Anolis alvarezdeltoroi was described in 1996 from a single female specimen collected in the Northern Highlands region of Chiapas, Mexico. Since its description, *A. alvarezdeltoroi* has been infrequently collected and officially documented only from Chiapas, and its phylogenetic position within *Anolis* has remained unknown. This species inhabits the inside of limestone caves.

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Morphology and ecology of the Mexican cave anole *Anolis alvarezdeltoroi*

Simon Scarpetta[1], Levi Gray[2], Adrián Nieto Montes de Oca[3], María del Rosario Castañeda[4], Anthony Herrel[5], Jonathan B. Losos[4], Roberto Luna-Reyes[6], Noé Jiménez Lang[7], and Steven Poe[2]

[1]*Department of Biology, Stanford University, Stanford, California 94305, United States.*
Email: scas100@stanford.edu (SS, Corresponding author)

[2]*Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico 87131, United States.*

[3]*Laboratorio de Herpetologia, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, D.F. 04510, Mexico.*

[4]*Harvard Museum of Comparative Zoology, 26 Oxford St., Cambridge, Massachusetts 02138, United States.*

[5]*UMR 7179 C.N.R.S/M.N.H.N., Département d'Ecologie et de Gestion de la Biodiversité, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France and 2) Ghent University, Evolutionary Morphology of Vertebrates, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium.*

[6]*Coordinación Técnica de Investigación, Secretaría de Medio Ambiente e Historia Natural, Av. de los Hombres Ilustres s/n, Fracc. Francisco y Madero, CP 29000, Tuxtla Gutiérrez, Chiapas, Mexico.*

[7]*El Colegio de la Frontera Sur. Periférico Sur s/n, Barrio de María Auxiliadora, CP 29290, San Cristóbal de Las Casas, Chiapas, Mexico*

Abstract: We redescribe the ecologically unusual lizard *Anolis alvarezdeltoroi*, previously known from a single specimen, based on newly collected and previously unidentified preserved specimens from the type-locality region in Chiapas, as well as new localities in Veracruz and Oaxaca. We include information on color, morphological variation, and natural history. *Anolis alvarezdeltoroi* occupies limestone caves, an unusual habitat for anoles. We found individuals active on limestone surfaces during the day at heights from 0.42 to 5 m, and sleeping mainly in cave interiors, with some individuals observed on ceilings deep within caves.

Key Words: Anoles, caves, Mexico, morphology, natural history

Resumen: Se redescribe a la lagartija de ecología inusual *Anolis alvarezdeltoroi*, conocida previamente de un solo ejemplar, con base en ejemplares recolectados recientemente y ejemplares preservados no identificados previamente de la región de la localidad tipo en Chiapas, así como de nuevas localidades en Veracruz y Oaxaca. Se incluye información sobre su coloración, variación morfológica, e historia natural. *Anolis alvarezdeltoroi* vive en cuevas en roca caliza, un hábitat inusual para las lagartijas del género *Anolis*. Observamos individuos activos durante el día en la superficie de la roca en alturas de 0.42 a 5 metros, y individuos durmiendo principalmente en el interior de cuevas, donde algunos individuos se observaron en el techo a considerable profundidad dentro de las mismas.

Palabras Claves: Anolis, cuevas, México, morfología, historia natural

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INTRODUCTION

Lizards of the genus *Anolis* are known for their many adaptations to a multitude of different environments. Most Caribbean *Anolis* have been found to conform to six convergent and specialized groups called ecomorphs, which share similar morphology and ecology somewhat independent of phylogeny and geography (e.g., Williams, 1972, 1983; Irschick et al., 1997; Losos et al., 1998). The ecological diversity of island forms is well documented (Irschick et al., 1997; Nicholson et al., 2005; Losos et al., 2006), but mainland forms are relatively less well researched and may occupy an even greater diversity of niches (Pinto et al., 2008; Schaad and Poe, 2010; pers. observ.). One of the more novel and fascinating of both mainland and island anole ecologies is the occupation of the interior and exterior surfaces of limestone caves—an environment rarely occupied by lizards of any genus—by the Mexican taxon *A. alvarezdeltoroi*.

