



Endemic to Mexico, snakes of the genera *Ophryacus* and *Mixcoatlus* are some of the most unusual pitvipers in the country. The taxonomy and natural history of members of these genera has not been studied extensively, perhaps because individuals are difficult to encounter in the field and thus rarely are deposited in museum collections. A specimen collected in 2010 in western Veracruz did not match any of the known species in these genera, resulting in a two-year study. Pictured here is a new species of *Ophryacus* from Zilcatipan, Municipio de Huayacocotla, Veracruz, Mexico. 📷 © Iván Ahumada-Carrillo



A new species of *Ophryacus* (Serpentes: Viperidae: Crotalinae) from eastern Mexico, with comments on the taxonomy of related pitvipers

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ABSTRACT: The genus *Ophryacus* is endemic to Mexico, where it ranges along the Sierra Madre Oriental from Hidalgo and northern Veracruz south to the Sierra Madre del Sur in Guerrero and Oaxaca. We obtained new material of *Ophryacus* and compared it to specimens from all previously documented populations of *O. undulatus*. We examined scutellational characters and proportional differences, and found strong evidence to support the existence of at least three species within this genus. One species is undescribed and another currently is in the synonymy of *O. undulatus*. We describe a new species of *Ophryacus* from eastern Mexico, and remove *Bothrops sphenophrys* from the synonymy of *O. undulatus* and formally place it in *Ophryacus*. We provide comparative morphological data and a key for the known species of *Ophryacus* and *Mixcoatlus*. We also discuss the ecological and geographical distribution of *Ophryacus* and *Mixcoatlus* and include a distribution map for all the species with supraocular horns. Finally, we comment on the conservation implications for the horned pitvipers of Mexico.

Key Words: Biogeography, conservation implications, external morphology, Hidalgo, *Mixcoatlus*, Oaxaca, Puebla, Sierra Madre del Sur, Sierra Madre Oriental, taxonomy, Veracruz

RESUMEN: El género *Ophryacus* es endémico a México con una distribución que abarca desde la Sierra Madre Oriental en Hidalgo y el norte de Veracruz hasta la Sierra Madre del Sur en Guerrero y Oaxaca. Se obtuvo nuevo material de *Ophryacus* y se comparó con especímenes de todas las poblaciones previamente documentadas. Examinamos caracteres de escamación y diferencias proporcionales, y encontramos evidencia significativa que confirman la existencia de al menos tres especies en este género. Una especie no está descrita y la otra actualmente esta sinonimizada con *O. undulatus*. Describimos una especie nueva de *Ophryacus* del este de México y removemos *Bothrops sphenophrys* de la sinonimia de *O. undulatus* y la colocamos formalmente en *Ophryacus*. Proporcionamos datos morfológicos comparativos y la claves para las especies conocidas de *Ophryacus* y *Mixcoatlus*. También discutimos la distribución geográfica y ecológica de *Ophryacus* y *Mixcoatlus* e incluimos un mapa de distribución para todas las especies con cuernos supraoculares. Finalmente comentamos sobre las implicaciones de conservación para todas las víboras de fosea cornudas de México.

Palabras Claves: Biogeografía, Hidalgo, implicaciones de conservación, *Mixcoatlus*, morfología externa, Oaxaca, Puebla, Sierra Madre del Sur, Sierra Madre Oriental, taxonomía, Veracruz

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INTRODUCTION

Mexico is considered a megadiverse country and a biodiversity hotspot that continues to produce species previously unknown to science at an impressive rate (Wilson and Johnson, 2010; Flores-Villela and García-Vázquez, 2013; Wilson et al., 2013a, b). New species of amphibians, lizards, and small colubrid snakes are being discovered with regularity (e.g., Feria-Ortíz et al., 2012; Nieto-Montes de Oca et al., 2013, 2014; Bryson et al., 2014; Grummer and Bryson, 2014; Köhler et al., 2014; Campbell, 2015; Reyes-Velasco et al., 2015). Venomous snakes, and specifically pitvipers, have been well studied in Mexico for the last century (see Campbell and Lamar, 2004, and references therein). Nevertheless, several new species of pitvipers have been described from Mexico in the last 20 years, including one species of *Cerrophidion* (López-Luna et al., 1999) and four of *Crotalus* (Alvarado-Díaz and Campbell, 2004; Campbell and Flores-Villela, 2008; Bryson et al., 2014). Furthermore, Jadin et al. (2011) removed *Agkistrodon browni* Shreve, 1938, from the synonymy of *Cerrophidion barbouri* (Dunn, 1919) and placed both species and *Ophryacus melanurus* (Müller, 1923) in a new genus, *Mixcoatlus*, and Anderson and Greenbaum (2012) removed *Crotalus ornatus* Hallowell, 1854, from the synonymy of *Crotalus molossus* Baird and Girard, 1853. Recent phylogenetic or phylogeographic studies also have been undertaken on the following genera of Mexican pitvipers: *Crotalus* (Bryson et al. 2011a, b; Reyes-Velasco et al., 2013; Bryson et al., 2014); *Agkistrodon* (Porras et al., 2013); *Atropoides* (Jadin et al., 2010); and *Cerrophidion* (Jadin et al., 2011, 2012). The monotypic genus *Ophryacus* Cope, 1887, however, has not undergone a recent review.

The genus *Ophryacus* has had a long but intermittent taxonomic history. Jan (1859) described *Trigonocephalus (Atropus) undulatus* on the basis of two syntypes from “Mexique” (= Mexico). *Trigonocephalus (Atropus) undulatus* first was placed in the genus *Ophryacus* by Ferrari-Pérez (1886). McDiarmid et al. (1999), however, considered this a nomen nudum and commented on the situation, and formally regarded the genus as having been described by Cope (1887). Thereafter, various authors have placed the species in different genera, including *Bothrops*, *Lachesis*, *Trimeresurus*, and *Bothriechis* (see Campbell and Lamar, 2004). Smith (1960) described *Bothrops sphenophrys* on the basis of a single specimen from La Soledad (Municipio de Candelaria Loxicha), Oaxaca, and speculated that this species likely was closely related to *B. undulatus* (= *O. undulatus*). In an unpublished dissertation, Burger (1971) resurrected the genus *Ophryacus*, within which he placed *O. undulatus*, and considered *B. sphenophrys* a junior synonym of *O. undulatus*. Campbell and Lamar (1989) followed this arrangement, and commented on the synonymy of *B. sphenophrys* with *O. undulatus*. *Ophryacus* was considered a monotypic genus until Gutberlet (1998) placed *Porthidium melanurum* Müller, 1923, in *Ophryacus*, based on morphology and ecology. Jadin et al. (2011) removed *O. melanurus* from *Ophryacus* and assigned it to the newly erected genus *Mixcoatlus*, which currently includes three species (*M. melanurus*, *M. browni*, and *M. barbouri*), and considered it a sister group to *Ophryacus* on the basis of molecular evidence. Herein, we follow the taxonomy proposed by Jadin et al. (2011), but for comparative purposes (see below) consider all species of *Ophryacus* and *Mixcoatlus* as closely related.

In 2010, while conducting herpetological surveys in little-explored areas of east-central Hidalgo and western Veracruz, we collected a specimen that did not match any of the recognized species of *Ophryacus* or *Mixcoatlus*. We made two more trips in 2013, during which we collected four additional individuals. This discovery triggered our interest in the genus *Ophryacus*, and a subsequent examination of museum specimens confirmed that these

specimens represent a taxon distinctive from *O. undulatus*. We found this population to be in *Ophryacus*, as opposed to *Mixcoatlus*, based on the presence of raised canthals with the same shape as the supraocular horns, divided subcaudals, a lack of palatine teeth, and the presence of a short, straight tail spine (Jadin et al., 2011). Nevertheless, the specimens we collected were not assignable to *O. undulatus*, as they differed in several important morphological characters. In these specimens, the supraocular horn is separated from the eye by one or two rows of supraocular scales, a condition not present in *O. undulatus*. Also, the shape of the raised canthals and supraocular horn is rounded, and not pointed as in *O. undulatus*. Furthermore, the members of this new population show less scale division on the head, resulting in fewer supralabials, fewer interrials, and fewer intersupraoculars than in *O. undulatus*. A long, plate-like upper preocular is present in *O. undulatus*, whereas in this population the upper preocular is short and square. Finally, the members of this new population show a unique color pattern on the head, consisting of a pale yellowish cream or white triangular marking behind the eye that extends from just below the supraoculars diagonally down onto the 5th and 6th supralabials, and occasionally farther back. Secondary pale markings of the same color also are present on the 1st and 3rd supralabials, whereas the color of the 2nd and 4th supralabials is the same as the ground color of the head. These markings are not present in *O. undulatus*. On the basis of 10 individuals examined, herein we describe the population of *Ophryacus* from the eastern Sierra Madre Oriental as a distinct species (Figs. 1, 2, 3), and compare this new species to other species of *Ophryacus* and *Mixcoatlus* present in the Sierra Madre Oriental (Fig. 4). Additionally, we examined new material from a population of *Ophryacus* that was described by Smith (1960) as *Bothrops sphenophrys*, but later was relegated to the synonymy of *O. undulatus* by Burger (1971) and Campbell and Lamar (1989, 2004). We found convincing morphological evidence, including supraocular horn shape and size, tail length, and subcaudal scale counts, that supports the distinctiveness of this population and its recognition as a species of *Ophryacus* (Figs. 5, 6, 7). We compare this species to related species in the Sierra Madre del Sur (Fig. 8), and also compare the head scutellation of all species of *Ophryacus* and *Mixcoatlus* (Figs. 9, 10). Finally, we mapped all of the available museum specimens and photographic vouchers with reliable locality data (Fig. 11). We also include photos of the type localities of the new species described herein, as well as of the third species of *Ophryacus* we revalidate (Fig. 12).

MATERIALS AND METHODS

Materials and Techniques

We collected snakes in the field during the day and night, and for future molecular analysis took DNA samples of muscle tissues and preserved them in 96% ethanol. We fixed specimens in buffered formalin (diluted to 10% of stock solution) and then transferred them to 70% ethanol for permanent storage in scientific collections. We recorded the colors in life based on notes taken on individuals in the field, and also from high quality digital photographs deposited in the University of Arizona Photographic Species Voucher Collection (UAZ-PSV). All museum abbreviations follow Sabaj-Pérez (2014), and we define those not listed. We examined specimens from every known population of *Ophryacus* and *Mixcoatlus*. We examined specimens in Mexican collections in person, as follows: MZFC, CNAR, EBUAP, Universidad Autónoma de Guerrero (UAG) and ENCB-IPN. To determine which species of *Ophryacus* are present in collections outside of Mexico, we examined high-quality digital images of all non-Guerrero specimens of *O. undulatus* in the following collections: AMNH, FMNH, USNM, KU, CU, and UIMNH (Appendix 1). We did not examine all the specimens from Guerrero in collections because there are many and all are from three general localities; however, we examined several specimens from each general locality. We plotted all the specimens examined on a distribution map (Fig. 11).

For terminology of scutellation and protocols for counting scales, we followed Burger (1971), Werman (1992), Gutberlet (1998), Campbell and Lamar (2004), and Jadin et al. (2011), with some deviations. Our counts are as follows: intersupraocular scales are those between the supraocular horns, not including the horns; interrials scales include the last upper supralabial; intercanthal scales are those between the canthals, but not including them; canthals are all the raised scales along the canthus rostralis, between the internasals and the supraoculars; postrostral internasals are all the scales between the nasals, immediately behind the rostral; anterior intercanthals are the scales immediately behind the postrostral internasals, between the canthals but not including them; and posterior intercanthals are the last row of scales between the canthals, but not including the canthals, anterior to the intersupraoculars.

Our abbreviations are as follows: TotL = total length; SVL = snout–vent length; TL = tail length; HL = head length; HW = head width; NW = neck width; HD = distance between supraocular horns; EW = eye width (= diameter); HoH = horn height; HoW = horn width; UPL = upper preocular length; UPH = upper preocular height; VS = ventral scales; and SS = subcaudal scales. We took measurements of the body and tail to the nearest 1 mm using a millimeter ruler, and those of the head, horns, and scales under a dissecting microscope using digital Vernier calipers. We counted dorsal scale rows behind the head at a distance of 1.5 times the HL, at midbody, and before the vent at a distance of 1.5 times the HL.

