RESEARCH ARTICLE

Horned Lizards (*Phrynosoma*) of Sonora, Mexico: Distribution and Ecology

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Mexico is recognized globally as a mega-diversity country. The state of Sonora has very diverse fauna, flora, and vegetation. The diversity of horned lizards in the genus *Phrynosoma* (Phrynosomatidae) in the state of Sonora is a reflection of the landscape and biotic diversity. In this paper, we summarize the distribution and ecology of eight species of *Phrynosoma* in Sonora.

Methods

Study area

The great biodiversity of Sonora is the result of complex biogeography and ecology. The elevation in Sonora ranges from sea level at the Gulf of California to over 2600 m in the Sierras Los Ajos and Huachinera (Mario Cirett-G., pers. comm., 2017). The Sierra Madre Occidental (SMO) reaches its northern limits in eastern Sonora and western Chihuahua. North of the SMO, the Madrean Archipelago or Sky Islands Region extends to the Mogollon Rim in central Arizona. Sky Islands are isolated mountain ranges with crowns of oak woodland and/or pine-oak forest surrounded by lowland 'seas' of desertscrub, desert grassland, foothills thornscrub, or tropical deciduous forest (Van Devender et al. 2013). There are 55 Sky Islands and Sky Island complexes connected by oak woodland in the Madrean Archipelago, 32 of them in Sonora (Deyo et al. 2013).

Six biotic provinces with characteristic animals, plants, and vegetation converge in the Madrean Archipelago. The Rocky Mountains and Colorado Plateaus to the north have cold temperate climates. To the northeast, winter rainfall-dominated Mediterranean chaparral extends from California east to central Arizona. In the mid-continent, Great Plains grassland occurs from Canada south to the Mexican Plateau, and west to southern New Mexico, southeastern Arizona, and northeastern Sonora. The Chihuahuan biotic province reaches its southwestern limit in northeastern Sonora. In much of this area, Chihuahuan desertscrub occurs on rocky slopes adjacent to grassland in the adjacent valleys. The desert grassland of southeastern Arizona is replaced by foothills thornscrub about 100 kilometers south of the Arizona border as winter freezing temperatures decline. This ecotone is really the transition between the New World tropics and northern temperate biotas. Tropical deciduous forest is on the lower slopes of the Sierra San Javier, the southernmost Sky Island (Van Devender et al. 2013). The Sierra Madre Occidental reaches its northern limit in eastern Sonora, with Madrean species present in the oak woodland and pine-oak forests in the higher elevations of the Sky Islands. West of the Madrean Archipelago, desertscrub vegetation is present in the Sonoran Desert lowlands of western and central Sonora.

Phrynosoma records

Eight species of *Phrynosoma* are reported from Sonora (Enderson et al. 2010; Rorabaugh and Lemos 2016). Distribution records from various sources and many photo vouchers are publicly available in the Madrean Discovery Expeditions (MDE) database (*madreandiscovery.org*)

Results

Phrynosoma cornutum, Texas Horned Lizard (Harlan, 1824)

In the United States, *Phrynosoma cornutum* ranges from Colorado and Kansas south to Texas and west to Arizona. Texas horned lizards may also be native to Louisiana and Arkansas. Introduced populations are found in the Carolinas, Georgia, northern Florida, and in the Honolulu area on Oahu Island in Hawaii (Hunsaker and Breese 1967). In Mexico, it is found throughout the Mexican Plateau as far south as Aguascalientes, San Luis Potosí, and Zacatecas (Arenas et al. 2014). In Sonora, *P. cornutum* is known in Chihuahuan desertscrub and desert grassland at 1136 to 1492 m elevation close to the Arizona border in the Agua Prieta-Naco area (Figs. 1 and 2). The southernmost record at Fronteras (49 km south of the border) was collected in June 1935 by Barry Campbell from the University of Michigan. He was in route to the Sierra El Tigre, where he made an important herpetological collection, including the first state records for Mexican Plateau Horned Lizard (*P. orbiculare*), Twin-spotted Rattlesnake (*Crotalus pricei*), and Ridge-nosed Rattlesnake (*C. willardi*). One animal was seen on Mesa las Víboras 30 km east of Agua Prieta. In this area, the vegetation is a unique dwarf (less than a meter tall) velvet mesquite (*Prosopis velutina*) scrub on reddish clay soils.

