

Morphology and distribution of the night lizard *Lepidophyma zongolicum* (Xantusiidae)

Antonio Esaú VALDENEGRO-BRITO¹, José Daniel LARA-TUFIÑO^{2,3}, Juan Carlos SÁNCHEZ-GARCÍA^{1,3}, Rodrigo Gabriel MARTÍNEZ-FUENTES^{1,3}, Diego GARCÍA-MORALES¹, Romina Itzel CERVANTES-BURGOS¹, Uriel GARCÍA-SOTELO¹, Miguel Ángel DE LA TORRE-LORANCA⁴ and Uri Omar GARCÍA-VÁZQUEZ^{1, *}

1. Laboratorio de Sistemática Molecular, Carrera de Biología, Unidad de Investigación Experimental Zaragoza, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Batalla 5 de mayo s/n, Col. Ejército de Oriente, 09230, CDMX, México.

2. Departamento de Biología Evolutiva, Museo de Zoología, Facultad de Ciencias, UNAM, AP.70-399 México, Ciudad de México 04510, México.

3. Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Circuito de Posgrados, Ciudad Universitaria, Ciudad de México 04510, CDMX, México.

4. Herping Zongolica, Finca Santa Martha Ecosuites Km 32 Carretera Federal Orizaba-Zongolica, Ocotepc, Los Reyes, Veracruz, México. C.P.95000.

* Corresponding author: U.O. García-Vázquez, E-mail: urigarca@gmail.com.

Received: 29 March 2022 / Accepted: 08 September 2023 / Available online: November 2023 / Printed: December 2023

Abstract. *Lepidophyma zongolicum* is known from only seven specimens (type series) collected in the Sierra Negra of Puebla, Mexico. Here, we report 18 additional records from the Sierra de Zongolica and Sierra de Atoyac in central Veracruz, Mexico. We built a species distribution model that predicts suitable areas for *L. zongolicum* in the mountains of central Veracruz southward to eastern Puebla and northern Oaxaca. Morphologically our new material is readily assigned to *L. zongolicum*, but the specimens exhibit variation in the number of dorsal scales, paravertebral scales, dorsal interwhorls, and tail coloration that is previously undocumented for the species. The morphological variation recorded in the specimens allowed us to establish a better diagnosis for the species. Additionally, the new records corroborated the secretive habits and preferential microhabitats of this enigmatic lizard and helped to infer the species potential distribution, showing the species real distribution is likely more extensive than previously known.

Keywords: Sierra de Zongolica, Sierra de Atoyac, Veracruz, montane cloud forest, maximum entropy, morphology.

Introduction

Night lizards of the genus *Lepidophyma* A. Duméril in Duméril and Duméril, 1851 occur from Nuevo León and Colima on the Atlantic and Pacific versants of Mexico, respectively, to southeastern Panama (Bezy 2019, Arenas-Moreno et al. 2021, Lara-Tufiño & Nieto Montes de Oca 2021). Although this genus has a broad distribution, 19 of the 23 described species have relatively small distributions, often restricted to specific mountain ranges (Arenas-Moreno et al. 2021, Lara-Tufiño & Nieto Montes de Oca 2021). Additionally, members of the genus are secretive and are seldom observed outside of sheltered microhabitats, which include caves, rock crevices, or decaying tree trunks (Bezy 2019). Due to these factors, few specimens have been collected for most *Lepidophyma* species, which has led to imprecise diagnoses and scarce knowledge about their geographic distribution (Bezy 2019). Similar problems exist for species in other genera of Middle American squamates, making it valuable to publish novel data even from a handful of additional specimens when they become available (e.g., Scarpetta et al. 2015, Clause et al. 2016, Sánchez-García et al. 2019).

Lepidophyma zongolica (Fig. 1) was named as a reference to the type locality in the Sierra de Zongolica, Veracruz (García-Vázquez et al. 2010). However, Bezy (2019) changed the specific epithet to *zongolicum* because *Lepidophyma* is neuter. *Lepidophyma zongolicum* is only known from seven specimens from the Sierra Negra in southern Puebla, collected at 94–120 m elevation in tropical evergreen forest. The southern portions of Sierra de Zongolica in the states of Puebla are commonly called the Sierra Negra. According to the original description, *L. zongolicum* is characterized by the following combination of characters: 40–49 gular scales, 174–184 dorsal

scales, 100–106 scales along the paravertebral row, 61–68 scales (all sizes) in the paravertebral row, 21–28 lateral tubercle rows, 33–43 femoral pores, 27–30 fourth toe lamellae, 4 dorsal interwhorls, and 2–3 ventral interwhorls (García-Vázquez et al. 2010).



