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Problems with imperfect locality data: distribution and conservation status of an enigmatic pitviper

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***Abstract.*—Vague geospatial biodiversity data can lead to confusion regarding the biogeography of poorly-known species, and also complicate efforts for their conservation. The Guatemalan Palm-pitviper, *Bothriechis bicolor* (Squamata: Viperidae), a striking yet rarely encountered inhabitant of wet Middle American montane forests, offers a case study germane to this problem. Using a literature- and specimen-based review coupled with novel field observations, this study shows that despite the high-profile status of *B. bicolor*, much of the current understanding of its distribution is conflicted. The results of this review clarify the lack of records for *B. bicolor* from Honduras, underscore its existence on both the Pacific and interior (Gulf of Mexico) slopes of the Sierra Madre de Chiapas, call into question its presumed minimum occupied elevation, and indicate a 68-km range extension into a Biosphere Reserve. Based in part on these findings, we recommend that *B. bicolor* be re-categorized as Vulnerable (criteria A4c+B1ab[iii]+B2ab[iii]) under the International Union for the Conservation of Nature Red List of Threatened Species. Several ambiguous localities for *B. bicolor* have helped to cloud both historical and contemporary conceptualizations of the distribution of this species, highlighting issues that often confront biodiversity scientists. Simple approaches for optimizing representations of the geographic range of a species are thus presented.**

Keywords. *Bothriechis bicolor*, georeferencing, Guatemala, Honduras, Mexico, Viperidae

***Resumen.*—Datos geoespaciales vagos de biodiversidad pueden generar confusión sobre la biogeografía de especies poco conocidas, y también complicar su conservación. La víbora de foseta de palma Guatemalteca *Bothriechis bicolor* (Squamata: Viperidae), un habitante llamativo pero rara vez encontrado de los bosques montanos húmedos mesoamericanos, ofrece un estudio de caso representativo de este problema. Usando una revisión basada en la literatura y en especímenes, junto con nuevas observaciones de campo, mostramos que a pesar del estado de alto perfil de *B. bicolor*, gran parte de la comprensión actual de su distribución está en conflicto. Nuestros resultados aclaran la falta de registros de *B. bicolor* en Honduras, enfatizan su existencia en las vertientes tanto del interior (Golfo de México) como del Pacífico de la Sierra Madre de Chiapas, cuestionan su supuesta elevación mínima ocupada, y corroboran una extensión de su área de distribución de 68 km en una Reserva de la Biósfera. Basándonos en parte en estos resultados, recomendamos que el estatus de *B. bicolor* se actualice a Vulnerable (criterios A4c+B1ab[iii]+B2ab[iii]) en la Lista Roja de Especies Amenazadas de la Unión Internacional para la Conservación de la Naturaleza. Varias localidades ambiguas para *B. bicolor* han contribuido a oscurecer las conceptualizaciones históricas y contemporáneas de la distribución de esta especie, destacando los problemas que a menudo enfrentan los científicos de la biodiversidad. Por lo tanto, se presentan enfoques simples para optimizar las representaciones de la distribución geográfica de una especie.**

Palabras clave. *Bothriechis bicolor*, georreferenciación, Guatemala, Honduras, México, Viperidae

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Introduction

Detailed understanding of the distribution of a species is vital for the accurate interpretation of its natural history, biogeography, and conservation needs (Boitani et al. 2011; Bloom et al. 2017). Museum records are a key subset of global biodiversity data (Graham et al. 2004; Newbold 2010; Holmes et al. 2016; Ríos-Muñoz and Espinosa-Martínez 2019). Like all datasets, however, museum collections can contain problematic records. In particular, historical vouchers collected prior to the availability of field GPS technology often lack sufficiently descriptive locality data (Murphey et al. 2004; Wieczorek et al. 2004; Newbold 2010; Bloom et al. 2017). Such vague locality data can influence the accuracy of downstream analyses such as species distribution models, although that influence is often minimal and can be modulated (Graham et al. 2008; Velásquez-Tibatá et al. 2016). Modeling applications aside, imprecise or even erroneous characterizations of species distributions can also occur, including for rarely seen species (Peterson and Nieto-Montes de Oca 1996; Ervin et al. 2013; Mendelson et al. 2016; Correa Q 2017). These problems can be especially prevalent in understudied tropical areas, and sometimes remain unaccounted for by the contemporary scientific community. This reality necessitates both periodic updates for poorly studied species, and occasional reminders for careful scholarship and record-keeping (Clause et al. 2016; Reyes-Velasco and Ramírez-Chaparro 2019; Ríos-Muñoz and Espinosa-Martínez 2019).

The Palm-pitvipers (Squamata: Viperidae: *Bothriechis*) are a Western Hemisphere clade that exemplifies many of these issues. Ranging from southern Mexico to northern South America, the 11 described species of *Bothriechis* are semi-arboreal, usually occupy wet highland forests, and have diversified largely in allopatry (Campbell and Lamar 2004; Mason et al. 2019). As colorful, visually striking snakes with medically-relevant venom, *Bothriechis* are high-profile animals among many human communities (Luna-Reyes and Suárez-Velázquez 2008; Meléndez 2008; Auliya et al. 2016). Nonetheless, authors have long lamented the paucity of *Bothriechis* samples available for study, and the geographic ranges of many species suffer from ambiguity (Bogert 1968; Jiménez-Lang et al. 2002; Townsend et al. 2013).