Geographical Data

We determined Mexican place names and localities from the Pueblos America website (www.PueblosAmerica.com, 2014) and Google Earth (2013). For distributional data and to create maps, we consulted the Global Biodiversity Information Facility online database (www.gbif.org; accessed 12 December 2014); when exact locality data were not available, we contacted the contributing institution for locality information. Aside from the collections listed above, we also included locality data from specimens housed in the following collections: CAS, CM, TCWC, UTA, and the Instituto Tecnológico Superior del Oriente del Estado de Hidalgo (ITAH). We also consulted Canseco-Márquez and Gutiérrez-Mayén (2010) for additional records, as well as researchers working in the area (see Acknowledgments).

RESULTS

In 2010, we searched for rattlesnakes in eastern Hidalgo and west-central Veracruz in an attempt to define the eastern distributional limits of *Crotalus aquilus* (Klauber, 1952). On the evening of 16 September 2010, we found a bright green adult male pitviper crossing a road at approximately 2250 h. Although superficially the pitviper was similar to *O. undulatus*, it also showed conspicuous differences from individuals of that species we had seen from other localities in southern Veracruz, Puebla, Oaxaca, and Guerrero (Fig. 3A). This colorful new pitviper, which appears to be endemic to the Sierra Madre Oriental of eastern Mexico, shall be known as:

Ophryacus smaragdinus sp. nov.

Figs. 1–3, 4A, C, 9A, B, C

Ophryacus undulatus—Flores-Villela et al. (1992). *Texas Journal of Science* 44: 249.

Ophryacus undulatus—Camarillo (1995). *Bulletin of the Maryland Herpetological Society* 31: 196.

Ophryacus undulatus—Campbell and Lamar (2004). *The Venomous Reptiles of the Western Hemisphere* p. 454 (in part).

Ophryacus undulatus—Mendoza-Paz et al. (2006). *Herpetological Review* 37: 109 (in part).

Ophryacus undulatus—Ramírez-Bautista et al. (2010). *Lista Anotada de los Anfibios y Reptiles del Estado de Hidalgo, México* p. 77.

Ophryacus undulatus—Solano-Zavaleta et al. (2010). *Herpetological Review* 41: 381.

Ophryacus undulatus—Ramírez-Bautista et al. (2014). *Los Anfibios y Reptiles de Hidalgo, México: Diversidad, Biogeografía y Conservación*. p. 177.

Holotype (Fig. 1): An adult female, MZFC 29290, collected by Jason M. Jones and Iván T. Ahumada-Carrillo on 2 November 2013 at Los Ocotes (20.601542, -98.469708; datum WGS 84; elev. 2,150 m asl), Zilacatipan, Municipio de Huayacocotola, Veracruz, Sierra Madre Oriental, Mexico.

Paratypes: Seven specimens. MEXICO: HIDALGO: El Potrero, Municipio de Tenango de Doria (20.314922, -98.229653; datum WGS 84; elev. 2,200 m), an adult male collected 25 August 1990 by students of the Escuela Nacional Estatal y Profesional de Iztacala, UNAM (MZFC 21140); “Doria,” Municipio de Tenango de Doria (20.314922, -98.229653; datum WGS 84; elev. 2,200 m), an adult male collected on 14 July 1990 by Efraín Hernández-García (MZFC 04825). OAXACA: San Martín Caballero, Municipio de San José Tenango (18.108175, -96.633981; datum WGS 84; elev. 1,360 m), an adult male collected 25 May 1994 by Mario Mancilla-Moreno (MZFC 13556); San Martín Caballero, Municipio de San José Tenango (18.108175, -96.633981; datum WGS 84; elev. 1,360 m), a juvenile female collected 28 May 1994, collector unknown (MZFC 13557). PUEBLA: Xucayucan,

Municipio de Tlatlauquitepec (19.895744, -97.471700; datum WGS 84; elev. 1,630 m), a juvenile female collected 27 May 2005 by Israel Solano-Zavaleta (MZFC 17663). VERACRUZ: Cerro La Campana, Ticuautipan, Municipio de Xico (19.439500, -97.078078; datum WGS 84; elev. 2,045 m), a subadult female collected on 26 October 2003 by Itzel Durán Fuentes (MZFC 20582); and Zilacatipan, Municipio de Huayacocotla (20.655761, -98.424894; datum WGS 84; elev. 1,790 m), a subadult female, collected on 2 November 2013 by Jason M. Jones and Iván T. Ahumada-Carrillo (MZFC 29289).

Diagnosis: *Ophryacus smaragdinus* can be distinguished from all other pitvipers in North America by the combination of the following characters: absence of a rattle; divided subcaudal scales; presence of a supraocular horn that is not in immediate contact with the eye; fewer than 30 interriotal scales; and usually fewer than 10 supralabials on each side of the head (Fig. 2). A distinctive white, cream, or pale yellow triangular marking is present on the lateral surfaces of the head, starting just below the suboculars and extending diagonally onto the 5th and 6th supralabials; this pale marking often extends onto the 7th and 8th (if present) supralabials. Secondary pale markings also are present on the 1st and 3rd supralabials, whereas the color of the 2nd and 4th supralabials is the same as the



Fig. 1. (A) General view of the holotype of *Ophryacus smaragdinus* sp. nov. (MZFC 29290) from Los Ocotes, Municipio de Huayacocotla, Veracruz. Dorsal (B) and ventral (C) views of holotype in preservative.

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ground color of the head. This pale-colored triangular marking and the associated secondary pale markings are diagnostic for this species, and when viewing photographic material are helpful in distinguishing it from its congeners (Fig. 9A, B, C).

Description: Adults of this moderate-sized, stout pitviper reach a total length of ca. 450–600 mm. The tail comprises 12–15% of the total length and is prehensile. The head is wide, with a rounded snout from a dorsal profile and a blunt (not pointed) snout from a lateral profile. The head scalation is as follows: the rostral is broader than high; supraocular horns are present, rounded and taller than wide, and separated from the eye by one or occasionally two rows of small supraocular scales; 3–5 canthals are present between the nasals and the supraocular scales; the canthals are prominent but rounded, and not pointed; the raised canthals form a slight ridge along the canthus rostralis; the loreals do not project laterally; there are 1–4 postrostral internasals, which are small and keeled; the row directly posterior to the internasals contains 5–7 anterior intercanthals, which are heavily keeled and not noticeably large or flat; 7–9 posterior intercanthals, 11 intersupraoculars, and 22–29 interrials are present; the scales on the dorsal surfaces of the snout and head are heavily keeled; the postnasal is separated from the 1st supralabial, and the prelacunal scale is separated from the 2nd supralabial, usually by one subfoveal; the sublacunal scale is divided; 2–3 interlacunolabials (includes lacunal and supralabial) and 3–4 (not 5) interoculabials (includes subocular and supralabial) are present; there are three preoculars, the upper one is the largest, but usually only measures 25–50% of the eye width (maximum 65%); the middle preocular is not fused with the supralacunal and the lower preocular usually is not in contact with the eye; a loreal is present and divided; prefoveals and subfoveals usually are present; usually there is one row of 4–6 supraoculars between the horn and the eye, and occasionally a second row of supraoculars is present, consisting of 2–3 scales; there are 3–5 suboculars, 3–5 postoculars, and usually 7–9 supralabials (maximum 10). The ventrals are 155–166; the subcaudals are 39–46; the dorsal scale rows are 21–21–17; and the subcaudals are divided. The color pattern is as follows: the ground color is emerald or olive green, brown or tan, and adults are not gray; 37–46 dark blotches are present on the dorsal surface of the body; the dark blotches are outlined in black, and usually are dark brown or contain a paler shade of brown in the middle, although often the green ground color is so pronounced that the centers of the blotches appear green; the dorsal blotches usually are broken up middorsally, and interconnected by an undulating dark stripe on some or most of the body; a row of lateral blotches is present, at the same interval as the dorsal blotches, and usually occupies the 3rd, 4th, and 5th dorsal scale rows; these blotches sometimes are faded or indistinct in adults, but typically are obvious in juveniles; the tail usually is the same dark color as the dorsal blotches, and contains 5–12 pale bands that usually are interrupted dorsally; the head is the same color as the body, and contains black spots and markings; and a dark postocular stripe is present and usually is outlined in black along the lower edge.

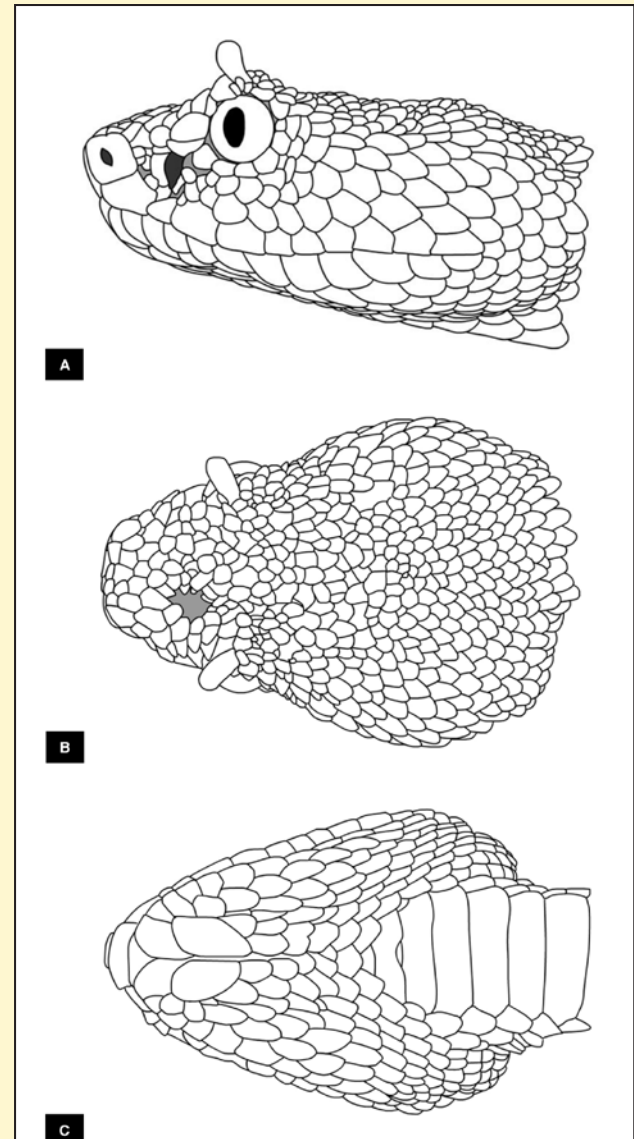


Fig. 2. Lateral (A), dorsal (B), and ventral (C) views of the head of the holotype *Ophryacus smaragdinus* sp. nov. (MZFC 29290) from Los Ocotes, Municipio de Huayacocotla, Veracruz.

Drawings © Jason M. Jones



Fig. 3. Variation in *Ophryacus smaragdinus* sp. nov. (A) specimen (UAZ 57622-PSV) from Los Ocotes, Municipio de Huayacocotla, Veracruz; (B) specimen (UAZ 57620-PSV) from Los Ocotes, Municipio de Huayacocotla, Veracruz; (C) specimen (UAZ 57626-PSV) from Santa Catarina, Municipio de Acaxochitlán, Hidalgo; (D) paratype (MZFC 17663) from Xucayucan, Municipio de Tlatlauquitepec, Puebla; (E) paratype (MZFC 4825) from Doria, Municipio de Tenango de Doria, Hidalgo; and (F) paratype (MZFC 13556) from San Martín Caballero, Municipio de San José Tenango, Oaxaca.

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Comparisons: *Ophryacus smaragdinus* is morphologically similar to *O. undulatus* and species of the genus *Mixcoatlus*, including *M. melanurus*, *M. browni*, and, to a lesser degree, *M. barbouri*. *Ophryacus smaragdinus* can be distinguished from *O. undulatus* by the presence of a supraocular horn that is separated from the eye by one or two rows of small supraocular scales (Figs. 2A, 9A, B, C), as well as by the presence of fewer supralabials (often seven or eight on at least one side, but no more than 10), whereas in *O. undulatus* usually 11 or more are present on each side, but no fewer than nine. In *O. smaragdinus* 1–4 postrostral internasals are present, followed by a row of 5–7 anterior intercanthals, all of which are small and distinctly keeled. In contrast, 2–3 postrostral internasals are present in *O. undulatus*, which lack a keel and are followed by a row of 5–7 anterior intercanthals, of which the

outer ones are large and flat and the smaller inner scales are slightly keeled. In *O. smaragdinus* 22–29 interrials are present, whereas in *O. undulatus* there are 31–36. The upper preocular in *O. smaragdinus* is shorter than in *O. undulatus*, with a length of 25–50% of the eye diameter, compared to 70% or more in the latter species (Figs. 9, 10). The condition of the canthals also differs in the two species; whereas they might be prominent in both, the canthals of *O. smaragdinus* are rounded and slightly elevated, but those in *O. undulatus* are pointed and raised into horns (Figs. 9, 10). Finally, although the coloration of both species is variable, individuals of *O. smaragdinus* can be distinguished from those of *O. undulatus* by the presence of a white, cream, or pale yellow triangular marking that extends from the posterior portion of the eye diagonally onto the 5th and 6th supralabials. This triangular marking is not present in *O. undulatus* (Figs. 4, 9). See Table 1 here and below for a comparison of the distinctive characters among the various species.