Figure 1. *Lepidophyma zongolicum*, adult female (not collected) from the type locality. Photo: Adam G. Clause.

Recent fieldwork in central Veracruz yielded a sample of 18 additional records of *L. zongolicum*. This material extends the known geographic range for this species and shows notable morphological variation. Here, we report on this novel distributional and morphological data and generate a potential distribution model for the species to establish a more accurate morphological diagnosis, identify the microhabitats it occupies, and identify the sites where conservation strategies are necessary.

Material and methods

During the monitoring of amphibians and reptiles from 2017 to 2020 in the Sierra de Zongolica and Sierra de Atoyac de Veracruz, we found 18 specimens of *L. zongolicum*. The individuals were detected through a direct search method, searching potential microhabitats from ground level up to three m in height, considering the species natural history (García-Vázquez et al. 2010, Bezy 2019). We euthanized collected specimens with 6% pentobarbital sodium, fixed them in 10% buffered formalin, preserved them in 70% ethanol, and deposited them in the herpetological collection of the Museo de Zoología, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México (MZFZ). In the case of uncollected specimens, we deposited photographic vouchers in the digital collection of the Museo de Zoología, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México (MZFZ-IMG).

Morphological data

Scale terminology follows Bezy & Camarillo-Rangel (2002) as modified by Gauthier et al. (2008). We counted scales using a Carl Zeiss (model 2004017913) dissecting microscope and measured with a caliper to the nearest 0.1 mm. We recorded ten meristic characters, including the count of the following scales: gulars (GUL), middorsal scales (DOR), dorsal scales in the row immediately above the paravertebral tubercle row (DAPVR), granular and tubercular scales in the paravertebral tubercle row (PVR), fourth toe lamellae (FTL), lateral tubercle rows (LTR), femoral pores (FPT), dorsal interwhorls (IWD2), and ventral interwhorls (I WV2). DOR, DAPVR, PVR, and LTR were counted between the levels of the axilla and groin. We also recorded the presence/absence of an anterior frontal scale (AFS). To describe specimen coloration in preservatives, we rely on color names (plus color codes in parentheses) that correspond to those in the color catalog of Köhler (2012).

Species distribution model (SDM)

We built a distribution model to estimate the potential geographic distribution of *L. zongolicum*. Occurrence data were collected from scientific literature and fieldwork. For current climate data, we downloaded as shape files 19 bioclimatic variables from Cuervo-Robayo et al. (2013) for Mexico, with high resolution (30 arc seconds) for the monthly average climatic period 1910–2009 (available at <http://idrisi.uaemex.mx/distribucion/superficies-climaticas-para-mexico>). We created the potential distribution model for *L. zongolicum* with all 19 bioclimatic variables and packages “maxnet” (Phillips et al. 2017), “ENMeval” (Muscarella et al. 2014) and “kuenm” (Cobos et al. 2019) in the R v. 4.3.1. software (R Core Team, 2021). Package “maxnet” is the open-source version of Maxent and compares the

distribution of environmental variables measured at background locations to the distribution of environmental variables at known presence locations (Phillips et al. 2017, Helmstetter et al. 2021). We removed occurrence data duplicates to avoid pseudoreplication, and we subsetted the occurrences data for training and testing models with the method partitioning Jackknife with ENMeval v. 2.0 package (Muscarella et al. 2014) in the R v. 4.3.1. software (R Core Team, 2021) for k-fold cross-validation. We used the partitioned occurrence data subsets and the parameterizations selected with ENMeval v. 2.0 since models will compare the environment at occurrence localities to the environment at background localities. We sampled random points from a background extent, we created a buffer of 70 km, considering as a natural barrier the presence of the River Papaloapan, and that includes all occurrence localities by cropping our global predictor variable rasters to a smaller region, and we sampled 29,863 random points from the background. We calculated the AUC ratio and associated p-value for the partial ROC performance metric with the R package kuenm (iterations = 500, omission rate $E = 5$, and bootstrap resampling of 50% of testing data; Cobos et al. 2019). Model response types (feature classes: L, LQ, LQH, H; L= Linear, Q = quadratic, H = hinge; Elith et al. 2011) and regularization multiplier values (RM: 1:5). We selected a model with delta AICc equal to 0 from the ENMeval object using the tune.args of our optimal model and plotted the final prediction model of *L. zongolicum*.