Within this genus, the scientific understanding of the Guatemalan Palm-pitviper, *Bothriechis bicolor* (Bocourt 1868), is particularly poor and outdated. Reported only from a handful of localities in mesic montane forests of Nuclear Central America, most research on this enigmatic, colorful species relates to its taxonomy (see Campbell and Lamar [2004] for a synonymy) or evolutionary history (reviewed by Mason et al. [2019]). Importantly, the *B. bicolor* literature also includes old statements that warrant clarification. Published sources offer differing assertions regarding which Central American countries *B. bicolor* occupies, whether it occurs within interior (Gulf of Mexico) drainages, and its presumed elevational range. Moreover, the two most recent dot-locality range maps for the species are over 10 years old and need to be updated (Campbell and Lamar 2004; Köhler 2008). These two maps, which show *B. bicolor* occurring only in Mexico and Guatemala, are also contradicted by more recent polygon-based range maps (Campbell and Muñoz-Alonso 2014; Mason et al. 2019) that show *B. bicolor* occuring broadly in Honduras.

The objective of this contribution is to resolve these ambiguities in the known geographic distribution of *B. bicolor* by reviewing the literature and museum collections, supplemented with unpublished records from the authors and others. The findings of this review are then leveraged to re-evaluate the International Union for the Conservation of Nature (IUCN) Red List categorization for this little-known species, and attention is drawn to some common inaccuracies in biodiversity data and how to mitigate them.

Materials and Methods

To assemble museum-vouchered locality information, the online VertNet specimen portal (http://vertnet.org/) was queried together with the specimen holdings of the Colección Zoológica Regional of the Secretaría de Medio Ambiente e Historia Natural (CZR-HE, also as IHNHERP), the Museo de Zoología "Alfonso L. Herrera," Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC-HE), and the Colección Herpetológica of El Colegio de la Frontera Sur, San Cristóbal de Las Casas (ECO-SCH). For certain problematic records, institutional curators or the collector/observers were contacted directly to seek additional data for those records. Queries directed to the Colección Nacional de Anfibios y Reptiles, Instituto de Biología, Universidad Nacional Autónoma de México (CNAR), and to the online citizen science platforms iNaturalist and HerpMapper, did not return novel data. Subsequently, this dataset was cross-referenced with literature-based information. These sources were identified from queries of ISI Web of Science using the Latin name of *B. bicolor* and all synonyms as search terms. For pre-existing museum records that were not previously published in the literature, written permission was obtained from all living original collectors to release their records herein. Localities identified from these museum- and literature-based searches were georeferenced using the Mapa Digital de México, PueblosAmerica, and GifeX online platforms following the point-radius georeferencing protocol described by Wieczorek et al. (2004). Each unique locality is defined as being at least 1 airline km from any other locality. To accommodate this geospatial filter in cases of closely clustered records, only the most centrally-located record was selected for reporting herein as a locality. Conversely, when elevation data for multiple records from the same mountain clearly segregated those

records by over 1 airline km, they were considered to be separate localities.

This dataset was supplemented with the authors' personal field records for *B. bicolor* obtained from 2004–2019. Some of these records were mentioned previously (Luna-Reyes 1997, 2019), but detailed, vouchered information for them is provided here for the first time. For all records, one or more digital photographic vouchers were deposited at the Los Angeles County Museum of Natural History (LACM PC; where the PC indicates "photo collection"). When possible, physical voucher material was also deposited at the MZFC-HE, including both liver tissue preserved in 95% ethanol, and a whole-body specimen fixed in a 10% dilution (by volume) of 37% formalin and preserved in 70% ethanol. Animal collection and handling were authorized under SEMARNAT permit #FAUT-0093 issued to Adrián Nieto-Montes de Oca, and UGA IACUC AUP #A2016 02-001-Y2-A0. All novel material was diagnosed as *B. bicolor* based on the presence of 27 or more interrictal scales (Campbell and Smith 2000).

The World Database on Protected Areas (available from Protected Planet at http://www.protectedplanet.net) was used to determine which georeferenced localities for *B. bicolor* lie within a government protected area. The IUCN Red List categorization of *B. bicolor* was then re-evaluated using guidelines available from the IUCN Standards and Petitions Committee (2019). For geographic range calculations, a minimum convex polygon was drawn around all geospatially explicit *B. bicolor* localities to estimate the extent of occurrence of the species, and all grid cells containing one or more of these localities were summed across a 2 × 2 km grid to estimate the area of occupancy of the species. Additionally, the Environmental Vulnerability Score (EVS) for *B. bicolor* (see Johnson et al. 2015a) and its national protected status in both Mexico (SEMARNAT 2010) and Guatemala (CONAP 2009) were revisited. Because *B. bicolor* is commercially desirable (Meléndez 2008; Auliya et al. 2016), reported locality data were obscured by rounding GPS coordinates to the nearest hundredth of a decimal degree.

Results

Seven potential Guatemalan and Mexican localities were conservatively excluded from the results reported below, due to suspect or imprecise data. All seven localities are also omitted from Table 1, and four are omitted from Fig. 1 while the remaining three are indicated with question marks. The type locality for *B. bicolor*, and the potential minimum elevation for the species, are included among these records, emphasizing their scientific importance. Given this importance, the problems associated with all seven localities are thoroughly reviewed in the **Discussion** section.

