



ANNOTATED LIST OF SPECIES

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Amphibians (Amphibia, Anura and Caudata) and reptiles (Reptilia, Squamata) from the headwaters of Río Guázaro on the Caribbean versant of Veraguas province, western Panama

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Abstract

We present a list of amphibian and reptile species encountered from 16–20 July 2016 in the upper drainage of Río Guázaro, Parque Nacional Santa Fé, Veraguas, Panama. We collected 10 amphibian and 10 reptile species and observed three additional amphibian and one additional reptile species. Our collected material provides the first records from Veraguas province for the amphibians *Bolitoglossa schizodactyla* Wake & Brame, 1966 and *Diasporus* aff. *quidditus* (Lynch, 2001), as well as for the reptiles *Basiliscus plumifrons* Cope, 1876, *Micrurus stewarti* Barbour & Amaral, 1928, and *Sibon argus* (Cope, 1876). Although relatively small in species and specimen numbers, our collection represents the first documented herpetological inventory on the largely unexplored Caribbean versant of Veraguas in 50 years.

Keywords

Biodiversity, Cocuyos de Veraguas, Cordillera Central, frogs, inventory, lizards, salamanders, snakes

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Introduction

Despite its small size, the Republic of Panama, as part of the Lower Central American biodiversity hotspot (Myers et al. 2000), exhibits high numbers and densities of amphibian and reptile species (Jaramillo et al. 2010; Wilson and Johnson 2010; Lotzkat 2014; Hertz 2015; Batista 2016). To date, 229 amphibian (Hertz 2015; Batista 2016; Batista et al. 2016a; Arias et al. 2016, 2018, 2019; Gray

2018; Hill et al. 2018; Elizondo-Lara 2021) and 274 reptile (Lotzkat 2014; Batista et al. 2015, 2016b, 2019, 2020; Lotzkat et al. 2016; Batista and Wilson 2017; Poe and Ryan 2017; Lotzkat unpubl. data) species have been documented to occur in Panama. Historically, herpetological research in Panama has been unevenly distributed geographically, with most faunistic studies concentrated

in central Panama (Ibáñez et al. 2001). However, during this millennium an increasing amount of fieldwork has been performed both in the western and eastern portions of the country (e.g., Lotzkat 2014; Hertz 2015; Batista 2016).

Bordered to the west by the Comarca Ngöbe-Buglé and Chiriquí province, and to the east by the provinces of Colón, Coclé, Herrera, and Los Santos, Veraguas (Fig. 1) is the second largest Panamanian province (IGNTG 2008) and the only one that has both Caribbean and Pacific shorelines. In its northern half, it is traversed by western Panama's Cordillera Central, that is, the easternmost portion of the Talamancan or Lower Central American highlands sensu Savage (2002). Within Veraguas this mountain range is composed of five principal massifs, attaining elevations well above 1400 m a.s.l., separated by interjacent saddles as low as approximately 700 m a.s.l. This mountain range forms the continental divide along all of its roughly east-west course through the province. Well above 80% of the province's continental land area lies to the south of this crest and accordingly drains to the Pacific Ocean. While these areas are largely subject to strong anthropogenic impacts, the Caribbean versant of extreme northern Veraguas, which is wholly within the district of Santa Fé, has retained much of its original forest cover and only recently has seen the construction of a single paved road leading from Santa Fé along the western provincial border to Calovébora on the Caribbean coast.

While the Pacific drainage of Veraguas has received some herpetological attention at least since the beginning of the 1990s, especially in terms of local and regional faunistic inventories being compiled and more or less accessibly published (e.g., Martínez and Rodríguez 1994, 2005; Martínez et al. 1995; de la Riva 1997; Pérez-Santos and Martínez 1997; Martínez 1999; Martínez et al. 1999, Carrizo 2000, 2010; ANAM 2005; Stadler 2010), the Caribbean North has apparently only experienced two noteworthy episodes of herpetological collecting to date. The first took place in the early second half of the 19th century around Cocuyos de Veraguas (alternatively [mis-]spelled Cocuyas, Cucuyas, or Cucuyos), a long-abandoned gold mine near the Río Concepción at approximately 08°45′N, 081°00′W (Myers 1974; locality 1 in Fig. 1). Here, R.W. Mitchell collected a number of specimens which he sent to the Academy of Natural Sciences of Philadelphia, where Edward Drinker Cope subsequently described five reptile species explicitly from Cocuyos (Cope 1860: Tantilla reticulata; Cope 1861a: Amastridium veliferum; Cope 1861b: Leptophis

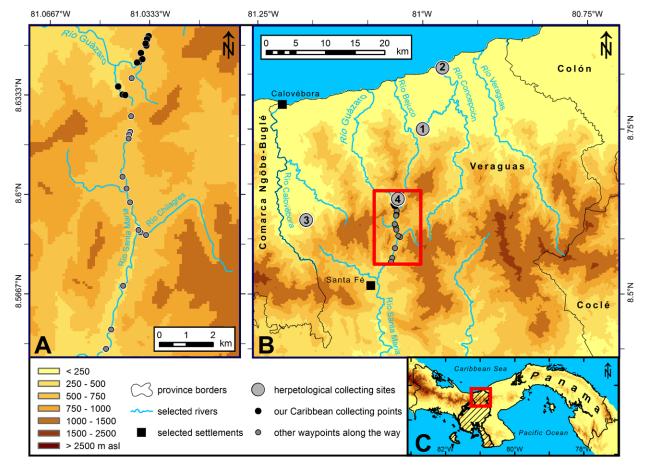


Figure 1. Map of our collecting sites in northern Veraguas province of western Panama. **A.** Detail map of the study area and our access route. **B.** Map of northern Veraguas province. The provenances of herpetofaunal collections mentioned in the text are numbered as follows: 1 = Cocuyos de Veraguas (Cope 1860, 1861a, 1861b, 1861c, 1862b, 1868); 2 = mouth of Río Concepción (Myers 1971); 3 = Alto Ortiga: Los Olivos (Flores et al. 2018a, 2018b); 4 = this study: headwaters of Río Guázaro (detailed in A). **C.** Overview map of Panama. The hatched area shows the total extent of Veraguas province.

depressirostris and Oxybelis brevirostris; Cope 1861c: Norops lionotus). Given that their respective types were collected by the same R.W. Mitchell in "Veraguas", Peters (1960) and Lotzkat (2014) concluded that Cocuyos can also confidently be assumed as the type locality of four additional reptile species described by Cope (1860: Rhadinaea vermiculaticeps; Cope 1861c: Norops lemurinus; Cope 1862b: N. limifrons; Cope 1868: Dipsas articulata).

Almost a century after Cope's last description of a reptile species from Cocuyos, the second episode of noteworthy herpetological collecting in Caribbean Veraguas occurred when Charles W. Myers spent three days near the mouth of the Río Concepción (Myers 1971; locality 2 in Fig. 1). Here, he secured the holotype of Norops procellaris (Myers, 1971), presently considered a junior synonym of Norops carpenteri (Echelle, Echelle & Fitch, 1971), and encountered six other species of anoles (i.e., Dactyloa frenata, Norops biporcatus, N. humilis, N. lemurinus, N. limifrons, and N. lionotus). Their KU collection numbers suggest that during his stay at the lower Río Concepción, Myers also collected specimens of several snake species (i.e., Chironius grandisquamis, Phrynonax poecilonotus, Sibon annulatus, Xenodon rabdocephalus, and Bothrops asper) that were later examined or referred to by other authors (e.g., Savage and McDiarmid 1992; Pérez-Santos 1999; Cadle and Myers 2003).

Since Myers' visit to the Río Concepción, there are only scattered records of singular collecting efforts in the Caribbean drainage of Veraguas. The Museo de Vertebrados de la Universidad de Panama houses specimens of Atelopus varius (MVUP 106A, B, C, and 107; Tejera and Dupuy 2003), Corytophanes cristatus (MVUP 290), and Norops lemurinus (MVUP 292, catalogued as Anolis tropidogaster but examined and re-identified by SL) collected in 1978 at "Cocuyo", "Cocuyito", and "Minas de Cocuyo" (all of which can be interpreted to refer to Cocuyos), respectively, by E. Durán, and a specimen of Atelopus varius (MVUP 1301) from "Calovébora, Río Luis, El Guabal" collected in 1991 by I. Quezada. Very recently, Flores et al. (2018a) provided a photo voucher (UTADC 8721) for a Sphaerodactylus lineolatus which E. E. Flores encountered in 2016 at Alto Ortiga, Los Olivos (locality 3 in Fig. 1) and which the same authors later re-identified as S. homolepis (Flores et al. 2018b).