Results

We obtained 18 new records of *L. zongolicum* from seven localities in Veracruz: 14 specimen-based and 4 photo-based, respectively (Table 1). All specimens were found in rock crevices, under tree cover (tropical evergreen forest or coffee shade), or inside caves. These specimens represent the first record of *L. zongolicum* for Veracruz and extend the distribution range by 48 km in a straight line from the northern of the nearest town localities in El Tepeyac, Eloxochitlán, Puebla (García-Vázquez et al. 2010). These records increase the number of *Lepidophyma* species documented in this state to five (*L. flavimaculatum*, *L. sylvaticum*, *L. tuxtlae*, *L. pajapanense*, and *L. zongolicum*) (Bezy 2019). Additionally, with this new record of *L. zongolicum* in Veracruz, the state’s reptile diversity has increased to 238 species (Torres-Hernández et al. 2021), second only to the state of Oaxaca with 322 species (Mata-Silva et al. 2021).

Table 1. New localities for *Lepidophyma zongolicum*. Coordinates in datum WGS 84; N – number of collected individuals.

Locality	Coordinates and elevation	Date	N	Voucher numbers	Microhabitat	Source
Road between Rancho Nuevo and Tepeyac, Puebla	18.487°, -96.85352°; 125 m	07.06.2006	3	MZFC-HE 22180–182	Rock crevice	García-Vázquez et al. 2010
El Tepeyac, Eloxochitlán, Puebla	18.48772°, -96.85047°; 94 m	06.07.2007	4	MZFC-HE 22183–186	Rock crevice	García-Vázquez et al. 2010
Tepezcuintles cave, Aticpac, Zongolica, Veracruz	18.56942°, -96.88153°; 326 m	09.01.2016 01.11.2015 14.12.2015	1 1 2	MZFZ 3409 MZFZ 3413 MZFZ 3407–08	Rock crevice into cave	This study
El Boqueron, Zongolica, Veracruz	18.60211°, -96.88422°; 227 m	20.02.2019 28.02.2019	1 4	MZFZ 4369 MZFZ 4370–73	Rock crevice	This study
Ejido Caballo Blanco, Atoyac, Veracruz	18.86336°, -96.73302°; 449 m	20.06.2019	1	MZFZ 4374	Rock crevice	This study
Finca La Gloria, Tezonapa, Veracruz	18.63338°, -96.81810°; 931 m	15.07.2020	2	MZFZ-IMG 288, 291	Rock crevice	This study
Atoyac, Veracruz	18.92211°, -96.76733°; 538 m	29.10.2020	4	MZFZ 4409–12	Rock crevice and hole on the ground	This study
San Gabriel, Tezonapa, Veracruz	18.57321°, -96.72487°; 510 m	16.06.2021	1	MZF-IMG 359	Rock crevice	This study
Reserva Forestal La Luisa, Tezonapa, Veracruz	18.62710°, -96.88744°; 183 m	22.08.2021	1	MZF-IMG 360	Rock crevice	This study

Morphological variation

The meristic characters of the specimens examined from Veracruz (range and average in parentheses) are congruent with most diagnostic characters reported for the type series of *L. zongolicum* (Table 2). However, DAPVR (92–98, \bar{X} = 95.1) and PVR (52–59, \bar{X} = 54.2) in the examined specimens do not overlap with those reported for the type series (DAPVR [100–

106, \bar{X} = 103.3] and PVR [61–68, \bar{X} = 64.2]). Another difference was found in the number of dorsal interwhorls (IWD2): three in most individuals from Veracruz (except MZFC 3413 with four) vs four in the type series. Additionally, four specimens from Aticpac, Boquerón, and Veracruz have an anterior frontal scale in contact with the frontonasal and frontal scale (Table 2; Fig. 2).

Table 2. Variation in selected features of collected specimens of *Lepidophyma zongolicum*. See methods for abbreviations. Specimens in bold correspond to the type series. M: male; F: female.