Mexico is recognized globally as a mega-diversity country. The state of Sonora has very diverse fauna, flora, and vegetation. The diversity of horned lizards in the genus *Phrynosoma* (Phrynosomatidae) in the state of Sonora is a reflection of the landscape and biotic diversity.

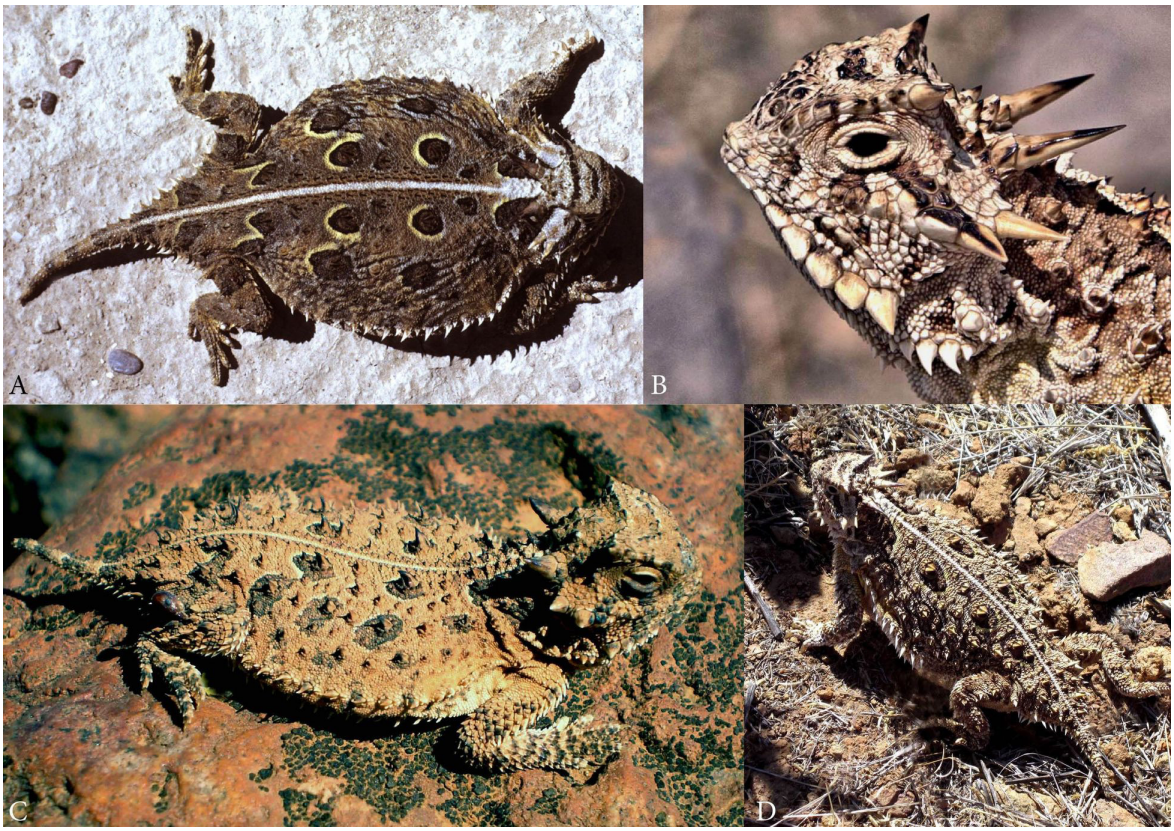

Figure 1. *Phrynosoma cornutum*. **A.** South of Ojinaga, Chihuahua, July 1972. Photo by Thomas R. Van Devender. **B.** Pat Hills, south of Willcox, Arizona, May 2015. Photo by Chris Roll. **C.** Mesa Las Víboras, east of Agua Prieta, Sonora, April 2008. Photo by Thomas R. Van Devender. **D.** Pat Hills, Arizona, May 2015. Photo by Chris Roll.

