An expeditionary collection and analysis of amphibians and reptiles from Nicaragua with an updated checklist of new species records

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Introduction

From May to June of 2018, we conducted an expedition, in partnership with the University of Michigan Museum of Zoology, to survey and collect amphibian and reptile species across Nicaragua's northern, central, and southern eco-regions. Our work coincided with the onset of the rainy season, which causes an annual pulse in activity in reptiles and amphibians. Our aim was to maximize the habitat and taxonomic diversity we surveyed, so we chose our survey locations based on those goals. We worked in three locations spanning Nicaragua's diverse landscape, visiting six forest formations in the country (Holdridge 1967). Below, we describe the biogeographic context and history of biological collection in Nicaragua, discuss the physiogeographic features of the country, and describe our field and analytical methods.

Scientific collecting expeditions, during which biological specimens are captured, preserved, and deposited into natural history museums along with associated data, remain the best way for scientists to understand the processes that generate and maintain biodiversity (Holmes et al. 2016). Such expeditions produce vast amounts of data, including but not limited to: genetic, morphological, ecological, behavioral, distribution, and climatic data, all of which can be garnered from a single specimen (Davis Rabosky et al. 2019; von May et al. 2019). Furthermore, specimens represent snapshots in time and can be used to infer climatic and habitat changes
(DuBay and Fuldner 2017) and how those changes have influenced species through time (Weeks et al. 2020). Historically, collecting expeditions have been dominated by western scientists that travel to countries, often in the tropics, collect specimens independently or with the assistance of local people(s), and return the specimens to their home institution (Das and Lowe 2018). Unfortunately, there has been a systemic failure to recognize the contribution of local scientists, indigenous peoples, and/or field assistants in the process of scientific collection. Collaborative, reciprocal science is often more productive, beneficial to all parties, and can result in higher quality science (Golden et al. 2014; Linn et al. 2017). In the spirit of continuing the legacy of invaluable collecting expeditions while also engaging reciprocally with our international colleagues, we present here the results of a herpetological expedition to Nicaragua.

Central America as a whole is a globally important biodiversity hotspot, and Nicaragua plays a particularly key biogeographic role in the region (Gutiérrez-García and Vázquez-Domínguez 2013). The southern boundary of Nicaragua lies along a major fault line in the region, making it a key meeting place for North and South American biotas. Repeated marine inundations of this intercontinental terrestrial connection formed a secondary barrier to dispersal that fully disappeared only 3.1-2.7 Ma. Such recent interchange of ancient evolutionary lineages situates Nicaragua as a globally important focus for furthering research in fields such as biogeography, community ecology, and population genetics. Despite its size, habitat complexity, and biological diversity, Nicaragua has one of the highest deforestation rates in the world, including a decrease of 20% in forest cover in the last 20 years (Hansen et al. 2013). The rate of habitat destruction increases the urgency of biodiversity surveys in Nicaragua. Nicaragua has the lowest recorded number of recorded amphibian and reptile taxa of the countries in Central America that border both the Pacific Ocean and the Caribbean Sea (Incer 1975; Köhler 2008; Sunyer 2009, 2014). This lower described diversity is attributed to the country's relatively smooth topography, which

doesn't promote altitude-driven isolation processes that occur in the neighboring countries of Honduras and Costa Rica (Savage 2002; Marshall 2007; Köhler 2008). However, the turbulence in Nicaragua caused by civil wars from 1979 to 1990, and the subsequent lag in research, may indicate that the biodiversity of the country has been underestimated. Since the 2000s, biodiversity research in the country has slowly recovered, increasing the number of known species of amphibians and reptiles, mammals, and birds (Múnera-Roldán et al. 2007; Köhler et al. 2013; Sunyer 2014; Gutierrez Rodriguez and Sunyer 2016; Fernández et al. 2017; Loza et al. 2017; Costea et al. 2018; Salazar-Saavedra et al. 2018; Martínez-Fonseca et al. 2019, 2020; Medina-Fitoria and Martínez-Fonseca 2019). Given the rate of new species descriptions, Nicaragua's biodiversity is likely underappreciated. A sense of urgency propels future research, as high rates of habitat destruction constantly threaten to reduce unknown biodiversity before it can be described in the scientific literature. Our field expedition was part of the ongoing effort to increase our knowledge of herpetological diversity and distributions in Nicaragua. We combined traditional collection techniques in under-surveyed locations with genetic work that can be used to identify genetically-differentiated but morphologically cryptic lineages.

Physiographic Regions and Habitat Types in Nicaragua

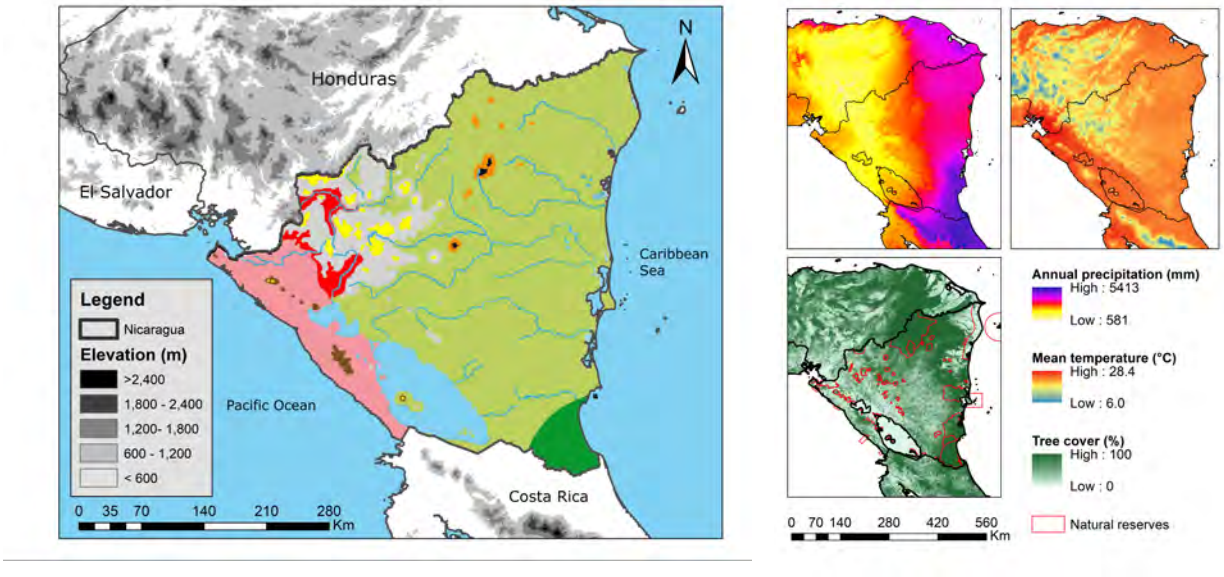


Figure 1: Biotic and abiotic variables across Nicaragua, including major physiogeographic regions. Main forest formations in Nicaragua: LWF (dark green); LMF (light green); LDF (pink); LAF (red); PWF (orange); PMF (gray); PDF (brown); LMWF (black); LMMF (yellow). See text for abbreviations (Modified from Sunyer 2009 and Holdridge 1957).

Nicaragua lies in the center of the American continent, covering an area greater than 130,000 square kilometers. It is the largest country in the Central American isthmus, a land bridge that separates the Pacific Ocean from the Caribbean Sea. In this area many northern and southern flora and fauna meet, resulting in a unique profile of species diversity in the country (Sunyer

2009). Biogeographically, Nicaragua is divided into three main bio-regions (Figure 1A): 1) Pacific Lowlands (PL) in the West are dominated by a young and active volcanic chain and tectonic uplifting and depressions filled by the two largest freshwater lakes in the region; 2) the Caribbean Lowlands (CL) in the East are dominated by sedimentary soils that slowly drain into Caribbean sea; and 3) the Central Highlands (CH), located between the Pacific and Caribbean Lowlands, is part of the nuclear Central American formation that links with the lower Sierra Madre in Southern Mexico (Vinson and Brineman 1963; Incer 1975; MARENA 1999; Sunyer 2009). According to (Holdridge 1967) and (Sunyer and Köhler 2010), nine main forest formations are distributed across nine bioregions: Lowland Arid Forest (LAF), Lowland Dry Forest (LDF), Premontane Dry Forest (PDF), Lowland Wet Forest (LWF), Lowland Moist Forest (LMF), Lower Montane Moist Forest (LMMF), Premontane Moist Forest (PMF), Premontane Wet Forest PWF), Lower Montane Wet Forest (LMWF) (Figure 1A). These forest formations take into consideration only a few abiotic factors (e.g., precipitation, latitude, elevation, evapotranspiration rate) and do not necessarily reflect influences such as soil types or biological community composition, and boundaries between forest types do not necessarily represent strict boundaries for most species distributions (Figure 1B).

In our species accounts, we use several more general terms to describe the different macrohabitats in which we collected specimens. Nicaragua, like most of other countries in Central America, does not have a standardized nomenclature for vegetative formations and some definitions can be vague in the literature. We refer as “upland forest” to non-riparian areas in any of the nine formations. The “pine forests” in Nicaragua appear in mainly in PMF and LMF with different pine species dominating lower (Pinus caribaea) and high elevation ecosystems (e.g., P. oocarpa). Due to species ranges comprising more than one forest type across Nicaragua and Central America we refer as “dry forests” to LAF, LDF, and most PDF areas. Rainforest involve LMF, LWF and transitional areas to higher elevations of with high precipitation like PMF and PWF. The term “cloud forest” is a very widespread term in used in the neotropics and usually refers to high-elevation, high-precipitation LMMF, PMF, and LMWF formations.

Our first collection location (Figure 2) was Las Brisas del Mogotón, in Nueva Segovia Department in northwestern Nicaragua, near the border with Honduras and part of the Cordillera Dipilto-Jalapa Natural Reserve in the Central Highlands (Incer 1975; Marshall 2007). These areas correspond to the oldest geological formations in Central America (Vinson and Brineman 1963; Incer 1975). We sampled three distinct habitats with different biotic communities along an altitudinal gradient. At lower elevations (<600 m), we sampled lowland arid forest. This vegetative formation is characterized by strong seasonality of rain with less than a 1000 mm of total annual precipitation, caused by the “rain shadow” effect caused by the country’s highest mountains to the east. Vegetation is deciduous with abundant shrubs. Most of the original vegetation has been highly disturbed by cattle ranching and seasonal crops of potato, corn, beans, and other grains. At intermediate elevation (600-1200 m) we encountered Premontane Moist Forest with annual precipitation ~2000 mm. This habitat is dominated by upland oak-pine forest and represents the southernmost boundary of the distribution of natural pine in the western hemisphere (Incer 1975). Along ridgelines, this forest was open with a thick litter layer. Drainages and riparian areas are more thickly forested, with deciduous trees interspersed with the pines. In recent years, this area has been opened to medium-intensity coffee cultivation. The highest elevations (1200-2100 m) represent Lower Montane Moist Forest. Here, annual

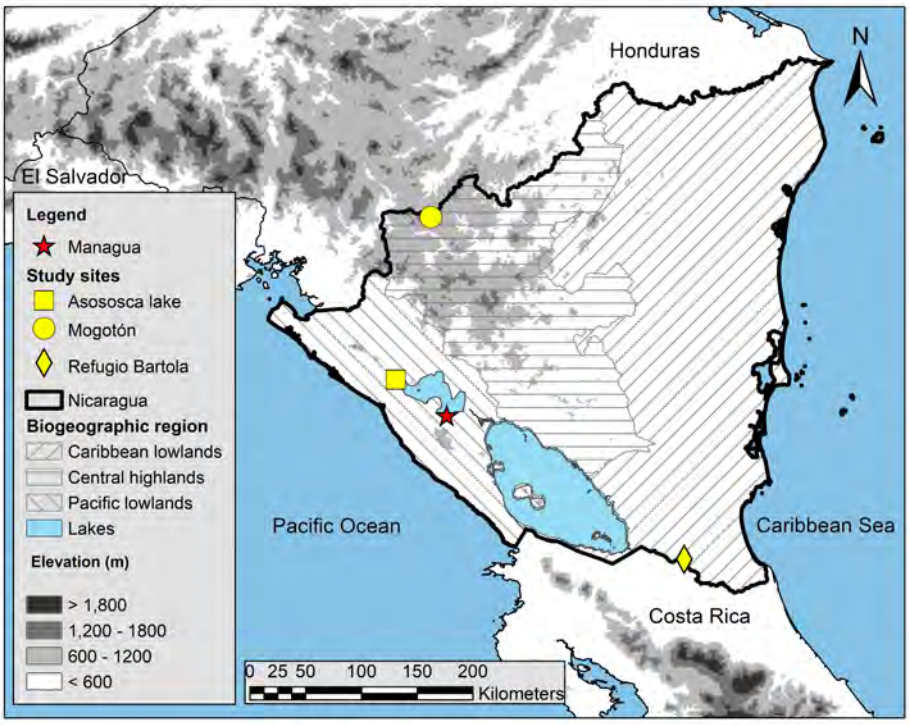


Figure 2: collection locations overlaid on elevation and biogeographic region in Nicaragua.

precipitation is usually above 2000 mm, with less seasonality and a more even rain distribution across the year. The formation is dominated by large, close-growing deciduous trees. Bromeliads are common, both on trees and growing on the deep litter layer in the ground. Occasional gaps in the canopy were filled by thick stands of herbaceous vegetation, dominated by bamboo.

Our second site, Asososca lake (Also known locally as "Laguna del Tigre"), is one of the many volcanic lakes in the Pacific Lowlands in the Department of León. We also sampled forested habitat on private land 6 km Southeast from Asososca lake, a volcanic lake part of the Natural Reserve Pilas-El Hoyo Volcanic complex near the town of Puerto Momotombo. A volcanic chain dominates this ecoregion with Lowland Dry Forests as the main vegetation formation (<600m) (Incer 1975; Marshall 2007). Annual precipitation in this region is 1000-2000 mm with two well defined seasons: rainy and dry. The rainy season extends from mid-May to late-November. The area's soil is formed from geologically recent volcanic material with igneous rock and gravel, often with little topsoil development. Lowland Dry Forest represents the most endangered habitat of the American continent, with less than two percent of the original extent remaining (Portillo-Quintero and Sánchez-Azofeifa 2010). The forest is composed of deciduous trees with relatively small diameters and short height, but larger trees are present near permanent water and streams. Historically, the Pacific of Nicaragua has suffered intensive anthropogenic disturbance since the pre-colonization Indian-American establishments. Today, the landscape is dominated by a mosaic of seasonal crops and secondary growth forest at early regeneration stages. Most of the original forest is limited to the surroundings of the Asososca lake.

Finally, we sampled in the Río San Juan department, part of the Caribbean Lowland ecoregion in southeastern Nicaragua near the border with Costa Rica. Refugio Bartola is one of over 70 private reserves in Nicaragua and the herpetologically richest locality in the country (Sunyer and

Pierson 2015). Bartola sits at the confluence of the Río Bartola and the Río San Juan; the latter is a main component of the "Nicaraguan depression", a biogeographic barrier for many species in the region (Savage 2002; Marshall 2007). Our site was in a transition zone of the Caribbean slope at about 60m of elevation between the Lowland Moist Forest with an annual precipitation of 2000-4000mm and the even wetter Lowland Wet Forest (>4000mm). The western side of the refuge borders fragmented habitat, including cattle fields, palm oil plantations, and residential areas. The eastern side of the reserve abuts the Indio-Maíz Biosphere Reserve, one of Central America's largest unfragmented areas (Jordan et al. 2016). We worked in a variety of habitats across the study site. The edges of the Río San Juan are dominated by emergent vegetation, which harbors a variety of frog species. The forest has several smaller streams, with smaller riparian zones that provide overhanging vegetation used by a variety of amphibian and reptile species. In November 2016, Hurricane Otto flattened the forest in some areas of Refugio Bartola and the neighboring Indio-Maíz (Brown 2017). These places have very thick, re-growing vegetation, with small sapling trees and thick growth of vines and other epiphytes. Other areas have older-growth tropical rainforest, with variable thickness of understory.

Field, Laboratory, and Analysis Methods

We intend for our species accounts to function as an easily-referenced guide for future herpetological work in Nicaragua. In addition to data collected at the time of capture for the specimens we collected, we will provide information derived from the existing literature on the known range, ecology, and behavior of each species we encountered. We hope that this information will facilitate herpetological work both by guiding collectors who are interested in sampling particular species, and by identifying specimens that are of particular scientific value for Central American herpetology. We organize our species accounts taxonomically by order, and within orders alphabetically by family. We provide a brief introduction to each family, discussing distinguishing characteristics, global diversity, and diversity within Nicaragua. For each species, we describe identifying field marks, report relevant data on our collected samples, describe the current state of knowledge about the species' range, and where applicable reference published literature on the species' ecology or phylogeography.

In the field, we collected a set of morphological, ecological and behavioral metadata associated with each specimen. Specifically, we collected basic morphometric data (snout-vent length, mass, and tail length where applicable), GPS coordinates of the capture location, and standardized ecological and behavioral observations made at the specimens' point of capture where available. Our ecological data include macrohabitat type (such as upland forest or riparian habitat), the substrate on which the animal was resting at the time of encounter (such as ground, leaf, trunk, or branch), perch height and diameter, and a description of the behavior the animal at the time of encounter. We report general habitat-use trends per species in the species accounts, and make these specimen-specific data available in a supplementary table.

We include a subset of the morphometric and ecological data in each species account, focusing on the data that will be helpful for identification or to guide species-specific searches. We report snout-vent length (SVL) for all specimens: SVL is a commonly reported metric of body size, and is sometimes used as a field mark for species identification. We include descriptions of macro-

and microhabitats in which species were captured to aid in future targeted searches. In addition, we highlight ecological observations we made that have not been previously reported.

We sequenced the 16S barcode gene from a selection of specimens. We chose this gene because it is widely used to identify organisms to species, so a large amount of comparative material is available in public databases (Vences et al. 2012). When genetic sequences from conspecifics from two or more other Central American countries are available from NCBI's GenBank, we show a gene tree to visualize regional genetic clusters. We aligned the sequences, with an added a congeneric or confamilial outgroup, using the program Muscle through its online portal (Edgar 2004), then built a tree in RAxML with 1000 bootstraps (Stamatakis 2014). To display these data, we have color-coded GenBank reference sequences by country of origin, in addition to displaying their GenBank accession numbers and country of origin as tip labels. Locations south of Nicaragua are increasingly darker shades of red, while locations to the north are increasingly darker shades of blue. We will code sequences from our sampling sites in Nicaragua by listing collection location and collection ID as tip labels on the tree. All of our sequences are accessioned in GenBank, and their accession numbers are available in the attached species database.

We stress that with our single-gene trees built from few sequences are not definitive representations of the phylogeographic history of our species. Rather, we present these gene trees as a starting point for future work and as a tool to identify phylogeographic patterns of intraspecific relatedness that may be repeated across different species. In gene trees, sample names (at the tips of the trees) that are directly connected by lines are the most similar genetically. Connecting lines within the body of the tree indicate deeper genetic relationships. In our figures, we label connection points within the tree with a 'bootstrap value' between 0 and 100, which represents our confidence in the placement of a branch at that location. Values below 90 should be considered relatively unreliable representations of evolutionary history. In general, tree structures in which samples from countries cluster together may indicate isolation by distance, in which limited migration across a species' range leads to localized genetic differentiation (see Lithobates forreri figure for example). In contrast, gene trees that look 'stepped,' with some samples branching off early and others clustered at the tip can indicate directional migration patterns. In this case, the earlier-branching samples represent the ancestral locality, while more nested samples represent more recent range expansions (see Craugastor bransfordii figure for example of a nested tree representing a possible Panama to Nicaragua expansion). We again emphasize that our gene trees should not be treated as definitive, but rather as starting points for more-detailed future studies.

We present range maps for each species, including both the locations in which we captured the species, and records of vouchered specimens from Honduras, El Salvador, Nicaragua, and Costa Rica available in the Global Biodiversity Information Facility (GBIF). Data from GBIF was acquired by defining the search based on: "Species=XXXX", "Basis of record= Preserved specimens", "Location =Including coordinates" and "Country or Area = Guatemala; Honduras; El Salvador; Nicaragua; Costa Rica". We paired these point localities with a range polygon from the International Union for the Conservation of Nature (IUCN) Red List assessments, which are available for the majority of species we discuss. While these two data sources do not represent the totality of knowledge on a species, they do reflect relative sampling effort in different

countries and locations. In addition, IUCN and GBIF data are widely-used options for large-scale biodiversity analyses. If these reflect relatively lower sampling in large geographical regions, biodiversity analyses could be systematically biased for the country. By presenting these data sources, we plan to indicate potential directions and severity of potential biases. In addition, we indicate which of our samples are departmental records and range extensions after a thorough literature review. Our intention is to identify which of our observations represent range extensions and provide a quick reference for future collectors to identify their own potential range-extending observations, although full determination of a range extension requires a thorough survey of archived specimens that are not available on GBIF.

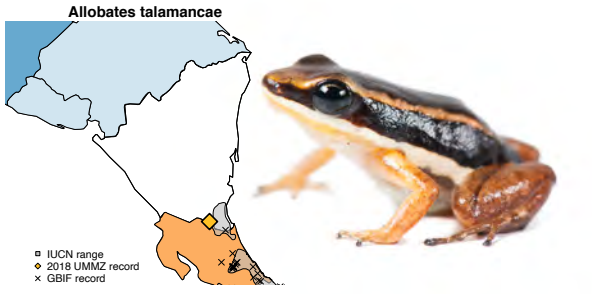
Class Amphibia

Order Anura

Family Aromobatidae

Members of this family were formerly placed in the family Dendrobatidae with the other dart frogs but recently were separated based on genetic evidence. No single morphological character separates all Aromobatids from members of the superfamily Dendrobatoidea, but Aromobatids are generally small and cryptically colored (Grant et al. 2006). Five genera and over 80 species are described from central and south America but only one species reaches Nicaragua.

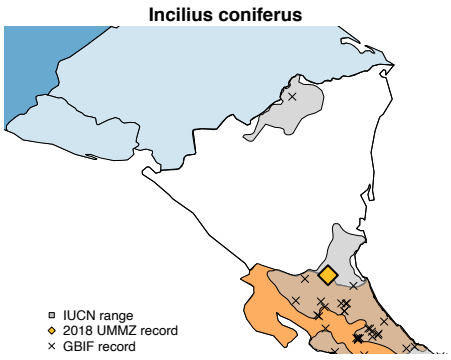
Allobates talamancae a small, cryptic species easily recognized by two pairs of light lines (four total) from the tailbone to the eye (dorsolateral lines) in a mostly black to dark brown body with a white ventral surface. Males have a black throat (Savage 2002). This species is diurnal and active in the leaf litter of the wet forests from southern Nicaragua to Colombia from sea level to 800 m elevation. We encountered one individual, RAB3229, on the west bank of the Bartola river moving along the ground under a clump of bamboo during the day. The frog had an SVL of 21 mm.

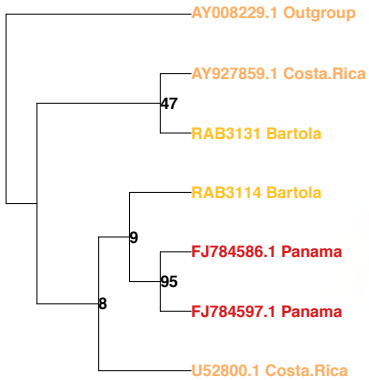


Family Bufonidae

The “true toads” are a diverse family with over 35 genera, with native species distributed across all continents except Australia and Antarctica (Pramuk et al. 2007). Most species have a pair of parotid glands behind the eyes that produce a variety of toxins including bufotoxin. The purpose of these toxins is to protect the animal from predators, by inducing anything from a foul taste to serious cardiac distress. We encountered five of the seven species of the family recorded from Nicaragua.

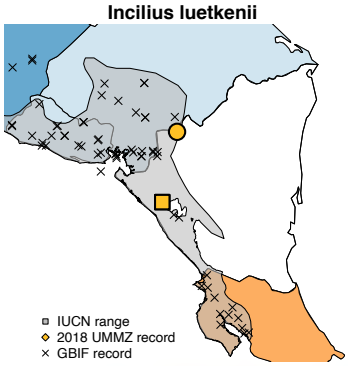
Genus Incilius Members of this toad genus are generally medium-sized in Nicaragua and fit the classic toad body form with a robust body, relatively small limbs, warty skin, and moderately-sized parotid glands. Systematic studies of the family Bufonidae have not recovered specific morphological features that distinguish the genus from other members of the family (Frost et al. 2006; Mendelson III et al. 2011).