Fig. 4. Species of Crotalinae from the Sierra Madre Oriental of eastern Mexico: (A) *Ophryacus smaragdinus* sp. nov. from the vicinity of Los Ocotes, Municipio de Huayacocotla, Veracruz; (B) *O. undulatus* (UAZ 57623-PSV) from Puerto del Aire, Municipio de Acultzingo, Veracruz; (C) *O. smaragdinus* sp. nov. (UAZ 57626-PSV) from Santa Catarina, Municipio de Acaxochitlán, Hidalgo; (D) *O. undulatus* (UAZ 57627-PSV) from the vicinity of Zongolica, Municipio de Zongolica, Veracruz; (E) *Mixcoatlus melanurus* (UAZ 57628-PSV) from 1.6 km W of San Andrés Cacaloapan, Municipio de Tepanco de López, Puebla; and (F) *Cerrophidion petlalcalensis* from Cerro Petlalcalca, Municipio de San Andrés Tenajapa, Veracruz.

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Table 1. Variation of selected morphological characters among the species of *Ophryacus* and *Mixcoatlus melanurus*. We separated populations of *O. undulatus* from the Sierra Madre del Sur and from the Sierra Madre Oriental to show some differences between the two populations. We also included the available information on the type specimen of *Ophryacus undulatus* (Jan, 1859). HCO = horn in contact with eye; HTS = horn tip shape; HS = horn shape; IN = internasal shape; SSh = snout shape; SL = supralabials; IOL = interoculabials (including subocular and supralabial); %TL/TotL = % tail length of total length (males); ISO = number of scales between the horns (intersupraoculars); IR = number of interriectals (range); VS = ventrals; FM = facial markings; UP L/H = upper preocular length/height; UPL/EyeW = upper preocular length/eye width ratio; and Canth = canthal condition.

Characters	<i>Ophryacus smaragdinus</i> sp. nov.	<i>Ophryacus undulatus</i> (SMDS)	<i>Ophryacus undulatus</i> (SMOri)	<i>Ophryacus sphenophrys</i> new comb.	<i>Ophryacus undulatus</i> TYPE	<i>Mixcoatlus melanurus</i>
HCO	No	Yes	Yes	Yes	Yes	Yes
HTS	Rounded	Pointed	Usually Pointed	Pointed	Rounded	Slightly Pointed
HS	Thin and tall	Thin and tall	Thin and tall	Wider than tall	Thin and tall	Wide
IN	Heavily keeled	Slightly keeled	Flat, unkeeled	Slightly keeled	Flat	Flat
SSh	Blunt	Pointed	Pointed	Pointed	Slightly pointed	Blunt
SL	7–10	10–12	9–12	10	12	10–12
IOL	3–4	4–5	3–4	3	3	4–5
%TL/TotL	12.4–15%	11.9–14.2 %	8.8–13.4%	17.3%	—	9–12.5%
ISO	11	15–22	13–18	10–12	12	9–12
IR	22–29	31–36	31–36	33	—	27–29
VS	154–166	165–174	160–174	171	170	141–152
FM	Triangular pale marking laterally	No pale marking	No pale marking	No pale marking	—	No pale marking
UPL/H	1–1.8 × long as high	1.8–2.9 × long as high	2.1–3.3 × long as high	1.5 × long as high	—	1.1–2 × long as high
UPL/EyeW	25–66%	70–80%	80–100%	65%	70%	30–50%
Canth	Slightly raised, rounded	Prominent and pointed	Prominent and pointed	Pointed then fused with horn	Not visibly pointed	Flat

Ophryacus smaragdinus can be distinguished from *O. undulatus* from the Pacific versant of the Sierra Madre del Sur, Oaxaca (*Ophryacus sphenophrys* new comb.; see below) by the presence of a supraocular horn that is not in immediate contact with the eye, and which is taller than wide (Fig. 2). In *O. undulatus* from the Pacific versant of the Sierra Madre del Sur, Oaxaca, the horn is wider than tall and in contact with the eye (Figs. 6A; 10C, D). Furthermore, four characters also are useful in distinguishing the two species. Values for *O. undulatus* from the Pacific versant of the Sierra Madre del Sur, Oaxaca follow those for *O. smaragdinus*: a shorter tail in males (less than 15% of SVL, compared to over 17%), fewer supralabials (usually 7–9, vs. 10), fewer interriectals (22–29, as opposed to 33), and fewer subcaudals (39–46, as opposed to 51–57).

Ophryacus smaragdinus can be distinguished from *M. melanurus* by the presence of divided subcaudals, a supraocular horn that is separated from the eye by one or two rows of small supraoculars, and fewer supralabials (7–9 vs. 10–14 in *M. melanurus*). Furthermore, *M. melanurus* is gray and not green, whereas *O. smaragdinus* is green or brown and not gray (Fig. 4). *Ophryacus smaragdinus* can be distinguished from the other two species of *Mixcoatlus* by the presence of supraocular horns, as well as by the number of intersupraoculars (11 in *O. smaragdinus* vs. 1

in *M. browni* and 3–4 in *M. barbouri* (Figs. 9, 10). Additionally, in *O. smaragdinus* one or two scales are present between the subocular and the supralabials, whereas in *M. browni* and *M. barbouri* the suboculars are in contact with the supralabials (Figs. 9, 10).

Description of the Holotype: The holotype (MZFC 29290) is an adult female with the following characteristics: rostral broader than high (4.9 mm × 2.5 mm); four internasals; canthals 5/5 (all bilateral scale counts are left/right), prominent but rounded; large supraocular horn with the tip rounded, $\frac{2}{4}$ times as high as wide; supraocular horn separated from the eye by one row of supraoculars; 11 intersupraoculars between the horns (not counting the horns); nasal indistinctly divided above and below the naris; loreals 2/2; preoculars 3/3, with upper preocular the largest, longer than high, but only by 15%, UPL/EW ratio is 0.62; middle preocular small, in contact with the supralacunal but not fused with it; lower supraocular medium-sized, squarish, not in contact with the eye; supraoculars 6/6; suboculars 3/3; postoculars 3/4; six anterior intercanthals; nine posterior intercanthals; scales on the frontal region and intersupraoculars small, rounded and distinctly keeled; 28 interriectals; supralabials 10/10, suboculars separated from the supralabials by two rows of small scales; sublacunal separated from the 1st and 2nd supralabials by one subfoveal scale; prefoveals 3/3; subfoveals 4/3; postfoveals 4/3; infralabials 11/11; mental broader than long (3.6 mm × 2.2 mm), two pairs of chin shields flank mental groove; six gular scales between the chin shields and 1st ventral; 165 ventrals; 41 subcaudals; cloacal scute (= anal plate) single; subcaudals divided; tail spine short, pointed with a slight upward turn; dorsal scales rounded, keeled; and dorsal scale rows 21-23-17 (Figs. 1, 2).

The measurements are as follows: TotL = 552 mm; SVL = 489 mm; TL = 63 mm; HL = 27 mm; HW = 18 mm; and NW = 7.7 mm. The TL = 11.3% of the TotL; the HL = 49% of the TotL; the HL/HW ratio = 1.52. The HoH = 2.9 mm; the HoW = 1.3 mm; and the HoH = 2.23 times the HoW. The HD = 9.4 mm; the EW = 3.7 mm; the UPL = 2.3 mm; the UPH = 2 mm; the UPL to UPH ratio = 1.15; and the UPL to EW ratio = 0.63.

The coloration in life is emerald green with dark dorsal blotches along the entire length of the body (Fig. 1). The dorsal blotches are olive green to brownish-olive in the center, and outlined in black. Occasionally these blotches are divided middorsally and become offset to form a discontinuous undulating middorsal stripe. Corresponding lateral blotches accompany each dorsal blotch, and usually consist of 4–6 scales located on the 4th, 5th, and 6th dorsal scale rows. When the dorsal blotches are split and offset, their accompanying lateral blotch is aligned with the dorsal blotch on each side. Several dorsal blotches show a tendency for additional splitting, albeit laterally, and result in two accompanying lateral blotches; thus, 46 lateral blotches are present on the right side and 47 on the left. Black speckling is present on all the body scales, sparsely on the pale-colored emerald scales of the ground color and more heavily on the darker olive or brown scales inside the dark dorsal blotches. The lateral blotches are smaller than the dorsal blotches, and thus consist almost exclusively of the black outline with olive and brown speckling in the middle. The dorsal ground color of the head and body are the same, emerald on the sides and olive on top. Paired black spots are present in the interorbital region, and another pair in the parietal region. The horns are lime green with black lines. Two undefined blotches are discernable on the posterior portion of the head, which extend posteriorly onto the nuchal area; the blotches are olive green in the middle and outlined in black, with black flecking, similar to the dorsal blotches. Distinctive yellowish-cream spots are present on the sides of the head, with the first blotch restricted to the anterior two-thirds of the 1st supralabial. The second pale blotch is restricted to the 3rd supralabial and the adjacent subfoveal, and is outlined in black. The third and most distinctive pale blotch is triangular in shape, starting just below the posterior border of the eye and extending diagonally onto the 6th, 7th, and 8th supralabials, and posteriorly is outlined in black. A dark green postocular stripe is present, starting at the posterior border of the orbit and extending diagonally toward the rictus, and includes the 9th and 10th supralabials. The tail is dark brownish-gray with a pattern of 11 thin pale green bands that are broken middorsally and offset. The gular region is pale cream and contains sparse black speckling. The venter is yellow anteriorly grading to lime-green posteriorly, and covered with black speckling; the speckling is moderately sparse anteriorly and progressively denser posteriorly. The subcaudals follow the same trend as the ventral coloration, with a lime-green ground color and dense black speckling on the anterior two-thirds of the tail; the posterior one-third of the underside of the tail is yellow with almost no black speckling (Fig. 1). In preservative, the holotype turned pale bluish-green, with the dark dorsal blotches brown and outlined in black. Black speckling is present on all the body scales. The underside of the head and neck is orangish-brown, and the rest of the underside is cream with dark gray speckling (Fig. 1B, C).

