



The Leptotyphlopidae, descriptively called threadsnakes or wormsnakes, is one of five families comprising the most ancient but highly specialized clade of snakes, the Scolecophidia, which dates back to the Jurassic Period (ca. 155 mya). Scolecophidians are the least studied and poorest known group of snakes, both biologically and taxonomically. Due to their subterranean habitat, nocturnal lifestyle, small size, and drab coloration, these snake are extremely difficult to find and seldom are observed or collected. *Epictia* is one of six genera found in the New World, with a distribution extending throughout Latin America. Whereas most *Epictia* are uniform brown or black, some species are brightly colored. *Epictia tenella*, the most wide-ranging member of the genus, occurs throughout much of northern South America. Pictured here is an individual from Trinidad that exhibits several distinctive features, including yellow zigzag stripes, relatively large bulging eyes, contact of the supraocular and anterior supralabial shields, and the presence of numerous sensory pits on the anterior head shields.

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## Morphological review and taxonomic status of the *Epictia phenops* species group of Mesoamerica, with description of six new species and discussion of South American *Epictia albifrons*, *E. goudotii*, and *E. tenella* (Serpentes: Leptotyphlopidae: Epictinae)

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**ABSTRACT:** I examined the “*Epictia phenops* species group” of Mesoamerica, and recognize 11 species as valid (*E. ater*, *E. bakewelli*, *E. columbi*, *E. magnamaculata*, *E. phenops*, plus four new species from Mexico, one from Honduras, and one from Panama). *Epictia goudotii* does not occur in Panama, but only in South America. I used head shields, color patterns, and visceral characters to differentiate the Mesoamerican taxa, and compared these species externally and internally with *E. albifrons*, *E. goudotii*, and *E. tenella* of South America. I selected a neotype for *E. albifrons* from a topotypic series, and provide identification keys for the genera of tribe Epictini, the scolecophidians of the state of Pará, Brazil, members of the “*E. phenops* species group,” and the *Epictia* of Mesoamerica and northern South America.

**Key Words.** *Epictia ater*, *E. bakewelli*, *E. columbi*, *E. magnamaculata*, distribution, morphology, neotype, new species, viscera

**RESUMEN:** Examiné el “grupo de especies de *Epictia phenops*” de Mesoamérica, y reconozco 11 especies como válidas (*E. ater*, *E. bakewelli*, *E. columbi*, *E. magnamaculata*, *E. phenops*, además de cuatro nuevas especies para México, una en Honduras y otra en Panamá). *Epictia goudotii* no ocurre en Panamá, solamente en Suramérica. Usé las escamas dorsales de la cabeza, patrón de coloración y características viscerales para diferenciar los taxones de Mesoamérica, y comparé estas especies externa e internamente con *E. albifrons*, *E. goudotii* y *E. tenella* de Suramérica. Seleccioné un neotipo para *E. albifrons* de la serie topotípica, y proporciono unas claves de identificación para los géneros de la tribu Epictini, los scolecófidos del estado de Pará, Brasil, miembros del “grupo de especies de *E. phenops*” y los *Epictia* de Mesoamérica y norte de Suramérica.

**Palabras Claves:** *Epictia ater*, *E. bakewelli*, *E. columbi*, *E. magnamaculata*, distribución, morfología, neotipo, nuevas especies, vísceras

**Citation:** Wallach, V. 2016. Morphological review and taxonomic status of the *Epictia phenops* species group of Mesoamerica, with description of six new species and discussion of South American *Epictia albifrons*, *E. goudotii*, and *E. tenella* (Serpentes Leptotyphlopidae: Epictinae) 3: 216–374.

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**Received:** 2 April 2016; **Accepted:** 8 May 2016; **Published:** 29 June 2016.

## INTRODUCTION

Among all snakes, the Scolecophidia are unsurpassed in their difficulty of identification, scale counting, head shield identification, accuracy of illustration, and discovery of diagnostic characters of systematic and taxonomic value. In part, this situation results from their minute to small size, rarity of collection and field observations due to their secretive habits and fossorial lifestyle, and simplification of the general serpentine body plan. The Leptotyphlopidae is the sister group to the Typhlopoidea (Gerrhopilidae, Typhlopidae, and Xenotyphlopidae), and together they form the sister group to the Anomalepididae (Vidal et al., 2010; Pyron et al., 2013; Pyron and Wallach, 2014). Even within the five scolecophidian families (Anomalepididae with 18 species; Gerrhopilidae with 18 species; Leptotyphlopidae with ca. 130 species; Typhlopidae with ca. 400 species; and Xenotyphlopidae with a single species; Wallach et al., 2014; Uetz and Hošek, 2016), the Leptotyphlopidae, by far, is the most difficult group to study. Not only are members of this family the smallest of all snakes, but they also exhibit no variation in the number of longitudinal scale rows. In most of the 130 known species, only 14 scale rows are present throughout the body (which is the same as the 13-13-13 alethinophidian scale row formula with unenlarged ventrals), but 16 longitudinal rows are present in a few species. Their internal anatomy also is reduced to a minimum, with the respiratory system consisting of only a single, short, right lung (whereas, in addition to the right lung, a tracheal lung also is present in all the other scolecophidian families, and a left lung is found in some Typhlopidae). Thus, characters in the Leptotyphlopidae are at a premium.

Based on a molecular analysis, Adalsteinsson et al. (2009) divided the genus *Leptotyphlops* (*sensu lato*) into the following 11 genera: *Epacrophis* Hedges, Adalsteinsson, and Branch *In* Adalsteinsson et al., 2009; *Epictia* Gray, 1845; *Guinea* Hedges, Adalsteinsson, and Branch *In* Adalsteinsson et al., 2009 (= *Tricheilostoma* Jan, 1861); *Leptotyphlops* Fitzinger, 1843; *Mitophis* Hedges, Adalsteinsson, and Branch *In* Adalsteinsson et al., 2009; *Myriopholis* Hedges, Adalsteinsson, and Branch *In* Adalsteinsson et al., 2009; *Namibiana* Hedges, Adalsteinsson, and Branch *In* Adalsteinsson et al., 2009; *Rena* Baird and Girard, 1853; *Siagonodon* Peters, 1881; *Tetracheilostoma* Jan, 1861; and *Tricheilostoma* Jan, 1861 (= *Trilepida* Hedges, 2011). Six genera were recognized within the subtribe Epictina, tribe Epictini, and subfamily Epictinae (*Epictia*, *Mitophis*, *Rena*, *Siagonodon*, *Tetracheilostoma*, and *Trilepida*) and can be identified by using the following key.

### Key to the genera of the tribe Epictini

- 1a. Supraocular absent . . . . . *Siagonodon*
- 1b. Supraoculars present . . . . . 2
- 2a. Supraoculars large, wider than long . . . . . *Epictia*
- 2b. Supraoculars small, as long as wide . . . . . 3
- 3a. Supralabials 4 (3–4 in *M. leptepileptus*) . . . . . 4
- 3b. Supralabials 2–3 . . . . . 5
- 4a. Total middorsals < 200 . . . . . *Tetracheilostoma*
- 4b. Total middorsals > 250 . . . . . *Mitophis*
- 5a. Venter brown; supralabials 3 . . . . . *Trilepida*
- 5b. Venter white; supralabials usually 2 (3 in *R. bressoni*,  
*R. dissecta*, and *R. mypoica*) . . . . . *Rena*

The three confusing species that form the focal point of this study are *Epictia albifrons* (Wagler *In* Spix, 1824) from Brazil, *Epictia goudotii* (Duméril & Bibron, 1844) from Colombia, and *Epictia phenops* (Cope, 1875) from Mexico. This complex of species variously has been referred to as the *albifrons* species group, the *goudotii* species group, and the *phenops* species group, with the majority of researchers considering *E. albifrons* and *E. goudotii* to be species complexes sorely in need of revision (Taylor, 1939; Schmidt and Walker, 1943; Thomas, 1965; Wilson and Hahn, 1973; Franco and Pinto, 2009; Ugueto and Rivas, 2010). These three species and their relatives are

remarkably similar in external appearance, and various subspecies previously have been allocated to these taxa (Dunn and Saxe, 1950; Roze, 1966; Peters et al., 1970).

For 150 years enormous confusion has existed with three species, each involving multiple species or subspecies, along with a number of presently undescribed forms. Klauber (1939: 59) stated that, “it was immediately evident that *L. albifrons*, as usually defined, is a complex of a number of species and subspecies.” Schmidt and Walker (1943: 305) referred to “the *Leptotyphlops albifrons* of authors is an *omnium gatherum* of species of varying degrees of distinctness.” Schmidt and Inger (1951: 456) noted that “the *albifrons* of authors having been shown to be a complex of quite distinct species.” Thomas (1965: 6) claimed that “there is obviously more than one species involved in the material I have seen” when referring to South American *albifrons*. Wilson and Hahn (1973: 120) remarked that the *albifrons* complex was in “a notorious state of taxonomic confusion.” Vanzolini et al. (1980: 15) stated the *albifrons* group to be very difficult, with examples from very diverse regions that show apparent *E. albifrons* characters, but in reality consist of more than one species. Vanzolini (1996: 281–282) remarked that *E. albifrons* was “certainly a composite concept” and he hoped that his description of *L. borapeliotes* was a “reasonable beginning for the dissection of the complex.” Ugueto and Rivas (2010: 218) remarked that, “a revision of the taxonomic status of the *E. goudotti-albifrons* complex is urgently needed.” Chaves et al. (2013: 2) most recently commented that, “the taxonomy of *Epictia* (formerly *Leptotyphlops*) in Central America is in need of revision.”

The following taxa, listed with their original orthography, have been considered related to *E. albifrons*, either as species group members, subspecies, or synonyms (Peters et al., 1970; Hahn, 1980; McDiarmid et al., 1999; Börschig, 2007; Franco and Pinto, 2009; Adalsteinsson et al., 2009; Koch et al., 2014; Wallach et al., 2014): *Stenostoma albipunctum* Jan, 1861 (= *E. albipuncta*); *Leptotyphlops alfredschmidti* Lehr et al., 2002 (= *E. alfredschmidti*); *Leptotyphlops amazonicus* Orejas-Miranda, 1969 (= *E. signata*); *Epictia antoniogarciai* Koch et al., 2014 (= *E. antoniogarciai*); *Leptotyphlops ater* Taylor, 1940 (= *E. ater*); *Leptotyphlops australis* Freiberg and Orejas-Miranda, 1968 (= *E. australis*); *Leptotyphlops bakewelli* Oliver, 1937 (= *E. bakewelli*); *Leptotyphlops borapeliotes* Vanzolini, 1996 (= *E. borapeliotes*); *Epictia clinorostris* Arredondo and Zaher, 2010 (= *E. clinorostris*); *Leptotyphlops collaris* Hoogmoed, 1977 (= *E. collaris*); *Leptotyphlops columbi* Klauber, 1939 (= *E. columbi*); *Leptotyphlops diaplocius* Orejas-Miranda, 1969 (= *E. diaplocia*); *Stenostoma fallax* Peters, 1857 (= *E. goudotii*); *Stenostoma flavifrons* Weyenberg In Napp, 1876a, b (= *E. albipuncta*); *Leptotyphlops gadowi* Duellman, 1956 (= *E. bakewelli*); *Stenostoma goudotii* Duméril & Bibron, 1844 (= *E. goudotii*); *Epictia hobartsmithi* Esqueda et al. In Mumaw et al., 2015 (= *E. hobartsmithi*); *Leptotyphlops magnamaculata* Taylor, 1940 (= *E. magnamaculata*); *Leptotyphlops albifrons margaritae* Roze, 1952 (= *E. magnamaculata*); *Stenostoma melanoterma* Cope, 1862 (= *E. melanoterma*); *Leptotyphlops melanurus* Schmidt and Walker, 1943 (= *E. melanura*); *Leptotyphlops munoai* Orejas-Miranda, 1961 (= *E. munoai*); *Leptotyphlops nalis* Taylor, 1940 (= *E. ater*); *Leptotyphlops nicefori* Dunn, 1946 (= *Rena nicefori*); *Leptotyphlops peruvianus* Orejas-Miranda, 1969 (= *E. peruviana*); *Stenostoma phenops* Cope, 1875 (= *E. phenops*); *Glauconia albifrons rubrolineata* Werner, 1901 (= *E. rubrolineata*); *Leptotyphlops rufidorsum* Taylor, 1940 (= *E. rufidorsa*); *Epictia septemlineata* Koch et al., 2014 (= *E. septemlineata*); *Stenostoma signatum* Jan, 1861 (= *E. signata*); *Leptotyphlops striatula* Smith and Lafe, 1945 (= *E. striatula*); *Leptotyphlops subcrotilla* Klauber, 1939 (= *E. subcrotilla*); *Leptotyphlops teaguei* Orejas-Miranda, 1964 (= *E. teaguei*); *Leptotyphlops tenella* Klauber, 1939 (= *E. tenella*); *Typhlops (Stenostoma) tessellatum* Tschudi, 1845 (= *E. tessellata*); *Leptotyphlops tricolor* Orejas-Miranda and Zug, 1974 (= *E. tricolor*); *Typhlops undecimstriatus* Schlegel, 1839 (= *E. undecimstriata*); *Glauconia bilineata unicolor* Werner, 1913 (= *E. unicolor*); *Epictia vanwallachi* Koch et al., 2014 (= *E. vanwallachi*); *Leptotyphlops vellardi* Laurent, 1984 (= *E. vellardi*); and *Leptotyphlops weyrauchi* Orejas-Miranda, 1964 (= *E. weyrauchi*).

The molecular analysis of Adalsteinsson et al. (2009) revealed that *E. goudotii* is represented by multiple species (Table 1). Their six samples labeled *E. “goudotii”* in fig. 12 included the following: *E. goudotii*-1 (= *E. bakewelli* from Michoacán); *E. goudotii*-2 and -3 (= *E. bakewelli* from Oaxaca); *E. goudotii*-4 (= *E. phenops* from Guatemala); *E. goudotii*-5 (= *E. phenops* from Tehuantepec, Oaxaca); and *E. goudotii*-6 (= sp. nov. from Veracruz). Samples 1–3 form a western Mexico clade representing *E. bakewelli*, samples 4–5 form a southwestern Mexico clade representing *E. phenops*, and sample 6 forms an eastern Mexico clade representing a new species, described below. Adalsteinsson et al. (2009) also sampled *E. “albifrons”* from Guyana (= *E. tenella*), *E. magnamaculata* from the Bay Islands of Honduras, and *E. columbi* from the Bahamas.



**Table 1.** Molecular data for *Epictia* based on the studies of Adalsteinsson (2008), Adalsteinsson et al. (2009), and McCranie and Hedges (2016). \* = data unavailable to author.

GenBank No.	Locality	Voucher	Adalsteinsson	Adalsteinsson et al.	McCranie/Hedges	Species
KP171710, KP171718	Honduras: Potrerillos	FMNH 283741	—	—	<i>E. ater</i> -1	<i>E. ater</i>
KP171711	Honduras: Potrerillos	USNM 581843	—	—	<i>E. ater</i> -2	<i>E. ater</i>
GQ469122, GQ469221	Mexico: Oaxaca	UTA 57498	<i>L. goudotii</i> -3	<i>E. goudotii</i> -3	<i>E. bakewelli</i> -1	n. sp.
GQ469121, GQ469220	Mexico: Michoacán	UTA 54554	<i>L. goudotii</i> -1	<i>E. goudotii</i> -1	<i>E. bakewelli</i> -2	<i>E. bakewelli</i>
GQ469123, GQ469217	Mexico: Oaxaca	UTA 53657	<i>L. goudotii</i> -2	<i>E. goudotii</i> -2	<i>E. bakewelli</i> -3	n. sp.
*	*	*	—	—	<i>E. bakewelli</i> -4	n. sp.
GQ469212, GQ469089	Bahamas: San Salvador	USNM 576215	<i>L. columbi</i> -1	<i>E. columbi</i> -1	<i>E. columbi</i> -1	<i>E. columbi</i>
GQ469211, GQ469090	Bahamas: San Salvador	SBH 192936	<i>L. columbi</i> -2	<i>E. columbi</i> -2	<i>E. columbi</i> -2	<i>E. columbi</i>
GQ469213, GQ469091	Bahamas: San Salvador	SBH 192979	<i>L. columbi</i> -3	<i>E. columbi</i> -3	<i>E. columbi</i> -3	<i>E. columbi</i>
GQ469214, GQ469092	Bahamas: San Salvador	SBH 192980	<i>L. columbi</i> -4	<i>E. columbi</i> -4	<i>E. columbi</i> -4	<i>E. columbi</i>
GQ469215, GQ469093	Bahamas: San Salvador	SBH 192981	<i>L. columbi</i> -5	<i>E. columbi</i> -5	<i>E. columbi</i> -5	<i>E. columbi</i>
KP171713	Honduras: Guanaja	USNM 581844	—	—	<i>E. magnamaculata</i> -1	<i>E. magnamaculata</i>
KP171714, KP171719	Honduras: Isla Grande	UNAH 256774	—	—	<i>E. magnamaculata</i> -2	<i>E. magnamaculata</i>
GQ469094, GQ469216	Honduras: Utila	SBH 172915	<i>L. goudotii</i> -7	<i>E. magnamaculata</i>	<i>E. magnamaculata</i> -3	<i>E. magnamaculata</i>
KP171715, KP171720	Honduras: Ocotepeque: Antigua	FMNH 283737	—	—	<i>E. phenops</i> -1	n. sp
KP171716, KP171721	Honduras: Ocotepeque: Antigua	FMNH 283735	—	—	<i>E. phenops</i> -2	n. sp
*	*	*	—	—	<i>E. phenops</i> -3	n. sp
GQ469119, GQ469219	Mexico: Veracruz: Catemaco	UTA 52658	<i>L. goudotii</i> -6	<i>E. goudotii</i> -6	<i>E. phenops</i> -4	n. sp
GQ469124, GQ469222	Mexico: Oaxaca:San Isidro	ENEPI 6752	<i>L. goudotii</i> -5	<i>E. goudotii</i> -5	<i>E. phenops</i> -5	<i>E. phenops</i>
GQ469117, GQ469218	Guatemala: Huehuetenango	UTA 42208	<i>L. goudotii</i> -4	<i>E. goudotii</i> -4	<i>E. phenops</i> -6	<i>E. phenops</i>
GQ469096, GQ469223	Guyana: Kurpukari	ROM 20503	<i>L. albifrons</i> -2	<i>E. albifrons</i> -2	<i>E. albifrons/tenella</i> -1	<i>E. tenella</i>
GQ469043, GQ469224	Guyana: Baramita	ROM 22487	<i>L. albifrons</i> -1	<i>E. albifrons</i> -1	<i>E. albifrons/tenella</i> -2	<i>E. tenella</i>
GQ469097, GQ469224	Guyana: Baramita	—	—	—	<i>E. albifrons/tenella</i> -2	<i>E. tenella</i>

A more recent molecular study focusing on Mesoamerican *Epictia*, by McCranie and Hedges (2016), revealed three additional undescribed species masquerading under the names of *E. bakewelli* and *E. phenops* (Table 1). Their samples presented in fig. 2 (of which some were identical to those of Adalsteinsson et al., 2009) included the

following: *E. bakewelli*-1 (= sp. nov. from Oaxaca); *E. bakewelli*-2 (= *E. bakewelli* from Michoacán); *E. bakewelli*-3 and -4 (= sp. nov. from Oaxaca); *E. phenops*-1 and -2 (= sp. nov. from Honduras); *E. phenops*-3 and -4 (= sp. nov. from Veracruz); and *E. phenops*-5 and -6 (= *E. phenops* from Oaxaca and Guatemala). McCranie and Hedges (2016) referred to the Middle American complex as the *E. goudotii* species group. As I will show below, *E. goudotii* does not occur in Panama and is not closely related to the Mexican and Central American species, all of which comprise the “*Epictia phenops* species group.”

## MATERIALS AND METHODS

I examined 323 specimens of *Epictia* from Mexico, Central America, the West Indies, and northern South America, and dissected 59 to examine the viscera. I included scale count data from eight literature sources (1943–2016), bringing the total number of summarized specimens to more than 525 (Table 2). The museum acronyms follow Leviton et al. (1985) and Sabaj Pérez (2014), except for the following: ARH = A. R. Hardy field number; CBF = Charles B. Fugler field number; CHP = Círculo Herpetológico de Panamá; CSL = Carl S. Lieb field number; DKR = D. K. Richards field number; DWM = D. W. Morris field number; EF = UMMZ field series; EHT = Edward H. Taylor field number; EHT-HMS = Edward H. Taylor and Hobart M. Smith field number; EWA = E. Wyllis Andrews field number; JAO = James A. Oliver field number; JC = John Cadle field number; JEW = John E. Winbery field number; JRM = James R. McCranie; JRM = John R. Meyer field number; LBSC = California State University, Long Beach field series; RAT = Richard A. Thomas field number; RWA = Ralph W. Axtell field number; SBH = S. Blair Hedges field number; TBM = Thomas B. MacDougall field number; and VW = Van Wallach field number. With regard to elevation, NSL signifies “near sea level.”

