017), and Cruz-Sáenz et al. (2017).

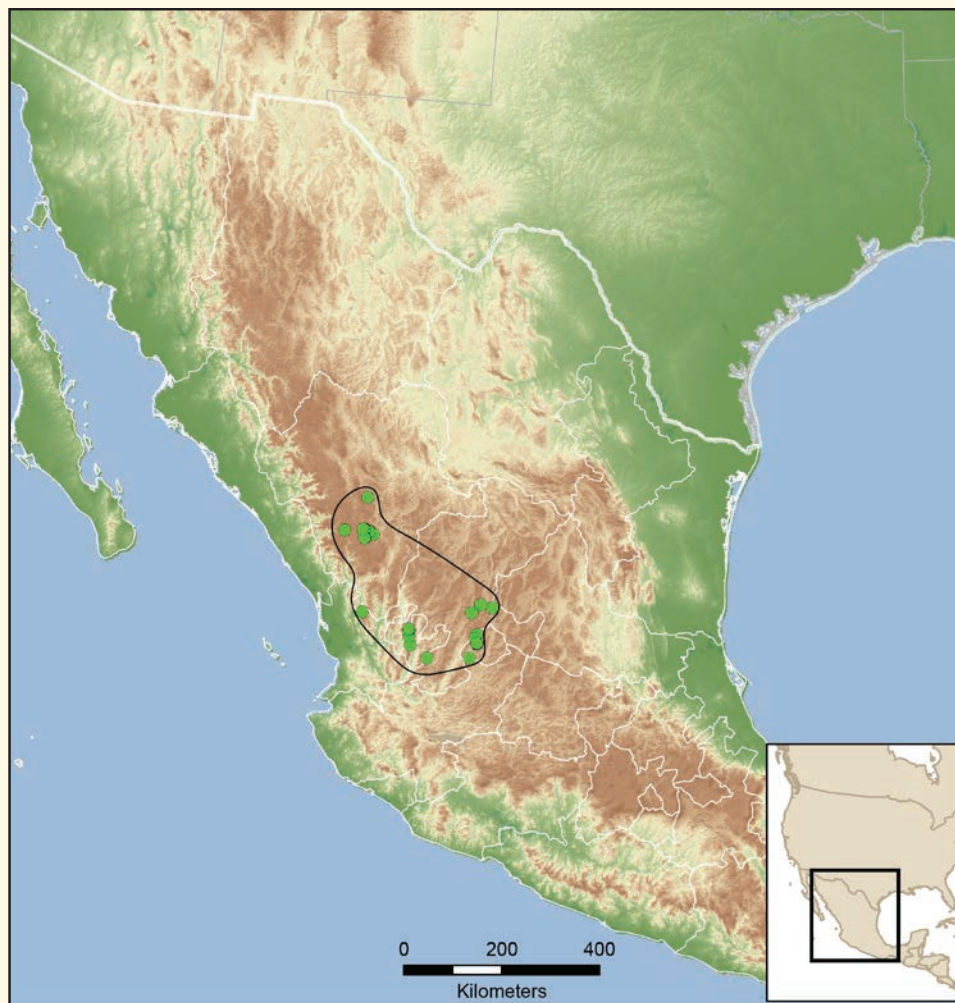


Fig. 5. Distribution map of *Lampropeltis greeri*.

The northernmost record of *L. greeri* is ~30 km (by air) WNW of Canatlán, Durango (UTADC 2599; Savage and Hansen, 2009; 24.58141°N, 104.93548°W). The range extends southward across the Sierra Madre Occidental into Nayarit, where *L. greeri* is known from a single locality at Mesa de Nayar (UTADC 6833–6835; Hansen et al., 2011; 22.42838°N, 104.84609°W).

East of the main north–south axis of the Sierra Madre Occidental, *L. greeri* occupies outlier ranges in Zacatecas (Cerro de la Virgen on southern margin of Cd. Zacatecas, TNHC 100779, approximately 22.74501°N, 102.55035°W; La Ciénega, MZFC 23706, 21.66683°N, 103.51244°W), Aguascalientes (Sierra Fría, UAA-CV-R263, approximately 22.18087°N, 102.58879°W, Carbajal-Márquez and Quintero-Díaz, 2014; vic. of Mesa Montoro, Quintero-Díaz et al., 2001, MZFC 13655), and Jalisco (Sierra del Laurel, 21.72980°N, 102.69890°W, Hansen and Bryson, 2009).



Fig. 6. Habitat of *Lampropeltis greeri* in Durango and Zacatecas, Mexico. (A, B) Rancho Santa Bárbara, Municipio de Durango, Durango, near type locality, elev. 2,260–2,360 m, August of 2003 and August of 2005; (C, D) Sierra Madre Occidental near Otinapa, Municipio de Durango, Durango, elev. 2,365 m, July of 2007; (E) Cerro de la Virgen, south side of Ciudad Zacatecas, Municipio de Guadalupe, Zacatecas, elev. 2,625 m, June of 2011; and (F) vicinity of La Ciénega, Municipio de Atolinga, Zacatecas, elev. 2,328 m, September of 2008.

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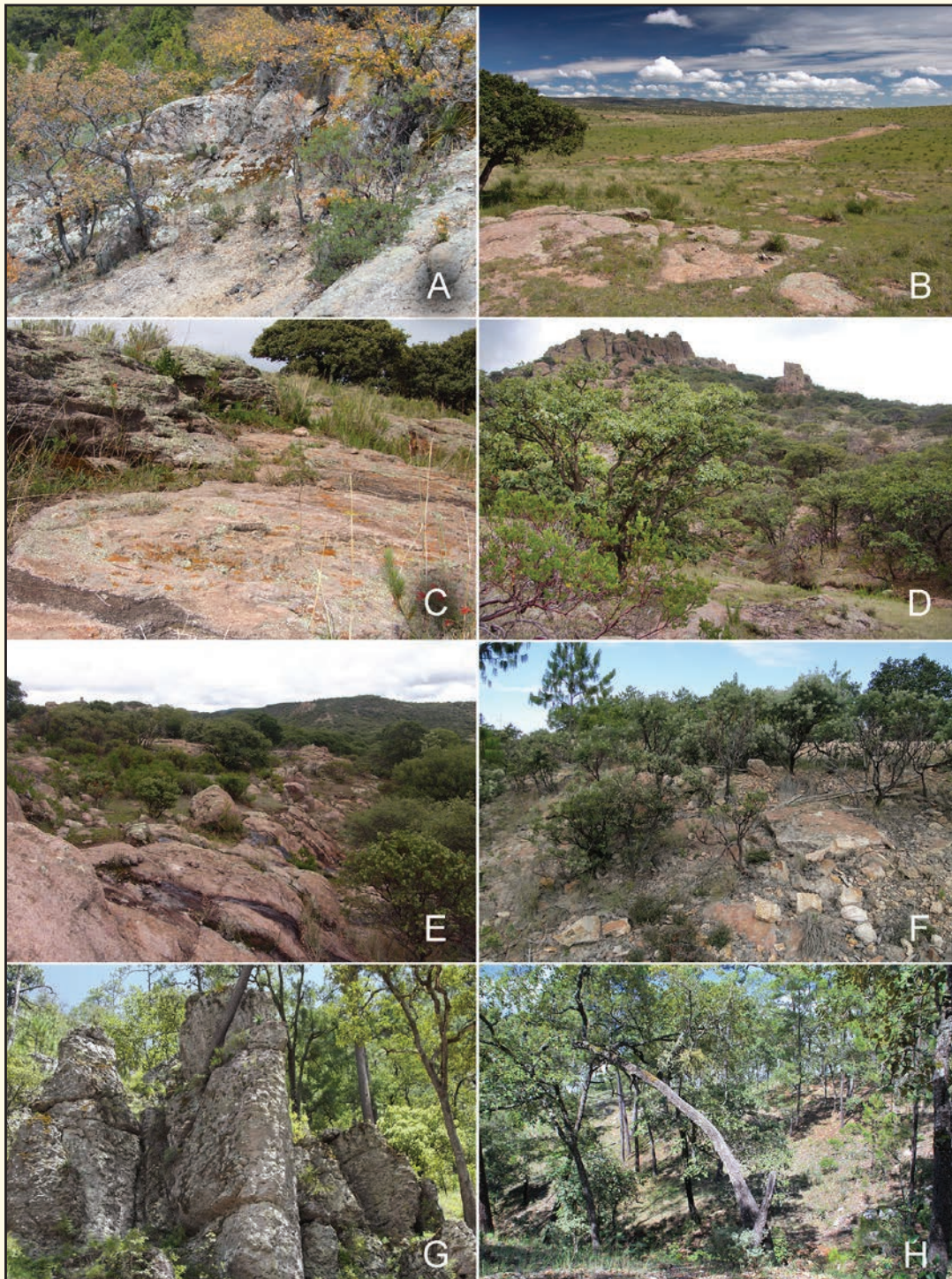


Fig. 7. Habitat of *Lampropeltis greeri* in Aguascalientes, Jalisco, and Nayarit, Mexico. (A) Sierra Fría, Municipio de San José de Gracia, Aguascalientes, elev. 2,350 m, April of 2015; (B, C) Mesa Montoro, Municipio de San José de Gracia, Aguascalientes, elev. 2,384 m, July of 2006; (D, E) Sierra del Laurel near La Ciénega, just south of border with Aguascalientes, Municipio de Villa Hidalgo, Jalisco, elev. 2,440 m, July of 2006. (F, G) Sierra de los Huicholes, vicinity of El Astillero, Municipio de Bolaños, Jalisco, elev. 2,300 m, July of 2011; and (H) Mesa de Nayar, Municipio de El Nayar, Nayarit, elev. 2,220 m, August of 2010.

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Over most of its range, *L. greeri* is closely associated with Madrean pine-oak woodland, with some regional variation, and almost always in association with rocks (Figs. 6, 7). In Durango, *L. greeri* occurs in rock outcroppings within pine-oak woodland (Hubbs, 2004; Savage and Hansen, 2009; R. Bryson Jr., J. Forks, and T. D. Hibbitts, pers. comm.). In Aguascalientes, the species has been found in oak savanna (Quintero-Díaz et al., 2001; RWH, pers. observ.) and oak-juniper forest (Carbajal-Márquez and Quintero-Díaz, 2014). In Jalisco, *L. greeri* has been found in an oak-manzanita community in the Sierra del Laurel (Hansen and Bryson, 2009), and in pine-oak forest in the Sierra de los Huicholes (Ahumada-Carrillo et al., 2014). Cruz-Sáenz et al. (2017) erroneously reported this species from the Tepalcatepec Depression physiographic region in Jalisco. The single known locality for Nayarit lies within pine-oak forest (Hansen et al., 2011). In Zacatecas, *L. greeri* has been recorded from oak forest (Ahumada-Carrillo et al., 2011).

An enigmatic specimen obtained in 1964 from 2.74 km S of Transcoso (= Trancoso), Zacatecas (MCZ 162279; Liner and Dundee, 1977), from high elevation Chihuahuan Desert (elev. ~2,119 m), is notable in its occurrence beyond the present distribution of Madrean woodland. Although reported as *L. mexicana*, one of the collectors, Ernest A. Liner (Liner, 1996; and pers. comm.), stated that the snake was of the “*greeri* morph” and also noted that *Opuntia* was locally abundant. Presently, this region has experienced severe habitat degradation due to modification for agriculture, and thus it is not possible to infer historical habitat conditions. Our examination of the specimen confirms its affiliation with *L. greeri*, based on color pattern and ventral scale counts.

Lampropeltis greeri occurs over a narrow elevational range. The lowest elevation record is from 2,104 m at Río Chico, 42 mi. E of El Salto on Mex 40, Durango (LACM 107231). The highest elevation is attained in the Sierra Fría of Aguascalientes, at 2,603 m (UAA-CV-R263; Carbajal-Márquez and Quintero-Díaz, 2014).

Lampropeltis leonis

Lampropeltis leonis occurs in the northern segment of the Sierra Madre Oriental of northeastern Mexico, at latitudes of 23.21–25.38°N, in the states of Coahuila, Nuevo León, and Tamaulipas. We obtained 45 valid records for *L. leonis* representing 35 discrete localities (Fig. 8). Despite its long popularity in herpetoculture, this species remains poorly known in the wild, where it can be difficult to find. Additionally, some older records are accompanied by vague locality data, making it difficult to plot those on a map or to accurately estimate the elevation. Although Lemos-Espinal and Dixon (2013) listed *L. leonis* (reported as *L. mexicana thayeri*) as occurring in San Luis Potosí, we are not aware of any specimens from that state. Published sources of distributional information concerning *L. leonis*, including discussions of biogeography, are: Loveridge (1924), Smith (1944), Smith and Taylor (1950), Liner (1964), Gehlbach (1967), Liner et al. (1976), Garstka (1982), Liner (1992), Hilken and Schlepper (1998), Salmon et al. (2001), Salmon et al. (2004), Lazcano et al. (2007), Lemos-Espinal and Smith (2007), Farr et al. (2009), Lazcano et al. (2010), Lemos-Espinal and Smith (2015b), Lemos-Espinal and Cruz (2015), Farr (2015), Contreras-Lozano et al. (2015), Terán-Juárez et al. (2016), Nevárez-de los Reyes et al. (2016a), and Nevárez-de los Reyes et al. (2016b).

The northernmost record is from the vicinity of Los Lirios, Coahuila (Gartska, 1982; 25.39097°N, 100.58538°W). The southernmost locality for Nuevo León is from Mex Hwy 61, ~2.4 km by rd NNE jct with Hwy 120 (UANL 3776; 23.75468°N, 100.10841°W). On the Gulf Coast-facing slope of the Sierra Madre Oriental, snakes that can be confidently assigned to *L. leonis* have been found as far south as the Miquihuana region, near the type locality of *Lampropeltis thayeri* (Loveridge, 1924).

A noteworthy specimen is from 39.7 mi. (by Mex 101) NE jct Mex 101 and Mex 80, Tamaulipas (AMNH 107290; approximately 23.212484°N, 99.679196°W). This snake was collected as a DOR and no photographs were taken prior to preservation (M. Rubio, pers. comm.). Nevertheless, based on pattern elements and ventral scale counts (W. Farr, pers. comm.), we assign this specimen to *L. leonis*, which constitutes the southernmost record for this species.

Lampropeltis leonis is closely associated with the Sierra Madre Oriental and outlier ranges, including its interface with bordering Chihuahuan Desert. This species occupies habitats from Chihuahuan Desert Scrub and Chihuahuan Desert/Tamaulipan Thorn Scrub to pine-oak woodland, usually in close association with rock-strewn slopes (Farr et al., 2015; Lemos-Espinal and Cruz, 2015) (Figs. 9, 10). It also occurs on relatively level terrain in intermountain valleys in Nuevo León, where it has been found in rock piles created by farmers clearing land for crops.

Lampropeltis leonis occupies an elevational range of 1,036–2,268 m. The low elevation record is for Cañon de Santa Rosa, Nuevo León (elev. 1,036 m, UANL 5773; Salmon et al., 2001). High elevation records include 20 mi. N of La Ascención, Nuevo León (elev. ~2,268 m, UTA 6135), Sierra Zapalinamé, Coahuila (elev. 2,268 m, UANL 7693), and 6 km SW of San Antonio de las Alazanas, Nuevo León (elev. 2,182 m, TNHC 100780).

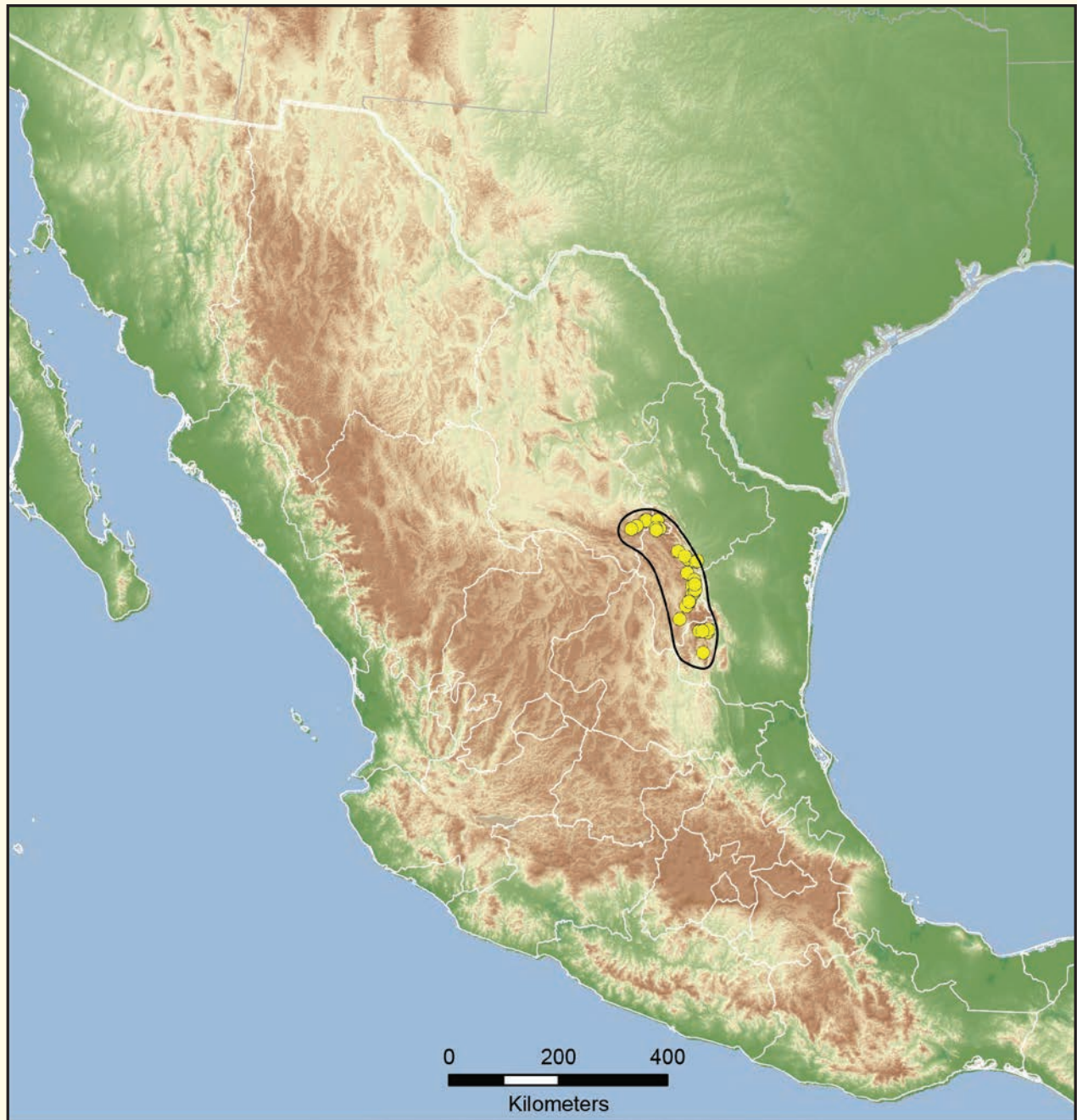


Fig. 8. Distribution map of *Lampropeltis leonis*.