Variation: We examined 10 individuals of *O. smaragdinus*, including the type-series and two additional topotypical individuals, a juvenile male and an adult female that were not collected. Of these, there were three juveniles and seven adults. We consider snakes under 350 mm TotL to be either juveniles or sexually immature, and those above 350 mm as adults. Our consideration is based on studies of other Mexican high-elevation pitvipers that set the limit between 300 (Dorcas, 1992) and 350 mm (Holycross and Goldberg, 2001; Holycross et al., 2002). We provide the size and proportion character ranges separately for adults (ad.) and juveniles (juv.) wherever ontogenetic changes might influence their values (Campbell, 1989; Holycross and Goldberg, 2001). The variation is as follows: TotL 368–590.2 mm (\bar{x} = 491.4 mm; n = 6) ad., 214–348.4 mm (\bar{x} = 288.8 mm; n = 3) juv.; SVL 422–523.2 mm (\bar{x} = 436 mm; n = 7) ad., 185–302 mm (\bar{x} = 249 mm; n = 3) juv.; TL 46–82 mm (\bar{x} = 62.6 mm; n = 6) ad., 29–46.4 mm (\bar{x} = 39.9 mm; n = 3) juv.; HL 16.3–27.0 mm (\bar{x} = 23.1 mm; n = 7) ad., 13.7–16.8 mm (\bar{x} = 15.5 mm; n = 3) juv.; HW 11.8–19.6 mm (\bar{x} = 16.3 mm; n = 7) ad., 9.7–11.2 mm (\bar{x} = 10.6 mm; n = 3) juv.; HL/TotL 3.9–5.4% (\bar{x} = 4.6%; n = 6) ad., 4.4–5.4% (\bar{x} = 5.3%; n = 3) juv.; TL/TotL 12.4–15% (\bar{x} = 12.8%; n = 6) ad., 13.3–14.5% (\bar{x} = 13.8%; n = 3) juv.; VS 153–166 (\bar{x} = 160; n = 10); SC 39–46 (\bar{x} = 43.1; n = 8); dorsal scale rows 19–22 behind the head (\bar{x} = 21; n = 10), 21 or 23 at midbody (\bar{x} = 21.2; n = 10), and 16–18 anterior to the vent (\bar{x} = 17; n = 10); internasals 1–4 (\bar{x} = 2.6; n = 9); anterior intercanthals 8–10 (\bar{x} = 6.1; n = 7); interrials 22–28 (\bar{x} = 25.2; n = 9); canthals five on each side, but one individual has six on one side (\bar{x} = 5.1; n = 6); postoculars 3–4 (\bar{x} = 3.3; n = 6); supraoculars (between horn and eye, not counting horn) 5–6 (\bar{x} = 5.2; n = 4); HoH 2.9–3.3 mm (\bar{x} = 2.8 mm; n = 7) ad., 1.9–2.2 mm (2.0 mm; n = 3) juv.; HoW 0.74–1.3 mm (\bar{x} = 1.0 mm; n = 7) ad., 0.75–0.95 mm (\bar{x} = 0.9 mm; n = 3) juv.; HoH to HoW ratio 1.8–4.4 times higher than wide (\bar{x} = 2.23; n = 10); HD 6.3–10.4 mm (\bar{x} = 8.7 mm; n = 7) ad.; 5.2–6.6 mm (\bar{x} = 5.7 mm; n = 3) juv.; HD to HW ratio 0.48–0.60 (\bar{x} = 0.52; n = 10); HD to HL ratio 0.30–0.44 (\bar{x} = 0.35; n = 10); EW 2.6–4.2 mm (\bar{x} = 3.3 mm; n = 10); HoH to EW ratio 0.63–0.94 (\bar{x} = 0.78; n = 10); supraocular horn separated from eye by 1–2 supraocular scale rows (\bar{x} = 1.1; n = 10); UPL 1.3–2.3 mm (\bar{x} = 1.93; n = 6) ad., 0.71–1.22 mm (\bar{x} = 0.94 mm; n = 3) juv.; UPH = 0.90–2.0 mm (\bar{x} = 1.2 mm; n = 6) ad., 0.57–1.1 mm (\bar{x} = 0.82 mm; n = 3) juv.; UPL to UPH ratio 1.1–1.9 times long as high (\bar{x} = 1.4; n = 9); UPL to EW ratio 0.26–0.66 (\bar{x} = 0.46; n = 9); supralabials 7–10 (\bar{x} = 8.5; n = 9.5); interoculabials, including suboculars and supralabials 3–4 (\bar{x} = 3.7; n = 9.5); interlacunolabials, including lacunals and supralabials 2–3 (\bar{x} = 2.5; n = 9.5); infralabials 9–11 (\bar{x} = 10.4; n = 5); and gular scales between chin shields and 1st ventral 5–6 (\bar{x} = 5.5; n = 5). The dark dorsal blotches range from 37 to 46; the blotches are independent, split middorsally, or interconnected by an undulating stripe. One or two lateral blotches accompany each dorsal blotch (Fig. 3).

Distribution and Natural History: *Ophryacus smaragdinus* apparently is restricted to montane cloud forest, humid pine-oak woodland, and pine forest (Fig. 12A), but also has been found in disturbed areas with secondary vegetation. Although this species appears to be less arboreal than what has been reported for *O. undulatus* in Guerrero and Oaxaca (Campbell and Lamar, 2004: 452), it has been collected at a height of up to 1 m in low bushes (Flores-Villela et al., 1992). Other individuals have been found under fallen logs, in woodpiles, and on the ground in vegetation. Whereas most individuals have been encountered during the day, one individual from Veracruz (UAZ-57622-PSV) was found crossing a road at 2258 h during foggy weather.

Ophryacus smaragdinus has been collected in east-central Hidalgo, west-central Veracruz, northeastern Puebla, and north-central Oaxaca, where it ranges along the humid eastern slopes of the Sierra Madre Oriental from at least as far north as Zilacatipan, in the municipality of Huayacocotla, Veracruz, south to at least San Martín Caballero, in the municipality of San José Tenango, Oaxaca. Its elevational distribution ranges from about 1,400 m in Oaxaca to at least 2,340 m in Hidalgo and Veracruz (see Fig. 11).

Etymology: The specific epithet is derived from the Latin word *smaragdinus*, an adjective meaning “emerald-green,” in reference to the emerald green ground coloration exhibited by most individuals of this species.

Remarks: A taxonomic question that became evident during our review of *Ophryacus* was the status of *Bothrops sphenophrys* Smith 1960, which was synonymized with *O. undulatus* by Campbell and Lamar (1989). Smith (1960) described *B. sphenophrys* from a single specimen collected by W. Leslie Burger in south-central Oaxaca. Upon examining all of the preserved specimens of *Ophryacus* in Mexican collections, we found a second specimen assignable to *B. sphenophrys*, as defined by Smith (1960). The specimen (MZFC 16680) is an adult male found between Buenavista Loxicha and La Soledad, in the municipality of Candelaria Loxicha, Oaxaca, fewer than 4 km from where the type specimen of *B. sphenophrys* was collected (Figs. 6, 7, 10D). A third specimen assignable

to *B. sphenophrys* was collected in 2013 at the type locality in Oaxaca (Figs. 5, 8A, 10C). Although this specimen has not been deposited in a formal collection, we had the opportunity to examine high quality digital photographs and review measurements taken from the animal. After reviewing the new material available for *B. sphenophrys*, we concluded that the species is assignable to the genus *Ophryacus*, as defined by Jadin et al. (2011), and the name is applied here. *Ophryacus sphenophrys*, new comb., presents divided subcaudals, raised canthals, a short and straight tail spine, and the absence of palatine teeth, all of which are diagnostic of *Ophryacus* (Jadin et al., 2011). Smith (1960) identified eight diagnostic characters used to distinguish *B. sphenophrys* from *O. undulatus*. Most of these characters fall within the range of variation for *O. undulatus*, and thus Campbell and Lamar (1989, 2004) considered *O. sphenophrys* as a junior synonym of *O. undulatus* and included the characters listed for *O. sphenophrys* in their *O. undulatus* account; however, they did not re-examine the type specimen of *O. sphenophrys* or topotypic material of *O. undulatus* from the Sierra Madre Oriental. With the collection of additional material assignable to *O. sphenophrys*, we decided to review all the morphological characters known to be of importance in *Ophryacus*, to determine the validity of the taxon *O. sphenophrys*.

Although many of the characters listed by Smith (1960) fall within the range of variation for *O. undulatus*, several important morphological characters are not evident in *O. undulatus*, which consistently distinguish *O. sphenophrys* from *O. undulatus*. A broad supraocular horn is present on *O. sphenophrys*, which is 1.5 times as wide as it is tall on MZFC 16680 (Fig. 6), and twice as wide as tall on both the holotype (UIMNH 6262) and the third individual examined by us (Fig. 5, 10C). Although Campbell and Lamar (1989) indicated that this character might not be of significance, we found no specimen of *O. undulatus* with a subocular horn that is wider than 66% the height of the horn. The wide horn of *O. sphenophrys* is the only supraocular, and it contacts the upper preocular (Figs. 5, 6, 8A,

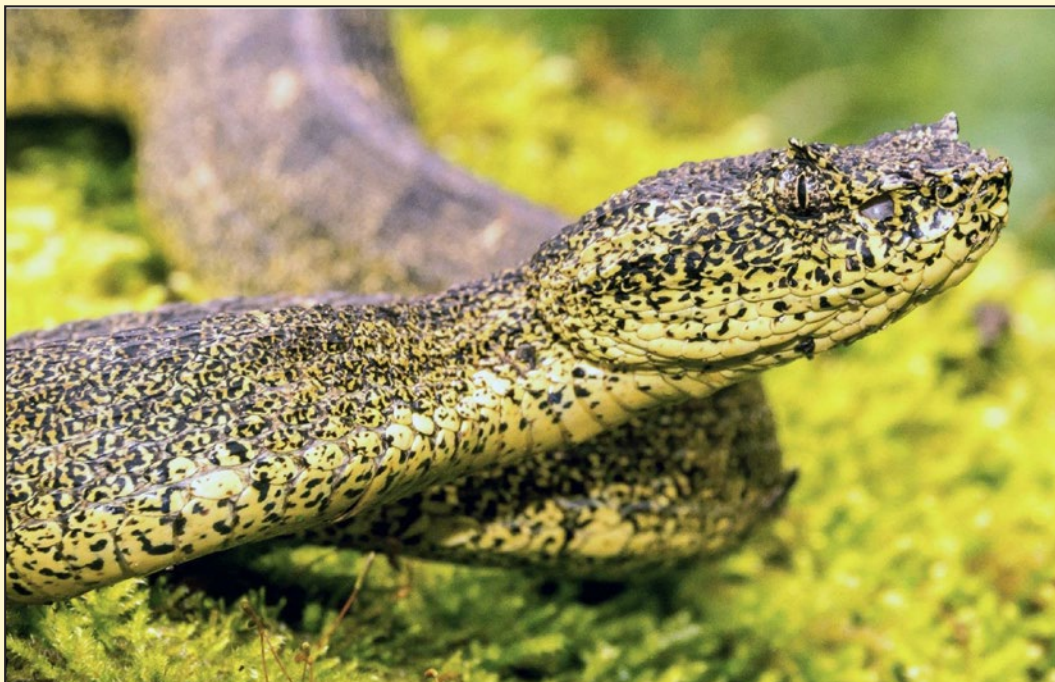



Fig. 5. Lateral view of the head of topotypic *Ophryacus sphenophrys* in life from Parador La Soledad, Municipio de Candelaria Loxicha, Oaxaca.  © Eli García-Padilla

10C, D). At least three supraoculars are present in *O. undulatus*, and the longest horn is not in contact with the upper preocular. Another important character is that the tail of male *O. sphenophrys* is proportionally longer than that of any other species of *Ophryacus*. The tail length is 16.3–17.3% ($n = 3$) of the total length in male *O. sphenophrys*, whereas typically it is 11–13% (one with 14.5%; $n = 6$) in male *O. undulatus*. Also, 51–57 subcaudals ($n = 3$) are present in male *O. sphenophrys*, whereas 36–51 ($n = 6$) are present in male *O. undulatus*. Finally, the head scales

of *O. sphenophrys* show less division than those of *O. undulatus*. In *O. sphenophrys* there are 10–12 intersupraoculars, the holotype with 10 and MZFC 16680 with 12 (Fig. 6). Although this falls within the ranges indicated by Campbell and Lamar (1989, 2004) for *O. undulatus sensu lato*, it no longer does with the description of *O. smaragdinus*. The range of supraoculars for *O. undulatus* now is 13–22, and at least 15 supraoculars are present in all of the *Ophryacus* not assignable to *O. sphenophrys* we examined from the Sierra Madre del Sur of Guerrero and Oaxaca. Similarly, four anterior intercanthals are present in *O. sphenophrys*, whereas in *O. undulatus* there are at least five (one specimen), and usually nine or 10. Likewise, *O. sphenophrys* exhibits one large scale between the suboculars and the 4th and 5th supralabials, for a total of three interoculabials, whereas all of the *O. undulatus* we examined from the Sierra Madre del Sur of Guerrero and Oaxaca exhibit at least two and often three scales between the suboculars and the supralabials, for a total of 4–5 interoculabials (Figs. 8B, C, D, 10A, B).

As no detailed description of the coloration of *O. sphenophrys* in life exists, we provide one here. The one adult specimen of *O. sphenophrys* for which we have photographs in life (Figs. 5, 10C) shows a bright yellow ground color with black stippling and reticulations over the entire dorsal and lateral surfaces of the body, and 40 dark brown and black pairs of dorsal blotches that are offset on either side of the body but connected by an undulating middorsal stripe. Small lateral blotches are present on the 1st, 2nd, and 3rd dorsal scale rows, which lack some of the stippling and thus appear bright yellow, like the ground color. The head is the same color as the body, with black stippling throughout; however, the stippling is most dense on the dorsal surface of the head behind the interorbital area and least dense on the postorbital area and between the eyes, suggesting a remnant of a postorbital stripe and pale interorbital area. A dark blotch in the shape of the letter “M” is present on the parietal portion of the head, starting immediately posterior to the horns and extending two thirds of the way to the neck. A pair of dark nuchal spots that resembles two scythes facing each other is present on the posterior part of the head; the spots extend approximately 12 scales onto the neck. The venter is yellow and flecked with small black spots; the flecking increases in density from the chin and gular region to the subcaudals.