Anolis alvarezdeltoroi was described from a single adult female (Nieto Montes de Oca, 1996) from 19.5 km N, 8.1 km W of Ocozocoautla, Chiapas, Mexico (16°56'N, 93°27'W), elev. 940 m. This species has been collected infrequently since its description, and currently is documented only from the state of Chiapas. Two unidentified anoles in the Museum of Vertebrate Zoology collection, however, were secured from the interior of caves in southern Veracruz on October 14–15, 1984. We identified these as *A. alvarezdeltoroi*, and embarked on fieldwork to obtain additional specimens in the area. In 2010 and 2011, personnel from the University of New Mexico (UNM) and collaborators at Universidad Nacional Autónoma de México (UNAM) undertook three expeditions to locate the "cave anole," *A. alvarezdeltoroi*. Subsequently, researchers from Harvard University collected additional data at a site where UNM researchers had found multiple individuals. Our efforts have resulted in the collection of several new specimens of *A. alvarezdeltoroi*, including some from new localities, and the first ecological data for this species.

Here we present a redescription of *A. alvarezdeltoroi* based on newly collected and previously preserved specimens from the type-locality region in Chiapas, and from new localities in Veracruz and Oaxaca. We also present natural history data for this enigmatic and ecologically interesting species. While Nicholson et al. (2012) would call this species *Norops alvarezdeltoroi*, we call this anole by the generic name *Anolis* rather than *Norops* based on arguments in Poe (2013). That is, we consider the division of *Anolis* into multiple genera by Nicholson et al. (2012) as scientifically unnecessary and arbitrary. See alternative, generic splittings of *Anolis* in Poe (2013: fig. 1). For different opinions, see Nicholson et al. (2014) and Johnson et al. (2015).

MATERIALS AND METHODS

Morphology

We examined 18 specimens of *Anolis alvarezdeltoroi*. Sixteen were collected during our recent expeditions, and three are from museum collections or previous description of the species (Nieto Montes de Oca, 1996). Museum abbreviations are listed as per Sabaj Pérez (2010) except for the acronym NJL, which is an abbreviation for a field number of an uncatalogued specimen in the MZFC.

We made measurements with digital calipers on preserved specimens, and provide them in millimeters (mm), usually to the nearest 0.1 mm. We measured snout–vent length (SVL) from the tip of the snout to the anterior edge of the cloaca; head length from the tip of the snout to the anterior edge of the ear opening; femoral length from the longitudinal midline of the body laterally to the knee, which was bent at a 90° angle; head width at the broadest part of the head between the posterolateral corners of the orbits; tail length from the anterior margin of the cloaca to the tip of the tail; and length of the fourth (i.e., longest) toe of the hind limb from the proximal limit of the toe to the tip of the claw. The scale terminology and characters used mainly follow standards established by Williams et al. (1995) for species descriptions of *Anolis* lizards.

Observations

We observed individuals of *A. alvarezdeltoroi* at night on 27 December 2011 at 2 km N of La Chinantla, Veracruz (17.29834, -94.45433; elev. 95 m) and on 2 January 2012 at ca. 24 km N of Ocozocoautla, on the road to Apic Pac, Chiapas (16.93078, -93.4532; elev. 780 m). During our observations, we noted their sleeping perch height and perch substrate. We collected a sample of these animals and preserved them for morphological and molecular studies. The specimens were euthanized with sodium pentobarbital, fixed in 10% formalin, rinsed, and stored in 70% ethyl alcohol.

We searched for lizards during daylight hours at 2 km N of La Chinantla, Veracruz on 12–15 August 2013. For each animal observed, we noted its location unless it was moving away when first seen. We captured animals for morphological measurements (not reported), and released them at the end of the study; consequently, no animal provided more than one data point.