Based on the literature- and specimen-based review, 29 geospatially explicit, independent localities exist for *B. bicolor*. These localities are distributed across the Sierra Madre de Chiapas mountain range in southern Mexico (18 localities) and southwestern Guatemala (11 localities) from 900–2,090 m asl (Fig. 1, Table 1). In Mexico, records exist only from the state of Chiapas, while in Guatemala records exist from the departments of Chimaltenango, Escuintla, San Marcos, Sololá, and Suchitepéquez. Campbell and Smith (2000) inadvertently listed *B. bicolor* specimens from Volcán de Atitlán, department of Suchitepéquez, as having originated from the department of Sacatepéquez. Additionally, Meléndez (2008) implied that the species is known from both the Sacatepéquez and Guatemala departments. Although we suspect that *B. bicolor* does, in fact, occur in these two departments, this remains unverified. Historical records for *B. bicolor* also exist for Honduras, but these records are all now attributed to a congener that was described 20 years ago (Campbell and Smith 2000). The conflicted literature surrounding this issue is covered in detail in the **Discussion** section.

All 11 Guatemalan localities for *B. bicolor* lie in Pacific drainages. However, in Mexico 11 of the 18 localities for the species (61%) occur on interior slopes facing the Central Depression of Chiapas that eventually drain into the Atlantic via the Gulf of Mexico (Table 1). These 11 localities occur at distances up to 11 airline km (mean = 2.8 airline km) from the Continental Divide, which runs along the spine of the Sierra Madre de Chiapas.

Of the 29 total localities summarized above, 14 are reported here for the first time (Fig. 1, Table 1). These novel records, which originate from unpublished museum specimens and the recent field expeditions of the authors, lie within several large gaps which existed in the previously known range of *B. bicolor*. More importantly, they also extend the range of the species 68 km to the northwest, and represent the first vouchered records from the federally protected Reserva de la Biósfera La Sepultura and Reserva de la Biósfera Volcán Tacaná (Campbell and Muñoz-Alonso 2014).

Including these two biosphere reserves, five Mexican protected areas and one Guatemalan protected area with at least one verified record of *B. bicolor* were identified. In total, 62% of all verifiable *B. bicolor* localities lie within a protected area. This figure is likely an underestimate, however, because imprecise locality data for three other records prevented confirmation of whether they lie within or just outside of a reserve (Table 1).

Despite the majority of *B. bicolor* populations occurring in protected areas, we conservatively recommend re-categorizing the species as Vulnerable (criteria A4c+B1ab[iii]+B2ab[iii]) on the IUCN Red List of Threatened Species, and code this category change as Nongenuine: New information (IUCN Standards and Petitions Committee 2019). This is a two-category jump compared to the prior evaluations of this species in 2007 and 2012 as Least Concern (Campbell and Muñoz-Alonso 2014). For unknown reasons, Acevedo et