Fig. 9. Habitat of *Lampropeltis leonis* in Coahuila and Nuevo León, Mexico. (A) Chorro Canyon, Municipio de Arteaga, Coahuila, elev. ~2,100 m, September of 2008; (B) vicinity of San Antonio de las Alazanas, Municipio de Galeana, Nuevo León, at the border with Coahuila, elev. 2,280 m, April of 2010; (C) northwest of Galeana from the lower slopes of Cerro Potosí, Municipio de Galeana, Nuevo León, elev. ~2,100 m, August of 2005; (D) Santa Rosa Canyon near Iturbide, Municipio de Iturbide, Nuevo León, elev. ~1,200 m., August of 2005; (E and F) northeast of La Ascensión, Municipio de Aramberri, Nuevo León, elev. 1,920 m, July of 2008; (G) northwest of Aramberri, Municipio de Aramberri, Nuevo León, elev. 1,860 m, August of 1985; and (H) vicinity of La Escondida, Municipio de Aramberri, Nuevo León, elev. ~1,530 m, July of 2005.



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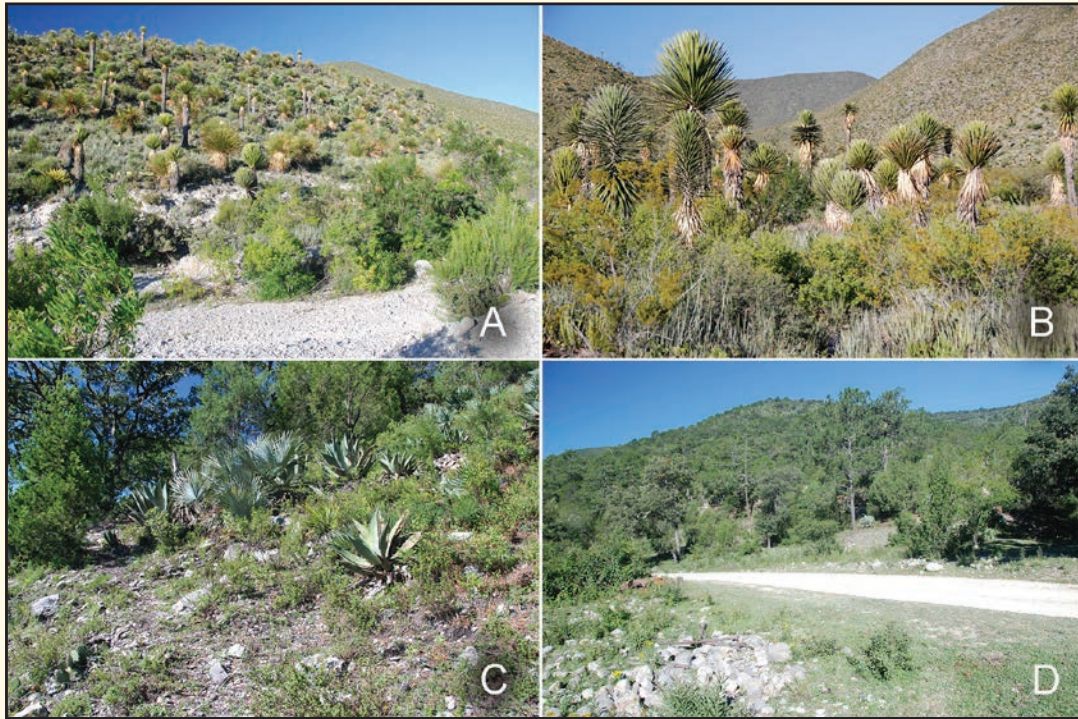


Fig. 10. Habitat of *Lampropeltis leonis* in Tamaulipas, Mexico. (A, B) Vicinity of Miquihuana, Municipio de Miquihuana (type locality for *Lampropeltis thayeri*), elev. ~1,830 m, August of 2008; and (C, D) vicinity of Ávila y Urbina, Municipio de Jaumave, elev. 1,740 m, August of 2008.

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Lampropeltis mexicana

Lampropeltis mexicana, as defined herein, occurs in eastern parts of the Central Plateau and adjacent Sierra Madre Oriental in Mexico, where it has been documented from the states of Aguascalientes, Guanajuato, Hidalgo, México, and San Luis Potosí. Records span latitudes of 19.65–22.72°N. This species almost certainly occurs in southeastern Zacatecas and possibly Tamaulipas (Terán-Juárez et al., 2015). We obtained 45 valid records representing 18 discrete localities (Fig. 11). The largest number of specimens, both in scientific collections and in captivity, has been obtained from the mountains in eastern San Luis Potosí, generally in the area of Valle de los Fantasma and nearby Alvarez. Published sources of distributional information concerning *L. mexicana* (*sensu stricto*), including discussions of biogeography, include Garman (1884), Dugès (1897), Smith and Taylor (1950), Gehlbach and Baker (1962), Gehlbach (1967), Morafka (1977), Garstka (1982), Camarillo Rangel (1983), Hilken and Schlepper (1998), Canseco-Márquez et al. (2004), Vázquez-Díaz and Quintero-Díaz (2005), Flores-Villela et al. (2010), Lavín-Murcio and Lazcano (2010), Lemos-Espinal and Dixon (2013), Cruz-Elizalde et al. (2014), Terán-Juárez et al. (2015), Hansen et al. (2016), and García-Vázquez et al. (2017).

The northernmost record is from Sierra La Trinidad, San Luis Potosí (MZFC 26940; 22.72025°N, 100.38489°W). This species ranges as far south as ~7.8 km by air ENE of Jilotepec, México (UTA-DC 8646; 19.96500°N, 99.46459°W; Hansen et al., 2016).

The earliest records of this species are from San Luis Potosí (Garman, 1884), followed by a report from Guanajuato (Dugès, 1897). In Aguascalientes, this species is known from a single specimen (UAA, uncatalogued; G. Quintero-Díaz, pers. comm.) obtained at La Tinajuela, Municipio de Asientos, in the far eastern part of the state (22.05931°N, 101.91070°W; Vázquez-Díaz and Quintero-Díaz, 2005).

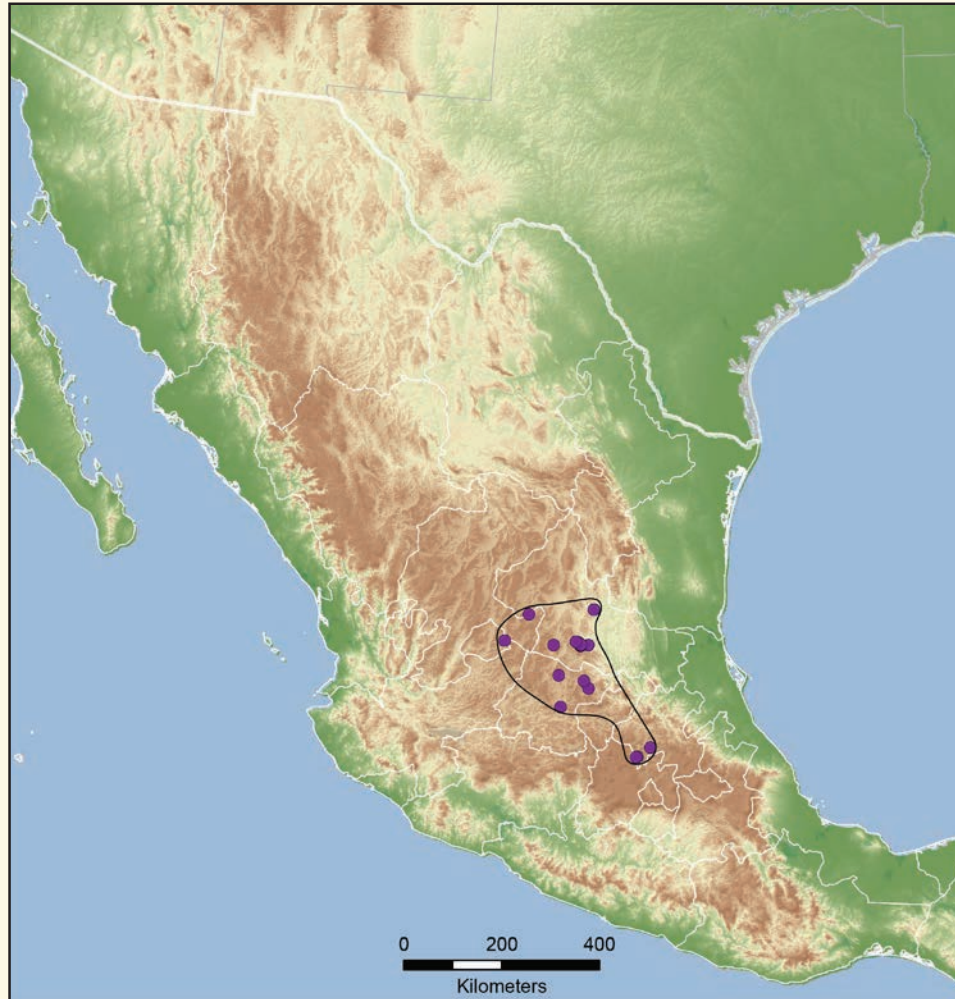


Fig. 11. Distribution map of *Lampropeltis mexicana*.

Smith and Smith (1976) erroneously listed *L. mexicana* among species known to occur in the state of México; this mistake was corrected by Camarillo Rangel (1983). Similarly, Ramírez-Bautista et al. (2010, 2014) misinterpreted data from Bryson et al. (2007) and included *L. mexicana* in the herpetofauna of Hidalgo. This error was noted by Lemos-Espinal and Smith (2015a). A recent report, however, provided the first records of this species from both Hidalgo and México (Hansen et al., 2016). This species was erroneously omitted from a list of the herpetofauna known from Guanajuato (Leyte-Manrique et al., 2015).

An unusual specimen from the San Luis Potosí–Zacatecas border region was collected 52 miles (~84 km) WNW of Cd. San Luis Potosí, elev. 2,290 m (CM 59980; Morafka, 1977; Garstka, 1982). The geography, habitat (high-elevation Chihuahuan Desert; see Morafka, 1977: plate 9), and number of ventral scales (191) are suggestive of *L. mexicana*, but the relatively slender build and color pattern resemble *L. alterna* or *L. leonis*. Perhaps this specimen influenced Garstka’s (1982) placement of *greeri*, *leonis*, and *mexicana* in a monotypic *L. mexicana*. Based on our examination of this specimen we tentatively allocate it to *L. mexicana*, although additional specimens from this region would be helpful.

A single specimen was collected in 1962 reportedly from Río Verde, San Luis Potosí (KU 85010, elev. ~991 m; Garstka, 1982). This area, however, is an unlikely location for *L. mexicana*, given that it is a lower-elevation farming region that lacks suitable habitat for this species. Perhaps this specimen originated from the mountains just west of Río Verde, where *L. mexicana* is fairly common.

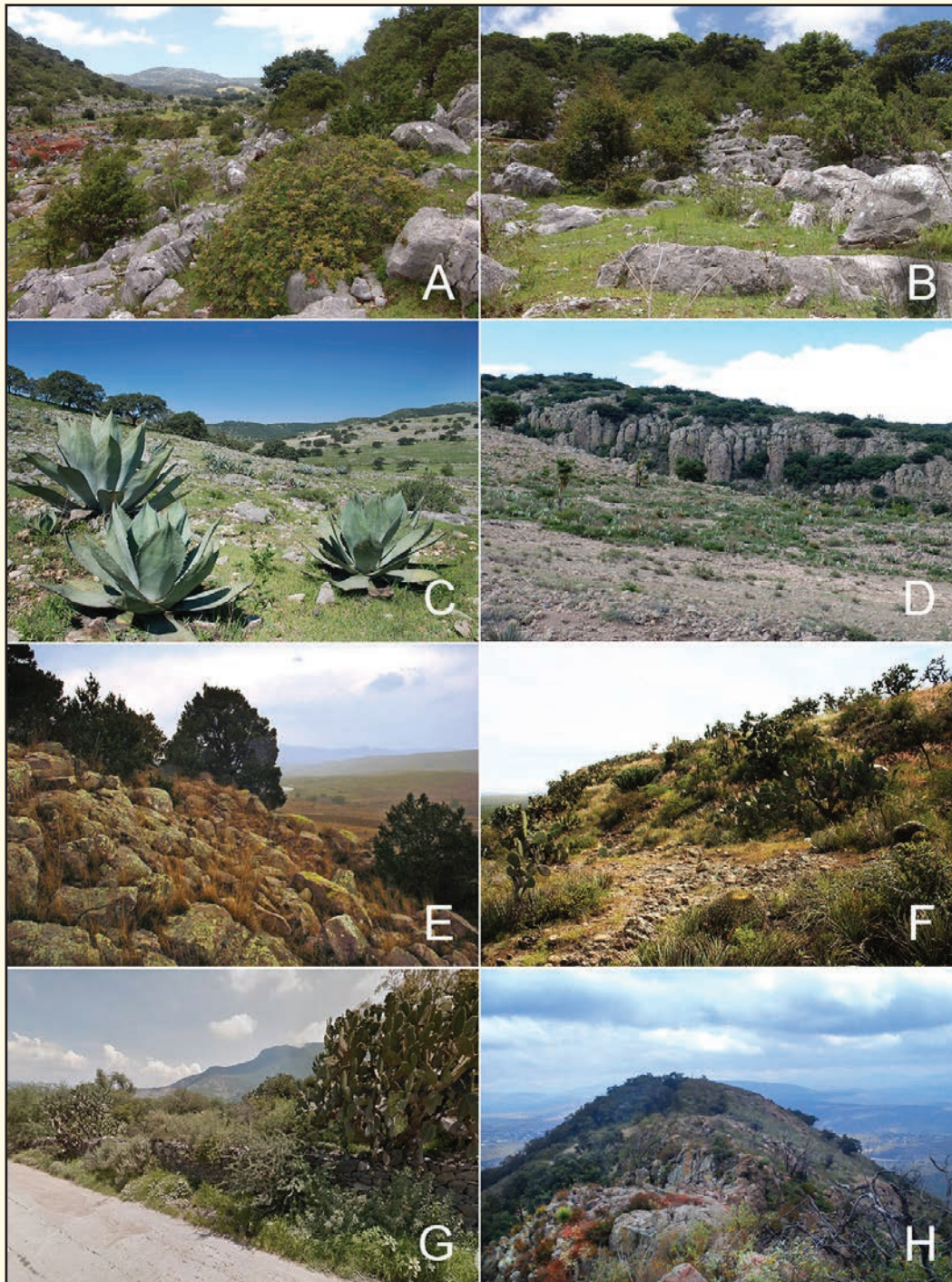


Fig. 12. Habitat of *Lampropeltis mexicana* in San Luis Potosí, Guanajuato, and Hidalgo, Mexico. (A) Valle de los Fantasma, Municipio de Zaragoza, San Luis Potosí, elev. ~2,200 m, July of 2005; (B) vicinity of Alvarez, Municipio de Zaragoza, San Luis Potosí, elev. ~2,380 m, July of 2005; (C) Sierra la Trinidad near Guadalcázar, Municipio de Guadalcázar, San Luis Potosí, elev. ~2,100 m, July of 2008; (D) Hwy 70 east of Ciudad San Luis Potosí, Municipio de Zaragoza, San Luis Potosí, elev. ~2,200 m, July of 2006; (E) Sierra San Miguelito, Municipio de Villa de Arriaga, San Luis Potosí, elev. ~2,409 m, June of 2016; (F) Sierra de las Pozos, Municipio de San Luis de la Paz, Guanajuato, elev. ~2,150 m, August of 2015; (G) vicinity of Mixquiahuala, Municipio de Mixquiahuala de Juárez, Hidalgo, elev. ~2,040 m; and (H) Cerro de la Campana, Municipio de Tepeji del Río de Ocampo, Hidalgo, elev. ~2,350 m, November of 2016.

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Garstka (1982) examined a specimen from near Armadillo de los Infantes (= Armadillo de los Infante, ~30 km by air NE of Cd. San Luis Potosí), San Luis Potosí, citing E. Wagner as the source of the snake; however, Wagner (pers. comm.) does not recall collecting any snakes from that area. Thus, we did not include the locality in our distribution map, although it lies within the expected range for this species.