We were unable to locate photos of MZFC 16680 in life, but the specimen, collected in 2003, is in good condition (Figs. 7, 10D). The dorsal surfaces are olive-gray, with a peppering of black flecks over the entire body. Two rows of darker gray-green blotches are present on each side of the dorsum; most are fused middorsally by rhombs, but less so on the anterior portion of the body. The lateral surfaces are the same color as the remainder of the dorsum, except for on the lower four scale rows where the ground color is more yellow. Large dorsolateral spots that lack speckling are present; the spots are similar in color to the dorsal coloration and outlined in black, and typically are located on the 2nd, 3rd, and 4th dorsal scale rows and usually are two or three scales long and three scales tall. The tail

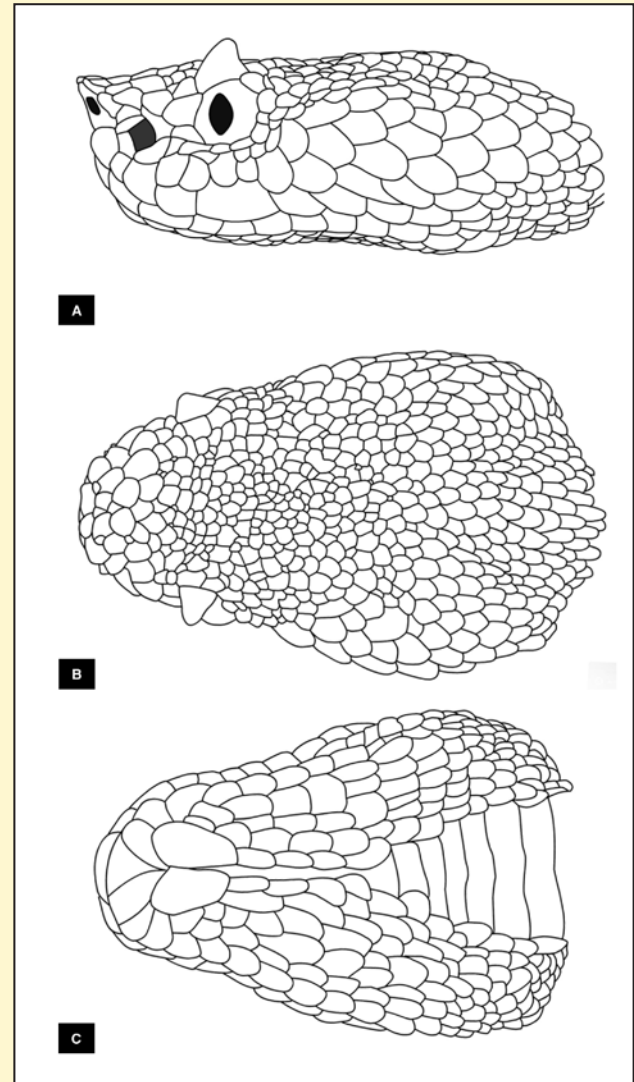


Fig. 6. Lateral (A), dorsal (B), and ventral (C) views of the head of a toptypical *Ophryacus sphenophrys* (MZFC 16680) from near la Soledad, Municipio de Candelaria Loxicha, Oaxaca.

Drawings © Jason M. Jones

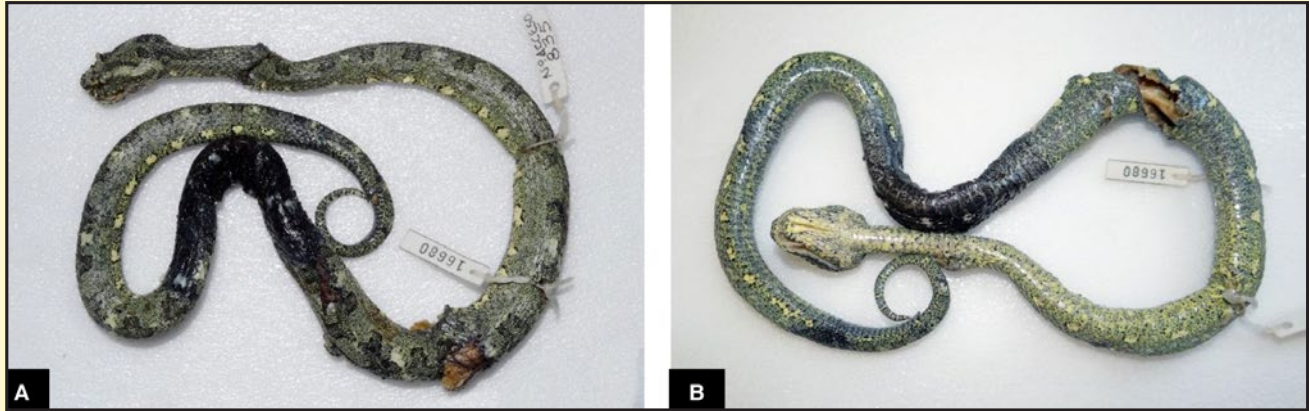


Fig. 7. Dorsal (A) and ventral (B) views of a topotypical *Ophryacus sphenophrys* (MZFC 16680) from near la Soledad, Municipio de Candelaria Loxicha, Oaxaca, in preservative. © Christoph I. Grünwald

is a darker olive-green than the body, and contains pale yellow banding. The head scales are speckled with green, yellow, and black. No discernable marks, stripes, or pale markings are present on the labials. An indistinct pale gray-green postocular stripe is present, which lacks black markings. A pale cream interorbital marking is present, followed by a pair of similar dark blotches that extend onto the neck. These blotches are broken up into three pairs, one directly behind the horn, one on the posterior portion of the head, and another on the neck. The venter is yellow with black speckling along the length of the body.

Key to the Species of *Ophryacus* and *Mixcoatlus*

- 1a. No supraocular horns present on head, five or fewer intersupraocular scales, middorsal scales at midbody moderately slender and pointed, subocular series in contact with supralabials **2**
- 1b. Supraocular horns present on head; nine or more intersupraocular scales; middorsal scales at midbody broad and obtusely rounded; suboculars separated from supralabials by at least one scale **3**
- 2a. One intersupraocular; 19–22 interriectals; no subfoveals *Mixcoatlus browni*
- 2b. Three intersupraoculars; 22–26 interriectals; a single subfoveal. *Mixcoatlus barbouri*
- 3a. Subcaudals entire; canthals flat; fewer than 152 ventrals *Mixcoatlus melanurus*
- 3b. Subcaudals divided; canthals raised, either pointed or rounded; more than 154 ventrals **4**
- 4a. Supraocular horn not in contact with eye, separated by one or two small scales; rounded canthals and supraocular horn; 10 or fewer supralabials; 22–29 interriectals, pale triangular marking extends diagonally from eye onto 5th and 6th supralabials. *Ophryacus smaragdinus*
- 4b. Supraocular horn in direct contact with eye; pointed canthals and supraocular horn; nine or more supralabials; 31–36 interriectals; no pale triangular marking on lateral sides of head. **5**
- 5a. Supraocular horn wider than tall and in contact with upper preocular; tail more than 17% of total length in males; upper preocular 1.5 times longer than high; 10–12 intersupraoculars (not counting horns) and only four anterior intercanthals (lowest count). *Ophryacus sphenophrys*
- 5b. Supraocular horn taller than wide and not in contact with upper preocular; tail 14% or less of total length in males; upper preocular usually twice or more longer than high; 13 or more intersupraoculars (not counting horns) and five or more anterior intercanthals (lowest count). *Ophryacus undulatus*

DISCUSSION

History of *Ophryacus undulatus* and Origin of the Type Specimen

Jan (1859) described *Trigonocephalus (Atropus) undulatus* on the basis of two specimens from “Mexique” collected by Sumichrast in the 1850s. Jan did not designate a holotype and provided data only for one of the two syntypes. Later, Smith and Taylor (1950: 350) restricted the type locality to “Orizaba, Veracruz, México.” This restriction was inferred based on the assumption that the origin of the type specimens of *Ophryacus undulatus* was the same locality as other animals collected by Sumichrast around the same time. Sumichrast (1882: 45) later stated that *O. undulatus* “no es raro en la región Alpina de Orizaba,” so we reviewed his writings about his collections (Sumichrast, 1864, 1870, 1873, 1881, 1882) and it was not possible to restrict the type locality beyond “Mexique.” Further, this situation is complicated because the specimens were lost during the Second World War (S. Scali, pers. comm.), and thus were not examined by recent reviewers of this species (Smith, 1960; Campbell and Lamar, 1989, 2004). Because the syntypes were destroyed, we were unable to examine them for the characters now known to be diagnostic for species of *Ophryacus*. Thus, we were limited to analyzing the available information in the description and the accompanying figures.

We reviewed the original description of *O. undulatus* (Jan, 1859). Although Jan mentioned two snakes, he provided counts for only one and the figures pertain to only one specimen. The animal he described measured 56 cm in total length, and is the one destroyed and no longer at the Museo Civico di Storia Naturale di Milano (Wallach et al., 2014). Details of the second animal are unknown, as Jan did not provide scale counts, characters, or drawings for the second specimen. We tried to locate the second specimen to identify the species, but it also has been lost or destroyed (S. Scali, pers. comm.). We included all the characters of morphological importance that can be drawn from Jan’s description in our table as “*O. undulatus* Type” (Table 1). From the characters listed, Jan clearly had a specimen of *O. undulatus*, as defined herein, and not of *O. smaragdinus*. The illustration in the description shows the supraocular horn in contact with the eye, as in *O. undulatus*, and not separated from the eye by a row of small scales, as in *O. smaragdinus*. Jan described a specimen with 12 supralabials on both sides, a common characteristic for *O. undulatus*, and opposed to no more than 10, a character present in *O. smaragdinus*. Furthermore, the specimen depicted shows large and flat internasals, in comparison to the smaller and heavily keeled internasals present in *O. smaragdinus*. Finally, the upper preocular is large, at least 65% of the eye width, which also precludes it from being *O. smaragdinus*. One peculiar feature of Jan’s specimen is that he depicted 12 intersupraoculars between the horns, and all the specimens of *O. undulatus* we examined have counts of 13 or more, and usually above 15. Perhaps Jan did not recognize some of the smaller scales as intersupraoculars, and left them out of the drawing. After Jan’s description, Sumichrast obtained several more specimens of *O. undulatus*, presumably from the same area as the original material. He sent one of the specimens to the British Museum (Natural History) and two to the USNM. Although we were unable to examine the specimen in the British Museum, Boulenger (1896) provided a description. Whereas he did not indicate specific scale counts for the specimen from Orizaba, he provided the ranges of some characters from all the specimens available to him. The high number of supralabials (11) and intersupraoculars between the horns (14–20) confirm that all four specimens, including the one from “Orizaba,” are assignable to *O. undulatus*. The two specimens at the USNM from Sumichrast (USNM-6319 and USNM-331408) also are assignable to *O. undulatus*. The skulls have been removed from both specimens, which obscures some of the distinguishing characters, but clearly show too many intersupraoculars to be *O. smaragdinus* (14–16 vs. 11, in *O. smaragdinus*); they also contain an elongated upper supraocular, which cannot be measured to the eye diameter due to the condition of the specimens, but this character is obvious when comparing the length by the height (2.7–3.3 times as long as it is tall vs. 1–1.8 times as long as it is tall, in *O. smaragdinus*) (See Table 1).

Sympatry and Syntopy of *Ophryacus*

A common question for the student of any group of closely related taxa is whether they are ecologically isolated, or if they maintain their identity when coming into sympatry. With the description of *O. smaragdinus*, three closely related species (*O. smaragdinus*, *O. undulatus*, and *Mixcoatlus melanurus*) now are known to inhabit the Sierra Madre Oriental in eastern Mexico. The latter two species occur sympatrically at least in one locality, as collections contain specimens of both species from El Tejocote, in the municipality of Santiago Tenango, Oaxaca (see Fig. 11). Despite

heavy collecting in this area, no hybrids between *O. undulatus* and *M. melanurus* have been reported. In Veracruz, *O. smaragdinus* and *O. undulatus* have been collected in close proximity at Cerro Petlalcala and Zongolica, respectively (M. de la Torre-Loranca and M. López-Luna, pers. comm.), and although they have not been collected at the same locality they might occur sympatrically in the mountains south of Orizaba or even farther south in Oaxaca. In the Sierra Madre del Sur of Oaxaca, *O. sphenophrys* and *O. undulatus* have been collected within 7 km of one another. Despite the proximity of these localities, these species maintain their distinctiveness (see Fig. 8C).