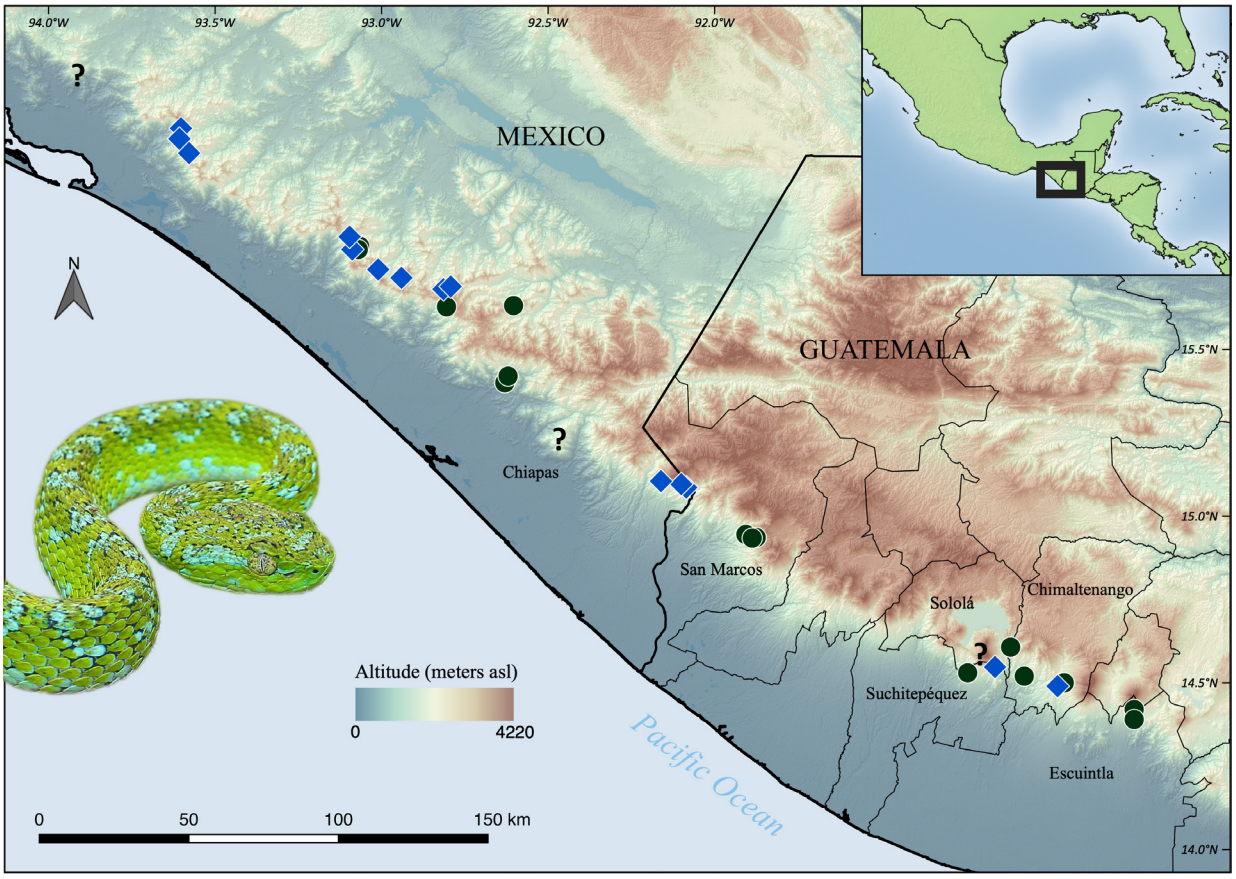

Fig. 1. Geographic distribution of the Guatemalan Palm-pitviper, *Bothriechis bicolor*, based on a review of the literature and museum collections. Circles indicate previously published records, diamonds indicate new records, and question marks approximate the locations of selected problematic records discussed in the text. The easternmost question mark represents the type locality for *B. bicolor*. The inset illustrates specimen MZFC-HE 33491 (juvenile, snout-vent length 322 mm) in life.

al. (2010) reported the species as Near Threatened. Our proposed IUCN Vulnerable re-categorization agrees with a suggestion by Johnson et al. (2015a), but unlike those authors, we base our recommendation on the IUCN Red List criteria. In the **Discussion** section, we justify our assumptions and decisions in the context of those criteria.

The IUCN recommendation offered here is congruent with the most recently published Environmental Vulnerability Score (EVS) for this species of 14 out of 20, which is at the lower boundary of the High Vulnerability category (Johnson et al. 2015a). Among the EVS values published earlier for *B. bicolor* (Acevedo et al. 2010; Wilson et al. 2013; Johnson et al. 2015b), only the Guatemala-specific work by Acevedo et al. (2010) offers a different evaluation (EVS of 15). Our IUCN recommendation is also congruent with the governmental imperiled species listings that carry legal weight across the range of *B. bicolor*. In Mexico, *B. bicolor* is categorized as Amenazada (Threatened) [SEMARNAT 2010], and in Guatemala it is considered a Category 3 species under the Listado de Especies Amenazadas (List of Threatened Species) [CONAP 2009]. We recommend no changes to the EVS, SEMARNAT, or CONAP listings for *B. bicolor* at this time.

Discussion

Ambiguity in the Distribution of *B. bicolor*

This study highlights the ambiguity that can exist concerning species distributions. This ambiguity can potentially lead to erroneous biogeographical conclusions, and complicate conservation assessments. By exploring these issues as they relate to *B. bicolor*, several sources of ongoing scholarly confusion are resolved and the need for greater awareness of problems associated with imprecise biodiversity information are highlighted.

Perhaps the greatest ambiguity in the literature associated with *B. bicolor* is whether the species is known from Honduras. Historically, many authors placed the species in Honduras (Bogert 1968; Meyer and Wilson 1971; Wilson and Meyer 1982; Wilson 1983; Wilson and Meyer 1985; Campbell and Lamar 1989; Crother et al. 1992; Wilson and McCranie 1994; McDiarmid et al. 1999). However, all Honduran material ascribed to *B. bicolor* by these authors was subsequently referred to the newly described species *B. thalassinus* (Campbell and Smith 2000). No new Honduran *Bothriechis* material has since been forthcoming other than Honduran populations announced as the newly described species *B. guifarroi*,

Table 1. Vouchered, geospatially explicit localities for the Guatemalan Palm-pitviper, *Bothriechis bicolor*, based on a review of the literature and museum collections. Datum WGS 84 for all coordinates.