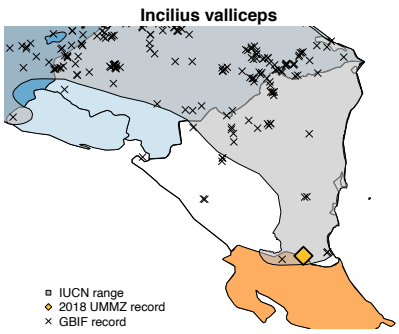


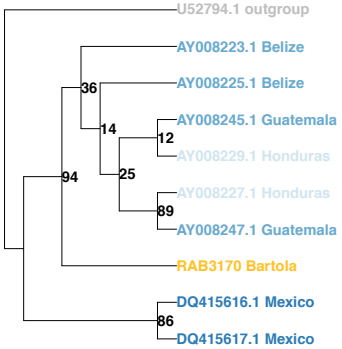
Incilius coniferus a medium-sized toad that can be distinguished from similar species by small parotid glands (less than half the size of the upper eyelids). Parotid glands are large bumps above and behind the eyes in amphibians and are especially prominent in toads. The species has slender limbs relative to other Bufonids (Savage 2002). Finger II (counting from the inside of the hand) is longer than finger I. Coloration can be variable, but green is the most common. This species is semi-arboreal and can be found at night perching on vegetation up to 2 m above ground in wet and moist forests up to 1500 m of elevation from Nicaragua to Colombia and Ecuador. We vouchered two individuals at Bartola, RAB3114 and RAB3131, which had SVLs of 34 mm and 68 mm respectively. We encountered both of them at night in upland forest perching above the ground on vegetation or fallen logs. Our 16S tree is not well-resolved, but shows Nicaraguan samples clustering near Costa Rican samples, while the sequences from Panama cluster together in a strongly supported group. Further sampling is necessary to determine if this pattern arises from standard isolation by distance across Central America, or a pattern of recent range expansion.





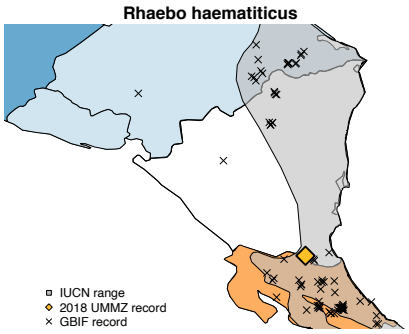
Incilius leutkenii a medium-sized species widely distributed in the dry areas from Guatemala to Costa Rica. Males can be easily identified by a uniform yellow coloration and white underparts. Most females are light brown. This species can be further distinguished by parotid glands (raised bumps above and behind the eyes) about the half of the size of the upper eyelid and very well-defined cranial crests (raised ridges of hardened, often darker skin) on the top of the head (Savage 2002). We encountered two adult individuals in Las Brisas del Mogotón, RAB3044 and RAB3054, with SVLs of 89 mm and 95 mm. RAB3044 was encountered in a puddle on a dirt road in lowland dry forest, while RAB3054 was found moving across leaf litter on a slope. A further two adult individuals, RAB3095 and RAB3105, were found at Asososca lake with SVL of 74 mm and 84 mm. Both were found on the ground at night, one near the lake and one in upland forest.

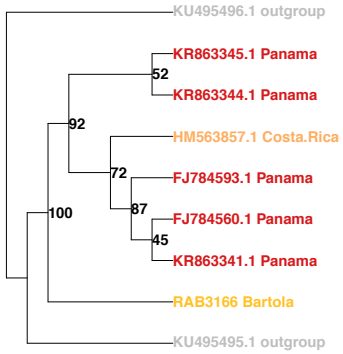




Incilius valliceps a medium-sized species with distinct cranial crests (hardened ridges of skin on top of the head) that can be identified by the ellipse-shaped parotid glands (raised bumps behind the eyes) that are equal in size or larger than the upper eyelid. This species ranges from Veracruz, México to northwestern Costa Rica (Klank et al. 2020) and can be found mostly in wet forest from sea level to 2000 m (Savage 2002). We collected one adult individual at Bartola, RAB3170, with an SVL of 60mm. We found this individual moving across leaf litter at night in upland forest. Our 16S tree showed that our sample represents an outgroup to a cluster of weakly-differentiated sequences from Honduras, Guatemala, and Belize. Samples from Mexico form a well-supported sister clade to the more southerly samples.





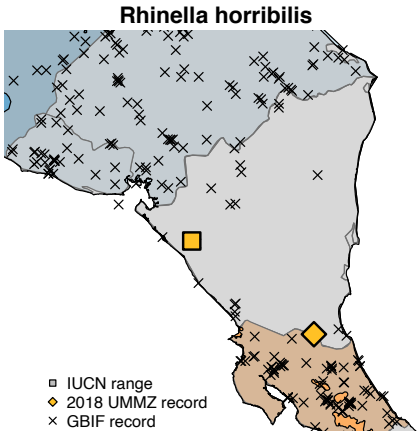




Rhaebo haematiticus a small to medium sized species primarily found in wet forests, often associated with riparian areas. The species ranges from Honduras to Ecuador, from sea level to 1300 m. In Nicaragua, the species is unmistakable with contrasting dorsolateral lines (running from snout to tailbones) and smooth, reddish-brown skin with no cranial crests (Savage 2002). Rhaebo haematiticus is a leaf litter dweller that feeds on small arthropods.

We collected two young individuals, RAB3166 and RAB3237, at Bartola with SVLs of 27 mm and 25 mm respectively. We found both animals moving across the ground during the day in upland forest. Our 16S tree indicates that our samples are genetically distant from other available Central American sequences. We note that in our analysis, one sample from Costa Rica nests within one of two clades from Panama. In other studies, samples from Ecuador had similarly idiosyncratic relationships to complex genetic structures within Panamanian samples (Ron et al.

2015), which the authors took to indicate cryptic diversity in the lineage. We suggest that our results might similarly indicate cryptic diversity within the R. haematiticus species in Central America. If so, further sampling throughout the species' range could resolve relationships between groups.



Rhinella horribilis one of the most common amphibian species in Nicaragua. This medium to large toad is abundant

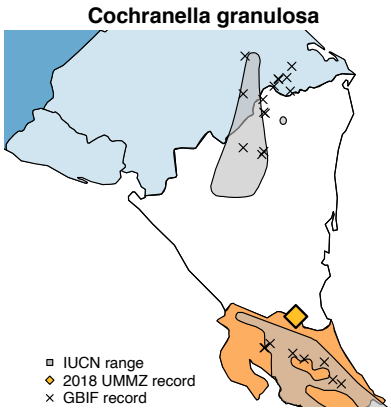


in a wide variety of habitats from the southern United States to Peru. It is unmistakable due to its large size, tuberculated skin, and very large parotid glands (raised bumps behind the eyes) several times the size of the upper eyelids (Savage 2002). Coloration ranges from bright yellow to brown. We collected two adult specimens at Asososca lake, RAB3089 and RAB3096, with SVL of 119 mm and 118 mm. Both were encountered moving across the ground near the lake at night. We also encountered a younger specimen at Bartola, RAB3171, with an SVL of 66 mm. It was captured in upland forest near a small stream, moving over leaf litter.

Family Centrolenidae

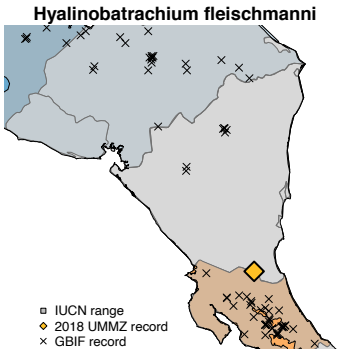
Commonly known as "glass frogs," this stunningly unique family comprises 160 species across twelve genera (Guayasamin et al. 2009). These hylid frogs owe their name to the translucent ventral skin found in many species, through which the internal viscera are visible (Cisneros-Heredia and Mcdiarmid 2007). We collected four species across four genera at Refugio Bartola. In all four species we collected, the internal organs are wrapped in a white, slightly reflective sheath that can be seen through the skin. These are mostly small-bodied, arboreal frogs, with dorsal coloration varying from light lime to dark green. Glass frogs are also characterized by green bones as a result of green bile salts, and are distributed from Central to South America, through Venezuela, Bolivia, Argentina, and Southern Brazil.

Cochranella granulosa can be identified by its blue-green dorsal (back) coloration with scattered dark spots, a snout that is flat and rounded in profile, dark green bones, and a white stripe on the upper lip (Savage 2002; Cisneros-Heredia and Mcdiarmid 2007). The species



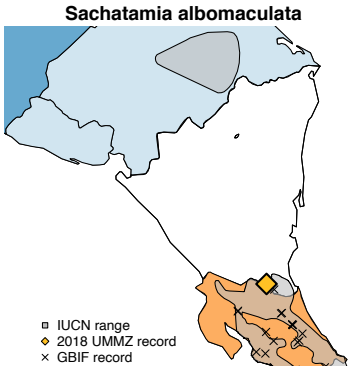


ranges from Honduras to Panama. We collected two individuals at Bartola, RAB3218 and RAB3219, in riparian habitat. Both had SVLs of 27 mm. We encountered both individuals at night, at rest on leaves in trees overhanging the river. One specimen was recorded 3 m above the river.



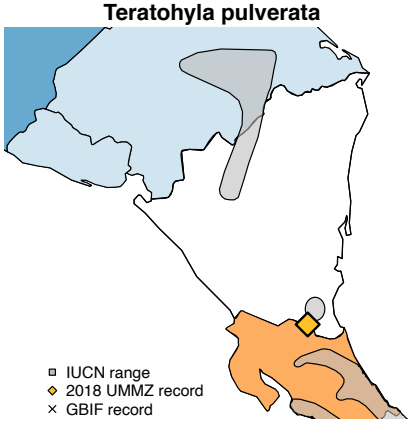
Hyalinobatrachium fleischmanni can be distinguished from similar species by its pale green dorsal (back) coloration with yellow spots, forward-directed eyes, and white bones (Savage 2002; Cisneros-Heredia and Mcdiarmid 2007). This frog ranges from Mexico to Costa Rica. We collected two individuals of this species at Bartola in riparian habitat, RAB3221 and RAB3222. The frogs had SVLs of 25 and 26 mm. Both were found during the night, at rest on leaves 1m high overhanging the river.

Sachatamia albomaculata a blue-green frog that ranges from Honduras south to Colombia and from sea level up to 1500 m, and can be distinguished from similar species by its shortened white sheath over the internal organs compared to other glass frogs, white stripe on the upper lip, and small silver bumps on the dorsal (back) surface (Savage 2002; Cisneros-Heredia and Mcdiarmid 2007). In Nicaragua it is found up to 400 m (McCranie et al. 2019). We collected two individuals from riparian habitat at Bartola, RAB3220 and RAB3223. Both were found during the night, at rest on leaves overhanging the river. They had SVLs of 24 and 25 mm.





Teratohyla pulverata can be identified by its lime green dorsal (back) coloration with yellow spots, snout that is rounded and flattened in profile, and light green bones (Savage 2002; Cisneros-Heredia and Mcdiarmid 2007). This frog ranges from Honduras south to Colombia. We found three individuals at Bartola in riparian habitat, RAB3183, RAB3184, and RAB3198. Their SVLs ranged from 18 to 21 mm. All were found during the night, at rest on leaves in trees overhanging the river.



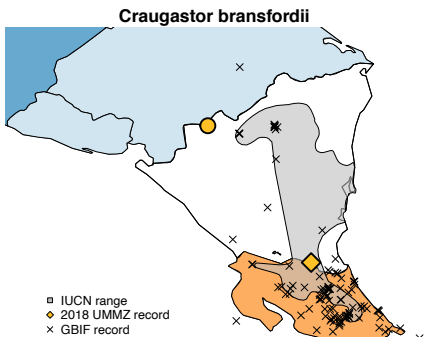
Families Craugastoridae and Eleutherodactylidae

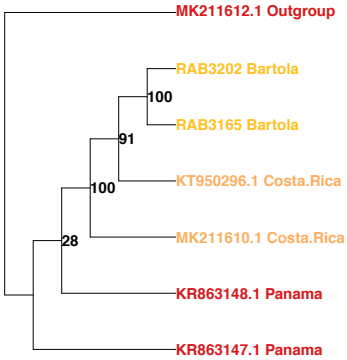
These families are composed of small, direct-developing frogs, which occur throughout South America, Central America, and the Caribbean. We group the families here because of their physical and ecological similarity. Until recently, all members of these families in Nicaragua were included in the genus *Eleutherodactylus* (Hedges et al. 2008). We keep them grouped here because they are physically and ecologically similar and can easily be mistaken for each other.

Family Craugastoridae
Twelve species, from the genera *Craugastor* and *Pristimantis*, are known from Nicaragua. We sampled six species across our three sampling sites.

Genus *Craugastor* Members of this genus in Nicaragua can be distinguished from similar frogs in the field by the following combination of morphological traits: 1) head no wider than the body, 2) lack of cranial crests, 3) distinct external ears, usually larger in males, 4) toes often without expanded tips (Hedges et al. 2008).

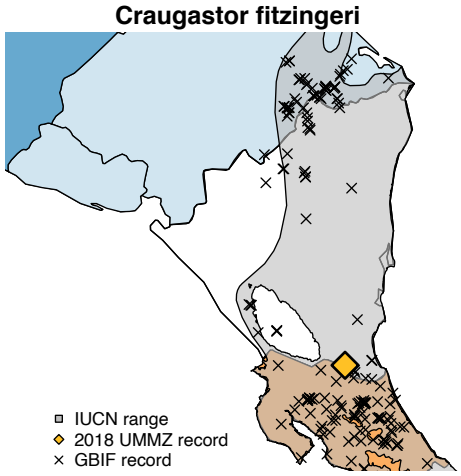
Craugastor bransfordii a small brown frog with reddish coloration on its hindquarters that can be identified by the large tubercles (protruding, generally rounded, fleshy bumps) on the bottom of its feet. The tubercles at the base of the thumb are not larger than the tubercles on the palm of the hand (Savage 2002). The species ranges from northern Nicaragua to Panama. In Bartola, we encountered two specimens, RAB3165 and RAB3202. They had SVLs of 23 and 26 mm respectively and were also hopping over leaf litter at night in upland forest. Our 16S gene tree indicates that the Nicaraguan specimens are nested within a Costa Rican clade, which are in turn nested inside the Panamanian sequences. This tree topology could indicate a relatively recent expansion north from Panama by this species, although further work would be necessary to establish such a pattern.







Craugastor fitzingeri a small, brown frog that can be distinguished by slight toe webbing and the pattern on the underside of their chin. The chin is largely pale with dark speckles, with an un-speckled line along the center, running from the nose toward the tail (Savage 2002). This species ranges from Honduras to Colombia at elevations up to 1455 m. We vouchered five *C. fitzingeri* at Bartola, RAB3116, RAB3123, RAB3128, RAB3154, and RAB3182, with SVLs ranging from





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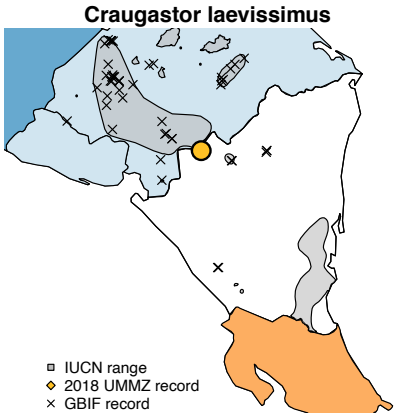
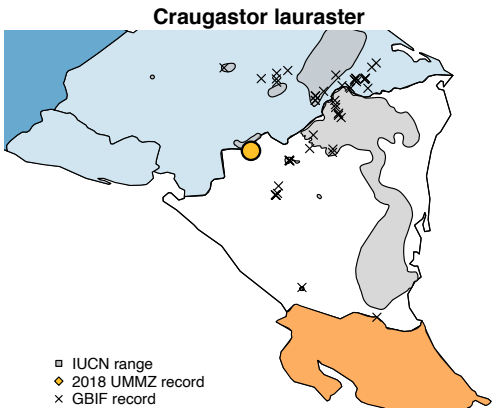
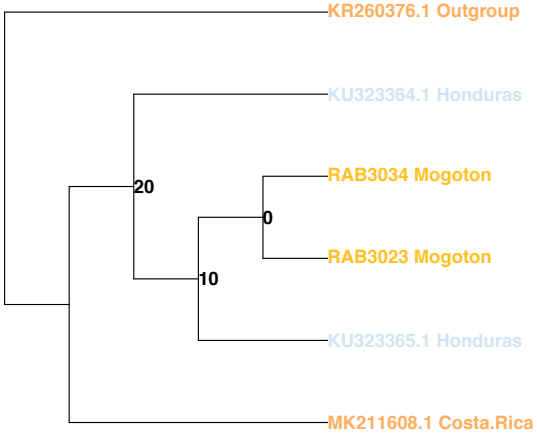
to 32 mm. We found them resting on leaves and shrubs at night in upland forest, with perch heights ranging from 0.3 to 1.5 meters above the ground.



Craugastor laevissimus a small brown frog that can be distinguished from other similar species by warty dorsal (back) skin, smooth ventral (underside) skin, and light dorsolateral stripe (down the center of the back) (Hedges et al. 2008). Its known range extends throughout highlands between 1000 and 1640 m in Honduras and into southwestern Nicaragua. We vouchered two specimens, RAB 3030 and RAB3073, in Las Brisas de Mogotón. They had SVLs of 31 mm and 24 mm respectively. We found the animals hopping across the ground at night in pine forest.

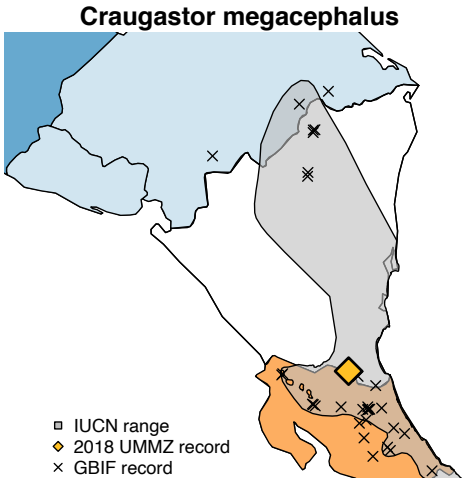
Craugastor lauraster a small, brown frog that can be distinguished from similar species by its black eye mask and banded rear legs. It ranges across southern Honduras and northern Nicaragua up to 1535 m (Hedges et al. 2008,





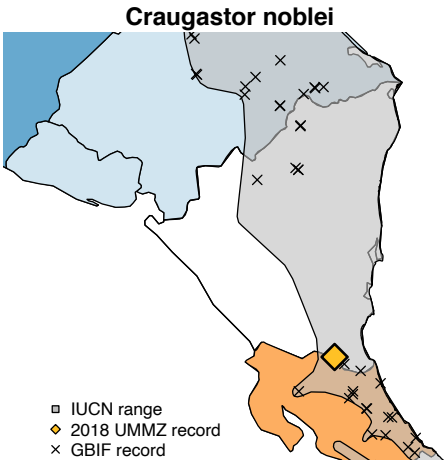
McCranie et al. 2019). We vouchered three specimens in Mogotón, RAB3032, RAB3034, and RAB3077, all with an SVL of 21 mm. We found all specimens in the leaf litter at night. One was calling, one was still, and one was moving. Two specimens were in upland forest, while the third, RAB3034, was found near a stream. Our 16S sequences cluster within Honduran samples, reflecting their geographical proximity to the populations that occupy the Honduran highlands.

Craugastor megacephalus can be distinguished from related species by its very large head and its paired cranial crests (ridges of hardened skin on the top of the head) (Savage 2002). It occurs from eastern Honduras to Panama at elevations up to 1295 m. We found two specimens at Bartola, RAB3196 and RAB3201, with SVLs 22 and 24 mm. We found one individual moving along a fallen branch in upland forest.





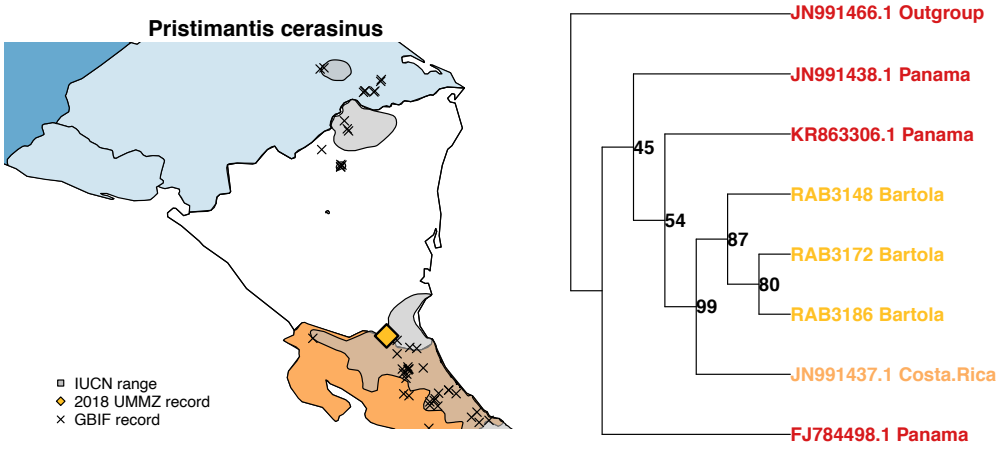
Craugastor noblei can be distinguished from similar species by the webs that extend along the base of its toes, larger toe disks on outer fingers compared to inner fingers, and long eye mask that starts on the nose and continues onto its flanks (Savage 2002). It ranges from Honduras to Panama up to 1330 m. We vouchered two specimens at Bartola, RAB3231 and RAB3185, with SVLs of 58 and 70 mm. We found both specimens three meters above the ground on branches in upland forest.





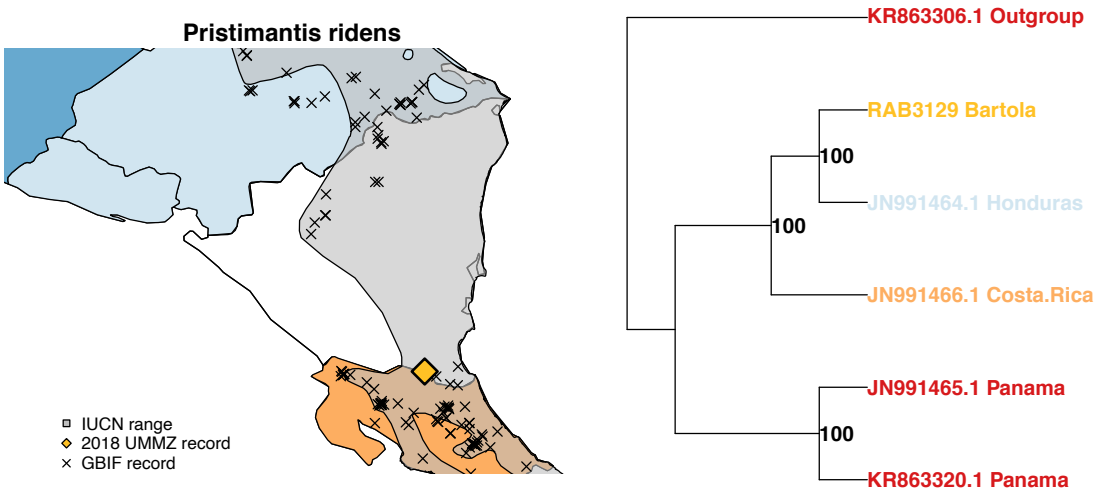
Genus *Pristimantis* Members of the genus in Nicaragua can be identified by the following morphological characters in the field: 1) head and body are equal width, 2) toe tips wider than the rest of the toe (many *Craugastor* species have to tips no wider than the rest of the toes) (Hedges et al. 2008).

Pristimantis cerasinus a small, light brown frog with darker dorsal markings and dark bars on the limbs that can be distinguished from similar frogs because it lacks toe webs, has large, pointed tubercles (protruding, generally rounded, fleshy bumps) on the heel, and its fifth toe (counting from the inside of the hand) does not reach the last tubercle on the bottom of toe four (Savage 2002; McCranie and Wilson 2003). It occurs from Honduras to Panama up to 1360 m. We found three specimens at Bartola, RAB3148, RAB3172, and RAB3186, with SVLs ranging from 22 to 26 mm. RAB3172 and RAB3186 were both found at night, resting on leaves within a meter of the ground in upland forest. In contrast to other Eleutherodactylid and Craugastorid species we sampled, our *Pristimantis cerasinus* samples showed strong genetic differentiation from all available sequences from the species. Bartola *P. cerasinus* had 5% genetic differentiation from both *P. cerasinus* and *P. cruentus* sequences. However, the Bartola specimens nest within Costa Rica and Panama sequences, indicating that raising the Nicaraguan specimens to a new species is not warranted. However, further work on the species might show why their genetic differentiation is stronger than ecologically similar, phylogenetically related frogs over the same Panama to Nicaragua geographic span.