Phrynosoma ditmarsi, Rock Horned Lizard (Stejneger, 1906)

Phrynosoma ditmarsi is endemic to the state of Sonora (Fig. 2). The species was first collected on the Carl S. Lumholtz expeditions to Mexico in 1890–91 from "Sonora." Two additional specimens collected "a short distance over the border of Arizona, in old Mexico, state of Sonora" in 1897 were described as a new species by Stejneger (1906). The species was not found again for 73 years, when mining engineer Paul Geiger discovered it on Rancho El Alacrán in the Sierra Manzanal (now called the Sierra Alacrán) southeast of Cananea (Lowe et al. 1971). Today it is known from the Sierras Alacrán and Manzanal near Cananea south through the Sierras la Púrica, Nacozari (Burkhardt and Trageser 2015), la Madera, Babiácora, Lampazos, and Murrieta (Turner et al. 2017; Fig. 3). It is recorded from the western edge of the Sierra Madre Occidental near Nácori Chico and Ónavas (Perrill 1983), and was recently found in lowland areas at Bacerac, Colonia Aribabi, and Subitatechi. It typically lives in desert grassland-oak woodland transition, but has been found in oak woodland, desert grassland, foothills thornscrub, and tropical deciduous forest at 950 to 1679 m elevation. *P. ditmarsi* is only occasionally encountered in rocky habitats away from paved roads.

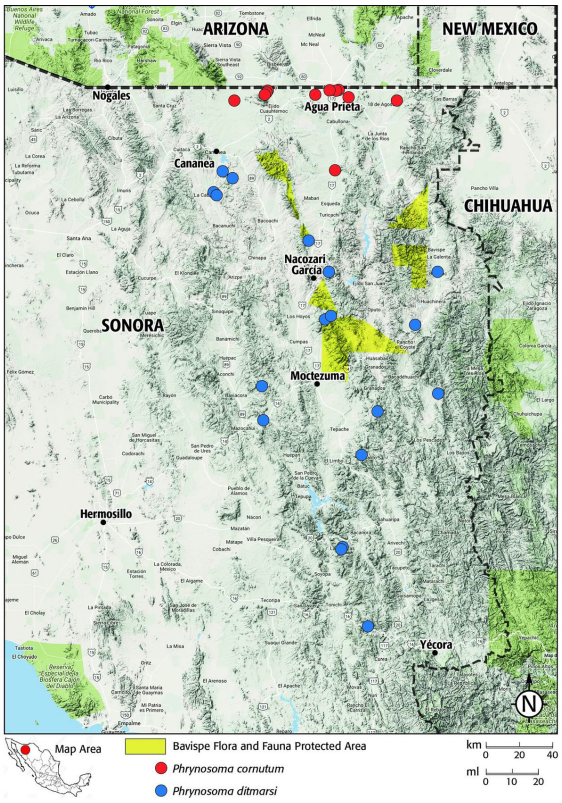

Figure 2. Known distribution of *Phrynosoma cornutum* and *P. ditmarsi* in Sonora, Mexico.

Phrynosoma ditmarsi is endemic to the state of Sonora (Fig. 2). The species was first collected on the Carl S. Lumholtz expeditions to Mexico in 1890–91 from "Sonora." Two additional specimens collected "a short distance over the border of Arizona, in old Mexico, state of Sonora" in 1897 were described as a new species by Stejneger (1906).

Figure 3. *Phrynosoma ditmarsi*. **A.** Rancho la Palma, east-northeast of San José de Babiácora, Sonora, September 2004. Photo by Erik F. Enderson. **B.** Top of head. Rancho Subitatechi, Sonora, November 2016. Photo by Ana L. Reina-Guerrero. **C.** Rancho las Tierras de Jimenez, Sierra de Murrieta, Sonora, August 2014. Photo by Stephen L. Minter. **D.** Side view of head. Rancho Subitatechi, Sonora. Photo by Ana L. Reina-Guerrero. **E.** *Sceloporus*-like keeled scales on chest. Rancho Subitatechi, Sonora. Photo by Ana L. Reina-Guerrero. **F.** Front view of head. Rancho Subitatechi, Sonora. Photo by Ana L. Reina-Guerrero.

***Phrynosoma goodei*, Goode's Horned Lizard (Stejneger, 1893)**

Phrynosoma goodei occurs from Punta Sargento on the coast of the Gulf of California to the Colorado River in western Sonora and north to the Gila River and east to the Tucson area in Arizona. It is found in sandy and rocky habitats in Sonoran desertscrub (Figs. 4 and 5). Formerly, it was considered a subspecies of *P. platyrhinos*.