A specimen from 3 km W of Bustamante, Tamaulipas (UTADC 8512; 23.43263°N, 99.79096°W; reported by Terán-Juárez et al., 2015 as *L. mexicana*) is known only from a blurry photo of a live snake. Although based on geography this might be a *L. leonis*, it differs in color pattern from the handful of geographically closest *L. leonis* specimens collected from near Miquihuana in southwestern Tamaulipas. Collectively, snakes from this area show little variation in color pattern, unlike populations of *L. leonis* in Nuevo León and Coahuila, and are coral-snake mimics. The Bustamante snake shows pattern elements seen in some *L. mexicana* (*sensu stricto*) as well as in *L. leonis* from Nuevo León, and this is a region where the ranges of *leonis* and *mexicana* might be expected to meet. Due to the poor-quality photo and lack of a specimen from which to obtain ventral scale counts, we withhold assignment to species pending collection of additional material from this region.

Lampropeltis mexicana occurs in rocky, open habitats, from high-elevation desert to mesic oak forests. Collecting sites just east of Cd. San Luis Potosí in San Luis Potosí and in the Sierra de las Pozos in Guanajuato are rocky, treeless landscapes (Fig. 12d,f). Conditions, however, appear much wetter in the mountains of eastern San Luis Potosí near Alvarez, where summer weather includes rain and fog; the habitat here consists of limestone outcrops in patchy oak forest (Fig. 12a–b).

Lampropeltis mexicana occupies a relatively narrow elevational zone. The lowest confirmed elevation is 1,194 m at Santa Catarina, San Luis Potosí (UTA 11271; but see comment above regarding KU 85010 from Río Verde, San Luis Potosí), and the maximum elevation is 2,438 m at Alvarez (MCZ 19022–19025).

Lampropeltis ruthveni

Any discussion of the distribution of *L. ruthveni* must take into account the long period of confusion involving this species and *L. triangulum arcifera* (recently synonymized with *L. polyzona* by Ruane et al., 2014). *Lampropeltis ruthveni* occurs along the southern part of the Central Mexican Plateau and adjacent Transvolcanic Belt. This species has been recorded from Jalisco, Michoacán, Guanajuato, Querétaro, and Hidalgo, with an east–west range of ~570 km. We obtained 57 valid records representing 32 discrete localities (Fig. 13).

Published sources of distributional information concerning *L. ruthveni* (sometimes presented as *L. triangulum arcifera*), including discussions of biogeography, are: Blanchard (1920a), Martín del Campo (1940), Taylor (1940), Smith and Taylor (1950), Duellman (1965), Williams (1970, 1978), Armstrong and Murphy (1979), Garstka (1982), Williams (1988), Campbell and Lamar (2004), Hubbs (2004), Tinoco Navarro (2005), Gómez-Mendoza (2007), Dixon and Lemos-Espinal (2010), Flores-Villela et al. (2010), Roth-Monzón et al. (2011), Alvarado-Díaz et al. (2013), Ochoa-Ochoa et al. (2014), Hansen et al. (2015), Hernández-Melo and Fernández-Badillo (2015), Grünwald et al. (2016), Fernández-Badillo et al. (2016), Lemos-Espinal and Dixon (2016), and Cruz-Sáenz et al. (2017).

The westernmost record is from near Cerro la Campana, Jalisco (UTADC 8556; 20.36986°N, 104.59936°W; Grünwald et al., 2016). The eastern range limits are reached at Rancho El Durazno, Hidalgo (19.90186°N, 99.37630°W; Roth-Monzón et al., 2011).

Recent discoveries have expanded the range to include the states of Hidalgo (Roth-Monzón et al., 2011) and Guanajuato (Hansen et al., 2015). Undoubtedly, *L. ruthveni* also occurs in the state of México.

In a molecular phylogenetic study, Bryson et al. (2007) included a sample of *L. ruthveni* purportedly originating from “near Jalpan, Querétaro.” Relatedly, Heimes (2016), citing Bryson et al. (2007), listed the Jalpan Valley as an isolated population of *L. ruthveni*. The Jalpan Valley, however, is a low-elevation (elev. ~760 m) xeric thornscrub area that we do not consider suitable habitat for *L. ruthveni* or *L. mexicana*. The Jalpan sample used in Bryson et al. (2007) was from a snake at the Dallas Zoo that never was deposited in a museum collection. Given this, and since the specimen lacked precise information concerning the circumstances of collection, we cannot confidently associate it with a specific place and did not include it in our range map.



Fig. 13. Distribution map of *Lampropeltis ruthveni*.

Campbell and Lamar (2004: plate 1143) included a photo of a snake identified as *L. mexicana* reportedly collected on “Mexican Highway 120, 9.6 km west-northwest of Jalpan, Querétaro, Mexico, elevation 1,981 m.” According to David G. Barker (pers. comm.), who took the photo in 1988, the snake depicted is a *L. ruthveni* from Tapalpa, Jalisco. We examined a higher resolution image supplied by Barker and confirmed the identification as *L. ruthveni*.

Tipton (2005) included Oaxaca as part of the species’ range, although there are no records from that state. Wallach et al. (2014) listed Morelos as part of the range of *L. ruthveni*, but we are not aware of any records from that state.

Lampropeltis ruthveni occurs in open, rocky habitats, generally in or near oak or pine-oak forests (Fig. 14; Armstrong and Murphy, 1979; Garstka, 1982; Hansen et al., 2015; Grünwald et al., 2016). In northeastern Michoacán, this species occurs in treeless mesquite grassland (Duellman, 1965). Collection sites range from humid to semi-arid, and some populations persist in landscapes immediately adjacent to croplands (Hansen et al., 2015).

The elevational range of *L. ruthveni* is from 1,925 to 2,667 m. The lowest elevations are found at the western extreme of the range, e.g., near Cerro la Campana, Jalisco (1,925 m; Grünwald et al., 2016). Two records exceed an elevation of 2,600 m: Cañon de Rio Galindo, Querétaro (elev. 2,650 m; MCZ 161010–161011); and 0.4 rd mi SE of Amealco on road to La Piedad, Mexquititlan Hwy, Querétaro (elev. 2,667 m; TCWC 52508).

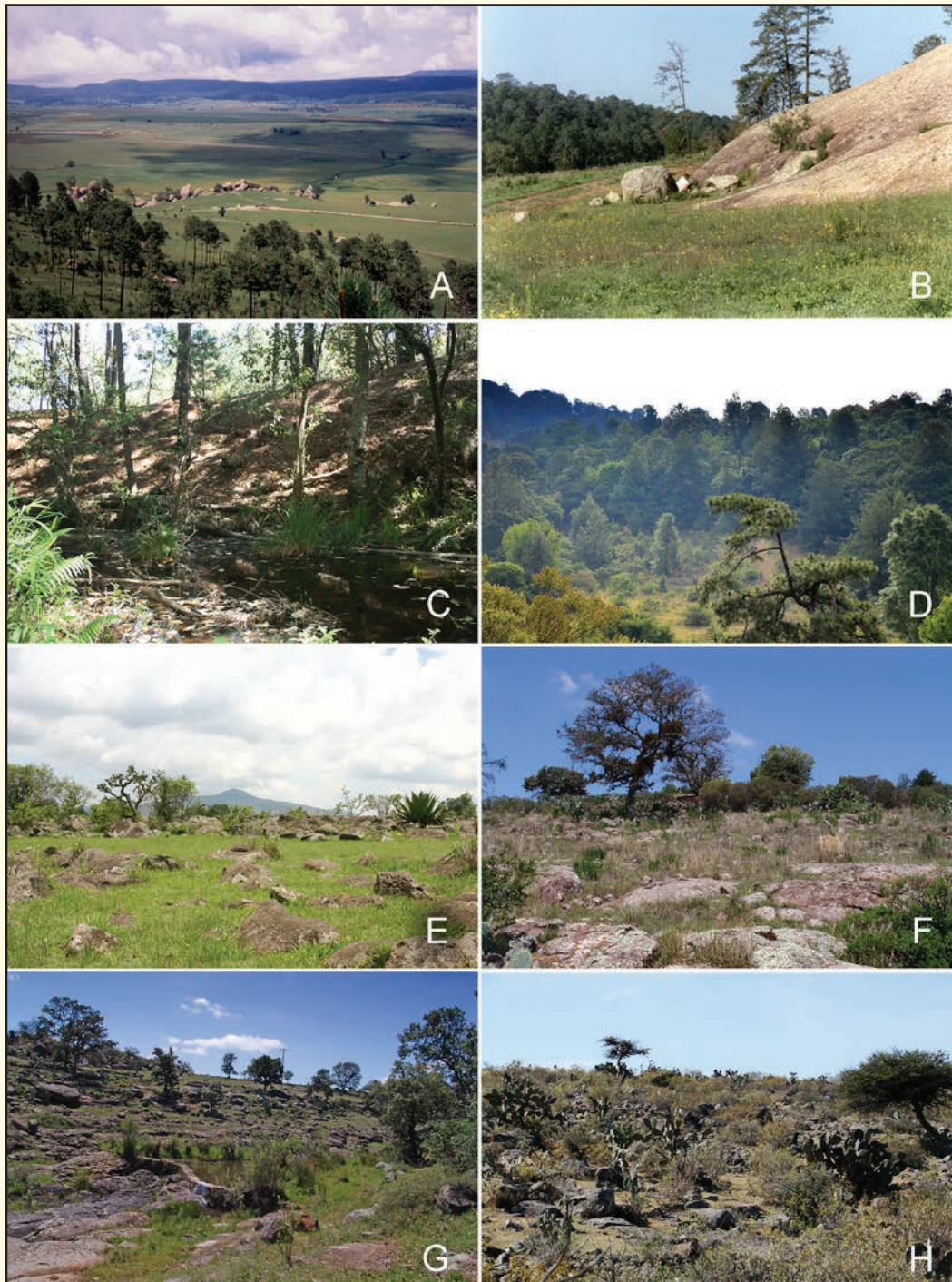


Fig. 14. Habitat of *Lampropeltis ruthveni* in Jalisco, Michoacán, Querétaro, and Hidalgo, Mexico. (A, B) Rancho San Francisco, near Tapalpa, Municipio de Tapalpa, Jalisco, elev. ~2,198 m, August of 1998; (C) Sierra de Quila, Municipio de Tecolotlán, Jalisco, elev. 1,995 m, March of 2014; (D) southeastern margin of Morelia, Municipio de Morelia, Michoacán, elev. 2,019 m, June of 2015; (E) 9 km by air NE of San Jose de Gracia, Municipio de Marcos Castellanos, Michoacán, elev. 2,073 m, August of 2007; (F, G) near Amealco, Municipio de Amealco de Bonfil, Querétaro, elev. 2,650 m, June of 2006; and (H) El Sendo, ~7 km WNW of Zócalo de Nopala, Municipio de Nopala de Villagrán, Hidalgo, elev. 2,245 m, August of 2008.

© Blake Thomason (A, B), Ivan T. Ahumada-Carrillo (C), Juan Manuel Gonzalez-Villa (D), Chris Rodriguez (E), Christoph Grünwald (F, G), and Andres Alberto Mendoza-Hernández, courtesy of Andrea Roth-Monzón (H)

Lampropeltis webbi

The rarest species of *Lampropeltis*, *L. webbi*, is known from five specimens, of which only one was alive at the time of collection. This species also occupies one of the smallest ranges of any *Lampropeltis* species, with all records clustered along a short section of Hwy 40 in the Durango–Sinaloa border region of the Sierra Madre Occidental (Fig. 15). Published sources of distributional information concerning *L. webbi*, including discussions of biogeography, include Bryson et al. (2001), Bryson et al. (2005), and Ochoa-Ochoa et al. (2014). Heimes (2016: 92–93) erroneously included Nayarit in the range of *L. webbi* and included a photo of a snake labeled as that species (fig. 108), which actually is a *L. greeri* from Mesa de Nayar, Nayarit (Hansen et al., 2011).

The holotype (UANL 5684) was collected in 2000 as a freshly hit DOR 4.0 km W of El Palmito on Hwy 40, elev. 2,000 m, Sinaloa, and initially was reported as a range extension for *L. mexicana* (Bryson et al., 2001; Bryson et al., 2005). A second specimen, obtained as a DOR in Durango in 1968, was discovered in a small museum

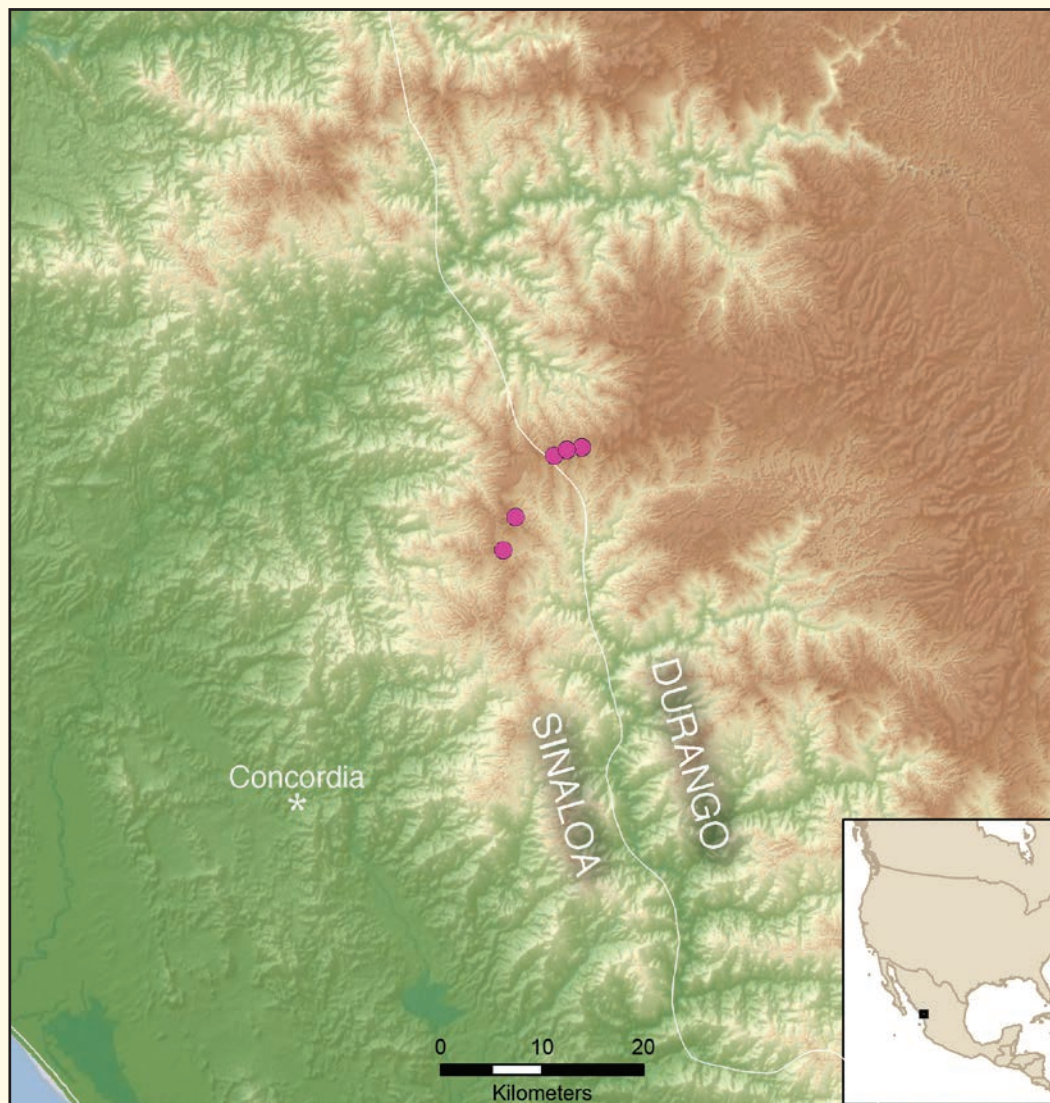


Fig. 15. Distribution map of *Lampropeltis webbi*.

collection by R. G. Webb (paratype described in Bryson et al., 2005; formerly Fort Worth Museum of Science and History 6716, now TCWC 100530). Since the description, two additional DOR specimens and one live individual have been found, all clustered around the Durango–Sinaloa border. Four of the five snakes were found on the road at night. Collectively, these records span a small area, with the two most distant localities separated by only 13 km. The elevational range is 2,000–2,394 m.

All records are associated with a transition between the lower-elevation Tropical Deciduous Forest that faces the Pacific Ocean and the higher and drier Madrean Woodland mostly on the eastern-facing slopes (Fig. 16). Webb (1984: 222) described this area as follows: “... [it] covers rugged, mountainous terrain at the highest elevations in large barrancas and canyons, and is best developed on south-facing slopes. Steep, boulder-strewn hillsides with rock outcrops, interrupted by small, relatively level areas, are covered in most places with a tall pine-oak woodland and often a dense understory of herbs, shrubs, and thick tangles of vines....” Webb (1984) also noted that this humid pine-oak community occurred for ~51 km along Hwy 40 at elevations of 1,798–2,408 m. Given that this formation extends for a considerable distance both north and south of the Hwy 40 corridor, we anticipate that the range of *L. webbi* will be extended with additional fieldwork.