RESULTS AND DISCUSSION

The description of external morphological variation in *Anolis alvarezdeltoroi* is based upon the holotype (ENCB 12940) and the following specimens: MSB 94836–94837, 94839, 94841, 94842, 94845, 94846, 94852; MVZ 229607–229608; NJL 107, 162, 164–166, POE 4097-4098; UOGV 397). Snout–vent length 53.3–74.0 (= 65.2 ± 4.9) in nine adult males (one juvenile male was excluded), 49.6–66.5 (= 60.4 ± 5.3) in nine adult females; ratio of head length to SVL 0.25–0.28 (= 0.26 ± 0.01) in males, 0.22–0.28 (= 0.27 ± 0.02) in females; ratio of head width to SVL 0.14–0.17 (= 0.16 ± 0.01) in males, 0.11–0.18 (= 0.16 ± 0.02) in females; ratio of ear height to head length 0.12–0.16 (= 0.13 ± 0.01) in males, 0.10–0.18 (= 0.13 ± 0.02) in females; ratio of femoral length to SVL 0.35–0.38 (= 0.36 ± 0.01) in males, 0.31–0.39 (= 0.35 ± 0.03) in females; ratio of tail length to SVL for the eight male specimens with complete tails 1.66–2.08 (= 1.81 ± 0.17), and 0.99–2.05 (= 1.77 ± .44) for the five female specimens with complete tails; and ratio of length of fourth toe to SVL 0.19–0.21 (= 0.21 ± 0.01) in males, 0.16–0.25 (= 0.22 ± 0.03) in females.

Dorsal head scales smooth or with weak single (in supraocular disc) or multiple keels (on snout); frontal depression deep; rostral extends anteriorly beyond mental; 7–11 (= 9.3 ± 1.2) scales across snout between second canthals; supraorbital semicircles in contact or separated by up to 3 scales; suboculars in contact with supralabials or separated by one scale row; 1–3 (= 2.2 ± 0.6) elongate superciliary scales; 6–9 (= 7.1 ± 0.9) loreal rows; elongate anterior nasal scale contacts sulcus between rostral and first supralabial; ratio of length of interparietal to head length 0.05–0.09 (= 0.07 ± 0.01); ratio of length of interparietal to length of largest scale adjacent to lateral edges of interparietal 1.9–2.7 (= 2.3 ± 0.4); ratio of length of interparietal to ear height 0.39–0.64 (= 0.56 ± 0.1), 3–5 (= 3.9 ± 0.6) scales between interparietal and supraorbital semicircles; preoccipital absent; 8–12 (= 9.5 ± 1.1) supralabials to center of eye; postrostrals 4–7 (= 6.1 ± 1.1); 4–8 (= 6.5 ± 1.2) postmentals; some enlarged scales present in supraocular disc, decreasing gradually in size laterally; mental partially divided posteriorly, extending posterolaterally beyond rostral, with posterior border in shallow concave arc or straight; 0–2 (= 0.6 ± 0.6) poorly differentiated or slightly enlarged sublabials; shallow axillary pocket present; enlarged postcloacal scales absent; nuchal, dorsal, and caudal crests absent; dorsal scales slightly to distinctly keeled; approximately 2–3 very slightly enlarged middorsal scale rows, 7–13 (= 9.9 ± 2.1) longitudinal dorsal rows in 5% of SVL; ventral scales in transverse rows, smooth, 7–13 (= 8.8 ± 1.3) ventral scales in 5% of SVL; middorsal caudal scales jumbled, not in regular rows; limb and supradigital scales muticarinate; toepads expanded; and 11–18 (= 14.4 ± 1.9) expanded lamellae under fourth toe.

Color in Life

The color in life is described from photos and notes of male specimens unless otherwise noted (see Fig. 1). Head yellowish brown; ridges above and below eyes yellow; broad yellowish and brown lateral stripes extend posteriorly from eye to nape; iris blue; pale narrow lateral bands in blue, yellow, and pink, often outlined by a medium brown, sometimes broken; many pale spots on flank interspersed between and around bands; blue-green sheen on flanks, especially near hind limbs, but can extend across the flank almost to the head; limbs faintly banded, alternating between light brown and cream (not very distinct on some specimens); tail starkly banded brown and cream; dewlap dark red in males with white scales in single rows, black in females with white scales in single rows (Fig. 3); a poorly defined pale middorsal stripe (Fig. 2) is present in most females but not observed in males.