The descriptions of the viscera follow Wallach (1991, 1996, 1998a, b), Broadley and Wallach (1996, 1997a, b, 2007), and Wallach and Boundy (2005). The external morphology follows Boundy and Wallach (2008), Broadley et al. (2014), Francisco et al. (2012), Hahn and Wallach (1998), Lehr et al. (2002), Wallach (2003c), and Wallach and Hahn (1997). When describing the head shields, length and depth refer to the longitudinal axis of the snake, and width, breadth, and height to the transverse axis. The traditional vertebral scale posterior to the rostral is the prefrontal, but it has been fused with the rostral in the majority of leptotyphlopids so the first post-rostral scale in *Epictia* is the frontal or, in the case of *E. ater* and *E. bakewelli*, the postfrontal (Wallach, 2003b; McCranie, 2011). The orientation of the parietals and occipitals may be transverse (Fig. 2E) to the body axis, or oblique (Fig. 6A) when the lateral edges are angled anteriorly. The posterior transverse borders of the supraoculars are parallel (Fig. 7G), or oblique (Fig. 10C) to those of the supranasals. The cloacal shield can be semilunate (Fig. 5AP), or subtriangular (Fig. 5AR) in shape (Broadley and Wallach, 2007), and I describe a truncated, pyramidal cloacal shield in *E. albifrons* (Fig. 13AL). The termination of the tail in *Epictia* is a variable character, but the typical condition is a small apical spine. I define the various forms of this spine as: (1) a needle-like spine (Fig. 6H); (2) a tapered thorn (Fig. 13AH); (3) a horizontally compressed spike (Fig. 5AS); (4) a broad horizontally compressed vertical blade (Fig. 4V); and (5) a cone or conical termination lacking a sharp point (Fig. 12Q). Specimens with a terminal cone might have supported a spine that wore away from use, but no available data or observations suggest this is the case.

The color pattern of sclecophidians often is difficult to observe and describe accurately due to three factors involving the actual scale outline, pigmentation of the skin beneath it (which usually does not correspond to the shape of the scale), and reflection of light off the scales (Fig. 6E). Snakes in the genus *Epictia* often are described as silver in coloration (i.e., Buurt, 2005), but this is an artifact of the reflection of light from the enlarged free edges of the costal scales, which consist of 20–30% of the scale’s length (Jackson and Reno, 1975; Fig. 3E). This silvery condition is seen in some of the photographs presented below due to reflection of light (Fig. 4bZ, aE). Upon closer examination a regular pattern of brown and yellow stripes actually exists, and the width of the yellow stripes that border the brown stripes along the center of each scale row varies from a stripe equal to or wider than its adjacent brown stripes (i.e., *E. bakewelli*, *E. magnamaculata*, and *E. tenella*) to merely a pale outline of the scales (i.e., *E. ater*, *E. columbi*, and *E. goudotii*), in which case the snake appears as uniform brown or black.

Four basic color patterns are present in *Epictia*, including a uniform dark coloration and three striped patterns. Snakes with a uniform pattern may or may not have pale outlines around each scale, and I refer to this midbody pattern as unstriped (U; Fig. 3D) or outlined (O; Fig. 1S). In those species with a pattern of dark (brown or black) and pale (yellow, white, or silver) stripes, I define the midbody stripe formula as the number of dark dorsal, lateral,

and ventral stripes. A formula of 3 + 2/2 + 0 indicates 3 middorsal dark stripes, 2 lateral dark stripes, and no mid-ventral stripes, for a total of 7 dark stripes (Fig. 13U). In one striped pattern, 7–11 dark stripes are somewhat similar in width on each scale row, and they are separated by pale stripes of equal width (i.e., 7 + 0). The second and third striped patterns (which I abbreviate as the 3D + 4L middorsal pattern; Figs. 2H, 4cI) present 3 middorsal dark stripes separated by 4 pale stripes. The second striped pattern contains 7 dark stripes, of which 2 are lateral and form a pair of broader dark stripes separated by a narrower pale stripe (midbody formula = 3 + 2/2 + 0; Fig. 2J). The third striped pattern contains 5 dark stripes, since only a single broad dark lateral stripe covers 2–3 scale rows (midbody formula = 3 + 1/1 + 0; Figs. 9J, 10K).

**Table 2 [a, b].** Morphometric means, ranges, and ratios of external morphological characters of the *Epictia phenops* species group plus *E. albifrons*, *E. goudotii*, and *E. tenella*. *n* E = sample size of examined specimens; *n* T = sample size of specimens for scutellation statistics; LOA = total length (in mm); TL = tail length (in mm); TMD = total middorsals between rostral and apical spine; SC = subcaudals; MBD = midbody diameter (in mm); MTW = midtail width (mm); L/W = length/width ratio; RTL = relative tail length (TL/LOA × 100); RTW = relative tail width (TL/TW); RRW = relative rostral width (RW/HW); RS = rostral shape; RA = rostral apex; RL = rostral length (pre-eye = not reaching eye level, ant. eye = reaching anterior eye level, mid-eye level, post-eye = reaching posterior eye level, post-ocular = nearly reaching posterior border of ocular shield); RSS = rostral spot size (S = small, indistinct and partially covering rostral, M = moderate, distinct and covering entire rostral, L = large, distinct and extending beyond rostral onto supranasal and frontal); DF = discrete frontal; SOP = supraocular proportion (W/L); SOS = supraocular shape; SOB = supraocular and supranasal borders; POO = parietal-occipital orientation (T = transverse, O = oblique); PVS = pale paravertebral stripes contact occipitals and parietals; OS = ocular shape; Eye = eye shape; RES = relative eye size (eye height/ocular shield height) = small < 0.40, moderate = 0.40–0.45, large > 0.45); EB = eye beneath which shields (O = ocular, SN = supranasal, ASL = anterior supralabial); POS = pale preocular spot; ASL = anterior supralabial (S = short, not or just reaching lower eye level, M = moderate, reaching eye level, T = tall, contacting supraocular); LOC = labial-ocular contact; POG = preoral groove; IL = number of infralabials; CS = cloacal shield shape (S = semilunate, T = subtriangular, P = pyramidal, triangular with truncate apex); CSC = cloacal shield color (B = uniform brown, BV = pale brown with dark vermiculations, Y = uniform yellow, 1 = lacking yellow cloacal ring, 2 = yellow cloacal ring present); DCS = pale dorsocaudal spot in number of mean scales and range; SCS = pale subcaudal spot in number of mean scales and range; RCS = relative caudal spot length (SCS/DCS); AS = apical spine (C = cone, S = spine, T = thorn, HS = spike, B = blade); TC = throat color (D = dark, L = pale); MSF = midbody stripe formula (dorsal/lateral/ventral, U = unstriped, O = scales thinly outlined); DSN = dark stripe number; DSS = dark stripe shape (D = diamond-shaped spots, R = rectangular-shaped spots, O = oval-shaped spots, T = triangular-shaped spots, — = unstriped); DS = dark dorsal stripes; LS = dark lateral stripes; VS = dark ventral stripes; LSW = pale stripe width (N = narrow, < 0.25 costal width; M = moderate, 0.25–0.50 costal width; B = broad, > 0.50 costal width); LSB = pale stripe borders (S = straight, Z = zigzag); and CPT = color pattern type (1 = unicolored or weakly outlined; 2 = 7–9 dark stripes of equal width; 3 = middorsal pattern of 3D + 4L with midbody formula of 3 + 2/2 + 0; and 4 = middorsal pattern of 3D + 4L with midbody formula of 3 + 1/1 + 0).

(Table 2a)							
	<i>E. ater</i>	<i>E. bakewelli</i>	<i>E. columbi</i>	<i>E. magnamaculata</i>	<i>E. phenops</i>	<i>E. martinezi</i>	<i>E. pauldwyeri</i>
	Central America	SW Mexico	Bahamas	Caribbean Islands	N Mesoamerica	Honduras	Panama
<i>n</i> E	53	3	2	54	83	6	6
<i>n</i> T	77 f	21 f	12 g	83 de	168 afh	6	6
LOA	125.4 (72–183)	146.6 (117–181)	136.0 (86–183)	141.5 (76–220)	131.5 (53–195)	143.8 (71–169)	105.2 (67–129)
TL	7.7 (3.5–11.0)	8.1 (7.0–12.5)	10.5 (9–13)	8.8 (4.0–11.5)	7.3 (3.0–12.0)	10.7 (5.0–14.0)	5.1 (3.0–7.0)
TMD	237.5 (212–266)	253.3 (245–269)	246.8 (243–265)	238.7 (219–262)	243.5 (216–277)	256.3 (248–260)	211.8 (202–226)
SC	18.4 (14–22)	19.2 (16–22)	18.2 (13–22)	17.3 (15–21)	16.3 (12–22)	19.8 (16–23)	12.7 (10–14)
MBD	2.3 (1.3–3.4)	2.9 (1.9–3.7)	2.8 (1.6–3.8)	2.8 (1.9–4.5)	2.4 (1.1–4.3)	3.1 (1.8–3.5)	2.3 (1.5–2.9)
MTW	2.1 (1.2–2.6)	2.5 (1.7–2.9)	1.8 (1.7–1.8)	2.3 (1.1–3.5)	2.1 (1.0–3.2)	2.0 (1.3–2.3)	2.0 (1.3–2.3)
L/W	52.3 (41–74)	52.9 (48–62)	53.3 (42–64)	53.6 (38–72)	56.9 (33–77)	46.0 (39–50)	45.7 (43–49)
RTL	6.2% (4.2–8.7%)	6.9% (5.8–9.5%)	6.6% (4.5–8.7%)	6.2% (4.8–8.5%)	5.5% (3.5–7.8%)	7.4% (5.5–8.8%)	4.8% (3.6–6.1%)
RTW	3.5 (2.2–4.8)	4.1 (3.6–4.4)	4.2 (3.3–5.3)	3.8 (2.8–5.9)	3.5 (2.0–5.4)	4.2 (3.3–5.2)	2.5 (1.8–3.1)

RRW	0.41 (0.34–0.56)	0.34 (0.31–0.37)	0.37 (0.23–0.47)	0.35 (0.22–0.50)	0.37 (0.22–0.48)	0.41 (0.37–0.51)	0.47 (0.42–0.53)
RS	waisted	waisted	sagittate	sagittate	sagittate	parallel	subtriangular
RA	triangular	rounded	truncated	oval	truncated	truncated	rounded
RL	post-eye	post-eye	post-eye	pre-eye	mid-eye	mid-eye	mid-eye
RSS	S	M	0	L	S–M	M	M
DF	0	0	+	+	+	+	+
SOP	1.5	1.25	2.0	1.5	2.0	2.5	1.5
SOS	pentagonal	pentagonal	pentagonal	pentagonal	pentagonal	pentagonal	pentagonal
SOB	parallel	parallel	parallel	parallel	oblique	oblique	parallel
POO	trans.	trans.	obl.	trans.	trans. or obl.	obl.	trans.
PVS	0	+	0	+	0	0	0
OS	hexagonal	hexagonal	hexagonal	hexagonal	hexagonal	hexagonal	hexagonal
Eye	oval	oval	oval	oval	oval	oval	oval
RES	0.43 (0.35–0.50)	0.43 (0.42–0.43)	0.45 (0.45–0.46)	0.45 (0.36–0.51)	0.42 (0.34–0.51)	0.50 (0.47–0.54)	0.43 (0.38–0.48)
EB	O–SN–ASL	O–SN	O–SN–ASL	O–SN–ASL	O	O–SN	O–SN
POS	0	0	0	0	0	+	0
ASL	M	M	M	M	M	M	M
LOC	0	0	0	0	0	0	0
POG	0	0	+	0	0	0	0
IL	4	4	4	4	4	4	4
CS	T	T	S	T	S (T)	S	T
CSC	B1 (B2)	Y2	B1	BV2	B1 (BV2)	B1	Y2
DCS	2.3 (0–3)	2.9 (0–4)	1.8 (0.5–2)	4.2 (0–6)	1.2 (0–3.5)	2.4 (1.5–3.5)	2.3 (2–3.5)
SCS	11.7 (6.5–17.5)	8.9 (3–13)	5.2 (2–7)	3.9 (0–7)	8.5 (0–13.5)	7.5 (5.5–9)	1.8 (1–2.5)
RCS	5.1	3.1	1.8	0.9	7.1	3.1	0.8
AS	S / T	HS	C	B	S / HS	T	HS
TC	D	L	D	D	D / L	L	D
MSF	U or O	3 + 2/2 + 0	U or O	3 + 3/3 + 1/1	3 + 1/1 + 0	3 + 2/2 + 0	7 + 0
DSN	—	7	—	11	5	7	7
DSS	—	rect.	—	rect. or dia.	tri.	dia.	dia.
DS	U or O	3D + 4L	U or O	3D + 4L	3D + 4L	3D + 4L	3
LS	U or O	2 + 2	U or O	3 + 3	1 + 1	2 + 2	2 + 2
VS	U or O	U or O	U or O	1 + 1	U or O	U or O	U or O
LSW	—	B	—	M–B	N–B	M	N
LSB	—	straight	—	straight	zigzag	zigzag	zigzag
CPT	1	3	1	3	4	3	2

(Table 2b)

	<i>E. resetari</i>	<i>E. schneideri</i>	<i>E. vindumi</i>	<i>E. wynni</i>	<i>E. goudotii</i>	<i>E. albifrons</i>	<i>E. tenella</i>
	Veracruz	S Mexico	Yucatan	NE Mexico	N South America	Brazil	South America
<i>n</i> E	6	12	46	16	6	14	16
<i>n</i> T	15 ac	12	46	21	13 d	14	33 b
LOA	122.7 (79–142)	123.6 (83–181)	142.8 (72–163)	147.2 (125–163)	110.2 (73–164)	121.0 (63–168)	147.3 (71–215)
TL	6.3 (5.0–8.5)	8.5 (5.0–11.5)	8.5 (4.0–11.0)	5.7 (6.0–9.5)	4.4 (3.5–6.0)	6.6 (3.0–9.0)	9.3 (5.0–14.0)
TMD	246.2 (238–258)	246.8 (243–265)	243.6 (230–253)	249.8 (242–260)	242.6 (227–260)	212.6 (206–218)	224.5 (215–233)
SC	17.7 (15–20)	18.2 (13–22)	17.8 (15–23)	16.3 (14–20)	13.8 (11–16)	13.1 (11–15)	17.2 (13–20)
MBD	2.1 (1.3–3.0)	2.8 (1.6–3.8)	2.4 (1.3–3.7)	3.0 (2.3–3.8)	1.9 (1.5–2.9)	2.4 (1.2–3.2)	3.2 (1.9–4.6)
MTW	1.9 (1.2–2.5)	2.3 (1.3–3.0)	2.1 (1.2–2.9)	2.4 (2.0–2.8)	1.5 (0.9–2.5)	2.4 (1.2–3.2)	2.7 (1.6–3.3)
L/W	54.1 (40–60)	53.3 (42–64)	53.6 (40–70)	47.8 (43–58)	59.8 (48–76)	40.0 (35–49)	48.5 (37–60)



RTL	6.0% (4.9–6.5%)	6.6% (4.5–8.7%)	6.5% (5.1–9.0%)	5.7% (4.4–6.9%)	4.7% (3.5–6.6%)	5.4% (4.3–6.4%)	6.4% (5.1–7.8%)
RTW	3.6 (3.2–4.2)	4.2 (3.3–5.3)	3.8 (2.8–5.7)	3.3 (2.5–4.3)	3.3 (2.0–3.9)	2.7 (2.1–3.6)	3.5 (2.8–4.1)
RRW	0.35 (0.27–0.41)	0.37 (0.23–0.47)	0.37 (0.24–0.44)	0.36 (0.29–0.42)	0.50 (0.42–0.60)	0.31 (0.25–0.37)	0.29 (0.26–0.34)
RS	sagittate	waisted	sagittate	subtriangular	triangular	sagittate	subtriangular
RA	oval–truncated	truncated	truncated	truncated	truncated	truncated	oval–truncated
RL	mid-eye	post-eye	post-eye	pre-eye	pre-eye	post-eye	pre-eye
RSS	M	S	M	S	0 (S)	M	L
DF	+	0	+	+	+	+	+
SOP	2.0	2.0	2.0–3.0	2.0	1.5–2.0	2.0–2.5	3.0–4.0
SOS	pentagonal	pentagonal	pentagonal	pentagonal	pentagonal	pentagonal	hexagonal
SOB	parallel	parallel	oblique	parallel	parallel	parallel	oblique
POO	trans.	trans.	trans.	trans.	trans.	obl.	trans.
PVS	0	0	0	0	0	0	+
OS	hexagonal	hexagonal	hexagonal	hexagonal	hexagonal	hexagonal	pentagonal
Eye	round	oval	round	round	round	oval	round
RES	0.44 (0.41–0.47)	0.45 (0.45–0.46)	0.47 (0.40–0.50)	0.42 (0.38–0.50)	0.43 (0.39–0.46)	0.42 (0.38–0.45)	0.44 (0.36–0.51)
EB	O–SN	O–SN–ASL	O–SN	O	O–SN	O–SN–ASL	O
POS	0	0	0	0	0	0	0
ASL	M	M	M	M	S	M	T
LOC	0	0	0	0	0	0	+
POG	0	0	0	0	+	0	0
IL	4	4	4	3	4	4	4
CS	S	S	S	T	T	P	T
CSC	B2	BV2	BV1	BV2	B1	B1	BV1
DCS	1.3 (1–2)	1.8 (0.5–2)	1.7 (1–3)	0.4 (0–1)	0.5 (0–3)	1.0 (0–1)	1.1 (0–2)
SCS	7.3 (5.5–9)	5.2 (2–7)	9.8 (8–13)	4.0 (0–8)	0.7 (0–2)	2.5 (1–4)	1.8 (1–3)
RCS	5.6	1.8	5.8	10.0	1.4	2.5	1.6
AS	HS	HS	HS	T	C–N	T	C
TC	D	L	D	D / L	D	L	D
MSF	3 + 2/2 + 0	3 + 1/1 + 0	7–9 + 0	3 + 2/2 + 0	U or O	7 + 0	7 + 0
DSN	7	5	7–9	7	—	7	7
DSS	dia.	rect.	dia.	dia. or tri.	—	dia.	oval
DS	3D + 4L	3D + 4L	3	3D + 4L	U or O	3	3
LS	2 + 2	1 + 1	2–3 + 2–3	2 + 2	U or O	2 + 2	2 + 2
VS	U or O	U or O	U or O	U or O	U or O	U or O	U or O
LSW	M	M	M	M–B	—	M–B	M–B
LSB	zigzag	straight	zigzag	zigzag	—	zigzag	zigzag
CPT	3	4	2	3	1	2	2

<sup>a</sup> includes data from Smith (1943)

<sup>b</sup> includes data from Hoogmoed (1977)

<sup>c</sup> includes data from Pampa-Ramírez (2010)

<sup>d</sup> includes data from Pinto et al. (2010)

<sup>e</sup> includes data from McCranie (2011)

<sup>f</sup> includes data from McCranie and Hedges (2016)

<sup>g</sup> includes data from Klauber (1939) and Riley (1981)

<sup>h</sup> includes data from Woodbury and Woodbury (1944)

I used the following abbreviations in the text: SRF = scale row formula; TSR = midtail scale rows; TMD = total number of middorsals between rostral and apical spine; SC = subcaudals, excluding apical spine; LOA = total length; SVL = snout–vent length; TL = tail length; MBD = horizontal midbody diameter; MTD = horizontal midtail diameter; RW = midrostral width; HW = head width at interocular level; ED/OH relative eye size (vertical eye diameter/maximum ocular shield height); L/W = relative body proportion (total length/midbody diameter); TL/LOA = relative tail length, TL/TW = relative tail width (tail length/midtailwidth ratio); RW/HW = relative rostral width; AT = anterior tip of organ; MP = organ midpoint; PT = posterior tip of organ; IPB or RB or B = intrapulmonary bronchus, right bronchus or bronchus; and KOL = kidney overlap (kidney overlap/right kidney AT–left kidney PT). I summarize the visceral data means in Table 3.

**Table 3.** Morphometric means of visceral characters expressed as % SVL, ratios, or mensural characters of the *Epictia phenops* species group plus *E. albifrons*, *E. goudotii*, and *E. tenella*. ATE = *E. ater*, BAK = *E. bakewelli*, COL = *E. columbi*, MAG = *E. magnamaculata*, PHE = *E. phenops*, MAR = *E. martinezi*, PAU = *E. pauldwyeri*, RES = *E. resetari*, SCH = *E. schneideri*, VIN = *E. vindumi*, WYN = *E. wyntni*, GOU = *E. goudotii*, ALB = *E. albifrons*, TEN = *E. tenella*; SHYPT = sternohyoideus posterior tip; SHY/SHG = sternohyoideus length/snout–heart gap; HL = heart length; HMP = heart midpoint; RLL = right liver length; TLMP = total liver midpoint; TLS = total (left + right) liver segments; ALA = anterior liver asymmetry (right liver lobe anterior tip–left liver lobe anterior tip/total liver length); PLT = posterior liver tail (left liver lobe posterior tip–right liver lobe posterior tip/total liver length); GBMP = gall bladder midpoint; GB–KG = gall bladder–kidney gap; TGMP = total gonad midpoint; TTS = mean total (right + left) testis segments; G–KG = gonad–kidney gap; TKMP = total kidney midpoint; K–VG = kidney–vent gap; K–VI/RLg = kidney–vent interval/right lung; RCL = rectal caecum length; RC–VI = rectal caecum–vent interval; NTR = number of trachea rings; RLgL = right lung length; RBL = right bronchus length; RLgMP = right lung midpoint; RLgPT = right lung posterior tip; H–LgD = heart–lung distance; H–LD = heart–liver distance; T/B–GBD = trachea/bronchus–gall bladder distance; and H–KD = heart–kidney distance.