In July 2016, three of us (GW, MH, and SL) set out from Santa Fé to cross the continental divide to the Caribbean versant of Veraguas, originally with the intention to collect topotypical material of several Copeian reptile species at Cocuyos. After realizing that we would be unable to reach this locality and safely return within the timeframe we had allotted to this venture, we decided to establish a camp (locality 4 in Fig. 1) next to the banks of Río Guázaro, about 12 km in a straight line from the approximate coordinates provided for Cocuyos by Myers (1971). There we concentrated on collecting specimens. In the present paper, we report on the results of

our fieldwork in the vicinity of Río Guázaro and provide the first published herpetofaunal inventory exceeding 10 species for a locality in Caribbean Veraguas.

Study Area

Due to considerable delays around Santa Fé, we reached the end of the dirt road at Piragual on the Río Santa María (08.5482°N, 081.0480°W; southernmost waypoint in the detail map in Fig. 1A) by car in the late afternoon of 15 July 2016. Following the trail frequented by local people as the traditional route to the Caribbean, we soon crossed the Río Santa María (at 08.5547°N, 081.0462°W) and continued upstream along its eastern banks until reaching the rancho (i.e., a shelter: in this case, a well-built palm-thatched roof supported by sturdy wooden posts) known as "Chilagres" at the junction of the Río Chilagres and Río Santa María (08.5872°N, 081.0363°W), where we spent the first night. On 16 July, we crossed the Santa María again just below the mouth of the Río Chilagres to continue along the trail towards the Caribbean. This trail crosses the main course of the Río Santa María three more times: first at 08.5973°N, 081.0399°W, and second at 08.6020°N, 081.0411°W, near a place called "tres bocas" because two rivers empty into the Río Santa María very close to each other. Near tres bocas, two trails leading to Cocuyos diverge: "El de Arriba" (i.e., the upper one) leading along higher mountain crests and allegedly without good water supply goes to the right, whereas "El de Abajo" (i.e., the lower one) leading through valleys with abundant water supply, follows the Río Santa María to the left. For obvious reasons, we chose El de Abajo. After crossing the Santa María's main course for the fourth time after the Chilagres rancho at 08.6060°N, 081.0424°W, the trail leaves the steepening banks of the river before descending again to one of its principal tributaries some 1.4 km in a straight line north at 08.6187°N, 081.0404°W. After crossing this tributary three times within approximately 260 m in a straight line and passing a provisional palm-thatched shelter, El de Abajo very steeply ascends the continental divide which it reaches at 08.6262°N, 081.0395°W and 760 m a.s.l. and then abruptly plunges down the Caribbean slopes. Descending these, heavy rainfalls and nightfall made us seek shelter in a rather luxurious rancho (a wooden hut completely made of planks, in a small clearing at 08.6361°N, 081.0439°W; Fig. 2A) that was indicated to us by two indigenous men travelling the trail the opposite direction. Fortunately, we met these travellers at a trail bifurcation (08.6333°N, 081.0415°W) where the larger branch, which we would intuitively have considered to continue to Cocuyos, continues straight ahead towards the abovementioned rancho while the real El de Abajo branches off rather inconspicuously to the right. After spending the night at this rancho, we continued on El de Abajo until deciding to set up camp at Río Guázaro, the first large river on the Caribbean versant crossed by El de Abajo at 08.6443°N, 081.0369°W, about



Figure 2. Representative habitats around the headwaters of Río Guázaro. **A.** Clearing with wooden *ranchos* where we collected the *Atelopus varius* specimen MHCH 3199 at daytime. **B.** Río Guázaro just below the crossing of El de Abajo. **C.** Creek in forest just above junction with Río Guázaro at the crossing of El de Abajo. **D.** Section of El de Abajo trail through forest near Río Guázaro.

70 m in a straight line downstream from this crossing. We stayed here from 17–20 July to explore the immediate surroundings (Fig. 2B–D) and the subsequent portion of El de Abajo up to its third crossing of a small stream (08.6531°N, 081.0337°W) approximately 1 km north of the Río Guázaro crossing. We returned to Santa Fé on 20–21 July.

Methods

We performed explorative fieldwork and documented and preserved the specimens following the methodology detailed by Lotzkat (2014). We located all animals by opportunistic searching and caught them by hand or with the aid of a snake hook. We euthanized specimens by a pericardial injection of T61 (Intervet International, Unterschleißheim, Germany). We removed tissue samples to be stored in 98% non-denatured ethanol before injecting a solution of 5-10 mL absolute formalin in 98% ethanol into the body cavity and thighs and finally storing the specimens in 70% ethanol. In the field, coordinates and elevations were recorded using a Garmin GPSMAP 64s. Specimens were collected under scientific permit SE/A-60-16 issued by the Dirección de Áreas Protegidas y Vida Silvestre of the Panamanian Ministerio de Ambiente (MiAmbiente), who also certified the compliance of our strictly scientific and

non-commercial collection and utilization purposes with the Nagoya protocol. All specimens collected by us were deposited in the collections of Museo Herpetológico de Chiriquí (MHCH) in Davíd, Panama, and Senckenberg Forschungsinstitut Frankfurt (SMF) in Frankfurt am Main, Germany. SL further examined specimens in the collection of the Museo de Vertebrados de la Universidad de Panamá (MVUP), and GK examined specimens in the collections of the Museum of Comparative Zoology at Harvard University (MCZ) as well as the Field Museum of Natural History (FMNH). Collection acronyms follow Sabaj Pérez (2016). Specimen identification was carried out via direct comparison to securely identified specimens in the abovementioned collections and consultation of relevant literature (Savage 2002; Köhler 2008, 2011; Lotzkat 2014; and the specific references mentioned in the results section). Amphibian nomenclature follows Frost (2021), reptile nomenclature is adopted from Uetz et al. (2021). All illustrations were enhanced and Figures 2-6 also produced in Adobe Photoshop (Adobe Systems Inc.). The map (Figure 1) was created in ArcGIS 10.3 for Desktop (ESRI Inc.) employing our own waypoints and several datasets of Lotzkat (2014). All coordinates are in WGS 1984 datum, all elevations in meters above sea level and rounded to the nearest 10 m. Distances were measured in DIVA-GIS (https://www.diva-gis.org/) using the datasets of Lotzkat (2014) and the specific references mentioned in the results section.

We deposited our occurrence dataset at the Global Biodiversity Information Facility (Lotzkat et al. 2021; https://doi.org/10.15468/fbq2fj).

Results

We collected 10 amphibian and 10 reptile species and observed individuals of two additional amphibian and one additional reptile species which escaped but could readily be identified to species. MH and GW each briefly saw a caecilian which they could not identify more precisely.

We provide a complete list of all 24 species which we encountered and the 33 specimens we collected in Table 1, and all photographed species are in Figures 3–6.

Our collection includes voucher specimens of two amphibian and three reptile species which have not been reported previously from Veraguas province. We provide the first records from Veraguas province for the amphibians *Bolitoglossa schizodactyla* Wake & Brame, 1966 and *Diasporus* aff. *quidditus* (Lynch, 2001), as well as for the reptiles *Basiliscus plumifrons* Cope, 1876, *Micrurus stewarti* Barbour & Amaral, 1928, and *Sibon argus* (Cope, 1876). For these five species, as well as for those for which we cannot substantiate our identifications with

Table 1. Amphibian and reptile species encountered near the headwaters of Río Guázaro. Museum voucher numbers are given for all collected specimens, approximate coordinates (latitude and longitude in decimal degrees) and elevation (meters above sea level, rounded to the nearest ten) also for the respective uncollected individuals of additional species.