Fig. 1. An adult male *Anolis alvarezdeltoroi* from Ejido Veinte Casas, Municipio de Ocozocoautla de Espinosa, Chiapas, Mexico.

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Fig. 2. An adult female *Anolis alvarezdeltoroi* from Ejido Veinte Casas, Municipio de Ocozocoautla de Espinosa, Chiapas, Mexico.

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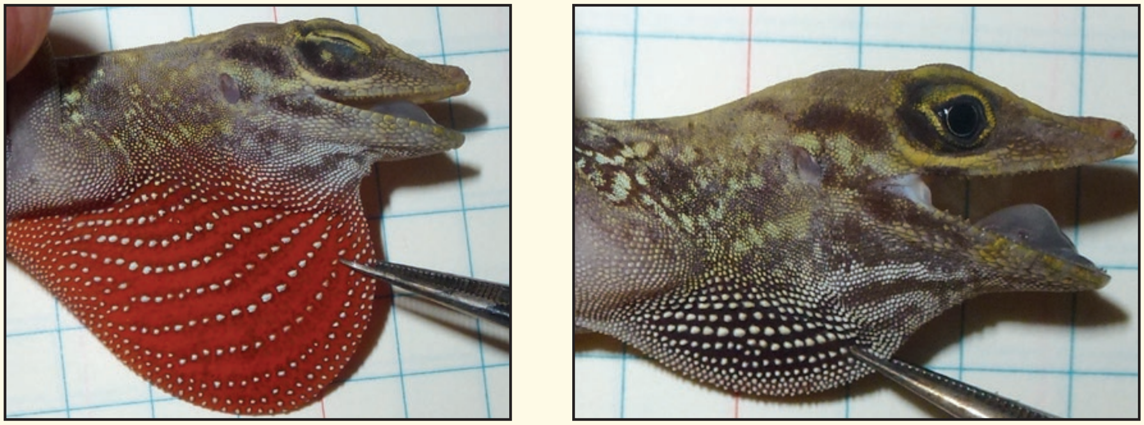

Fig. 3. Dewlap of *Anolis alvarezdeltoroi* (A, male, B, female) from Veracruz, Mexico. © Steven Poe

Ecology

We collected specimens of *A. alvarezdeltoroi* in karst limestone habitat surrounded by pasture and tropical evergreen forest. Many individuals found at night were sleeping vertically ~0.5–10 m up on limestone walls, both inside and outside of caves. Some adults were sleeping upside-down on a cave ceiling at heights of approximately 15 m from the cave floor (Fig. 4). We collected specimens throughout approximately 40 m of the cave length that was open on either side; i.e., we found specimens in the cave interior up to 20 m from a cave entrance. In the middle of this passage, some small holes in the walls also provided entry into the cave. We found an adult female from the type-locality region sleeping upside-down under an overhanging limestone boulder at a height of ~0.5 m. Juveniles often slept vertically on dangling vegetation along the limestone walls near the cave entrance (Fig. 5).

We summarize the diurnal observation data in Table 1. All the specimens collected during the day were on vertical rock walls, except for one male found on a 15 cm liana at a height of 2.0 m. Juveniles perched the highest (= 2.59), females perched the lowest (= 1.56), and males perched intermediately (= 2.26). The body axes of some animals were oriented vertically on their perch (50% for males, 25% for females, and 33% for juveniles), but most were not.

We are aware of at least two other anoles*, A. bartschi* of western Cuba and *A. lucius* from throughout Cuba, which are associated with karst habitat. We are unaware of any instances of *A. bartschi* being found deep in cave interiors as in *A. alvarezdeltoroi*, but *A. lucius* has been encountered deep within small and large caves, and the eggs of *A. lucius* have been found stuck to the limestone walls of these caves similar to those of some gecko species (Hardy, 1957). *Anolis bartschi* appears to possess the same short-bodied, long-hind limbed morphology present in *A. alvarezdeltoroi.* The similarity of these species in habitat use and morphology may indicate the presence of a "cave" ecomorph in *Anolis* shared across islands and the mainland, or may suggest broader convergence with other saxicolous anoles that possess long hind limbs such as *A. gadovii*.