Fig. 16. (A–D) Habitat of *Lampropeltis webbi* along the Hwy 40 corridor in the Durango–Sinaloa border region of Mexico, elev. ~2,100 m (photos A–C taken in July of 2014, and D in July of 2006). © Jason Jones (A–C), and Chris Rodriguez (D)

Remarks: The ranges of species in the *mexicana* group are allopatric, with no documented instances of range overlap, although several species pairs are nearly parapatric (Fig. 17). We determined the straightline distances between nearest localities of geographically adjacent species using Google Earth. In the Sierra Madre Occidental, the nearest records of *L. alterna* and *L. greeri* are 67 km apart; although barriers that might separate these species are not readily apparent, the canyon of the Río Santiago (Durango) might constitute a limit on northwestern expansion for *L. greeri* and thus prevent contact with *L. alterna*. *Lampropeltis greeri* and *L. mexicana* have been found within 68 km of one another in Aguascalientes, but the intervening terrain seems to lack suitable habitat for either species. *Lampropeltis webbi* and *L. greeri* both occur in the Sierra Madre Occidental of western Durango, and have been found within 54 km of one another. The intervening area contains high-elevation, cold ridgelines dotted with open grasslands, which may represent an ecological barrier. The distance between the nearest populations of *L. mexicana* and *L. ruthveni* in Hidalgo is only 13 km. In the Sierra Madre Oriental, the nearest populations of *L. leonis* and *L. mexicana* are 90 km apart. The ranges of *L. alterna* and *L. leonis* approach in the region south and east of Saltillo, Coahuila. The nearest records for each are separated by less than 18 km.

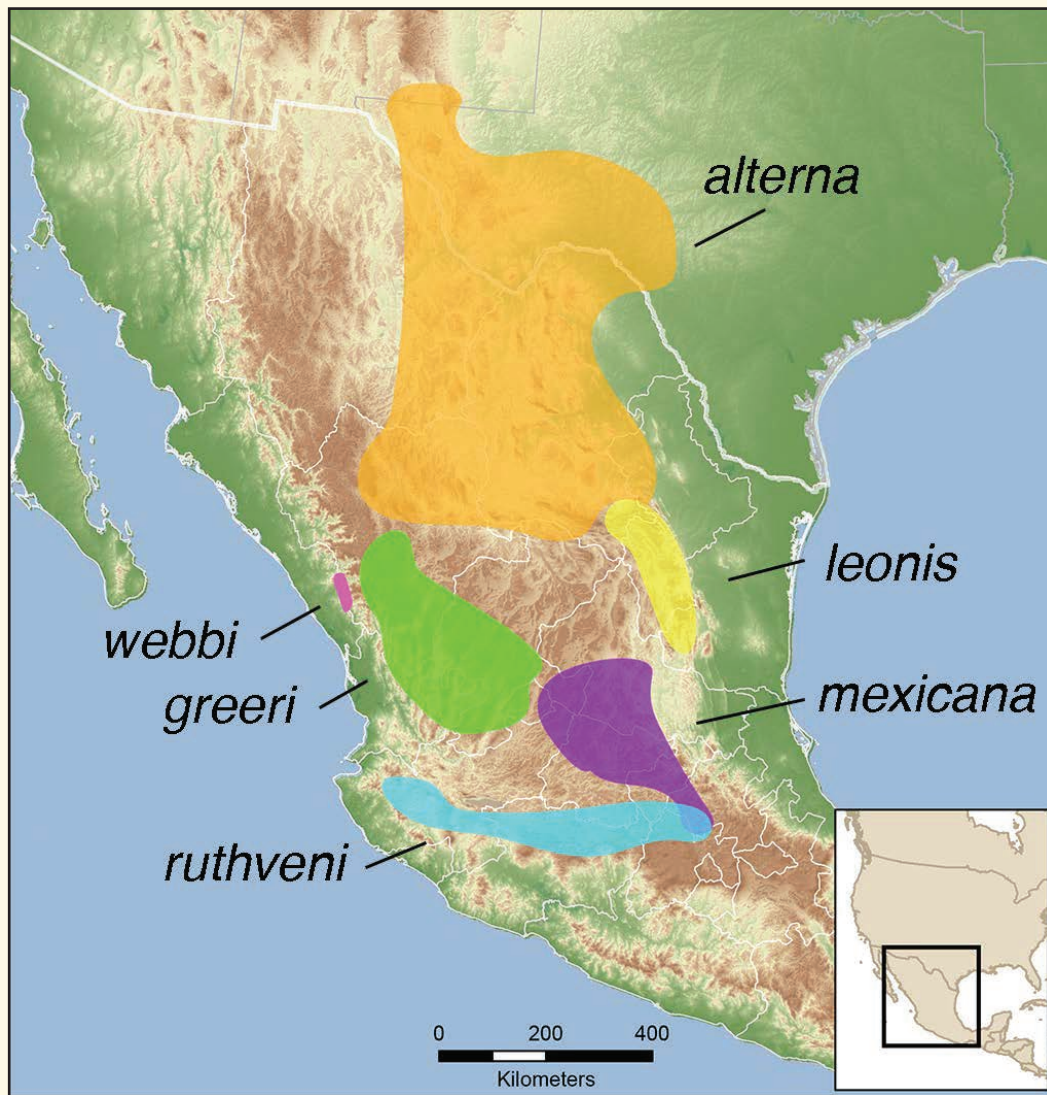


Fig. 17. Map of the combined ranges of species in the *Lampropeltis mexicana* group.

TAXONOMIC ACCOUNTS

Originally, the concept of a “*mexicana* group” of species of *Lampropeltis* was suggested by Hobart Smith (Smith, 1942, 1944) and later supported by Webb (1961), Gehlbach and Baker (1962), Tanzer (1970), Miller (1979), Garstka (1982), and Hilken and Schlepper (1998). The composition of this group has changed slightly with the recognition of *L. ruthveni* (Garstka, 1982), the description of *L. webbi* (Bryson et al., 2005), and the subsequent confirmation of the latter’s affiliation with the *mexicana* complex (Ruane et al., 2014). The taxonomic rank and recognition of some taxa, however, has changed from species to subspecies and back again. Bryson (2002) and Bryson et al. (2007) initially called into question the monophyly of this group, at least with respect to *L. alterna*. Mitochondrial DNA sequences suggested paraphyly relative to *L. triangulum*, although possibly as a result of ancient hybridization and mitochondrial introgression (Bryson et al., 2007). More recent studies (Pyrone et al., 2013; Figueroa et al., 2016; Chen et al., 2017) using nuclear (or nuclear + mitochondrial) sequence data and different analytical methods, also have suggested that a monophyletic *mexicana* clade might require modification. Regardless, questions concerning recognition of a *mexicana* group and its membership do not affect the present examination of species-level diversity (Table 4).

On the basis of allopatric distributions and unique combinations of morphological and color pattern characters, we consider *alterna*, *greeri*, *leonis*, *mexicana*, *ruthveni*, and *webbi* as species-level taxa, diagnosable based on a range of discrete characters. All but *mexicana* initially were described as distinct species. Furthermore, our viewpoint is supported by the apparent lack of character convergence where ranges of adjacent species approach each other. We therefore consider hybridization unlikely, supporting recognition of these taxa as species rather than subspecies (for those who still follow this taxonomic category).

Table 4. Chronology of taxonomic and nomenclatural changes in species of the *Lampropeltis mexicana* group. We also include references that address evolutionary relationships.

Year	Author(s)	Action
1884	Garman	Description of <i>Lampropeltis mexicana</i> (as <i>Ophibolus triangulus mexicanus</i>) based on two specimens from near Cd. San Luis Potosí, San Luis Potosí, Mexico.
1893	Günther	Description of <i>Lampropeltis leonis</i> (as <i>Coronella leonis</i>) based on a specimen from Nuevo León, Mexico, and transferred Garman’s <i>Ophibolus triangulus mexicanus</i> to <i>Coronella</i> , as <i>C. mexicana</i> .
1897	Dugès	Erected a new genus and species (<i>Oreophis boulengeri</i>) for a snake from Guanajuato, which later was placed in the synonymy of <i>L. mexicana</i> by Blanchard (1921).
1902	Brown	Description of <i>Lampropeltis alterna</i> (as <i>Ophibolus alternus</i>) from the Davis Mountains of Texas, United States.
1917	Stejneger and Barbour	Referred <i>Ophibolus alternus</i> Brown to <i>Lampropeltis</i> and emended the species name to match the gender of the genus, thus <i>L. alterna</i> .
1920a	Blanchard	Description of <i>Lampropeltis ruthveni</i> based on a complete head + skin from Patzcuaro, Michoacán, Mexico.
1920b	Blanchard	In a synopsis preceding his 1921 monograph, included both <i>mexicana</i> and <i>leonis</i> as species of <i>Lampropeltis</i> , without discussion. A more detailed treatment would follow in his 1921 publication.
1921	Blanchard	In a monograph of the kingsnakes, transferred <i>Coronella mexicana</i> and <i>Coronella leonis</i> to <i>Lampropeltis</i> , as <i>L. mexicana</i> and <i>L. leonis</i> , respectively. He regarded <i>Oreophis boulengeri</i> Dugès as a junior synonym of <i>L. mexicana</i> .

1922	Dunn	Unaware of Blanchard's (1921) action, Dunn independently determined that <i>Oreophis boulengeri</i> Dugès was a junior synonym of <i>Lampropeltis mexicana</i> .
1924	Loveridge	Description of <i>L. thayeri</i> based on a specimen collected at Miquihuana, Tamaulipas, Mexico. Loveridge clearly distinguished this taxon from <i>L. mexicana</i> , although he erroneously assigned four recently collected specimens of <i>L. mexicana</i> to <i>L. leonis</i> .
1942	Smith	Based on examination of 12 specimens of <i>L. mexicana</i> from San Luis Potosí, he suggested that hemipenial characters placed <i>L. mexicana</i> within the <i>triangulum</i> group. He also elaborated on his earlier report (Smith, 1941) of a <i>L. alterna</i> collected from just west of Saltillo, Coahuila; on the basis of hemipenial morphology and color pattern, he noted a relationship between <i>L. alterna</i> and <i>mexicana</i> . He suggested that <i>L. leonis</i> (still known only from the type specimen), together with <i>alterna</i> and <i>mexicana</i> , belonged in a “ <i>mexicana</i> subgroup.” Additionally, Smith proposed placement of <i>ruthveni</i> and <i>thayeri</i> in a “ <i>pyromelana</i> subgroup” with <i>knoblochi</i> (then considered a full species), <i>pyromelana</i> , and <i>zonata</i> .
1944	Smith	Reported on the collection of three snakes from near Galeana, Nuevo León, which he assigned to <i>L. thayeri</i> ; until this time, that species had been known only from the type specimen. Examination of this new material caused Smith to modify composition of his “ <i>mexicana</i> subgroup” to include <i>thayeri</i> , <i>leonis</i> , <i>alterna</i> , and <i>mexicana</i> .
1950	Flury	Description of <i>L. blairi</i> based on a specimen from Terrell County, Texas, United States. This species later would be synonymized with <i>L. alterna</i> by Tanzer (1970).
1952	Zweifel	Discussed evolutionary relationships of <i>L. zonata</i> and putative relatives, including <i>L. ruthveni</i> .
1953	Tanner	Identified the eastern part of the Central Plateau of Mexico as the likely area of origin for <i>L. mexicana</i> (<i>sensu lato</i>).
1961	Webb	Description of <i>L. greeri</i> from the Sierra Madre Occidental of Durango, Mexico. Webb linked this new species with others of the <i>mexicana</i> group based on color pattern.
1962	Gehlbach and Baker	Placed <i>alterna</i> , <i>blairi</i> , <i>greeri</i> , <i>mexicana</i> , and <i>thayeri</i> as subspecies of a wide-ranging <i>L. mexicana</i> (the oldest of these names). They proposed that this “ <i>mexicana</i> complex” was distinct from the milksnakes (<i>L. doliata</i> = <i>L. triangulum</i>), <i>pyromelana</i> , and <i>zonata</i> . They continued to recognize <i>L. leonis</i> as a distinct species.
1965	Gehlbach and McCoy	Regarded a specimen obtained from 42 mi S of Cd. Durango (UCM 21061) to be a <i>L. alterna</i> x <i>mexicana</i> intergrade, although our examination suggests this is a <i>L. greeri</i> . They placed <i>greeri</i> in the synonymy of <i>L. m. mexicana</i> .
1967	Gehlbach	Overview of <i>L. mexicana</i> , which at the time included <i>alterna</i> , <i>blairi</i> , <i>mexicana</i> , and <i>thayeri</i> . He suggested that <i>alterna</i> and <i>blairi</i> were color pattern polymorphs of a single geographic race, a hypothesis later confirmed by Tanzer (1970). He did not address the status of <i>L. leonis</i> .
1970	Tanzer	Followed Gehlbach's construction of <i>L. mexicana</i> as a broadly defined taxon, inclusive of <i>alterna</i> , <i>mexicana</i> (+ <i>greeri</i>), and <i>thayeri</i> . He demonstrated that <i>alterna</i> and <i>blairi</i> were pattern morphs of the same taxon, and that the name <i>alterna</i> had priority, thereby reducing <i>blairi</i> to a junior synonym of <i>L. mexicana alterna</i> . He also reported the first <i>alterna</i> from Durango, and pointed out that pattern element similarities between this specimen and the single known example of <i>L. leonis</i> suggested that the latter might be part of the <i>mexicana</i> complex. He noted the potential for polymorphism in other taxa within the <i>mexicana</i> complex, but pointed out that the subspecies <i>mexicana</i> , because of distinctive scutellation and coloration, should not be considered a polymorph.

1973	Blaney	In an overview of the genus <i>Lampropeltis</i> , recognized <i>leonis</i> as a distinct species, but later in the same account wrote: “It is not possible to distinguish <i>L. leonis</i> from <i>L. mexicana</i> and Tanzer (1970) has implied that they be considered synonyms, a suggestion with which I concur.” In our view, this is a mischaracterization of what Tanzer (1970) wrote, quoted here: “This pattern [referring to an <i>alterna</i> from Durango] is similar to that of <i>L. leonis</i> (Gunther, 1893), which is known only from the type specimen, and it suggests that <i>leonis</i> may be part of the <i>mexicana</i> complex.” Tanzer also noted: “With the distinct differences in pattern observed in <i>alterna</i> and <i>blairi</i> , it is not difficult to see how differences in the patterns of the other subspecies and of <i>L. leonis</i> could be due to polymorphism.” Thus, nowhere does Tanzer offer an opinion as to the validity of <i>leonis</i> , but he suggested that the phenomenon of polymorphism should be sought among other members of this group.
1978	Williams	In the published version of his Ph.D. dissertation (1970), Williams considered <i>L. ruthveni</i> to be a junior synonym of <i>L. triangulum arcifera</i> . Although additional specimens of <i>ruthveni</i> were by then present in museum collections, all were referred to <i>L. triangulum</i> .
1982	Garstka	Presented the first modern survey of the <i>mexicana</i> group based on examination of new material and available museum specimens. He resurrected <i>L. ruthveni</i> from synonymy of <i>L. triangulum</i> , and recognized <i>L. alterna</i> as a species distinct from <i>L. mexicana</i> . He considered all remaining taxa (<i>greeri</i> , <i>leonis</i> , <i>mexicana</i> , <i>thayeri</i>) as part of a monotypic <i>L. mexicana</i> .
1988	Williams	In this revised edition of his <i>L. triangulum</i> monograph, Williams acknowledged Garstka’s (1982) confirmation of <i>L. ruthveni</i> as a distinct species belonging to the <i>mexicana</i> species group.
1990	Collins	In a checklist, Collins adopted Garstka’s (1982) taxonomy recognizing <i>alterna</i> as a distinct, but monotypic species.
1990	Van Devender	Presented a scenario to account for phenotypic variation in United States populations of <i>L. alterna</i> and discounted Garstka’s (1982) elevation of <i>alterna</i> to species status apart from <i>L. mexicana</i> . He did not offer data in support of this view, but dismissed Garstka’s evidence as “weak and unconvincing.”
1992	Van Devender et al.	In the context of a wide-ranging defense of subspecies in herpetological taxonomy, cited similarity of color pattern elements in <i>alterna</i> and <i>thayeri</i> as possible evidence for gene exchange. By extension, they offered support for continued recognition of these forms as subspecies of <i>L. mexicana</i> .
1992	Frost et al.	Criticized Van Devender et al. (1992) for their advocacy of lumping <i>L. alterna</i> into <i>L. mexicana</i> , pointing out logical inconsistencies in their statements.
1994	Van Devender and Bradley	Disputed Garstka’s elevation of <i>alterna</i> to species status, suggesting that the characters used to diagnose <i>alterna</i> (e.g., iris color, head shape) were insufficient to warrant species-level distinction. They considered the Texas populations of <i>L. alterna</i> to consist of two subspecies, stating that pattern differences between eastern and western snakes warranted subspecies recognition.
1998	Hilken and Schlepper	Without presenting new data, recommended a <i>mexicana</i> complex comprised of <i>L. alterna</i> (with <i>alterna</i> and <i>blairi</i> as subspecies), <i>L. mexicana</i> (with three subspecies: <i>greeri</i> , <i>mexicana</i> , <i>thayeri</i>), and <i>L. ruthveni</i> .
1999	Rodríguez-Robles et al.	In a phylogeographic survey of <i>L. zonata</i> using mitochondrial DNA sequences, placed that species in a group comprised of <i>alterna</i> , <i>mexicana</i> , <i>pyromelana</i> , and <i>triangulum</i> .
2000	Crother	In a checklist of United States/Canadian herpetofauna, Crother followed Hilken and Schlepper (1998) in recognizing two subspecies of <i>L. alterna</i> , despite considerable contravening evidence. This arrangement was abandoned in the next edition (Crother, 2008).