Specimen	Sex	SVL	GUL	DOR	DAPVR	PVR	FPT	FTL	LTR	AFS	IWD2	IWV2
MZFC 22186 (Holotype)	M	72	46	179	102	64	38	30	26	No	4	3
MZFC 22180	?	69.2	45	174	103	68	43	28	28	No	4	3
MZFC 22181	?	61.5	42	180	106	61	36	27	22	No	4	2
MZFC 22182	?	35.2	49	175	100	66	40	28	27	No	?	?
MZFC 22183	?	38.7	45	176	104	64	36	29	24	No	4	3
MZFC 22184	?	71.4	45	184	102	64	33	29	24	No	4	3
MZFC 22185	?	71.8	40	182	106	64	39	29	21	No	4	2
MZFC 3407	F	68.79	51	192	98	59	39	31	25	Yes	3	2
MZFC 3408	F	72.1	51	173	98	52	40	29	26	Yes	3	2
MZFC 3409	M	70.52	52	182	94	49	40	29	30	No	3	2
MZFC 3413	F	55.16	48	171	94	55	40	27	28	Si	4	3
MZFC 4369	M	41.99	49	180	92	55	40	29	22	Si	3	2
MZFC 4370	M	64.47	49	172	98	54	40	24	26	No	3	2
MZFC 4371	F	50.15	50	178	96	58	41	23	27	No	3	2
MZFC 4372	?	44.35	56	183	96	57	40	29	30	No	3	2
MZFC 4373	F	48.31	50	172	96	56	40	32	28	No	3	2
MZFC 4374	M	56.52	47	171	92	50	40	29	25	No	3	2
MZFC 4409	M	63.84	49	174	93	48	37	29	29	Yes	3	2
MZFC 4410	F	64.53	48	171	93	52	36	32	28	No	3	2
MZFC 4411	F	56.60	48	171	91	51	40	32	29	No	3	2
MZFC 4412	F	40.39	48	171	93	50	35	29	27	No	3	2

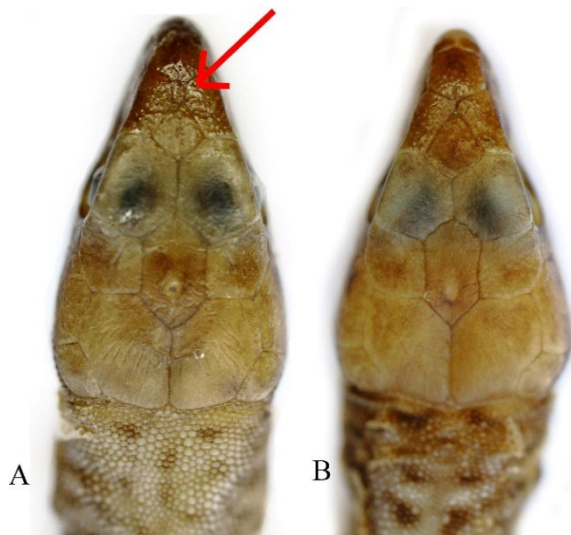


Figure 2. Dorsal head scutellation of *Lepidophyma zongolicum* specimens from Aticpac, Veracruz, Mexico. A: Presence of anterior frontal scale inserted between the prefrontal and frontal scales (MZFC 3413), the red arrow indicates the anterior frontal scale; B: Absence of anterior frontal scale (MZFC 3409)

In preservative, the colors of the specimens were as follows. Head dorsal surface Tawny Olive (C17) with Burnt Umber (C48) diffuse irregular marks in all specimens, except

Clay Color (C18) with Warm Sepia (C40) irregular marks in MZFC 3413, 4409 and 4410. Lateral surface Pale Tawny Olive (C17) with Dark Grayish Brown (C284) blotches suggesting a postocular stripe in all individuals. Supralabial and infralabial scales are Cream White (C52) with a Dark Grayish Brown (C284) blotch in each scale in all specimens. Granular throat scales are Cream White (C52) with Olive (C126) dots in all specimens.

Body dorsal and lateral background color Drab Gray (C256) in juveniles (MZFC 3413, 4369, 4371–4374, 4411 and 4412) and Medium Fawn (C257) in adults (MZFC 3407–3409, 4370, 4409 and 4410); Vandyke Brown (C282) blotches on the dorsal and lateral surfaces in all specimens; dorsal blotches roughly rectangular, arranged in two paravertebral rows (one immediately next to each paravertebral tubercle row), and lateral blotches reticulated throughout the body. Venter Cream White (C52) with dots or diffuse irregular marks in all specimens.

Forelimbs and hindlimbs have the same background color as the dorsal and lateral body surfaces, and Raw Umber (C22) diffuse blotches and dots in all individuals. The dorsal surface of fingers and toes is Cream White (C52) with Dark Brownish Olive (C127) bands in all specimens.