	ATE	BAK	COL	MAG	PHE	MAR	PAU	RES	SCH	VIN	WYN	GOU	ALB	TEN
Sample Size	6	2	1	10	15	2	3	2	3	5	3	1	2	4
Character														
SHYPT	14.3	13.4	11.7	13.8	13.8	14.4	14.7	12.8	12.7	13.3	14.0	13.7	14.3	10.1
SHY/SHG	0.80	0.80	0.75	0.84	0.85	0.67	0.87	0.73	0.83	0.87	0.84	0.82	0.56	0.56
HL	4.7	3.6	4.3	4.5	4.6	3.7	5.2	3.9	3.9	4.4	4.2	6.0	4.7	5.4
HMP	20.0	18.6	17.8	18.7	18.6	18.7	19.4	19.4	17.2	17.5	18.6	19.7	18.6	20.5
RLL	36.5	35.2	34.4	38.8	40.0	36.5	36.0	39.1	36.6	37.5	40.8	41.2	39.1	35.8
TLMP	49.9	45.2	46.1	48.6	48.8	47.0	47.8	47.8	46.2	46.1	49.5	48.9	48.5	48.4
TLS	57.8	70.5	63.0	66.7	64.9	73.0	57.0	53.5	72.7	61.0	62.0	56.0	49.5	73.5
ALA	0.13	0.12	0.18	0.12	0.08	0.11	0.09	0.13	0.09	0.12	0.07	0.11	0.03	0.07
PLT	0.10	0.13	0.10	0.11	0.14	0.16	0.08	0.15	0.16	0.14	0.13	0.16	0.22	0.06
GBMP	68.6	63.3	64.3	71.1	69.7	66.3	65.9	70.1	65.6	67.2	70.6	70.6	67.8	67.9
GB–KG	13.9	19.9	18.8	12.3	14.4	14.2	13.3	15.1	15.3	16.6	13.6	15.0	19.2	12.3
TGMP	78.0	78.6	80.5	81.2	80.4	77.2	76.9	80.7	76.4	79.7	80.9	84.2	83.3	78.8
TTS	10.6	8.0	—	7.5	11.1	3.8	8.0	—	—	5.0	10.0	5.5	7.0	6.5
G–KG	0.2	2.7	1.6	0.2	1.4	0.2	–0.5	2.5	2.6	2.5	1.0	–2.1	–0.6	–1.6
TKMP	85.5	86.6	87.5	86.9	87.8	85.3	83.3	88.5	84.4	87.6	87.5	89.5	90.5	84.4
K–VG	11.0	10.3	8.6	10.3	9.2	10.7	13.3	8.9	12.9	9.3	9.8	7.7	6.8	12.4
KVI/RLg	0.50	0.34	0.48	0.40	0.25	0.51	0.67	0.38	0.49	0.45	0.39	0.32	0.25	0.50
RCL	1.4	1.3	2.0	1.3	1.3	1.1	1.6	1.7	0.7	1.2	1.7	1.3	3.2	2.2
RC–VI	12.3	11.3	9.8	10.0	9.7	11.2	13.5	8.9	12.9	10.4	11.3	8.6	7.4	11.3
NTR	89.4	100.2	102.4	92.7	93.0	88.0	76.0	88.4	100.2	96.5	94.6	85.4	77.4	76.8
RLgL	27.8	30.9	26.6	28.9	31.4	24.2	31.6	24.8	32.2	27.5	33.8	27.9	30.2	32.4
RBL	17.7	19.6	19.5	18.7	19.4	20.1	21.9	17.3	20.0	17.7	20.8	14.6	19.8	19.2
RLgMP	36.3	35.9	33.2	35.4	36.6	32.7	37.8	33.7	35.3	33.5	37.6	36.7	36.0	39.4
RLgPT	50.1	51.3	46.5	49.9	52.3	44.8	53.6	46.1	51.4	47.2	54.5	50.6	51.1	55.6

H-LgD	16.2	17.3	15.4	16.7	18.0	14.0	18.4	14.4	18.1	16.0	19.0	17.0	17.4	18.9
H-LD	29.8	26.6	28.3	29.9	30.2	28.3	28.4	28.4	29.0	28.6	30.9	29.2	29.9	28.0
T/B-GBD	48.1	42.8	44.0	50.7	48.9	45.0	43.3	50.1	45.3	47.9	49.3	51.1	46.9	46.3
H-KD	65.4	68.0	69.7	68.3	69.2	66.6	63.9	69.1	67.2	70.1	68.9	69.8	71.9	63.9

The various proportional ratios include the length/width ratio (total length/midbody diameter); relative tail length (tail length/total length); relative tail width (tail length/midtail diameter); relative rostral width (midrostral width/head width at interocular level); relative eye size (eye height/ocular height); and relative caudal spot (pale subcaudals/pale dorsocaudals). I define the length of the dorsal rostral as short (when not reaching anterior eye level = pre-eye), moderate (extending to within the interocular level = mid-eye), and long (when extending past the posterior eye level = post-eye). I also employed two liver lobe ratios, including the anterior liver extension (right liver lobe AT–left liver lobe AT/total liver length) and the posterior liver tail (left liver lobe PT–right liver lobe PT/total liver length). In addition to characters of the viscera being calculated as gaps, intervals, and various points (AT, MP, PT), I define another character as the distance: this character is measured from the midpoint of one organ to the midpoint of another organ. When the trachea-bronchus length is calculated as part of a distance character (i.e., trachea/bronchus–kidney distance), it is written as “trachea/bronchus” rather than “trachea-bronchus” to prevent confusion with signifying the ratio of trachea length/bronchus length. I define total organ length as the sum of the left and right organ lengths and total organ midpoint as the mean of the left and right organ midpoints. I present the statistics in Table 6 in following format:  $\bar{x} \pm SD$  (range) *n*.

The meristic and morphometric characters follow Broadley and Wallach (2007a) and Francisco et al. (2012). I used digital calipers (ISO 9001 by Tresna Instruments) for head, body, and tail measurements to the nearest 0.1 mm, and used a clear plastic mm ruler to measure the body and tail lengths to the nearest 0.5 mm. I photographed most of the specimens at the FMNH with a Leica MZ75 Stereomicroscope (6.3× to 50× with a 10× eye piece) with a SPOT Insight Color Camera (Model no. 3.2.0). Joe Martinez photographed *E. columbi*, *E. martinezi*, some *E. goudotii*, and the paratype of *E. tenella* at the MCZ with a JVC3-CCD (model no. KY-F75U) camera attached to a Leica MZ125 automontage microscope (0.8× to 10.0×). I am most appreciative of Joe’s photographic efforts, because without his excellent images this project would be incomplete. I oriented all of the photographs in Figs. 1–14 with the anterior direction of the snake toward the right (head) and the posterior direction toward the left (tail), and in Fig. 15 (hemipenes) the anterior direction is toward the right (when specimen is horizontally aligned) or toward the top of the page (when specimen is vertical in position). I prepared the maps using Google Earth (2015, version 7.1.5.1557) by searching localities by name or entering the geographic coordinates expressed in map datum WGS 84. Purple stars represent the type locality of each species, red dots represent specimens I examined, and yellow dots represent records taken from the primary literature, online museum databases, and Internet photographs. In the *E. phenops* and *E. ater* maps, the star symbol represents the frontal-rostral condition opposite to that described for the species (i.e., a star for *E. phenops* indicates a fused frontal-rostral shield and a star for *E. ater* represents a discrete and separate frontal shield). I was not able to confirm the distribution of snakes within several Mexican states. In cases where a species has been reported from a state but I did not find a museum voucher specimen or published locality to confirm its presence, I omitted those states from the distribution of the species and discuss this matter under the remarks.

Samples of scolecophidians for internal examination are limited by several factors: rarity of most species, fossorial lifestyle resulting in the paucity of specimens in collections, and permission for dissection. Some studies on visceral data suggest, however, that a relatively small sample size (i.e., 5–10 specimens) adequately represents the variation found in a population, rather than the *n* = 30 requirement stated in statistical texts (Wallach, 1991, 1998a; Wong, 1994). Also, in previous studies of snake viscera I found that a mean difference of at least 2% between visceral characters indicates specific distinctness (Broadley and Wallach, 1996, 1997a, b, 2002, 2007a, b, 2009; Franzen and Wallach, 2002; Lehr et al., 2002; Pyron and Wallach, 2014; Shea and Wallach, 2000; Wallach, 1991, 1994, 1997, 1998a, 1999, 2000, 2001, 2003a, 2005; Wallach and Boundy, 2005; Wallach and Glaw, 2009; Wallach and Ineich, 1996; Wallach et al., 2010). In the following accounts for new species, I made comparisons with every other member of the *E. phenops* complex, in addition to *E. albifrons*, *E. goudotii*, and *E. tenella*. In the diagnostic comparisons between species, I used two different measurements. When the range of values for a character are

exclusive and do not overlap, I indicated the minimum and maximum values separating the two species by “greater than or equal to” and “less than or equal to” symbols (i.e.,  $\leq 8.5$  vs.  $\geq 10.0$ ) to illustrate the gap between the ranges of the two species. When the ranges of a character overlap but the mean values were greater than or equal to 2%, I listed the mean values (i.e., 48.4% vs. 51.6%).

Francisco et al. (2012) defined three differences in the dark dorsal stripes of *Epictia* as taxonomic characters: line-shaped (Figs. 2B, 4J), triangular-shaped (Fig. 6D), and rectangular-shaped (Fig. 9H) spots. To these, I propose two additional character states of diamond-shaped (Fig. 5X) and oval-shaped (Fig. 14R) spots. I called the prominent sensory scale organs or touch corpuscles present in leptotyphlopids (Jackson and Reno, 1975; Orejas-Miranda et al., 1977) sensory pits.

## RESULTS

I provide a summary of the diagnostic external (Table 2) and internal characters (Table 3) for the 14 species examined and discussed in this study, which incorporates my proposed taxonomic arrangement. The species accounts below are arranged alphabetically in the following order: the five currently recognized species in Mesoamerica; new descriptions of four Mexican species, one Honduran species, and one Panamanian species; and the three northern South American species that are related to, or have been confused with, the Mesoamerican taxa. The six new Mesoamerican species of *Epictia* increase the known number of species in the genus to 40.

The status of *E. albifrons* and *E. tenella* currently is controversial (Franco and Pinto, 2009; Ávila-Pires et al., 2010; Wallach et al., 2014; Mumaw et al., 2015), but I am proposing an arrangement whereby both species are recognized. If the neotype designation of MCZ R-2885 for *E. albifrons* by Mumaw et al. (2015) were considered valid (see discussion below under Remarks for *E. albifrons*), however, then *E. tenella* would become a subjective synonym of *E. albifrons*, which would necessitate combining the data herein for the two species' descriptions. The scale counts, descriptive material, photographs, and maps presented below for *E. tenella* would refer to *E. albifrons*, since it would become the senior synonym.

### *Epictia ater* (Taylor, 1940)

Figs. 1A–AA, 15A–F, 16A–H

*Stenostoma albifrons*—Cope, 1887: 63 (part).

*Glauconia albifrons*—Boulenger, 1893: 63 (part).

*Leptotyphlops albifrons*—Amaral, 1930: 138 (part); Dunn and Saxe, 1950: 160; Taylor, 1951: 19, 27–28 (part); 1954: 677 (part); Heyer, 1965: 56, 82; List, 1966: 44, 107; Van Devender and Cole, 1977: 5; Cogger and Zweifel, 1992: 34, col. fig., 1998: 34, col. fig.

*Leptotyphlops* (= *Glauconia*) *albifrons*—Wettstein, 1934: 31 (part).

*Leptotyphlops ater* Taylor, 1940: 536–538, fig. 4, 1944: 156, 1955: 562–563; Dunn and Saxe, 1950: 161; Cochran, 1961: 194; Heyer, 1967: 267; Orejas-Miranda *In* Peters et al., 1970 and 1986: 170; Smith and Smith, 1976: S-B-128, S-C-37, S-D-2; Hahn, 1980: 15; Wallach, 1998a: 552; Savage, 2002: 558–559, pl. 333; Solórzano, 2004: 124–129, fig. 22, map; Bolaños et al., 2005: 18, 193–197, 1343–1347; Porras, 2006a: 21, 2006b: 35; Savage and Bolaños, 2009: 18; Sasa et al., 2010: 526; Sunyer and Köhler, 2010: 492; Illescas-Palomo et al., 2011: 231; McConnell, 2013: 24, col. fig. 28, 199 (map).

*Leptotyphlops nasalis* Taylor, 1940: 535–536, fig. 3, 1944: 156; Cochran, 1961: 194; Orejas-Miranda *In* Peters et al., 1970 and 1986: 171; Hahn, 1980: 22; Villa, 1983: 37, 1990: 473.1, fig; Villa et al., 1983: 85; Sokolov, 1988: 355; Martínez-Sánchez, 1990: 11; Frank and Ramus, 1995: 251; Wilson and McCranie, 1998: 18, 31, 35; Köhler, 1999a: 91, 2001: 123, fig. 98a, map; McDiarmid et al., 1999: 38; Sasa Marin, 2000: 150; Savage, 2002: 559; Wrobel, 2004: 287; Rueda-Pereira, 2007: 84; Delhay, 2009: 181; Sunyer and Köhler, 2010: 492; Beolens et al., 2011: 261; Wallach et al., 2014: 275.

*Leptotyphlops albifrons ater*—Cochran, 1961: 194; Hahn, 1980: 15; Illescas-Palomo et al., 2011: 231.

*Leptotyphlops albifrons nasalis*—Cochran, 1961: 194.

*Leptotyphlops phenops*—Campbell and Howell, 1965: 133; Wilson, 1968: 166; Meyer, 1969: 409–411, map 105 (part); Scott, 1969: 69–72, map 2 (part); Smith and Smith, 1973: 184, 306; Wilson and Hahn, 1973: 120–123 (part); Wilson, 1979: 25; Wilson et al., 1979: 25; Kettunen and Davis, 2004: 23; Kettunen, 2005: 100; Gutiérrez-Espeleta and Van Gysegem, 2005: 135, 136, 139, 144, 145; Wilson and Townsend, 2007: 145.



*Leptotyphlops bakewelli*—List, 1966: 6, 43–44, 60–65, 94–97, 107, pls. 1–3, fig. 3, pl. 18, fig. 11, pl. 19, fig. 2; Cundall and Irish, 2008: 369, 371, 373, 597, 730; McDowell, 2008: 542, 545, 765.

*Leptotyphlops goudotii ater*—Orejas-Miranda In Peters et al., 1970 and 1986: 170; Hahn, 1980: 15; Illescas-Palomo et al., 2011: 231; EOL, 2015: 457414.

*Leptotyphlops goudotii phenops*—Orejas-Miranda In Peters et al., 1970 and 1986: 170 (part); Hahn, 1980: 16 (part).

*Leptotyphlops goudotii* (sic)—Savage, 1973: 13; Wilson and Meyer, 1985: 20–21, fig. 25 (part); Savage and Villa, 1986: 25, 194; Villa et al., 1988: 85 (part); Vences et al., 1998: 37–38; Muurmans and Farmer, 2004: 15–16.

*Leptotyphlops goudotii ater*—Smith and Smith, 1976: S-B-128, S-C-37; Tipton, 2005: 24 (part); Varin, 2008: 122.

*Leptotyphlops goudotii*—Hahn, 1979: 2–3 (part); Wilson, 1983: 125; Johnson, 1984: 119 (part); Weyer, 1990: 48 (part); Smith and Smith, 1993: 591; Wilson and McCranie, 1994: 148, 1998: 18, 31, 35 (part); Garel and Matola, 1996: 38 (part); Günther, 1999: 91, fig. 129a; Marineros, 2000: 139 (part); Wilson et al., 2001: 139 (part).

*Leptotyphlops goudotii*—Savage, 1980: 16; Wilson and Meyer, 1982: 23 (part); Scott, 1983: 406; Scott et al., 1983: 372; Savage and Villa, 1986: 16; Johnson, 1989: 37, 63; Frank and Ramus, 1995: 250 (part); Sasa and Solórzano, 1995: 118; Hedges, 1996: 111, 115 (part); Greene, 1997: 149–150, col. photo; Campbell, 1998: 186–187 (part), fig. 113 (col. photo); Wallach, 1998a: 490 (part); Köhler, 1999a: 91 (part), 1999b: 214, 2001a: 123, fig. 98b, map, 2001b: 12, fig. 11b (part), 2003a: 171 (part), 2003b: 279 (part), 2008: 183–184, map (part); McDiarmid et al., 1999: 31–32 (part); León-Soler and Solórzano, 2000: 1,019; Sasa Marín, 2000: 150 (part); Stafford and Meyer, 2000: 173–174, pl. 96 (part); Leenders, 2001: 216–217, 2 figs., pl. 60 (lower), 2003: 201; Wilson et al., 2001: 117, 124, 139, 141, 149, 152 (part); Wilson and McCranie, 2002: 92, 2004: 21; Salazar et al., 2004: 43; Gutiérrez-Espeleta and Van Gysegheem, 2005: 135, 136; Anonymous, 2006: 139; Casteñeda and Marineros, 2006: 10; Lovich et al., 2006: 11, 14; Porras, 2006a: 21, 2006b: 35; Porras and Solórzano, 2006: 21; Rueda-Pereira, 2007: 84; Cundall and Irish, 2008: 597, 730; Delhay, 2009: 180; Sunyer, 2009: 51, 154, 163; Sasa et al., 2010: 526; Sunyer and Köhler, 2010: 505; Townsend and Wilson, 2010a: 478, 2010b: 693, 698 (part); Wilson and Townsend, 2006: 96, 2010: 811 (part); Wilson and Johnson, 2010: 137, 233 (part); Guevara-Alonso, 2012: 74; Vergner, 2012: 16.

*Leptotyphlops goudotii* (sic) *ater*—Hahn, 1980: 15; Villa, 1983: 36.

*Leptotyphlops goudotii* (sic) *phenops*—Villa, 1983: 37.

*Leptotyphlops* (sic) *goudotii*—Greene, 1999: 149.

*Leptotyphlops goudotii* (sic)—Alemán-Mejía, 2008: 101 (part).

*Epictia ater*—McCranie, 2009: 16, 2011: 43–47, pl. 4, fig. B, map 11, 2015: 378–379 (part); Bolaños et al., 2011: 16; Townsend, 2011: 158, 2014: 246; Abarca-Alvarado, 2012: 267; Chaves et al., 2013: 1–7; Cambronero-Mena, 2014: 28; Chaves et al., 2014: 39; Gallo-García and Mendoza, 2014: 24–25, 30, 52, 62, 65, 77, fig. 27 (col. photo), 79, 86, 88; McCranie et al., 2014: 101; Solís et al., 2014: 137; Stark et al., 2014: 309–311, figs. 1, 2; Sunyer, 2014: 197; Wallach et al., 2014: 275–276 (part); Johnson et al., 2015a: 92; Stark, 2015: 161; McCranie and Hedges, 2016: 6, 16–18, figs. 2, 4; Wilson and Johnson, 2016: 38.

*Epictia goudotii*—Canseco-Márquez and Gutiérrez-Mayén, 2010: 252 (part); Wilson and Johnson, 2010: 101; McConnell, 2013: 24; Muñoz-Chacón and Johnston, 2013: 107, col. photo.

*Epictia nasalis*—Wilson and Johnson, 2010: 101; Pinto and Curcio, 2011: 61; Çinar, 2012: 122; CONABIO, 2012: 52; Spangler, 2015: 342.

*Epictia goudotii ater*—Çinar, 2012: 121.

*Crishagenus nasalis*—Hoser, 2012: 33.

**Holotype:** USNM 79957, a 185 mm (LOA) specimen collected by Henry C. Kellers (USN) in 1928–1929, from “Managua, Nicaragua” [= Managua, Departamento de Managua, Nicaragua, 12°08'N, 86°15'W, elev. 100 m asl].