***Phrynosoma hernandesi*, Greater Short-Horned Lizard (Girard, 1858)**

Phrynosoma hernandesi ranges from Alberta and Saskatchewan in Canada to North Dakota and Montana south to Utah, Nevada, Arizona, and New Mexico in United States, and Chihuahua, Durango, and Sonora in Mexico. The taxonomy of the *P. douglasii* species complex, including *P. hernandesi*, was reviewed by Montanucci (2015). In Sonora, it is known in the Municipalities of Agua Prieta, Cananea, Cumpas, Fronteras, Ímuris, Naco, Nacozari de García, and Nogales, where it lives at 1294 to 2470 m elevation in desert grassland, plains grassland oak woodland, and pine-oak forest (Fig. 6 and 7). *P. hernandesi* can tolerate cooler temperatures than most other Sonoran horned lizards.

***Phrynosoma mcallii*, Flat-tailed Horned Lizard (Hallowell, 1852)**

Phrynosoma mcallii species occurs in northwestern

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Figure 4. *Phrynosoma goodei*. All Pinacate Biosphere Reserve, Sonora. **A.** February 2008. Photo by James O. Rorabaugh. **B.** Top of head. March 2012. Photo by Thomas R. Van Devender. **C.** Photo by Thomas R. Van Devender. **D.** Side of head. March 2012. Photo by Thomas R. Van Devender. **E.** Front view of head. Photo by Thomas R. Van Devender. **F.** Detail of scales on back. March 2012. Photo by Thomas R. Van Devender.

Phrynosoma modestum ranges from southeastern Colorado, western Texas, and southern New Mexico to southeastern Arizona in the United States. In Mexico, it occurs on the Mexican Plateau from Chihuahua and Coahuila south to Aguascalientes, San Luis Potosi, and Zacatecas.

Sonora, northeastern Baja California, southwestern Arizona, and southeastern California (Figs. 5 and 8). It lives in sandy Sonoran desertscrub at 0 to 300 m elevation (Rodríguez 2002). This species has an unusually flattened body, a long, broad, flat tail, dagger-like horns, no external openings, and color matches the soil very well.

Phrynosoma modestum, Round-tailed Horned Lizard (Girard, 1852)

Phrynosoma modestum ranges from southeastern Colorado, western Texas, and southern New Mexico to southeastern Arizona in the United States. In Mexico, it occurs on the Mexican Plateau from Chihuahua and Coahuila south to Aguascalientes, San Luis Potosi, and Zacatecas. In Sonora, it has been found only near Agua Prieta at 1211 to 1326 m elevation in Chihuahuan desertscrub and desert grassland (Figs. 9 and 10). Neonate *Phrynosoma* are more similar to each other than adults. *P. modestum* is a small, paedomorphic species, where the adults retain juvenile morphology in plain color patterns, simple dorsal scales, and modest horn development. Adults match the color of the soil very well, and simply hide among the stones in the open to avoid predators.

Phrynosoma orbiculare, Mexican Plateau Horned Lizard (Linneaus, 1758)

Phrynosoma orbiculare is a Mexican species that ranges from the Sierra Madres Occidental and Oriental and the Mexican Plateau south to Puebla and Veracruz, and to western Chihuahua and the Yécora area in easternmost Sonora (Enderson et al. 2014, Van Devender et al. 2017; Fig. 7). A disjunct population in the Sierra

el Tigre, Municipality of Nacozari de García is 225 kilometers north of Yécora (Van Devender et al. 2015). It was recently found in between these two populations near Mesa Tres Ríos, Municipality of Nácori Chico in the northernmost Sierra Madre Occidental 149 km north-northeast of Yécora (Cabrera-H. et al., in press). In Sonora, this species lives in pine-oak forest at 1720 to 2412 m elevation (Fig. 11). It is common in the Sierra el Tigre, but less so in the Yécora area.