Tail background color Fawn (C46) with Cream White (C52) diffuse irregular blotches and bands (complete or incomplete) in all specimens (Figure 3a), but specimens from Atoyac (MZFC 4409–4412) present a conspicuous pattern of

Cream White (C52) complete bands interspersed with Fawn (C46) bands (Fig. 3b).

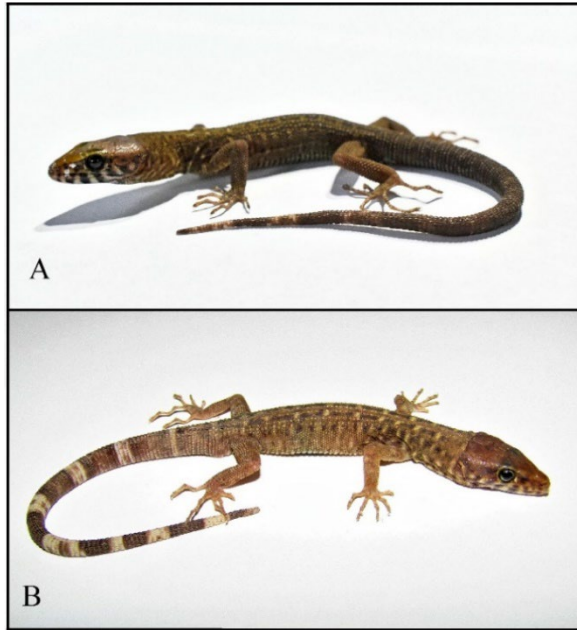


Figure 3. Dorsolateral view of two specimens of *Lepidophyma zongolicum* from Veracruz, Mexico. A: Specimen MZFF-IMG 292 from Tezonapa (photo by Maximiliano Monroy Sánchez); B: Specimen MZFF 4409 from Atoyac, showing a conspicuous tail pattern of cream-white complete bands interspersed with fawn bands.

Species distribution modeling

Based on fieldwork and published records, we compiled a list of 25 records for *L. zongolicum* from nine localities. After

eliminating duplicate occurrences, the final database consisted of 12 presence records. We selected the best model from 20 generated. The final model LQ_rm1 (linear-quadratic) showed optimal values of area under curve AUC= 0.85 (average/sd AUC calculated on the validation datasets, the data withheld during cross-validation), omission rate, or.mtp = 0.11 (average/sd omission rate with threshold as the minimum suitability value across occurrence record) and Akaike’s Information Criterion AICc = 0 (AIC corrected for small sample sizes), which we considered indicative of good model performance. According to Phillips et al. (2017) the environmental variables that showed the greatest contribution and therefore considered to generate the model chosen according to COR statistics (measured by correlation with 0/1 evaluation data encoding observed absences/presences) observed in the graphics cloglog are: mean temperature of driest quarter ($\beta = -0.7780$), precipitation seasonality ($\beta = 0.1861$), precipitation of warmest quarter ($\beta = 0.6398$), max temperature of warmest month ($\beta = 1.2044$), isothermality ($\beta = 1.7199$), and precipitation of driest quarter ($\beta = 5.7305$) (Fig. 4).

The species distribution model (Fig. 5) suggests the presence of *L. zongolicum* in the southern Sierra Madre Oriental and the province of Oaxaca, in central Veracruz (municipalities of Cordoba and Orizaba), extending southward along the Sierra de Zongolica in Veracruz a small region in southeast Puebla and Sierra Mazateca in Oaxaca bordering a small region of Papaloapan River with a lower probability of suitable conditions towards the northern Oaxaca in Sierra Juárez. The state with the highest area predicted as suitable for the species is Veracruz, followed by Oaxaca, and finally Puebla. The SDM of *L. zongolicum* shows that it can probably be found in the protected natural areas of Parque Nacional Cañon del Río Blanco in Veracruz and a small zone in the Reserva de la Biosfera Tehuacán-Cuicatlán.