Taxon	Voucher	Latitude	Longitude	Elevation
Class Amphibia				
Order Anura				
Family Bufonidae				
Atelopus varius (Lichtenstein & Martens, 1856)	MHCH 3199	08.6361	-081.0439	460
	SMF 100838	08.6453	-081.0357	500
Rhaebo haematiticus Cope, 1862a	Fig. 3C	08.6333	-081.0415	500
Family Centrolenidae				
Hyalinobatrachium fleischmanni (Boettger, 1893)	MHCH 3232	08.6453	-081.0357	500
	SMF 100868	08.6442	-081.0375	470
Sachatamia albomaculata (Taylor, 1949)	SMF 100902	08.6453	-081.0357	500
Teratohyla pulverata (Peters, 1873)	MHCH 3283	08.6442	-081.0375	470
Teratohyla spinosa (Taylor, 1949)	MHCH 3284	08.6443	-081.0369	470
	SMF 100909	08.6442	-081.0375	470
Family Craugastoridae				
Craugastor crassidigitus (Taylor, 1952)	SMF 100852	08.6442	-081.0375	470
Pristimantis cruentus (Peters, 1873)	MHCH 3265	08.6531	-081.0337	650
	SMF 100894	08.6531	-081.0337	650
	MHCH 3266	08.6531	-081.0337	650
Family Eleutherodactylidae				
Diasporus aff. quidditus (Lynch, 2001)	MHCH 3219	08.6443	-081.0369	470
Family Hylidae				
Agalychnis lemur (Boulenger, 1882)	MHCH 3195	08.6531	-081.0337	650
Family Ranidae				
Lithobates warszewitschii (Schmidt, 1857)	observed	08.6474	-081.0362	590
Order Caudata				
Family Plethodontidae				
Bolitoglossa schizodactyla Wake & Brame, 1966	SMF 100845	08.6531	-081.0337	650
Order Gymnophiona				
Gymnophiona sp.	observed	08.6333	-081.0415	500
	observed	08.6474	-081.0362	590
Class Reptilia				
Order Squamata				
"Sauria"				
Family Corytophanidae				
Basiliscus plumifrons Cope, 1876	MHCH 3203	08.6442	-081.0375	470
	SMF 100843	08.6442	-081.0375	470
Family Dactyloidae				
Norops capito (Peters, 1863)	MHCH 3246	08.6499	-081.0344	600
N. humilis (Peters, 1863)	observed	08.6499	-081.0344	600
N. limifrons (Cope, 1862b)	MHCH 3253	08.6453	-081.0357	500
	MHCH 3254	08.6474	-081.0362	590
	SMF 100883	08.6474	-081.0362	590

axon	Voucher	Latitude	Longitude	Elevation
N. lionotus (Cope, 1861c)	MHCH 3256	08.6453	-081.0357	500
	SMF 100887	08.6453	-081.0357	500
	MHCH 3257	08.6442	-081.0375	470
	SMF 100886	08.6442	-081.0375	470
Family Gymnophthalmidae				
Echinosaura panamensis Barbour, 1924	MHCH 3221	08.6453	-081.0357	500
Serpentes				
Family Dipsadidae				
Imantodes cenchoa (Linnaeus, 1758)	SMF 100870	08.6499	-081.0344	600
Sibon argus (Cope, 1876)	SMF 100904	08.6335	-081.0423	480
Family Elapidae				
Micrurus stewarti Barbour & Amaral, 1928	MHCH 3241	08.6520	-081.0342	630
Family Viperidae				
Bothrops asper (Garman, 1883)	MHCH 3205	08.6453	-081.0357	500
	SMF 100849	08.6442	-081.0375	470
Porthidium nasutum (Bocourt, 1868)	SMF 100893	08.6506	-081.0347	610
	MHCH 3264	08.6520	-081.0342	630

preserved voucher specimens, and for the emblematic harlequin toad *Atelopus varius*, we provide more detailed information in their respective species accounts below.

Atelopus varius (Lichtenstein & Martens, 1856) Figure 3A, B

New records. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Río Luis: Parque Nacional Santa Fé: near El de Abajo trail: clearing with plantain plantation and ranchos; 08.6361°N, 081.0439°W; 460 m elev.; 17.VII.2016; GW, MH, SL leg.; MHCH 3199. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Calovébora: Parque Nacional Santa Fé: tributary flowing into Río Guázaro at crossing of El de Abajo trail; 08.6453°N, 081.0357°W; 500 m elev.; 17.VII.2016; GW, MH, SL leg.; SMF 100838.

Identification. Both individuals are clearly referable to the genus *Atelopus* by their general habitus typical for this genus, including long and slender arms, smooth skin, and the absence of a tympanum. They were further identified as *A. varius* based on the absence of differentiated glandular areas, slightly swollen tips of fingers and toes, and contrasting chocolate brown and yellow coloration (Savage 2002; Köhler 2011).

Remarks. Atelopus varius is a polymorphic species exhibiting considerable variation in color and coloration pattern, including yellow, greenish, orange, or red ground color with black to chocolate brown areas of varying extent (Köhler 2011). The dorsal color patterns of our specimens MHCH 3199 and SMF 100838 more or less resemble the color patterns f and k figured by Savage (2002: 192, fig. 7.19) for Costa Rican A. varius. Both also are more or less similar in color pattern to the lecto- and paralectotypes of A. varius, which are thought to originate from the Pacific versant of Veraguas and to have lacked red markings (Savage 1972; Lötters et al. 1998). Interestingly, our specimens also resemble in their pattern although they differ in color from two adult specimens (SMF 89822 and AH 218) reported by Hertz et al.

(2012) and figured by Köhler (2011: 101: figs. 208, 211) from Cerro Negro, the nearest known exact locality to our collecting sites (ca. 9–10 km SSW on the Pacific versant; Hertz et al. 2012). While the Cerro Negro specimens, which SL has seen and photographed in life, had a bright yellow ground color with pitch black markings and a few conspicuous bright red dorsal blotches, our specimens from the Caribbean versant had a relatively pale-yellow ground color with orange shading only dorsally and on palms and soles (SMF 100838) or ventrally (MHCH 3199), respectively, and chocolate brown instead of black markings dorsally and ventrally.

Rhaebo haematiticus Cope, 1862a

Figure 3C

New record. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Río Luis: Parque Nacional Santa Fé: El de Abajo; 08.6333°N, 081.0415°W; 500 m elev.; 16.VII.2016; GW, MH, SL obs.; around 18:45 while it was actively moving about on the ground during heavy rain; not collected.

Identification. With its comparably smooth skin, large parotoid glands, dark face mask, and absence of cranial crests, *R. haematiticus* has a unique appearance and cannot be confused with any other Panamanian anuran. As evident in Figure 3C, the individual, which managed to escape following photography, is a representative of this species.

Diasporus aff. quidditus (Lynch, 2001)

Figure 4C

New record. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Calovébora: Parque Nacional Santa Fé: eastern banks of Río Guázaro, next to crossing of El de Abajo; 08.6443°N, 081.0369°W; 470 m elev.; 17.VII.2016; GW, MH, SL leg.; MHCH 3219.

Identification. The tiny frog was identified as a member of the genus *Diasporus* by its general habitus, pale markings at the dorsal base of finger and toe discs, absence of



Figure 3. Amphibian specimens from the upper Río Guázaro watershed. **A.** Atelopus varius, MHCH 3199. **B.** Atelopus varius, SMF 100838. **C.** Rhaebo haematiticus, uncollected specimen. **D.** Hyalinobatrachium fleischmanni, male SMF 100868. **E.** Sachatamia albomaculata, SMF 100902. **F.** Teratohyla pulverata, MHCH 3283. **G.** Teratohyla spinosa, MHCH 3284. **H.** Craugastor crassidigitus, SMF 100852.

toe webbing, and fifth toe being longer than third when both are adpressed against the fourth toe. The specimen was identified as *D. quidditus* by its small size, lanceolate to papillate disc covers on the third finger and toe, and prominent lateral fringes along the fingers (Köhler 2011; Hertz et al. 2012; Batista et al. 2016a). This identification was corroborated by direct comparison with males from Cerro Azul, whose identity had been revealed by their very distinctive calls and call positions (see Batista et al. 2016a) and confirmed by Abel Batista.

Distribution. First record from Veraguas province, extending its documented distribution approximately 49 km west from Parque Nacional General de División Omar Torrijos Herrera ("El Copé"), Coclé (MVUP 1832, USNM 572444; Hertz et al. 2012) and more than 130 km from central Panama around the Canal, which has variously been considered the western extreme of the species' distribution (Lynch 2001; Köhler 2011; Batista et al. 2016a).

Remarks. In their revision of *Diasporus* from eastern Panama, Batista et al. (2016a) shared their insights on ecological differences between Colombian and Panamanian populations referred to this species and questioned their conspecificity. Consequently, they referred to the populations from eastern and central Panama as *D*. aff. *quidditus*. Our specimen is clearly conspecific with the populations from Cerro Azul in central Panama, and thus assignable to the taxon referred to as *D*. aff. *quidditus* by Batista et al. (2016a).