Phrynosoma solare, Regal Horned Lizard (Gray, 1845)

Phrynosoma solare ranges from southwestern New Mexico and Arizona in the United States south through Sonora to northern Sinaloa in Mexico. In Sonora, it lives from near sea level to 1400 m elevation in Chihuahuan and Sonoran desertscrub, desert grassland, coastal and foothills thornscrub, tropical deciduous forest, and open oak woodland (Figs. 10 and 12). It occurs on Tiburón Island in the Gulf of California. It is very widely distributed and the most common species in Sonora. The basic body coloration can be shades of gray, tan, brown, orange, or red, generally re-

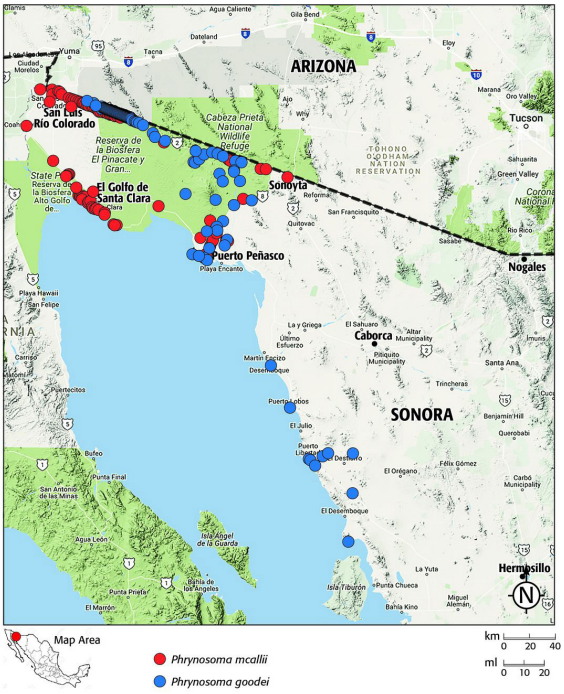

Figure 5. Known distribution of *Phrynosoma goodei* and *P. mcallii* in Sonora, Mexico.

Phrynosoma solare ranges from southwestern New Mexico and Arizona in the United States south through Sonora to northern Sinaloa in Mexico. In Sonora, it lives from near sea level to 1400 m elevation in Chihuahuan and Sonoran desertscrub, desert grassland, coastal and foothills thornscrub, tropical deciduous forest, and open oak woodland.

Figure 6. *Phrynosoma hernandesi*. **A.** Cañada el Pinalito, Sierra Elenita, Sonora, September 2015. Photo by Thomas R. Van Devender. **B.** Front view of head after squirting blood from eye. Sierra la Púrica, July 2013. Photo by Charles Hedgcock. **C.** Sierra la Púrica, July 2013. Photo by Charles Hedgcock. **D.** Side view of head. Sierra la Púrica, July 2013. Photo by Charles Hedgcock. **E.** Sierra la Púrica, July 2013. Photo by Charles Hedgcock. **F.** Juvenile color matching stones in bare area in desert grassland near Cananea, Sonora, September 2014. Photo by Thomas R. Van Devender.

flecting local substrates. The back can be patternless, or with various pattern elements, including an oval mid-dorsal light area, spots, three transverse bands, and a mid-dorsal stripe (Figs. 12A, C, E, and G.). The head can be the same color as the body, but the four largest horns are typically a contrasting reddish brown.

Discussion

Diversity and Habitat

The state of Sonora with eight species has the greatest diversity of *Phrynosoma* of any state in Mexico or the United States. The most commonly encountered species are *P. hernandesi* and *P. solare* in the east and *P. goodei* and *P. mcallii* in the west. *Phrynosoma goodei*, *P. mcallii*, and *P. solare* live in sparse desertscrub in the Lower Colorado River Valley subdivision of the Sonoran Desert from the Gulf of California in western Sonora inland to Arizona, California, and Baja California. *P. goodei* and *P. solare* are in the Central Gulf Coast subdivision of the Sonoran Desert along the coast of the Gulf of California. *P. solare* is the only horned lizard present in the Arizona Upland and Plains of Sonora subdivisions in northern and central Sonora, but also lives in desert grassland and tropical vegetation to the east. *P. cornutum* and *P. modestum* occur in Chihuahuan desertscrub and desert grassland near Agua Prieta and Naco.