**Etymology:** This species is named after its typical coloration, from the Latin word *ater*, meaning black.

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 72–183 ( $\bar{x}$  = 125.4) mm; (4) total middorsals = 212–266 ( $\bar{x}$  = 237.3); (5) subcaudals = 14–22 ( $\bar{x}$  = 18.4); (6) relative body proportion = 41–74 ( $\bar{x}$  = 52.3); (7) relative tail length = 4.2%–8.7% ( $\bar{x}$  = 6.2%); (8) relative tail width = 2.2–4.8 ( $\bar{x}$  = 3.5); (9) relative rostral width = 0.34–0.56 ( $\bar{x}$  = 0.41); (10) relative eye size = 0.38–0.53 ( $\bar{x}$  = 0.46); (10) rostral waisted with a posterior constriction and triangular arrowhead-shaped apex; (11) supralabials 2, moderate anterior

supralabial reaching mid-eye level but not in contact with supraocular; (12) frontal fused with rostral, apex triangular; (13) supraoculars large and pentagonal, twice as broad as deep, with posterior border parallel to that of supranasal; (14) widest anteriormost vertebral scale 4<sup>th</sup>; (15) parietals and occipitals subequal, oriented transversely; (16) infralabials 4; (17) cloacal shield subtriangular in shape; (18) head brown with a small pale spot on upper rostral; (19) dorsum uniform brown to black, with or without pale scale edges (no stripes); (20) venter uniform brown to pale brown; (21) midbody stripe formula (U or O) and middorsal pattern (U or O); (22) tail with a pale terminal spot covering 0–3 ( $\bar{x}$  = 2.3) dorsocaudals and 6.5–17.5 ( $\bar{x}$  = 11.7) subcaudals (ventral/dorsal ratio 5.1); and (23) apical termination usually in a small spine.

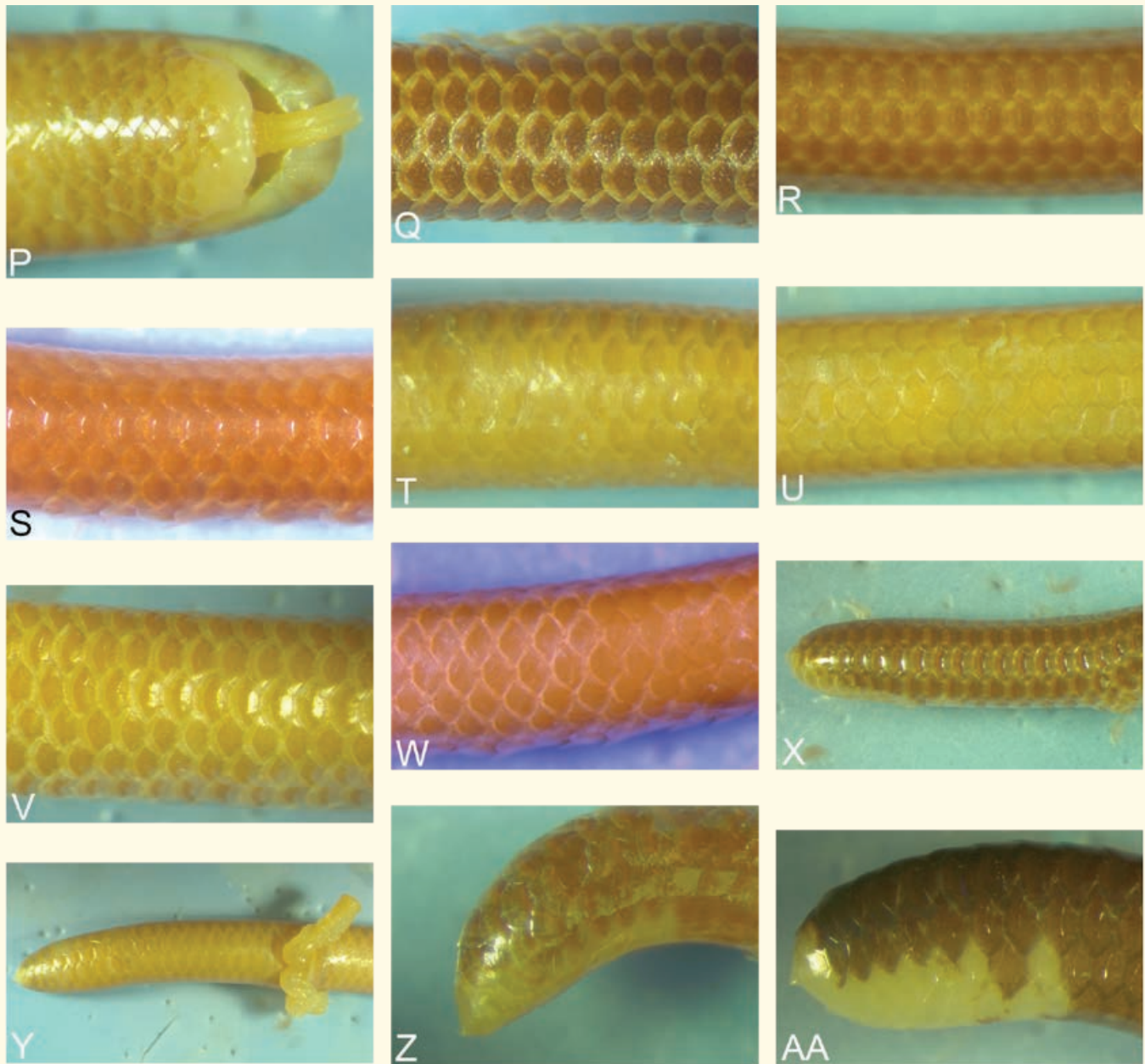
**Description:** Head broader than neck, all head shields with prominent sensory pits that appear as depressions in the scales; head tapered in dorsal profile, with a slightly truncated snout; rostral waisted posteriorly at site of fusion with frontal shield, parallel-sided anteriorly, with triangular apex (= fused frontal) extending beyond the level of the eyes and in contact with supraoculars (Fig. 1D, G); postfrontal slightly broader than deep (or as wide as long), subhexagonal in shape with rounded posterior contours; interparietal and interoccipital distinctly broader than deep; broadest anteriormost vertebral scale 4<sup>th</sup>; supraoculars large and pentagonal, 1½–2 times as wide as long; parietals usually slightly longer than occipitals, occasionally equal in length, both shields oriented transversely; lateral profile rounded; nasal completely divided, suture forming a deep V-shaped angle along anterior supralabial and infranasal (Fig. 1I), nostril oval and positioned nearer to rostral than supralabial; infranasal twice as tall as wide, narrowing toward lip; supralabials 2 (Fig. 1L), anterior supralabial moderate in height with nearly parallel sides, reaching orbit and extending approximately to mid-eye level and taller than posterior supralabial, its labial border usually 1½ times as long as that of infranasal (but varies from one to two times); ocular large, twice as tall as broad, roughly hexagonal with nasal and labial borders equal in length, slightly concave border with supranasal; eye large with distinct pupil and iris, slightly oval or elliptical in vertical plane, equal in depth to lip-orbit gap (ED/OH = 0.38–0.53, = 0.46), protuberant but not visible in dorsal view; posterior supralabial as long as deep or slightly taller than long, shorter than anterior supralabial, posterior border rounded; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 4, 1<sup>st</sup> to 3<sup>rd</sup> small, broader than deep, the 4<sup>th</sup> elongated and hidden from view with closed mouth (Fig. 1N); costal scales rounded and imbricate, in 14 rows throughout; cloacal shield triangular; apical spine minute (Fig. 1X, Z), horizontal or angled downward, projecting from a vertically compressed cone in Nicaragua and Costa Rica, but a vertically compressed narrow blade in El Salvador and Honduras.

Overall coloration in life is chocolate brown to jet-black, with a faint or nonexistent rostral spot and a large subcaudal spot (midbody formula = U or O). Closer inspection of the dorsum in preserved material reveals a pale, narrow border around each dark scale, resulting from a lack of pigment in the free margins of the scales (Fig. 1Q–S; middorsal pattern = O); venter paler than dorsum, generally pale brown with faintly outlined scales (Fig. 1U–W). Head black, purple or dark brown with a small irregular or indistinct pale spot on upper rostral (not including the fused frontal portion, which is dark); lateral head with a broad but short yellow bar along lower half of posterior supralabial and ocular, and lower lip yellow (Fig. 1L–N). Tail uniform dark above and below; cloacal shield paler than surrounding cloaca, which sometimes also is surrounded by a pale ring (Fig. 1Y), the shield itself is pale with brown vermiculations covering ½ of the scale; tail with a yellow tip consisting of a large yellow spot ( $\bar{x}$  = 11.7 subcaudals) ventrally, a very small dorsal spot ( $\bar{x}$  = 2.3 dorsocaudals), and a pale apical spine; and base of spine consists of a vertically compressed cone, with a tiny terminal spike directed horizontally or downward at a 30°–45° angle (Fig. 1Z–AA).

Savage (2002) described the hemipenes of *E. ater* from Costa Rica. The hemipenis of KU 174119, KU 174121, and KU 174135, from Nicaragua (Fig. 15A–G), is single, the organ length 4.5–5.0 mm with a distal cap that is capitate or semicapitate on asulcate side, cap with 15 fringed papillae, distal portion of trunk with 5–7 rows of calyces (1 mm), medial portion (2 mm) with 7–10 elongate ridges of spinose calyces, and proximal base (1.5 mm) with 2–3 longitudinal rugae on either side of sulcus; and sulcus spermaticus with simple sinistral sulcus whose lips are bordered by numerous serrations, and sulcus curves counterclockwise and then extends straight up organ to tip.







**Fig. 1.** Morphological variation in *Epictia ater*. (A, B) dorsal and ventral views of holotype of *Leptotyphlops nasalis* (USNM 16134); (C, D, E, F, G, H) dorsal head (KU 174134, KU 183846, LACM 154162, MVZ 40398, KU 102495, KU 42332); (I, J, K, L) lateral head (KU 183846, KU 174135, MVZ 40398, KU 291287); (M, N, O, P) ventral head (KU 174135, KU 183846, MVV 40398, KU 174135); (Q, R, S) dorsal midbody (KU 174135, LACM 154161, MVZ 40398); (T) lateral midbody (KU 174121); (U, V, W) ventral midbody (LACM 154161, KU 174135, MVZ 40398); (X) lateral tail (LACM 154161); (Y) ventral tail (KU174121); and (Z, AA) lateral apical spine (KU 291287, MVZ 40398).  
 📷 © USNM webpage (A, B), and remaining photos by Van Wallach

**Distribution:** *Epictia ater* is broadly distributed in Mesoamerica, including Guatemala (Izabel); western Honduras (Choluteca, Comayagua, Copán, Cortés, Francisco Morazán, Gracias a Dios, Intibucá, Lempira, Santa Barbara, Valle, Yoro, including Isla Zacate Grande, elev. NSL–1,350 m); El Salvador (Morazán, San Miguel, San Salvador, 250–960 m); western Nicaragua (Carazo, Chinandega, Estelí, Granada, Managua, Rivas, elev. 40–1,100 m); and northwestern Costa Rica (Alajuela, Guanacaste, N Puntarenas, including Islas Murciélagos, San José, elev. NSL–1,125 m), overall elev. NSL–1,350 m (Map 1).





**Map. 1.** Distribution of *Epictia ater* in upper Central America.

**Ecology:** This species frequents pine-oak forest in El Salvador (Köhler et al., 2006). In Honduras it inhabits lower montane rainforest, evergreen and semi-evergreen seasonal forest, tropical deciduous forest, short-tree savanna, and thorn woodland (Johnson, 1989), subtropical wet forest, hardwood cloud forest, and humid pine-oak forest (Wilson et al., 2001) and lowland arid, dry and moist forest, and premontane dry and moist forest (McCranie, 2011). In Nicaragua it occurs in lowland arid forest and premontane wet forest (Sunyer and Köhler, 2010) and dry tropical forest (Guevara-Alonso, 2012). In Costa Rica it is found within lowland dry forests and wet premontane wet forests (Bolaños et al., 2005; Sasa et al., 2010).

**Remarks:** Both *Leptotyphlops ater* Taylor, 1940 and *L. nasalis* Taylor, 1940 were described from Managua, Nicaragua. As first revisers, Dunn and Saxe (1950), who considered the taxa synonymous, selected *E. ater* as the name for the Nicaraguan population. Cochran (1961) considered both taxa as subspecies of *E. albifrons*. Orejas-Miranda (In Peters et al., 1970) rejected the action of Dunn and Saxe (1950) and recognized *E. nasalis* as a full species with *E. ater* as a subspecies of *E. goudotii*, an arrangement followed by Hahn (1980) and McDiarmid et al. (1999). Savage (2002) demonstrated that the Nicaraguan–Costa Rican population is allopatric to *E. goudotii* to the south, and applied the name *E. ater* to the lower Mesoamerican population. Apparently, the frontal is fused to the rostral (southwestern Mexico in the north and Costa Rica in the south) in two populations. A discrete frontal is present in the population from southern Mexico–Guatemala–El Salvador–western Honduras. *Epictia ater* now is the name applied to the Mesoamerican population that occurs on the Pacific versant in El Salvador, western Honduras, western Nicaragua, and northwestern Costa Rica (McCranie, 2011). Wallach et al. (2014) again synonymized *E. nasalis* with *E. ater*.

The fusion of the frontal with the rostral occurs in three species (*E. bakewelli* from Colima to Oaxaca in SW Mexico, a new species described below from Guerrero and Oaxaca, and *E. ater* from Honduras to Costa Rica in Central America). *Epictia phenops* is distributed in Mexico and Central America, and in a presumed hybridization region from southeastern Guatemala to western El Salvador there is some variation in this character. A fused frontal-rostral is present in some specimens of *E. phenops*, whereas the typical condition is a separate frontal and rostral shield. Oliver (1937) reported one of 19 specimens (5%) from the Tehuantepec region and Smith (1943) cited one of 35 Mexican specimens (3%) that lacked a discrete frontal; Flores-Benabib and Flores-Villela (2008) mentioned two of four specimens (50%) from La Loma, Tamaulipas, with a fused frontal and rostral; and Mertens (1952) listed one of five specimens (20%) from San Salvador, El Salvador, with a frontal-rostral fusion. Some variation has been reported in the fusion of the frontal and rostral in *E. ater* (Wilson and Hahn, 1973; McCranie, 2011), where three of 36 specimens (8%) lack the fusion and retain a discrete frontal. All three specimens, however, came from near the border of El Salvador (one from Ocotepeque, described below as a new species) or Guatemala (two from Copán) (J. McCranie, pers. comm.). Two infralabials are fused on the right side of the holotype of *L. ater* (of which the catalogue number is in error in fig. 4 with USNM 79947) and both supraoculars are fused to the supranasals in the holotype of *L. nasalis* (Taylor, 1940).

McCranie (2011) summarized these data from 28 Honduran specimens of *E. ater*: LOA 76–176 mm ( $\bar{x}$  = 131.0), TMD 212–244 ( $\bar{x}$  = 229.1), SC 14–21 ( $\bar{x}$  = 17.2), LOA/MBD 57–96, and TL/LOA 4.7–8.1. McCranie and Hedges (2016) further summarized 30 specimens as follows: dorsal caudal spots 0–2 and ventral caudal spots 4–12.

I refer three specimens from El Salvador (KU 183846, KU 291287, MVZ 40398) with a fused frontal-rostral to *E. ater*, based upon a suite of characters that more closely resemble *E. ater* than *E. phenops* (total middorsals, tail length, relative tail length, midbody diameter, length/width ratio, tail length/width ratio, rostral width, head width, relative rostral width, cloacal shield shape, and pale ventral and dorsal tail spots).

### ***Epictia bakewelli* (Oliver, 1937)**

Figs. 2A–O, 15H

*Stenostoma albifrons*—Bocourt, 1882 *In* Duméril et al., 1870–1909: 505, pl. 29, figs. 10, 10A, B (part); Amaral, 1930: 138 (part); Smith and Smith, 1976: S-B-190, S-F-31 (part).

*Glauconia albifrons*—Boulenger, 1893: 63 (part); Ihering, 1911: 308–309 (part); Amaral, 1930: 138 (part); Smith and Smith, 1976: S-B-97, S-C-37, S-D-1, S-F-17, S-F-20, S-F-23 (part).

*Leptotyphlops albifrons*—Amaral, 1930b: 138 (part).

*Leptotyphlops bakewelli* Oliver, 1937: 16–18, fig. 1a; Taylor, 1939: 1, pl. 1, figs. 13, 14, 1944: 185; Smith and Taylor, 1945: 24 (part); Peters, 1952: 47; Cochran, 1961: 194; Marx, 1976: 88; Smith and Smith, 1976: S-B-128, S-C-37, S-D-4, S-F-12, S-F-17, S-F-23, S-F-30 (part), 1993: 590 (part); Kluge, 1984: 63; Estes et al., 1988: 245, fig. 34A–C; Renous et al., 1991: 37, fig. 13L; Casas-Andreu et al., 1997: 48; Cundall and Irish, 2008: 369, 371, 373, 597; McDowell, 2008: 542, 545; Pampa-Ramírez, 2010: 10; Illescas-Palomo et al., 2011: 231.

*Leptotyphlops phenops*—Klauber, 1940: 151; Zweifel, 1960: 123.

*Leptotyphlops phenops bakewelli*—Smith, 1943: 445; Smith and Taylor, 1945: 24, 1950: 328 (part); Peters, 1952: 47, 1954: 20, 1960b: 332; Maldonado-Koerdell, 1953: 129; Duellman, 1954: 21, 1958: 15; Cochran, 1961: 194; Duellman, 1961: 89, 1965: 654; Thomas, 1965: 1–2; Smith and Smith, 1976: S-B-130, S-C-37, S-D-30, S-F-17, S-F-21, S-F-23, S-F-30 (part); Webb and Baker, 1969: 143; Gaviño de la Torre et al., 1979: 709, 713 (map), 717; Pampa-Ramírez, 2010: 10; Illescas-Palomo et al., 2011: 231.

*Leptotyphlops gadowi* Duellman, 1956: 93–94, fig. 1, 1961: 89, 1965: 654, 663, 679–680, 701; Smith and Taylor, 1966: 23; Smith and Smith, 1976: S-B-128, S-C-37, S-D-17, S-F-23, S-G-4, 1993: 591, 709; Huacuz-Elias, 1995: 40, map 5; Wallach, 1998a: 552; Illescas-Palomo et al., 2011: 231; Wallach et al., 2014: 276.

*Leptotyphlops phenops cf. bakewelli*—Thomas, 1965: 9.

*Stenostoma phenops*—Smith and Smith, 1976: S-F-52.

*Leptotyphlops goudotii bakewelli*—Smith and Smith, 1976: S-B-129, S-C-37, S-D-18 (part); Orejas-Miranda *In* Peters et al., 1970 and 1986: 169 (part); Liner, 1994: 90, 2007: 54 (part); Wallach, 1998a: 490 (part); Liner and Casas-Andreu, 2008: 122 (part); Pampa-Ramírez, 2010: 10; Illescas-Palomo et al., 2011: 231.

*Leptotyphlops phenops phenops*—Smith and Smith, 1976: S-B-130 (part).

- Leptotyphlops goudoti*—Smith and Smith, 1976: S-B-129, S-C-37, S-D-18, 1993: 591, 709 (part); Hahn, 1979: 230.2–3 (part); Flores-Villela, 1993: 35 (part); García, 2006: 43 (part); Álvarez-Romero et al., 2008: 287, 325; Antonio, 2010: Anexo 4.38, 4.39; Santamaría and Flores-Villela, 2006: 119, 125, 127, 139.
- Leptotyphlops goudoti bakewelli*—Smith and Smith, 1976: S-B-128–130, S-C-37, S-G-4, 1993: 590–591, 593, 709 (part); Camarillo-Rangel et al., 1985: 85; Saldaña de la Riva, 1987: 39, 251–252 (part); Sánchez-Herrera and López-Forment, 1988: 739, 749–750; Camarillo-Rangel and Smith, 1992: 40; Pérez-Ramos et al., 2000: 32 (part); Tipton, 2005: 24 (part); Varin, 2008: 122 (part).
- Leptotyphlops goudotii*—Smith and Smith, 1976: S-B-129, S-C-37, S-D-18, S-F-12 (part); Frank and Ramus, 1995: 250 (part); Hedges, 1996: 111, 115 (part); McDiarmid et al., 1999: 31 (part); Sasa Marín, 2000: 150 (part); Köhler, 2001a: 123 (part), 2001b: 12, fig. 11B (part); 2008: 183–184, map (part); Casas-Andreu et al., 2004: 389; Adalsteinsson, 2008: 6, 29, 41, 47, figs. 3.2, 3.5 (part); Cundall and Irish, 2008: 597; URS Corp., 2008: 177; Aguilar-Miguel and Casas-Andreu, 2009: 420; Aguilar-Miguel et al., 2009: 180; Anonymous, 2009: 69 (part); CONABIO, 2009: 17 (part); Wilson and Johnson, 2010: 137, 233 (part); Wilson and Townsend, 2010: 811 (part); Alvarado-Díaz et al., 2013: 142, 153; Wilson et al., 2013: 44 (part).
- Leptotyphlops gaudoti* (sic) *bakewelli*—Casas-Andreu and López-Forment, 1978: 292; Casas-Andreu, 1982: 263; Casas-Andreu et al., 1997: 48; LFTAIPG, 2000: 256; MEXTENIS, 2006: 64; Anonymous, 2007c: 226.
- Leptotyphlops goudotii phenops*—Hahn, 1980: 15–16 (part); Kluge, 1984: 63.
- Leptotyphlops goudotii bakewelli*—Pérez-Higareda and Smith, 1991: 29 (part).
- Leptotyphlops gadovi* (sic)—Wiens, 1993: 414.
- Epictia goudotii*—Adalsteinsson et al., 2009: 7, 10, 17, 31, 46, figs. 3A, 12 (part); Urben et al., 2014: 1409.
- Epictia goudoti*—CONABIO, 2012: 52 (part).
- Epictia goudotii bakewelli*—Çinar, 2012: 121.
- Epictia bakewelli*—Wallach et al., 2014: 276 (part); Mata-Silva et al., 2015: 23, 41 (part); McCranie and Hedges, 2016: 4, 6, 18–20, figs. 2, 4 (part); Schätti and Stutz, 2016: 4; Wilson and Johnson, 2016: 38 (part).