Country	Department or state	Municipality	Locality[1]	Latitude	Longitude	Elevation (m)[2]	Slope (versant)	Protected area[3]	Voucher(s) and original source[4]
Guatemala	Chimaltenango	Pochuta	Finca Pacayal, nr Pochuta [=Finca El Pacayal, near San Miguel Pochuta]	14.52	-91.07	ca. 1,200	Coastal (Pacific)	none	MCZ 31941, Crother et al. 1992
Guatemala	Chimaltenango	Yepocapa	11 km S of Finca Victoria ca. 1200 m vicinity of Yepocapa Chimaltgo [=Chimaltenango]	14.49	-90.97	ca. 1,200	Coastal (Pacific)	none	UMMZ 131661, this work
Guatemala	Chimaltenango	Yepocapa	Yepocapa	14.50	-90.95	ca. 1,400	Coastal (Pacific)	none	USNM 127973, Bogert 1968
Guatemala	Escuintla	Palín or Escuintla	S slope Volcán de Agua, Finca Rosario Vista Hermosa	14.42	-90.74	1,370	Coastal (Pacific)	none	UTA R-24758–24759, Campbell and Smith 2000
Guatemala	Escuintla	Palín or Escuintla	S slope Volcán de Agua, Finca Rosario Vista Hermosa	14.39	-90.74	900	Coastal (Pacific)	none	UTA R-39238, Campbell and Smith 2000
Guatemala	San Marcos	Esquipulas Palo Gordo	Aldea La Fraternidad, lado oeste	14.94	-91.88	ca. 1,700–1,800	Coastal (Pacific)	none	UTA R-39412, Campbell and Smith 2000
Guatemala	San Marcos	San Rafael Pie de la Cuesta	Aldea Patí, near San Rafael Pie de la Cuesta	14.95	-91.91	ca. 1,140	Coastal (Pacific)	none	UTA R-38149, Campbell and Smith 2000
Guatemala	San Marcos	San Rafael Pie de la Cuesta	Aldea Feria, Finca America El Vergel	14.93	-91.89	ca. 1,480	Coastal (Pacific)	none	UTA R-39413–39422, Campbell and Smith 2000
Guatemala	Sololá	San Lucas Tolimán	Finca Santo Tomás Pachuj	14.61	-91.11	1,200	Coastal (Pacific)	CDLA	UTA R-46613, Campbell and Lamar 2004
Guatemala	Suchitepéquez	Patulul	3.3 km NW (by air) of entrance to Finca San Jerónimo Miramar, SE slope of Volcán Atitlán	14.55	-91.16	1,300	Coastal (Pacific)	CDLA	MVZ 270073, this work
Guatemala	Suchitepéquez	Santa Bárbara	Olas de Moca, near Finca La Moka	14.53	-91.24	ca. 900	Coastal (Pacific)	CDLA	FMNH 20162, Bogert 1968
Mexico	Chiapas	Acacoyagua or Escuintla	Dist Soconusco Mt Ovando [=Cerro Ovando]	15.40	-92.63	1,200	Coastal (Pacific)	REBITRI[5]	UMMZ 87707, Bogert 1968
Mexico	Chiapas	Acacoyagua or Escuintla	Mt Ovando [=Cerro Ovando]	15.42	-92.62	2,000	Coastal (Pacific)	REBITRI[5]	UMMZ 94644, Bogert 1968
Mexico	Chiapas	Ángel Albino Corzo	Road to Pablo Galeana (Mex 157), 50 road km SE of Ángel Albino Corzo	15.63	-92.60	1,430	Interior (Atlantic)	ZSCEPELP	MZFC-HE 30395, Clause et al. 2016
Mexico	Chiapas	Ángel Albino Corzo	1.5 km due SW (airline) of Ejido Santa Rita, 14 km S and 6 km W (airline) of Nueva Palestina	15.68	-92.81	1,500	Interior (Atlantic)	REBITRI	LACM PC 2505–2507, this work
Mexico	Chiapas	Ángel Albino Corzo	1.0 km due E (airline) of Ejido Santa Rita, 13 km S and 4 km W (airline) of Nueva Palestina	15.69	-92.79	1,550	Interior (Atlantic)	REBITRI	LACM PC 2508, this work
Mexico	Chiapas	Cacahoatán	Benito Juárez Montecristo, 3.0 km S and 5.5 km W (airline) of the peak of Volcán Tacaná	15.10	-92.16	1,800	Coastal (Pacific)	REBIVTA	LACM PC 2503–2504, this work
Mexico	Chiapas	La Concordia	2.5 km due W (airline) of Finca Nueva Linda, 1.4 km N and 3.7 km W (airline) of the peak of Cerro El Cebú	15.84	-93.10	1,570	Interior (Atlantic)	REBITRI & APFFLF	LACM PC 2497–2498, this work

Table 1 (continued). Vouchered, geospatially explicit localities for the Guatemalan Palm-pitviper, *Bothriechis bicolor*, based on a review of the literature and museum collections. Datum WGS 84 for all coordinates.

Country	Department or state	Municipality	Locality[1]	Latitude	Longitude	Elevation (m)[2]	Slope (versant)	Protected area[3]	Voucher(s) and original source[4]
Mexico	Chiapas	La Concordia	0.7 km SSW (airline) of Campamento El Quetzal on trail to Monterrey, 2.2 km due SW (airline) of the peak of Cerro Quetzal	15.72	-92.94	1,630	Interior (Atlantic)	REBITRI	LACM PC 2499–2502, this work
Mexico	Chiapas	La Concordia	Finca Santa Teresa, 5 km due NNW (airline) of Finca Custepec, 23 road km SSE of Nuevo Paraíso and Yaj Noptic	15.74	-93.01	1,400	Interior (Atlantic)	REBITRI & APFFLF	LACM PC 2509–2515, this work
Mexico	Chiapas	La Concordia	Reserva de la Biósfera El Triunfo, Polígono V, El Santuario	15.80	-93.09	1,680	Interior (Atlantic)	REBITRI & APFFLF	CZR-HE 1833, this work
Mexico	Chiapas	La Concordia	Near Cerro Cebú [=Cerro El Cebú]	15.81	-93.07	1,570	Interior (Atlantic)	REBITRI & APFFLF	UTEP G-2015.4, Meneses-Millán and Garcia-Padilla 2015
Mexico	Chiapas	La Concordia	Rancho Bélgica Uno	15.80	-93.07	1,400	Interior (Atlantic)	REBITRI & APFFLF	photos in book: Heimes 2016
Mexico	Chiapas	Mapastepec	Cañada Honda, ca. 3 km due S (airline) of Campamento El Triunfo [=Cañada Honda (near El Triunfo)]	15.63	-92.81	ca. 1,530	Coastal (Pacific)	REBITRI	photo in book: Campbell and Lamar 2004
Mexico	Chiapas	Tonalá	2.9 km due SW (airline) of Ejido Sierra Morena [=Ejido Sierra Morena, campamento Las Limas]	16.13	-93.61	1,390	Coastal (Pacific)	REBISE	ECO-SCH 3932, this work
Mexico	Chiapas	Unión Juárez	Colonia Talquián, Volcán Tacaná	15.09	-92.09	1,650	Coastal (Pacific)	REBIVTA[5]	MVZ 159460, this work
Mexico	Chiapas	Unión Juárez	Volcán Tacaná	15.10	-92.10	2,090	Coastal (Pacific)	REBIVTA	MZFC-HE 26545, this work
Mexico	Chiapas	Villa Corzo	1.7 km due NW (airline) of Ejido Sierra Morena, 3.7 km S and 1.2 km E (airline) of the peak of Cerro Tres Picos	16.16	-93.60	1,460	Interior (Atlantic)	REBISE & APFFLF	MZFC-HE 33491, this work
Mexico	Chiapas	Villa Corzo	Reserva de la Biósfera La Sepultura, Rancho Solo Dios	16.09	-93.58	1,465	Interior (Atlantic)	REBISE & APFFLF	CZR-HE 2352, this work