Pristimantis ridens can be distinguished from similar species by its pointed snout tip, pointed tubercles (protruding, generally rounded, fleshy bumps) above the eyes, and lack of heel tubercles (Savage 2002). It occurs from Honduras to Colombia up to 1600 m. In Nicaragua is only recorded up to 1360 m (McCranie et al. 2019). We found one specimen at Bartola, RAB3129, with an SVL of 29 mm. We encountered the specimen sitting on a leaf at night in upland forest, 0.75 m above the ground. Our 16S gene tree shows that the Bartola specimen shares more genetic similarity to conspecifics from Honduras, despite being geographically closer to Costa Rica. This result could support the 'Nicaraguan depression' hypothesis as a biogeographic barrier for this species. The Costa Rica, Nicaragua, and Honduras specimens in turn form a geographical cluster that is distinct from the Panamanian *P. ridens*. The strong separation of the Panama *P. ridens* in our data is a key similarity with a much broader study of *P.*

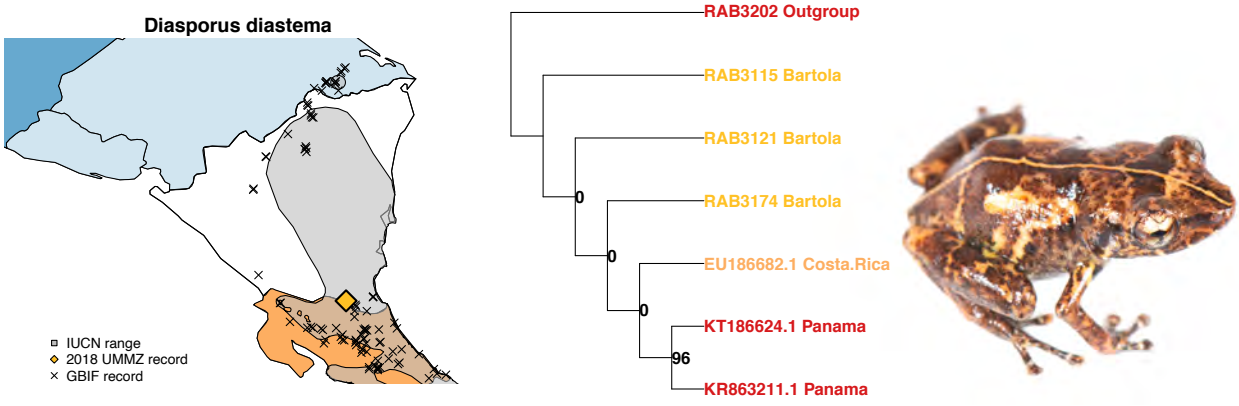
ridens phylogeography that used a different mitochondrial gene (Wang et al. 2008). The 2008 study lacked samples from Nicaragua, but showed that Honduran *P. ridens* were genetically similar to Costa Rican frogs. The authors hypothesized the species occupied higher-elevation habitats across Central America for over 10 million years, then expanded into lowland wet forest habitats more recently. Our gene tree may indicate that the Honduran/Northern Nicaraguan highlands were the source of the lowland Nicaraguan frogs, rather than the closer Costa Rican highlands. Further genetic work across the species' range could identify the location of the geographic break between the Honduras-Nicaragua genetic group and the Costa Rica group. Identifying such a break might provide insight into the historical biogeography and habitat use of the species. In addition to further genetic work, more extensive sampling in eastern Nicaragua might demonstrate whether there is continuous geographical connectivity between the known southern Nicaraguan and northern Nicaraguan/Honduras populations.



Family Eleutherodactylidae

Diasporus diastema is the only member of the family known from Nicaragua.

Diasporus diastema an abundant grey to brown frog that can be identified by their uniformly pigmented thighs, lack of webbing on feet, and lack of heel tubercles (protruding, generally rounded, fleshy bumps) (Savage 2002). It occurs from Honduras to Panama up to 1620 m. Its lowland form in Nicaragua is found up to 1465 m and has very smooth skin both dorsally and ventrally, while some highland populations include individuals with large tubercles across the dorsal (back) surface (Sunyer 2009, McCranie et al. 2019). We vouchered four lowland-

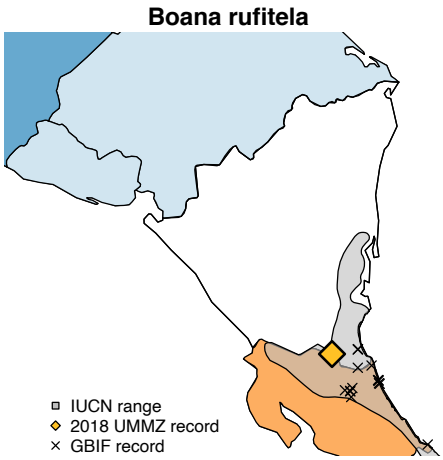


phenotype specimens from Bartola, RAB3113, RAB3115, RAB3121, and RAB3174. Their SVLs ranged from 17 to 23 mm. We encountered the specimens at rest on leaves at night, between 1 and 2 m above the substrate. Our 16S tree failed to find well-supported differentiation between Costa Rican and Nicaraguan samples, making it difficult to draw phylogeographic conclusions. One potential cause for this pattern could be extensive gene flow across the range of this abundant and widespread species. The taxonomy of this species is complex, and some or all Nicaraguan populations may be better described as *Diasporus chica*.

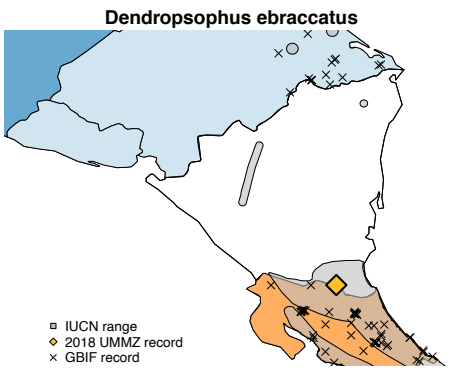
Family Hylidae

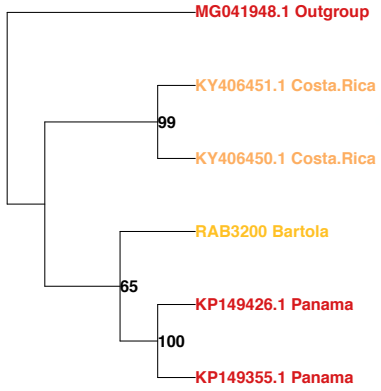
Hylids, commonly known as the treefrogs, are one of the most speciose frog families and includes some very emblematic species. Most species are highly adapted for arboreal life with long thin legs, long fingers with adhesive disks on the fingertips, and wide interdigital membranes. We encountered 7 of the 17 species present in Nicaragua, with most species present at Bartola.

Boana rufitela is a relatively rare species characterized by a green coloration with red interdigital (between the toes) membranes. Eyes are twice the size of the tympanic membrane (external ears) and the species lacks an axillar membrane (between legs and body) (Savage 2002). The species is found in the lowland wet forests from southern Nicaragua to Panama at elevations up to 650 m. It is associated with slow-flowing rivers and ponds. At Bartola, we collected one adult individual, RAB3181, with an SVL of 57 mm, resting on a leaf two meters above the ground in upland forest.



Dendropsophus ebraccatus a distinctive species with large yellow or white patches on the back and limbs. The axillar membrane (between leg and body) is well developed and interdigital membrane extends halfway up the fingers of the hand and ¾ the length of the toes. Sexual dimorphism is present with females 37 mm of SVL and males 28 mm (Savage 2002). The species ranges from Mexico to Colombia in elevations up to 1600 m. We collected two female individuals, RAB3200 and RAB3236, at Bartola. The former, with an SVL of 35 mm, was found in a riparian area and deposited eggs in the bag when transported to camp. The later had an SVL of 37 mm and was found about a meter above ground in a heliconia plant in a disturbed area

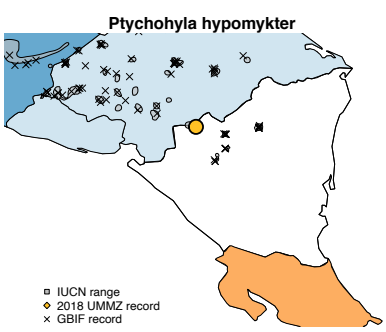


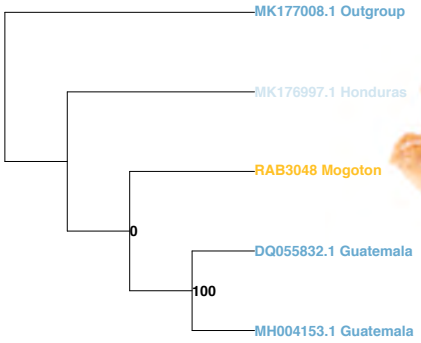




within the Refugio Bartola property. The 16S tree topology is unusual, with the Bartola specimen weakly placed as an outgroup to Panamanian samples. One possibility is that this species follows several other amphibians in having a major phylogeographic break across the Nicaraguan depression, leading the Nicaraguan sample to differ strongly from more southerly samples and therefore accounting for the uncertain placement of the Nicaraguan sample. Further sampling in the northern area of the species' range could resolve this unusual tree topology.

Ptychohyla hypomykter can be identified by the rounded snout, bronze eyes, and interdigital membrane 1/3 the length of the fingers in the hands and 90% of the length of the toes. Color can be variable but the most common pattern is brown with light brown dorsal patches and white ventral surface. Males have 35 to 66 small nuptial pads with enlarged spines (McCranie and Wilson 1993). Nuptial pads are darkened, roughened areas of skin on the bottom of the feet in male frogs. The species occurs mostly in wet mountainous forest from Guatemala to Nicaragua at elevations of 320 m to 2070 m. We collected three individuals at Las Brisas de Mogotón. The first, RAB3047, was a female with an SVL of 42 mm. The second, RAB3048, was a juvenile with an SVL of 36 mm. Our third specimen,
RAB3075, had an SVL of 35 mm. All individuals were

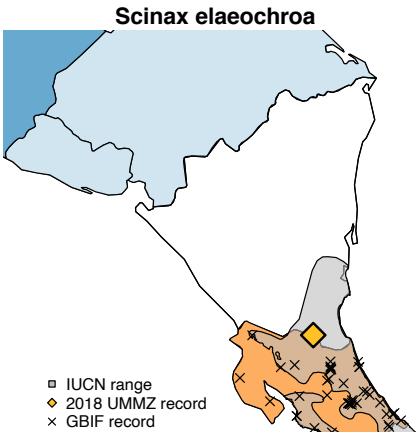






found at rest on top of ferns and epiphytes in the understory in cloud forest. This species is known from cloud forest patches in Honduras and northern Nicaragua. The 16S tree is poorly resolved, indicating the need for further sampling across this species' complex and fragmented range.

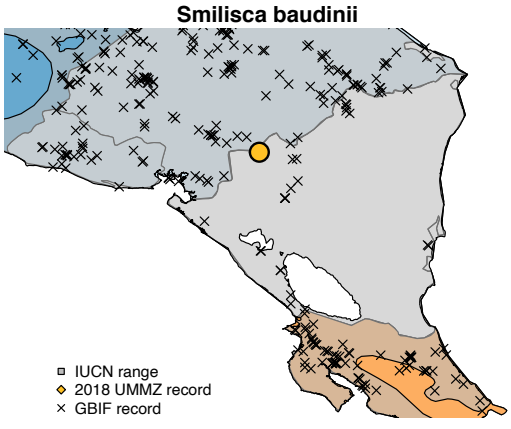
Scinax elaeochroa is a small species of frog, easily identified by the evident green bones which can be seen from the underparts of limbs. Its coloration can be variable, usually green and easily changed to brown after capture. No interdigital membrane is present in the hands, and the disk of the third finger (counting from the inside of the hands) is larger than the tympanic membrane (external ear). No markings on thighs (Savage 2002). This species can be distinguished from the glass frogs by its opaque dorsal skin. The species is relatively common in lowland moist and wet forests from Nicaragua to Panama at elevations from sea level to 1200 m. We encountered two individuals at Refugio Bartola, RAB3169 and RAB3234, with SVL of 38 mm and 33.5 mm respectively.

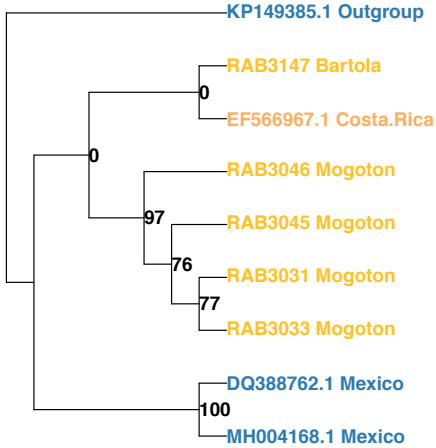




Genus *Smilisca* These medium-sized treefrogs are distinguished from other members of the family by characters visible on the bone (Starrett 1960). However, many members of the genus have vocal sacs that bulge to the side during calling, and members of the genus tend to be more heavily built than other hylids in Nicaragua.

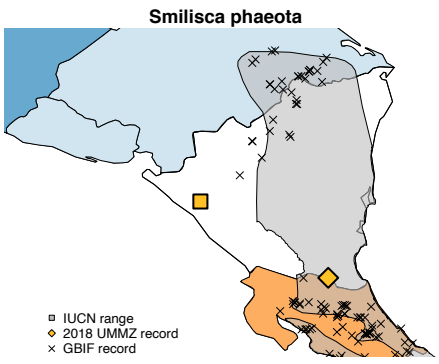
Smilisca baudinii a medium-sized frog, very variable in coloration and the only member of the genus that inhabits the lowland dry forests of Nicaragua, due to their ability to hibernate in desiccation-proof cocoons (Mcdiarmid et al. 1987). It can be distinguished from other species in the genus by presenting a much thinner trans-ocular strip (reaching across the back of the head between the eyes), and clear markings on the lips and thighs. The species can be found in other forest types from Mexico to Costa Rica at elevations up to 1950 m, but in Nicaragua has there are records only up to 1350 m (Savage 2002; McCranie 2017, McCranie et al. 2019). Two individuals in amplexus, a female (RAB3045) and a male (RAB3046), were found in pine forest of Las Brisas de Mogotón. These two individuals had SVL of 50 mm and 59 mm respectively. In addition, we collected RAB3031 and RAB3033, with SVLs of 59 mm and 68 mm respectively. Both were in standing water on dirt roads in mixed pine forest-shade grown coffee, and the latter was a male calling.

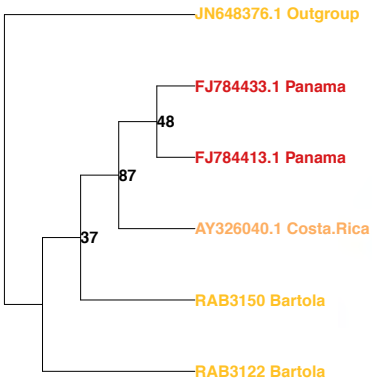




Smilisca manisorum a species recently separated from *S. baudinii*. McCranie (2017) suggests that *S. baudinii* is a species complex, with the previously-synonymized species *Smilisca* [*Hyla*] *manisorum* occupying lowland eastern Honduras, Nicaragua and Costa Rica. *Smilisca manisorum* can be distinguished from *S. baudinii* by its larger adult size, greater amount of toe webbing, and flatter metatarsal tubercle (protrusions at the base of the foot by the wrist joint) (McCranie 2017). We collected a specimen (RAB3147) that matched this description at Refugio Bartola. The individual has an SVL of 60 mm. The precise distribution of *Smilisca baudinii* and *S. manisorum* are uncertain, but they seem to appear in Nicaragua in a west-east gradient. Our Mogotón (RAB3031, RAB3033) and Asoscosa lake (RAB3045-3046) samples most likely belong to *S. baudinii*, while our Bartola samples would be assigned to *S. manisorum*. Further morphological and genetic work could confirm this proposed taxonomic division and resolve the phylogeographic history of this widespread species. Our 16S tree shows a strong separation between our Mogotón and Bartola S. *baudinii*-*S. manisorum* samples, with the Bartola sample clustering with the Costa Rican samples as predicted by the McCranie species complex hypothesis. Further sampling of this widespread potential species complex will be necessary to resolve species boundaries and historical biogeography of the taxon.

Smilisca phaeota a medium-sized arboreal frog, relatively common species identified by the trans-ocular dark strip (running across the eyes) that covers the tympanum (external ear) and fades away right after the axilla (armpits) into a reticulated pattern of large, unevenly shaped spots. Many but not all individuals have a green patch under the eye and immaculate upper lip (Savage 2002). This species can be found in wet forests from Honduras to Ecuador at elevations up to 1455 m. We collected three individuals. The first was a gravid female, RAB3104, encountered at Asososca lake at rest in a pool of water in upland forest. This specimen had an SVL of 74 mm. We collected two individuals at Bartola, RAB3122 and RAB3150, the former with an SVL of 46 mm and the latter with an SVL of 44 mm. RAB3122 was encountered five meters high in a *Cecropia* spp. tree in upland forest. Our 16S tree shows samples from Costa Rica and Peru nested within the Nicaraguan samples, possibly indicating a southward range expansion by the species. However, the tree is poorly supported and should be interpreted with caution. Further work on the species in Central America is necessary to determine its historical biogeography.

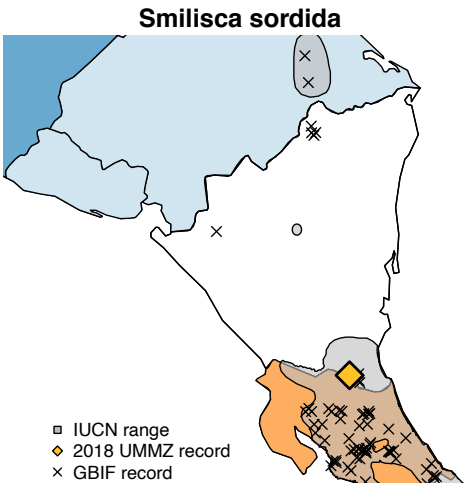






Smilisca sordida a medium-sized species that can be identified by an inter-ocular dark band connecting both eyes at the top of the head. It lacks an axillar (armpit) membrane. The tympanic

membrane (external ear) is separated from the eye by a distance equal to 2/3 of the diameter of the membrane (Savage 2002). The species ranges from Honduras to Panama, in mostly lowland wet forests and elevations up to 1525 m but in Nicaragua is only reported up to 420 m (McCranie et al. 2019). We collected two at Bartola, RAB3149 and RAB3151, with SVL of 42 mm and 56 mm respectively. Both individuals were moving across the ground in a riparian area. Their riparian association may relate to their breeding strategy of constructing basins in streambeds for their eggs and tadpoles (Malone
2006).



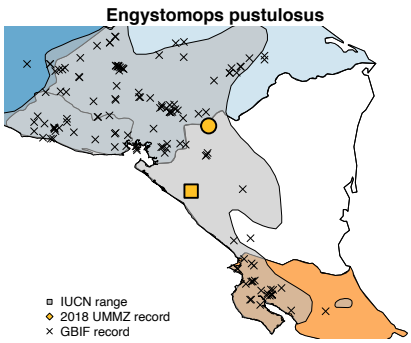


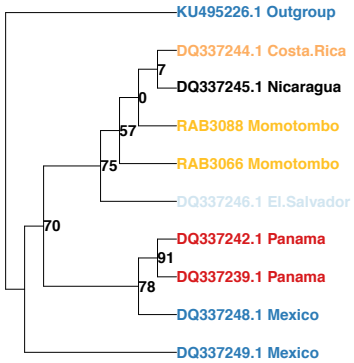
Family Leptodactylidae

This family includes a variety of species adapted to different habitats and behaviors. Members of this family are distributed from the Southern United States to Southern Chile and Argentina. They lack membranes and adhesives disks on fingers and toes. Recently, the family has gone under extensive revision (de Sá et al. 2014). Members of the Eleutherodactylidae and other groups like Craugastoridae used to be considered part this family. Four species of the revised Leptodactylidae are known in Nicaragua. We encountered three species from two genera across our three study sites.

Engystomops pustulosus a relatively small species with a maximum of SVL of 35 mm. It can be recognized by the tuberculated tympanic membrane (external ear with rounded bumps) and warty dorsal skin. The first finger (counting from the inside of the hand) is longer than the second, and toes have small fringes. A clear white line is often present from the chin to the throat (Nascimento et al. 2005). The species is very common in the lowland dry forests, savannas, and disturbed environments from Mexico to Colombia and Venezuela at elevations up to 1540 m. We found two individuals, RAB3066 and RAB3088. The first one was at lower elevation in Las Brisas de Mogotón with an SVL of 29 mm. The second one was found at Asososca lake and had an SVL of 26 mm. Both individuals were found in temporary pools, with RAB3066 in a dry creek bed and RAB3088 on a road near an agricultural field. In Costa Rica, *E. pustulosus* is represented by two ecologically distinct lineages: a southern group that occurs in wet forest, and a northern group that inhabits dry forest. Both geography and habitat indicate that our samples

belong to the dry-forest group, but further sampling and genetic work on the specimens from western Nicaragua and Costa Rica could confirm that association (Pröhl et al. 2010). The 16S sequence from the sample clusters in a poorly-resolved group with another Nicaragua sample and a Costa Rican sample. The tree overall is poorly supported, with Panamanian samples clustering with Mexican samples, and so should be interpreted with caution.

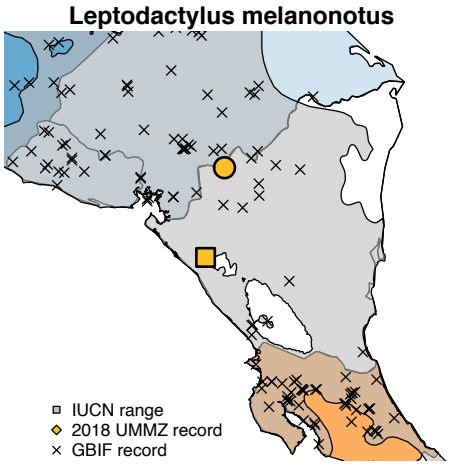






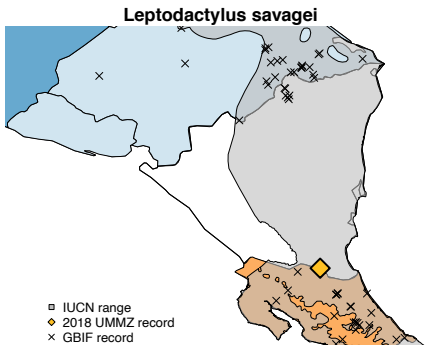
Genus *Leptodactylus* Members of this genus are long-limbed, medium to large frogs. In body form they are similar to the distantly-related *Lithobates*, but can be distinguished by the lack of webbing on the feet and lack of expanded toe tips (Savage 2002).

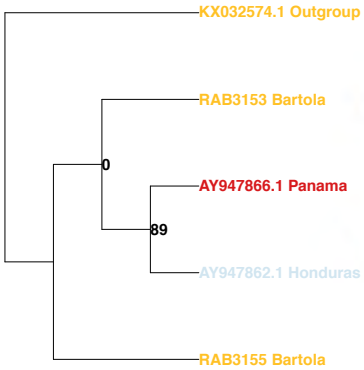
Leptodactylus melanonotus is recognizable by a tuberculated dark dorsal surface (skin has rounded bumps), smooth mostly white belly, and lack of strong dorsolateral folds (paired skin folds running along the back from the neck area to above the back legs). Males have nuptial claws made of darkened, rough skin on thumbs but not in the chest. Tympanic membrane (external ear) is 0.5 to 0.7 times the eye size. Orange or yellow band on the lips extends to the shoulders. This is a common species of the lowlands of Mexico to Ecuador at elevations up to 1550 m in a variety of habitats, including disturbed environments (de Sá et al. 2014). We found two individuals, RAB3067 and RAB3090. The first individual was found at lower elevation in a riparian area of Mogotón and had an SVL of 38 mm. The second was found at Asososca lake and had an SVL of 44 mm.