To better understand how three closely related species can occur in the same mountain ranges and still retain their specific identity, we mapped all of the known *Ophryacus* and *Mixcoatlus* collecting localities using Google Earth. We then overlaid the different elevation and precipitation layers (HerpMx_Map_Pack, developed by J. Jones, produced from data obtained directly from INEGI in 2005, and available at www.herp.mx/pubs/HERPMX-Mexico-Map-Pack-v1.0.kmz), and found that the three species appear to be segregated to habitats with differing rainfall



Fig. 8. Species of Crotalinae in the Sierra Madre del Sur of southern Mexico. (A) *Ophryacus sphenophrys* from Parador La Soledad, Municipio de Candelaria Loxicha, Oaxaca; (B) *O. undulatus* (UAZ 57624-PSV) from La Trinidad, Municipio de Ajuchitlán del Progreso, Guerrero; (C) *O. undulatus* juvenile from highway between Buenavista Loxicha and Tierra Blanca, Municipio de San Agustín Loxicha, Oaxaca; (D) *O. undulatus* (UAZ 57625-PSV) from the vicinity of La Guitarra, Municipio de General Heliodoro Castillo, Guerrero; (E) *Mixcoatlus barboursi* from Paraje Montero de Zaragoza, Municipio de Malinaltepec, Guerrero; and (F) *M. browni* from Cerro Teotepec, Municipio de General Heliodoro Castillo, Guerrero.

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Fig. 9. Head scalation of *Ophryacus* and *Mixcoatlus* from the Sierra Madre Oriental of eastern Mexico. (A) *O. smaragdinus*, sp. nov. (UZA 57622-PSV) from Los Ocotes, Municipio de Huayacocotla, Veracruz; (B) *O. smaragdinus*, sp. nov. (UZA 57620-PSV) juvenile from the type locality; (C) *O. smaragdinus*, sp. nov. (MZFC 13556) from San Martín Caballero, Municipio de San José Tenango, Oaxaca; (D) *M. melanurus* from San Andrés Cacaloapan, Municipio de Tepanco de López, Puebla; (E) *O. undulatus* (UZA 57623-PSV) from Puerto del Aire, Municipio de Acultzingo, Veracruz; and (F) *O. undulatus* from the vicinity of Los Reyes, Municipio de Zongolica, Veracruz.

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regimes. All of the *O. smaragdinus* we examined came from the humid eastern slopes of the Sierra Madre Oriental, where the annual precipitation ranges from 1,800 mm to over 4,500 mm. Records of *O. undulatus* with precise collecting data from the Sierra Madre Oriental are from seasonally dry pine-oak forest present on the drier western slopes of this mountain range, where the annual precipitation ranges from 500 mm to 1,800 mm. All the records of *M. melanurus* for which we have precise collecting data came from xeric tropical scrub and oak woodland present in the dry interior valleys and associated mountain ranges, where the annual precipitation ranges from 300 mm to approximately 1,000 mm. In the Sierra Madre del Sur, *O. undulatus* and *O. sphenophrys* have been collected in close proximity to one another. Apparently, *O. sphenophrys* is restricted to cloud forest on the lower elevation windward slopes of the Sierra Miahuatlán portion of the Sierra Madre del Sur, and *O. undulatus* is restricted to the seasonally dry pine-oak forest at higher elevations and on the drier leeward slopes of the Sierra Madre del Sur. These results suggest that the ecological separation of the three species in the same mountain ranges might be correlated with differences in annual precipitation. This would be an important factor in defining the ranges of *Ophryacus*, as well as in identifying conservation priorities.

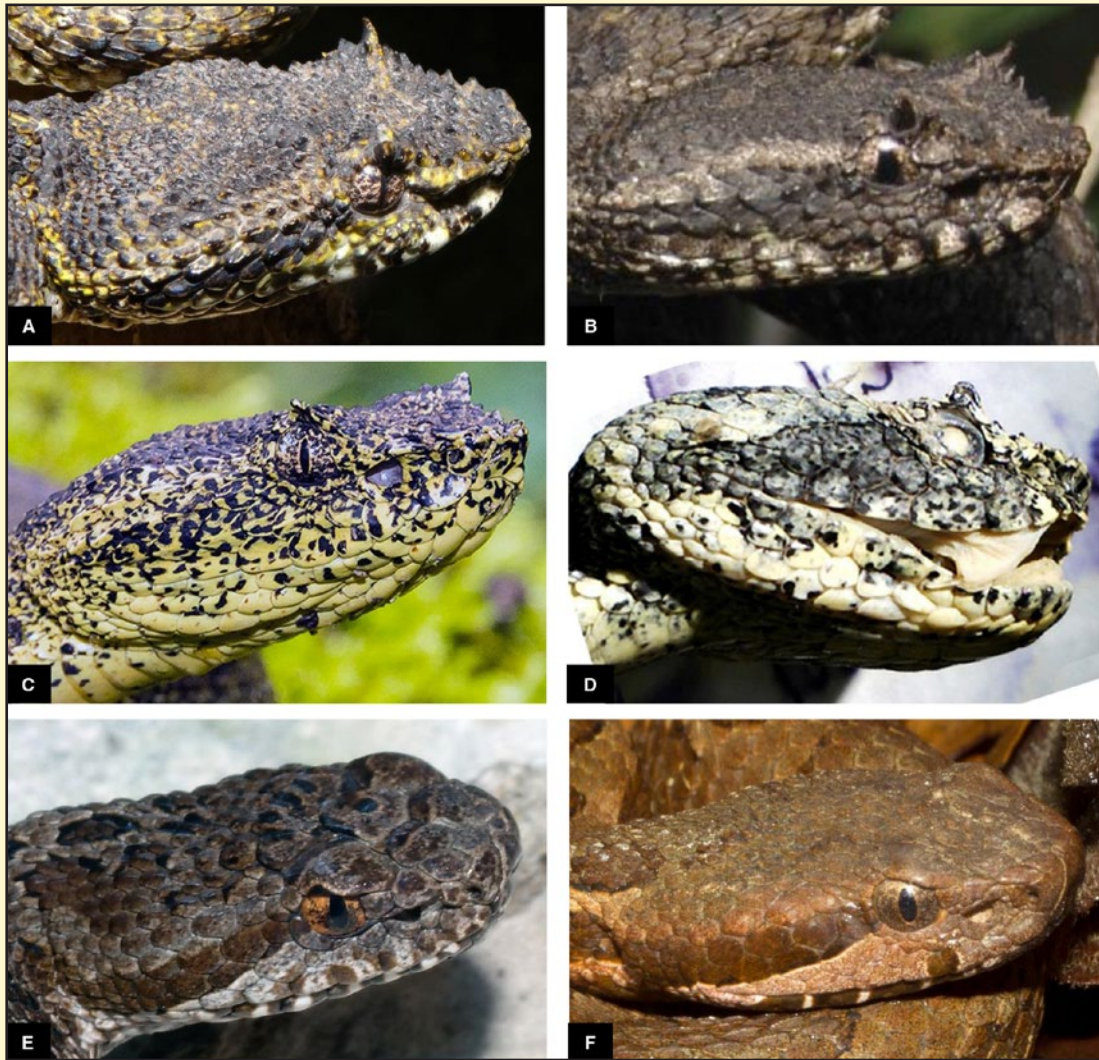


Fig. 10. Head scalation of *Ophryacus* and *Mixcoatlus* from the Sierra Madre del Sur of Southern Mexico. (A) *O. undulatus* (UAZ 57625-PSV) from La Trinidad, Municipio de Ajuchitlán del Progreso, Guerrero; (B) *O. undulatus* (UAZ 57629-PSV) juvenile from La Guitarra, Municipio de General Heliodoro Castillo, Guerrero; (C) *O. sphenophrys*, from Parador La Soledad, Municipio de Candelaria Loxicha, Oaxaca; (D) *O. sphenophrys* (MZFC 16680) from between La Soledad and Buenavista Loxicha, Municipio de Candelaria Loxicha, Oaxaca; (E) *M. browni* from Cerro Teotepec, Municipio de General Heliodoro Castillo, Guerrero; and (F) *M. barbouri* from Paraje Montero de Zaragoza, Municipio de Malinaltepec, Guerrero.

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Distribution of *Ophryacus* and *Mixcoatlus*

With the description of *O. smaragdinus* and the resurrection of *O. sphenophrys* and *M. browni* (Jadin et al., 2011), we consider it necessary to review the known geographical distribution of all the species of *Ophryacus* and *Mixcoatlus*, as presently understood. *Ophryacus smaragdinus* apparently is restricted to the humid windward slopes of the Sierra Madre Oriental in eastern Mexico. Its distribution ranges from the municipality of Huayacocotla, in north-western Veracruz, southeastward along the eastern edge of the Sierra Madre Oriental, through east-central Hidalgo, northeastern Puebla, and west-central Veracruz. This species is narrow in distribution, occurring only at elevations from about 1,400 to 2,400 m on the humid windward slopes. Although this might seem like a broad elevational range, the mountains in this region fall off abruptly onto the coastal plain to form deep *barrancas*, and therefore such a wide elevational range often encompasses only a few kilometers. In southern Veracruz, *O. smaragdinus*

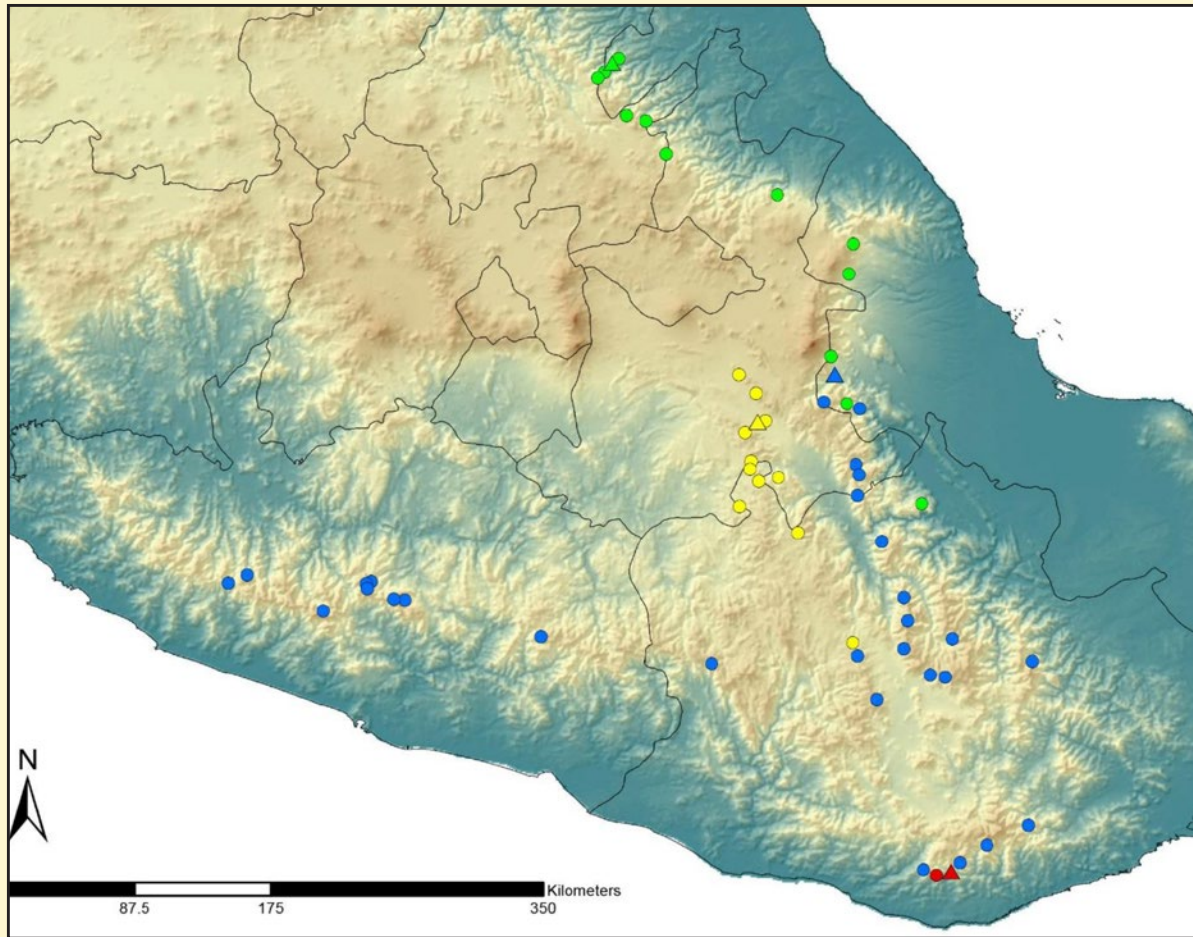


Fig. 11. Geographical distribution of members of subfamily Crotalinae with supraocular horns. Green dots represent records of *Ophryacus smaragdinus* sp. nov., and green triangle denotes the type locality; blue dots represent records of *O. undulatus*, and blue triangle the proposed location of the type locality (Smith and Taylor, 1950); red dots represent records of *O. sphenophrys*, and red triangle denotes the type locality; yellow dots represent records of *Mixcoatlus melanurus* and yellow triangle represents the type locality.

has been found only on the humid slopes of Cerro de Orizaba and Cerro Petlalcala (M. López-Luna and M. de la Torre-Loranca, pers. comm.). Although *O. smaragdinus* has been recorded only from one locality in Oaxaca, this population suggests that this species occurs at least as far south as the Río Santo Domingo drainage. This drainage might prove to be a formidable barrier to its distribution, however, as *O. smaragdinus* is absent from the Sierra de Juárez and the Sierra Mixe despite what appears to be suitable habitat in both ranges.