[1] Square brackets "[ ]" indicate alternative or more precise catalog-based or literature-based locality descriptions for the indicated specimen.

[2] All elevations are rounded to the nearest 10 m, and elevations preceded by "ca." are rough estimates due to imprecise locality data.

[3] Cuenca del Lago Atitlán (CDLA), Reserva de la Biósfera La Sepultura (REBISE), Reserva de la Biósfera El Triunfo (REBITRI), Reserva de la Biósfera Volcán Tacaná (REBIVTA), Área de Protección de Flora y Fauna La Frailescana (APFFLF), Zona Sujeta a Conservación Ecológica Pico El Loro-Paxtal (ZSCEPELP).

[4] Colección Zoológica Regional de la Secretaría de Medio Ambiente e Historia Natural (CZR-HE); Field Museum of Natural History (FMNH); Natural History Museum of Los Angeles County photographic collection (LACM PC); Musuem of Comparative Zoology, Harvard University (MCZ); Museo de Zoologiá "Alfonso L. Herrera," Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC-HE), Musuem of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Michigan Museum of Zoology (UMMZ); Smithsonian Institution National Museum of Natural History (USNM); University of Texas at Arlington (UTA); University of Texas at El Paso Biodiversity Collections (UTEP).

[5] Locality may actually lie outside the reserve boundary, but locality data are too imprecise for exact determination.

together with a possibly undescribed species (Townsend et al. 2013). The taxonomic validity of either *B. thalassinus* or *B. guifarroi* has never been questioned in the literature. As such, although a number of authors (Taggart et al. 2001; Wilson and McCranie 2002; Campbell and Muñoz-Alonso 2014; Pla et al. 2017; Mason et al. 2019) later attributed Honduran populations of *B. thalassinus* to *B. bicolor*, they either universally overlooked the description of *B. thalassinus* or mistakenly considered the two species roughly sympatric in Honduras. All other recent works (Köhler 2008; Castoe et al. 2009; Townsend and Wilson 2010; Wilson and Johnson 2010; McCranie 2011; Townsend et al. 2013; Solís et al. 2014; Wallach et al. 2014; McCranie 2015) have not recognized *B. bicolor* as a member of the Honduran herpetofauna. Importantly, these works include all modern, authoritative treatments and checklists of the Honduran snake assemblage (Townsend and Wilson 2010; McCranie 2011; Solís et al. 2014; McCranie 2015). Given the uncontroversial transfer of all Honduran *B. bicolor* material to the binomial *B. thalassinus* by Campbell and Smith (2000), and given that no Honduran *B. bicolor* vouchers have since been reported, we here affirm that *B. bicolor* is undocumented from Honduras. The nearest *B. bicolor* vouchers (Finca Rosario Vista Hermosa, Table 1) were obtained ca. 150 airline km west of the Honduras border.

Another major ambiguity relating to the geographic distribution of *B. bicolor* is the comparatively large number of problematic localities that have been treated inconsistently in the literature. Supplementing brief coverage by Bogert (1968), these seven problematic localities are discussed below because they encapsulate issues commonly posed by geographic data.

Bocourt (1868) gave the type locality for *B. bicolor* as "Des forêts de Saint-Augustin, département de Solola (Guatémala), sur le versant occidental de la Cordillère. 610 mètres d'altitude." Nonetheless, only a tiny corner of the department of Sololá lies at 610 m asl. The locality description conceivably refers to Finca San Agustín, department of Suchitepéquez, ca. 550–700 m asl on the slopes of Volcán Atitlán, ca. 8 km south of the border with the department of Sololá. This is consistent with the claim by several authors (McDiarmid et al. 1999; Campbell and Lamar 2004) that the type locality probably lies on Volcán Atitlán. However, Wallach et al. (2014) erroneously georeferenced the type locality to the department of Sacatepéquez in the urban zone of the city of Antigua at ca. 1,530 m asl, adding additional confusion to the published literature. Assuming that Bocourt's types did, indeed, originate from somewhere on Volcán Atitlán, they are also essentially topotypic with a specimen from the vague locality "cuesta de Atitlan im westlichen Guatémala" that Müller (1877, 1878) used to describe "*Bothrops* (*Bothriechis*) *Bernoullii*" (see detailed discussion by McDiarmid et al. [1999]). Müller's taxon was subsequently synonymized with *B. bicolor*, but the fact remains that the provenance of the types for both binomials is inexactly known.