**Holotype:** UMMZ 80228 (field no. JAO 256), a 138 mm (LOA) specimen collected by James A. Oliver and Anderson Bakewell on 26 July 1935, from “Paso del Río, Colima, Mexico” [= Periquillo, Hacienda Paso del Río, Colima, Mexico, 18°54'N, 103°53'W, elev. 30 m asl].

**Paratypes** (4): MEXICO: COLIMA: Paso del Río, collected by Hobart M. Smith on 8 July 1935, FMNH 100625 (field no. EHT-HMS 3370/5477); Hacienda Paso del Río, found dead in road just west of mill by James A. Oliver on 26 July 1935, UMMZ 80229A–B (field no. JAO 286A–B); MICHOACÁN: La Salada, collected by Edward W. Nelson and Edward A. Goldman on 23 March 1903, USNM 46340.

**Etymology:** This species was named in honor of one of its collectors, Anderson Bakewell, who accompanied James A. Oliver on a herpetological collecting expedition to Colima, Mexico, from June to August 1935.

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 117–181 ( $\bar{x}$  = 146.6) mm; (4) total middorsals = 245–269 ( $\bar{x}$  = 253.3); (5) subcaudals = 16–22 ( $\bar{x}$  = 19.2); (6) relative body proportion = 48–62 ( $\bar{x}$  = 52.9); (7) relative tail length = 5.8%–8.5% ( $\bar{x}$  = 6.9%); (8) relative tail width = 3.6–4.4 ( $\bar{x}$  = 4.1); (9) relative rostral width = 0.31–0.37 ( $\bar{x}$  = 0.34); (10) relative eye size = 0.42–0.44 ( $\bar{x}$  = 0.43); (10) rostral waisted with a posterior constriction, apex rounded; (11) supralabials 2, moderate anterior supralabial reaching mid-eye level, but not in contact with supraocular; (12) frontal fused with rostral; (13) supraocular blocky, about as broad as deep, with posterior border parallel to that of supranasal; (14) widest anteriormost vertebral scale 2<sup>nd</sup>; (15) parietals and occipitals subequal, oriented transversely; (16) infralabials 4; (17) cloacal shield semilunate in shape; (18) head brown with a moderate pale spot on upper half of rostral; (19) dorsum with 3 brown middorsal stripes of rectangular-shaped spots separated by 4 broad straight yellow stripes, and a pair of broader brown midlateral stripes separated by a moderate yellow stripe (= 7 dark stripes); (20) venter uniform pale yellow with diffuse brown vermiculations on each scale; (21) midbody stripe formula (3 + 2/2 + 0), and middorsal pattern (3D + 4L); (22) tail with a pale terminal spot covering the 0–4 ( $\bar{x}$  = 2.9) dorsocaudals and 3–13 ( $\bar{x}$  = 8.9) subcaudals (ventral/dorsal ratio 3.1); and (23) apical spine a tiny horizontal spike.



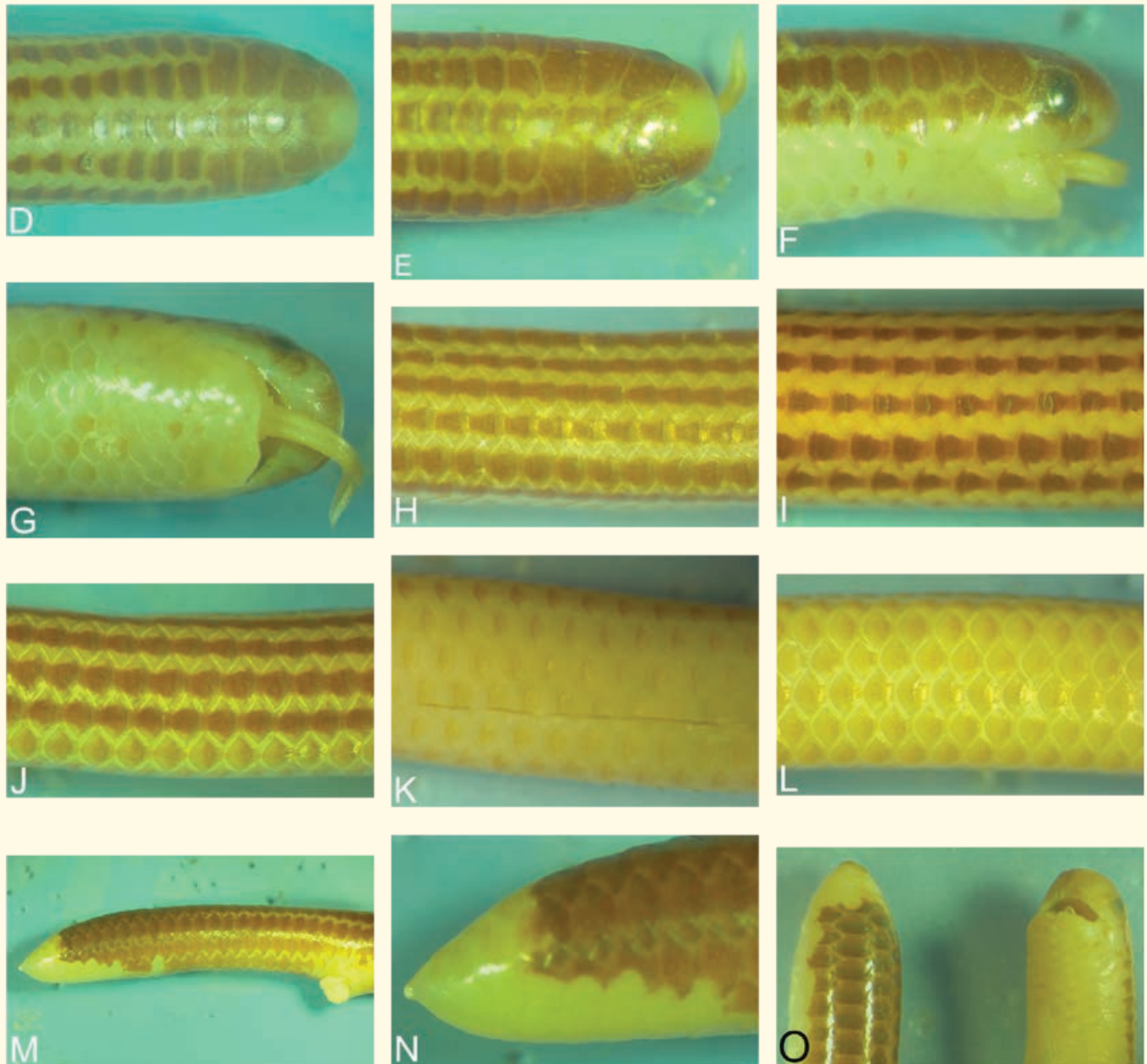
**Description:** Head not broader than neck, all head shields with prominent sensory pits that appear as depressions in scales; head tapered in dorsal profile with a rounded snout (Fig. 2D); rostral waisted posteriorly at site of fusion with frontal shield, parallel-sided anteriorly with rounded apex (= fused frontal) extending beyond interocular level and in contact with supraoculars; postfrontal enlarged, slightly broader than deep (or as wide as long), subhexagonal in shape with rounded posterior contours, more than  $\frac{1}{2}$  of the size of the supraoculars, interparietal and interoccipital distinctly broader than deep; broadest anteriormost vertebral scale 2<sup>nd</sup>; supraoculars squarish or quadrangular with parallel borders, less than  $1\frac{1}{2}$  times as wide as long (Fig. 2D); parietals slightly longer than occipitals, both shields oriented transversely; lateral head profile rounded; nasal completely divided, suture forming a deep V-shaped angle along anterior supralabial and infranasal, nostril slit-like and positioned close to rostral border; infranasal twice as tall as wide, narrowing toward lip; supralabials 2, anterior supralabial moderate in height with nearly parallel sides, reaching orbit and extending approximately to mid-eye level, its labial border usually  $1\frac{1}{2}$  times (occasionally 2 times) as long as that of infranasal; ocular large,  $1\frac{1}{2}$ –2 times as tall as broad, roughly hexagonal with nasal and labial borders equal in length, slightly concave border with supranasal; eye large with distinct pupil and iris, distinctly oval or elliptical in vertical plane, equal to or slightly less than the distance between the lip and orbit ( $ED/OH = 0.42$ – $0.44$ ,  $\bar{x} = 0.43$ ), slightly protuberant and barely visible in dorsal view; posterior supralabial as long as deep or slightly broader than deep, taller than anterior supralabial, posterior border rounded; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 4, with 1<sup>st</sup> to 3<sup>rd</sup> small and 4<sup>th</sup> elongated; costal scales rounded and imbricate in 14 rows throughout; cloacal shield subtriangular; and apical spine a horizontally-compressed spike supported on a conical base (Fig. 2N).

Coloration in life bicolored with yellow and brown stripes, a moderate yellow rostral spot, and a large yellow subcaudal spot. In preserved specimens, dorsum golden brown to brown with 4 broad, straight, yellow stripes that are equal to or greater than the width of the 3 moderate brown stripes at midbody (Fig. 2H; middorsal pattern = 3D + 4L), which appear as connected strings of rectangles; 2 broad midlateral brown stripes separated by a moderate yellow stripe, all with straight borders (Fig. 2I, J); thus, 7 dark stripes are present, with a midbody stripe formula of 3 + 2/2 + 0. Venter immaculate yellow (sometimes with faint brown diffusion) or pale yellowish-tan (Fig. 2C, L). Head brown like dorsum, with a yellow spot on anterior part of rostral and pale paravertebral stripes extending to occipitals and parietals. Lateral head brown with large pale spot on lower half of the posterior supralabial and ocular, each shield with a yellow triangle rather than a horizontal bar. Chin and throat immaculate yellow (Fig. 2C). Cloacal shield yellow with a pale yellow cloacal ring. Tail brown with its apex covered by a small yellow spot that is 3.1 times as long ventrally ( $\bar{x} = 8.9$  subcaudals) as dorsally ( $\bar{x} = 2.9$  dorsocaudals) (Fig. 2M).

The hemipenis of NLU 40758, from Colima, Mexico (Fig. 15H), is incompletely everted, with only the base visible. The bulbous, nude basal portion, however, is similar to that of *E. magnamaculata* (Fig. 15I, J) and three of the new species described below (Fig. 15O–R).







**Fig. 2.** Morphological variation in *Epictia bakewelli*. (A, B) dorsal and ventral views of holotype of *E. bakewelli* (UMMZ 80228); (C) paratype of *E. bakewelli* (UMMZ 80229); (D, E) dorsal head (NLU 40757, NLU 40758); (F) lateral head (NLU 40758); (G) ventral head (NLU 40758); (H, I) dorsal midbody (NLU40758, NLU 40757); (J) lateral midbody (NLU 40758); (K, L) ventral midbody (NLU 40757, NLU 40758); (M) lateral tail (NLU 40758); (N) lateral apical spine (NLU 40758); and (O) head and tail (NLU 40757).

© UMMZ webpage (A, B), Greg Schneider (C), and remaining photos by Van Wallach

**Distribution:** *Epictia bakewelli* is a Mexican endemic known to occur in southwestern Mexico (Colima, Michoacán, México, Guerrero, and W Oaxaca), overall elev. NSL–1,950 m (Map 2).



**Map. 2.** Distribution of *Epictia bakewelli* in southwestern Mexico (Colima to Oaxaca).

**Ecology:** This species occurs in tropical semi-deciduous forest and arid scrub forest (Duellman, 1965). The type and two of the paratypes were collected in a humid area of semiarid woods (Oliver, 1937).

**Remarks:** Kluge (1984: 63) and the UMMZ database list only J. A. Oliver as the collector of the holotype. Wilson (1968) first suggested that *Epictia bakewelli* might be a species distinct from *E. phenops*. Romo-García and Gallardo-Arroyo (2007: 96, 187) listed *E. phenops* as occurring in the Río Laja region of Guanajuato (21°05'50"N, 100°55'30"W, elev. 1,950 m), but this information remains unconfirmed (voucher specimens unknown). Smith (1943) and Mata-Silva et al. (2015) reported *E. bakewelli* from the coastal plain of Tehuantepec. This species has been also reported from Jalisco (i.e., Smith and Taylor, 1945; Uetz and Hošek, 2016), but I am not aware of any voucher specimens or primary literature citations. *Epictia bakewelli* and *E. phenops* appear to be sympatric near Aguas Blancas, just northwest of Acapulco, Guerrero. McCranie and Hedges (2016) reported TL/LOA ratios of 4.7–8.0%, dorsal caudal spots 0–4, and ventral caudal spots 1–11, data that could not be included in Table 2 because of the lack of mean values.

The molecular study of McCranie and Hedges (2016) revealed that *E. bakewelli* is polyphyletic and composed of at least three separate species. One undescribed species probably is represented by UTA 53657 from between Mazunte and Piontepanoc, and the other by UTA 57498 from between Puerto Escondido and Puerto Angel, both coastal localities in Oaxaca, Mexico.



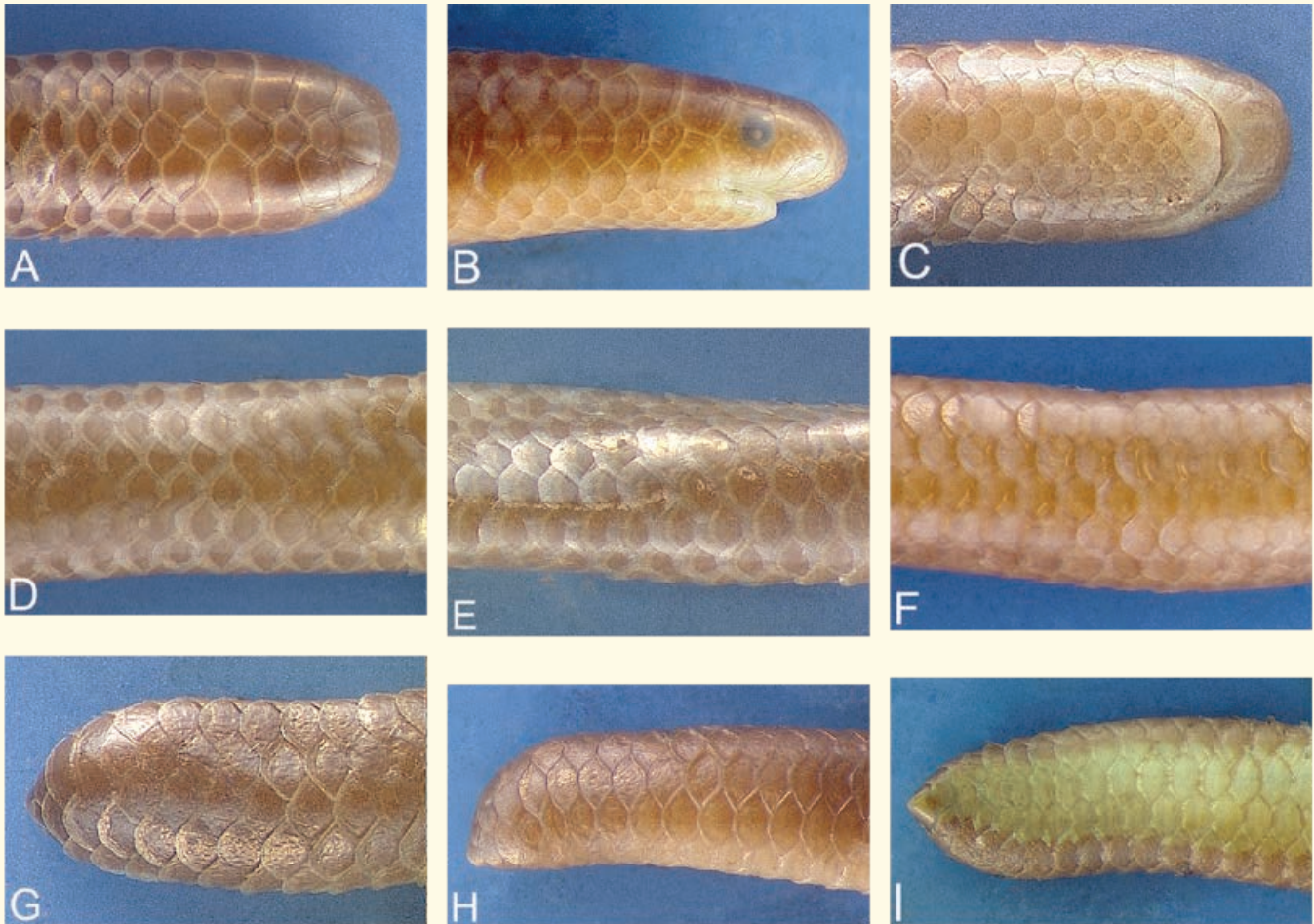
***Epictia columbi* (Klauber, 1939)**

Figs. 3A–I, 16I

*Leptotyphlops albifrons*—Stejneger, 1905: 335; Barbour, 1914: 324, 355 (part), 1930: 107 (part), 1935: 130 (part), 1937: 149 (part).*Glauconia albifrons*—Werner, 1917: 203 (part).*Leptotyphlops columbi* Klauber, 1939: 62–64, fig. 3A, B; Legler, 1959: 112; R. Thomas, 1965: 7; 1975: 188; McCoy and Richmond, 1966: 261; Buden, 1975: 174; Schwartz, 1978: 45; Hahn, 1980: 10; Riley, 1981: 233–234; Schwartz and Henderson, 1985: 83, 113; 1988: 223; 1991: 618–619, map; Thomas et al., 1985: 219; Sokolov, 1988: 355; Olson et al., 1990: 13; Welch, 1994: 29; Frank and Ramus, 1995: 250; Heise et al., 1995: 260; Hedges, 1996: 111, 115, 2006: 238, fig. 6; Powell et al., 1996: 89, pl. 7, fig. A; Franz and Buckner, 1998: 39–40; Wallach, 1998a: 480, 1998b: 184; Crother, 1999: 320; Duellman, 1999: 362; Mattison, 1999: 146; McDiarmid et al., 1999: 25; Morrone, 2001: 54; Hayes et al., 2004: 236; Wrobel, 2004: 285; Tipton, 2005: 22; Vidal and Hedges, 2002: 983–984, fig. 2, 2004: Elec. App. 5; Vidal and David, 2004: 784; Adalsteinsson, 2008: 12, 20, 31, 33, 44, 54, 61, 63; Delhay, 2009: 180; Adalsteinsson et al., 2009: 7, 10, fig. 3A; Crother et al., 2009: 4; Franco and Pinto, 2009: 241; Henderson and Powell, 2009: 374; Alamillo, 2010: 8, fig. 2; Beolens et al., 2011: 57; Hillbrand et al., 2011: 165.*Leptotyphlops colombi*—Barbour and Loveridge, 1946: 142.*Epictia columbi*—Adalsteinsson et al., 2009: 10, 17, 46, fig. 12A; Hillbrand et al., 2011: 165 (col. photo); Knapp et al., 2011: 60, 78; Buckner et al., 2012: 107; Çinar, 2012: 121; Pinto and Fernandes, 2012: 43; Pyron et al., 2013: fig. 1, App. S1: 72; Wallach et al., 2014: 276; Giery, 2015: 5 (photo); McCranie and Hedges, 2016: 4, 8, 20, 22, fig. 2.*Crishagenus columbi*—Hoser, 2012: 33.**Holotype:** CM R-1364, a 183 mm (LOA) specimen collected by W. W. Worthington in 1909, at “Watling Island, Bahama Islands” [= San Salvador Island, Bahama Islands, 24°03'N, 74°29'W, elev. NSL].**Paratypes** (4): CM R-1360, CM R-1362, MCZ R-48773 (exchange of CM R-1363 to MCZ in 1945), and SDSNH 32760 (exchange of CM R-1361 to SDNHM on 31 August 1939), collected by Willis W. Worthington in 1909 on Watling’s Island, Bahamas.**Etymology:** This species was named in reference to Christopher Columbus, who is credited with discovering the New World, with the first landfall supposedly on San Salvador Island.**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 86–183 ( $\bar{x}$  = 136.0) mm; (4) total middorsals = 240–265 ( $\bar{x}$  = 255.6); (5) subcaudals = 22–25 ( $\bar{x}$  = 23.7); (6) relative body proportion = 49–69 ( $\bar{x}$  = 58.3); (7) relative tail length = 5.7%–8.9% ( $\bar{x}$  = 7.6%); (8) relative tail width = 4.3–6.3 ( $\bar{x}$  = 5.1); (9) relative rostral width = 0.27–0.44 ( $\bar{x}$  = 0.35); (10) relative eye size = 0.35–0.41 ( $\bar{x}$  = 0.38); (10) rostral short and sagittate with a truncated apex, extending to anterior eye level; (11) supralabials 2, moderate anterior supralabial just reaching eye level; (12) frontal subhexagonal, longer than wide; (13) supraoculars large, twice as broad as deep, posterior borders parallel to posterior supranasal borders; (14) widest anteriormost vertebral scale 3<sup>rd</sup> or 4<sup>th</sup>; (15) parietals and occipitals subequal, oriented obliquely; (16) infralabials 4; (17) cloacal shield semilunate in shape; (18) head brown, lacking a pale spot on rostral; (19) dorsum uniform blackish-brown to black (no stripes); (20) midventral 3 rows uniform reddish-brown to yellowish-brown, with a sharp demarcation between the dorsal and ventral color, at least anteriorly; (21) midbody stripe formula (U) and pattern (U); (22) dorsum of tail uniform brown, ventral 3 rows pale yellow; and (23) apical spine a laterally compressed cone.**Description:** Head only slightly distinct from neck, snout rounded in dorsal view (Fig. 3A); head shields with prominent sensory pits; rostral sagittate and short, triangular in shape with a truncated apex, not reaching the interocular level; frontal subhexagonal with rounded edges, 1½ times as long as broad; postfrontal smaller than frontal; interparietal and interoccipital longer than wide; broadest anteriormost vertebral scale 3<sup>rd</sup> or 4<sup>th</sup>; supraoculars large and pentagonal, twice as broad as deep, posterior borders parallel to supranasal borders; parietals and occipitals subequal in size, oriented obliquely to body axis; lateral head profile with rounded snout; nasal completely divided, suture forming a shallow V-shaped angle (Fig. 3B), nostril oval and positioned near the rostral border; infranasal as tall as the anterior supralabial and approximately equal in width with its lower border 1½ times as broad as that of the anterior supralabial; supralabials 2, anterior supralabial moderate in height, reaching mid-eye level, taller than posterior supralabial; ocular hexagonal, twice as tall as broad with dorsal border wider than ventral border, anterior border nearly straight; eye small in size with a distinct pupil, less than the lip-orbit gap (ED/OH = 0.45–0.46,  $\bar{x}$  =

0.46), nearly round in shape, situated along upper anterior border of ocular and barely visible in dorsal view; posterior supralabial taller than anterior supralabial, pentagonal in shape with a rounded posterior margin; ventral rostral with a preoral groove; mental butterfly-shaped, infralabials 4, 1<sup>st</sup>, 2<sup>nd</sup>, and 3<sup>rd</sup> short and squarish with 4<sup>th</sup> largest and elongated; costal scales imbricate and rounded in 14 rows throughout; cloacal shield semilunate; and tail terminates in a laterally-compressed cone directed ventrally at a 45° angle.