2002	Bryson	Developed phylogenetic and biogeographic scenarios for <i>L. mexicana</i> -group species and <i>L. triangulum</i> based on mitochondrial DNA sequences. Notably, <i>L. alterna</i> was not recovered as a monophyletic taxon relative to <i>L. triangulum</i> (<i>sensu lato</i>).
2005	Bryson et al.	Description of <i>Lampropeltis webbi</i> as a new species from the Pacific versant of the Sierra Madre Occidental in the Durango–Sinaloa border region. This species was found to be distinctive based on mtDNA sequence differences and morphological characters.
2007	Bryson et al.	In an expanded version of an earlier work (Bryson, 2002), suggested that <i>L. mexicana</i> and <i>L. triangulum</i> , as then constituted, were not monophyletic groups.
2007	Liner	In a checklist of the Mexican herpetofauna, followed Hilken and Schlepper (1998) in resurrecting sub-species for <i>L. mexicana</i> (<i>greeri</i> , <i>mexicana</i> , <i>thayeri</i>), but retained <i>L. alterna</i> as monotypic.
2008	Liner and Casas-Andreu	In a checklist of the Mexican herpetofauna, followed Hilken and Schlepper (1998) in recognizing sub-species for <i>L. mexicana</i> (<i>greeri</i> , <i>mexicana</i> , and <i>thayerii</i> [sic]) and for <i>L. alterna</i> , with <i>L. a. alterna</i> listed as occurring in Mexico.
2008	Crother	In the sixth edition of the checklist of United States herpetofauna, <i>L. alterna</i> was treated as monotypic.
2013	Pyron et al.	Included <i>L. alterna</i> , <i>mexicana</i> , <i>ruthveni</i> , and <i>webbi</i> , as well as <i>pyromelana</i> and <i>zonata</i> , in a large-scale phylogenetic study based on mitochondrial sequence data in Bryson et al. (2007). Although the sequence data were the same, the resulting topology differed in that <i>alterna</i> was placed in a clade containing the <i>getula</i> complex + <i>L. extenuatum</i> , which in turn was the sister group to <i>L. triangulum</i> .
2014	Ruane et al.	Although focused on the <i>L. triangulum</i> group using both mitochondrial and nuclear gene sequences, Ruane et al. included samples of <i>alterna</i> , <i>mexicana</i> (inclusive of <i>greeri</i> and <i>mexicana</i> , but not <i>leonis</i>), <i>ruthveni</i> , and <i>webbi</i> . Concluded that <i>webbi</i> probably belongs in a <i>mexicana</i> group rather than with <i>L. pyromelana</i> + <i>zonata</i> , and appears to be the sister species to <i>L. ruthveni</i> . Overall, their conclusions relative to <i>mexicana</i> -group species, based on both nuclear and mitochondrial sequences, corroborated older studies based on morphology.
2014	Wallach et al.	In a compendium of extant snake species, considered <i>greeri</i> and <i>leonis</i> as synonyms of <i>L. mexicana</i> . They stated that <i>alterna</i> is “probably a subspecies of <i>L. mexicana</i> ” citing Bryson et al. (2007). Bryson et al. (2007) did not make this suggestion, however, and it is possible that Wallach et al. misinterpreted the former’s phylogenetic tree as evidence for that relationship despite clear problems in using mtDNA sequence data to make such inferences.
2016	Heimes	Recognized three subspecies of <i>L. mexicana</i> (<i>greeri</i> , <i>mexicana</i> , and <i>thayeri</i>).
2016	Figuerroa et al.	Used nuclear and mitochondrial sequences to generate a molecular phylogeny for > 1,600 species of snakes. They recovered a clade that included <i>alterna</i> with northern <i>triangulum</i> + <i>getula</i> -group species. A second clade included <i>mexicana</i> (<i>sensu lato</i>), <i>ruthveni</i> , and <i>webbi</i> , but also tropical milksnakes and montane kingsnakes (<i>knoblochi</i> , <i>pyromelana</i>). These results do not support the monophyly of a <i>mexicana</i> group and are also at odds with other recent molecular-based phylogenies (e.g., Ruane et al., 2014; Chen et al., 2017).
2017	Chen et al.	Used nuclear gene sequences to generate a species tree for Old and New World ratsnakes. They recovered a <i>mexicana</i> clade consisting of <i>webbi</i> + (<i>ruthveni</i> + <i>mexicana</i> [<i>sensu lato</i>]), with <i>alterna</i> recovered as sister to a clade of <i>pyromelana</i> + <i>zonata</i> . These results call into question the monophyly of a <i>mexicana</i> group inclusive of <i>alterna</i> .

***Lampropeltis alterna* (Brown)**

Ophibolus alternus Brown, 1902: 612

Lampropeltis alterna, Stejneger and Barbour, 1917: 87

Lampropeltis blairi Flury, 1950: 215

Lampropeltis mexicana alterna, Gehlbach and Baker, 1962: 298

Lampropeltis mexicana blairi, Gehlbach and Baker, 1962: 298

Lampropeltis alterna alterna, Hilken and Schlepper, 1998: 100

Lampropeltis alterna blairi, Hilken and Schlepper, 1998: 101

Type specimen: ANSP 14977.

Type locality: “Davis Mountains, Jeff Davis county, Texas.” Collected by Edmund Meyenberg, 1901. Restricted by Rhoads and Salmon (2012) to vicinity of Madera Canyon, Little Aguja Canyon, and Big Aguja Canyon, near headwaters of Toyah Creek, Jeff Davis County, Texas, United States.

Distribution: Extreme southeastern New Mexico and southwestern Texas, United States, southward into Coahuila, Durango, and Nuevo León in Mexico, at elevations from 384 to 2,311 m. Probably occurs in Chihuahua and possibly in Zacatecas.

Diagnosis: A moderate-sized (maximum TL = 1,467 mm) species of kingsnake most similar to *L. greeri* and *L. leonis*, differing from those species by the presence of a silver-gray iris (golden-brown to dark brown in *L. greeri*, golden-brown in *L. leonis*), the head noticeably distinct from neck (only slightly so in *L. greeri* and *L. leonis*), the eyes prominently protruberant (vs. only slightly so in *L. greeri* and *L. leonis*), and by higher ventral scale counts (211–230 vs. 197–204 in *L. greeri* and 194–212 in *L. leonis*) (Fig. 18). Additionally, black head cap markings are lacking or indistinct in *L. alterna* populations from near the range of *L. greeri*; conversely, such markings are present in nearly all individuals of *L. greeri* (Figs. 19–22).

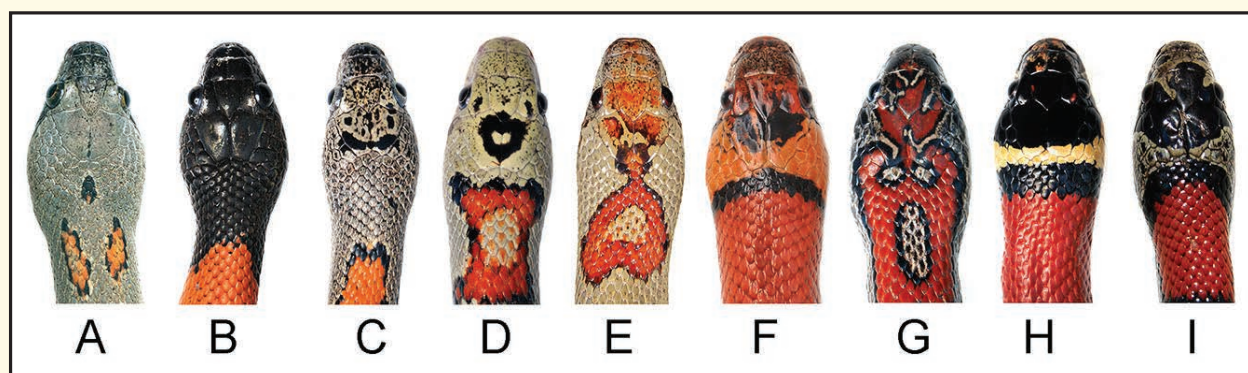


Fig. 18. Head shape and pattern in species of the *Lampropeltis mexicana* group. (A) *L. alterna* (~20 km NW of Ramos Arizpe, Municipio de Ramos Arizpe, Coahuila); (B, C) *L. alterna* (Christmas Mountains, Brewster County, Texas); (D) *L. greeri* (Rancho Santa Bárbara, Municipio de Durango, Durango); (E) *L. leonis* (SE of La Escondida, Municipio de Aramberri, Nuevo León); (F) *L. leonis* (tricolor phenotype, captive specimen); (G) *L. mexicana* (Valle de los Fantasma, Municipio de Zaragoza, San Luis Potosí); (H) *L. ruthveni* (vicinity of Tapalpa, Municipio de Tapalpa, Jalisco); and (I) *L. webbi* (just west of Durango border, Municipio de Concordia, Sinaloa).



Fig. 19. Variation in *Lampropeltis alterna* from the United States: New Mexico and western part of range within Texas. (A) Brokenoff Mountains, Otero County, New Mexico; (B) Carlsbad Caverns National Park, Eddy County, New Mexico; (C) Paisano Gap west of Alpine, Presidio County, Texas; (D) 32 km S of Alpine, Brewster County, Texas; (E, F) 9.6 km S of Alpine, Brewster County, Texas; (G) FM 170, Presidio County, Texas; and (H) Christmas Mountains, Brewster County, Texas.

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Fig. 20. Variation in *Lampropeltis alterna* from the United States: central part of range within Texas. (A, B) Boy Scout Road, Davis Mountains, Jeff Davis County, Texas; (C) Musquiz Canyon, Davis Mountains, Jeff Davis County, Texas; (D, E) north of Sanderson, Terrell County, Texas; (F) Sanderson, Terrell County, Texas; and (G, H) Black Gap Wildlife Management Area, Brewster County, Texas.

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Fig. 21. Variation in *Lampropeltis alterna* from the United States: central and eastern part of range within Texas. (A) Howard Draw, Crockett County, Texas; (B, C) vicinity of Iraan, Pecos County, Texas; (D, E) Castle Mountain, Upton County, Texas; (F) west of Langtry, Valverde County, Texas; and (G, H) Hwy 277, Valverde County, Texas.

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Fig. 22. Variation in *Lampropeltis alterna* from Mexico. (A–C) Northwest of Ramos Arizpe, Municipio de Ramos Arizpe, Coahuila; (D) Sierra de Jimulco, Municipio de Viesca, Coahuila; (E) west-northwest of Monterrey, Municipio de García, Nuevo León; and (F–H) vicinity of Santiago Papasquiaro, Municipio de Santiago Papasquiaro, Durango.

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Remarks: Van Devender and colleagues (1990, 1992, 1994) advocated for the continued placement of *alterna* within *L. mexicana*, but presented no evidence in support of this arrangement and we found their arguments unconvincing, as did Frost et al. (1992). Similarly, Hilken and Schlepper (1998), without presenting new information, recommended recognition of two subspecies within *L. alterna*. The broad geographic sampling of specimens, especially in the United States part of the range, and captive breeding data involving locality-specific snakes clearly illustrate the geography of color pattern variation and pervasive pattern polymorphism (Tanzer, 1970; Miller, 1979). These data do not support the recognition of subspecies, at least not for the well-sampled populations in the United States.

***Lampropeltis greeri* Webb**

Lampropeltis greeri Webb, 1961: 326

Lampropeltis mexicana greeri, Gehlbach and Baker, 1962: 298

Lampropeltis mexicana mexicana, Gehlbach and McCoy, 1965: 37

Lampropeltis mexicana, Garstka, 1982: 29

Lampropeltis mexicana greeri, Hilken and Schlepper, 1998: 101

Type specimen: MSU 190

Type locality: “Rancho Santa Barbara (Weicher Ranch), 29 miles west-southwest of Ciudad Durango, Durango, México, ca. 7400 ft.” Collected by J. Keever Greer and Robert G. Webb on 18 July 1958.

Distribution: Southeastern Sierra Madre Occidental and outlier ranges to the south, from southwestern Durango to Nayarit, and eastward to Zacatecas, Aguascalientes, and Jalisco, at elevations from 2,104 to 2,603 m.

Diagnosis: A moderate-sized (maximum TL = 1,156 mm) tricolored kingsnake most similar to *L. alterna* and some populations of *L. leonis*. It differs from nearest populations of *L. alterna* by the presence of a golden-brown to dark brown eye color (vs. silver-gray in *L. alterna*), black head cap markings (mostly absent in *L. alterna*), the head only slightly distinct from the neck (vs. prominently so in *L. alterna*), the eyes only slightly protruberant (vs. prominently so in *L. alterna*), and lower ventral scale counts (197–204 in *L. greeri* vs. 211–230 in *L. alterna*) (Fig. 18).

Although the ranges of *L. greeri* and *L. leonis* are separated by ~270 km, the dorsal patterns of some individuals of the highly polymorphic *L. leonis* are similar to those seen in *L. greeri*. *Lampropeltis greeri* differs from *L. leonis* in lacking pronounced pattern polymorphism (with the exception of the population from Sierra del Laurel, Jalisco, where modest levels of pattern variation are evident), the snout/head color matches the body ground color (only in some individuals of *L. leonis*), the presence of postocular black markings (rare in *L. leonis*), and the lack of ontogenetic color pattern change (often pronounced in some pattern types of *L. leonis*) (Figs. 23, 24).

Remarks: Following Webb’s (1961) description of *L. greeri*, the species was sunk by Gehlbach and McCoy (1965), who considered it to fall within the known variation of *L. m. mexicana*. We view that decision as ill advised, given the distinctive morphology and color pattern of *L. mexicana* (*sensu stricto*), as well as the occurrence of *greeri* and *mexicana* in different biogeographic regions of Mexico. Although the distinctiveness of *greeri* relative to other taxa in the *mexicana* complex has long been recognized by herpetoculturists, that name has been mostly absent in the scientific literature from 1965 until its resurrection by Hilken and Schlepper (1998). Their arrangement, with *greeri* as a subspecies of *L. mexicana*, has been adopted by some authorities (Liner and Casas-Andreu, 2008; Heimes, 2016), while others have considered *greeri* as part of a monotypic *L. mexicana* (Wallach et al., 2014).

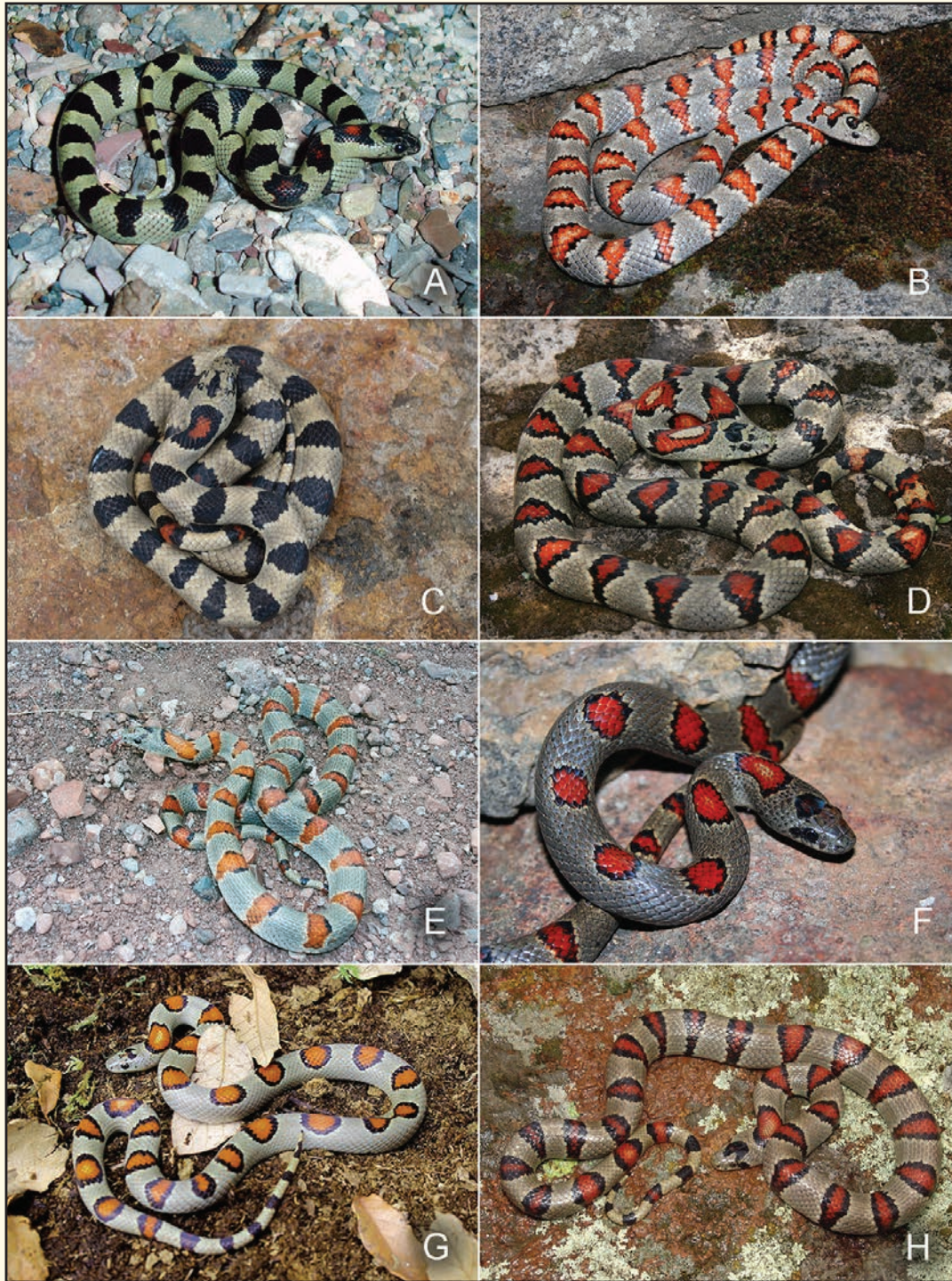


Fig. 23. Variation in *Lampropeltis greeri* from Durango, Zacatecas, and Aguascalientes, Mexico. (A) West-northwest of Canatlán, Municipio de Canatlán, Durango, elev. 2,306 m; (B) Rancho Santa Bárbara, Municipio de Durango, Durango, elev. ~2,300 m; (C) Rancho Santa Bárbara, Municipio de Durango, Durango, elev. ~2,260 m; (D) vicinity of Otinapa, Municipio de Durango, Durango, elev. 2,414 m; (E) Cerro de la Virgen, near Ciudad Zacatecas, Municipio de Guadalupe, Zacatecas, elev. 2,625 m; (F) La Ciénega, Municipio de Atolinga, Zacatecas, elev. 2,328 m; (G) Mesa Montoro, Municipio de San José de Gracia, Aguascalientes, elev. 2,350 m; and (H) Mesa Montoro, Municipio de San José de Gracia, Aguascalientes, elev. 2,385 m.