Anolis alvarezdeltoroi may be found sympatrically with several other anoles. Up to 14 species of *Anolis* have been found near known localities for *A. alvarezdeltoroi* (pers. observ.). Although there is significant overlap in distribution among *A. alvarezdeltoroi* and other anoles, the unusual habitat preference of *A. alvarezdeltoroi* suggests minimal ecological overlap with other *Anolis* in the region. *Anolis compressicauda* displays a similar range and has also been found at cave entrances (pers. observ.), but typically is found only on the ground. Other lizards found alongside *A. alvarezdeltoroi* on limestone walls and crevices were species of *Lepidophyma* and *Xenosaurus*.

Fig. 4. A male of *Anolis alvarezdeltoroi* from Veracruz, Mexico, approximately 12 m up and 15 m from the nearest cave entrance; includes inset close up. © Steven Poe

Fig. 5. An adult female *Anolis alvarezdeltoroi* perched on a tree trunk, from Zona Sujeta a Conservación Ecológica La Pera, Municipio de Berriozábal, Chiapas, Mexico. © Roberto Luna Reyes

Table 1. Diurnal observation data; listed are the average heights of rock wall perches for male, female, and juvenile lizards, ± the SD range distance from the rock to the nearest structure on which the lizard could perch, e.g., tree, liana, root, followed by the range of height observations.

	Perch Height (m)	**Distance to Nearest Vegetation (m)**
Males (*n* = 15)	2.26 ± 0.13	0.42–5.00
Females (*n* = 8)	1.56 ± 0.72	0.64–3.00
Juveniles (*n* = 6)	2.59 ± 1.05	2.50–4.00

DISTRIBUTION AND CONSERVATION

Anolis alvarezdeltoroi is distributed in the Chimalapas region of Oaxaca and Veracruz and the El Ocote region of Chiapas, at elevations from 90 and 1,200 m (Fig. 6). The distribution spreads east of the El Ocote Biosphere Reserve to north of Berriozabal, Chiapas. Our collections represent two new state records for this species, in Oaxaca and Veracruz, respectively (Appendix I).

Anolis alvarezdeltoroi appears to be dependent on karst limestone caves and sinks. Nearby forest habitat often is degraded—sometimes severely—yet populations of *A. alvarezdeloroi* appear to be healthy as long as the karst habitat is preserved. We do not know how extensive the appropriate habitat is within Chimalapas and El Ocote. Our limited experience in the region suggests the habitat is uncommon and patchy. The species is protected via the El Ocote Biosphere Reserve, which is a known biodiversity hotspot in Mexico that protects numerous other species such as jaguars, howler monkeys, tapirs, and harpy eagles (SEMARNAT, 2001).