In Chiapas, Juliá-Zertuche and Varela-Juliá (1978) reported a record from "Colonia Ejidal Morelos, Mpio. de Huixtla, Chis. […] y a unos 500 m. de altitud aproximadamente" as the type locality for another taxon, *Bothriechis ornatus*, that was also later synonymized with *B. bicolor*. The only community or site in the Municipio (Municipality) de Huixtla with the word "Morelos" in its name that we could identify is the hamlet of José María Morelos, but it sits at ca. 1,350 m asl, over 3 airline km from the 500 m contour. To our knowledge, no other *Bothriechis* vouchers have since reached a museum collection from anywhere within 15 airline km of the Municipio de Huixtla, leaving this locality vague and open to interpretation.

Three additional Chiapas localities cannot be confidently placed because they lack elevation data, no verbatim place names are identifiable, and they could plausibly correspond to two or more sites separated by over 10 airline km with imperfectly matching names. These three localities are as follows: "Catharinas (=Catarina la Grande?)" (Greene 1971), "Chicharras" or variations thereof (Smith 1941; Bogert 1968; Campbell and Lamar 2004), and "Finca La Lucha" (Greene 1971).

Lastly, we are aware of an unvouchered 1994 sight record of a snake identified as *B. bicolor* from Rancho El Recuerdo in the Municipality of Jiquipilas, within what is now the Reserva de la Biósfera La Sepultura. If accurate, this would extend the range of the species ca. 40 km to the NW and would halve the distance between *B. bicolor* and known populations of its congener *B. rowleyi* near Cerro Baúl (Bogert 1968). In 2018 and 2019, the authors unsuccessfully searched for *Bothriechis* near Rancho El Recuerdo on Cerro La Palmita. Several damaging wildfires had recently swept through this forested region (Myers 2011), which might have influenced these survey results. However, until verifiable material reaches a museum, we consider the existence of *Bothriechis* in the vicinity of Cerro La Palmita uncertain.

Ambiguity in Elevation Range and Biogeography of *B. bicolor*

Intertwined with the problematic localities discussed above is ambiguity in the elevational range of *B. bicolor*. Based on material of sound provenance, the species is known from 900–2,090 m asl (Table 1). Yet, as indicated above, the problematic "Saint-Augustin" and "Colonia Ejidal Morelos" localities supposedly originate from 610 and 500 m, respectively. Additionally, Crother et al. (1992) list a minimum elevation of 457 m for specimens from Finca Rosario Vista Hermosa in Guatemala, but this was likely in error because museum catalogue data for those specimens list no elevation below 1,300 m asl. Despite prior authors consistently accepting 500 m as the lower elevation limit, for reasons articulated above, we consider the underlying data questionable. Confirmation

of the geospatial validity of the seven problematic historical records, and thus of the true minimum elevation for *B. bicolor*, will necessitate targeted re-surveys. Nonetheless, this could prove particularly challenging because lower-elevation habitats are more degraded relative to those at higher elevations (Campbell and Lamar 2004; Campbell and Muñoz-Alonso 2014; Godínez-Gómez and Mendoza 2019), increasing the likelihood that low-elevation *B. bicolor* populations could now be extirpated. Climate change may have also pushed low-elevation *B. bicolor* populations upslope (Elsen et al. 2020), which would further complicate re-surveys to verify the lower elevation limit of the species.

The final source of confusion relating to the distribution of *B. bicolor* is biogeographical. All published sources indicate a strictly Pacific-versant range for *B. bicolor*, other than Clause et al. (2016) who were the first to explicitly state that *B. bicolor* occurs on interior-draining (Gulf of Mexico) slopes of the Sierra Madre de Chiapas. However, several prior authors beginning with Luna-Reyes (1997) had also reported localities from the Atlantic versant of that mountain range (Meneses-Millán and García-Padilla 2015; Heimes 2016). Although Pacific drainages still harbor the majority of *B. bicolor* localities range-wide, our results emphasize that the species can no longer be accurately characterized as having a Pacific-versant distribution, at least in Mexico. We encourage field workers to be attentive to the possibility of encountering this species on both sides of the Continental Divide in the Sierra Madre de Chiapas. Future discovery of new *B. bicolor* localities will likely further improve understanding of how widely its range spans the Continental Divide, as would development of a rigorous ecological niche model for the species (Wisz et al. 2008; Ríos-Muñoz and Espinosa-Martínez 2019).

More broadly, this work underscores the fact that the distribution of many organisms in southern Mexico remains poorly resolved, even at coarse spatial scales. The 68-km range extension for *B. bicolor* reported herein is one of several range extensions exceeding 50 km for highland squamates (Morales et al. 2015; Hidalgo-García et al. 2018; Valdenegro-Brito et al. 2018) and salamanders (Bouzid et al. 2015; Barrio-Amorós et al. 2016) reported in the last five years from Chiapas and Guatemala. Future survey efforts in remote, mountainous areas throughout Mesoamerica hold additional promise for wildlife discoveries of high biogeographical and conservation value.