Leptodactylus savagei is one of the largest amphibians in Nicaragua, easily identifiable by large eyes that produce a strong eyeshine when pointed with headlamps, and almost circular snout with barred or spotted upper lip. The species is mostly nocturnal and terrestrial, with semi-fossorial behavior. A dark line through the eye that bends towards the shoulder and a pair of dorsolateral folds (paired skin folds running along the back from the neck area to above the back legs) are also characteristic of this species. Usually found near burrows. It can be found in lowland moist and wet forests from Honduras to Colombia at elevations up to 1000 m (de Sá et al. 2014, McCranie et al. 2019). We encountered two individuals at Bartola, RAB3153 and RAB3155, in a riparian area near their burrows. Corresponding SVLs were 116 mm and 148 mm. While being photographed, RAB3155 displayed a "high stand" defensive behavior. Our 16S tree incongruously groups Honduran and Panamanian samples, while the position of the Bartola specimens is poorly resolved. Caution should be using in interpreting the tree.



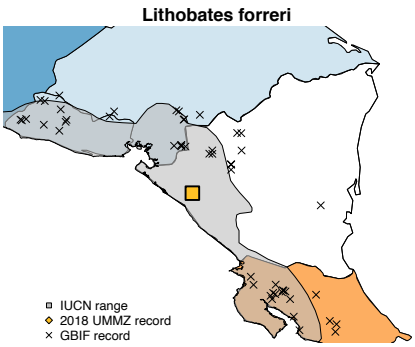


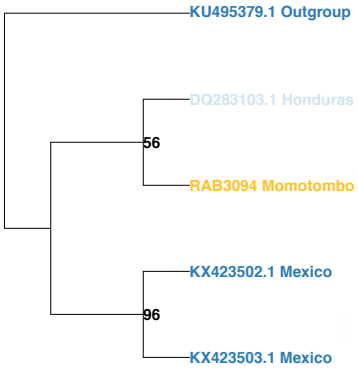


Family Ranidae

The Ranidae are commonly called "true frogs," and species in this group can be found across the world. This group has the widest distribution of any frog family. Family characteristics include: smooth, moist skin, strong hindlimb and webbed toes, and a visible tympanum; eggs laid in water that hatch into tadpoles; individuals are terrestrial and aquatic; inhabiting a wide range of habitats. *Lithobates* (Hillis and Wilcox 2005) is the genus used for the *palmipes* subgroup (Yuan et al. 2016). We sampled four species of *Lithobates*, found across all three sampling sites.

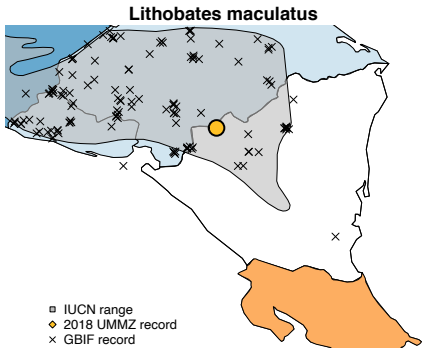
Lithobates forreri is known from southern Sonora to Jalisco, Mexico, and down through Nicaragua into northern Costa Rica. In Nicaragua the species is found up to 1280 m. The species might represent a species complex (Luque-Montes et al. 2018, McCranie et al. 2019). This is a moderately large frog, with a maximum SVL of 120 mm. It has well developed dorsolateral folds of skin running from the eye to the base of the hind limb. Dark brownish spots are present on the dorsal surface. Hind limbs have dark bands. This species generally resides in ponds (Grismer 2002). We found a single individual of this species: RAB3094 was an adult male, found at Asososca lake resting on leaf litter near the lake, with an SVL of 65 mm. The 16S tree groups our sample with a sequence from Honduras, rather than Mexico, possibly indicating a pattern of isolation by distance across northern Central America.

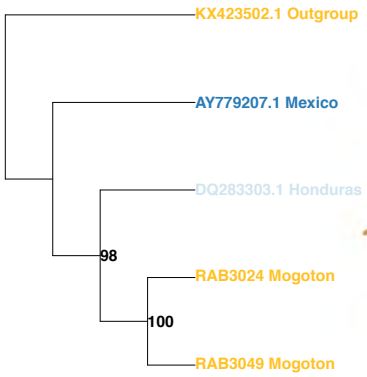






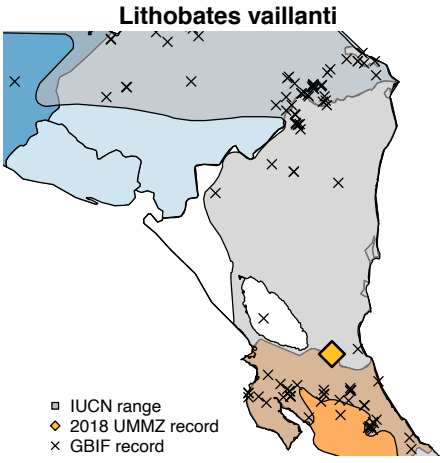
Lithobates maculatus ranges from Guatemala to Nicaragua. In Nicaragua the species is found up to 1700 m. It can be identified by a tympanum (external ear) smaller than the eye, a single metatarsal tubercle (protrusions at the base of the foot by the wrist joint) on the hind foot, dorsolateral folds (paired folds of skin running along the back from the neck area to above the back legs) having a black border, and a black face mask (Hillis and de Sá 1988). We collected two individuals of this species at Las Brisas de Mogotón (RAB3024 and 3049), both in pine forest. RAB3024 had SVL 80 mm and was found at rest in the leaf litter. RAB3049 had SVL 57 mm and was found at rest in standing water near a quickly-flowing stream. The 16S tree groups our sample with a sequence from Honduras, with a Mexican sequence as an outgroup. This tree topology suggests a north to south expansion history for the species.





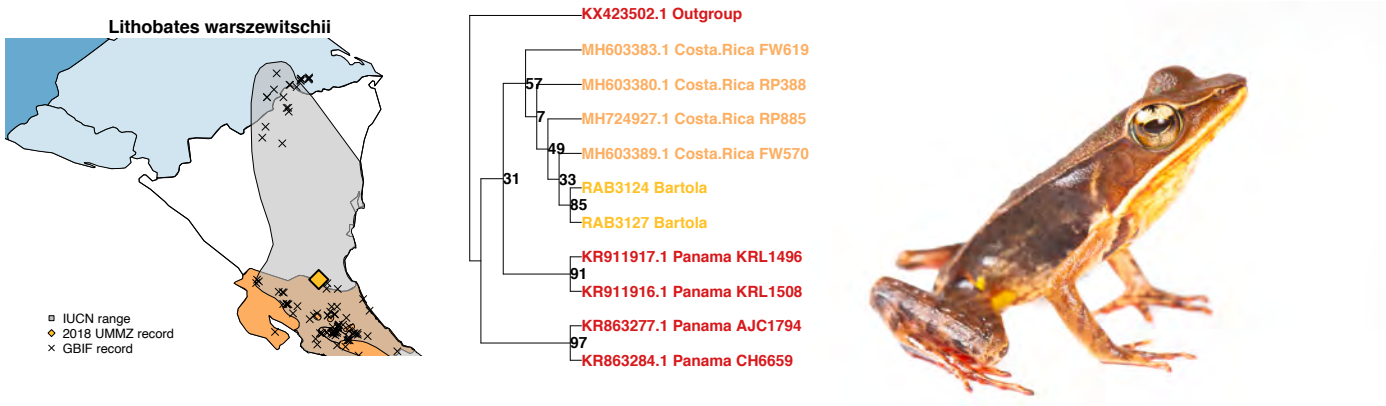


Lithobates vaillanti is known from the Caribbean slopes from Veracruz, Mexico to northern Colombia and Ecuador. In Nicaragua the species is found up to 900 m. Additionally, it is found on the Pacific slopes from Oaxaca, Mexico to Ecuador. It prefers deep pools of slow-moving or still water. It is a large Ranid species, with females having an SVL 76-125 mm and males 67-94 mm. In coloration, males have a brighter green dorsum while females are tan-brown and may possess green along the edges of the dorsum. Its tympanum (external ear) is larger than the eye, and fingers have no webbing. Dorsal surface and outer areas of legs are covered in small, white-tipped projections (Savage 2002). We collected two individuals of this species, RAB3118-3119 at Bartola, both of



which were found in a riparian area. RAB3118 had an SVL of 42 mm while RAB3119 was a gravid female with SVL 113 mm.

Lithobates warszewitschii a smaller species of the *palmipes* group, related to *L. maculatus*: females have a maximum SVL of 63 mm and males 48 mm. The tympanum (external ear) is prominent but smaller than the eye, and feet have two metatarsal tubercles (protrusions at the base of the foot by the wrist joint). While color varies in this species, one distinguishing feature is the presence of yellow spots on the posterior surface of the thighs. This species is found in humid environments, from sea level to ~2000 m. They range from southeast Honduras to eastern Panama up to 1000 m (Hillis and de Sá 1988). Individuals are often found on the forest floor. We collected two individuals of this species at Bartola. RAB3124 had an SVL of 32 mm and was found moving across leaf litter in upland forest. RAB3127 had an SVL of 44 mm. It was found at rest on the ground. This species may form a species complex. In a previous region-wide study, individuals sampled from Costa Rica and Panama did not group perfectly by collection location, and within-site genetic diversity is higher than would be expected if all individuals belonged to a single species (Cryer et al. 2019). Our samples nested within the Costa Rica samples sequenced by Cryer. Our sampling indicates that the historical biogeography of the species is a straightforward story of northward expansion in the northern portion of the species' range, in contrast to the complex biogeography in Panama and further south. We include the Cryer sample names in our figure for readers wishing to reference their paper.



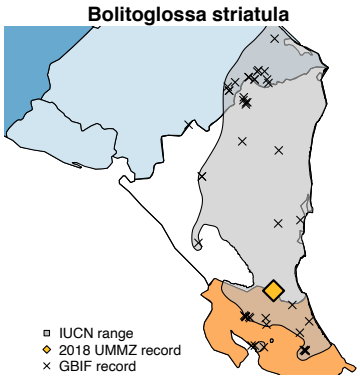
Order Caudata

Family Plethodontidae

The lungless salamanders are the most diverse family of salamanders in the world and the only family of salamanders in the neotropics. Most of the 400 species of this family are distributed across the Americas, and all members of this family have elongated bodies and a naso-labial groove (a groove extending from the upper lip to the nostril). They reproduce by internal fertilization and most species have direct development (Parra-Olea et al. 2004). Nine species from three genera (*Bolitoglossa, Oedipina, Nototriton*) are present in Nicaragua, including 5 endemics.

Bolitoglossa striatula is the most wide-spread species of salamander in Nicaragua. It can be identified by the two ventral-lateral stripes and yellow venter. The species can reach a total

length of 130 mm with a tail up to 55% of that length. The species ranges from Honduras to Costa Rica, in most of the lowland wet forests in elevations up to 1,380 m (Sunyer et al. 2012). We encountered three individuals at Bartola. The first two, RAB3117 and RAB3152, both had an SVL of 61 mm. The former had a tail length of 61 mm and the later had almost no tail at all, probably because of some predation attempt, but signs of regeneration were evident. We found them in a riparian area up in leaves of small plants in the understory. The third individual, RAB3203, had an SVL of 49 mm and a tail length of 44 mm, and was found in a palm frond further away from water. All individuals were found at night. The recent description of two localized species in southern Nicaragua indicates that further cryptic diversity in this species complex might be uncovered by morphological and genetic work (Sunyer 2009).





Order Gymnophiona

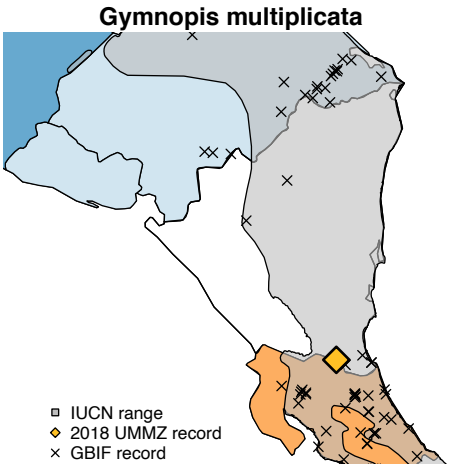
Family Dermophiidae

This family is composed by terrestrial caecilians with fossorial life styles distributed to the tropical areas of the Americas and Africa (San Mauro et al. 2014). Two species of different genera occur in Nicaragua, but do not overlap in distribution. *Dermophis mexicanus* can be found in the Pacific area of the country and *Gymnopis multiplicata* in the Caribbean lowlands.

Gymnopis multiplicata reaches 500 mm of length with 112-133 primary and 64 to 117 secondary annuli (grooves encircling the body to form segments, aligning with the vertebrae). It has a small tentacle that lies anterior to the eye. The eye is covered by skin and bone. Teeth are monocuspid, recurved, and shorter in height in the posterior part of the jaw. The species is viviparous. The species can be found from Southern Guatemala to western Panama in wet forests and elevations of up to 1400 m (Wake 1988). We collected three specimens at Bartola, RAB3167, RAB3175, and RAB3197. SVL measurements were 274 mm, 143 mm, and 370 mm respectively. RAB3175 was found at rest under a large log while the other specimens were moving on the ground surface in upland forest at night.

Class Reptilia

Order Squamata



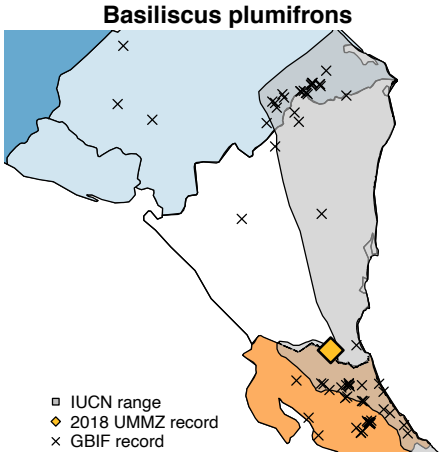


Family Corytophanidae

Of the Iguanid lizards, members of the genus *Basiliscus* and *Corytophanes* are some of the most notable (Vieira et al. 2005). The head and dorsal crests of basilisks give them the appearance of a dragon. They are able to run across water on the hind legs, giving them the nickname "Iguana Jesucristo" - the notable characters enabling them to do such are toe-fringes and a heavy tail that acts as a counter-balance to the upright body. Basilisks are found near water, especially streams, ponds or swamps. They eat insects, spiders and sometimes small vertebrates. *Corytophanes*, or the 'helmeted iguanas' are known only from Mexico, Central America and northwestern South America. They have a laterally flattened body and a prominent, bony head crest for which they are named.

Genus *Basiliscus* This genus can be identified by their relatively large body, long and muscular rear legs, toes with fringed scales, and the fleshy (not bony) crest on their heads (Savage 2002).

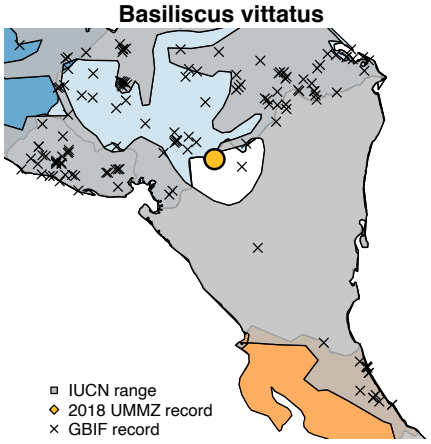
Basiliscus plumifrons a large green lizard with one or two rows of pale spots running parallel to the spine. Adult males possess a head crest with two distinct lobes, differentiating this species from congeners. Juveniles have a uniformly colored chin region. The species is known from Honduras to Panama from sea level to 780 m elevation (Savage 2002). Maximum known SVL is 240 mm. We collected two individuals at Bartola. RAB3136 was an adult female with an SVL of





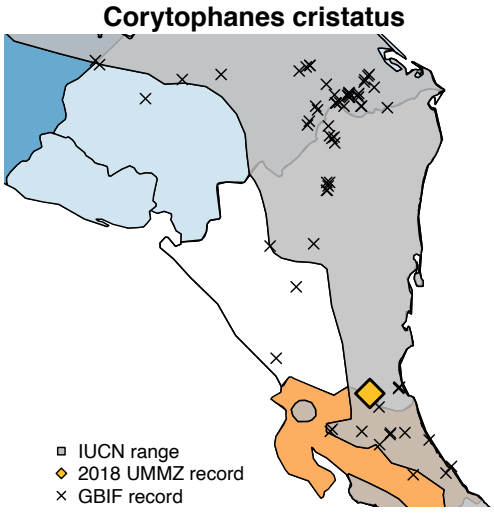
103 mm. It was found in a riparian area. RAB3159 was found at rest on a woody vine, also in a riparian area. It was an adult male with an SVL of 218 mm.

Basiliscus vittatus distinguished by keeled ventral scales, 1-2 mental shields (scales on the bottom of the chin at the tip of the snout) that contact the infralabials (scales that line the bottom lip), and a single, triangular head crest. It is known from Jalisco and Tamaulipas, Mexico to Panama from sea level to 1500 m. SVL goes up to 170 mm (Savage 2002). We collected two individuals from Las Brisas de Mogotón: RAB3058 and RAB3062. The former was a juvenile female with an SVL of 81 mm; it was found sleeping on a tree branch in the shrub layer. The latter was also found sleeping on a tree branch. RAB3062 is an adult female with an SVL of 138 mm. Both were found in a riparian area in montane pine forest.





Corytophanes cristatus an arboreal lizard that can vary in color from dark brown to olive green, with yellow spots or crossbands. The venter is pale brown with sporadic dark spots. Males are distinguished by the hemipenal bulge at the base of the tail, large helmets, and relatively large heads. The helmet extends past the bony skull process, unlike congeners. It can further be characterized by smooth scales on the dorsal surface of the head. The species is known from Veracruz, Mexico to Colombia from sea level to 1640 m in tropical and subtropical rain forest (Townsend et al. 2004). In Nicaragua it is reported up to 1100 m. Two individuals were collected

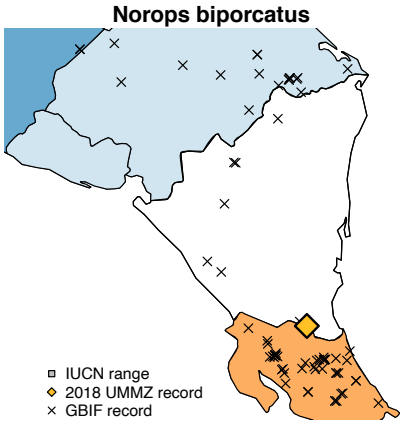




from Bartola; both were found at rest on tree trunks in upland forest. RAB3210 had an SVL of 125 mm and RAB3212 88 mm.

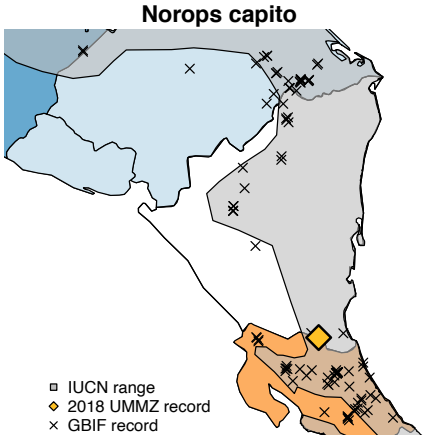
Family Dactyloidae

The anole lizards (genus *Norops* in Central America) represent the most speciose group of iguanian lizards, with over 400 species currently described (Nicholson et al. 2012). Most species are arboreal, dwelling in trees or bushes, but some are terrestrial and reside in leaf litter. Others still are semi-aquatic and occur only in proximity of water. In Nicaragua, there are 17 species of *Norops* lizards; our surveys resulted in 13 species.



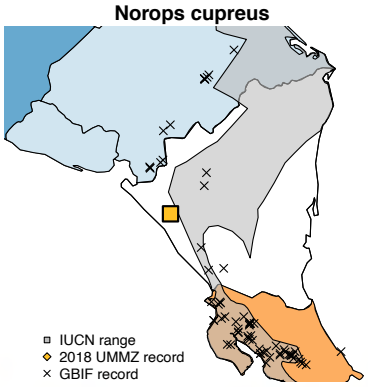
Norops biporcatus known from Southern Mexico to northern South America at elevations up to 2000 m. In Nicaragua the species is found up to 1300 m. This lizard is green in body, though like many anoles capable of rapidly changing color to brown. Males have a blue and orange dewlap, while females have a white or blue dewlap with dark speckling. The species has keeled ventral scales (scales have a raised ridge running from the head toward the tail) (Armstead 2017). We collected two specimens from Bartola. Both were found at rest in the shrub layer (one on a palm frond) in upland forest, at perch heights of 127 and 200 cm. RAB3157 was a male with SVL 86 mm and tail 200 mm. RAB3216 had an SVL 93 mm and a tail length of 150 mm. A recent gene tree based on the mitochondrial gene COI recovered strong genetic differentiation between specimens collected in central Costa Rica relative to those collected in northern Costa Rica and Honduras (Armstead 2017). Further sampling in southern Nicaragua will fill in the phylogeographic history of the northern Costa Rica-Honduras clade, and identify whether the recovered split is a clean break or a more complex zone of intergradation.





Norops capito is found at elevations from sea level to 1300 m on the Caribbean side of Central America from southern Mexico to Panama. The body is grey with green markings, with a yellow-green dewlap and smooth scales with offset rows (thickest portion of scales don't line up) (Savage 2002). This species has eyes that are relatively large and surrounded by a strongly developed ring of supraorbital scales and a relatively short and upturned snout (Köhler et al. 2005). Many specimens have a dark bar running between the eyes, and continuing diagonally

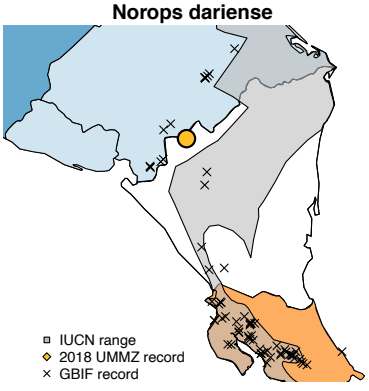
down to the corner of the mouth. We collected a single specimen from Bartola, RAB3190. The lizard was found at rest on a tree trunk in the sun in upland forest at a perch height of approximately 150 cm. The specimen had SVL 82 mm and tail length 143 mm.





Norops cupreus a grey to brown lizard, with males having a large dewlap with a basal orange to red-orange color. The dewlap fades to pink then yellow at the margins. The four central rows of dorsal scales (the scales along the spine) are strongly keeled (scales have a raised ridge running along the long axis of the scale) (Savage 2002). The type locality for this species is in Nicaragua, and the species ranges from Honduras to Costa Rica from sea level to 1250 m. Known maximum SVL is 57 mm. We found two specimens (RAB3082, 3086) near Asososca lake in the lowland dry forest. The specimens had SVLs of 48 and 44 mm respectively.

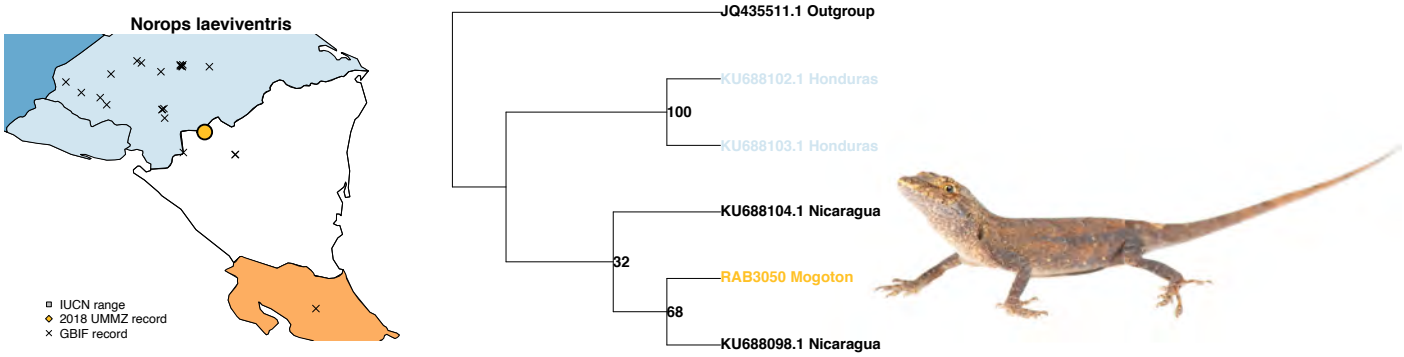
This species is part of a taxonomically complex group of anoles. A population of the species from eastern El Salvador and Guatemala was elevated to a full species (Köhler and Kreutz 1999), leaving the range of *N. cupreus* encompassing Pacific dry forest from Honduras to Costa Rica. In addition, the taxon *N. dariense* (discussed below) has been variably described as a separate species in a work focusing on Costa Rican animals (Savage 2002; Sunyer 2009), and as a subspecies of *N. cupreus* in publications concerned with Honduran or Nicaraguan animals (McCranie and Köhler 2015). In addition, some or all Nicaraguan populations may warrant being identified as *Norops intermedius*. We suggest that further geographical sampling and genetic work throughout the species' range in Nicaragua could provide valuable insights into whether the current classification represents several distinct species, a species complex, or a single species with variable color and scalation. Specifically, a contact zone occurs in central Nicaragua, which may illuminate complex ecological and evolutionary relationships between the two taxa (McCranie and Köhler 2015, McCranie et al. 2019).