Lithobates warszewitschii (Schmidt, 1857)

Figure 4F (uncollected specimen from Río Chilagres)

New record. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Calovébora: Parque Nacional Santa Fé: El de Abajo ca. 350 m N of Río Guázaro; 08.6474°N, 081.0362°W; 590 m elev.; 18.VII.2016; GW, MH, SL obs.; around 17:00 while actively moving about on the ground during heavy rain; not collected.

Identification. Before it escaped, this frog was identified as *Lithobates warszewitschii* due to its relatively smooth skin, pronounced canthal ridge continuing posterior to eye as a dorsolateral glandular ridge, and green mottling on the dorsal surfaces of head and body (Savage 2002; Köhler 2011).

Bolitoglossa schizodactyla Wake & Brame, 1966 Figure 4G, H

New record. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Calovébora: Parque Nacional Santa Fé: El de Abajo next to third creek crossing after Río Guázaro, ca. 1 km N of Río Guázaro; 08.6531°N, 081.0337°W; 650 m elev.; 18.VII.2016; GW, MH, SL leg.; SMF 100845.

Identification. This salamander was readily identified as *B. schizodactyla* owing to its fully webbed hands and feet, unstriped dorsum, and yellow venter with a broad

dark brown midventral stripe (Savage 2002; Köhler 2011).

Distribution. First record from Veraguas province, filling the gap between the records from the Valiente peninsula, Bocas del Toro (113 km WNW; KUMNH-CWM 4259, 4290–4291; Wake and Brame 1966), and El Copé, Coclé, Panama (49 km E; USNM 572791–572794; Hertz et al. 2013).

Gymnophiona sp.

New record. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Río Luis: Parque Nacional Santa Fé: path leaving El de Abajo to the left; 08.6333°N, 081.0415°W; 500 m elev.; 16.VII.2016; MH, obs.; approximately 18:45 while actively moving about on the ground during heavy rain; not collected • Distrito de Santa Fé: Corregimiento de Calovébora: Parque Nacional Santa Fé: El de Abajo ca. 350 m N of Río Guázaro; 08.6474°N, 081.0362°W; 590 m elev.; 18.VII.2016; GW obs.; approximately 17:00 while actively moving about on the ground near the roots of an overturned tree during heavy rain; not collected.

Identification. Unfortunately, both of the bluish caecilians slipped through MH's and GW's hands, respectively, and rapidly disappeared, thus preventing any identification, although both were predominantly blue in colour. So far, 11 named species of caecilians have been reported from Panama (Savage and Wake 2001; Jaramillo et al. 2010; Köhler 2011; Hertz 2015; Batista 2016; AmphibiaWeb 2021; Elizondo-Lara 2021; Frost 2021; STRI 2021). Members of the genus Oscaecilia are very slender and elongate, and are gray in color, which renders them unlikely candidates for our sightings. While only Caecilia volcani Taylor, 1969 and Gymnopis multiplicata Peters, 1874 have previously been reported from Veraguas (Martínez et al. 1999; Young et al 1999; Köhler 2011; Hertz 2015), any of the described Panamanian species of Caecilia, Dermophis, and Gymnopis represent possible candidates because their general appearance matches the recollections of MH and GW, and with the exception of the newly reported C. guntheri (Elizondo-Lara 2021), all are known to occur on the Caribbean versant of Panama. Therefore, the specific and even generic identities of our observed specimens will remain pure conjecture.

Basiliscus plumifrons Cope, 1876

Figure 5A, B

New records. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Calovébora: Parque Nacional Santa Fé: banks of Río Guázaro, ca. 70 m downstream from crossing of El de Abajo trail; 08.6442°N, 081.0375°W; 470 m elev.; 19.VII.2016; GW, MH, SL leg.; adult male SMF 100843, adult female MHCH 3203.

Identification. Recognized as members of the genus *Basiliscus* by the presence of scaly lateral fringes along the outer toes and knob-like keels on the subdigital lamellae. The two adult individuals were identified as *B*.

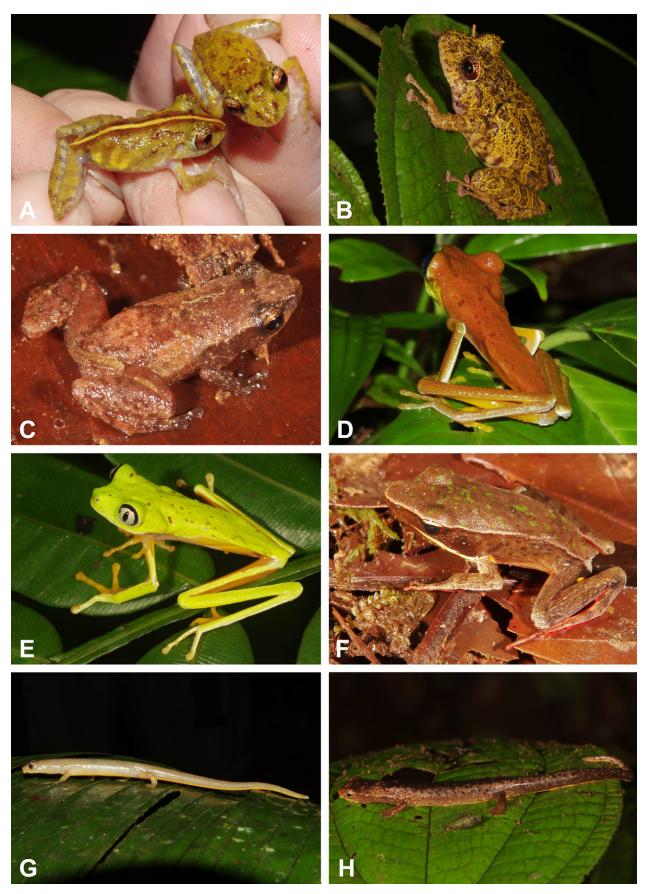


Figure 4. Amphibian specimens from the upper Río Guázaro watershed. **A.** *Pristimantis cruentus*, juveniles MHCH 3265 and SMF 100894 at night just after capture. **B.** *Pristimantis cruentus*, MHCH 3266 at daytime. **C.** *Diasporus* aff. *quidditus*, MHCH 3219. **D.** *Agalychnis lemur*, MHCH 3195 at nighttime. **E.** *Agalychnis lemur*, MHCH 3195 at daytime. **F.** *Lithobates warszewitschii*, uncollected specimen from Río Chilagres. **G.** *Bolitoglossa schizodactyla*, SMF 100845 at nighttime. **H.** *Bolitoglossa schizodactyla*, SMF 100845 at daytime.

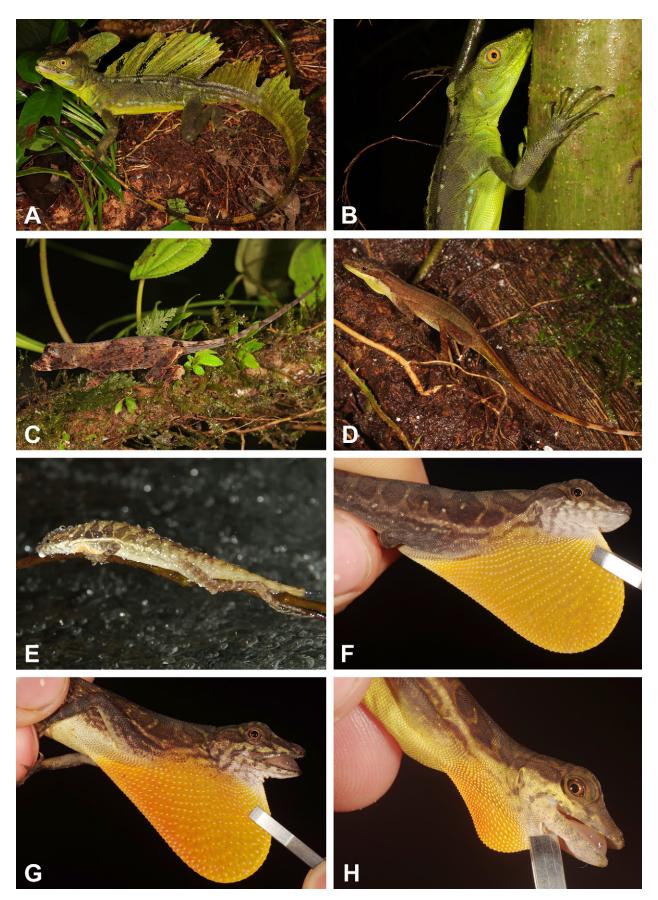


Figure 5. Reptile specimens from the upper Río Guázaro watershed. **A.** *Basiliscus plumifrons*, adult male SMF 100843. **B.** *Basiliscus plumifrons*, adult female MHCH 3203. **C.** *Norops capito*, juvenile MHCH 3246. **D.** *Norops limifrons*, adult female SMF 100883. **E.** *Norops lionotus*, adult male MHCH 3257 in sleeping position a few centimeters above Río Guazaro. **F.** *Norops lionotus*, dewlap of adult male SMF 100886. **H.** *Norops lionotus*, dewlap of adult female SMF 100887.