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Fig. 24. Variation in *Lampropeltis greeri* from Jalisco and Nayarit, Mexico. (A–C) Sierra del Laurel, Municipio de Villa Hidalgo, Jalisco, at border with Aguascalientes, elev. 2,435–2,545 m; (D) vicinity of Santa Catarina, Sierra de Huichola, Municipio de Mezquitic, Jalisco, elev. 2,550 m; (E) El Astillero, Sierra de Huichola, Municipio de Bolaños, Jalisco, elev. 2,300 m, road-killed specimen showing extreme pattern reduction; (F–H) Mesa de Nayar, Municipio de El Nayar, Nayarit, elev. 2,220 m.

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Lampropeltis leonis* (Günther)Coronella leonis* Günther, 1893: 110*Lampropeltis leonis*, Blanchard, 1920b: 4*Lampropeltis thayeri*, Loveridge, 1924*Lampropeltis mexicana thayeri*, Gehlbach and Baker, 1962: 298 (in part)*Lampropeltis mexicana*, Garstka, 1982: 29 (in part)*Lampropeltis mexicana thayerii*, Liner and Casas-Andreu, 2008: 118 (unjustified emendation)

Fig. 25. Variation in *Lampropeltis leonis* from Coahuila and Nuevo León, Mexico. (A) Chorro Canyon, Municipio de Arteaga, Coahuila, elev. 2,042 m; (B) vicinity of San Antonio de las Alazanas, Municipio de Arteaga, Coahuila, elev. 2,280 m; (C) vicinity of San Antonio de las Alazanas, Municipio de Galeana, Nuevo León (near border with Coahuila), elev. 2,180 m; (D) Sierra Zapalinamé, Municipio de Saltillo, Coahuila, elev. 2,283 m; and (E, F) northeast of La Ascensión, Municipio de Aramberri, Nuevo León, elev. 1,920 m.

© David G. Barker (A), José Luis Jibaja, courtesy of David Lazcano (B), Michael S. Price (C), Manuel Nevárez-de los Reyes (D), and Robert W. Hansen (E, F)

Type specimen: BMNH 89.7.3.41 (re-registered as 1946.1.4.10)

Type locality: “Mexico, Nuevo Leon.” Collected by W. Taylor, date not stated.

Distribution: Northern Sierra Madre Oriental and margins of Chihuahuan Desert in the states of Coahuila, Nuevo León, and Tamaulipas in northeastern Mexico, at elevations from 1,036 to 2,268 m.

Diagnosis: A moderate-sized (maximum TL = 1,219 mm) species of kingsnake characterized by extensive intra-populational and geographic pattern variation, including a coralsnake mimic pattern and a melanistic phenotype. This species is most similar to some populations of *L. alterna* and *L. greeri*, but differs from *L. alterna* by the presence of a golden-brown iris (vs. silver-gray in *L. alterna*), the head is only slightly distinct from the neck (vs. noticeably distinct in *L. alterna*), the eyes protrude only slightly from the outline of the head (vs. prominently so in *L. alterna*), and lower ventral scale counts (194–212 in *L. leonis* vs. 211–230 in *L. alterna*) (Fig. 18).



Fig. 26. Variation in *Lampropeltis leonis* from Nuevo León and Tamaulipas, Mexico. (A) Cañon Santa Rosa, vicinity of Iturbide, Municipio de Iturbide, Nuevo León, elev. 1,245 m; (B) just south of La Escondida, Municipio de Aramberri, Nuevo León, elev. 1,835 m; (C) MX Highway 61 southeast of La Escondida, Municipio de Aramberri, Nuevo León, elev. 2,015 m; (D) captive-bred offspring of female shown in (C); (E) 16 airline km ENE of Miquihuana, Municipio de Miquihuana, Tamaulipas, elev. 1,740 m; and (F) 31 airline km NW of Jaumave, Municipio de Jaumave, Tamaulipas, elev. 1,703 m.

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Compared to *L. greeri*, *L. leonis* exhibits high levels of pattern polymorphism as well as melanism. The snout and head color matches the body ground color only in some individuals of *L. leonis*, compared to matching in all specimens of *L. greeri* examined. Most individuals of *L. leonis* lack black post-ocular markings, which are present in *L. greeri*. Ontogenetic color pattern change is common in captive-bred *L. leonis* and absent in *L. greeri* (Figs. 25, 26).

Remarks: Most recent authors have used the epithet *thayeri* (usually as a subspecies of *L. mexicana*) rather than *leonis*. The genesis of this priority of name usage is not clear, although Blaney's (1973) commentary (see Table 4) offers insight. In our view, if the populations of *mexicana*-group snakes in Nuevo León and adjacent areas of Coahuila and Tamaulipas warrant taxonomic recognition apart from *L. mexicana*, as we believe they do, then the name *Lampropeltis leonis* (Günther, 1893) has priority over *Lampropeltis thayeri* Loveridge, 1924. Therefore, we regard *L. thayeri* Loveridge, 1924 as a junior synonym of *L. leonis*. We note, however, that snakes occurring on the Gulf Coast-facing slopes of the northern Sierra Madre Oriental, including the type locality for *L. thayeri*, appear to have a fixed coral-snake-mimic pattern and show little evidence of color pattern polymorphism as seen in *L. leonis* from Nuevo León (Figs. 24, 25). If the Tamaulipan populations prove to be distinctive, the name *L. thayeri* is available.

Lampropeltis mexicana (Garman)

Ophibolus triangulus mexicanus Garman, 1884: 66

Coronella mexicana Günther, 1893: 110

Oreophis boulengeri Dugès, 1897: 284

Lampropeltis mexicana, Blanchard, 1920b: 7

Lampropeltis mexicana mexicana Gehlbach and Baker, 1962: 298

Type specimen: MCZ 4652, 4653 (syntypes designated by Blanchard, 1920b).

Type locality: "Mexico, near [Ciudad] San Luis Potosí." Collected by E. Palmer, August 1879.

Distribution: Eastern parts of the Central Mexican Plateau eastward into the Sierra Madre Oriental in Mexico. Confirmed records exist for the states of Aguascalientes, Guanajuato, Hidalgo, México, and San Luis Potosí, at elevations from 1,194 to 2,438 m. It may also occur in Tamaulipas (Terán-Juárez et al., 2015).

Diagnosis: A moderate-sized (maximum TL = 1,156 mm) species of kingsnake most similar to some individuals of *L. leonis* (Tamaulipas). The presence of black-bordered red blotches or bands on a gray or brown ground color is distinctive. A black postocular dash is present in *L. mexicana* (rare in *L. leonis*). Red head markings typically are elaborate, and often are tri-lobed; in *L. leonis*, the dorsal head markings, if present, differ from those seen in *L. mexicana* (Fig. 18). *Lampropeltis mexicana* also differs from *L. leonis* in lacking pattern polymorphism. Sexual dichromatism is evident in captive-bred *L. mexicana*, as adult males tend to be more brightly marked, a character discernible even in some captive-produced hatchlings. This species does not exhibit the degree of ontogenetic pattern change commonly seen in non-coral-snake pattern phenotypes of *L. leonis*. The dorsal blotches of individuals from the northern part of the range (Sierra La Trinidad, San Luis Potosí) are elongated, compared to snakes from more southern localities (Fig. 27). The ventral scale counts (190–200) are slightly lower, but partly overlap those for *L. leonis* (194–212).

Remarks: The composition of *L. mexicana* has varied since its description in 1884. Most workers have treated this taxon as something of a composite that variously included *alterna*, *greeri*, *leonis*, *mexicana*, and *thayeri*, with or without the recognition of subspecies. Our concept of this taxon is much narrower and corresponds in large part to the description and range of the former subspecies *L. m. mexicana* (Gehlbach, 1967), although with a modified distribution to reflect recent field discoveries.



Fig. 27. Variation in *Lampropeltis mexicana* from San Luis Potosí and Guanajuato, Mexico. (A, B) Sierra La Trinidad near Guadalcázar, Municipio de Guadalcázar, San Luis Potosí, elev. 2,127 m; (C) vicinity of Alvarez, Municipio de Zaragoza, San Luis Potosí, elev. 2,381 m; (D) Valle de los Fantasma, Municipio de Zaragoza, San Luis Potosí, elev. 2,199 m; (E) Hwy 70 ~16 km W of turnoff to Alvarez, Municipio de Zaragoza, San Luis Potosí, elev. 2,200 m, DOR; (F) Sierra San Miguelito, Municipio de San Luis Potosí, San Luis Potosí, elev. ~2,415 m; (G, H) north of San Luis de la Paz, Municipio de San Luis de la Paz, Guanajuato, elev. 2,156 m.

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***Lampropeltis ruthveni* Blanchard**

Lampropeltis ruthveni Blanchard, 1920a: 8

Lampropeltis triangulum arcifera, Williams, 1978: 179 (in part)

Lampropeltis ruthveni, Garstka, 1982: 30

Type specimen: USNM 46558

Type locality: “Patzcuaro, Michoacan, Mexico.” Collected by E. W. Nelson on 2 August 1892. Garstka (1982) stated that the locality with the specimen is Potrenaro, Michoacán.

Distribution: Southern part of the Central Mexican Plateau and adjacent Transverse Volcanic Belt, at elevations from 1,925 to 2,667 m. Confirmed records exist for Jalisco, Michoacán, Guanajuato, Querétaro, and Hidalgo.

Diagnosis: A moderate-sized (maximum TL = 1,295 mm) species of kingsnake most similar to nearby populations of *L. polyzona* (formerly *L. triangulum arcifera*; see Ruane et al., 2014) (Fig. 28). A tricolor pattern, a black head, and often lighter markings on the snout, are present in both species; however, in *L. ruthveni* the head is broader and distinct from the neck, whereas in *L. polyzona* the head is only slightly distinct from the neck (Fig. 29). The body of *L. ruthveni* is relatively more robust compared to the more slender habitus of *L. polyzona*, and it also differs by a lower number of ventral scales (182–195 vs. 204–222 in nearby *L. polyzona*). Although these two species have not been found in sympatry, apparently reflecting different habitat and elevation preferences, the range of *L. ruthveni* largely is circumscribed by that of *L. polyzona*.

Remarks: *Lampropeltis ruthveni* received scant mention in the scientific literature following its description in 1920. Taylor (1940) reported on the second and third known specimens, both from Michoacán. Much later, however, Williams (1970, 1978) did not distinguish *ruthveni* from nearby *L. triangulum*, and thus considered *ruthveni* a synonym of that species.

Publications that followed Williams in both scientific and hobbyist literature often mistakenly reported on specimens of *ruthveni* under *L. triangulum arcifera*. Examples include Herman (1979), Armstrong and Murphy (1979), Tryon and Murphy (1982), Fitch (1985), Blatchford (1985), Slavens (1988), Campbell and Lamar (1989), Markel (1990), Applegate (1992), Thissen and Hansen (1996), and Bartlett and Markel (2005). The common name “Jalisco milk snake” frequently was used in hobbyist and herpetocultural literature, and although intended to represent *L. t. arcifera*, instead nearly always referred to *L. ruthveni*.

Subsequently, Garstka (1982) provided diagnostic characters for *L. ruthveni* that demonstrated its distinctiveness from *L. triangulum*. Williams (1988) acknowledged Garstka’s confirmation of *L. ruthveni* as a distinct species in the *mexicana* species group. Williams continued to confound these taxa, however, by including data on captive reproduction for *L. t. arcifera* based on the report by Tryon and Murphy (1982). As noted by Tryon and Murphy, the Dallas Zoo’s breeding pair of snakes was collected in Rancho San Francisco, Jalisco, an area where only *L. ruthveni* is present. Williams’ statement (p. 126) that “*arcifera* occurs between 2075 and 2317 m” was taken from Tryon and Murphy, and thus pertains to *ruthveni*. Moreover, Williams’ color figure (p. 98) of “*Lampropeltis triangulum arcifera*” is a *L. ruthveni*, and reportedly was based on a specimen at the San Antonio Zoo and collected from near Amealco, Querétaro (D. Blody, pers. comm.). In his list of referred specimens, Williams (1988) includes a mix of *ruthveni* and *triangulum* (*sensu lato*).

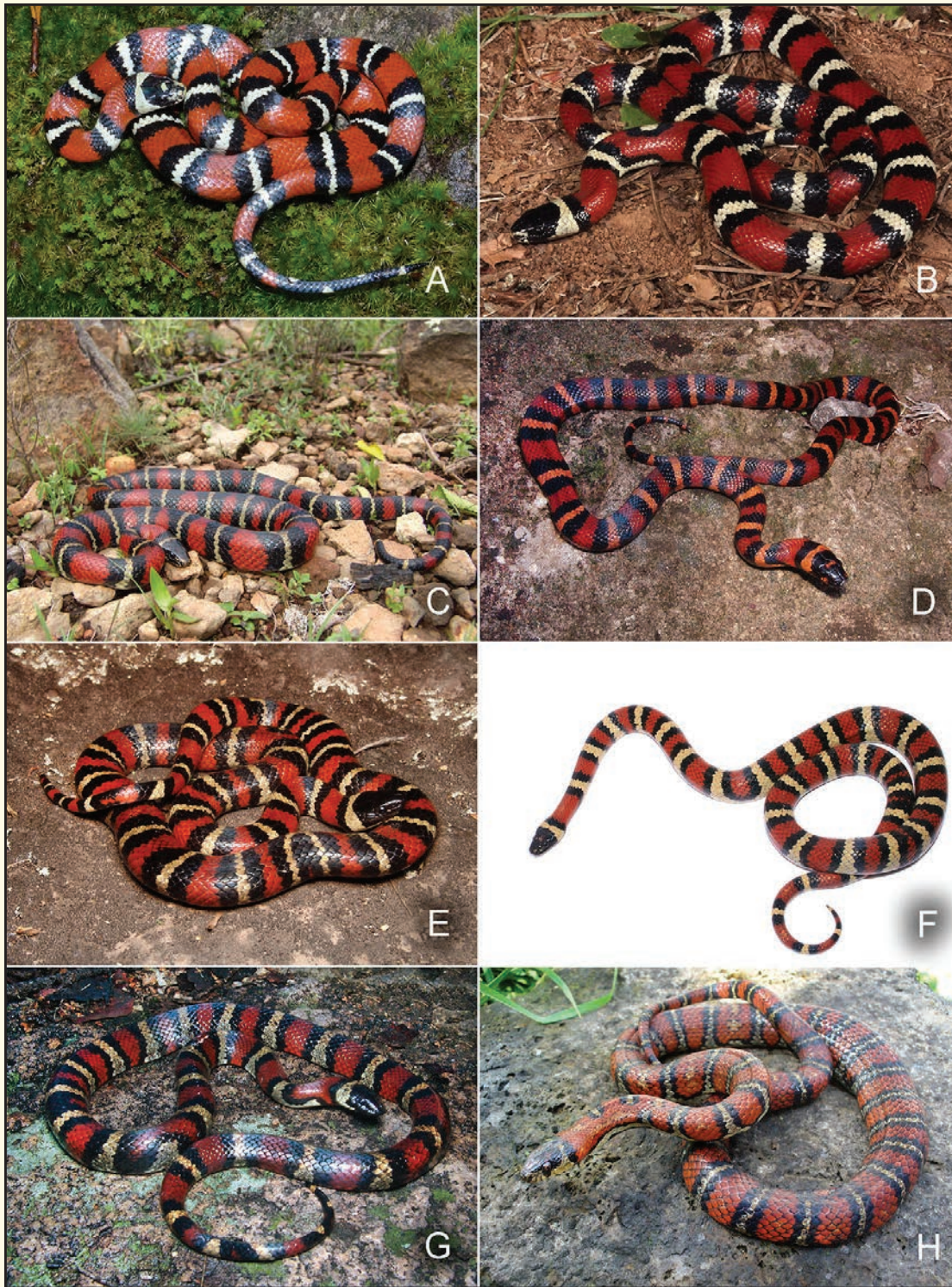


Fig. 28. Variation in *Lampropeltis ruthveni* from Jalisco, Michoacán, Guanajuato, Querétaro, and Hidalgo, Mexico. (A) Cerro la Campana, Municipio de Atenguillo, Jalisco, elev. 1,925 m; (B) Presa del Ohogado, 3 km S of Quila El Grande, Sierra de Quila, Municipio de Tecolotlán, Jalisco, elev. 1,975 m; (C) Tapalpa, ~1.5 km by air NE, Municipio de Tapalpa, Jalisco, elev. 2,207 m; (D, E) ~9 km by air NE of San José de Gracia, Municipio de Marcos Castellanos, Michoacán, elev. 2,073 m; (F) 6.3 km by air SE of Coroneo, Municipio de Coroneo, Guanajuato; elev. 2,222 m; (G) vicinity of Amealco, Querétaro, elev. 2,331 m; and (H) El Sendo, 6.75 km WNW of Zócalo de Nopala, Municipio de Nopala de Villagrán, Hidalgo, elev. 2,245 m.