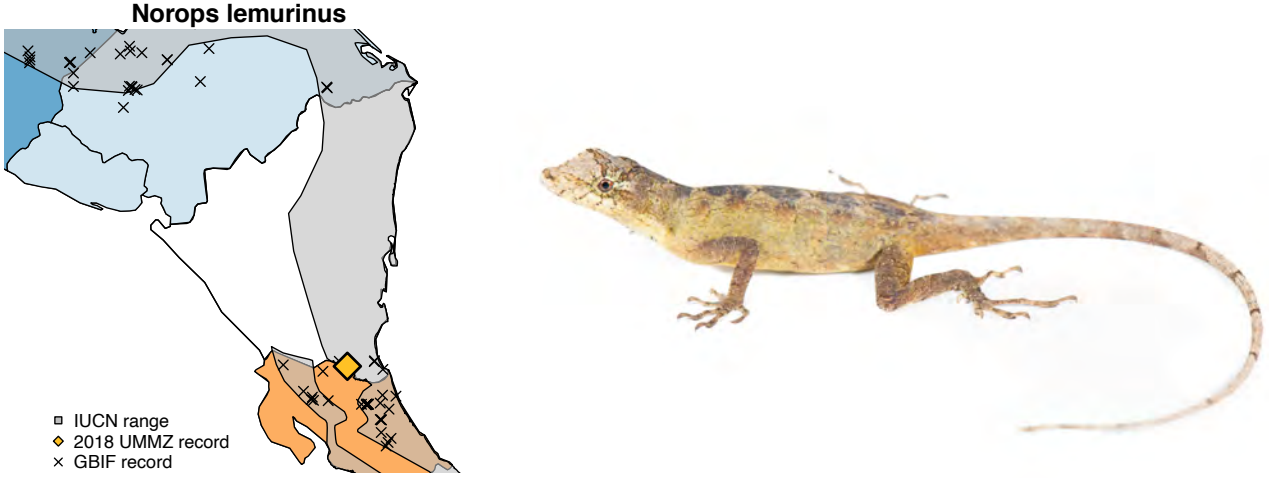
Norops dariense part of the *Norops cupreus* species group, discussed above, that ranges in highlands from Honduras to Costa Rica. It can be distinguished by its uniformly brown dewlap (Savage 2002; Sunyer 2009). We vouchered two specimens of this species near Mogotón in the cloud forest. One individual, RAB3028, was found near a riparian area, sleeping on a leaf in the shrub layer. RAB3026 was found moving across soil. The SVL of our animals ranged from 46 - 51 mm.

Norops laeviventris is known from Southern Mexico to Panama at elevations from 1160 to 2000 m. In Nicaragua the

species is found in the 1100 to 1515 m range. It is a small lizard (SVL to 52 mm) with greyish-brown body and white dewlap (McCranie and Köhler 2015). A single specimen (RAB3050; SVL 41 mm) was collected in the cloud forest near Mogotón. The animal was found sleeping on a fern in the understory. No IUCN range polygon is available for the species. Our 16S sampling strongly separates Nicaraguan and Honduran sequences, perhaps pointing to genetic differentiation across the species' range in this highland-specialist lizard.

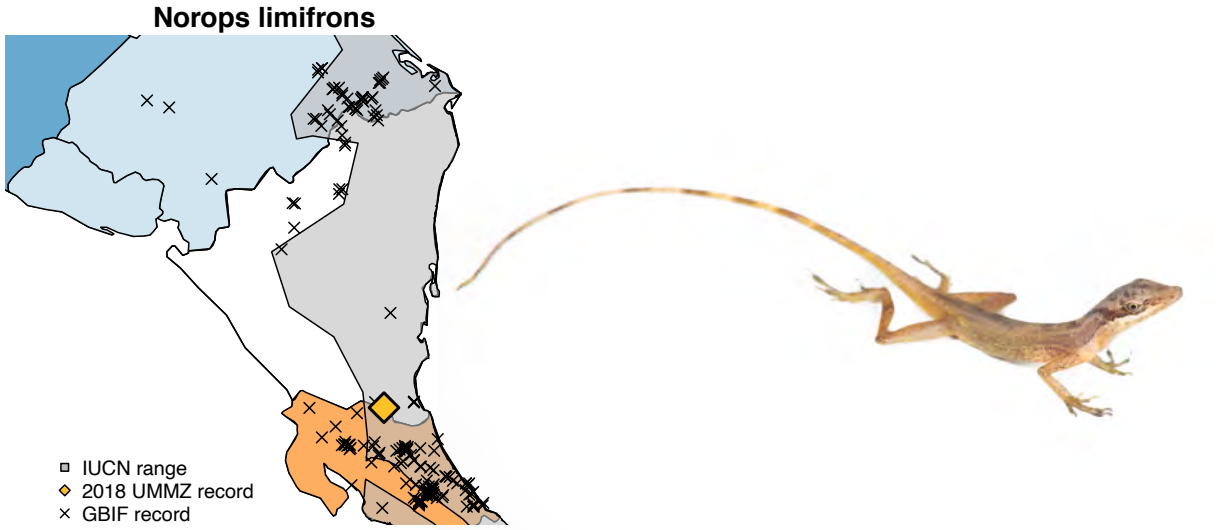


Norops lemurinus known from Central Veracruz to central Panama along Caribbean, sea level to 1080 m. It has an orange-red dewlap, two weakly enlarged dorsal scale rows (the scales along the spine), and relatively long hind limbs (McCranie and Köhler 2015). At Bartola, we collected three specimens of this species (RAB3177, 3192, and 3194). All of the animals were found sleeping on leaves in the shrub layer in upland forest. The animals had SVL's of 55, 45, and 60 mm respectively.

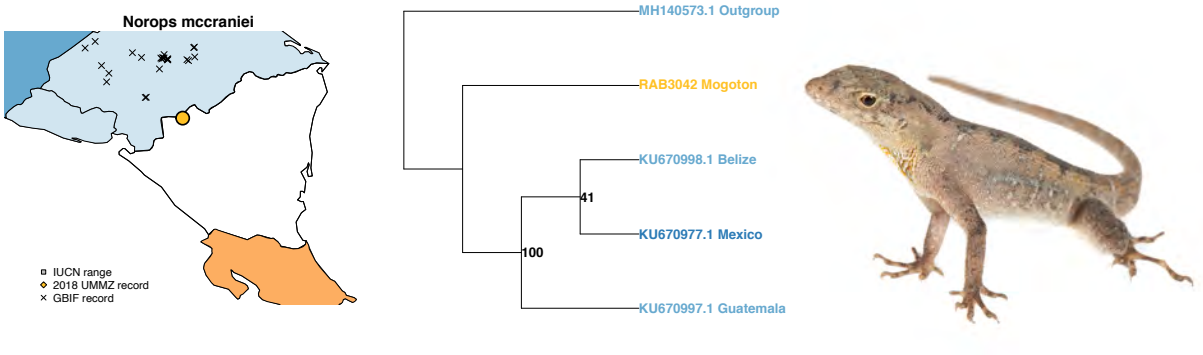


Norops limifrons distributed widely from Guatemala to Panama up to 1080 m. In Nicaragua the species is found up to 200 m. It has a grey/brown body and a white dewlap with a basal orange spot (Savage 2002; Sunyer 2009). Six specimens were collected at Bartola (RAB3139 – 3142, RAB3168, and RAB3180). Five were found in upland forest on branches, leaves or blades of

grass, and one was found near a riparian area. Our animals had SVLs of ranging from 35 to 93 mm. Distinct species with highly localized ranges have been proposed from *N. limifrons* in Panama (Köhler and Sunyer 2008), indicating that further morphological and genetic work throughout the taxon's range could uncover cryptic diversity.

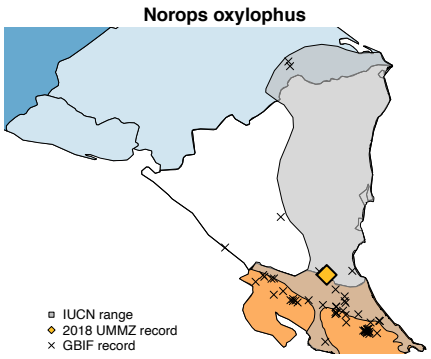


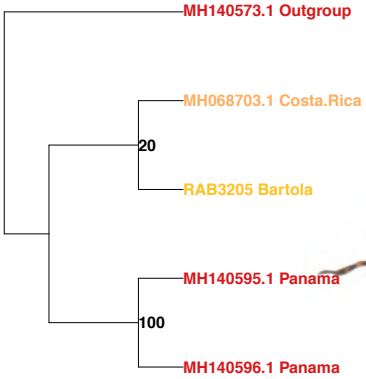
Norops mccraniei a short-limbed, grey to brown, mostly ground-dwelling anole. It can be distinguished by the enlarged, keeled scales (scales have a raised ridge running along the long axis of the scale) in front of the ear opening, and the large orange male dewlap with a dark streak in the center (Köhler et al. 2016). We found two animals (RAB3042, 3055) at Las Brisas de Mogotón. RAB3042 was located moving in the leaf litter. Both animals had SVL of 53 mm. Previous genetic work offers some evidence of a basal lineage occupying northeastern Honduras, with genetically nested lineages in central and southern Honduras (Köhler et al. 2016). This pattern could indicate an expansion southward and westward by the species. If this is the case, our samples would represent the extreme boundary of such an expansion.



Norops oxylophus a semiaquatic species with a yellow dewlap and dorsal scales smooth or weakly keeled (keeling refers to scales with a raised ridge running along the long axis of the scale), distinguishing it from the similar-looking *N. lionotus*. It is a uniform dark brown in color

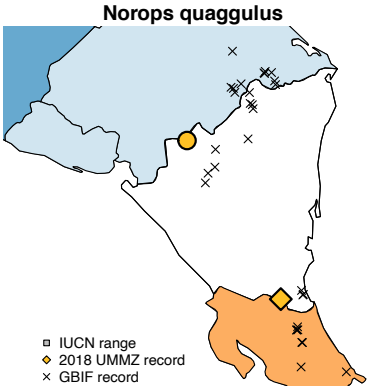
with cream-colored lateral stripes (stripes running from the neck to above the back legs). It ranges from Honduras to Panama up to 1100 m (Savage 2002). Morphological work suggests that it is adapted to seeking refuge in riparian vegetation while foraging in streams (Muñoz et al. 2015). Two specimens, RAB3161 and RAB3205, with SVLs 39 mm and 69 mm respectively, were collected at Bartola. RAB3161 was encountered near the riparian area; the animal was found at rest on a fallen branch. No IUCN range polygon is available for the species. Our 16S tree showed that our sample clustered with a Costa Rican sequence, and was differentiated from Panamanian sequences.







Norops quaggulus ranges from eastern Honduras to northeastern Costa Rica up to 1600 m (Phillips et al. 2015). It is a small, brown, terrestrial anole with eight to ten enlarged mid-dorsal scale rows (the scales along the spine), usually three enlarged scales above the eye, and a short, bilobed hemipenis (Savage 2002; Sunyer 2009). We collected two individuals at Las Brisas de Mogotón. RAB3040 had an SVL of 45 mm and RAB3076 had an SVL of 49 mm. Both specimens were encountered in upland pine forest, resting on soil or leaf litter. We collected three more individuals at Bartola, RAB3206, 3208, and 3209, with SVLs of 33, 37, and 34 mm. All occurred in upland forest, with one specimen sleeping on a leaf, one in the leaf litter, and one caught in a funnel trap.

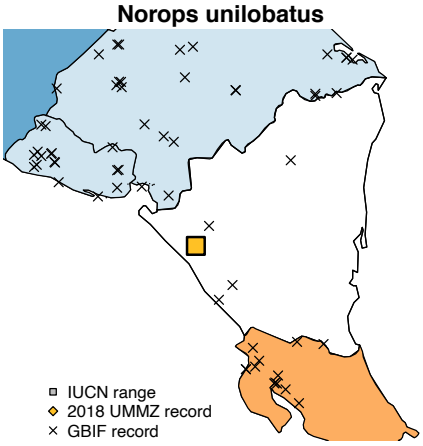




Norops quaggulus was separated from *N. humilis*, which ranges across southern Nicaragua, Costa Rica and into Panama, based on hemipenal morphology (Köhler et al. 2003). Phylogeographic work placed *N. quaggulus* as a monophyletic group nested within taxa identified as *N. humilis*. The *Norops humilis* taxon ranges from Panama to Costa Rica, indicating a history of northward expansion in this species complex (Phillips et al. 2015).

Norops unilobatus ranges from Mexico to Costa Rica at elevations from 0-1200 m. Males have a dewlap that is yellow-orange with a large blue-purple blotch, the species has short legs (longest toe of hindlimb does not pass external ear when bent forward along the body), and ventral scales

are strongly keeled (scales have a raised ridge running from the head toward the tail) (Köhler and Vesely 2010). We collected three specimens at Asososca lake (RAB3091, RAB3092 and RAB3111, SVLs 42, 45, and 46 mm respectively). RAB3091 and 3092 were found sleeping or at rest on leaves or branches near the lake. This species belongs to a complex that encompasses three taxa with distinct hemipenal and dewlap morphology (Sunyer 2009; Köhler and Vesely 2010). Our samples were taken from a zone of contact with *N. wellbornae* and *N. unilobatus,* species that were both formerly included under *N. sericeus*. Further genetic, ecological, and morphological work in the area could determine whether splitting *N. sericeus* into several species is taxonomically warranted.





Infraorder Gekkota

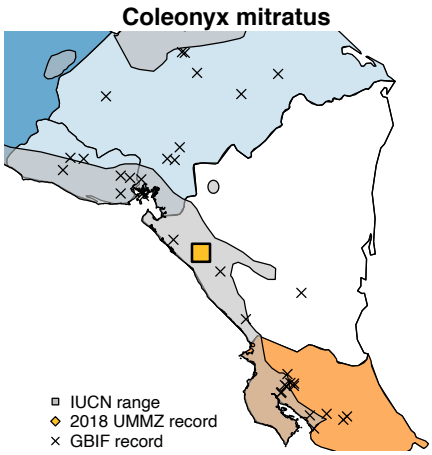
This infraorder of squamates comprises all of the families known as "geckos," as well as the limbless lizards in the family Pygopodidae. Of the seven gecko families, we found representatives of four: Eublepharidae, Gekkonidae, Phyllodactylidae, and Sphaerodactylidae (Han et al. 2004). Geckos are generally characterized by broadened adhesive lamellae on the underside of digits, allowing them to cling onto smooth, vertical surfaces. Further, many lack a movable eyelid. Some are nocturnal but others are diurnal.

Family Eublepharidae

This family contains 6 genera and 30 species. They occur across Asia, Africa, and North and Central America. Eublepharid geckos differ from "typical" geckos by a lack of adhesive toepads and a moveable eyelid. We found a single species in Nicaragua, *Coleonyx mitratus*.

Coleonyx mitratus a terrestrial, nocturnal lizard that is known to hide beneath rocks, fallen logs, and hollow tree trunks during the day. They are generally insectivorous. They move gracefully and have distinguishable, leopard-like spots on the light-colored dorsal surface. When frightened, they will widen the throat and assume an upright and stiff posture. They are distinguished by the other congeneric species in Central America, *Coleonyx elegans,* by a lack of scaly sheath covering the claws; a square first sublabial (scales on upper lip); and lack of small scales behind

internasals (the first scales on top of the tip of the snout that do not touch the mouth) (Savage 2002; McCranie 2018). This species is known from Guatemala to Costa Rica on the Pacific versant, to 1000 m elevation. SVL reaches 91 mm. We found two specimens at Asososca lake, both resting or moving across the ground at night in upland forest. RAB3081 had an SVL of 68 mm, while RAB3084 had an SVL of 80 mm.





Family Gekkonidae

This is the largest family of geckos, with ~1000 species and 61 genera. It contains the house geckos (Hemidactylus), day geckos (Phelsuma), and mourning geckos (Gehyra). We found a single species, *Hemidactylus frenatus,* which has been introduced to Nicaragua.

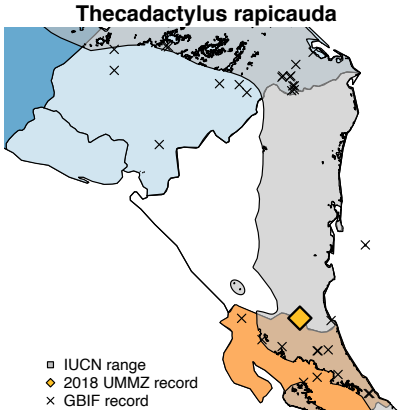
Hemidactylus frenatus one of five species of *Hemidactylus,* or "old world house geckos," have been introduced to Central America. They can be distinguished from other Gekkota genera in the region by a combination the presence of large tubercles (rounded protruding bumps) on the dorsal surface and a lack of tubercles on the upper surface of hind limbs and above the ear opening. They are usually associated with human activity and can be found in and around buildings. Their chirping vocalizations are distinct and can be heard at night. This species has been introduced to the Yucatán Peninsula, Guatemala, El Salvador, Nicaragua, Costa Rica, and Panama (Rödder et al. 2008; McCranie 2018). They are known from sea level to 1230 m. We vouchered one specimen, RAB3100, at Asososca lake. It had an SVL of 56 mm. We captured it during the day after it fell out of a thatched roof during a fight with another male.

Family Phyllodactylidae

This family of geckos contains approximately 150 species and 10 genera, distributed throughout the New World as well as northern Africa, Europe, and the Middle East.

Thecadactylus rapicauda a primarily arboreal, nocturnal gecko, recorded from perch heights up to 30 m and frequenting a variety of perches from trees to palm leaf axils to anthropogenic structures. This species can be distinguished from other neotropical geckos by the combination

of expanded sensorial pads under the bases of all digits, unique cloacal sacs and internal cloacal bones, and a deep subdigital sulcus beneath each toe that houses the claw and divides the lamellae into a double series (the wide, ridged toe pads are divided into two lobes each) (Russell and Bauer 2002; Savage 2002; McCranie 2018). The extensive distribution is more or less continuous from the Yucatán Peninsula through Panama, primarily on the Atlantic versant, to northcentral South America through Brazil, and on either side of the Andes in Ecuador and Colombia but mainly restricted to the eastern side in Peru and Bolivia. It is found from sea level up to at least 750 m, with some records reaching 1000 to 1500 m. Maximum reported SVL is 150 mm. We collected one male individual, RAB3239, at Bartola, with an SVL of 103 mm. It was encountered at night under a stack of logs in an abandoned shed at the riparian-upland forest interface. Our Bartola specimen falls in a sampling gap in a recent phylogeographic study of the species based on the mitochondrial gene CO1 (Kronauer et al. 2005). Samples from north of Nicaragua form a clade with lizards from Trinidad and Tobago, while samples from Costa Rica cluster with sequences from the Lesser Antilles. Sampling the species' Central American and



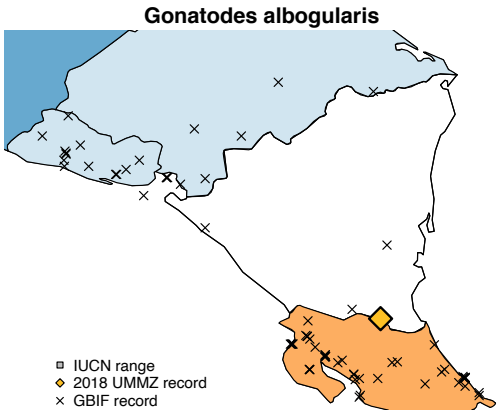


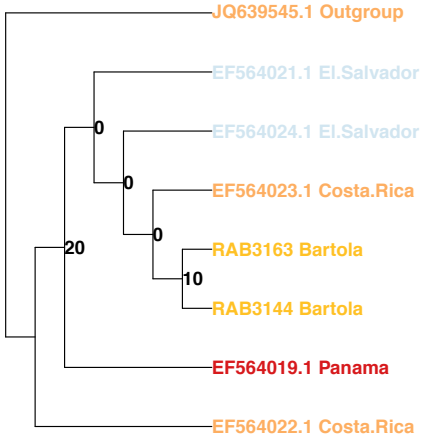
Caribbean ranges and sequencing more genes might resolve the complex biogeographic history of the northern range of *Thecadactylus rapicauda*.

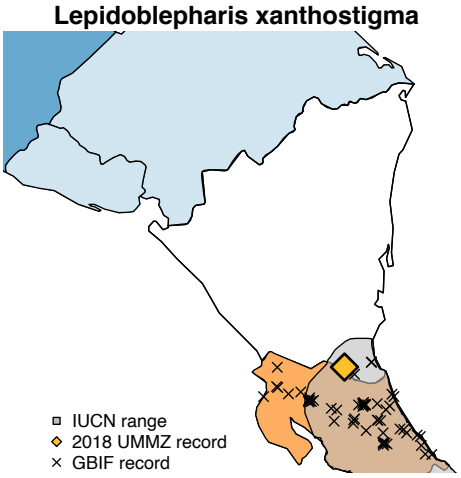
Family Sphaerodactylidae

This family contains over 200 species broadly distributed across the Americas, Caribbean, southern Europe, Africa, and Asia. We found species representing three genera.

Gonatodes albogularis diurnal and often brightly colored geckos. Many species in the genus are found in South America, and *G. albogularis* is the sole Central American representative. *Gondatodes albogularis* is widely distributed across Central America, into South America, and across the Caribbean islands. In Nicaragua the species is found up to 800 m. Females are cryptically colored, while males have a bright yellow head (Savage 2002). We encountered two specimens at Bartola, RAB3144 (SVL 80 mm), and RAB3163 (SVL 40 mm). The latter was encountered at the lodge at Bartola. Our 16S tree is poorly supported and should be interpreted with caution, perhaps due to extensive gene flow in this widespread and abundant species. The Bartola samples nested in a clade made up of El Salvadoran and one Costa Rican sample, while a second Costa Rican sequences and a Panamanian sequences formed outgroups.



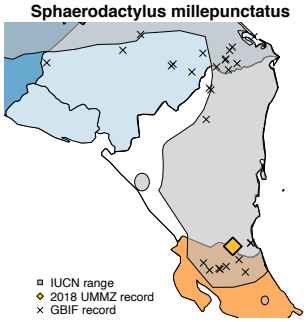




Lepidoblepharis xanthostigma a small, ground-dwelling lizard that lives in leaf litter, often near rotting logs, roots, or decaying plant matter, which provide needed humidity. Two species occur in Central America: *L. xanthostigma* and *L. santaemartae*, with three more proposed as Panamanian endemics (Savage 2002; Batista et al. 2015). *Lepidoblepharis xanthostigma* can be distinguished by juxtaposed dorsal scales (thickest portion of scales on back do not line up) and enlarged median subcaudal scales (large scales in a row along the bottom of the tail). This species is known from southern Nicaragua to Colombia, up to 1360 m elevation. In Nicaragua the species is reported up to 420 m. We encountered one individual, RAB3211, with an SVL of 26 mm. We found this specimen at Bartola, moving across the ground at night in upland forest. A revision of Panamanian *Lepidoblepharis* found extensive cryptic variation in the genus (Batista et al. 2015). This result may indicate undiscovered cryptic diversity throughout the rest of the species' Central American range. Alternatively, the genus might follow ecologically similar species in having a large amount of ancestral diversity in Panama, with more recent range expansions northward leading to fewer cryptic lineages in northern Central America. Further sampling in Costa Rica and Nicaragua could resolve this biogeographic question.



Sphaerodactylus millepunctatus a small, ground-dwelling lizard that can be found from Mexico to Costa Rica. In Nicaragua is found up to 960 m. It can be identified by distinct dorsal spots that are larger than single scales, by its two supranasal scales (scales above the nostrils) and single row of subcaudal scales (scales beneath the tail), and by its 42 to 57 dorsal scale rows (Savage



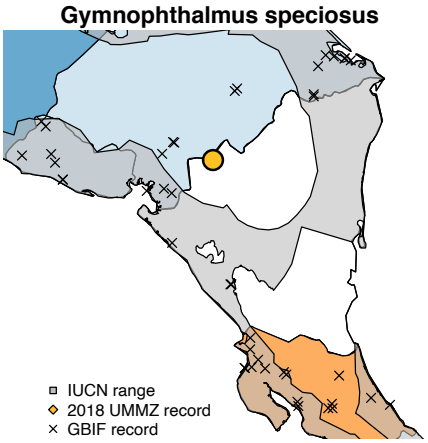


2002; McCranie and Hedges 2012). We encountered one specimen, RAB3228 (SVL 26 mm) at Bartola. It was found during the day under cover at the Bartola lodge.