Coloration in life uniform blackish-brown to black, without a pale rostral spot but with a pale, small, subcaudal spot, dorsum fading to brown in preservative; middorsal 9 rows dark brown (midbody formula and pattern = U or O), midventral 3 rows pale beige, and single ventrolateral row pale brown. Head brown, lacking pale rostral spot, posterior upper lip spot, and dorsal and ventral caudal spots (Fig. 3A, H). Tail entirely brown, median 3 rows of subcaudals pale beige, and apical cone brown.



**Fig. 3.** Morphological variation in *Epictia columbi*. (A) dorsal head (MCZ R-48773); (B) lateral head (MCZ R-48773); (C) ventral head (MCZ R-48773); (D) dorsal midbody (MCZ R-48773); (E) lateral midbody (MCZ R-48773); (F) ventral midbody (MCZ R-48773); (G) dorsal tail (MCZ R-48773); (H) lateral tail (MCZ R-48773); and (I) ventral tail (MCZ R-48773). © MCZ, Harvard University

**Viscera:** ( $n = 1$  female). Posterior tip of sternohyoideus muscle = 11.7%; sternohyoideus/snout–heart gap = 0.75; heart length = 4.3% with midpoint at 17.8%; snout–heart interval = 19.9%; heart–liver gap = 9.0% and interval = 47.7%; heart–gall bladder gap = 43.8%; liver lobes multipartite; right liver length = 34.4% with midpoint at 46.1% and 35 segments; left liver length = 24.6% with midpoint at 47.5% and 28 segments; anterior liver extension = 0.18 and posterior liver tail = 0.10; left liver/right liver = 0.72; liver–gall bladder gap = 0.4% and interval = 35.9%; gall bladder length = 1.2% with midpoint at 64.3%; gall bladder–gonad gap = 13.3%; liver–kidney gap = 20.3% and interval = 62.5%; gall bladder–gonad gap = 13.3% and interval = 18.4%; gall bladder–kidney gap = 18.8% and interval = 27.7%; right gonad length = 2.3% with midpoint at 79.3%; left gonad length = 0.8% with midpoint at

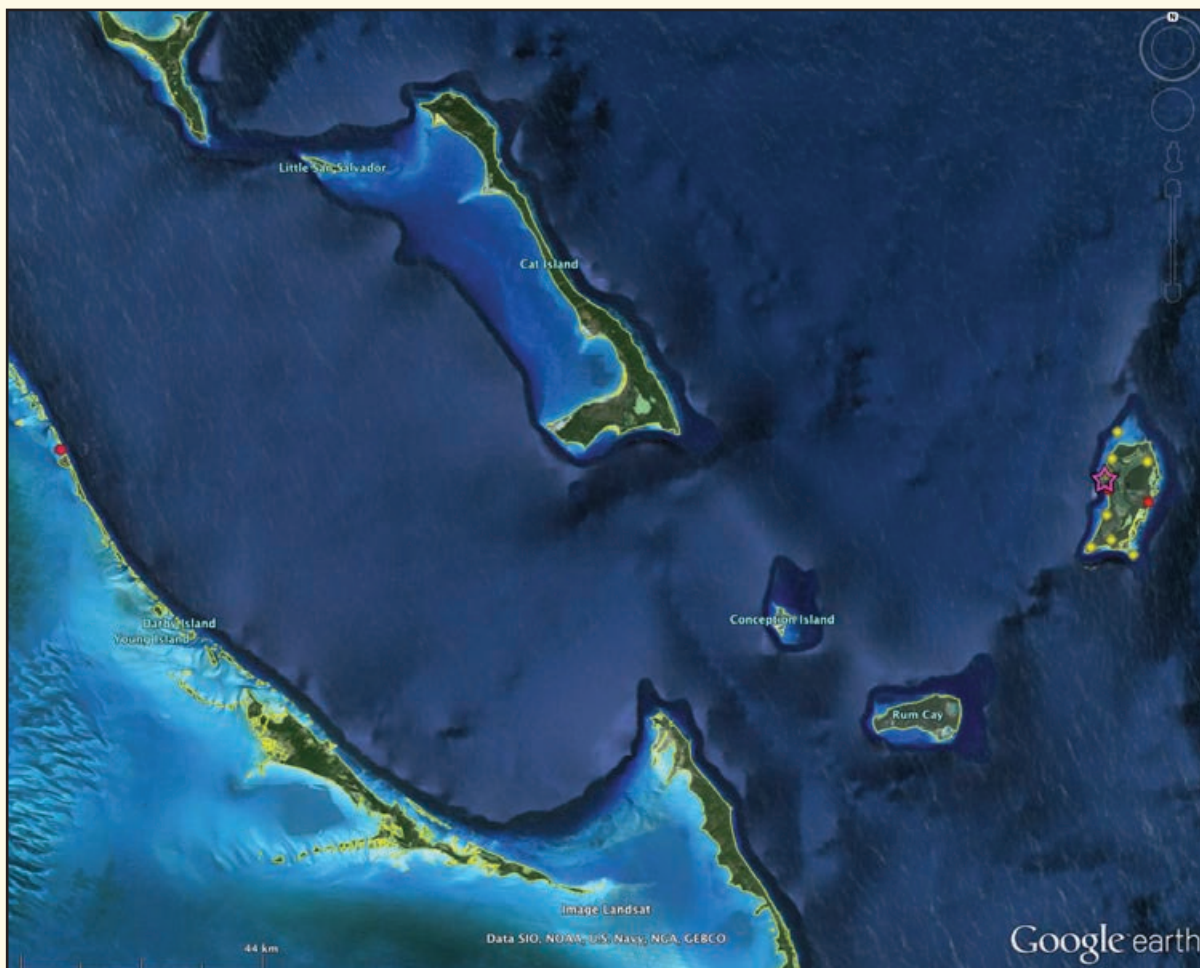


81.6%; gonad–kidney gap = 1.6% and interval = 13.3%; right adrenal midpoint = 80.7% and left adrenal midpoint = 81.6%; right kidney length = 3.9% with midpoint at 85.5%; left kidney length = 3.9% with midpoint at 89.5%; kidney overlap = none (unique among squamates); kidney–vent gap = 8.6% and interval = 16.4%; rectal caecum length = 2.0%; rectal caecum–vent interval = 9.8%. One egg and 4 follicles are present in the right ovary and 3 follicles in left ovary of the single female examined.

Respiratory system lacking tracheal lung and left lung complex; trachea length = 18.8% with midpoint at 10.5% and an estimated 192 tracheal rings or 102.4 rings/10% SVL; anterior lung tip at 18.4%; tracheal entry terminal; cardiac lung length = 1.6%; right lung length = 26.6% with midpoint at 33.2% with faveolar cranial third, characterized by a row of small foramina along the lung's border with the bronchial cartilages, trabecular middle third, and reticulate terminal third; posterior lung tip at 46.5%; right bronchus length = 19.5% with posterior tip at 39.5%; bronchus/right lung length = 0.74; trachea–bronchus length = 38.3% with midpoint at 20.3%; total lung length = 28.1% with midpoint at 46.5%; and trachea–bronchus/total lung length = 0.82.

Visceral distance data include heart–right lung distance = 15.4%; heart–liver distance = 28.3%; trachea–liver distance = 35.6%; liver–kidney distance = 41.4%; trachea–bronchus–gall bladder distance = 44.0%; right lung–adrenal distance = 48.0%; heart–gonad distance = 61.5%; trachea/bronchus–kidney distance = 67.2%; heart–kidney distance = 69.7%; and trachea–adrenal distance = 70.7%.

**Distribution:** *Epictia columbi* is a Bahama Island endemic known to occur on San Salvador (Watling's) Island and some of its satellites (Gauntlet Cay, Little Green Cay, and Low Cay), overall elev. NSL–2 m (Map 3). Franz and Buckner (1998) noted that this species might be found on islands of the Concepcion Bank.



**Map 3.** Distribution of *Epictia columbi* in the Bahamas.

**Ecology:** This species has been found under rocks in the blacklands, the higher elevation limestone areas bordering the mangroves and brackish lakes and ponds, and grasslands (Riley, 1981), in rotting logs (Schwartz and Henderson, 1991), and in pine bush adjacent to mangroves (Ryann Rossi *In* Giery, 2015).

***Epictia magnamaculata* (Taylor, 1940)**

Figs. 4aA–F, bA–AG, cA–AA, 15I–J, 16J–N

*Glauconia albifrons*—Boulenger, 1893: 63 (part); Günther, 1893 *In* 1885–1902: 85 (part); Werner, 1917: 203, 1925: 539 (part); Smith and Smith, 1976: S-B-97, S-C-37, S-D-1.

*Leptotyphlops albifrons*—Barbour, 1914: 324 (part), 1930: 107, 1935: 130, 1937: 149; Amaral, 1930b: 138 (part); Haas, 1930: 59, 73, figs. 90–92 (part), 1931: 127 (part); Brongersma, 1940: 117; Pérez-Santos, 1986: 72–73 (part); Buurt, 2001: 90, figs. 55, 66 (col. photos), 2005: 107–108, 128, col. photos 63 and 64, 2006: 313; Wilson and Hahn, 1973: 120–121; Cundall and Irish, 2008: 374, 597, 730 (part); García-Escobar and Lasso-Zapata, 2008: 50; González, 2008: 597; McDowell, 2008: 545, 562, 765 (part); Urrego et al., 2009: 27.

*Glauconia (Leptotyphlops) albifrons*—Werner, 1925: 540 (part).

*Leptotyphlops magnamaculata* Taylor, 1940: 532–533, fig. 1, 1944: 156; Dunn, 1945: 364; Cochran, 1961: 194; Alexander and Gans, 1966: 183; List, 1966: 6, 25, 29, 31, 78–83, 90–91, 98–99, 107, pls. 10–12, fig. 5, pl. 16, fig. 6, pl. 20, fig. 2; Orejas-Miranda *In* Peters et al., 1970 and 1986: 170; Schwartz and Thomas, 1975: 189; Hahn, 1980: 15; Schwartz and Henderson, 1988: 223; Sánchez et al., 1995: 317; Cundall and Irish, 1998: 597, 730; McCranie et al., 2005: 128; McDowell, 2008: 545, 765; Coral-Enríquez, 2011: 5; Illescas-Palomo et al., 2011: 231.

*Leptotyphlops phenops phenops*—Smith and Taylor, 1945: 24 (part).

*Leptotyphlops albifrons magnamaculata*—Dunn and Saxe, 1950: 159–160; Cochran, 1961: 194; Tamsitt and Valdivieso, 1963: 136; Valdivieso and Tamsitt, 1963: 78–79; Thomas, 1965: 7; Echternacht, 1968: 157; Medem, 1969: 179; Hahn, 1980: 15; Anonymous, 2005: 14; Illescas-Palomo et al., 2011: 231.

*Leptotyphlops (sic) albifrons*—Barriga-Bonilla et al., 1969: 78.

*Leptotyphlops phenops*—Meyer, 1969: 409–411, map 105 (part); Wilson and Hahn, 1973: 120–123 (part); Hahn, 1980: 15; Hudson, 1981: 377; McCranie et al., 2005: 128.

*Leptotyphlops goudotii goudotii*—Orejas-Miranda *In* Peters et al., 1970 and 1986: 170; Maclean et al., 1977: 43, 44, 46; Lancini and Kornacker, 1989: 104 (part); Mijares-Urrutia and Arends, 2000: 25 (part).

*Leptotyphlops goudotii magnamaculatus*—Orejas-Miranda *In* Peters et al., 1970 and 1986: 170; Peters and Orejas-Miranda, 1970: 322–323, fig. 4; Schwartz and Thomas, 1975: 189; Serna, 1977: 101; Hahn, 1980: 15; Branch, 1986: 293; Pérez-Santos, 1986a: 75, 85, fig. 33; Pérez-Santos and Moreno, 1988: 419, map 27; Schwartz and Henderson, 1988: 223; Börschig, 2007: 167; Adalsteinsson et al., 2009: 7, fig. 3A; Illescas-Palomo et al., 2011: 231; EOL, 2015: 1294336.

*Leptotyphlops goudoti*—Schwartz and Thomas, 1975: 189 (part); Schwartz, 1978: 45; Schwartz and Henderson, 1988: 223 (part); Smith and Smith, 1993: 591 (part); Henderson and Powell, 2009: 374 (part).

*Leptotyphlops goudoti magnamaculata*—Schwartz and Thomas, 1975: 189; Maclean et al., 1977: 4; Morgan, 1985: 43; Schwartz and Henderson, 1988: 223, 1991: 620, map; Tipton, 2005: 24; Varin, 2008: 122.

*Leptotyphlops goudoti magnamaculatus*—Maclean et al., 1977: 4.

*Leptotyphlops goudotti (sic)*—Wilson and Meyer, 1985: 20–21, fig. 25 (part).

*Leptotyphlops goudotii*—Thomas et al., 1985: 220; Wilson and Meyer, 1985: 20–21, fig. 25 (part); Wilson and Cruz-Díaz, 1993: 18; Frank and Ramus, 1995: 250 (part); Hedges, 1996: 111 (part); Köhler, 1996a: 27, 1998a: 375–376, fig. 4, 1998b: 143, 144, 2000: 2, cover photo, 2001b: 11, figs. 9, 10, 2001b: 11–12, figs. 9, 10, 11b, 2003a: 171, figs. 409, 410, map, 2008: 183–184, figs. 494, 495, map (part); Powell et al., 1996: 89; G. Cruz *In* Bermingham et al., 1998: 29; Wallach, 1998a: 490 (part), 552; Crother, 1999: 320; McDiarmid et al., 1999: 31 (part); Grismer et al., 2001: 135; Wilson et al., 2001: 117, 124, 139 (part); Powell, 2003: 37 (photo); Courrau and Andrakla, 2004: 22; Echternacht, 2005: 130, fig.; McCranie et al., 2005: 124, 127–128, 167, three col. photos (part); McCranie, 2006: 126; Anonymous, 2007b: 23, 2011: fig. 6; Adalsteinsson, 2008: 6, 29, 41, 47, figs. 3.2, 3.5; Cubas, 2009: 123; Townsend et al., 2011: 21; Anonymous, 2014: 107; McCranie and Valdés-Orellana, 2014: 46.

*Leptotyphlops goudotti goudotti (sic)*—Lancini, 1986: 170 (part).

*Leptotyphlops tenella*—Malhotra and Thorpe, 1999: 71, 122; Daltry, 2007: 108.

*Leptotyphlops tenellus*—Henderson, 2004: 312.

*Leptotyphlops* (sic) *albiprons* (sic)—Howard et al., 2004: 112.

*Leptotyphlops goudotii magnamaculata*—Anonymous, 2005: 37; Adalsteinsson et al., 2009: 17.

*Leptotyphlops* (sic) *albifrons*—CORALINA, 2007: 52.

*Leptotyphlops magnamaculatus*—Adalsteinsson, 2008: 25–26, 37.

*Epictia magnamaculata*—Adalsteinsson et al., 2009: 10, 17, 31, 46, fig. 12; McCranie, 2009: 16, 2011: 47–50, pl. 4, fig. C, map 11, 2015: 379; Arredondo and Zaher, 2010: 191; Pinto et al., 2010: 22–24, 28, fig. 13A–C; Wilson and Johnson, 2010: 101; Pinto and Curcio, 2011: 61; Townsend, 2011: 76, 158, 2014: 246; Çinar, 2012: 122; CONABIO, 2012: 52; Pinto and Fernandes, 2012: 46; Powell and Henderson, 2012: 92; Valencia, 2012: 8; Pantoja-Leite, 2013: 200; Caicedo-Portilla, 2014: 182; McCranie and Valdés-Orellana, 2014: 46; Solís et al., 2014: 137; Urben et al., 2014: 1409; Wallach et al., 2014: 277; Johnson et al., 2015a: 92; McCranie and Hedges, 2016: 4, 6–7, 14–16, figs. 2, 4, 5; Wilson and Johnson, 2016: 38.

*Epictia goudotii*—Ugueto and Rivas, 2010: 216–219, figs. 85A, E, 87, 88, pl. 7, fig. 1, map 25; McCartney, 2013: 88, 119, 128.

*Leptotyphlops albifrons magnamaculatus*—Coral-Enriquez, 2011: 7.

*Crishagenus magnamaculata*—Hoser, 2012: 33.

*Epictia goudotti* (sic)—Rivas et al., 2012: 27.

*Leptotyphlops albifrons margaritae*—Wallach et al., 2014: 277.

**Holotype:** USNM 54760, a 167 mm (LOA) female collected by F. J. Dyer on 9 April 1916, from “Utila Id., Honduras” [= Isla de Utila, Departamento de Islas de la Bahía, Honduras, 16°06'N, 86°55'W, elev. NSL–20 m asl].

**Etymology:** The specific epithet is derived from the Latin *magnus*, meaning large, and *macula*, meaning spot, a reference to the large yellow spot on the snout of the snake.

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 76–220 ( $\bar{x}$  = 141.5) mm; (4) total midodorsals = 219–262 ( $\bar{x}$  = 238.7); (5) subcaudals = 15–21 ( $\bar{x}$  = 17.3); (6) relative body proportion = 38–72 ( $\bar{x}$  = 53.6); (7) relative tail length = 4.8%–8.5% ( $\bar{x}$  = 6.2%); (8) relative tail width = 2.8–5.9 ( $\bar{x}$  = 3.8); (9) relative rostral width = 0.22–0.50 ( $\bar{x}$  = 0.35); (10) relative eye size = 0.40–0.54 ( $\bar{x}$  = 0.47); (10) rostral sagittate with rounded apex; (11) supralabials 2, moderate anterior supralabial reaching mid-eye level; (12) frontal subtriangular, as long as broad; (13) supraoculars large and pentagonal, 1½ times as broad as deep, with posterior borders parallel to posterior borders of supranasal; (14) widest anteriormost vertebral scale 5<sup>th</sup>; (15) parietals and occipitals subequal, oriented transversely; (16) infralabials 4; (17) cloacal shield subtriangular in shape; (18) head brown, with large pale rostral spot covering scales adjacent to rostral; (19) dorsum with 11 brown stripes of rectangular- or diamond-shaped spots bordered by broad yellow stripes (= 11 dark stripes); (20) midventral 3 rows uniform pale brown or gold; (21) midbody stripe formula (3 + 3/3 + 1/1) and middorsal pattern (3D + 4L); (22) tail with a pale terminal spot covering the 0–6 ( $\bar{x}$  = 4.2) dorsal scales and 0–7 ( $\bar{x}$  = 3.9) ventral scales (ventral/dorsal ratio 0.9); and (23) apical spine horizontally-compressed into broad vertical blade, sometimes with paired points.