Ophryacus undulatus occurs in both the southern Sierra Madre Oriental and the Sierra Madre del Sur. In the Sierra Madre Oriental it has been collected as far north as the municipality of Acultzingo, in west-central Veracruz, where it is restricted to elevations above 1,800 m on the moderately humid slopes of the western and upper portions of this mountain range. In Oaxaca *O. undulatus* has a much wider distribution, as it has been collected at various localities in the Sierra Madre Oriental of Oaxaca, from the northern border south through Cerro San Felipe, the Sierra de Juárez and the Sierra Mixe, as well as in the highlands on all sides of the valley of Oaxaca. It also is known to occur in the Sierra Madre del Sur from as far east as the municipality of Santo Domingo Chontecomatlán, Oaxaca, and as far west as La Trinidad, in the municipality of Ajuchitlán del Progreso, Guerrero. This suggests a more or less continuous distribution from the Isthmus of Tehuantepec to the mouth of the Río Balsas. Campbell and Lamar (2004) indicated an elevational range of 1,800–2,800 m for *O. undulatus*, which seems accurate, although *O. smaragdinus* and *O. sphenophrys* have been collected at lower elevations.

Ophryacus sphenophrys has been collected only at the type locality and one other locality in the same municipality, between La Soledad and Buenavista Loxicha. Both localities lie at moderate elevations on the extremely humid windward slopes of the Sierra Madre del Sur of south-central Oaxaca. Smith (1960: 267) indicated the elevation of La Soledad at “about 6,000 ft.” (= 1,829 m), but the elevation actually is 1,460 m. The second known locality lies at 1,340 m, so the known elevational range for this species is 1,340–1,460 m. For additional information, see Fig. 14.

Mixcoatlus melanurus has been collected only from the arid slopes of the northern, western, and southwestern edges of the Tehuacán-Cuicatlán Valley in southern Puebla and northern Oaxaca (see Fig. 11). Although Campbell and Lamar (2004) noted this species occurring at elevations from 1,600 to 2,400 m, the lowest confirmed record we have been able to find is from 1,880 m, from NE of Tepanco de López, municipality of Tepanco de López, Puebla, and the highest known elevation is around 2,400 m. Several peaks throughout its known distribution attain elevations of 2,650–2,700 m, and this species probably inhabits these areas.

Mixcoatlus browni is known only from the Sierra Madre del Sur of central and western Guerrero, where it has been collected in four clusters of localities: the vicinity of Omiltemi, municipality of Chilpancingo, Guerrero; on and around the Cerro Teotepec, municipality of General Heliodoro Castillo, Guerrero; the vicinity of Carrizal de Bravo, municipality of Carrizal de Bravo, Guerrero; and several localities in the municipality of Ajuchitlán del Progreso, Guerrero. This species has been reported to occur at elevations from 1,826 to 3,296 m (Jadin et al., 2011), but all records with precise collecting data are above 2,400 m. More populations of this species likely will be discovered in eastern Guerrero and adjacent Oaxaca.

Mixcoatlus barbouri has been reported from only two populations, one around Omiltemi, municipality of Chilpancingo, Guerrero, and a second in the municipality of Ajuchitlán del Progreso, Guerrero. Specimens have been collected at elevations from 2,300 to 2,608 m. Several authors have suggested that this species eventually will turn up in the Sierra Madre del Sur of Oaxaca (Campbell and Lamar, 2004). A recent discovery in eastern Guerrero (E. Centenero-Alcala, pers. comm.) emphasizes this possibility.

CONSERVATION IMPLICATIONS

Wilson and McCranie (1992) developed a conservation status algorithm known as the Environmental Vulnerability Score (EVS) for use with amphibians in Honduras. Since then it has been applied for use with both amphibians and reptiles inside and outside of Honduras (Wilson and McCranie, 2004; Wilson et al., 2010; Alvarado-Díaz et al., 2013; Porras et al. 2013; Johnson et al., 2015) and specifically in Mexico (Wilson et al., 2013a, b). We applied the EVS as outlined in Porras et al. (2013) to assess the conservation priority status of the species revisited herein. The EVS, however, initially was based on “forest formations” in Honduras, and we consider those significantly different from the “formations” present in Mexico. Thus, we developed a set of “biogeographical provinces” based primarily on the “natural regions” of Flores-Villela (1993), the “physiographic regions” of Johnson et al. (2010) and the “physiographic provinces” of more recent authors (Alvarado-Díaz et al., 2013; Mata-Silva et al., 2015). To delineate them, we used the program Google Earth to outline the physiographical provinces, and then overlaid them on a map created from data obtained from INEGI. We are including a map (Fig. 13) of the “biogeographical formations” we consider present in southern Mexico. We divided the Sierra Madre del Sur into biogeographical formations consisting of continuous elevations above 1,700 m. In total, the Sierra Madre del Sur of Guerrero and Oaxaca consists of three biogeographical formations that function as high elevation “islands.” The southern Sierra Madre Oriental abuts the central plateau and transverse ranges and thus is not divided by elevational barriers. We consider it, however, to consist of the following biogeographical formations: (1) from the Río Metztlán drainage south to the Perote–Xalapa section of Veracruz; (2) from Cofre de Perote and associated highlands to the gap in the Sierra Madre Oriente between Orizaba and Tehuacán; and (3) from the Orizaba–Tehuacán gap south to the Río Papaloapan drainage. Likewise, we divided the central mountains of Oaxaca and southern Puebla into biogeographical formations consisting of continuous habitat above 1,700 m, and consider the valley of Tehuacán–Cuicatlán as an independent formation. Using this definition of biogeographical formations and applying the EVS with the changes outlined by Porras et al. (2013), we determined the following EVS scores for the known species of *Ophryacus* and *Mixcoatlus*:

O. smaragdinus: $3 + 6 + 5 = 14$

O. sphenophrys: $5 + 8 + 5 = 18$

O. undulatus: $3 + 1 + 5 = 9$

M. melanurus: $3 + 6 + 5 = 14$

M. barbouri: $3 + 7 + 5 = 15$

M. browni: $4 + 8 + 5 = 17$

We note that these results vary slightly from those provided by Wilson et al. (2013b), who reported the following EVS scores for the group:

O. undulatus: $5 + 5 + 5 = 15$

M. melanurus: $5 + 7 + 5 = 17$

M. barbouri: $5 + 5 + 5 = 15$

M. browni: $5 + 7 + 5 = 17$



Fig. 12. (A) Photo of the type locality of *Ophryacus smaragdinus* sp. nov.; and (B) photo from near the type locality of *O. sphenophrys*.

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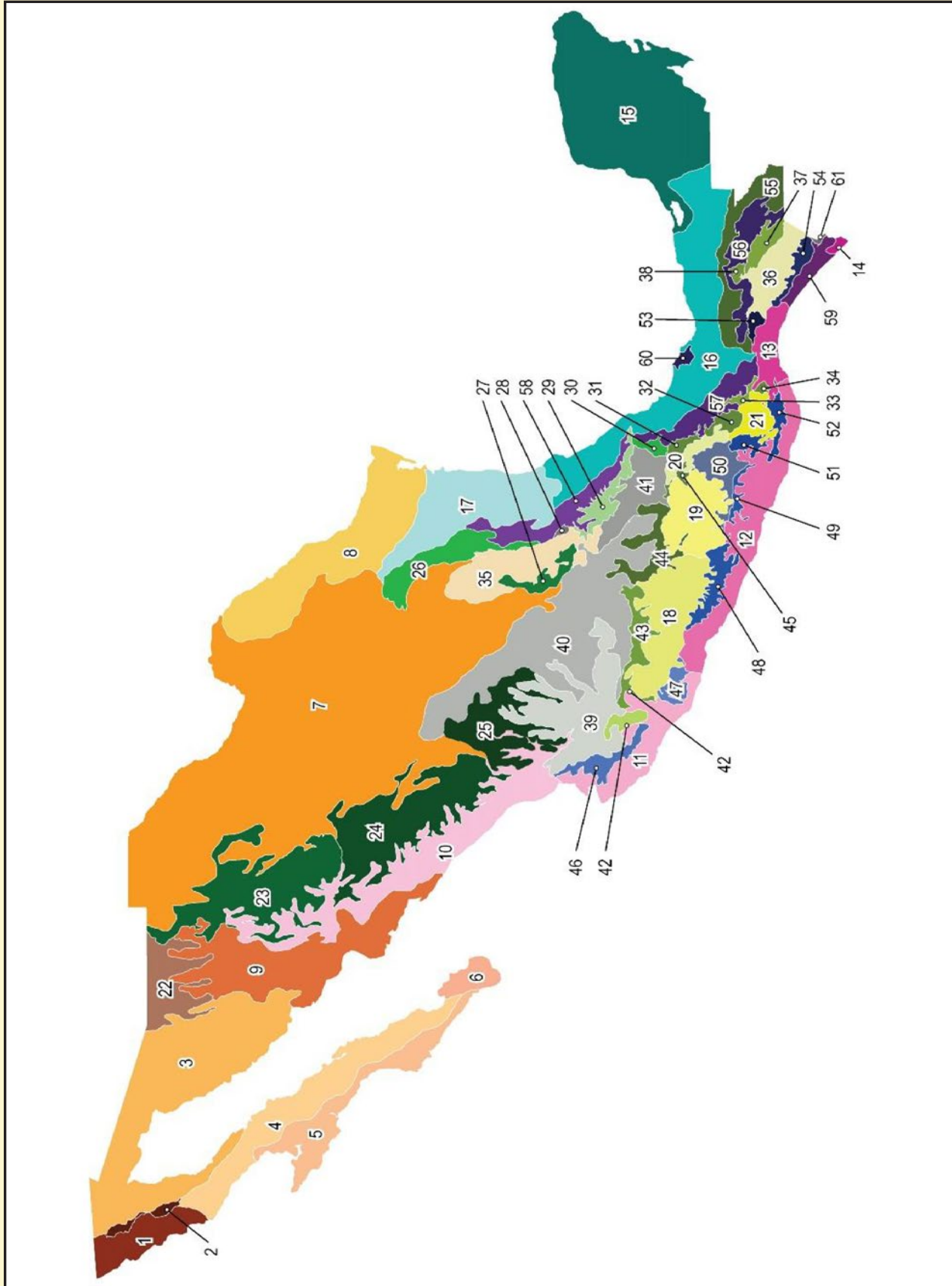


Fig. 13. Map of the Biogeographical Formations of Mexico, including the relevant areas inhabited by *Ophryacus* and *Mixcoatlus* used to apply the Environmental Vulnerability Scores (EVS). See following page for corresponding legend.