plumifrons based on their unique appearance of predominantly green coloration and bright yellow eyes, as well as smooth ventrals (vs. keeled in *B. vittatus*) and occipital scales similar in size to the supraoculars and gradually grading to smaller scales posteriorly (vs. larger than the supraoculars and well differentiated from the much smaller posteriorly adjacent scales in *B. basiliscus*) (Savage 2002; Köhler 2008; Lotzkat 2014).

Distribution. These are the first records from Veraguas province, filling the gap between the records from Río Caña de Arriba, Comarca Ngöbe-Buglé (75 km WNW; Batista et al. 2020), and Donoso, Colón (56 km NE; Batista et al. 2020).

Norops humilis (Peters, 1863)

New record. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Calovébora: Parque Nacional Santa Fé: El de Abajo, second creek crossing beyond Río Guázaro, ca. 680 m N of Río Guázaro; 08.6499°N, 081.0344°W; 600 m elev.; 18.VII.2016; GW, MH, SL obs.; not collected.

Identification. Although it escaped, the adult male individual could conclusively be identified as *N. humilis* by its red dewlap with yellow border and 8–12 middorsal rows of greatly enlarged and strongly keeled scales that markedly contrast with the much smaller lateral scales (Savage 2002; Köhler 2008; Lotzkat 2014).

Sibon argus (Cope, 1876)

Figure 6C

New record. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Río Luis: Parque Nacional Santa Fé: creek near El de Abajo; 08.6335°N, 081.0423°W; 480 m elev.; 16.VII.2016; SL leg.; SMF 100904.

Identification. The specimen is clearly assignable to the genus Sibon by 15 longitudinal rows without posterior reduction of smooth dorsal scales lacking apical pits, enlarged penultimate supralabial immediately posterior to the orbit, entire cloacal scute, loreal bordering the orbit, preocular absent, and the presence of a mental groove. Among the members of Sibon known from Panama and Costa Rica, it is readily diagnosable as *S. argus* because it lacks a postmental (vs. present in S. annulatus, S. lamari, and S. perissostichon) and 1st pair of infralabials separated by mental and chin shields (vs. in contact in S. noalamina and S. nebulatus), a blotched to ocellate dorsal color pattern extending only to the edges of the ventrals (vs. a banded pattern extending well onto or even across venter in all aforementioned species), and a very slender habitus with a blunt head and very large, bulging eyes (vs. head not very distinct from neck and eyes moderate and non-protruding in the similar-colored S. longifrenis; Savage 2002; Köhler 2008; Lotzkat et al. 2012; Lotzkat 2014).

Distribution. This is the first record from Veraguas province, filling the gap between the records from

Bosque Protector Palo Seco, Comarca Ngöbe-Buglé (131 km WNW; Hofer and Bersier 2001), and Parque Nacional General de División Omar Torrijos Herrera, Coclé (42 km E; Cadle and Myers 2003; Myers et al. 2007; Ray 2009; CHP 400 according to Lotzkat 2014).

Micrurus stewarti Barbour & Amaral, 1928 Figure 6D, E

New record. PANAMA – Provincia de Veraguas • Distrito de Santa Fé: Corregimiento de Calovébora: Parque Nacional Santa Fé: El de Abajo, ca. 900 m N of Río Guázaro; 08.6520°N, 081.0342°W; 630 m elev.; 18.VII.2016; GW, MH, SL leg.; MHCH 3241.

Identification. The specimen clearly belongs to the genus Micrurus by its cylindrical body and tail, small black eyes within the black head cap, smooth dorsals in 15 longitudinal rows without reduction, divided cloacal scute, loreal absent, upper jaw with two short fangs, and contrasting pattern of black and white rings. It differs from the other bicolored Micrurus known from Lower Central America (M. mipartitus and M. multifasciatus) in having 28 black body rings that are of two different, alternating widths (vs. 34 or more black body rings of similar width in M. mipartitus, 40 or more in M. multifasciatus). Our specimen exhibits the blackand-white morph of M. stewarti which has been regarded as a rare morph in the past (Ibáñez et al. 2003; Campbell and Lamar 2004) but currently is considered typical for the Caribbean versant, while red-and-black individuals are typical on the Pacific versant (Ray 2017). Nevertheless, our identification of MHCH 3241 as M. stewarti is somewhat tentative because although it exhibits other characteristics mentioned for this species in recent literature (Ibáñez et al. 2003; Campbell and Lamar 2004; Köhler 2008; Ray 2017), the specimen differs in certain aspects from the morphological descriptions available for this species. First, its black body rings are not as clearly dimorphic in width as considered typical for this species, in certain body regions it is not obvious whether a given ring should be considered a longer or a shorter one (narrow rings spanning 2.5–8 dorsals vs. 3–8 according to Campbell and Lamar 2004, broad rings spanning 5.5–8 dorsals vs. 8–14 according to Campbell and Lamar 2004). Second, it has more black body and tail rings than reported for this species (28 black body rings and 6 black tail rings vs. 13-25 and 3-5 according to Campbell and Lamar 2004, who gave a maximum of 25 black body rings known for this species in their description of this species on p. 194 but 21 in their comparisons with M. mipartitus and M. multifasciatus on pp. 202 and 203, respectively). Third, the male specimen has more ventrals (213) than the maximum reported for males of this species (207; Campbell and Lamar 2004). Whether our specimen simply exhibits hitherto undocumented extremes in the variability of the color pattern or represents a taxon distinct from M. stewarti remains to be clarified. However, we expect the former to be true, considering that this species is known only from a few specimens

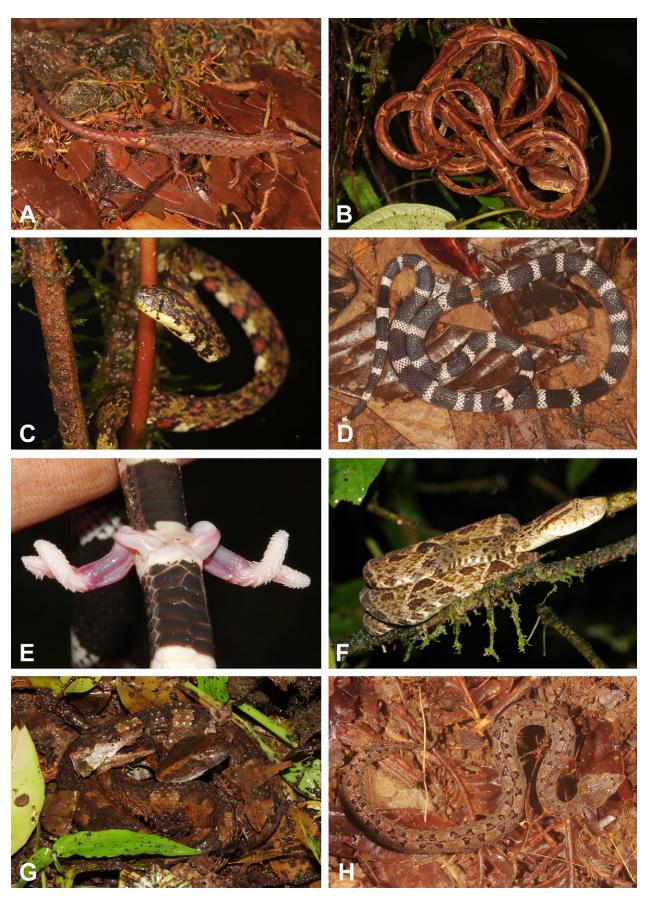


Figure 6. Reptile specimens from the upper Río Guázaro watershed. **A.** *Echinosaura panamensis*, adult female MHCH 3221. **B.** *Imantodes cenchoa*, adult female SMF 100870. **C.** *Sibon argus*, adult female SMF 100904. **D.** *Micrurus stewarti*, adult male MHCH 3241. **E.** *Micrurus stewarti*, hemipenes of adult male MHCH 3241. **F.** *Bothrops asper*, young male SMF 100849 as encountered on branches in the forest understorey. **G.** *Porthidium nasutum*, adult female SMF 100893. **H.** *Porthidium nasutum*, juvenile MHCH 3264.