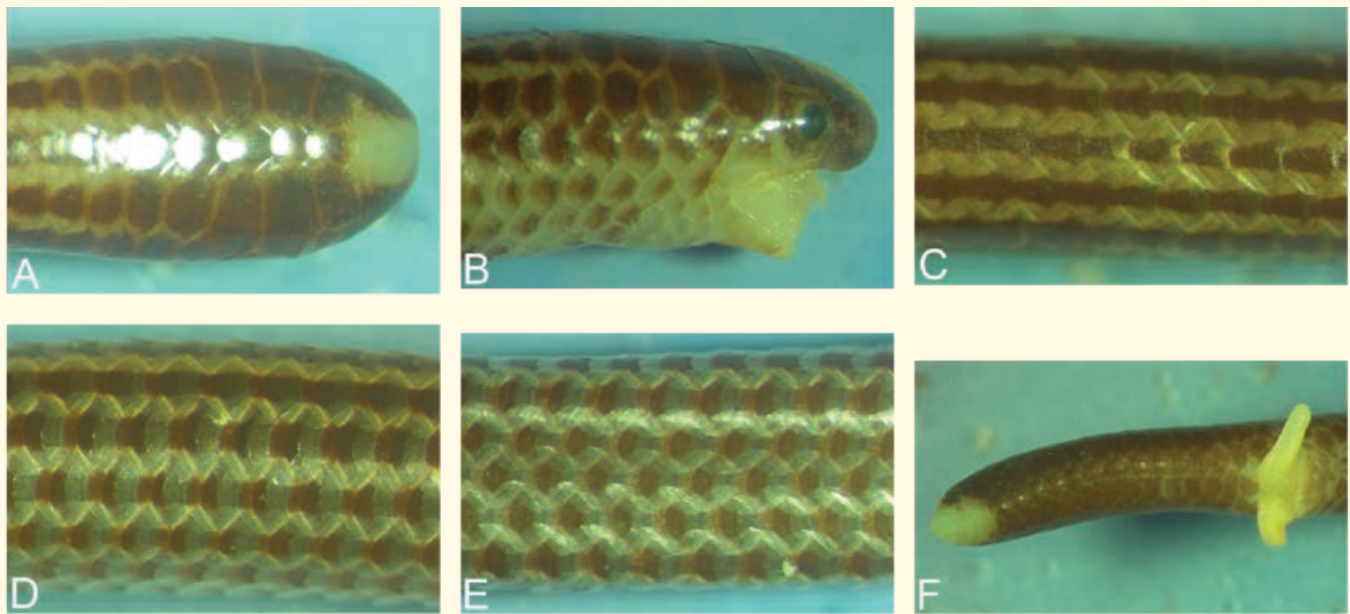
**Description:** Head broader than neck (Fig. 4cA), smoothly rounded in dorsal profile, all head shields with prominent sensory pits that appear as depressions in scales; rostral sagittate in shape with oval apex, extending to anterior or mid-eye level; frontal subhexagonal, slightly longer than wide; postfrontal, interparietal and interoccipital usually as broad as deep, subhexagonal in shape with rounded posterior contours, interparietal the largest vertebral scale; supraoculars large and blocky, 1½ times as wide as long with posterior borders parallel to those of supranasals; parietals and occipitals subequal in length or parietals slightly longer, both shields transverse in orientation (Fig. 4bC); broadest anteriormost vertebral scale 5<sup>th</sup>; lateral head profile rounded; nasal completely divided, suture forming a deep V-shaped angle along anterior supralabial and infranasal, nostril oval and positioned nearer the rostral than supralabial; infranasal 2–2½ times as tall as long, narrowing toward lip; supralabials 2, anterior supralabial moderate in height with nearly parallel sides, extending to level of pupil, its labial border equal to or half again as long as that of infranasal; ocular large, twice as high as long, hexagonal in shape with a convex supranasal border and concave lower anterior and posterior borders; eye large with distinct pupil but lacking visible iris, slightly oval or elliptical in vertical plane, slightly taller than its lip-orbit gap in Mexico and Honduras (ED/OH = 0.40–0.54,  $\bar{x}$  = 0.47), but less than the lip-orbit gap in Colombia (ED/OH = 0.27–0.33,  $\bar{x}$  = 0.30), protuberant but not visible in dorsal view; posterior supralabial taller than anterior supralabial, slightly taller than long with triangular



posterior border; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 4, 1<sup>st</sup> to 3<sup>rd</sup> small, twice as broad as long, the 4<sup>th</sup> shield elongated three times as long as broad and invisible when mouth is closed; costal scales rounded and imbricate in 14 rows throughout; cloacal shield subtriangular (Fig. 4cT); tail lacking typical tapering spine, terminating instead in the unique shape of a moderate to broad vertical blade (Colombia) or a blade with paired points (Honduras) (Fig. 4bAE, cV, W).

Coloration in life vividly bicolored with brown and yellow stripes, a large yellow cranial spot, and a small yellow caudal of equal size, above and below (Fig. 16M–Q). Midbody pattern of preserved material consists of 11 brown to dark brown dorsal and lateral stripes, consisting of rectangular-shaped spots (may be diamond-shaped in Colombia; Fig. 4cK), separated by moderate to broad yellow straight (rarely zigzag) stripes formed by their pale scale borders (Fig. 4aC, bS, cI), the 3 midventral rows uniform pale brown (midbody stripe formula = 3 + 3/3 + 1/1). This species is the only one with ventrolateral dark stripes. Honduran specimens typically show only 3 brown middorsal stripes, edged by 4 pale zigzag stripes of moderate thickness (middorsal pattern = 3D + 4L); midlateral 4 rows uniform brown; and midventral 3 rows pale brown due to heavy stippling (Fig. 4bY). Head dark brown with a distinctively large lemon yellow spot on snout that entirely covers rostral and adjacent portions of supranasals, frontal and supraoculars (Fig. 4aA, bC, cA); a pair of pale paravertebral stripes extends along occipitals and parietals, and sometimes contacts the frontal (Fig. 4cD); lateral head brown with a pale spot on lower edge of posterior supralabial and ocular, sometimes atypical bar (Fig. 4bJ) and other times a pair of pale triangles (Fig. 4aB, cF); a thin pale ring around upper lip. Tail normally brown with pale stripes, but sometimes unicolored brown; cloacal shield entirely pale or heavily infused with brown vermiculations; cloacal region pale white/yellow; and yellow tail spot symmetrically disposed with a mean dorsal spot of 4.2 dorsocaudals, a mean ventral spot of 3.9 subcaudals, and a ventral/dorsal ratio of 0.9.

Variation exists among insular populations of *E. magnamaculata* from the islands of Cozumel (off Yucatan, Mexico) in the north, through the Bay Islands and Swan Islands (off Honduras), to the Colombian islands of San Andrés and Providencia (off Nicaragua) in the south (Table 4). Typical clinal variation is seen, for example, with the number of total middorsals increasing from north to south, and the values of 12 other characters increasing or decreasing from Mexico to Colombia (Table 4 [A]). Among the other 40 characters (most are visceral), however, a



**Fig. 4a.** Morphological variation in Mexican *Epictia magnamaculata*. (A) dorsal head (LACM 127623); (B) lateral head (LACM 127623); (C) dorsal midbody (LACM 127623); (D) lateral midbody (LACM 127623); (E) ventral midbody (LACM 127623); and (F) ventral tail (LACM 127623).

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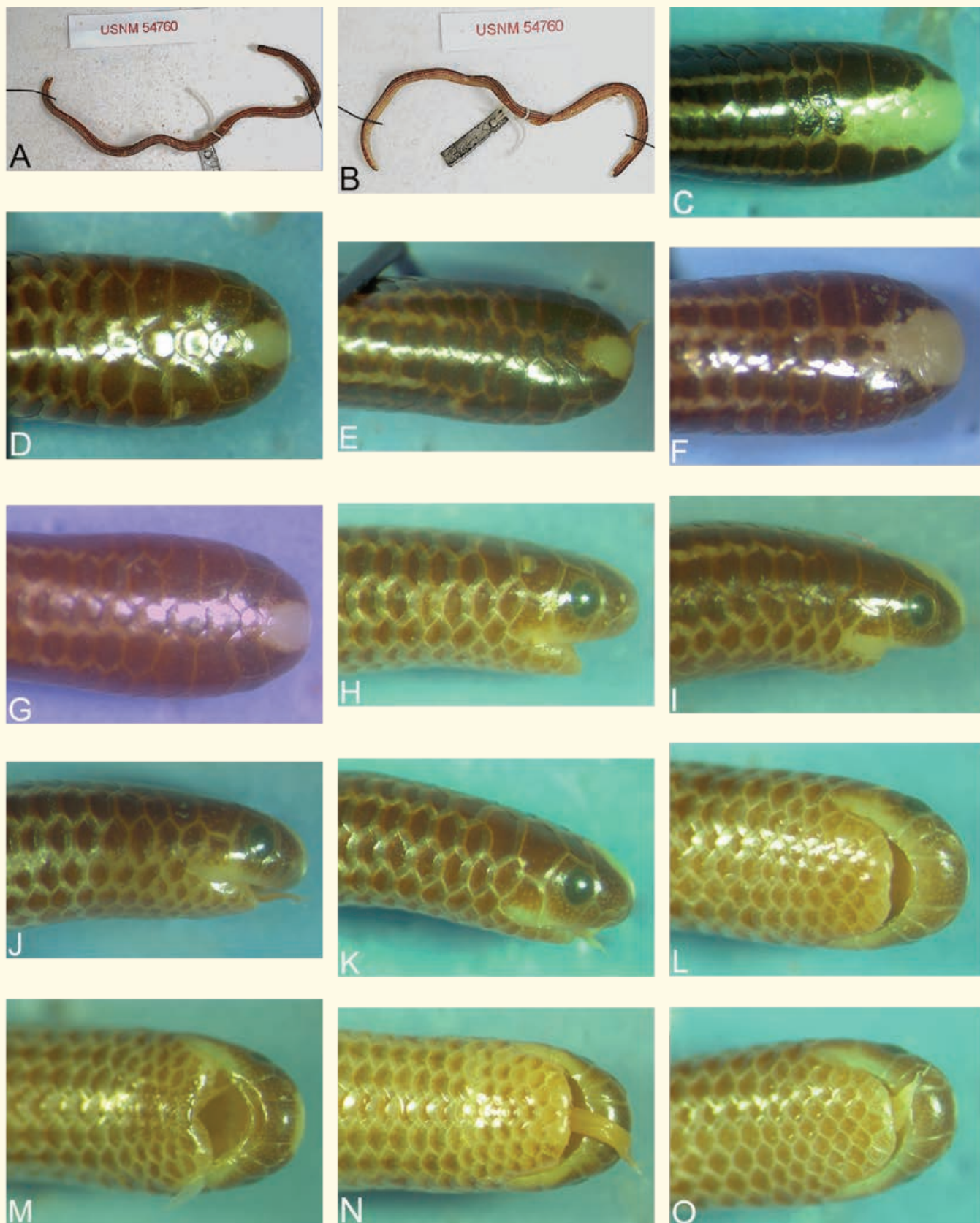


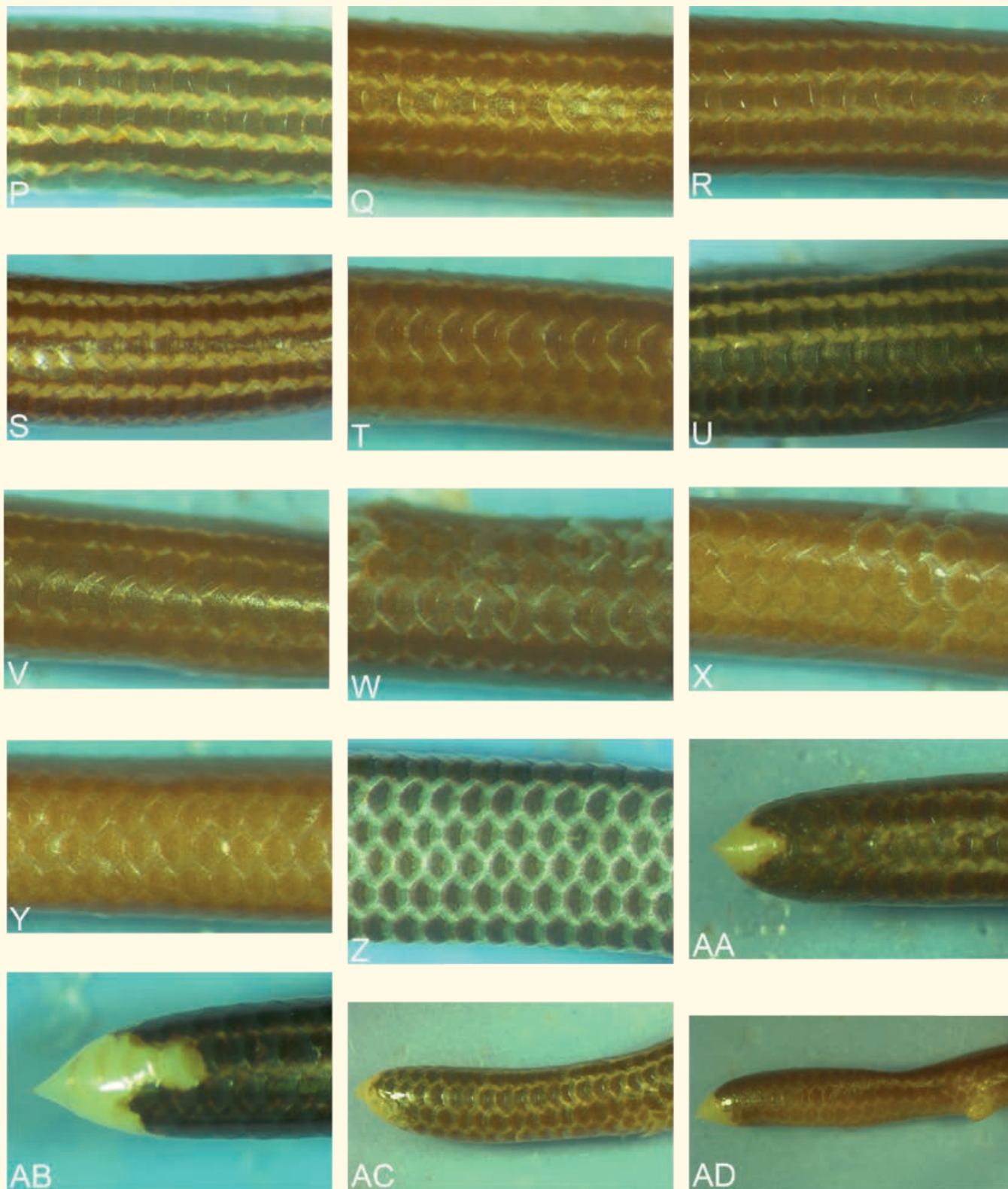
closer relationship is suggested between the Mexican and Honduran populations for six characters (Table 4 [B]), the Mexican and Colombian populations for four characters (Table 4 [C]), or the Honduran and Colombian populations for 30 characters (Table 4 [D]).

**Table 4.** Clinal variation in morphological and visceral character means (as % SVL or ratios) of *Epictia magnamaculata*. A = characters with clinal variation from north to south; B = characters indicating a Mexico–Honduras association; C = characters indicating a Mexico–Colombia association; D = characters indicating a Honduras–Colombia association; and M/V = *n* of specimens for morphology/viscera. See Materials and Methods and Tables 2 and 3 for character abbreviations.

Character	Mexico	Honduras	Colombia	Character	Mexico	Honduras	Colombia
M / V	<i>n</i> = 5 / 2	<i>n</i> = 24 / 5	<i>n</i> = 20 / 3	M / V	<i>n</i> = 5 / 2	<i>n</i> = 24 / 5	<i>n</i> = 20 / 3
<b>A</b>				<b>D</b>			
TMD	228	235	251	SC	14.7	17.8	17.2
DCS/SCS	2.5 / 2.75	3.3 / 3.5	4.5 / 4.9	HMP	17.9	18.9	18.8
HL	4.0	4.6	4.8	SHI	19.9	21.2	21.2
SAJ/HL	0.121	0.147	0.156	LLL	33.9	28.3	29.8
HLG	17.6	12.3	11.3	RLMP	50.7	47.8	48.5
PLT	0.06	0.11	0.15	LLMP	54.3	47.6	47.4
LGBG	3.5	2.2	1.9	GBL	1.3	1.6	1.6
GBGG	5.1	6.3	7.4	GBMP	77.7	68.7	70.6
RBL	16.5	18.6	20.2	GBKG	8.9	13.4	12.9
RBPT	36.4	39.9	41.4	GBKI	14.1	21.1	20.3
T+B	35.0	38.8	40.3	LGMP	87.2	80.9	82.5
TBMP	18.9	20.5	21.3	TGMP	86.1	79.2	81.4
RC/HL	0.47	0.29	0.23	TAMP	85.7	80.9	82.6
<b>B</b>				RKL	2.8	3.4	3.5
MBD	2.7	2.7	2.9	TKL	5.8	7.0	6.7
Tail L	8.0	8.3	9.8	KOL	0.53	0.16	0.15
RW/HW	0.32	0.33	0.35	RCL	1.7	1.2	1.1
RGL	3.2	3.4	2.7	RC/LK	0.55	0.34	0.36
TGL	6.0	6.1	5.5	TL	18.5	20.1	20.1
RLgL	29.3	29.9	27.1	TMP	10.6	11.2	11.1
<b>C</b>				NTR	153.0	189.8	188.7
LOA	149.0	128.2	167.5	TR/10% SVL	85.7	94.8	93.9
TL/LOA	6.0	6.7	6.0	KVI/RL	0.26	0.41	0.43
HW	2.1	1.8	2.1	H–L distance	32.8	28.8	29.7
MTW	2.5	2.2	2.5	T–L distance	40.1	36.6	37.3
L/W	55.0	47.4	57.1	RLg–A distance	54.7	44.7	47.9
HLG	7.9	8.6	7.7	TB–GB distance	58.9	48.2	49.3
TLS	72.0	59.4	75.3	H–G distance	67.2	58.6	61.4
KVI	12.7	17.1	15.8	TB–K distance	70.3	65.4	66.0
RLgMP	34.5	36.2	34.7	H–K distance	71.3	66.9	68.5
RLgPT	49.1	51.2	48.3	T–A distance	75.1	69.7	71.5

The hemipenes of specimens from Isla de Providencia, Colombia (AMNH 103852 and AMNH 103864), were described by Peters and Orejas-Miranda (1970). The hemipenis of FMNH 282651, from Isla de Roátan, Honduras (Fig. 15I), is a single organ with a simple sulcus spermaticus that mostly is nude except for a few papillae on the distal tip. The organ, which tapers gradually toward apex, is 2.2 mm in length, with a basal diameter of 0.65 mm and a distal neck diameter of 0.25 mm. The hemipenis of LACM 127623, from Isla de Guanaja, Honduras (Fig. 15J), which appears to be incompletely everted, also is a single, slightly tapering organ with a simple sulcus that extends around the posterolateral surface; the organ is 2 mm in length, naked and entirely smooth, lacking any ornamentation, and the basal portion is barely enlarged (1.0 mm in width).