Family Gymnophthalmidae

This family includes over 250 species worldwide (Pellegrino et al. 2001). They are known as spectacled lizards because the lower eyelids are transparent in many species. Their bodies are elongated with reduced limbs, well adapted to a semi-fossorial lifestyle. Most species are nocturnal or move secretly under the leaf litter of the forest. All species feed on arthropods and lay eggs. A single species is present in Nicaragua.

Gymnophthalmus speciosus a relatively small species with SVL up to 50 mm and tail about the same length. Most individuals have a tail with a red tip. The lighter brown dorsal color is contrasting with the darker scales along the side of the body. Front limbs have four fingers while the back legs have five (García-Roa and Sunyer 2012). The species inhabits the leaf litter in different habitats from Guatemala to Colombia at elevations from sea level to 1200 m. We encounter one adult female, RAB3061 at Mogotón with an SVL of 46mm. It was found in pine needle litter on a slope above a river.



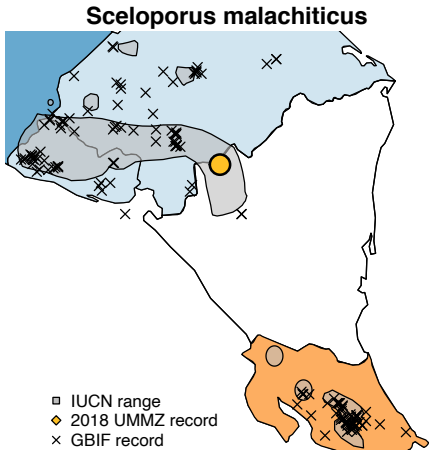


Family Phrynosomatidae

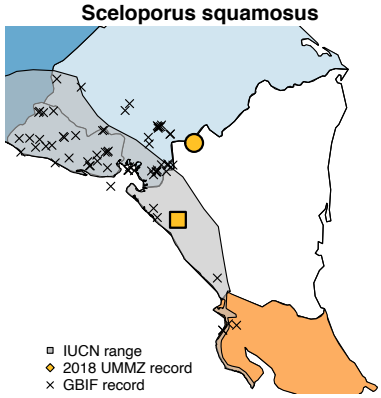
Genus *Sceloporus* some of the most commonly-encountered Iguanid lizards in the dry regions of Central America. Spiny lizards are small to medium sized diurnal lizards that feed on arthropods and smaller vertebrates. Species vary in habitat use from primarily ground dwelling and/or saxicolous, to highly arboreal (Wiens et al. 2010). We encountered all three species present in Nicaragua.

Sceloporus malachiticus a taxonomic designation within the *Sceloporus formosus* species group that has recently been broken into several species (McCranie, 2018). Nicaraguan populations of this species likely correspond to *S. hondurensis* or to an undescribed species (McCranie, 2018). *Sceloporus malachiticus* is a large green lizard with visibly pointed, rough scales that is generally found on trees, fence posts, and roofs. Males are highly territorial. In Nicaragua this

species is easily distinguished from congeners by coloration and body size. The lizard can appear dark grey or black when cold, but will never appear striped (Savage 2002). We found *S. malachiticus* at Mogotón: RAB3036 was found at rest at ground layer in the sun at an elevation of 1430 m, had SVL 80 mm and tail 91 mm. RAB3041 was also found at rest in the soil. Though *S. malachiticus* is known to be highly arboreal, our specimens were all found at ground level. We could not corroborate if our samples belong to the species *S. hondurensis* because there is no reference for 16S genotypes available of that species in GenBank.



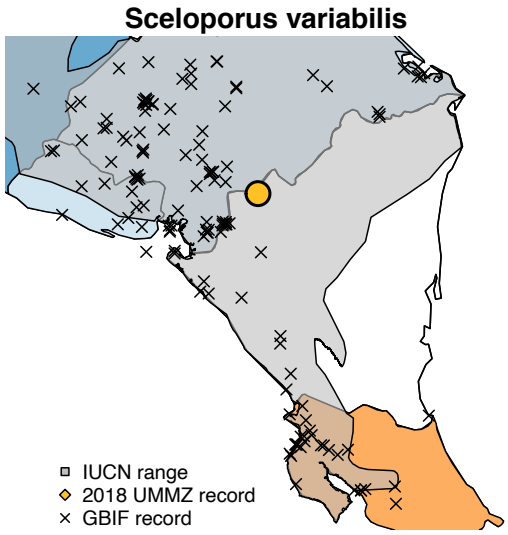
Sceloporus squamosus the only Nicaraguan species of the *S. siniferus* species group, which is made up of ground dwellers in arid environments. They are often seen on individual rocks or in rock piles. This species ranges from western Chiapas, Mexico along the pacific side of Central America into northwestern Costa Rica, in lowland arid and dry forests from sea level to 1000 m. It is a small *Sceloporus,* which can be recognized by its lack of a post-femoral dermal pocket (no small pit behind back legs), strongly keeled scales on the base of the tail and lower ventral surface (scales have a raised ridge running along the long axis of the scale), 6-12 femoral pores (row of enlarged pores along the back of the upper leg), and lack of enlarged post-cloacal scales (scales on the underside of the base of the tail) (McCranie 2018). We collected one specimen of *S. squamosus* from Mogotón: RAB3065 was found far upslope from a river in pine forest, and had an SVL 45 mm and tail length of 91 mm. We collected two specimens of *S. squamosus* near Asososca lake, in the lowland dry forest. RAB3083 was an adult male with SVL 49 mm and tail 113 mm, while RAB3107 had an SVL of 51 mm.





Sceloporus variabilis a small *Sceloporus* lizard with SVL up to 79 mm. In Nicaragua it is the sole representative of the *S. variablis* species group, of which the distinguishing feature is the presence of a postfemoral pocket (small pit behind back legs), distinguishing it from the similar-looking *S. squamosus* (McCranie 2018). Other significant characters include: 49-59 dorsal scales from the base of the head to the base of the tail; dorsal scales 2-3 times larger than lateral scales

(scale on sides of body) scales; 58-70 scales around the body; 57-79 ventral scales; 12-14 femoral pores (row of enlarged pores along the back of the upper leg). Coloration generally consists of two light dorsolateral lines (running from shoulders to above back legs) present with a series of dark spots; males possess paired pink, blue-bordered patches on the ventral surface. This species ranges from Texas, USA, along the Caribbean side of Mexico into northwest Costa Rica. It is found in savanna and dry forest at elevations from sea level to 1700 m. In Nicaragua the species is reported up to 1350 m.

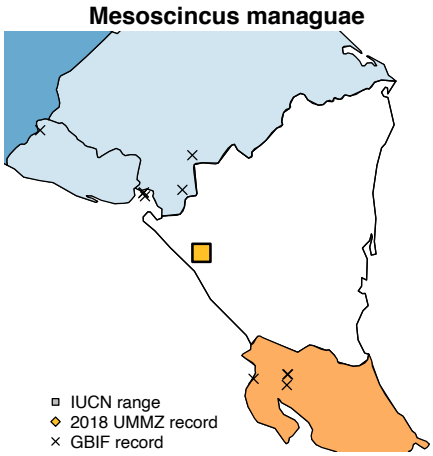


Recent genetic and morphometric work suggested that the *variabilis* species complex is polyphyletic, with the species *S. teapensis* and *S. smithi* nested within taxa formerly assigned to *S. variabilis* (Solis−Zurita et al. 2019). The authors suggest elevating all *S. squamosus* south of Mexico to species status under the name *S. olloporus*. However, all putative *S. olloporus* included in the study were collected in southern Mexico, so we do not apply the name to our specimens. Work in the southern range of the *variabilis* complex could further refine our understanding of the taxonomy and biogeographic history of the group. *Sceloporus variabilis* is generally described as a ground-dweller but is also seen on tree stumps or rocks. We collected two specimens at Mogotón (RAB3039, RAB3063), one female and one male. RAB 3039 (F) was an adult with SVL 56 mm and a tail length of 75 mm. It was found at rest in the soil in partial shade. RAB 3063 (M) had an SVL 62 mm and tail length of 53 mm. It was found in motion in the dry forest upslope from a nearby river. We collected on specimen at Asososca lake, RAB3106. It had an SVL of 36 mm.

Family Scincidae

The true skinks are a very diverse family, with over 1,500 species worldwide. This family formerly included other neotropical families like Mabuyidae and Sphenomorphidae (Linkem et al. 2016). The family is well adapted to semi-fossorial life with elongated smooth bodies and small limbs. Most species are insectivorous, but some larger species also prey on small vertebrates like lizards and even rodents. A single species occurs in Nicaragua with a type locality in Managua, the capital of the country.

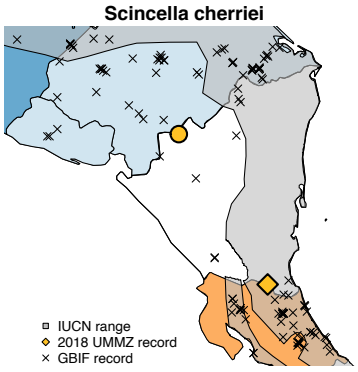
Mesoscincus managuae a large skink measuring up to 280 mm in total length. The relatively rare species inhabits the lowland dry forest in the Pacific of El Salvador to Costa Rica at elevations from sea level to 500 m. It is a diurnal leaf-litter dweller recognizable by the longitudinal black stripes (around the width of the body) and enlarged dorsal (back) scales (McCranie 2018). We collected one adult male, RAB3097, with an SVL of 81 mm and tail length of 127mm. It was found at Asososca lake under a dead log in the ground at night, near the lake shore.





Family Sphenomorphidae

The approximately 120 species within this family were formerly including in the family Scincidae. A single species, formerly classified formerly in the *Sphenomorphus* genus (Hedges 2014), is present in Nicaragua.



Scincella cherrei a relatively small species that reaches 50 mm of SVL and has a tail that can be longer that the rest of the body. The sides are marked by a thick black band that starts at the snout, crosses the eye and dissolves around mid-body. It has 30 to 34 scale rows at the mid-body has no enlarged nuchal scales (scales on the neck just posterior to the head scales) (Savage 2002; McCranie 2018). The species ranges from Mexico to Panama at elevations up to 1300 m in wet forests. We encountered two individuals at Mogotón, RAB3020 and RAB3021 with SVL of 44 mm and 55 mm respectively. Both individuals represent new elevation records for the species in Nicaragua (1320 m, 1350 m). The specimens had regenerated tails (45 mm, 32 mm). We encountered both individuals moving across pine litter at night. We also collected an adult male in Bartola, RAB3226, with an SVL 52 mm and tail length of 56mm. Individuals at Mogotón were found moving in the leaf litter at night, while the individual from Bartola was caught in a funnel trap in upland forest.



Family Teiidae

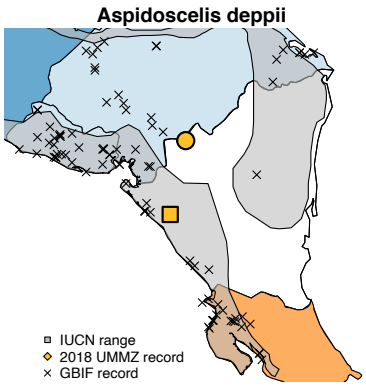
Teiidae is a family of autarchoglossan lizards widely distributed across the Americas and West Indies (Harvey et al. 2012). They are mainly terrestrial (with some semi-aquatic) and diurnal active foragers, characterized by well-developed limbs, a forked tongue, granular dorsal scales, and distinct transverse rows of ventral scales. 151 species across 18 genera are currently recognized (Tucker et al. 2016). We collected four species across two genera from three different

localities in Nicaragua. These genera, *Aspidoscelis* and *Ameiva*, represent the cnemidophorine clade of the subfamily Teiinae, along with *Cnemidophorus* and *Kentropyx*.

Genus *Aspidoscelis*

Lizards of the genus *Aspidoscelis*, commonly known as whiptail lizards, comprise a group of species distributed across North and Central America. Nearly one third of the species in this group are unisexual (all "female") lineages of interspecific hybrid origin, and reproduce asexually via parthenogenesis, in which embryos do not require fertilization by sperm (Reeder et al. 2002). *Aspidoscelis* lizards can be distinguished from all other Cnemidophorine taxa based on the combination of the following morphological traits, from (Reeder et al. 2002): absence of a basal tongue sheath; posterior portion of tongue clearly forked; smooth ventral scutes in eight rows across midbody; granular dorsal scales; absence of anal spurs in males; mesoptychial scales (scales of the anterior middle portion of the chest) abruptly enlarged over scales in gular fold (skin wrinkle under the neck just in front of front legs), becoming smaller anteriorly; three parietal scales (large scales at the top of the head behind the eyes); and three or four supraocular scales (scales above eyes). Both *Aspidoscelis* species discussed here have an unbroken row of enlarged scales (branchial and antibranchial scales) running down the outside of the front leg (McCranie 2018).

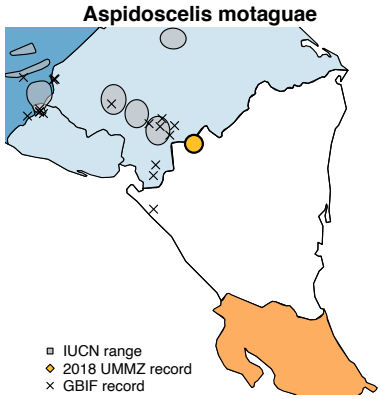
Aspidoscelis deppii a moderately-sized, slender whiptail ranges from Mexico to Costa Rica up to 1000 m. It has three supraoculars (enlarged scales above the eye), lacks further enlarged scales touching the enlarged forearm scale row, has black 'racing stripes' on a lighter background on the dorsal surface, and has a blue tail throughout life (McCranie 2018). We collected one individual, RAB3064, from Los Brisas del Mogotón in dry forest habitat, far up slope from a river. It had an SVL of 64 mm. Two individuals, RAB3108 and RAB3109, were collected from dry forest habitat near Asososca lake. They had SVLs of 81 and 92 mm. All were moving across the ground during the day.





Aspidoscelis motaguae a large, heavyset whiptail found from Mexico to northern Nicaragua in upland dry forest up to 1200 m, with its southernmost extent only recently published (Köhler et

al. 2013). It can be distinguished from similar species by its large size, the presence of more enlarged scales on the rear side of the enlarged forearm scale row, a spotted pattern on the dorsal surface and a red to brown tail, and four enlarged supraoculars (scales above the eye) (McCranie 2018). We collected one individual, RAB3070, from Mogotón in dry forest habitat, far up slope from a river. We encountered it moving across the ground during the day. It had an SVL of 140 mm.

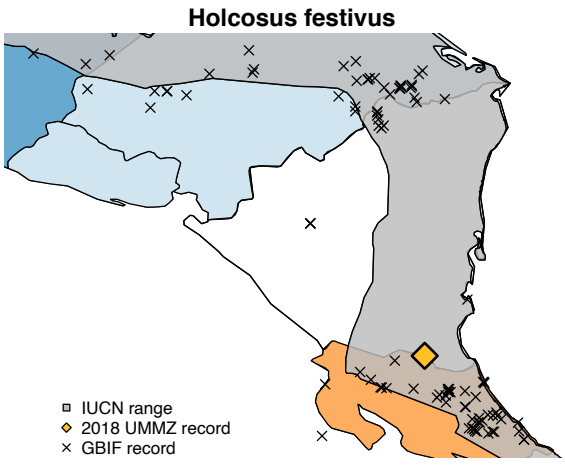


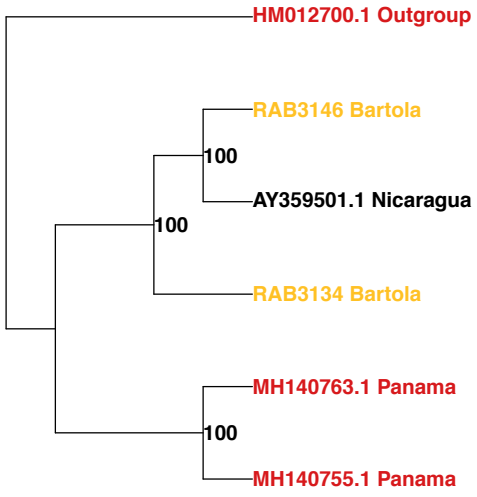


Genus *Holcosus*

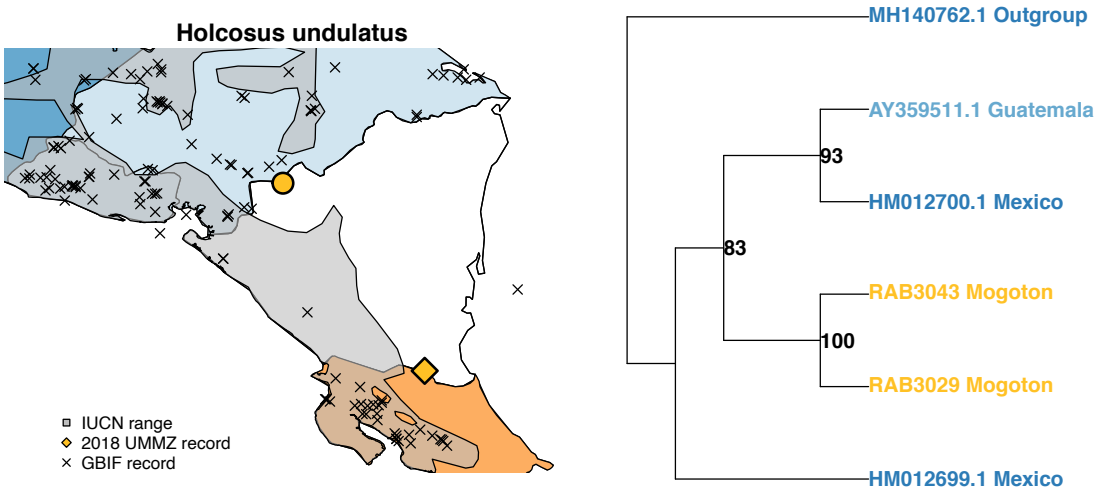
The species discussed below can be identified to genus using the following characteristics: 1) five scales (parietals) at the base of the head, where head scales meet body scales, 2) prefrontal scale (between frontal and internasal scales) not touching nasal scales, and 3) never more than one row of enlarged scales forming a collar (Savage 2002; McCranie 2018)

Holcosus festivus has uniformly small, granular throat scales and eight rows of ventral scales (Savage 2002). It is found from Mexico to Colombia. We collected three individuals of this species at Bartola, RAB3134, RAB3146, and RAB3225, two of which were encountered on the ground near fallen trees. They had SVLs 59 mm, 107 mm, and 49 mm respectively. The 16S tree strongly clusters our Bartola sample with another sequence available from Nicaragua, and separates the cluster from conspecific samples taken from Panama, indicating a possible isolation by distance pattern within Central America.





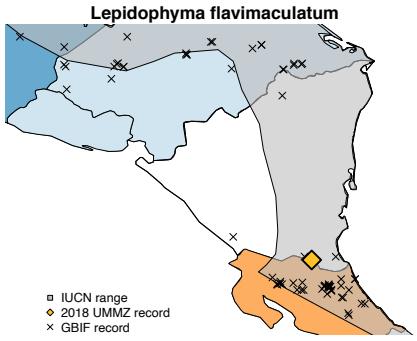
Holcosus undulatus a moderately-sized lizard ranging from Mexico to Nicaragua. It can be identified by an enlarged patch of scales on the throat, surrounded by smaller, granular scales and 12 rows of ventral scales (McCranie 2018). We encountered two members of this species at Las Brisas de Mogotón, RAB3029 (SVL 107 mm) and RAB3043 (SVL 48 mm). One was found under a rotting log during the day in pine forest. We vouchered a further two specimens at Bartola, both found moving across a muddy track at night. These specimens were RAB3145 (SVL 79 mm) and RAB3217 (SVL 67 mm). Our 16S sequences form northern Nicaragua cluster strongly together, while sequences taken farther north in the species' range form a separate clade, indicating a possible isolation by distance pattern.

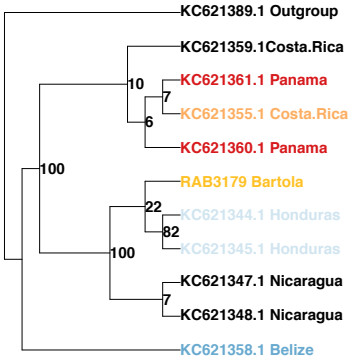


Family Xantusiidae

The family Xantusiidae contains three genera, *Lepidophyma*, *Xantusia*, and *Cricosaura*. *Lepidophyma* occurs in Central America, *Xantusia* in Mexico and southwestern North America, and *Cricosaura* is restricted to Cuba, where it may have survived the fallout of the end-Cretaceous asteroid impact that struck near the Yucatan peninsula (Noonan et al. 2013). All members of the family are cryptic lizards that tend to be closely associated with cover objects. *Lepidophyma flavimaculatum* is the only member of this family known from Nicaragua.

Lepidophyma flavimaculatum a cryptic and reclusive species of lizard occurs from Mexico to Panama up to 1000 m. It can be distinguished by its rough, almost conical dorsal scales, large smooth head scales, distinct neck, and dark coloration with white markings and is one of the few nocturnal species in Nicaragua (Savage 2002). We encountered one individual, RAB3179, living in a tree hole in upland forest at Bartola. It had an SVL of 37 mm, indicating its juvenile status. Adult SVL ranges from 60 to 102 mm (Savage 2002). Our 16S tree recovers three strongly supported clades, a Belize group, a Nicaragua-Honduras clade that includes our Bartola specimen, and a southern clade that includes Costa Rican and Panamanian samples. Within each clade, tree topology is poorly resolved. Our recovered tree topology could indicate a strong phylogeographic break in this species near the Nicaraguan depression, with extensive gene flow within each population unit in this widespread and abundant species.





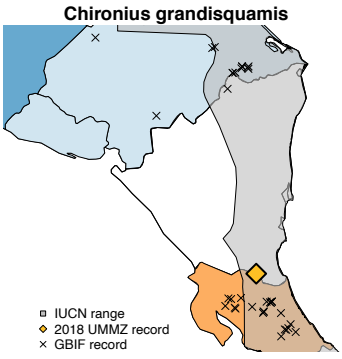


Suborder Ophidia

Family Colubridae

The family Colubridae comprises over 700 species. They are distributed worldwide, with high diversity in North and Central America. This group is morphologically and ecologically diverse, with terrestrial, arboreal, fossorial, and semi-aquatic ecomorphs (Figueroa et al. 2016). Many snakes in this group are putatively venomous, while others are powerful constrictors. In Nicaragua, we encountered 12 species.

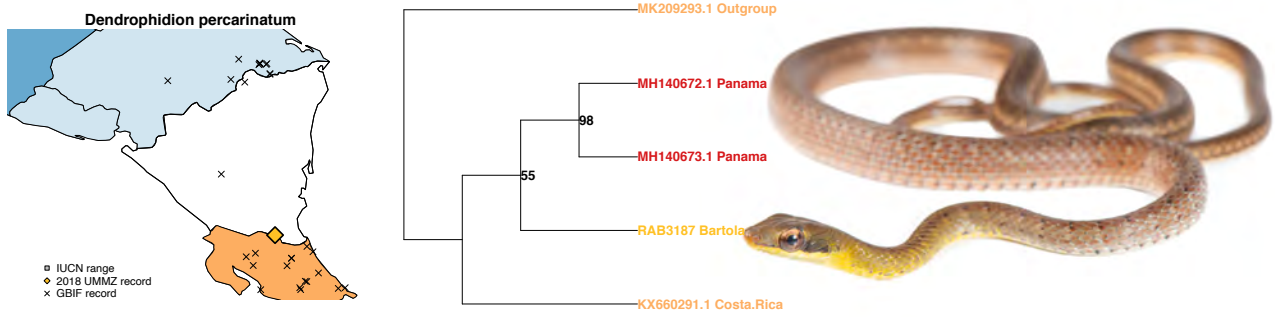
Chironius grandisquamis a large, predominantly arboreal snake. This genus is notable as the only Neotropical snakes with 10-12 dorsal scales at mid-body (Savage 2002). The large eyes are indicative of its diurnal behavior. It ranges from northern Honduras to northwestern Ecuador, up to 1600 m in rain and cloud forest. We captured a single individual, RAB3160, at Bartola; it was sleeping on a tree branch over the Río Bartola. The animal was an adult male with an SVL of 1150 mm.