There are three upland species of *Phrynosoma* in Sonora. *P. hernandesi* is common in desert grassland near Cananea, plains grassland east of Agua Prieta, and oak woodland and pine-oak forests in the Sky Islands (Sierras los Ajos, Avispas, Azul, Buenos Aires, Elenita, Madera [Oposura], Mariquita, Pan Duro, Púrica, and San Luis). *P. orbiculare* is a pine-oak forest species found in the Mexican Plateau and Sierra Madre Occidental reaching Sonora in the Yécora and Mesa Tres Río areas and in the Sierra el Tigre. Interestingly *P. hernandesi* has not been found in these areas.

Phrynosoma ditmarsi is endemic to Sonora (Turner et al. 2017). It is known from oak woodland and desert grassland from the Sierras Alacrán and Manzanal south of Cananea south through the Sierras la Púrica, Nacozari, la Madera, Babiácora, Lampazos, and Murrieta, and recently in desert grassland in the Río Bavispe Valley. Some of these localities are close to the western edge of the Sierra Madre Occidental, suggesting that it may eventually be found in Chihuahua.

Horned lizards are best known as desert-adapted lizards, and in Sonora five species occur in desertscrub in four subdivisions of the Sonoran Desert and the Chihuahuan Desert. But *Phrynosoma* also lives in desert grassland, coastal and foothills thornscrub, tropical deciduous forest, oak woodland, and pine-oak forest. Desert grassland with five species has the greatest diversity. *P. cornutum*, *P. modestum*, and *P. solare* are

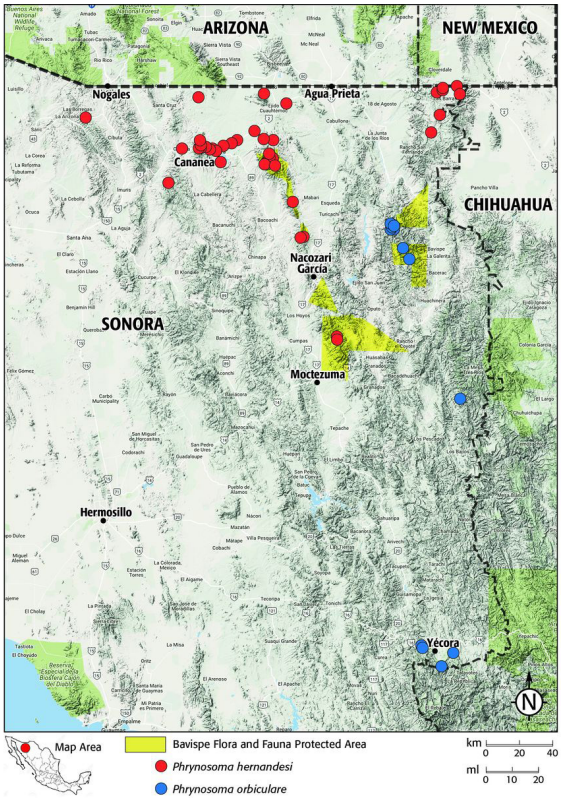

Figure 7. Known distribution of *Phrynosoma hernandesi* and *P. orbiculare* in Sonora, Mexico.

potentially sympatric near Agua Prieta in Chihuahuan desertscrub/desert grassland transition. *P. cornutum*, *P. ditmarsi*, and *P. hernandesi* are potentially sympatric in desert grassland in the Cananea area. *P. ditmarsi* and *P. solare* were found at the same locality in the Sierra Manzanal. *P. hernandesi* and *P. solare* both occur on Rancho el Aribabi in the Sierra Azul. In the Lower Colorado River Valley in northwestern Sonora and adjacent Arizona, *P. goodei*, *P. mcallii*, and *P. solare* potentially live in the same area. *Phrynosoma mcallii* prefers areas of fine-grained silica sand, while *P. goodei* specializes in granite-derived sands on desert bajadas (Rorabaugh pers. comm. 2018). They are sympatric in the sandy flats north of Puerto Peñasco. *Phrynosoma ditmarsi* and *P. hernandesi* both live in oak woodland and may co-occur in the Sierras Nacozari and la Púrica. *Phrynosoma hernandesi* and *P. orbiculare* both live in pine-oak forest, but not in the same areas.