(Ibáñez et al. 2003; Campbell and Lamar 2004; four vouchers, one photo record, and four literature reports in the occurrence dataset of Lotzkat 2014).

Distribution. First record from Veraguas province, filling the gap between the records from Puerto Armuelles, Chiriquí (207 km WSW; FMNH 35906 examined by GK) and Petaquilla, Río del Medio, Colón (47 km NE; Lotzkat 2014). Ray (2017) stated that *M. stewarti* occurs in Veraguas but neither provided a corresponding point on the species' distribution map nor referred to a specific locality or specimen.

Discussion

Admittedly, our collection is few in species and numbers of specimens when considering that three people spent four nights in the area studied. However, the necessities of fieldwork in remote rainforest areas can considerably decrease the efficiency even of experienced field herpetologists, especially during periods of prolonged and heavy rainfalls such as we experienced.

Despite this, our collection is significant as it represents the first documented herpetological inventory in 50 years on the largely unexplored Caribbean versant of Veraguas. Taking into consideration that Cope (1860, 1861a, 1861b, 1861c, 1862b, 1868) altogether stated nine reptile species to occur at Cocuyos whereas Myers (1971) listed seven anoles from the lower Río Concepción and must have collected at least five snake species in addition, our little list from Río Guázaro is simply the most species-rich herpetofaunal inventory published so far from Caribbean Veraguas.

Among the merely 20 collected species there are five (25%) new records at the province level. Four of these first province records (Bolitoglossa schizodactyla, Basiliscus plumifrons, Sibon argus, and Micrurus stewarti) were expected since these taxa are documented to occur both east and west of Veraguas, whereas the fifth (Diasporus aff. quidditus) represents a significant expansion of the species' documented range limits. Moreover, apart from the five species already mentioned in the introduction to have been reported or even described from northern Veraguas (Atelopus varius, Norops humilis, N. limifrons, N. lionotus, and Bothrops asper), the remaining species which we encountered near Río Guázaro (i.e., Agalychnis lemur, Craugastor crassidigitus, Pristimantis cruentus, Rhaebo haematiticus, Sachatamia albomaculata, Teratohyla pulverata, T. spinosa, Norops capito, Echinosaura panamensis, Imantodes cenchoa, and Porthidium nasutum) are herein reported for the first time from the Caribbean versant of this province.

Although Atelopus varius is the only amphibian species for which we could trace previously collected voucher specimens from Caribbean Veraguas, our records for this emblematic toad are important in times of amphibian declines. The finding of two individuals on the same day indicates a reasonable abundance of this species in our study area. This further supports

the suspicions formulated, among others, by Hertz et al. (2012) and Hertz (2015) that the populations of this species will recover from their disastrous declines in the wake of the chytrid wave.

Climate change is another major threat to biodiversity (IPBES 2019), and it is predicted that the Caribbean side of Mesoamerica will experience a comparably high impact from climate change during the next decades (Anderson et al. 2008). Since biodiversity inventories generate essential baseline data on life forms in space and time (McDiarmid et al. 2012), the local herpetofaunistic findings presented here ultimately contribute to our understanding of biodiversity and its changes within this particularly threatened biodiversity hotspot.

Last, although we did not accomplish our initial mission to visit Cocuyos and left several of the Copeian species described from this legendary type locality uncollected, our specimens of *Norops limifrons* and *N. lionotus* collected at Río Guázaro are currently the "most topotypical" fresh material that exists and will without doubt play an important role in upcoming taxonomic revisions of these nominal taxa.

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Authors' Contributions

Conceptualization: SL, GW, MH. Data curation: SL, GW, MH. Investigation: SL, GW, MH, GK. Resources: GK. Supervision: SL, GK. Validation: SL, GW, MH, GK. Visualization: SL, GW, MH. Writing – original draft: SL, GW, MH. Writing – review and editing: SL, GW, MH, GK.

References

- AmphibiaWeb (2021) University of California, Berkeley. https://amphibiaweb.org. Accessed on: 2021-04-17.
- ANAM (2005) Plan de Manejo del Parque Nacional Cerro Hoya. Panama City, Panama, 102 pp.
- Anderson ER, Cherrington EA, Flores AI, Perez JB, Carrillo R, E. Sempris E (2008) Potential impacts of climate change on biodiversity in Central America, Mexico, and the Dominican Republic. CATHALAC/USAID, Panama City, Panama, 105 pp.
- Arias E, Chaves G, Parra-Olea G (2018) A new species of *Craugastor* (Anura: Craugastoridae) from the montane rainforest of the Cordillera de Talamanca, Costa Rica. Phyllomedusa 17: 211–232. https://doi.org/10.11606/issn.2316-9079.v17i2p211-232
- Arias E, Hertz A, Parra-Olea G (2019) Taxonomic assessment of Craugastor podiciferus (Anura: Craugastoridae) in lower Central America with the description of two new species. Amphibian & Reptile Conservation 13 (1): 173–197.
- Arias E, Chaves G, Crawford AJ, Parra-Olea G (2016) A new species of the *Craugastor podiciferus* species group (Anura: Craugastoridae) from the premontane forest of southwestern Costa Rica. Zootaxa 4132 (3): 347–363. https://doi.org/10.11646/zootaxa.4132.3.3
- Barbour T (1924) Two noteworthy new lizards from Panama. Proceedings of the New England Zoölogical Club: 7–10.
- Barbour T, Amaral A do (1928) A new elapid from western Panama. Bulletin of the Antivenin Institute of America 1: 100.
- Batista A (2016) Taxonomy, diversity, and biography of the herpetofauna of eastern Panama. PhD thesis, Goethe-Universität, Frankfurt am Main, Germany, 308 pp. http://publikationen.ub.unifrankfurt.de/opus4/frontdoor/index/index/docId/41476. Accessed on: 2019-09-03.
- Batista A, Wilson LD (2017) A new record for *Leptophis cupreus* (Cope, 1868) (Squamata: Colubridae) for Panama and Mesoamerica. Mesoamerican Herpetology 4 (3): 671–672.
- Batista A, Mebert K, Lotzkat S, Wilson LD (2016b) A new species of centipede snake of the genus *Tantilla* (Squamata: Colubridae) from an isolated premontane forest in eastern Panama. Mesoamerican Herpetology 3 (4): 949–960.
- Batista A, Hertz A, Ponce M, Lotzkat S (2020) Notes of amphibians and reptiles from western Panama. Herpetology Notes 13: 219–229.
- Batista A, Vesely M, Mebert K, Lotzkat S, Köhler G (2015) A new species of *Dactyloa* from eastern Panama, with comments on other *Dactyloa* species present in the region. Zootaxa 4039 (1): 57–84. https://doi.org/10.11646/zootaxa.4039.1.2
- Batista A, Köhler G, Mebert K, Hertz A, Vesely M (2016a) An integrative approach to reveal speciation and species richness in the genus *Diasporus* (Amphibia: Anura: Eleutherodactylidae) in eastern Panama. Zoological Journal of the Linnean Society 178 (2): 267–311. https://doi.org/10.1111/zoj.12411
- Batista A, Ponce M, Garcés O, Lassiter E, Miranda M (2019) Silent pirates: Anolis sagrei Duméril & Bibron, 1837 (Squamata, Dactyloidae) taking over Panama City, Panama. Check List 15 (3): 455– 459. https://doi.org/10.15560/15.3.455

Bocourt MF (1868) Description de quelques chéloniens nouveaux appartenant à la faune Mexicaine. Annales des Sciences Naturelles, Zoologie et Paléontologie (Série 5) 10: 121–122.