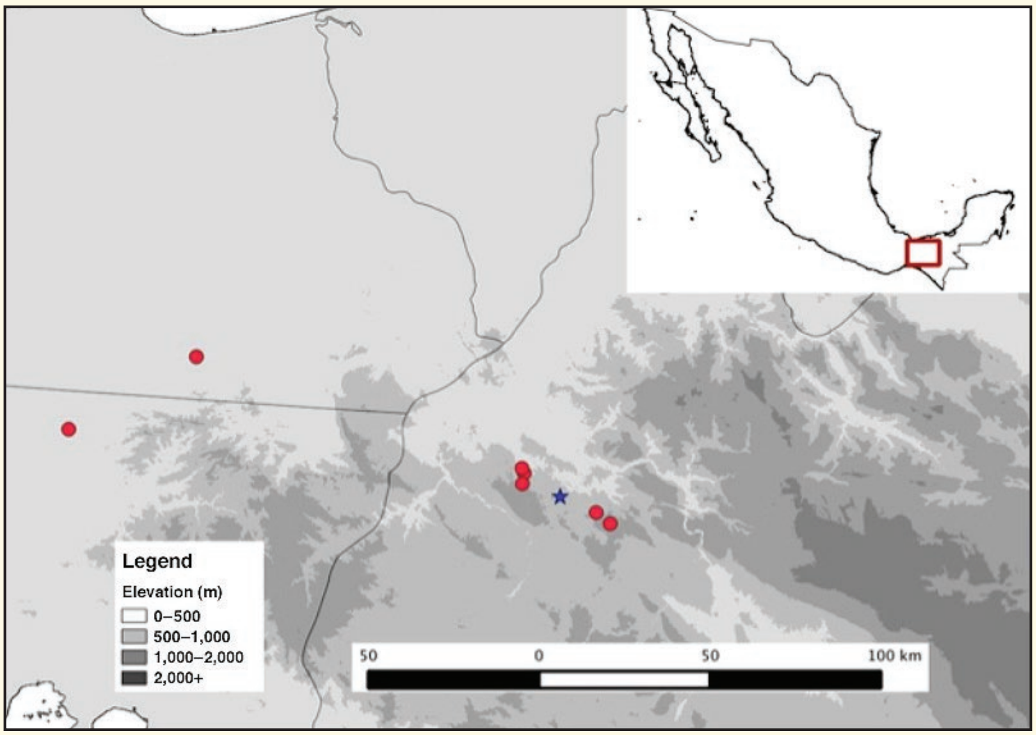

Fig. 6. Distribution map of *Anolis alvarezdeltoroi* in Mexico; includes type locality (blue star) and other localities (red circles).

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Appendix 1. List of Specimens Examined.

Anolis alvarezdeltoroi—MEXICO: MSB 94836–94837, 94841, 94845–6, 94852: Veracruz, 2 km N of La Chinantla (17.29834, -94.45433; elev. 95 m). MSB 94839: Chiapas, ca. 24 km N of Ocozocoautla, road to Apic Pac (16.93078, -93.4532; elev. 780 m). MSB 94846: Veracruz, 2 km N of Poblado Diez (La Chinantla) Uxpanapa (17.29834, -94.45433; elev. 95 m). MSB 94842: Oaxaca, ca. 25 km N of Chalchijapa (17.10345, -94.80348; elev. 103 m). MVZ 229607–229608: Veracruz, Benito Juárez Segundo, 44 mi. (rd.) NE Jct. Mex. Hwy. 185, 120 m. NJL 107: Rancho San Agustín, 12.5 km NW of Berriozábal, area known as El Pozo (16.860278, -93.316111). NJL 162: Ejido Veinte Casas, Sierra Veinte Casas, Reserva de la Biosfera Selva El Ocote (16.99462, -93.55135). NJL 164: Ejido Veinte Casas, Sierra Veinte Casas, Reserva de la Biosfera Selva El Ocote (16.96558, -93.55657). NJL 165: Ejido Veinte Casas, Sierra Veinte Casas, Reserva de la Biosfera Selva El Ocote (17.00802, -93.55804). POE 4097–4098: Veracruz, 2 km N of La Chinantla (17.29834, -94.45433; elev. 95 m). NJL 166: Ejido Veinte Casas, Sierra Veinte Casas, Reserva de la Biosfera Selva El Ocote (17.00803, -93.55803). UOGV 397 Chiapas, Ocozocoautla de Espinoza, El Limón, km 29 on Apic Pac-Ocozocuautla road (16.94477, -93.45419, elev.736 m).

Simon Scarpetta is a graduate student in paleontology at the University of Texas at Austin. He received his B.S. in Biology with an emphasis in ecology and evolution from Stanford University, where he studied phylogenetics and biogeography of *Ameiva* lizards. He also has been involved with lab and fieldwork at the University of New Mexico, studying *Anolis* lizards. Simon currently is interested in evolutionary morphology and biogeography of modern and fossil squamates.