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Fig. 29. Head shape differences in *Lampropeltis ruthveni* (left) and *L. polyzona* (right) from an area of near sympatry, Municipio de Atenguillo, Jalisco. Note the much narrower head of *L. polyzona*. © Ivan T. Ahumada Carrillo

Lampropeltis webbi Bryson, Dixon and Lazcano

Lampropeltis mexicana, Bryson et al., 2001: 123 (misapplication)

Lampropeltis webbi Bryson, Dixon and Lazcano, 2005: 208

Type specimen: UANL 5684.

Type locality: “4.0 km west of El Palmito on Hwy. 40, Municipio Concordia, Sinaloa, México (23°33'14.2"N, 105°50'47.2"W), 2000 m elevation.” Collected by Robert Bryson, Deron Hartman, and Javier Banda on 30 June 2000.

Distribution: Known only from a short section of Mex Hwy 40 in the Durango–Sinaloa border region, Sierra Madre Occidental, Mexico, at elevations from 2,000 to 2,394 m.

Diagnosis: Modified from Bryson et al. (2005) to include data on new specimens. A small species of kingsnake (TL: at least 756 mm) with a tricolor pattern most similar to taxa in the *mexicana* complex (Fig. 30). It differs from the geographically closest members of the *mexicana* complex, *L. greeri* and *L. ruthveni*, by the presence of a higher number of ventral scales (216–221 vs. 197–204 in *L. greeri*, and 182–196 in *L. ruthveni*), and by a different body and head pattern (Fig. 18).

Remarks: Originally, the type specimen was reported as a range extension for *L. mexicana* (Bryson et al., 2001), but mitochondrial sequence data revealed the distinctiveness of this taxon (Bryson et al., 2005). This species is known from five specimens. The holotype and paratype are juveniles (266 and 371 mm TL, respectively). Three additional adult specimens have been collected since the species description. The longest of these (MZFC 26939) is 756 mm TL. Based on this limited sample, *L. webbi* might be the smallest species in the *mexicana* group, though the discovery of additional specimens could alter this view.



Fig. 30. Variation in *Lampropeltis webbi* from Sinaloa and Durango, Mexico. (A) Only known living example of this species, Hwy 40 near Durango–Sinaloa border, elev. 2,012 m; (B) Holotype (UANL 5684), Hwy 40, 4.0 km W of El Palmito, Municipio de Concordia, Sinaloa, elev. 2,000 m; (C, D) DOR (MZFC 26939), Hwy 40, 7.5 mi E of El Palmito (Sinaloa), Municipio de Pueblo Nuevo, Durango, elev. 2,156 m; (E) DOR (UANL 7579), Hwy 40, 16.7 mi E of El Palmito (Sinaloa), Municipio de Pueblo Nuevo, Durango, elev. 2,394 m; and (F) Paratype (TCWC 100530), Hwy 40, 29.1 km SW of Buenos Aires, Municipio de Pueblo Nuevo, Durango, elev. 2,360 m.

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CONSERVATION

Although Mexico has attracted the attention of resident and foreign herpetologists for many decades, the number of species recorded continues to grow (Wilson et al., 2013; Uetz et al., 2016). This increase reflects a combination of new discoveries in previously underexplored regions, as well as the application of modern molecular tools to reveal cryptic diversity (e.g., Bryson et al., 2014). Because Mexico is recognized as a global biodiversity hotspot (Mittermeier et al., 2005; Wilson and Johnson, 2010), it is critically important to fully document that country's herpetofauna. We feel that underestimates of biodiversity, particularly with regard to cryptic species, present obstacles to conservation (see Bickford et al., 2007).

Various metrics and ranking systems have been developed to describe the degree of threat and to support the formulation of conservation priorities for the herpetofauna of Mesoamerica. Here we review the existing rankings and provide updated conservation assessments in light of our improved knowledge of species ranges, and to reflect the partitioning of *L. mexicana* into three species.

The IUCN Red List (IUCN, 2015) established categories to reflect the degree of conservation concern, ranging from Least Concern (typically for species that are widespread and abundant) to Critically Endangered. A Data Deficient category is provided in cases where a species' distribution and conservation threats are unknown. Although the IUCN is the most widely used system for evaluating conservation needs globally, herpetologists working in Mexico and Central America have noted deficiencies with the system. Specific concerns center on underestimating the threats facing a number of species (Terán-Juárez et al., 2016; Nevárez-de los Reyes et al., 2016a).

The SEMARNAT system, developed by Mexico's national wildlife agency, uses three categories (Endangered, Threatened, Special Protection), though not all species have been assessed (SEMARNAT, 2010).

The Environmental Vulnerability Score (EVS) originally was developed for assessing the conservation status of Honduran amphibians and reptiles (Wilson and McCranie, 1992), but subsequently has been applied to Mexican reptiles (Wilson et al., 2013). The EVS consists of a three-part scale that takes into account a species' geographical distribution, ecological distribution, and degree of human persecution. Recently, the EVS has been modified to incorporate the "biogeographical provinces" of Mexico (Grünwald et al., 2015), and we use this revised framework for updating the EVS values for the species of *Lampropeltis* discussed herein.

The Conservation Status Score (CSS) is derived from an assessment of geographic and ecological distribution, on a scale of 3 to 36, with lower numbers indicating species with small ranges and relatively narrow ecological tolerances (Wilson and Townsend, 2010). The CSS does not account for specific threats, however, such as commercial exploitation or habitat degradation. A low CSS can be viewed as indicating the potential for endangerment given small range sizes and narrow ecological tolerances.

Some limitations common to all of the above rating and ranking schemes are that they (1) fail to account for ongoing habitat loss (e.g., what percentage of historical range is potentially occupied?); (2) do not address impacts of global climate change (e.g., elevational shifts or loss of habitats); (3) lack any measure of "ecological resilience" (i.e., the extent to which some species are able to persist or even thrive in modified environments); and (4) do not prioritize evolutionary novelty (i.e., the extent to which a clade contributes to regional biodiversity; see Isaac et al., 2012, for a discussion of this viewpoint). These issues and others can be addressed in narrative fashion, but currently are not part of a formal framework that might be used in prioritizing conservation efforts.

We used all of the available information, included in our revised EVS values, to provide a summary assessment of the conservation status of each species.

Lampropeltis alterna.—Most of the United States range of this species is located in remote areas of low human population density and is unlikely to experience negative anthropogenic impacts in the foreseeable future. Road mortality likely is of some significance along the major highways that intersect *L. alterna* habitat; however, there are relatively few roads within its range. An exception lies in the Permian Basin of Texas—a region of intensive oil and natural gas extraction. The concentration of oil wells, along with networks of service roads, can easily be seen from satellite photos (Fig. 31) and has resulted in extensive habitat impacts in localized areas.

At one time, *L. alterna* was considered rare and fully protected in Texas; collection was prohibited from 1977 to 1986. Field searches by amateur and professional herpetologists later revealed this species to be relatively common over much of its range in Texas, and that perceptions of rarity reflected low levels of surface activity that were further restricted by atmospheric conditions (Tennant, 1984; Tennant et al., 1998).

In New Mexico, *L. alterna* is known only from two counties and a small number of specimens, is legally protected from collection, and is listed as endangered (Hakkila, 1994; Degenhardt et al., 1996; Painter et al., 2002; NMDGF, 2016). The relative scarcity of specimens known from New Mexico might reflect range-margin habitat conditions, but a markedly lower search effort due to the remote location of the known range, and legal restrictions, likely contribute to this data deficit. For example, we are aware of several anecdotal reports of individuals found by amateur herpetologists, who are reluctant to share this information with state conservation biologists out of concern for legal repercussions. Therefore, these observations and distributional data remain unavailable to researchers.



Fig. 31. The Yates Oil Field lies within the Permian Basin of West Texas, a region containing considerable reserves of oil and natural gas. The small town of Iraan, Pecos County, can be seen in the upper right of this satellite image.

© Google Maps

Although Painter et al. (2002) suggested that the New Mexico populations of this species were at risk from hobbyist or commercial exploitation, this assumption seems unlikely given (1) the low levels of surface activity, especially pronounced in the western parts of the United States range (e.g., El Paso, Hudspeth, and Culberson counties, Texas; Eddy and Otero counties, New Mexico); and (2) the general paucity of roads within *L. alterna* habitat in New Mexico. We note that removal of individual snakes from a local population, whether from collection or vehicle mortality, is confined to paved roads. Not only are roads scarce within the New Mexico range of *L. alterna*, they constitute a narrow ribbon imbedded within a much larger landscape of inaccessible habitat. Therefore, the proposition that a species like *L. alterna* that rarely is active on the surface and only can be hunted in a tiny fraction of its range could be impacted at an ecologically significant level by collection pressure seems unfounded.

A recent status report for threatened and endangered species in New Mexico stated, “the removal of even a small number of females from a population could significantly affect the population size” (NMDGF, 2016: 72). Here we note that *L. alterna* appears to fit an ecological pattern common among other species of temperate-zone colubrid snakes: the greater detectability of males reflects a combination of mate-searching behavior and reduced activity by reproductive females (Gregory et al., 1987). For example, in a sample of 295 *L. alterna* found active in Texas, only 90 (30.5%) were females (Miller, 1979; RWH, unpublished). Because the sex ratios of captive-hatched offspring are approximately 1:1 (Miller, 1979; RWH, GTS, unpublished), we consider this circumstantial evidence of reduced movements of adult females.

Hammerson and Santos-Barrera (2007) stated that “collectors perhaps have depleted roadside populations in some areas”...and that “captive breeding has generated a good supply of animals for the pet trade.” Miller (1979), however, found no evidence that numbers of snakes were reduced adjacent to the most heavily hunted roads.

Tennant and Allender (1980: 103) discussed the popularity of *alterna* among snake hunters in Texas, its value on the black market, and suggested that protected status came about because the “small population...in Texas came under such pressure from collectors that, in 1977, the species was awarded the slim protection of endangered status.” Tennant (1984) noted the proliferation of captive-produced offspring and speculated that this would reduce the demand for wild-collected snakes.

Although the majority of the range of *L. alterna* lies in Mexico, its distribution remains poorly known in that country (Nevárez-de los Reyes et al., 2016b). Moreover, most of the presumed Mexican range of *L. alterna* is in remote, roadless areas with low levels of human habitation. These areas should retain viable *L. alterna* habitat for the long-term. Nonetheless, portions of the range that are of special interest due to possible contact with *L. leonis* have been severely degraded. For example, at the southeastern extent of its range near Monterrey, Nuevo León, the habitat has been nearly eliminated as a consequence of housing developments and industrial activities (RWH and GTS, pers. observ.), but remaining habitat around Monterrey persists where the terrain is too steep to allow for housing construction (Fig. 32). A similar situation exists in the areas around Saltillo and Monclova in Coahuila. Even in “protected areas,” such as the Sierra Zapalinamé of Coahuila, illegal housing expansion continues without intervention from authorities. Finally, we know little about genetic variation across the range of *L. alterna* in Mexico, which spans ~535 km from east to west and includes habitats ranging from desert to high-elevation Madrean woodland.



Fig. 32. The approximate collection site for *Lampropeltis alterna* (UANL 5018) at the base of Cerro de la Silla on the outskirts of Monterrey, Municipio de Guadalupe, Nuevo León. Although the habitat of *L. alterna* has been nearly eliminated in and around Monterrey, small patches persist where the steep terrain prevents building construction.

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Current climate models predict a significant decline in the North American monsoon in response to global warming (Pascale et al., 2017). This change would result in reduced summer precipitation in the Trans-Pecos Region of Texas and adjacent areas of northern Mexico, potentially leading to range contraction in *L. alterna*, especially in the more arid parts of its range.

The Mexican conservation authority, considering only the range of *L. alterna* in Mexico, has classified this species as Threatened (SEMARNAT, 2010). Hammerson and Santos-Barrera (2007) considered this an IUCN Least Concern species, inclusive of the range across two countries. Wilson et al. (2013) calculated an EVS of 14 (Mexico only), which falls in the lower end of the High Vulnerability category (range of scores = 14–20). Wilson and Townsend (2010) assigned this species a CSS of 4 (range = 3–36, with lower numbers indicating greater vulnerability). In our assessment of *L. alterna* based on the most recent distributional data, we obtained an EVS of 14 for Mexico (same as that obtained by Wilson et al., 2013). We also applied the EVS concept to the United States portion of the range and obtained an EVS of 13.

Lampropeltis greeri.—The known range of this species occurs almost exclusively in rocky habitats within pine-oak or oak-dominated woodlands that are subject to low-impact use such as livestock grazing, timber harvesting, or small scale farming, including marijuana and opium poppy cultivation. The human population density in this area is relatively low. Although long considered endemic to Durango and Zacatecas, *L. greeri* recently has been recorded from Aguascalientes, Jalisco, and Nayarit (Quintero-Díaz et al., 2001; Hansen and Bryson, 2009; Hansen et al., 2011), thus expanding the known range. Overall, we consider this taxon's conservation status as stable. The Mexican conservation authority regards *L. mexicana* (*sensu lato*, inclusive of *greeri*, *leonis*, and *mexicana* by implication) as Threatened (SEMARNAT, 2010). Under the umbrella of *L. mexicana*, Vázquez-Díaz and Quintero-Díaz (2007) considered this an IUCN Least Concern species. Wilson et al. (2013) and Cruz-Sáenz et al. (2017) calculated an EVS of 15 (lower end of the High Vulnerability category), and Wilson and Townsend (2010) obtained a CSS of 7, both values determined as part of *L. mexicana*. In our assessment of *L. greeri* based on the most recent distributional data, we obtained an EVS of 14.

Lampropeltis leonis.—This species occupies a fairly small range, but occurs in habitats ranging from Chihuahuan Desert-edge to pine-oak woodlands. Habitat loss is concentrated in areas of human habitation, but overall the majority of the known range is largely intact. Even in areas where crops are grown, snakes continue to be found on the margins of fields, often where farmers have piled rocks cleared from their fields (C. Grünwald and M. Ingrasci, pers. comm.). Sources of mortality include indiscriminate killing by humans, focused especially on tricolor pattern variants of this species, as well as for *L. mexicana*, *L. ruthveni*, and presumably *L. webbi*, in the mistaken belief that these are venomous coral snakes (of which the ranges mostly do not overlap with *mexicana*-group kingsnakes). Such impacts, however, are in areas of human habitation and thus are not considered ecologically significant on a broader scale. Much of the habitat for *L. leonis* is in rugged, rocky, and otherwise challenging (for humans) terrain, but in light of the more restricted distribution of this species (as distinct from *L. mexicana*), we consider this taxon's conservation status as vulnerable. The Mexican conservation authority regards *L. mexicana* (*sensu lato*, inclusive of *greeri*, *leonis*, and *mexicana* by implication) as Threatened (SEMARNAT, 2010). Under the umbrella of *L. mexicana*, Vázquez-Díaz and Quintero-Díaz (2007) considered this an IUCN Least Concern species. Wilson et al. (2013) calculated an EVS of 15 (lower end of the High Vulnerability category), and Wilson and Townsend (2010) obtained a CSS of 7, both values determined as part of *L. mexicana*. Nevárez-de los Reyes et al. (2016a), considering this species as part of *L. mexicana*, argued for an IUCN rating of Endangered. In our reassessment of this taxon as a species distinct from *L. mexicana*, we obtained an EVS of 16.

Lampropeltis mexicana.—Our understanding of the range of *L. mexicana* (previously *L. m. mexicana*) has been altered not only by revising our concept of this species (i.e., adopting a narrower meaning of *L. mexicana* in contrast to earlier views as a wide-ranging, polytypic species), but also by recent discoveries of southward range extensions to include the states of Hidalgo and México (Hansen et al., 2016). Although much of the habitat for this species lies in relatively rugged terrain, large areas of the presumed historical range have been severely impacted by human activity, and we assume that populations of *L. mexicana* have been extirpated from many of these areas. Local people regard this species as venomous, and presumably individual snakes are killed as a result (Hernández Arciga, 2012). We regard this taxon as threatened over much of its range, and suggest that certain range segments might qualify for endangered status. The Mexican conservation authority regards *L. mexicana* (*sensu lato*, inclusive

of *greeri*, *leonis*, and *mexicana* by implication) as Threatened (SEMARNAT, 2010). Under the umbrella of *L. mexicana*, Vázquez-Díaz and Quintero-Díaz (2007) considered this an IUCN Least Concern species. Wilson et al. (2013) and Terán-Juárez et al. (2016) calculated an EVS of 15 (lower end of the High Vulnerability category) and Wilson and Townsend (2010) obtained a CSS of 7, both values determined as part of a more inclusive *L. mexicana*. Nevárez-de los Reyes et al. (2016a), considering this species as part of *L. mexicana*, recommended an IUCN rating of Endangered. In our reassessment of *L. mexicana* (*sensu stricto*), we obtained an EVS of 16.