Dendrophidion percarinatum known from rain forest habitat from northern Honduras to northwest Ecuador from 30 to 500 m elevation. In Nicaragua the species has been reported up to 260 m. It is a diurnal, medium sized, slender snake with large eyes. It can be distinguished from

congeners by scale counts: this species has 153-155 ventrals and 119-139 subcaudals (scales underneath the tail) (Savage 2002). The scale row reduction from eight too six occurs anterior to subcaudal 25 and differentiates this species from other species in the same genus (McCranie 2011). RAB3187, and adult male with an SVL of 497 mm, was the sole representative of this species from our trip. We encountered the specimen sleeping on a fallen tree branch in upland forest at Bartola. The 16S tree is poorly resolved and should be interpreted with caution. The location of the Nicaraguan specimen is particularly uncertain. Further genetic work throughout Central America can increase phylogeographic
resolution in this species.

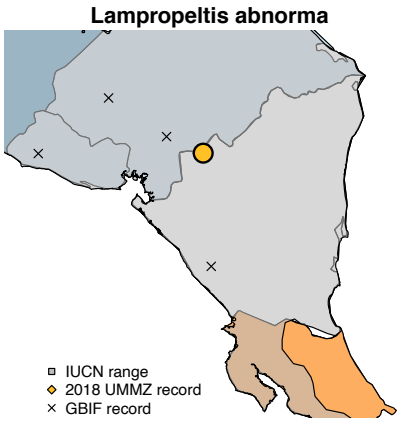


Drymarchon melanurus formerly considered a subspecies of *Drymarchon corais*. This species occurs from Veracruz, Mexico along the Pacific versant to South America up to 1500 m (Wüster et al. 2001). This is a large, fast, diurnal snake often encountered on the forest floor. As adults, the species is generally green to brown in dorsal color, sometimes with faded markings. Juveniles can be more vividly patterned. The species can be identified by a dark diagonal band on the neck and dark color on the ventral surface on the posterior portion of the body (Wüster et al. 2001). A single individual was collected at Las Brisas de Mogotón: RAB3059 was a large individual with an SVL of 1600 mm and a tail length of 1250 mm. It was found moving across the leaf litter in pine forest during the day.



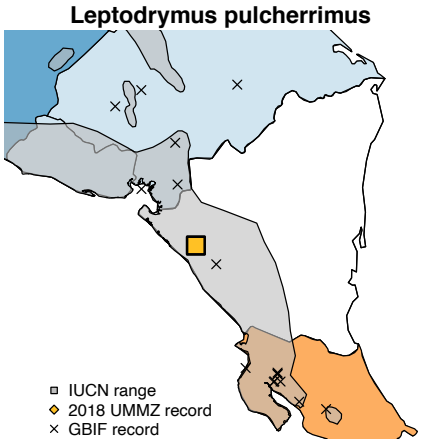
Lampropeltis abnorma previously considered a subspecies of *L. triangulum* (Ruane et al. 2014). It ranges from Mexico, to western Costa Rica up to 2000 m. Color can be variable, ranging from completely black to red with black banding, to the usual tricolored banding. The species can be

identified by its 19 to 23 dorsal scale rows, an entire scale just forward of the cloaca (anal scale), mostly divided scales on the bottom of the tail (subcaudals <65), and two small pits on the tail end of each scale (apical pits) (Savage 2002, McCranie 2011). We found one specimen of *L. abnorma* at Las Brisas de Mogotón. The animal was an adult female, RAB3060, with an SVL of 247 mm and tail of 41 mm. It was caught in a funnel trap in pine forest in a riparian zone.





Leptodrymus pulcherrimus a monotypic genus - this snake characterized by the presence of three postocular scales (scales directly behind the eye) and bright green coloration on the head and a cream dorsal stripe flanked by black on either side (McCranie 2011). The species is known from the Pacific side of Guatemala to Costa Rica, in savanna and dry forest from sea level to 1300 m (Savage 2002). We collected three animals from Asososca lake. The first, RAB3098, had an SVL of 502 mm. The second, RAB 3099, had an SVL of 623 mm. Both were adult females, and both were found sleeping in trees in upland forest. We found a single individual, RAB3103, also an adult female, with SVL of 532, sleeping in a tree branch near the lake shore. All individuals were found at night.





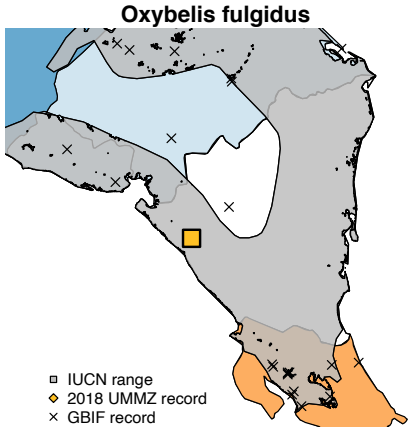
Mastigodryas alternatus ranges from Honduras to central Panama. Juveniles have pale cross bands, while adults are unicolored or possess longitudinal stripes. Unlike similar species, they

have a divided anal scale (the scale just anterior to the vent), 17 scale rows at mid-body, 15 scale rows just anterior to the vent, and two postocular scales (scales behind the eyes) (Savage 2002; Montingelli et al. 2019). Subcaudals in this species ranges from 82-107 in males, and 90-119 in females (McCranie 2011). This species is diurnal, and hunts lizards in savanna, dry forest, or rain forest habitats. A single specimen was collected from Bartola: RAB3191 had an SVL of 756 mm and was found sleeping on a branch in a riparian area.

Genus *Oxybelis*

The slender bodies and extremely pointed snouts of vine snakes make them incredibly cryptic in their habitat, but easily distinguished from other species when found. All species lack a loreal scale (a scale that falls between the scales touching the nostrils and the scales touching the eyes) and narrow pointy heads (McCranie 2011). These species are rear-fanged, with mild venoms (Heyborne and Mackessy 2013). When captured, members of this genus will gape exposing the blue-black inside of the mouth; they may also bite readily. These snakes are diurnal, and sleep coiled in trees or shrubs. In Nicaragua, we found two members of the genus *Oxybelis*.

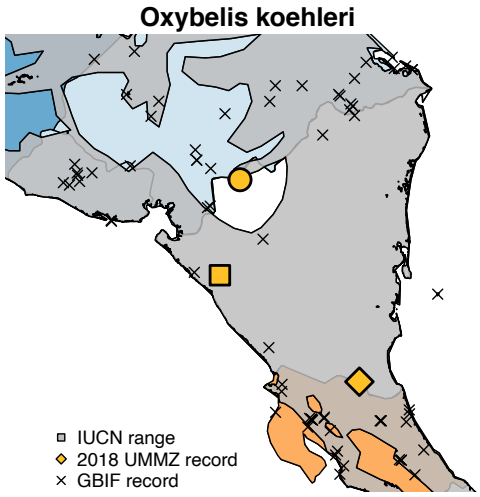
Oxybelis fulgidus known from Mexico (Isthmus of Tehuantepec) to Argentina, sea level to 1000 m, from a range of habitats including savanna, dry forest and wet forest. This species is distinguished from others in the genus by its uniform bright green dorsal coloration and yellow-brown ventral coloration (Savage 2002, McCranie 2011). We collected one specimen, RAB3079 with SVL 278 mm, at Asososca lake resting on a vine in upland dry forest.





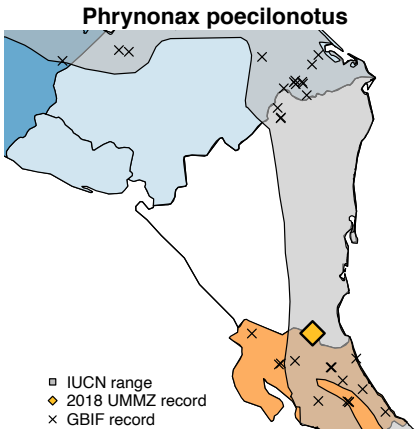
Oxybelis koehleri known from Guatemala to Costa Rica, from sea level to 1500 m in savanna, dry forest and wet forest. In Central America this species is distinguished from congeners by a brown or grey head, body and tail with small dark flecks (sometimes reddish), and 8-9 supralabials (scales on upper lip) (Savage 2002, McCranie 2011). We collected five specimens of *Oxybelis aeneus*, with individuals from each of our study sites. At Mogotón, we caught a single individual, RAB3056, a juvenile with an SVL of 355 mm. It was found near the riparian area in mixed pine forest. We caught two individuals at Asososca lake in upland dry forest, RAB3101, an adult male with SVL 725 mm, and RAB3012, an adult female with SVL 865 mm. Both were found at rest in tree branches. We caught two specimens at Bartola, both at rest on tree branches

in upland forest. RAB3189 was an adult male with SVL of 747 mm. RAB3143 was an adult female with SVL of 710 mm.



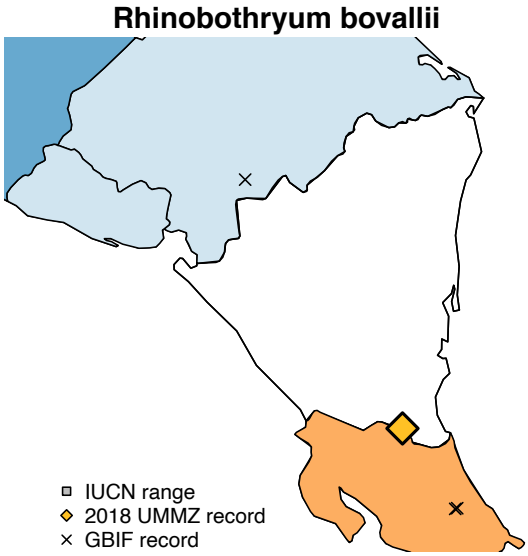


Phrynonax poecilonotus commonly found on the forest floor or on shrubs or trees in old growth rain forest. When threatened, the snake will inflate the anterior portion of the body in a characteristic threat display. *Phrynonax poecilonotus* is known from San Luis Potosi and Oaxaca, Mexico all the way to Brazil up to 1000 m. Its coloration is highly variable both between individuals and within individuals between the juvenile and adult stages. It can be distinguished by dorsal scales arranged in 21 to 25 oblique rows, with the scale rows near the spine keeled (scales have a raised ridge running along the long axis of the scale). It has a single anal scale (the scale anterior of the vent), single loreal, and eyes separated by at least two scales from the nasal scale (a preocular scale is present) (Savage 2002, McCranie 2011). This species has less than 155 ventral scales, and fewer than 85 subcaudals with the naris laterally placed (McCranie 2011). This species is diurnal and feeds mostly on birds, their eggs, and other arboreal mammals. We collected a single individual, RAB3207, at Bartola. The animal was an adult male with an SVL of 1150 mm. It was found at rest in a patch of sun on the ground, between rain showers.



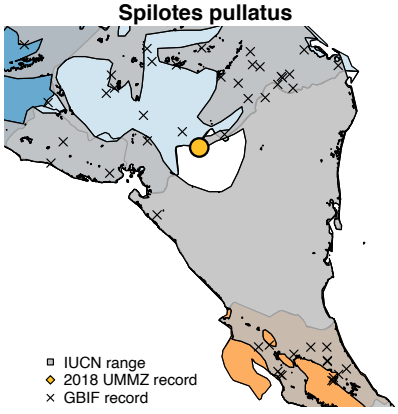


Rhinobothryum bovallii known as the "false tree coral." It is aptly named, as this snake displays red, white and black banding and is considered a mimic of the venomous coral snakes *Micrurus nigrocinctus* and *Micrurus alleni*. It is unique among coral snake mimics in having black head scales ringed in white (Savage 2002). The naris in this species is very large (McCranie 2011). This snake is rarely encountered in its habitat of lowland broadleaf rainforest, to the extent that it is unclear whether this species is mostly arboreal or terrestrial. This species is known from Honduras to Colombia, Venezuela, and Ecuador. We collected a single specimen at Bartola, RAB3018, which constitutes the first country record of this species in Nicaragua (Martínez-Fonseca et al. 2019). The specimen is an adult male with SVL 944 mm. Distinguishing characters include: broad and distinct head with upper enlarged shields black with pale edges; 238 ventral scales, 114 paired subcaudals.





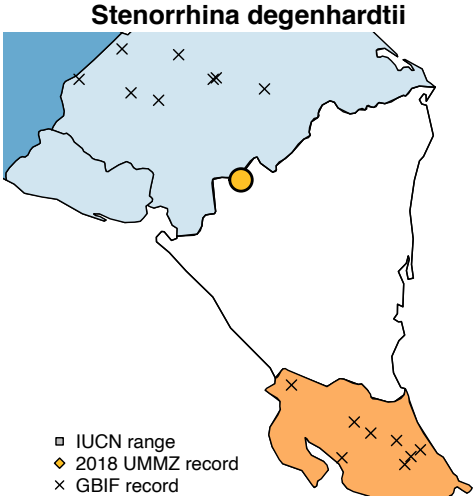
Spilotes pullatus known by Spanish name, "voladora," which means "flying one," and is an accurate representation of this species' arboreal nature and agility through vegetation. This species is the sole representative of the genus, and can be found from Mexico (Oaxaca, Tamaulipas) to Argentina from sea level to 1500 m. It is known from rain forest, wet forest and





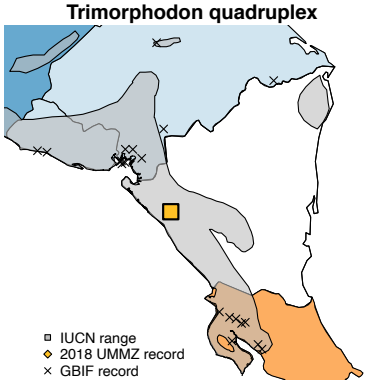
dry forest. It has striking yellow and black diagonal banding, with 14 to 18 keeled scale rows (scales have a raised ridge running from the head toward the tail) (Savage 2002). We caught a single individual of *Spilotes pullatus* in a mix of arid and dry forest and agricultural fields at Las Brisas de Mogotón: the animal, RAB3057, was located in a large tree, approximately 10 m high. With an SVL of 1670 mm, the specimen was a large male.

Stenorrhina degenhardtii a nocturnal and terrestrial species. It is known from southern Veracruz, Mexico to Ecuador and Venezuela, at elevations up to1650 m. It is found in both wet and dry forest. It is a small, robust snake with blotched ventral scales and a variable dorsal pattern. It can be identified by its upturned snout with an enlarged rostral scale (at the tip of the nose above the mouth and between the two nasal scales). The scales immediately behind the rostral but in front of the nostrils are fused into a single unit (Savage 2002). We caught a single individual, RAB3037, at Las Brisas de Mogotón in pine forest. It had an SVL of 226 mm. The snake was found moving across bare soil.





Trimorphodon quadruplex known as lyre snakes, the species is distributed across dry regions of southern Guatemala through northwestern Costa Rica. Members of the genus *Trimorphodon* have a distinctive dark arch or chevron on the back of the head, pointing toward the nose and continuing down behind the jaw line. *Trimorphodon quadruplex* can be identified by the light



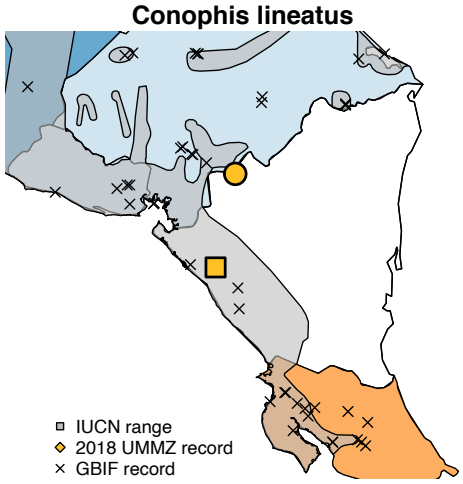


patches contained within the dark blotches along their dorsal surface, which make an irregular 'bullseye' pattern (Devitt et al. 2008). We collected two individuals of *T. quadruplex* at Asososca lake in lowland dry forest. RAB3085 was an adult female with an SVL of 842 mm; it was found in motion on a vine. RAB3078 was also an adult female with SVL 865 mm. It was also found moving along a woody vine.

Family Dipsadidae

The Dipsadines are a major South American radiation of rear-fanged snakes. The group contains around 700 species distributed across the western hemisphere (Vidal et al. 2010; Grazziotin et al. 2012). The taxonomy of the group remains an area of considerable research. The group contains species with a variety of ecological niches, including arboreal, terrestrial, and fossorial snakes, as well as highly aquatic species. Nicaragua contains 44 species from 26 genera, of which we captured 14 species from 11 genera.

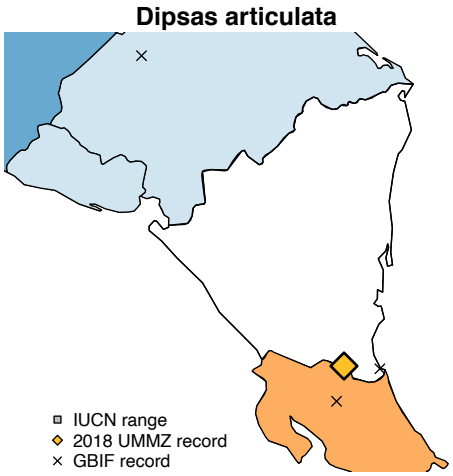
Conophis lineatus a medium-sized, heavy-bodied snake that can be found from Mexico to Costa Rica. It can be identified by its sandy-brown background color with two black lateral stripes running from nose to tail (Savage 2002). The rostral scale is curved upwards posteriorly and is distinctive of this species (McCranie 2011). We found two specimens, one at Las Brisas de Mogotón (RAB3072) and one at Asosoca Lake (RAB3087). We found both on the ground in lowland dry forest during the day. RAB3072 measured 631 mm with a 195 mm tail, while RAB3087 measured 602 mm with a 132 mm tail.





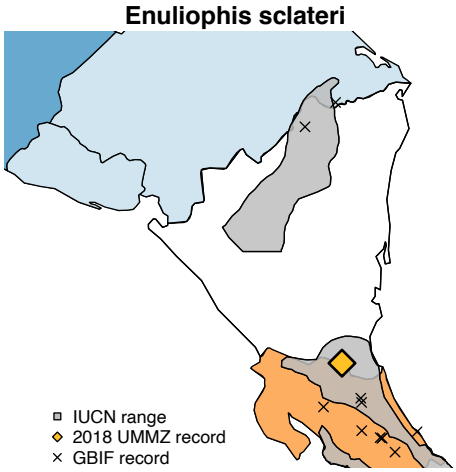
Dipsas articulata a small, arboreal snake that ranging from Nicaragua to Panama up to 700 m. It has large eyes, with thick black bands alternating with white to light tan bands (Savage 2002). A distinctive marks of this species is with the anterior chinshield (scale underneath chin) single and nearly rectangular (McCranie 2011). We found two specimens at Bartola, RAB3214 and RAB3240, both at night in upland forest near the banks of the Río Bartola. RAB3214 was moving through tall grasses at about one meter above the ground, while RAB3240 was moving

across a leaf at two meters above the ground. RAB3214 had an SVL of 299 mm and a tail measuring 125 mm, while RAB3240 had an SVL of 384 mm and a tail measuring 156 mm.



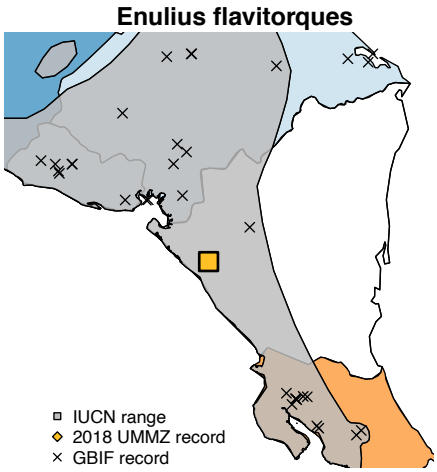


Enuliophis sclateri a small snake that occurs from northeastern Honduras to Colombia. Its coloration and size is similar to *Enulius flavitorques*, but the species can be distinguished by a white neck saddle that touches the eyes, the blunt snout, and 15 dorsal scale rows (Savage 2002). This species has less than 151 ventral scales and a pair of apical pits in most dorsal scales (McCranie 2011).We found one specimen at Bartola, RAB3215. We encountered this snake at night, moving on a dead stump at 1.5 m above the ground in upland forest. The snake is generally considered fossorial, so finding it above ground was unexpected (McCranie 2004). However, the closely-related *Enulius flavitorques* has been observed climbing trees, likely in pursuit of termites or arboreal lizard eggs (Brown et al. 2018). The specimen had an SVL of 177 mm and a tail of 122 mm.



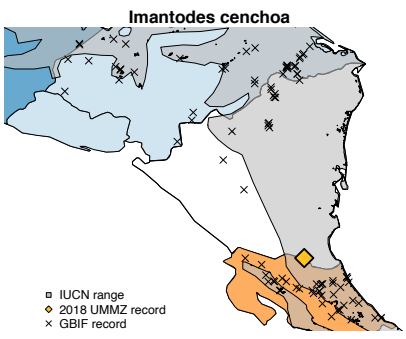


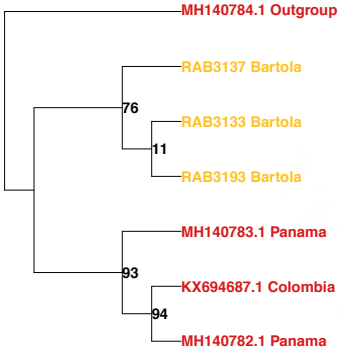
Enulius flavitorques a small, thin, fossorial snake that occurs from southern Mexico into Colombia and Venezuela. It can be identified by its black background color with a white saddle across the back of its neck behind its eyes, its shovel-shaped snout, and 17 dorsal scale rows (Savage 2002). Males of this species have more than 165 ventral scales and females more than 180 (McCranie 2011). We found two specimens, RAB3093 and RAB3112, on the ground at night in lowland dry forest near the shoreline of Asososca lake. RAB3093 was found by flipping a rock. RAB3093 had an SVL of 262 mm and a tail of 54 mm, while RAB3112 had an SVL of 186 mm and a tail of 78 mm.





Imantodes cenchoa an arboreal snake that can be distinguished by its long, thin neck, large head with protruding eyes, and light brown background color with darker saddles. It can be distinguished from all congeners in Nicaragua by the enlarged scale row along its spine three to four times the size of the adjacent dorsal scales (Savage 2002, McCranie 2011). The species is very widely dispersed, ranging from Mexico to Argentina. We sampled three *Imantodes cenchoa* in Bartola, RAB3133, RAB3137, and RAB3193. SVLs for these individuals were 658 mm, 526 mm, and 254 mm, respectively. We found specimens moving across woody or herbaceous branches at night in upland forest or the riparian zone, between 0.3 and 3 meters above the ground. Our 16S tree groups the Panamanian and South American snakes into one group, with the Bartola samples as a separate clade.

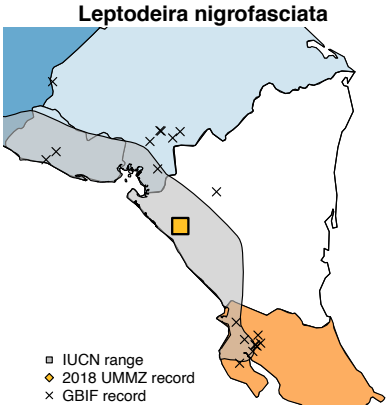






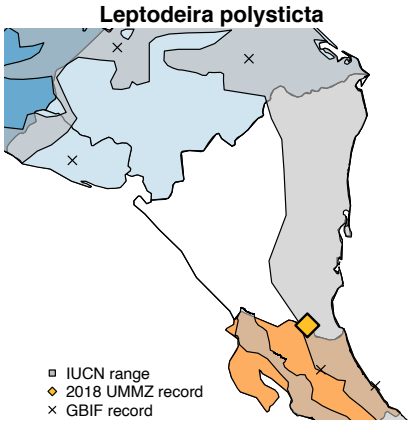
Genus *Leptodeira* is a widespread and abundant genus of arboreal snakes that range from Texas to Argentina. They can be identified by their divided nasal, anal, and subcaudal (underside of tail) scales, the presence of a loreal scale (a scale that falls between the scales touching the nostrils and the scales touching the eyes), and large eyes with an elliptical pupil. Considerable taxonomic uncertainty occurs within this genus (Daza et al. 2009; Barrio-Amorós 2019), with several recognized, wide-ranging species possibly being polyphyletic.