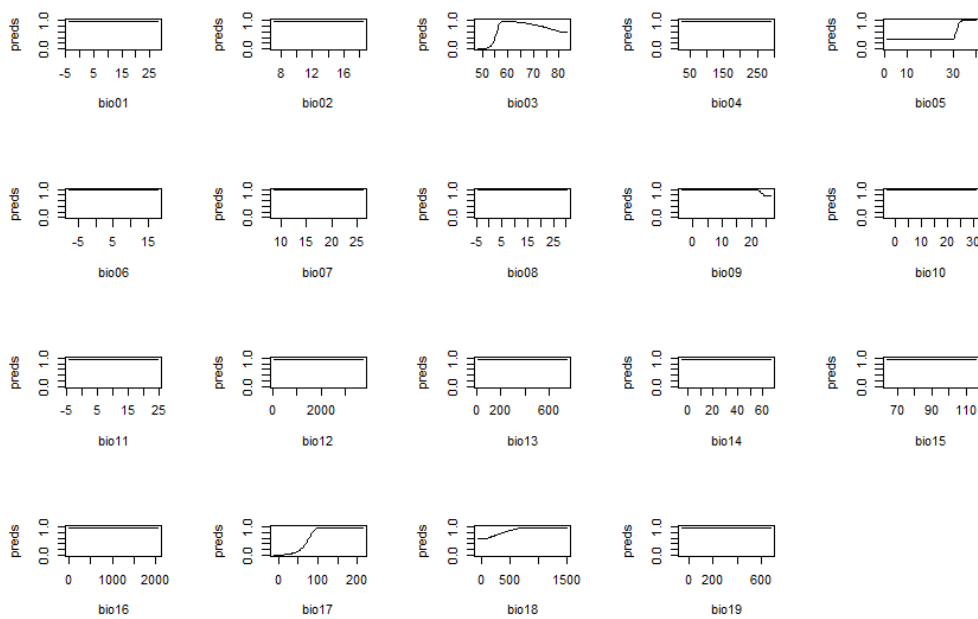


Figure 4. Marginal response curves for the predictor variables with non-zero coefficients in our model. Selected variables, BIO 03, BIO 05, BIO 09, BIO 15, BIO 17 and BIO 18.

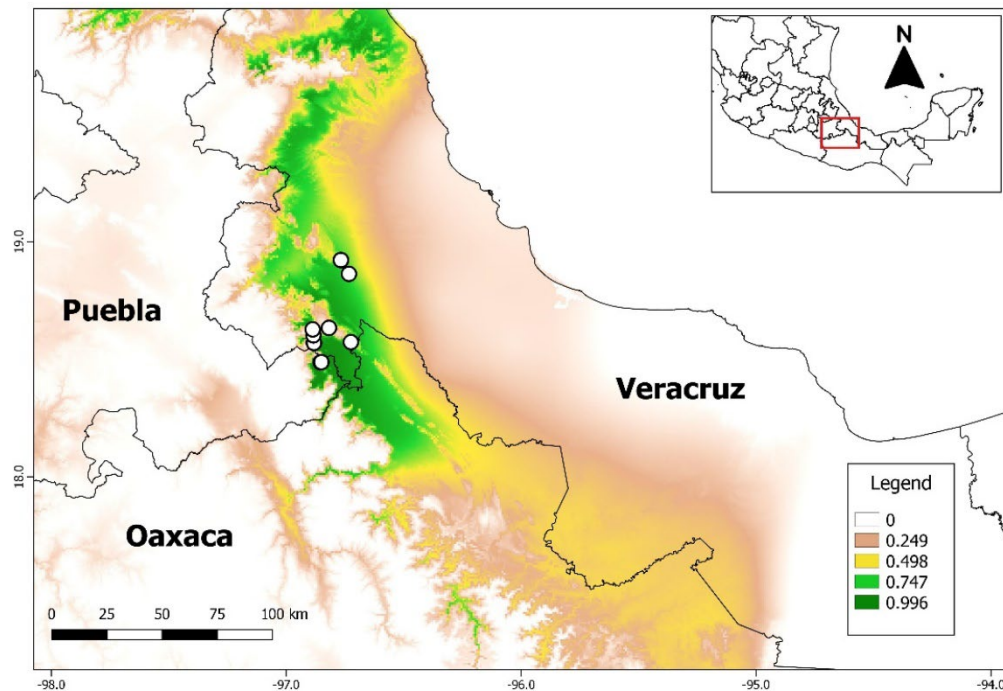


Figure 5. Species Model Distribution for *Lepidophyma zongolicum* in Mexico. Green colors represent suitable climatic conditions for the species.