Levi Gray grew up on a ranch in northern California, where he first gained an appreciation for local lizards, snakes, and frogs. After receiving his B.S. at UC Davis, Levi worked as a lab technician for several years in Dr. Bradley Shaffer's lab, working primarily on the California Tiger Salamander (*Ambystoma californiense*). Currently a Ph.D. student in Dr. Steve Poe's lab at the University of New Mexico, Levi's research focuses on speciation, systematics, and biogeography. Though generally interested in reptiles and amphibians, the focus of his dissertation work lies primarily on *Anolis* lizards in Mexico, with an emphasis on the most important state: Chiapas.

Adrián Nieto Montes de Oca received a Ph.D. in Biology (Systematics and Ecology) at the University of Kansas in 1994. He has been a Full Professor and Curator of Herpetology at the Museo de Zoología *Alfonso L. Herrera*, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, since 1994. Adrian has authored or co-authored about 55 research papers on amphibians and reptiles. His primary interest is in the systematics and biogeography of the amphibians and reptiles of Mexico.

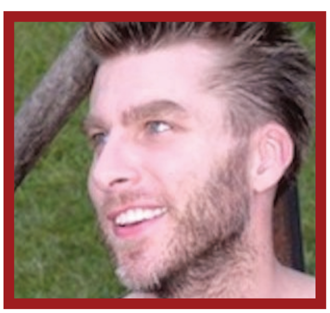
María del Rosario Castañeda obtained her B.S. in Biology from the Universidad de Los Andes in Bogotá, Colombia, and a Ph.D. from George Washington University in Washington, D.C. She was a postdoctoral researcher at Harvard University and currently is a postdoctoral researcher at Universidad del Valle in Cali, Colombia. Rosario is the co-chair of the IUCN Anoline Lizard Specialist Group. Her research primarily focuses on *Anolis* lizards, and combines field observations, DNA, and museum collections data to better understand how species are related, how and why different morphological and ecological attributes have evolved, and how population genetic data can be used toward conservation efforts.

Anthony Herrel is a permanent researcher employed by the French CNRS who works at the Muséum National d'Histoire Naturelle (MNHN) in Paris, and currently is the head of the FunEvol team at the MNHN. He also is a research associate in the Department of Biology at the Universities of Antwerp and Ghent in Belgium. Anthony's main research interest lies in the evolution of complex integrated systems. By combining a variety of experimental approaches and techniques in an explicit comparative framework, he tries to gain insights into the evolution of these systems. As model systems, he has chosen the feeding and locomotor system in vertebrates.

Jonathan Losos is an evolutionary biologist whose research takes a multi-disciplinary, integrative approach to understanding evolutionary diversification. Focusing on the diversity of lizards in the genus *Anolis*, Losos combines the studies of ecology, behavior, functional morphology, and systematics to address why the evolutionary radiation of anoles has been so successful and how particular species adapt to their environments. To address these questions, Losos and colleagues conduct field experiments in nature, sequence DNA, observe animals in their natural habitats, and bring lizards into the laboratory for functional and developmental studies.

Roberto Luna-Reyes is a Mexican herpetologist who earned his undergraduate and Master's degrees at the Universidad Nacional Autónoma de México (UNAM). He is a researcher at the Secretaría de Medio Ambiente e Historia Natural (SEMAHN) in the state of Chiapas, and a Professor at the Universidad de Ciencias y Artes de Chiapas (UNICACH). Roberto's main interests are systematics, biogeography, natural history, and conservation of amphibians and reptiles in Chiapas and Mexico.

Noé Jiménez-Lang studied biology at the Universidad de Ciencias y Artes de Chiapas (UNICACH), and currently is a Master's student at El Colegio de la Frontera Sur (ECOSUR) in the state of Chiapas. Noé's interests in herpetology include the ecology and conservation of Mexican amphibians and reptiles, and the management of natural resources and rural development.



Steven Poe is Associate Professor in the Department of Biology and Associate Curator in the Division of Amphibians and Reptiles of the Museum of Southwestern Biology at the University of New Mexico, United States. His research focuses on taxonomy, phylogenetics, and comparative evolution, especially of *Anolis* lizards. Steven enjoys experiencing the wonderful culture, scenery, and herpetofauna of Mexico.