IUCN Status of *B. bicolor*

Our recommendation to re-categorize *B. bicolor* from Least Concern to Vulnerable on the IUCN Red List of Threatened Species reflects advances in our understanding of its distribution, and the threats facing the species. We estimate the current extent of occurrence (EOO) and area of occupancy (AOO) for *B. bicolor* at 6,400 km^2 and 108 km^2, respectively. These estimates are well within the minimum thresholds for Vulnerable categorization, which are not exceeded even if all seven problematic localities for *B. bicolor* are added. Importantly, this estimated AOO value actually lies within the minimum threshold for Endangered categorization (AOO < 500 km^2). However, we consider our estimated AOO to be artificially low due to the severe lack of survey effort across intact, remote habitat within our estimated EOO. To ensure that our recommendation remains robust to future discoveries, we consider it premature to advocate for Endangered categorization. Regarding population size, we infer a reduction exceeding 30% within three generations, coupled with severe fragmentation of the range of this species and declines in habitat quality. We coarsely estimate generation length as 10 years for *B. bicolor*, based on available data for *Crotalus o. oreganus* and other *Bothriechis* spp. (Campbell and Lamar 2004; Maida et al. 2018). Widespread, historical deforestation is continuing across the range of *B. bicolor* (Campbell and Lamar 2004; Campbell and Muñoz-Alonso 2014; Cortina-Villar et al. 2019; Godínez-Gómez and Mendoza 2019; Elsen et al. 2020). This continuing forest loss even affects protected areas inhabited by the species, either because some land conversion remains legal within park boundaries or because socioeconomic issues prevent enforcement of forest protections (Figueroa and Sánchez-Cordero 2008; Acevedo et al. 2010; García-Amado et al. 2013). Additionally, recent climate change models for the Mexican portion of the Sierra Madre de Chiapas forecast over 90% loss of montane cloud forest by 2080 (Ponce-Reyes et al. 2012; Rojas-Soto et al. 2012). Across the entire mountain range, similar range reductions for hypothetical species are predicted due to climate change (Elsen et al. 2020). Climate change also exacerbates human-caused wildfires that likely impact western *B. bicolor* populations (Johnson et al. 2010; Myers 2011). The adaptability of *B. bicolor* probably modulates these pressures, given that it can persist in coffee fincas and often occupies montane moist forests below the cloud forest belt (Campbell and Lamar 2004; Acevedo et al. 2010; Johnson et al. 2010). However, fear-based killing of *B. bicolor* in coffee fincas, plus possible illegal collecting for the pet trade, negatively effects some populations to an unquantified degree. Although substantial uncertainty exists, we infer that observed and predicted habitat degradation coupled with targeted removal of individual snakes across the small range of this species justifies its threatened status.

General Considerations

The Sierra Madre de Chiapas, which supports only *B. bicolor* out of all recognized congeners, is rugged and biogeographically complex. The Guatemalan portion of the Sierra has been ascribed several alternative names in the literature, including the Pacific volcanic chain of

Guatemala (Acevedo et al. 2010; Solano-Zavaleta and Nieto-Montes de Oca 2018), the Volcanic Cordillera of Guatemala (Campbell and Lamar 1989; Mendelson 1997; Johnson et al. 2010; Campbell and Muñoz-Alonso 2014), the Guatemalan volcanic cordillera (Rovito et al. 2012), and the Fuegan area (Campbell and Vannini 1989). This volcanically-active portion of the mountain chain might best be considered a massif separate from the Sierra Madre de Chiapas. The Sierra's regular east-west turnover in highland species of squamates (Campbell and Brodie 1988; Campbell and Frost 1993; Solano-Zavaleta and Nieto-Montes de Oca 2018) and amphibians (Wake and Lynch 1976; Duellman 2001; Rovito et al. 2012) supports this consideration. Similar within-species geographic variation, and perhaps even cryptic species, could also exist within populations currently referred to *B. bicolor*. Most recently, Juliá Zertuche and Varela-Juliá (1978) erected the ill-diagnosed *Bothriechis ornatus* within the range of *B. bicolor*, but this taxon was soon questioned (Álvarez del Toro 1982) and later synonymized with *B. bicolor* (Campbell and Lamar 1989; McDiarmid et al. 1999; Campbell and Lamar 2004). Scarcity of physical samples coupled with uncertain locality data complicate efforts to revisit this issue. We thus invite students of the Mesoamerican herpetofauna, and especially managers of protected areas, to prioritize collection of physical samples of *B. bicolor* whenever possible.

In addition to this invitation, we also offer recommendations for addressing the confusing ambiguity in species distributions more generally. Echoing previous work (Clause et al. 2016), we encourage authors to be transparent when geographic distribution data is problematic, and account for uncertainty when it exists (Velásquez-Tibatá et al. 2016). In cases of data-deficient or confusing historical localities, and when confirmatory re-survey data are lacking, this approach is perhaps the most defensible. Wallach et al. (2014) offer a commendable model for how to do this. For modern field biologists, dual data-recording protocols that emphasize collection of both GPS coordinates and precise locality descriptors anchored to stable, unique place-names or notable landscape features offer another clear best-practice in our view. We concede that detailed locality descriptors are often challenging to devise in roadless, uninhabited areas with few well-known landmarks, such as the habitats often occupied by *B. bicolor*. Nonetheless, the free GoogleEarth platform provides a useful solution for accurately measuring distances (either airline or by road) from major named peaks or large towns when field-collected GPS coordinates are available for the locality. We model this approach in the locality descriptors for our new records in Table 1. If followed, these suggestions should help maximize data precision and improve appraisals of organismal biogeography and conservation needs.

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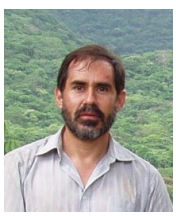

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