Discussion

The specimens we report herein were clearly assignable to *L. zongolicum* based on the combination of the following diagnostic characters: 40–49 GUL, 174–184 DAPVR, 21–28 LTR, 33–43 FPT, 27–30 FTL, and 2–3 IWV2 (García-Vázquez et al. 2010). However, we demonstrated that three characters previously considered diagnostic for *L. zongolicum* were uninformative: DAPVR, PVR, and IWD2. Additionally, the anterior frontal scale in two specimens from Aticpac and one from Atoyac has not been reported in *L. zongolicum* or any other xantusiid lizard (Gauthier et al. 2008, Bezy 2019). We documented an unusual coloration pattern within the genus in specimens from Atoyac (MZFZ 4409–4412): tail with cream-white complete bands interspersed with fawn bands. This variation discovered in the meristic and coloration characters for *L. zongolicum* demonstrates the importance of reporting additional specimens to generate an accurate morphological diagnosis, especially in species with few known specimens (e.g., *L. chicoasense*, *L. lineri*, *L. lipetzi*, *L. radula*, and *L. tarascae*; Guzmán-Villa et al. 1988, Bezy 2019), or that present a wide but disjunct geographic distribution (e.g., *L. flavimaculatum*, *L. smithii*, and *L. sylvaticum*; Bezy 1984, Bezy & Camarillo-Rangel 2002, Bezy 2019).

The results of the SDM suggest that *L. zongolicum* prefers warm climates where the annual temperature and humidity vary little and where strong rainfall occurs during the rainy season. The SDM also showed that *L. zongolicum* may inhabit the altitudinal range of 0–1300 m. It is congruent with our and literature data, given that the lowest known locality is at 94 m (type locality at El Tepeyac, Eloxochitlán, Puebla; García-Vázquez et al. 2010) and the highest known locality is at 931 m (La Gloria, Tezonapa, Veracruz; this work), so the true

elevation range of the species is likely broader than previously known. The area predicted by the model includes the biogeographic provinces of the southern region of the Sierra Madre Oriental and the province of Oaxaca in mountainous parts of central Veracruz in the municipalities of Orizaba, Cordoba, and Sierra de Zongolica, southward in the eastern Puebla and northern Oaxaca in Sierra Mazateca, with the Río Santo Domingo of Oaxaca forming the predicted southern limit of the species, this river representing the northern limit of Sierra Juárez (Razo-González et al. 2021). We observed a low probability of the presence of *L. zongolicum* in the Sierra Juárez of Oaxaca, likely to the close relationship between the Sierra de Juárez and Sierra de Zongolica concerning the Sierra Madre Oriental, because the biogeographic provinces of Oaxaca and Sierra Madre Oriental share biotic elements (Espinosa-Organista et al. 2004, León-Paniagua & Morrone 2009). Additional sampling efforts are needed to verify the predictions of the SDM, especially at sites with rocky formations under tree cover, which are the habitats where the species has been found.

Acknowledgments

Support for fieldwork was provided by Dirección General de Apoyo al Personal Académico, Universidad Nacional Autónoma de México (PAPIIT grant number IN-216619 and IN-218022) and Consejo Nacional de Ciencia y Tecnología (CONACyT A1-S-37838) to Uri García. To A. Clause and two anonymous reviewers for comments and review of the manuscript; Yeymy, Martha, and Miguelito (Mike Culebras) of Finca Santa Marthe Ecosuites for their hospitality during fieldwork. All specimens were taken under a collecting permit issued to Uri Omar García-Vázquez by the Mexican government's Secretaría de Medio Ambiente y Recursos Naturales (Permit number FAUT-0246).