- Boettger O (1893) Ein neuer Laubfrosch aus Costa Rica. Bericht der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main 24: 251–252.
- Boulenger GA (1882) Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum. Second Edition. Taylor & Francis, London, UK, xvi + 256 pp.
- Cadle JE, Myers CW (2003) Systematics of snakes referred to *Dipsas variegata* in Panama and western South America, with revalidation of two species and notes on defensive behaviors in the Dipsadini (Colubridae). American Museum Novitates 3409: 1–47.
- Campbell JA, Lamar WW (2004) The venomous reptiles of the western hemisphere. Cornell University Press, Ithaca, USA, 962 pp.
- Carrizo AR (2000) Estudio de la herpetofauna en la cuenca alta del Río Bermejito en Cerro Negro, Distrito de Santa Fe, Provincia de Veraguas. Tesis de Licenciatura, Universidad de Panamá, Centro Regional Universitario de Veraguas, Santiago, Panama, 69 pp.
- Carrizo AR (2010) Riqueza y abundancia de la herpetofauna de la cuenca alta del Río Santa María, Santa Fe, Veraguas. Master thesis, Universidad Autónoma de Chiriquí, Davíd, Panama, 123 pp.
- Cope ED (1860) Catalogue of the Colubridae in the Museum of the Academy of Natural Sciences of Philadelphia, with notes and descriptions of new species. Part 2. Proceedings of the Academy of Natural Sciences of Philadelphia 12: 241–266.
- Cope ED (1861a "1860") Descriptions of reptiles from tropical America and Asia. Proceedings of the Academy of Natural Sciences of Philadelphia 12: 368–374.
- Cope ED (1861b "1860") Catalogue of the Colubridae in the Museum of the Academy of Natural Sciences of Philadelphia. Part 3. Proceedings of the Academy of Natural Sciences of Philadelphia 12: 553–566.
- Cope ED (1861c) Notes and descriptions of anoles. Proceedings of the Academy of Natural Sciences of Philadelphia 13: 208–215.
- Cope ED (1862a) On some new and little known American Anura. Proceedings of the Academy of Natural Sciences of Philadelphia 14: 151–159.
- Cope ED (1862b) Contributions to Neotropical saurology. Proceedings of the Academy of Natural Sciences of Philadelphia 14: 176–188.
- Cope ED (1868) An examination of the Reptilia and Batrachia obtained by the Orton expedition to Equador and the Upper Amazon, with notes on other species. Proceedings of the Academy of Natural Sciences of Philadelphia 20: 96–140.
- Cope ED (1876 "1875") On the Batrachia and Reptilia of Costa Rica. Journal of the Academy of Natural Sciences of Philadelphia, ser. 2 8: 93–154.
- De la Riva I (1997) Herpetofauna (cocodrilos, tortugas y saurios) del Parque Nacional de Coíba (Panamá)—comentarios sobre su diversidad. In: Castroviejo S (Ed.) Flora y fauna del Parque Nacional de Coiba (Panamá): inventario preliminar. Madrid, Spain, 433–443.
- Echelle AA, Echelle AF, Fitch HS (1971) A new anole from Costa Rica. Herpetologica 27 (3): 354–362.
- Elizondo-Lara LC (2021) First record of *Caecilia guntheri* Dunn, 1942 (Gymnophiona, Caeciliidae) in Central America. Check List 17 (2): 649–653. https://doi.org/10.15560/17.2.649
- Flores EE, Page R, Aparicio D, Bordones E (2018a) Geographic distribution: Sphaerodactylus homolepis. Herpetological Review 49 (1): 74.
- Flores EE, Page R, Aparicio D, Bordones E (2018b) Geographic distribution: *Sphaerodactylus homolepis*: Erratum. Herpetological Review 49 (2): 288.
- Frost DR (2021) Amphibian species of the world 6.1, an online reference. American Museum of Natural History, New York, USA. https://amphibiansoftheworld.amnh.org/. Accessed on: 2021-04-17.
- Garman S (1883) On the reptiles and batrachians of North America.

- Memoirs of the Museum of Comparative Zoölogy at Harvard College 8 (3): 1–180.
- Gray AR (2018) Review of the genus *Cruziohyla* (Anura: Phyllomedusidae), with description of a new species. Zootaxa 4450: 401–426. https://doi.org/10.11646/zootaxa.4450.4.1
- Hertz A (2015) Integrative taxonomy and conservation status of amphibians in western Panama with an emphasis on the highlands of the Cordillera Central. PhD thesis, Goethe-Universität, Frankfurt am Main, Germany, 294 pp. http://publikationen.ub.uni-frankfurt.de/frontdoor/index/index/docId/37778. Accessed on: 2019-09-03.
- Hertz A, Lotzkat S, Köhler G (2013) New distribution records and variation of the two common lowland salamanders *Bolitoglossa* colonnea (Dunn, 1924) and *B. lignicolor* (Peters, 1873) in Panama (Amphibia: Caudata: Plethodontidae). Check List 9 (1): 83– 91. https://doi.org/10.15560/9.1.83
- Hertz A, Lotzkat S, Carrizo Diaz AR, Ponce M, Köhler G, Streit B (2012) Field notes on findings of threatened amphibian species in the central mountain range of western Panama. Amphibian and Reptile Conservation 6 (2): 9–30.
- Hill RL, Martin KG, Stanley E, Mendelson III JR (2018) A taxonomic review of the genus *Hemiphractus* (Anura: Hemiphractidae) in Panama: Description of two new species, resurrection of *Hemiphractus panamensis* (Stejneger, 1917), and discussion of *Hemiphractus fasciatus* Peters, 1862. Zootaxa 4429 (3): 495–512. https://doi.org/10.11646/zootaxa.4429.3.3
- Hofer U, Bersier L-F (2001) Herpetofaunal diversity and abundance in tropical upland forests of Cameroon and Panama. Biotropica 33 (1): 142–152.
- Ibáñez D. R, Solís FA, Jaramillo A. CA (2003) Color variation: Micrurus stewarti. Herpetological Review 34 (4): 376–377.
- Ibáñez D. R, Solís FA, Jaramillo A. CA, Rand AS (2001) An overview of the herpetology of Panama. In: Johnson JD, Webb RG, Flores-Villela OA (Eds.) Mesoamerican herpetology: systematics, zoogeography, and conservation. The University of Texas at El Paso, El Paso, Texas, USA, 159–170.
- IGNTG (Instituto Geográfico Nacional Tommy Guardia) (2008) Atlas Nacional de la República de Panamá 2007. Instituto Geográfico Nacional Tommy Guardia, Panama City, Panama, xii+290 pp.
- IPBES (Intergovernmental Panel on Biodiversity and Ecosystem Services) (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn, Germany, 56 pp.
- Jaramillo A. CA, Wilson LD, Ibáñez D. R, Jaramillo FE (2010) The herpetofauna of Panama: distribution and conservation status. In: Wilson LD, Townsend JH, Johnson JD, Murphy JB (Eds.) Conservation of Mesoamerican amphibians and reptiles. Eagle Mountain Press, Eagle Mountain, Utah, USA, 604–671.
- Köhler G (2008) Reptiles of Central America. Second edition. Herpeton Verlag, Offenbach, Germany, 400 pp.
- Köhler G (2011) Amphibians of Central America. Herpeton Verlag, Offenbach, Germany, 378 pp.
- Lichtenstein H, Martens E von (1856) Nomenclator Reptilium et Amphibiorum Musei Zoologici Berolinensis. Namenverzeichniss der in der zoologischen Sammlung der Königlichen Universität zu Berlin aufgestellten Arten von Reptilien und Amphibien nach ihren Ordnungen, Familien und Gattungen. Berlin, iv + 48 pp.
- Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio Decima, reformata, Tomus I. Lars Salvi, Stockholm, Sweden, 844 pp.
- Lötters S, Böhme W, Günther R (1998) Notes on the type material of the Neotropical harlequin frogs *Atelopus varius* (Lichtenstein & Martens, 1856) and *Atelopus cruciger* (Lichtenstein & Martens, 1856) deposited in the Museum für Naturkunde of Berlin (Anura, Bufonidae). Zoosystematics and Evolution 74 (2): 173–184. https://doi.org/10.1002/mmnz.19980740203
- Lotzkat S (2014) Diversity, taxonomy, and biogeography of the rep-