Conservation Status

We think that most of these horned lizards are reasonably common and not seriously threatened by habitat destruction. Horned lizard populations are locally impacted by human activities including cattle grazing, buffelgrass planting, mining, and disturbance near rural towns. Human interest in horned lizards was reflected by sculptures and myths in various American indigenous groups (Sherbrooke 2003). Before rigorous protection laws, horned lizards were commonly sold as pets in the United States, even though they quick-

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Figure 8. *Phrynosoma mcallii*. **A.** Southeast of El Golfo de Santa Clara, April 2017. Photo by S. Campbell. **B.** Top view of head. Machorro Canyon, east-southeast of El Golfo de Santa Clara, March 2011. Photo by A. Ferrell. **C.** Near San Luis Río, 1980. Photo by R. Wayne Van Devender. **D.** Side view of head. Southeast of El Golfo de Santa Clara, April 2017. Photo by S. Campbell. **E.** Near San Luis Río, 1973. Photo by R. Wayne Van Devender. **F.** Top view of head. North-northwest of El Golfo de Santa Clara. Photo by E. Scott.

ly died. In Bacerac, Sonora on the Río Bavispe, people occasionally keep camaleones as pets. This is of special concern because a *P. ditmarsi* was recently found in this town.

In the 1970s, University of Arizona students Wayne Howard and Michael D. Robinson collected large series of *P. cornutum* and *P. modestum* near Agua Prieta and Naco. In recent decades of relatively intense biological inventories, only a few individuals have been seen in these areas. One *P. modestum* area is now part of urban Agua Prieta. These species may have declined in Sonora, but are widespread in Chihuahua, Coahuila, and Texas.

Protection Status

Only *Phrynosoma mcallii* and *P. orbiculare* are listed as Threatened (Amenazada) in the Mexican endangered species law (NOM 059 SEMARNAT 2010). Curiously *P. ditmarsi* was also Threatened in earlier versions of the law, but delisted. The rest of the Sonoran species of horned lizards are not federally protected in Mexico or the United States. There has been an international effort to protect *P. mcallii* in the United States and Mexico. It is a high priority species in the Alto Golfo de California Biosphere Reserve in the Pinacate region of northwestern Sonora. It is illegal to collect *P. mcallii* in Arizona and California without a state scientific collection permit, and it has a Near Threatened status in the 2015 IUCN Red List. As a candidate for federal listing, it was extensively studied in Arizona and California, but not listed. Observations in the last eight years by vertebrate paleontologists prospecting for Pleistocene fossils in sedimentary badlands show that it is common near El Golfo de Santa Clara, Sonora (Fred Croxen, pers. comm. 2017).

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Figure 9. *Phrynosoma modestum*. **A.** Black Gap, Texas, June 1978. Photo by Thomas R. Van Devender. **B.** Side view of head. Black Gap, Texas, June 1978. Photo by Thomas R. Van Devender. **C.** Sierra Anibácachi, southwest of Agua Prieta, June 2007. Photo by R. Wayne Van Devender. **D.** Side view of head. Sierra Anibácachi, southwest of Agua Prieta, June 2007. Photo by R. Wayne Van Devender. **E.** Pat Hills, south of Willcox, Arizona, July 2010. Photo by Chris Roll. **F.** Top view of head. Pat Hills, south of Willcox, Arizona, July 2010. Photo by Chris Roll.

Protected Areas

Phrynosoma are present in protected areas in Sonora, although common or smaller species are not individually managed. There are six federal reserves managed by the Comisión Nacional de Áreas Naturales Protegidas (CONANP) in Sonora. *Phrynosoma hernandesi*, *P. ditmarsi* and *P. orbiculare* are in the Área de Protección de Flora y Fauna (APFF) Bavispe (formerly the Reserva Forestal Nacional y Refugio de Fauna Silvestre Ajos-Bavispe) in northeastern Sonora. *P. ditmarsi*, *P. cornutum*, *P. modestum*, and *P. solare* are known from nearby areas of conservation interest. *P. hernandesi* lives in the Área Natural Protegida Destinada Voluntariamente a la Conservación (ANPDVC) Sierra la Mariquita in northern Sonora. *P. hernandesi* and *P. solare* both occur on ANPDVC Rancho el Aribabi in northern Sonora. *P. solare* is in the proposed APFF Sierra Huérfana (= Sierra Mazatán) in central Sonora, and the APFF Sierra de Álamos-Río Cuchujaqui in southern Sonora. *P. goodei*. *P. mcallii*, and *P. solare* are in the El Pinacate y Gran Desierto de Altar Biosphere Reserve (administered by CONANP) in western Sonora.