Leptodeira nigrofasciata a black and white banded snake that ranges from Mexico to Costa Rica. It is the only member of the genus in Nicaragua with this color pattern (Savage 2002). We found two specimens in Lowland Dry Forest near the shores of Asososca lake, RAB3080 and RAB3110. RAB3080 was a juvenile with an SVL of 174 mm and a 48 mm tail, while RAB3110 was a larger individual with an SVL of 321 mm and a tail of 78 mm. We found the juvenile snake climbing a tree.





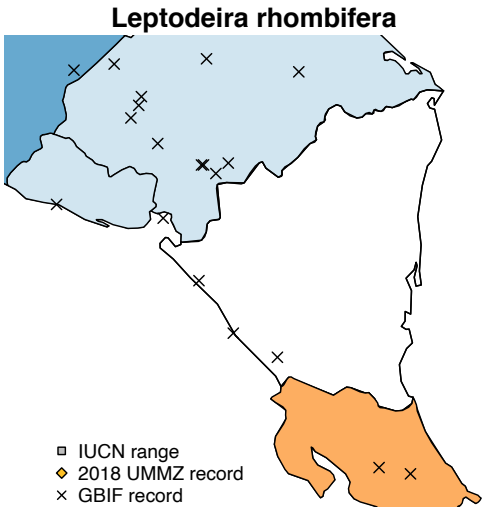
Leptodeira polysticta a wide-ranging species complex that occurs from Texas to Peru. In Nicaragua, the taxon was formerly known as *Leptodeira septentrionalis* (Daza et al. 2009; Barrio-Amorós 2019). They can be identified among similar-looking brown snakes with dark blotches by the lack of pattern on the ventral surface and separation between markings on the neck and the first dark blotch (Savage 2002; Barrio-Amorós 2019). We found three specimens, RAB3176, RAB3227, and RAB3232, all encountered at Bartola at night. RAB3176 was a gravid





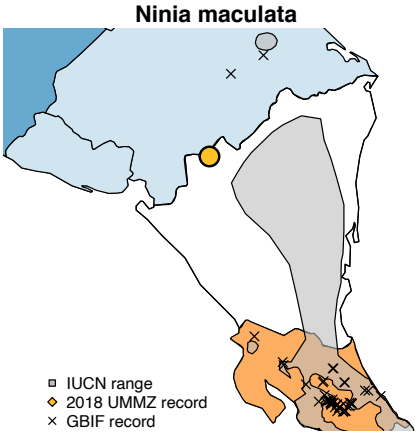
adult female with an SVL of 654 mm and tail of 179 mm. RAB3232 was also an adult, with an SVL of 574 mm and tail of 161 mm, found at rest on a palm frond. RAB3227 was a juvenile, with SVL of 158 mm and tail of 49 mm, found moving across a branch at 1.2 m above the ground near the river bank

Leptodeira rhombifera a taxon that may be synonymous with *Leptodeira annulata,* ranges from Guatemala to Panama. It forms a monophyletic clade within the paraphyletic *Leptodeira septentrionalis* (Daza et al. 2009; Barrio-Amorós 2019). It can be identified in the field by markings on the nape of the neck that connect to the dark blotching along the dorsal surface (Savage 2002; Barrio-Amorós 2019). We found one specimen, RAB3241, crossing a road in Tecompa, near the Pacific Ocean in the municipality of Jinotepe, in lowland dry forest. The species can be distinguished by its dark brown saddles on a light brown background. RAB3241 had an SVL of 665 mm and a tail of 190 mm.



Genus *Ninia* the coffee snakes are a genus of small, leaf litter dwelling snakes. They can be identified in the field by their keeled scales (scales have a ridge running along the long axis), their chin shields (two long scales running along the lower jaws), and their 17 to 19 scale rows (Savage 2002). As their name suggests, they can reach high abundance in coffee farms and other semi-disturbed habitats.

Ninia maculata a small, cryptic, ground-dwelling snake that occurs from Guatemala to Panama. It has a variable dorsal pattern of black saddles on a dark brown background, with strong black and white banding on the ventral surface (Savage 2002). We found one *Ninia maculata,* RAB3069, coiled between roots in pine litter in a riparian area in a transition zone between premontane moist forest and premontane wet forest at Las Brisas de Mogotón. This individual was found at 1570 m and represents a new altitudinal record for the species in Nicaragua (McCranie et al. 2019). The snake displayed a death feigning response when captured, including

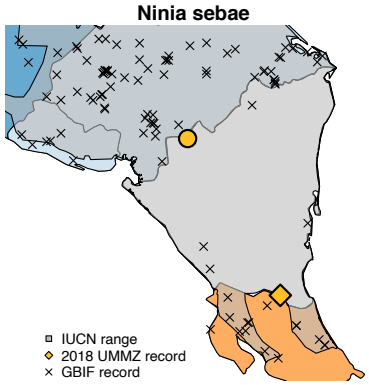




turning over to display its black and white banded ventral surface, then going limp. It had an SVL of 247 mm and a tail length of 65 mm. DNA evidence shows that Guatemalan *N. maculata* may be more closely related to Mexican *Nina pavimentata* than they are to Costa Rican *N. maculata* (Ingrasci 2011). Further sampling in Nicaragua will show whether this division represents monophyletic clades or a geographical cline with isolation by distance.

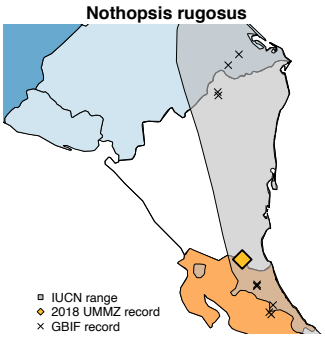
Ninia sebae a small, red-brown snake found from Mexico to Panama. The species has a black cap on the head, while the body shows variable patterns of black and yellow on the red background (Savage 2002). Some individuals have black and yellow banding or 'bull's eyes' along their bodies. We encountered all *Ninia sebae* at night. At Las Brisas de Mogotón, we found them moving across pine needle litter on the sandy bank of a stream in mixed pine forest and on a hillside near a coffee plantation. We also found them sheltering under rotting wood, both in natural pine forest and in shade-grown coffee areas. We collected individuals RAB3022 and RAB3023 at Mogotón, with SVLs of 191 and 232 mm, and tail lengths of 65 and 45 mm. We found one *Ninia sebae,* RAB3178, in Bartola, in upland habitat sheltering under a wooden plank in a clearing, with and SVL of 210 mm with a 70 mm tail.

The phylogeography of *N. sebae* in Central America is not fully resolved (Ingrasci 2011), but some mitochondrial and nuclear gene trees indicate that Mexican lineages of the snake are the most deeply divergent, indicating a north-to-south spread for the species. Further sampling in Nicaragua will help to determine whether a recovered clade of Honduran and Costa Rican snakes represents the true underlying genetic pattern of this species





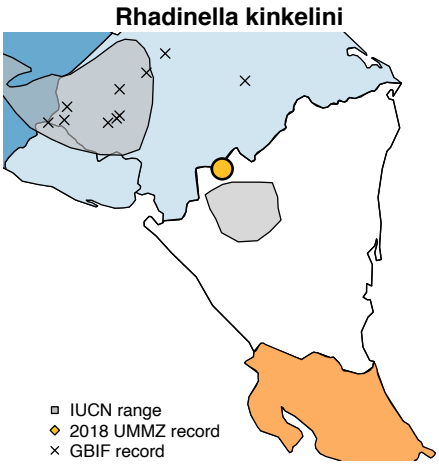
Nothopsis rugosus a rarely-encountered snake occurs from Honduras to Ecuador. It has rough dorsal scales, including irregular-shaped scales on the dorsal portion of the head, that give it an





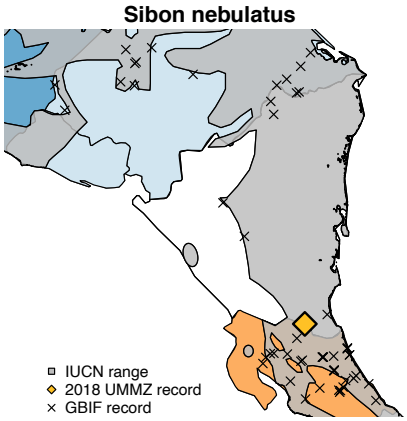
almost ‘beaded’ appearance, with its dorsal pattern composed of diamond-shaped dark blotches on a lighter background (Savage 2002). We found one specimen, RAB3188, at Bartola, moving over leaf litter on a rainy night in upland forest. It had an SVL of 257 mm and tail of 102 mm. This widespread species is distributed across eastern Nicaragua.

Rhadinella kinkelini a small snake that occurs from Mexico to Nicaragua at elevations of 1300 to 1900 m. It is distinguished by a black cap on the head with brown and black lateral stripes along the body, dark-edged supralabial scales (scales above the mouth), and a curving mark on the rostral scale (at the tip of the nose above the mouth) (Savage 2002). We found three specimens at Mogotón, RAB3027, 3035, and 3074, all moving along the ground at night in pine forest near a coffee plantation. They had SVLs of 222 mm, 187 mm, and 173 mm respectively, with tail lengths of 103 mm, 74 mm, and 82 mm.





Sibon nebulatus a wide-ranging arboreal snake that occurs from Mexico to Brazil. It is heavier-bodies than *Imantodes*, with similar bulbous head and eyes. Unlike other species in the same genus, this species has 15 dorsal scales through the body and first pair of infralabials are in





contact posterior to mental (McCranie 2011). It has diffuse black saddles extending onto the ventral surface, surrounded by a white border, on a grey background (Savage 2002). We sampled two *Sibon nebulatus* at Bartola, RAB3135 and 3138. Their SVLs ranged from 305 to 320 mm. We found them at night, moving across vegetation in the understory between 1 and 3 m above the ground. They occurred in upland habitat, and the species was highly abundant throughout Refugio Bartola.

Tretanorhinus nigroluteus a heavy-set, aquatic snake occurs from Mexico to Panama, and has successfully colonized islands along the Caribbean coast of Central America up to 750 m (Barquero and Arguedas 2019). In Nicaragua is found up to 220 m. It has an orange ventral surface, with a dark brown dorsal surface with small black saddles. As an aquatic snake, it has nostrils on the top of the snout to facilitate breathing while swimming (Savage 2002). We found one specimen, RAB3158, at night resting on submerged wood, under water, near the edge of Río Bartola. It had an SVL of 178 mm and tail of 88 mm. This widespread species is distributed across eastern Nicaragua.

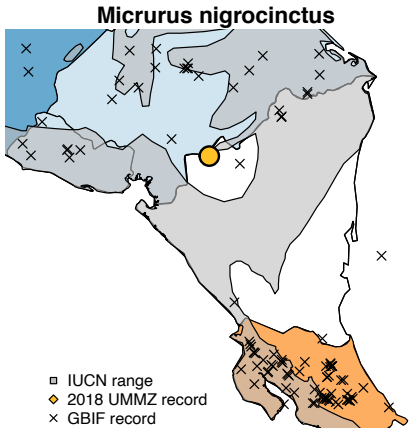


Family Elapidae

All new world true coral snakes belong to this family. In the Americas most species are of Neotropical range, but several species reach the subtropical regions of the southern United States. Most species are fossorial while some are semi-aquatic or associated with moist substrates. The family is venomous, with neurotoxic venoms delivered by short, fixed fangs. We encountered one of the four species of Nicaraguan elapids.

Micrurus nigrocinctus is the most widely distributed coral snake in Nicaragua and Central America and can be found in a variety of habitats up to 1400 m. It can be identified from the syntopic *M. alleni* by black coloration on the head that does not extend far past the eyes (Savage 2002). It ranges from Mexico to Panama. We collected two individuals. The first one was collected from the oak-pine forests of Las Brisas de Mogotón, RAB3053. The animal was an adult female with SVL 651 mm and was actively moving up bank at night in a small creek. The second, RAB3242, was an opportunistic encounter when our team was transiting from Bartola to Managua Airport in from Río Escalante-Chacocente Wildlife Reserve in the LDF at dusk, near

the Pacific coast of the country. The animal, an adult with SVL 651 mm, was crossing a dirt road at night. *Micrurus nigrocinctus moskitensis* is recognized to species level in Costa Rica and other countries but apparently is greatly hybridized with *M. n. nigrocinctus* in Nicaragua south east (Sunyer 2009).

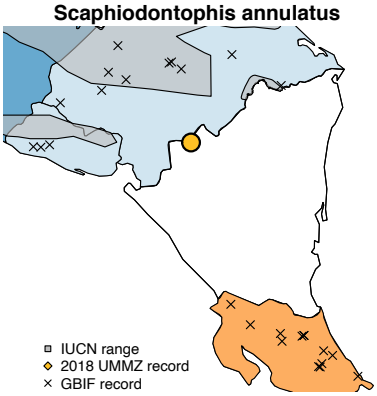




Family Sibynophiidae

This family of rear-fanged snakes is more closely related to the Colubrines than to Dipsidines. It contains two genera: *Scaphiodontophis* in Central America and *Sibynophis* throughout eastern Asia, the Pacific Islands, and the Indian subcontinent (Zaher et al. 2012). Nicaragua has one genus, *Scaphiodontophis*, with two species.

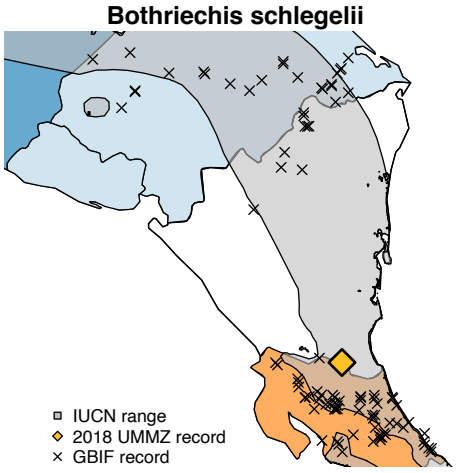
Scaphiodontophis annulatus a highly-variable snake that occurs from Mexico to Costa Rica. It has a background color of uniform brown, with red, yellow, and black triad bands occurring in sections along its length. Most specimens show tricolor banding near the head, and some show intermittent patches of the pattern along their bodies with remainder posterior part of the body showing three dotted lines (Savage 2002, McCranie 2011). We found two specimens at Las Brisas de Mogotón, RAB3019 and RAB3025. They had SVLs of 402 mm and 286 mm respectively, with tails of 227 mm and 232 mm. This species is one of the few snakes that lose their tails when under threat in a manner similar to lizards (Savage and Slowinski 1996), but the tails of the specimens we collected were complete. We located both specimens by digging through fallen pine needles at night near a coffee plantation.





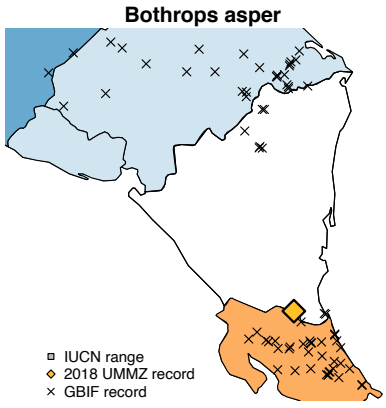
Family Viperidae
This is a family of venomous snakes, known for their large, forward-positioned, retractable fangs. With over 200 species worldwide, this group is diverse: many are familiar with the pit vipers (subfamily Crotalinae), which use heat-sensing pit organs to locate prey. Other subfamilies include Azemiopinae and Viperinae, the "true" or pitless vipers. All vipers have keeled scales and a stocky body with a short tail relative to other groups. Most are ovoviviparous, effectively giving birth to live young. We encountered four species of the ten species of viperid of Nicaragua.

Bothriechis schlegelii, called the eyelash pit-viper, is an emblematic species of the tropical wet forests of Central America with several color phases that can be found in the country. It ranges from Mexico to Colombia. It can be distinguished by the spiky "eyelash" scales above the eyes (Savage 2002). This species is arboreal and feeds on frogs, birds, and other small vertebrates. We captured one individual, RAB3224, in the "mossy green" color phase and was found perching on a branch about one meter above the water in a small tributary of the Río Bartola at dusk. The animal was an adult female with SVL of 445 mm.





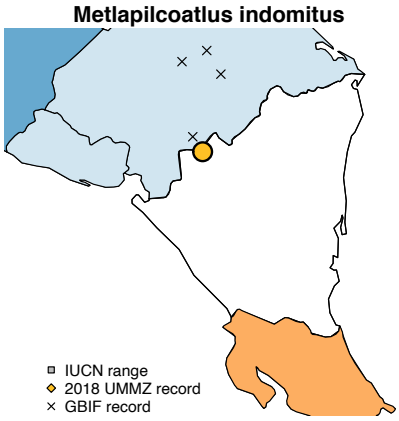
Bothrops asper can be identified by its dorsal pattern of dark triangular blotches with light outlines (Savage 2002). This species has nocturnal and crepuscular habits and reaches a





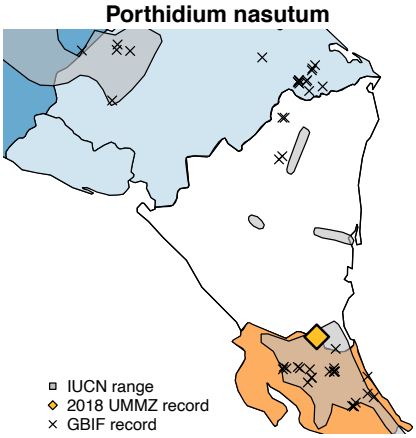
maximum SVL of 2.5 m. It ranges from Mexico to Colombia. It feeds mostly on small-to-medium sized vertebrates. Adults are terrestrial but some young individuals are found climbing in small bushes. The species occurs in both wet and transition zones to dry forest in Nicaragua (Martínez-Fonseca et al. 2016). Recent phylogeographic work groups Nicaraguan animals with Costa Rican animals. However, an extensive sampling gap occurs in Nicaragua. Further sampling of this species across the country will refine our understanding of the phylogeographic patterns of this species (Saldarriaga-Córdoba et al. 2017). We captured two young females in Bartola, RAB3213 and 3233, with SVL of 389 mm and 685 mm respectively.

Metlapilcoatlus indomitus generally found in remote areas with extensive primary growth. Juveniles prey on insects, frogs, and lizards, while adults usually eat small mammals. The species was originally described as endemic of Honduras, but is now known to occur in Nicaragua. It can be distinguished from congeners by its 140 ventral scales, and the dark coloration present on the posterior third of the venter (Smith and Ferrari-Castro 2008). We encountered an adult male, RAB3052, with SVL of 419 mm. It was killed and brought to us by workers of the coffee plantations in Las Brisas del Mogotón. Sunyer et al. (2017) erroneously recorded a photo voucher of this species from Cerro Mogotón, Nueva Segovia department, as *Cerrophidion wilsoni* in lapsus. RAB3052 represents the first official record of *M. indomitus* in the country and a range extension south from the closest specimen in Honduras





Porthidium nasutum a relatively common species from the lowlands of the Caribbean versant from Mexico to northwestern Colombia up to 1200 m. In Nicaragua is found in elevations up to





1200 m. The species is easily recognized by the "proboscis" at the tip of the nose and a usually white or light-colored dorsal line starting at the neck and running along the body and most of the tail (Savage 2002). We collected one individual, RAB3230, in Bartola. The animal was an adult male with SVL 297 mm, moving at ground level in the abundant leaf litter in upland forest at night. Previous genetic work has shown a single Honduran individual of this species 'nested' in Costa Rican specimens (Castoe et al. 2005), potentially indicating a south-to-north expansion history by the species. Sampling in Nicaragua to fill the gap between these specimens will untangle this idiosyncratic phylogeographic pattern.

Conclusions and future research priorities

The 2018 expedition resulted in a number of new departmental records for Nicaragua. From our work at Las Brisas del Mogotón, we recorded two amphibian and sixteen reptile departmental records for Nueva Segovia. The amphibians were the leaf litter frog *Craugastor laevissiums* and the toad *Incilius leutkenii*. The new snake records included the coffee snakes *Ninia maculata* and *Ninia sebae*, the vine snake *Oxybelis koehleri*, the indigo snake *Drymarchon melanurus*, the king snake *Lampropeltis abnorma*, the road guarder *Conophis lineatus*, and two semi-fossorial snakes, *Stenorrhina degenherdtii* and *Rhadinella kinkelini*. New lizard records were the anole lizards *Norops dariense*, *Norops laeviventris*, *Norops quaggulus*, and *Norops mccraniei*, the skink *Scincells cherriei*, the microteiid *Gymnophthalmus speciosus*, and the basilisk lizard *Basiliscus vittatus*. At our Asososca lake site, we recorded four departmental records for León. The records were the vine snake *Oxybelis koehleri*, the lyre snake *Trimorphodon quadruplex*, and the anole lizard *Norops cupreus*, as well as the invasive gecko *Hemidactylus frenatus*. Our Bartola site yielded one departmental record for Río San Juan, the glass frog *Hyalinobatrachium fleischmanni*. In total, the expedition contributed twenty-three departmental records for Nicaragua.

The country of Nicaragua is under-sampled for herpetological diversity relative to other Central American countries. The gap is most apparent in the eastern area of the country, which has historically been less populated and is still difficult to access despite the increasing new settlements in the last decades. The sampling distribution for many species has led to estimates of their total range that include a gap in eastern central Nicaragua. This sampling bias could lead to a systematic underestimate of the total biodiversity of the country. Specifically, a number of the species we discuss above show IUCN range polygons with a gap in lowland eastern Nicaragua, despite their documented occurrence in similar habitats in Honduras and Costa Rica. Range gaps for high-elevation specialists along the Pacific coast of Central America can be explained by relatively low elevation of western Nicaragua, but no such geographic explanation fits eastern Nicaragua. Instead, we hypothesize that the gaps most likely reflect an artefact in the range-polygon algorithm due to low sampling intensity in this area of the country. Species showing this pattern include the frogs *Incilius coniferus*, *Teratohyla pulverata*, *Cochranella granulosa*, *Sachatamia albomaculata*, *Craugastor laevissimus*, *Smilisca sordida*, and *Pristimantis cerasinus*. The snakes *Enuliophis sclateri* and *Porthidium nasutum* are also candidates for this pattern. In addition to the IUCN polygons, widely-used occurrence-only databases such as GBIF have lower sampling density in eastern Nicaragua. Biogeographic and ecological hypotheses based on this uneven data distribution could be vulnerable to biased outcomes similar to those illustrated in the IUCN range polygons.

Our 16S gene trees show a variety of potential categories biogeographic patterns repeated across Nicaraguan taxa. We stress that our low sample size per species and the use of a single gene means that the patterns we discuss should be treated with skepticism and considered only as a source of ideas for future work. We found five repeated patterns in the gene trees. The first involved three species from southern Nicaragua, the frogs *Rhaebo haematitcus*, *Diasporus diastema*, and *Smilisca phaeota*. The sequences from Nicaragua branched earlier with respect to sequences from Costa Rica and Panama, consistent with a biogeographic pattern in which the species expanded south from Nicaragua toward Panama and South America. Three more frog species, *Craugastor bransfordii*, *Lithobates warszewitschii*, and *Pristimantis cerasinus* show a reverse pattern, in which the gene trees show a pattern consistent with migration north from Panama toward Nicaragua. Two frogs, *Craugastor lauraster* and *Lithobates maculatus*, and the lizard *Holcosus undulatus,* and show gene tree patterns consistent with migration down to Nicaragua from ancestral populations further north in Central America.

Perhaps the most intriguing patterns are from species sampled from our most southerly site that group with conspecifics in Honduras or farther north, rather than more geographically adjacent samples from Costa Rica. The frogs *Incilius valliceps* and *Pristimantis ridens* and the lizard *Lepidophyma flavimaculatum* show this tree topology. These phylogeographic patterns may reflect reduced migration across the Nicaraguan depression. Such patterns could be relicts from the period prior to the meeting of the tectonic plates under Nicaragua and Costa Rica in the Pliocene, or from Pleistocene inundations of the area with salt water. Further sampling is necessary to understand which taxa show the 'Nicaraguan depression' phylogeographic pattern. The sparse sampling of reptile and amphibian taxa across Nicaragua is a problem for region-wide phylogeography and species delimitation. Without sampling in Nicaragua, studies that find genetic differentiation between Costa Rican and Honduran populations of a species cannot differentiate between a sharp genetic break between their samples or a gradual gradation in genetic differentiation (citations?). Sampling in Nicaragua, especially the under-sampled Caribbean region of the country, is critical to understanding the ecology and evolution not only of reptile and amphibian but also other taxa like mammals and plant species across Central America (Stevens 2001, Reid 2009, Martínez-Fonseca et al. 2020).

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