Biogeographical Formations of Mexico

- 1 Californian Mediterranean Chaparral Scrub
- 2 Peninsular Boreal Forest & Pine-Oak Woodland
- 3 Sonoran Desert Scrub
- 4 Peninsular Desert Scrub
- 5 Vizcaíno Desert Scrub
- 6 Peninsular Cape Region Mixed Habitat
- 7 Chihuahuan Desert Scrub
- 8 Tamaulipan Tropical Thornscrub
- 9 Sonoran Tropical Thornscrub
- 10 Sinaloan Tropical Dry Forest & Savanna
- 11 Coliman Tropical Dry Forest & Savanna
- 12 Guerreran Tropical Dry Forest & Savanna
- 13 Tehuantepec Tropical Dry Forest & Savanna
- 14 Guatemalan Tropical Dry Forest
- 15 Yucatecan Mixed Tropical Mixed Forest
- 16 Veracruzian Tropical Mixed Forest & Savanna
- 17 Tamaulipan Tropical Dry Forest
- 18 Lower Balsas Tropical Dry Forest & Thornscrub
- 19 Upper Balsas Tropical Dry Forest & Thornscrub
- 20 Tehuacán-Cuicatlán Tropical Dry Forest & Thornscrub
- 21 Valles de Oaxaca Tropical Dry Forest
- 22 Madrean Sky Islands Pine-Oak Woodland
- 23 Northern Sierra Madre Occidental Pine-Oak Woodland
- 24 Central Sierra Madre Occidental Pine-Oak Woodland
- 25 Southern Sierra Madre Occidental Pine-Oak Woodland
- 26 Northern Sierra Madre Oriental Pine-Oak Woodland
- 27 Potosian Sierra Madre Oriental Pine-Oak Woodland
- 28 Queretaran Sierra Madre Oriental Pine-Oak Woodland
- 29 Hidalgan Sierra Madre Oriental Pine-Oak Woodland
- 30 Veracruzian Sierra Madre Oriental Pine-Oak Woodland
- 31 Mazatecan Sierra Madre Oriental Pine-Oak Woodland
- 32 Sierra Juarez Pine-Oak Woodland
- 33 Sierra Mixe Pine-Oak Woodland
- 34 Sierra Sacamecate Pine-Oak Woodland
- 35 Potosian Inland Tropical Dry Forest & Thornscrub
- 36 Central Chiapanecan Depression Tropical Dry Forest
- 37 Central Chiapanecan Highlands Pine-Oak Woodland
- 38 Northern Chiapanecan Highlands Pine-Oak Woodland
- 39 Western Central Plateau Mesquite-Grassland & Pine-Oak Woodland
- 40 Central Mexican Plateau Mesquite-Grassland & Pine-oak Woodland
- 41 Eastern Central Plateau Mesquite-Grassland & Pine-oak Woodland
- 42 Jaliscan Transverse Ranges Pine-Oak Woodland
- 43 Michoacán Transverse Ranges Pine-Oak Woodland
- 44 Central Mexican Transverse Ranges Pine-Oak Woodland
- 45 Mixteca Poblana Pine-Oak Woodland & Mesquite Grassland
- 46 Jaliscan Sierra Madre del Sur Mixed Temperate Woodland
- 47 Coalcomán Sierra Madre del Sur Mixed Temperate Woodland
- 48 Guerreran Sierra Madre del Sur Mixed Temperate Woodland
- 49 Malinaltepec-Putla Sierra Madre del Sur Mixed Temperate Woodland
- 50 Mixteca Alta Pine-Oak Woodland & Mesquite Grassland
- 51 Central Oaxacan Sierra Madre del Sur Mixed Temperate Woodland
- 52 Miahuatlán Sierra Madre del Sur Mixed Temperate Woodland
- 53 Chimalapas Mixed Tropical Woodland
- 54 Sierra Madre del Sur de Chiapas Mixed Tropical Woodland
- 55 Chiapanecan Atlantic Tropical Rainforest
- 56 Chiapanecan Atlantic Cloud Forest
- 57 Veracruzian Atlantic Tropical Wet Forest
- 58 Huastecan Atlantic Tropical Wet Forest
- 59 Soconusco Pacific Tropical Wet Forest
- 60 Tuxtlán Atlantic Tropical Rainforest Forest
- 61 Fuegan Tropical Mixed Forest

The EVS score for *M. browni* and *M. barbouri* remains the same, and the lower EVS score for *M. melanurus* (14 as opposed to 17) and *O. undulatus* (9 as opposed to 15) is due to our application of the EVS category based on the methodology outlined by Porras et al. (2013). Both species are restricted to Mesoamerica (*sensu* Wilson and Johnson 2010), but neither is restricted to one physiographic region; both species have been collected in the Sierra Madre Oriental and the Sierra Madre del Sur, in both the Atlantic and Pacific drainages. Finally, we separated the Sierra Madre del Sur and the Sierra Madre Oriental into different biogeographical formations, which Wilson et al. (2013b) did not do. This approach more accurately reflects the conservation status of reptiles and amphibians in the large physiographic regions of Mexico; however, it begs for a standardized delineation of the “formations” in Mexico.

EVS scores of 14 or higher are considered in the “high vulnerability” category (Johnson et al., 2015). *Ophryacus smaragdinus* scored 14 and should be considered a priority by authorities and organizations leading conservation efforts in Mexico. Potential threats include habitat destruction, which is rampant in the Sierra Madre Oriental, as well as illegal collecting. Habitat destruction is present at the type locality (pers. observ.), and also can be seen at most localities where this species has been recorded (Google Earth, 2013). Photos of illegally collected and commercialized individuals of *O. smaragdinus* abound on the Internet and its social media sites (pers. observ.). *Mixcoatlus melanurus* also scored 14 and should be considered of conservation priority. Habitat destruction for goat herding and industrial agricultural practices are rampant throughout its range in the Tehuacán-Cuicatlán Valley, and thus the preservation of its unique habitat should be a priority. A secondary threat may be illegal collecting, as

this species also is available on the black market (pers. observ.). *Mixcoatlus barbouri* scored 15, largely due to its restricted range in the Sierra Madre del Sur of Guerrero. Much of its habitat is still intact however, and only partially affected by logging and habitat destruction. Its range includes one of the centers of narcotics production and distribution in Mexico, and while this activity is ongoing habitat destruction is limited due to the partial restriction of access to many of these areas. We have not seen this species commercialized. The EVS scores for *M. browni* (17) and *O. sphenophrys* (18) are extremely high, and suggest that these species are extremely vulnerable to any threat in their limited ranges. Again, habitat destruction is the most serious threat, and active logging and conversion of land for agricultural use is present at every locality where the two species are known to occur (pers. observ.). Climate change might pose an additional threat for *Mixcoatlus browni*, as the distribution of this species is restricted to isolated mountain peaks where minor temperature variation might be detrimental to its unique habitat (Wake and Vredenburg, 2008). We have not seen either of these species commercialized in or outside of Mexico. We suggest that all five species (*O. smaragdinus*, *O. sphenophrys*, *M. melanurus*, *M. barbouri* and *M. browni*) are candidates for immediate protection, and that every effort should be made to preserve their unique and restricted montane habitats.



Fig. 14. An adult *Ophryacus sphenophrys* collected near the type locality of La Soledad, Municipio de Candelaria Loxicha, Oaxaca. This paper was “in press” at the time of capture (16 December 2015), so coloration and meristic data for this individual does not appear in the text.

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When involved with conservation efforts, often we are asked to use common names in lieu of scientific names for better communication with the general public. Neither *O. smaragdinus* nor *O. sphenophrys* have been assigned common names, the accepted common name for *O. undulatus* might no longer be appropriate, and the remaining three species in the group (*M. melanurus*, *M. barbouri*, *M. browni*) have been referred to by different common names. Thus, we propose the following common names for these species:

Ophryacus smaragdinus = Emerald Horned Pitviper

Ophryacus sphenophrys = Broad-horned Pitviper

Ophryacus undulatus = Slender-horned Pitviper

Mixcoatlus melanurus = Black-tailed Horned Pitviper

Mixcoatlus barbouri = Barbour's Montane Pitviper

Mixcoatlus browni = Brown's Montane Pitviper

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Appendix 1. List of specimens examined.

Mixcoatlus barbouri ($n = 2$). MEXICO: Guerrero: MZFC 21430, 21432.

Mixcoatlus browni ($n = 3$). MEXICO: Guerrero: MZFC 16677, 21429, 21431.

Mixcoatlus melanurus ($n = 4$). MEXICO: Oaxaca: MZFC 8571, 9660; Puebla: MZFC 14364, 29288.

Ophryacus smaragdinus ($n = 8$). MEXICO: Hidalgo: MZFC 4825, 21140; Oaxaca: MZFC 13556–57; Puebla: MZFC 17663; Veracruz: MZFC 20582, 29289–90.

Ophryacus sphenophrys ($n = 1$). MEXICO: Oaxaca: MZFC 16680.

Ophryacus undulatus ($n = 11$). MEXICO: Guerrero: CNAR 24248, MZFC 4284, 2888–90, 2892; Oaxaca: MZFC 16977, 23864, 23866; Veracruz: CNAR 19732–33.

Appendix 2. List of material examined from digital images. Photos of live individuals are marked with an asterisk (*); those of preserved specimens in scientific collections are unmarked.

Mixcoatlus melanurus ($n = 1$). MEXICO: Puebla: UAZ 57628-PSV*.

Ophryacus smaragdinus ($n = 4$). MEXICO: Hidalgo: UAZ 57626-PSV*; Veracruz: UAZ 57620–22-PSV*.

Ophryacus sphenophrys ($n = 2$). MEXICO: Oaxaca: (UIMNH 6262), Municipio de Candelaria Loxicha: La Soledad (photos by Elí García-Padilla are not catalogued in scientific collections).

Ophryacus undulatus ($n = 34$). MEXICO: Guerrero: FMNH 202684, 38505, KU 85012, 91430, UIMNH 35015, UAZ 57624–25*-PSV, 57629*; Oaxaca: AMNH 91109, 97989–90, 102216–18, 103138, KU 116949, UCM 52513, UCM 52588–89, UCM 40071–72, 41214, UIMNH 46906, 52967, 56120, 56855, 63686–87, 63698, USNM 46466; Veracruz: USNM 6319, 331408, UAZ 57623-PSV*, 57627*.

Ophryacus sp. ($n = 1$). MEXICO: Veracruz: UIMNH 60830.





Christoph I. Grünwald is a German-Mexican herpetologist who for the last 15 years has led field expeditions to study herpetofauna. An expert in Mexican biogeography, he has been involved with the discovery of over 100 range extensions and dozens of state records for amphibians and reptiles from around the country. Christoph specializes in rattlesnakes and pitvipers, and many important discoveries have involved this group. He led the expedition that re-discovered *Crotalus lannomi*, which was feared extinct, and collaborated in the discovery, sampling, and description of two new rattlesnake species, *C. campbelli* and *C. tlaloci*. Recently, a new species of frog he discovered in 2005, *Eleutherodactylus grunwaldi*, was named in his honor. Currently he is leading research expeditions on Mexican rattleless pitvipers and direct-developing frogs. A co-founder of Biodiversa, A.C., an anti-extinction non-profit organization, Chris currently is developing a system of “micro-reserves,” aimed at preserving the most vulnerable, high-endemism localities in Mexico.



Jason M. Jones was born and raised in southern California, where he studied biology and marketing at the University of California, Irvine. He currently resides in Sinaloa, Mexico, and has spent the last 11 years studying and photographing the herpetofauna of the country, with an emphasis on rattlesnakes. During this time he co-led the rediscovery of *Crotalus lannomi* and also collaborated in the descriptions of *C. campbelli* and *C. tlaloci*, and extended the knowledge of the distribution of many small-bodied Mexican rattlesnake species. As a co-founder of Biodiversa, A.C., he is developing a strategy for conserving limited range reptile and amphibians species, specifically those restricted to isolated patches of cloud forest in the Sierra Madre del Sur.



Hector Franz-Chávez was born in Guadalajara, Mexico, and has had a passion for herpetology since childhood. He is a student of biology at the Universidad de Guadalajara (CUCBA), and his main interests include biogeography, natural history, and ecology of the herpetofauna of Mexico. He also is an avid nature photographer, and has collaborated in various herpetological inventories in different parts of Jalisco, and currently is working on an inclusive project on Mexican direct-developing frogs and several potentially new species of pitvipers. Hector has traveled extensively in the Sierra Madre Occidental and the Sierra Madre del Sur, where he has collected numerous specimens of interest.



Iván T. Ahumada-Carrillo originally is from Guadalajara, and received a degree in biology from the Universidad de Guadalajara (CUCBA). Currently he is an independent investigator who focuses on the biogeography of reptiles and amphibians in western Mexico. During his career, Iván has discovered dozens of range extensions and state records and has authored or co-authored numerous papers on biogeography, as well as a book entitled *Anfibios y Reptiles del Bosque La Primavera*. Recently he collaborated in the description of two new species of frogs, from Jalisco and Colima. Another interest is wildlife photography, and his work has been published throughout Mexico in educational materials, websites, scientific journals, and books.