Phrynosoma are also present on private protected natural areas in Sonora. The Cuenca Los Ojos Foundation (*cuencalosojos.org/*) owns six ranches in northeastern Sonora. *P. hernandesi* is common in plains grassland in the southern extension of the Animas Valley and in montane woodlands and forest in the nearby Sierra Pan Duro and San Luis. *P. solare* has been seen at Rancho Puerta Blanca. *P. cornutum* has not been reported from CLO but is likely to occur in Chihuahuan desertscrub on Rancho San Bernardino. *P. hernandesi* is on the Reserva los Fresnos owned by The Nature Conservancy near the Arizona border in northern Sonora, and *P. solare* is common in foothills thornscrub on the Northern Jaguar Reserve (*www.northernjaguarpro-*

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ject.org/northern-jaguar-reserve/) in east-central Sonora (Rorabaugh et al. 2011).

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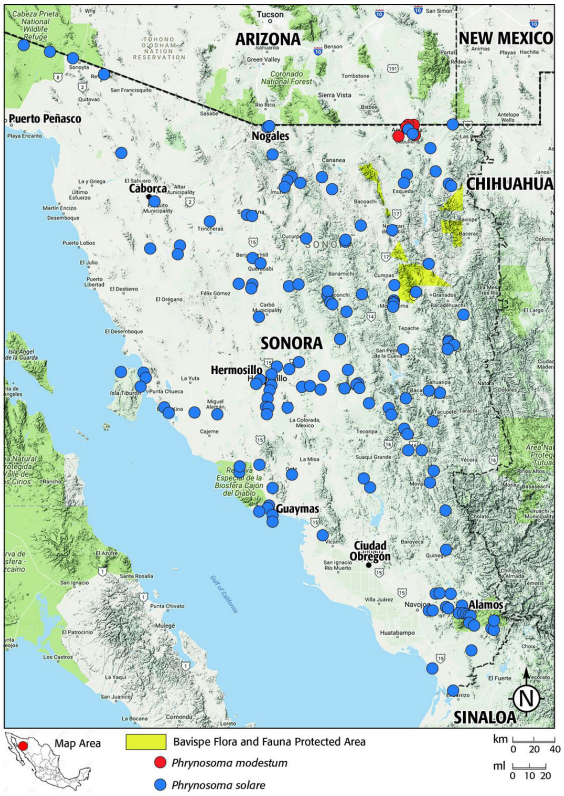

Figure 10. Known distribution of *Phrynosoma modestum* and *P. solare* in Sonora, Mexico.

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Figure 11. *Phrynosoma orbiculare*. **A.** Mesa del Campanero, west of Yécora, August 2010. Photo by Joseph Scheer. **B.** Side view of head of juvenile. Rancho el Tigre, Sierra el Tigre, August 2015. Photo by R. Wayne Van Devender. **C.** Rancho el Tigre, Sierra el Tigre, August 2015. Photo by R. Wayne Van Devender. **D.** Side view of head. Rancho el Tigre, Sierra el Tigre, August 2015. Photo by R. Wayne Van Devender. **E.** Pair found mating. Rancho el Tigre, Sierra el Tigre, August 2015. Photo by Guillermo Molina-Padilla. **F.** Rancho el Tigre, Sierra el Tigre, August 2015. Photo by R. Wayne Van Devender.

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Figure 12. *Phrynosoma solare*. **A.** La Mesa de San Patricio, south of Moctezuma, May 2012. Photo by Hugo Silva-Kurumiya. **B.** Top of head. West of Estancia, September 2012. Photo by Thomas R. Van Devender. **C.** North-northeast of Nácori Grande, July 2012. Photo by Thomas R. Van Devender. **D.** Side of head. West of Estancia, September 2012. Photo by Thomas R. Van Devender. **E.** East of Benjamín Hill, May 2009. Photo by Thomas R. Van Devender. **F.** Side of head. West of Estancia, September 2012. Photo by Thomas R. Van Devender. G. Hermosillo, July 2000. Photo by Thomas R. Van Devender. H. Dorsal pattern. West of Estancia, September 2012. Photo by Thomas R. Van Devender.