Lampropeltis ruthveni.—This species' preference for rocky habitats provides protection in some areas where bordering lands are converted for agricultural use. Although central Mexico is densely populated and human impact is expanding outward from this region, *L. ruthveni* persists in some disturbed habitats. The large-scale loss of habitat for industrial agriculture in Guanajuato and Querétaro, however, warrants a "Near Threatened" designation for those areas. In Hidalgo, Jalisco, and Michoacán, native habitats have been impacted on a smaller scale and we regard these populations as "Least Concern." The current range of this species is largely fragmented as a result of habitat loss, such that population connectivity no longer exists, a situation that will be amplified with human population growth and a warming climate (Sinervo et al., 2010). Flores-Villela et al. (2010) regarded *L. ruthveni* as a Threatened species under the SEMARNAT system. Ponce-Campos and Flores-Villela (2007) considered this an IUCN Near Threatened species. Wilson et al. (2013) and Cruz-Sáenz et al. (2017) calculated an EVS of 16 (lower end of the High Vulnerability category), and Wilson and Townsend (2010) obtained a CSS of 3. In our reassessment of this taxon in light of recent distribution records that extend the range into Guanajuato and Hidalgo, we obtained an EVS of 16.

Lampropeltis webbi.—The range of *L. webbi* appears to be fully contained within Mexico's largest concentration of illegal drug production, centered on the Durango–Sinaloa border region (Reed, 2015). Some small-scale farming and logging take place, but the steep, rugged terrain limits the extent of these activities. This taxon has not been evaluated under the SEMARNAT system. Flores-Villela (2007) placed this species in the IUCN Data Deficient category. Wilson et al. (2013) gave this species an EVS score of 16, and Wilson and Townsend (2010) calculated a CSS of 3. Our reassessment of this taxon based on additional material and reports from the field (C. Grünwald and J. Jones, pers. comm.) resulted in an EVS of 17.

SUGGESTIONS FOR FUTURE RESEARCH

Historically, attempts to characterize variation and infer relationships within the *Lampropeltis mexicana* group have been hampered by inadequate samples and a rudimentary understanding of ranges. This remains true today, with most localities in Mexico represented by single specimens, and many areas of potential occurrence have not been explored. Fieldwork should be prioritized with two goals in mind. One is to undertake focused field surveys in areas where species in the *mexicana* group have not been documented. Although a number of range extensions have been reported in the last 10+ years, we suggest that some important discoveries await, possibly including undescribed forms. An examination of our range maps will indicate where gaps exist, and thus suggest future survey targets. A second goal for fieldwork should be to examine areas of potential contact involving pairs of *mexicana*-group species. We suggest several specific targets.

(i) Although *L. alterna* is unvouchered from Chihuahua, the species almost certainly occurs in the northeastern part of the state (Carabias Lillo et al., 1997).

(ii) The large state of Zacatecas has received relatively little attention from field collectors. Although *L. greeri* is known from several localities in Zacatecas, much of the state is underexplored and *L. mexicana* and *L. alterna* likely will be found there.

(iii) Areas in northern Nuevo León and southeastern Coahuila present challenges for field workers given the rugged terrain, lack of road access in some places, and compromised habitats elsewhere. Nonetheless, our knowledge of the distribution of *L. alterna* and *L. leonis* in this region is fragmentary and new records will be valuable.

(iv) The present gap between southernmost records for *L. leonis* in Nuevo León and Tamaulipas and the northernmost confirmed record for *L. mexicana* near Guadalcázar, San Luis Potosí, contains unsampled outliers of the Sierra Madre Oriental. Specific targets for fieldwork should include the Sierra Azul (approximately 23.18079°N, 100.33786°W) and the Sierra Las Ventanas (= Sierra de Nanola) (approximately 22.99722°N, 99.94796°W).

(v) In Hidalgo and adjacent México, the ranges of *L. mexicana* and *L. ruthveni* approach one another and the two species appear to occupy similar habitats. Relatively little work has been done in this area, and we expect that additional populations of both species will be discovered.

(vi) Our knowledge of the biology of *L. webbi* obviously is constrained by low sample size, with all specimens coming from along Mex Hwy 40. Nevertheless, based on the north–south extent of the humid pine-oak forest in this area, this species potentially has a much larger range. Logistical challenges associated with the extremely rugged terrain, a lack of roads, and safety concerns related to illegal drug operations are obstacles to field research and should be taken into account by those considering fieldwork in this region.

(vii) The apparent range gap between the montane population of *L. alterna* in Durango (Ingrasci et al., 2008) and the northernmost record of *L. greeri* to the south (Savage and Hansen, 2009) contains what appears to be suitable habitat for one or both species.

(viii) Within the range of *L. leonis*, additional samples are needed from areas between known localities on the eastern slopes of the Sierra Madre Oriental (populations formerly referred to “*thayeri*”) and the more inland records in Nuevo León.

(ix) In the United States, additional records of *L. alterna* likely can be added for New Mexico and the adjacent areas of Texas. Because nearly all of the undersampled or unsurveyed areas of potential habitat in Texas lie on privately owned lands, access for researchers has been limited.

(x) The easternmost boundary for *L. alterna* in Texas should be explored, especially in light of anecdotal reports of snakes from the West Prong of the Nueces River (T. D. Hibbitts, pers. comm.).

CONCLUSIONS

The available distributional data for species in the *mexicana* group reveal a pattern of discrete geographic units. Although samples are lacking for some putative range gaps, there is no indication of hybridization between adjacent taxa. Based on morphology, color pattern, and allopatric ranges, we recognize six species-level taxa in the *mexicana* group. All but one of these originally was described as a full species. Our work sets the stage for more fine-scaled sampling in areas identified as potential contact zones, as well as for studies using newer molecular tools to examine historical gene flow and to infer evolutionary relationships. Our range maps, inclusive of estimated overall distribution, present several hypotheses that can be tested by future fieldwork.

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Appendix 1. List of specimens included in the distribution maps. Collection acronyms follow Sabaj (2016), except where noted.

Lampropeltis alterna.—MEXICO: COAHUILA: **Municipio de Castaños**: ASU 32853, TNHC 101581–101585; **Municipio de Cuatro Ciénegas**: UAZ 41687, FMNH 47090, TNHC 100776, 101586–101588, 101591–101592, UANL 3706; **Municipio de Ramos Arizpe**: TNHC 101593, 101673–101675, UF 24750, UANL 5016, Strecker Museum 10318, Ernest C. Tanzer 864 (now lost); **Municipio de Saltillo**: USNM 110819; **Municipio de Viesca**: TNHC 101594; DURANGO: **Municipio de Lerdo**: TNHC 101907; **Municipio de Rodeo**: TCWC 36892; **Municipio de Santiago Papasquiaro**: TNHC 100778, UTADC 1096, MZFC 26938; NUEVO LEÓN: **Municipio de Bustamante**: UANL 7662, 7672; **Municipio de García**: UANL 7405; **Municipio de Guadalupe**: UANL 5018; **Municipio de Hidalgo**: TNHC 100686; **Municipio de Mina**: UANL 6986; **Municipio de Monterrey**: UANL 459. USA: NEW MEXICO: **Eddy County**: UTEP 18600, MSB 52000, 71605; **Otero County**: MSB 96332; TEXAS: **Brewster County**: BUM 6444, CAS 200387, MCZ 15773, 162068, SDNHM 62753, SRSU 6483, 1558, 311, 4816, 4768, 2218, 1776, 1639, TCWC 72800, 72799, 72796, 69495, 82574–82575, 64458, 90216, 86031, 84896, 72798, 70060–70061, 70072, 64455–64456, 92940, TNHC 101595–101612, 101628–101635, USNM 328671, UTA 38306, 51451, 40365, 38781, 38996, 40365, 40818–40819, 51451, 17969; **Crane County**: UTA 40419; **Crockett County**: SRSU 6521–6522, TNHC 101636, UCM 63520, UF 106718, UTA 40371; **Culberson County**: Louisiana Technical University 41517 (now at University of Louisiana Monroe), TNHC 101637–101640, UMMZ 123494, UTADC 26756, UTEP 542 (not plotted); **Edwards County**: Fort Worth Museum 6308 (specimen now lost), UMMZ 122688, UTA 8674; **El Paso County**: TNHC 101641, UTEP 18912, 20598; **Hudspeth County**: TNHC 101642–101651, UTEP 1939, 2866, 9404; **Jeff Davis County**: ANSP 14977, SRSU 3037, TCWC 26181, 28343, 66189, 70409, 72797, 81188, 82576, 84947, 87476, 90683, 91926, 94376, TNHC 50697, 100777, 101652, 101676–101690, UMMZ 227026, USNM 328670, UTA 28895, 40372, UTADC 7459–7460; **Kinney County**: LSUMZ 55330, SBMNH 197, TCWC 26179; **Pecos County**: TNHC 7420, 66562, 89828, 101691–101693, UTA 40369–40370, 40827, 50566, 50583; **Presidio County**: CAS 178418, TCWC 64325–64326, 65365, 70067, 85093, 92942, TNHC 4181, 101704–101718, USNM 328672, UTA 7875, 35461, 38323–38325, UTEP 14724–14725; **Reeves County**: TNHC 101719; **Sutton County**: TNHC 101720; **Terrell County**: CAS 204040, KU CT 11963, LACM 28772, 66925, SRSU 3574, TCWC 70411, 71486, 82577–82580, 82580, 87478, 91915–91916, 92943, 94375, TNHC 4772, 89741, 894461, 95426, 101721, 101762–101780, UAZ 34527, USNM 328673, UTA 32599, 34540, 38390, 38545, 51452, 38389, UTEP 2689; **Upton County**: TNHC 95426, UTA 40418, 42518; **Val Verde County**: AMNH 102223, 107362, 169520–169522, ASNH 5705–5718, 8261, 10378, 12846–12847, 12895–12896, CAS 129650, 200388, FMNH 197798, KU 174807, 174944–174945, 175568, 180258, LACM 76568–76569, 102577, 109132, LSUMZ 81001, MCZ 156175, 157764–157765, 162067, SDNHM 60491–60492, 60494, 62754, SRSU 1567, 1620–1622, 1638, 1644, 2318, 2924–2927, 2948, 2973, 3019–3023, 3040, 3527–3528, 3575–3576, 4813, UAZ 35212, 41688, UMMZ 121400, 124029, 131410, 134105, 138256, 142688–142689, 170390, 172830, UTA 2633, 2941, 3921, 6680–6681, 7188, 7874, 8095, 8568, 8668, 8671, 8690, 9719, 28896, 33754, 35462, 37669–37670, 38369–38371, 38373, 38716, 40825–40826, UTEP 2545, 9038, TCWC 26180, 30515, 33759–33760, 62351, 64457, 67069, 68346, 70064, 70071, 70074–70075, 70412, 72251, 72801, 87863, 90142, 90412, 91319, 92468–92469, TNHC 33939–33940, 47223, 66037, 65730, 85170, 101781–101800, 101840–101847.

Lampropeltis greeri.—MEXICO: AGUASCALIENTES: **Municipio de San José de Gracia**: MZFC 13655, TNHC 101848–101853, UAA 263, 273, 322; DURANGO: **Municipio de Durango**: ASU 32854, CM 118916, LACM 107230–107231, 126257–126258, MCZ 157754, MSU 190, TNHC 101854–101866, UANL 5940, 6024, 7469, UTA 9013, 11272, **Municipio de Canatlán**: UTADC 2599; JALISCO: **Municipio de Bolaños**: UTADC 7519; **Municipio de Mezquitic**: TNHC 101867–101868, UTADC 7501, 7512, 7516–7517; **Municipio de Villa Hidalgo**: UTADC 2602–2604; NAYARIT: **Municipio de El Nayar**: UTADC 6833–6835; ZACATECAS: **Municipio de Atolinga**: MZFC 23706; **Municipio de Guadalupe**: MCZ 162279, TNHC 100779; **Municipio de Jerez**: UTADC 8938; **Municipio de Villanueva**: Escuela Nacional de Ciencias Biológicas, Mexico City (IPN-ENCB) 19769.

Lampropeltis leonis.—MEXICO: COAHUILA: **Municipio de Arteaga**: ITESM (Instituto Tecnológico y Escuela Superior de Monterrey) 2 specimens, uncatalogued (examined by Garstka, 1982; now lost), UANL 7705, UTA 12780; **Municipio de Saltillo**: TNHC 100687, UANL 7693; NUEVO LEÓN: **Municipio de Aramberri**: MCZ 156274–156277, 162091–162192, TNHC 101870–101878, UAZ 55938, UTA 6135, 16132; **Municipio de Doctor Arroyo**: UANL 3775–3776; **Municipio de Galeana**: FMNH 30819–30121, TNHC 100780, 101869 (formerly Ernest A. Liner 4022), 101879, TU 16483, UANL 1582; **Municipio de Iturbide**: UANL 5773, 6846, UTA 16133; TAMAULIPAS: **Municipio de Jaumave**: TNHC 101880, UANL uncatalogued (1 specimen), 6428, 6472; **Municipio de Miquihuana**: MCZ 18551, TNHC 101881, UANL 7954–7955; **Municipio de Tula**: AMNH 107290.

Lampropeltis mexicana.—MEXICO: AGUASCALIENTES: **Municipio de El Llano**: UAA (1 specimen, uncatalogued); GUANAJUATO: **Municipio de Guanajuato**: IBH (CNAR) 12716; **Municipio de San Diego de la Unión**: IBH (CNAR) 26352; **Municipio de San Luis de la Paz**: TNHC 101882–101885; HIDALGO: **Municipio de Mixquiahuala de Juárez**: CH-CIB 3357; **Municipio de Tepeji del Río de Ocampo**: Omar Avalos private collection; MÉXICO: **Municipio de Jilotepec**: UTADC 8646. SAN LUIS POTOSÍ: **Municipio de Guadalcázar**: MZFC 26940, TNHC 101886–101887; **Municipio de San Luis Potosí**: MZFZ IMG 14–16; **Municipio de San Nicolas Tolentino**: UTA 11271; **Municipio de Zaragoza**: AMNH 77602, MCZ 19022–19025, 24976–24981, UANL 5603, 6842–6844, uncatalogued (1 specimen), USNM 120823, UTA 35463–35464; **Municipio de Salinas**: CM 59980.

Lampropeltis ruthveni.—MEXICO: GUANAJUATO: **Municipio de Acámbaro**: UTADC 8581; **Municipio de Coroneo**: UTADC 8583; **Municipio de Yurida**: UTADC 8582; HIDALGO: **Municipio de Huichapan**: CH-CIB 037, TNHC 101888; **Municipio de Nopala de Villagrán**: MZFC-ID-5, MZFC 23645–23646; **Municipio de Tepeji del Río de Ocampo**: Roth-Monzón et al. (2011); JALISCO: **Municipio de Atemajac de Brizuela**: KU 155528; **Municipio de Atenguillo**: UTADC 8556; **Municipio de Tapalpa**: LACM 37307, TNHC 101889–101893, UTA 12345–12346, 27460–27464; **Municipio de Tecolotlán**: UTADC 8119; MICHOACAN: **Municipio de Chilchota**: MSU 7234; **Municipio de Marcos Castellanos**: TNHC 10194–10198; **Municipio de Morelia**: CHUM-INIRENA 564, 1244, FMNH 106013, TNHC 101899–101901, UIMNH 17780, UMSNH uncatalogued (Garstka, 1982); **Municipio de Patzcuaro**: USNM 46558; **Municipio de Quiroga**: LSUMZ 40433; **Municipio de Uruapan**: FMNH 104650, 105109–105110; **Municipio de Zinapécuaro**: CHUM-INIRENA 876; QUERÉTARO: **Municipio de Amealco de Bonfil**: MCZ 161010–161012, 162089, TCWC 52508, TNHC 101902–101903; **Municipio de Huimilpan**: TNHC 101904–101905.

Lampropeltis webbi.—MEXICO: DURANGO: **Municipio de Pueblo Nuevo**: MZFC 26939, TCWC 100530, UANL 7579; SINALOA: **Municipio de Concordia**: TNHC 101906, UANL 5684.





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Robert W. Hansen has a long-standing interest in the herpetofauna of Mexico and the American Southwest. His research interests include the ecology and systematics of plethodontid salamanders, work that has led to descriptions of three new species of *Batrachoseps* in California. He also is keenly interested in desert snake communities, and in an ongoing study begun in 1982, he and collaborators have examined the local distribution, relative abundance, and activity patterns of snakes along an elevational transect at the interface of the southern Sierra Nevada and Mojave Desert of California. His interest in the *Lampropeltis mexicana* complex began in 2004, when he became aware of and fascinated by the remarkable pattern polymorphism in some members of this group. An accomplished photographer, his photos of herpetological subjects have appeared in numerous books and journal articles. Since 1991, Hansen has been Editor of *Herpetological Review*, published by the Society for the Study of Amphibians and Reptiles. In 2015, he received the SSAR Presidential Award for Lifetime Achievement in Herpetology. He resides in the Sierra Nevada foothills of central California.



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Gerard T. Salmon is a naturalist interested in geographic distribution and conservation of North and Middle American amphibians and reptiles. He has been studying mexicana-group kingsnakes for more than 30 years in the field, museum collections, and in captivity. Although his career was in professional law enforcement (Sergeant, New York State Police, retired) or as an investigator (Texas Health and Human Services Commission), formerly he was employed at the Miami Serpenterium, and also has worked as a state park naturalist and endangered species consultant. Additionally, he volunteered in the Department of Herpetology at the Wildlife Conservation Society's Bronx Zoo and in the vertebrate collection at the University of Texas at Austin. Salmon has authored or co-authored several papers and notes in herpetological journals. A current project involves examining dietary preferences in Broad-banded Copperheads (with Harry Greene). Since 2005, he and Hansen have collaborated in studying the natural history of *mexicana* kingsnakes. He currently resides in the beautiful Texas Hill Country.