- tiles inhabiting the highlands of the Cordillera Central (Serranía de Talamanca and Serranía de Tabasará) in western Panama. PhD thesis, Goethe-Universität, Frankfurt am Main, Germany, 930 pp. http://publikationen.ub.uni-frankfurt.de/frontdoor/index/index/docId/37824. Accessed on: 2019-09-03.
- Lotzkat S, Hertz A, Köhler G (2012) A new species of *Sibon* (Squamata: Colubroidea: Dipsadidae) from the Cordillera Central of western Panama, with comments on other species of the genus in this area. Zootaxa 3485: 26–40. https://doi.org/10.11646/zootaxa.3485.1.2
- Lotzkat S, Hertz A, Köhler G (2016) A new species of *Celestus* (Squamata: Anguidae) from western Panama. Mesoamerican Herpetology 3: 962–975.
- Lotzkat S, Wehrenberg G, Haas M (2021) Amphibians (Amphibia, Anura and Caudata) and reptiles (Reptilia, Squamata) from the headwaters of Río Guázaro on the Caribbean versant of Veraguas province, western Panama. Version 1.4. Check List. Occurrence dataset https://doi.org/10.15468/fbq2fj accessed via GBIF.org on 2021-10-15.
- Lynch JD (2001) Three new rainfrogs of the *Eleutherodactylus diastema* group from Colombia and Panama. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 25 (95): 287–297.
- Martínez V (1999) Caracterización de la herpetofauna del Parque Nacional Cerro Hoya. In: Alvarado R, Hernández D (Eds.) Parque Nacional Cerro Hoya. Proyecto Desarrollo Sostenible del Parque Nacional Cerro Hoya y su Zona de Vecindad. Autoridad Nacional del Ambiente (ANAM) & ECO-GTZ, Panama City, Panama, 95–112.
- Martínez V, Rodríguez A (1994 "1992") Del primer inventario en "Cerro Tute". Amphibia: Caudata y Anura. Reptilia: Squamata. Sauria y Serpentes. Scientia (Panamá) 7: 29–53.
- Martínez V, Rodríguez A (2005) Datos preliminares sobre los anfibios y reptiles de Bahía Honda e Isla Canales de Tierra (Veraguas, Panamá). In: Castroviejo S, Ibáñez A (Eds.) Estudios sobre la biodiversidad de la región de Bahía Honda (Veraguas, Panama). Madrid, Spain, 571–626.
- Martínez V, Pimentel N, Hurdaneta A (1995 "1994") Diversidad herpetofaunistica en los cerros "Narices" y "La Anselma": Provincia de Veraguas. Distrito de Santa Fe. Scientia (Panamá) 9: 59–79.
- Martínez V, Rodríguez A, Rodriguez H (1999) Inventario herpetofaunístico preliminar en Isla Leones, Golfo de Montijo, Provincia de Veraguas, República de Panamá. Scientia (Panamá) 14: 79–94.
- McDiarmid RW, Foster MS, Guyer C, Gibbons JW, Chernoff N (2012) Reptile biodiversity: standard methods for inventory and monitoring. University of California Press, Berkeley, USA, 424 pp.
- Myers CW (1971) A new species of green anole (Reptilia, Sauria) from the north coast of Veraguas, Panama. American Museum Novitates 2470: 1–14.
- Myers CW (1974) The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. Bulletin of the American Museum of Natural History 153: 1–262.
- Myers CW, Ibáñez D. R, Cadle JE (2007) On the uniquely fragmented distribution of a rare Panamanian snake, *Dipsas nicholsi* (Colubridae: Dipsadinae). American Museum Novitates 3554: 1–18.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1038/35002501
- Pérez-Santos C (1999) Serpientes de Panamá. Madrid, Spain, 312 pp. Pérez-Santos C, Martínez V (1997) Serpientes del Parque Nacional de Coiba (Panama). In: Castroviejo S (Ed.) Flora y fauna del Parque Nacional de Coiba (Panama). Madrid, Spain, 445–456.
- Peters JA (1960) The snakes of the subfamily Dipsadinae. Museum of Zoology at the University of Michigan Miscellaneous Publications 114: 1–224.
- Peters WCH (1863) Über einige Arten der Saurier-Gattung *Anolis*. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1863: 135–149.

Peters WCH (1873) Über eine neue Schildrötenart, Cinosternon Effeldtii und einige andere neue oder weniger bekannte Amphibien. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1873: 603–618.

- Peters WCH (1874) Über neue Amphibien (Gymnopis, Siphonops, Polypedates, Rhacophorus, Hyla, Clyclodus, Euprepes, Clemmys). Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1874: 616–624.
- Poe S, Ryan MJ (2017) Description of two new species similar to Anolis insignis (Squamata: Iguanidae) and resurrection of Anolis (Diaphoranolis) brooksi. Amphibian & Reptile Conservation 11: e141.
- Ray JM (2009) Ecology of Neotropical arboreal snakes and behavior of New World mollusk-eating snakes. Ph.D. thesis, Old Dominion University, Norfolk, Virginia, USA, 154 pp. https://doi.org/10.25777/ysd1-2855
- Ray JM (2017) Snakes of Panama: a field guide to all species. CreateSpace, 214 pp.
- Sabaj Pérez MH (2016) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 6.5 (16 August 2016). American Society of Ichthyologists and Herpetologists. https://asih.org/sites/default/files/documents/symbolic_codes_for_collections_v6.5_2016.pdf. Accessed on: 2018-10-12.
- Savage JM (1972) The harlequin frogs, genus *Atelopus*, of Costa Rica and western Panama. Herpetologica 28 (2): 77–94.
- Savage JM (2002) The amphibians and reptiles of Costa Rica. A herpetofauna between two continents, between two seas. University of Chicago Press, Chicago, USA, xx+934 pp.
- Savage JM, McDiarmid RW (1992) Rediscovery of the Central American colubrid snake, *Sibon argus*, with comments on related species from the region. Copeia 1992 (2): 421–432. https://doi.org/10.2307/1446202
- Savage JM, Wake MH (2001) Reevaluation of the status of taxa of Central American caecilians (Amphibia: Gymnophiona), with comments on their origin and evolution. Copeia 2001 (1): 52–64. https://doi.org/10.1643/0045-8511(2001)001[0052:rotsot]2.0.co;2

- Schmidt O (1857) Diagnosen neuer Frösche des zoologischen Cabinets zu Krakau. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 24: 10–15.
- Stadler L (2010) Diversität, Taxonomie und Zoogeographie der Herpetofauna der Umgebung von Alto de Piedra (Veraguas, Panama). Diplomarbeit, Justus-Liebig-Universität, Gießen, Germany, 290 pp.
- STRI (Smithsonian Tropical Research Institute) (2020) Amphibians of Panama. STRI, Panama City, Panama. https://stricollections.org/portal/checklists/checklist.php?clid=3&pid=1. Accessed on: 2021-04-17.
- Taylor EH (1949) Costa Rican frogs of the genera Centrolene and Centrolenella. University of Kansas Science Bulletin 33 (4): 257–270.
- Taylor EH (1952) A review of the frogs and toads of Costa Rica. University of Kansas Science Bulletin 35 (5): 577–942.
- Taylor EH (1969) A new Panamanian caecilian. University of Kansas Science Bulletin 48 (12): 315–323.
- Tejera VH, Dupuy OA (2003) Anfibios del Museo de Vertebrados de la Universidad de Panamá. Catálogo. Universidad de Panamá, Autoridad Nacional del Ambiente, Fundacion Natura, Panama City, Panama, 208 pp.
- Uetz P, Freed P, Aguilar R, Hošek, J (Eds) (2021) The reptile database. http://reptile-database.org. Accessed on: 2021-04-17.
- Wake DB, Brame AH (1966) A new species of lungless salamander (genus *Bolitoglossa*) from Panama. Fieldiana Zoology 51 (1): 1–10.
- Wilson LD, Johnson JD (2010) Distributional patterns of the herpetofauna of Mesoamerica, a. biodiversity hotspot. In: Wilson LD, Townsend JH, Johnson JD, Murphy JB (Eds.) Conservation of Mesoamerican amphibians and reptiles. Eagle Mountain Press, Eagle Mountain, Utah, USA, 31–233.
- Young BE, Sedaghatkish G, Roca E, Fuenmayor QD (1999) El estatus de la conservación de la herpetofauna de Panamá. Resumen del primer taller internacional sobre la herpetofauna de Panamá. The Nature Conservancy y Asociación Nacional para la Conservación de la Naturaleza (ANCON), Arlington, Virginia, USA, 40 pp.