References

- Arenas-Moreno, D.M., Muñoz-Nolasco, F.J., Bautista-del Moral, A., Rodríguez-Miranda, L.A., Domínguez-Guerrero, S.F., Méndez-de la Cruz, F.R. (2021): A new species of *Lepidophyma* (Squamata: Xantusiidae) from San Luis Potosí, México, with notes on its physiological ecology. *Zootaxa* 4949: 115–130.
- Bezy, R.L. (1984): Systematics of xantusiid lizards of the genus *Lepidophyma* in northeastern México. *Contributions in Science, Natural History Museum of Los Angeles County* 349: 1–16.
- Bezy, R.L. (2019): Night lizards: field memoirs and a summary of the Xantusiidae. *ECO Herpetological Publishing and Distribution, Korea*.
- Bezy, R.L., Camarillo-Rangel, J.L. (2002): Systematics of xantusiid lizards of the genus *Lepidophyma*. *Contribution in Science, Natural History Museum of Los Angeles County* 493: 1–41.
- Clause, A.C., Schmidt-Ballardo, W., Solano-Zavaleta, I., Jiménez-Velázquez, G., Heimes, P. (2016): Morphological variation and natural history in the enigmatic lizard clade *Scopaeabronia* (Squamata: Anguinae: Bronia). *Herpetological Review* 47: 536–543.
- Cobos, M.E., Peterson, A.T., Barve N., Osorio-Olvera, L. (2019): kuenm: an R package for detailed development of ecological niche models using Maxent. *PeerJ* 7: e6281.
- Cuervo-Robayo, A.P., Téllez-Valdés, O., Gómez, M., Venegas-Barrera, C., Manjarrez, J., Martínez-Meyer, E. (2013): An update of high-resolution monthly climate surfaces for Mexico. *International Journal of Climatology* 34: 2427–2437.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J. (2011): A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43–57.
- Espinosa-Organista, D., Aguilar, C., Ocegueda, S. (2004): Identidad biogeográfica de la Sierra Madre Oriental y posibles subdivisiones bióticas. *Las Prensas de Ciencias, UNAM, México* 487–500.
- García-Vázquez, U.O., Canseco-Márquez, L., Aguilar-López, J.L. (2010): A new species of night lizard of the genus *Lepidophyma* (Squamata: Xantusiidae) from southern Puebla, México. *Zootaxa* 2657: 47–54.
- Gauthier, J., Kearney, M., Bezy, R.L. (2008): Homology of cephalic scales in xantusiid lizards, with comments on night lizard phylogeny and morphological evolution. *Journal of Herpetology* 42: 708–722.
- Guzmán-Villa, U., Flores-Villela, O., Schmidt-Ballardo, W. (1988): Variation, distribution, and taxonomic status of the xantusiid lizard *Lepidophyma tarascae*. *Herpetological Review* 29: 78.
- Helmstetter, N.A., Conway, C.J., Stevens, B.S., Goldberg, A.R. (2021): Balancing transferability and complexity of species distribution models for rare species conservation. *Biodiversity and Distributions* 27: 95–108.
- Köhler, G. (2012): *Color Catalogue for Field Biologists*. Herpeton Press. Germany.
- Lara-Tufiño, J.D., Nieto-Montes de Oca, A. (2021): A new species of night lizard of the genus *Lepidophyma* (Xantusiidae) from southern Mexico. *Herpetologica* 77: 320–334.
- León-Paniagua, L., Morrone, J.J. (2009): Do the Oaxacan Highlands represent a natural biotic unit? A cladistic biogeographical test based on vertebrate taxa. *Journal of Biogeography* 36: 1939–1944.
- Mata-Silva, V., García-Padilla, E., Rocha, A., DeSantis, D.J., Johnson, J.D., Ramírez-Bautista, A., Wilson, L.D. (2021): A reexamination of the herpetofauna of Oaxaca, Mexico: composition update, physiographic distribution, and conservation commentary. *Zootaxa* 4996: 201–252.
- Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P. (2014): ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models. *Methods in Ecology and Evolution* 5: 1198–1205.
- Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E. (2017): Opening the black box: an open-source release of Maxent. *Ecography* 40: 887–893.
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Razo-González, M., Márquez, J., Castaño-Meneses, G., Novelo-Gutiérrez, R. (2021): La complejidad biogeográfica de la Sierra de Juárez, Oaxaca, México, revelada a través del análisis de parsimonia de endemismos de especies de tricópteros (Insecta: Trichoptera). *Revista Mexicana de Biodiversidad* 92: e923808.
- Sánchez-García, J.C., Canseco Márquez, L., Pavón-Vázquez, C.J., Cruzado-Cortés, J., García-Vázquez, U.O. (2019): New records and morphological variation of *Rhadinaea marcellae* Taylor, 1949 (Squamata, Colubridae) from Sierra Madre Oriental, México. *Check List* 15: 729–733.
- Scarpetta, S., Gray, L., Nieto Montes de Oca, A., del Rosario Castañeda, M., Herrel, A., Losos, J.B., Luna-Reyes, R., Jiménez Lang, N., Poe, S. (2015): Morphology and ecology of the Mexican Cave Anole *Anolis alvarezdeltoroi*. *Mesoamerican Herpetology* 2: 261–270.
- Torres-Hernández, L.A., Ramírez-Bautista, A., Cruz-Elizalde, R., Hernández-Salinas, U., Berriozabal-Islas, C., DeSantis, D.L., Johnson, J.D., Rocha, A., García-Padilla, E., Mata-Silva, V., Fucsko, L.A., Wilson, L.D. (2021): The herpetofauna of Veracruz, Mexico: composition, distribution, and conservation status. *Amphibian & Reptile Conservation* 15 (2): 72–155.