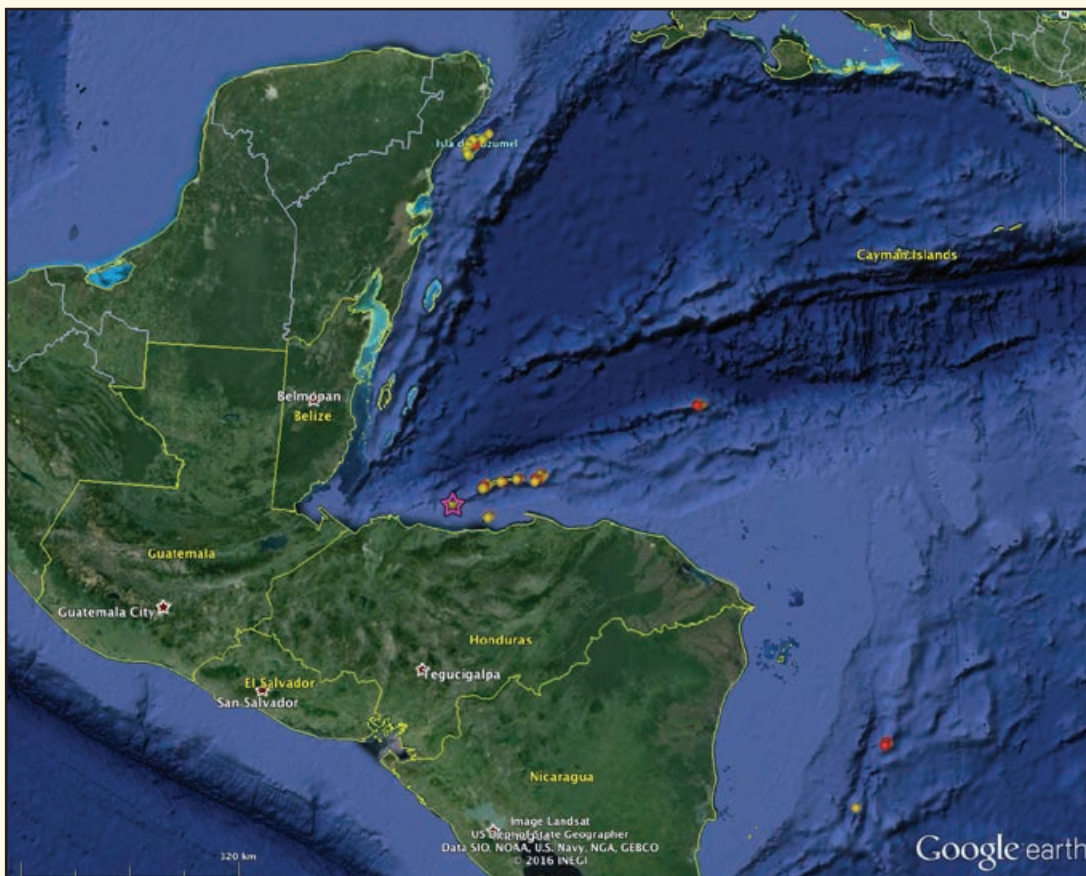






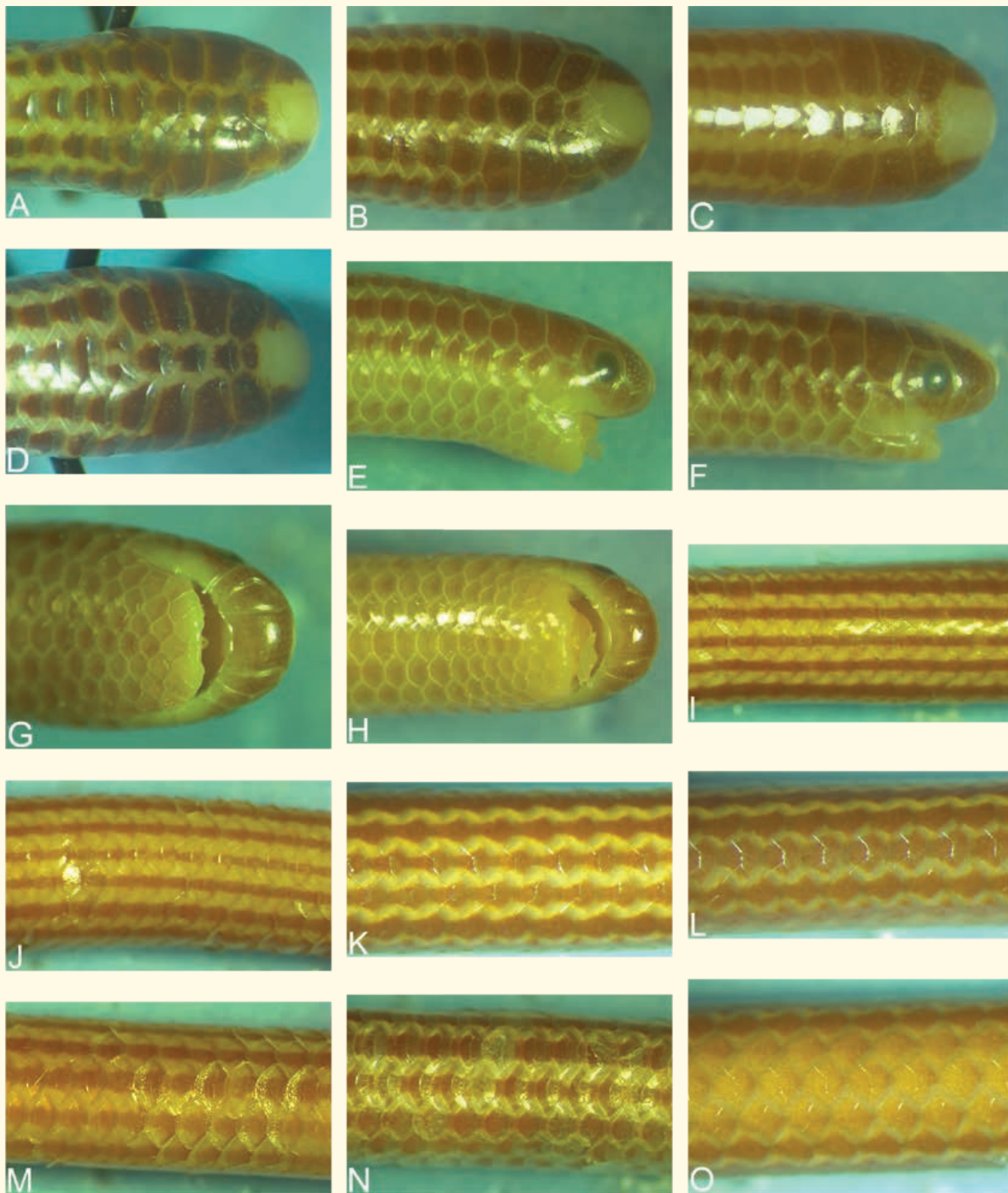
**Fig. 4b.** Morphological variation in Honduran *Epictia magnamaculata*. (A) dorsal view of holotype of *E. magnamaculata* (USNM 54760); (B) ventral view of holotype of *E. magnamaculata* (USNM 54760); (C, D, E, F, G) dorsal head (FMNH 282651, KU 101447, KU 101446, KU 203165, LACM 63429); (H, I, J, K) lateral head (KU 101447, KU 203163, KU 203165, LACM 63429); (L, M, N, O) ventral head (KU 101447, KU 203163, KU 101446, LACM 63429); (P, Q, R, S) dorsal midbody (KU 203163, LACM 63428, LACM 63429, KU 203165); (T, U, V) lateral midbody (LACM 63429, FMNH 282651, LACM 63428); (W, X, Y, Z) ventral midbody (KU 203163, LACM 63428, LACM 63429, FMNH 282651); (AA, AB) dorsal tail (KU 101446, FMNH 282651); (AC, AD) lateral tail (KU 101446, KU 101447); and (AE, AF, AG) lateral apical spine (KU 101447, FMNH 282651, KU 203163). © Van Wallach

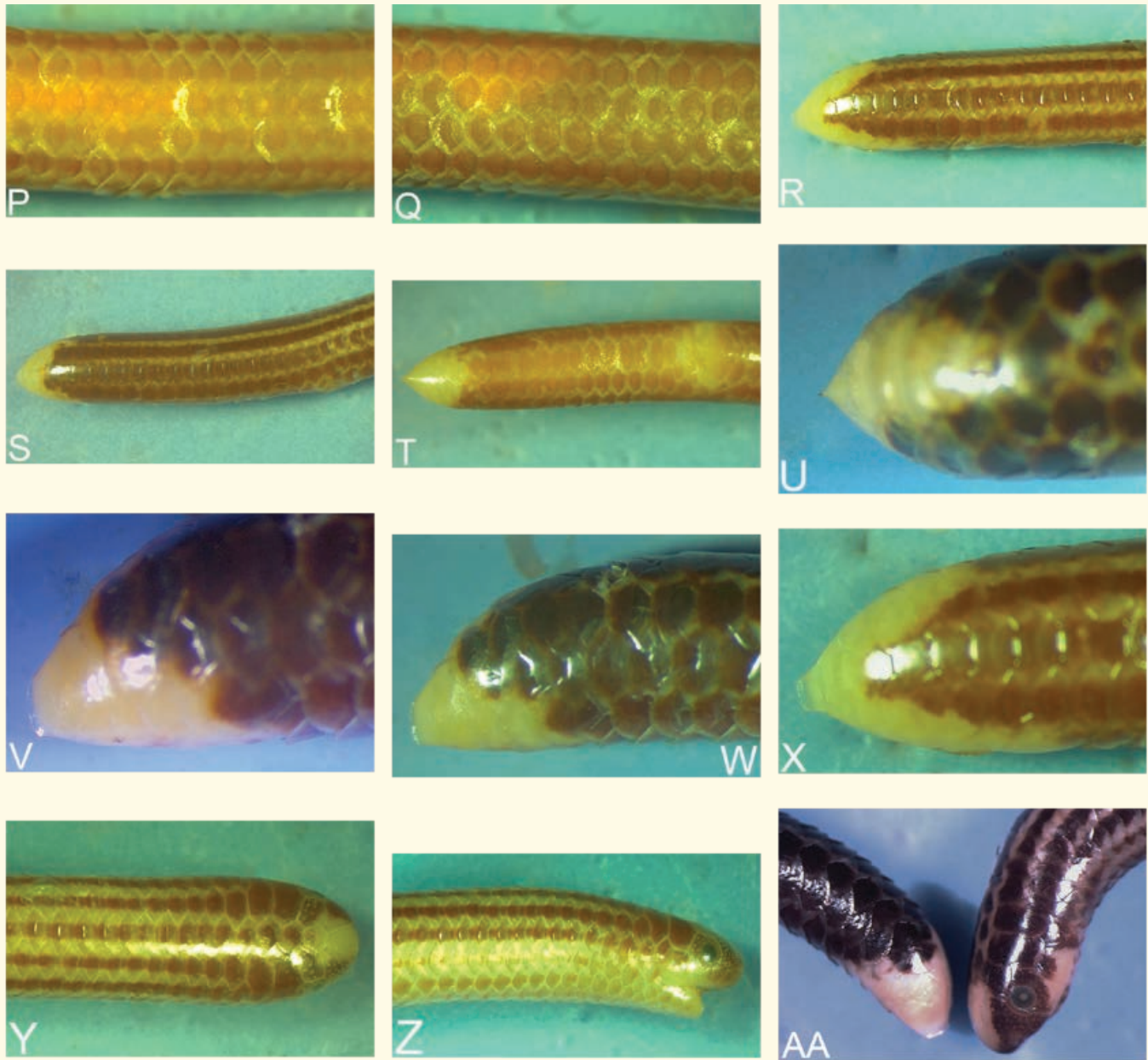
**Distribution:** *Epictia magnamaculata* is an insular endemic that inhabits Caribbean islands off southeastern Mexico (Quintana Roo: Cozumel, elev. NSL–25 m); northern Honduras (Islas de la Bahía [Bay Islands]: Bahía, Barbareta, Cayo Cochino Grande, Cayo Cochino Pequeño, Guanaja, Roatán, Utila; Islas del Cisne [Swan Islands]: Isla Pequeña [Little Swan], and Isla Grande [Big Swan], elev. NSL–25 m); and northern Colombia (Archipelago de Providencia, San Andrés and Santa Catalina: Providencia, San Andrés, and Santa Catalina, elev. NSL–200 m), overall elev. NSL–200 m (Map 4).




**Map. 4.** Distribution of *Epictia magnamaculata* on islands off Mexico and Central America.







**Fig. 4c.** Morphological variation in Colombian *Epictia magnamaculata*. (A, B, C, D) dorsal head (ANSP 25994, KU 269989, KU 269990, ANSP 25987); (E, F) lateral head (KU 269990, KU 269989); (G, H) ventral head (KU 269989, KU 269990); (I, J, K) dorsal midbody (KU 269989, KU 269988, ANSP 25991); (L, M, N) lateral midbody (ANSP 25991, KU 269988, KU 269989); (O, P, Q) ventral midbody (ANSP 25991); (R, S) lateral tail (KU 269988, KU 269989); (T) ventral tail (KU 269990); (U) dorsal apical spine (ANSP 25995); (V, W, X) lateral apical spine (ANSP 25995, ANSP 25994, KU 269988); (Y) dorsal neck (KU 269988); (Z) lateral neck (KU 269988); and (AA) lateral head and tail (ANSP 25992).  
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**Ecology:** This species inhabits tropical lowland hardwood rainforest in the Bay Islands of Honduras (McCranie et al., 2005). The holotype was collected in a banana plantation (Taylor, 1940).

**Remarks:** Dunn (1945: 364) remarked that *Epictia magnamaculata* was “almost equally allied to *L. goudotii* of Colombia and Panama and to *L. phenops* of Tehuantepec.” Thus, it was reduced to subspecies status and recognized as *Leptotyphlops albifrons magnamaculata* by Dunn and Saxe (1950), and as *L. goudotii magnamaculata* by



Orejas-Miranda *In* Peters et al. (1970). Meyer (1969) and Wilson and Hahn (1973) regarded it as a synonym of *L. phenops*. Adalsteinsson (2008) first confirmed the distinctness of this species with molecular data, and McCranie (2011) assigned the island populations of Cozumel (Mexico), Bahía, Swan, and Cayos Cochinos (Honduras), and San Andrés and Providencia (Colombia) to *E. magnamaculata*.

Pinto et al. (2010) reported the following statistics on *E. magnamaculata* from Colombia: LOA = 98–195 mm ( $\bar{x}$  = 154.5 mm); middorsals = 245–262 ( $\bar{x}$  = 252.6); subcaudals = 15–18 ( $\bar{x}$  = 16.8); LOA/MBD = 53–62 ( $\bar{x}$  = 57.9); TL/LOA = 4.8%–7.1% ( $\bar{x}$  = 6.0%); = TL/TW 2.8–4.0 ( $\bar{x}$  = 3.5); and RW/HW = 0.4–0.5 ( $\bar{x}$  = 0.4).

### ***Epictia phenops* (Cope, 1875)**

Figs. 5A–AV, 16O–R

*Stenostoma phenops* Cope, 1875: 128, 1887: 63; Troschel, 1877: 108; Sumichrast, 1880: 163, 179, 1881a: 269, 1881b: 282, 1882: 41; Garman, 1883: 6, 131; Velasco, 1892a: 75, 1892b: 78, 1893: 80, 1894: 40; Smith, 1939: 28; Klauber, 1940: 151 (part); Cochran, 1961: 214; Orejas-Miranda *In* Peters et al., 1970 and 1986: 170; Smith and Smith, 1976: S-B-191, S-C-37, S-D-30, S-F-7, S-F-31 (part); Hahn, 1980: 15; Smith, 1986: 421; Smith and Pérez-Higareda, 1986: 421; Pampa-Ramírez, 2010: 37; Illescas-Palomo et al., 2011: 231.

*Stenostoma phaenops*—Cope, 1879: 271, 1887: 63; Ferrari-Pérez, 1886: 183; Smith and Smith, 1976: S-B-191, S-C-37, S-D-30, S-F-31.

*Stenostoma albifrons*—Bocourt, 1882 *In* Duméril et al., 1870–1909: 505, pl. 29, fig. 10–10B (part); Smith and Smith, 1976: S-B-190, S-F-31 (part).

*Glauconia albifrons*—Boulenger, 1893: 63 (part); Günther, 1893 *In* 1885–1902: 85 (part); Dugès, 1896: 480 (part); Gadow, 1905: 195, 222, 1908: 363, 1930: 55; Smith and Smith, 1976: S-B-97, S-C-37, S-D-1.

*Leptotyphlops albifrons*—Amaral, 1930b: 138 (part); Smith, 1939: 28; Taylor, 1939: 1, pl. 1, figs. 11, 12 (part); Ahl, 1940: 248; Nicéforo-María, 1942: 86 (part); Pearse, 1945: 219; Alvarez del Toro, 1952: 71; Scortecchi, 1953: 651; Terent'ev, 1961: 254, 1965: 235; Freiberg, 1972: 459–460; Pampa-Ramírez, 2010: 10; Smith and Smith, 1976: S-B-127–128, S-C-37, S-D-1, S-F-6, S-F-30, 1993: 590, 709.

*Leptotyphlops phenops*—Smith, 1939: 28, 1957: 102; Klauber, 1940: 151 (part); Smith and Warner, 1948: 190–191, fig. 1S; Alvarez del Toro, 1960: 143–144, fig. 1, pl. (2 photos), 1973: 107, figs. 89, 90, 1982: 145, figs. 96, 97; Mertens, 1960: 94; Bogert, 1961: 507; Carr, 1963: 58; Reid and Lott, 1963: 141; Thomas, 1965: 1; Bellairs, 1969: pl. 26, 1970: pl. 26; Fitch, 1970: 121; McCoy, 1970: 139; Orejas-Miranda *In* Peters et al., 1970 and 1986: 170; Smith and Smith, 1973: 306, 1976: S-B-130, S-C-37, S-D-30, S-F-6, S-F-30 (part), 1993: 593; Groombridge, 1979: 669; Grimes, 1980: 191; Hahn, 1980: 15; Engelmann and Obst, 1982: 24; Hilty, 1982: 69; Athie-Lambarri, 1983: 245; Wallach, 1998a: 552; Ferri, 2000: 105 (part), col. photo; Gutiérrez-Espeleta and Van Gyseghem, 2005: 132; Kunz, 2006: 6; Baláz, 2007: 19; CONABIO, 2008: 5; Müller-González, 2010: 67, 106; Pampa-Ramírez, 2010: 10, 37; Caceros, 2011: 18, 94; Henríquez and Lara, 2011: 3; Illescas-Palomo et al., 2011: 231; Orellana-Pereira, 2011: 69; Mizuno and Kojima, 2015: 224.

*Leptotyphlops phenops phenops*—Smith, 1943: 444–445 (part), 1947: 70; Woodbury and Woodbury, 1944: 360; Smith and Taylor, 1945: 24 (part), 1950: 340; Stuart, 1948: 60, 1950: 23, 1954: 20, 1963: 85; Mertens, 1952a: 58–59, pl. 14, fig. 83, 1952b: 93; Maldonado-Koerdell, 1953: 130, 132; Cochran, 1961: 214; McCoy and Van Horn, 1962: 183; Lynch and Smith, 1965a: 168, fig. 1, 1965b: 58; Smith and Smith, 1976: S-C-37, S-D-30, S-F-30, 1993: 593; Müller, 1973: 13; Hahn, 1980: 15; Smith and Smith, 1976: S-B-130 (part), 1993: 593; Köhler, 1996b: 35; Dueñas et al., 2001: 96; Pampa-Ramírez, 2010: 10; Illescas-Palomo et al., 2011: 231.

*Leptotyphlops goudotii goudotii*—Orejas-Miranda *In* Peters et al., 1970 and 1986: 169; Lancini and Kornacker, 189: 104.

*Leptotyphlops goudotii phenops*—Orejas-Miranda *In* Peters et al., 1970 and 1986: 170; Smith and Smith, 1976: S-B-129 (part), S-C-37, S-F-30, 1993: 591, 709; Hahn, 1980: 15–16; Branch, 1986: 293, 295; Smith, 1986: 421–422, 1987: xxxiii; Smith and Pérez-Higareda, 1986: 421; Liner, 1994: 90, 2007: 54; Pérez-Higareda et al., 2007: 43, fig. 16 (part); Liner and Casas-Andreu, 2008: 122; Pampa-Ramírez, 2010: 10, 37; Illescas-Palomo et al., 2011: 231; EOL, 2015: 1281633.

*Leptotyphlops goudoti phenops*—Henderson and Hoevers, 1975: 32; Smith and Smith, 1976: S-B-129–130, S-B-191, S-C-37, S-G-4 (part), 1993: 591, 593, 709; Himmelstein, 1980: 29, 33; Flores-Villela et al., 1991: 172–173; Villafuerte and Flores-Villela, 1992: 53; Tipton, 2005: 24; Varin, 2008: 122.

*Leptotyphlops goudoti*—Ferguson, 1977: 497; Hahn, 1979: 230.2–3 (part); Campbell, 1982: 56, 276, 282, 290, 294, 297, 302, 308, 2001: 88; Weyer, 1990: 48 (part); Flores-Villela, 1991: 186, 1993: 35 (part); Smith and Smith, 1993: 591; Flores-Villela et al., 1995: 262 (part); Garel and Matola, 1996: 38 (part); Wilson and McCranie, 1998: 18, 31, 35, 45 (part);

Carabias-Lillo et al., 2000: 142; Núñez-Orantes and Muñoz-Alonso, 2000: 26; Anonymous, 2002: 36; Centro Turístico, 2003: 91; Grimshaw and Paz, 2004: 34; Peterson et al., 2004: 463; Álvarez-Romero et al., 2005: 5; Acevedo, 2006: 524; García, 2006: 43 (part); Paniagua, 2007: 99; Macip-Ríos and Casas-Andreu, 2008: 158; Luna-Reyes, 2009: 47–48; Martín-Regalado et al., 2011: 367; Luna-Reyes et al., 2012: 287, 294; Macossay-Cortéz et al., 2015: 18.

*Leptotyphlops bakewelli*—Hahn, 1980: 15.

*Leptotyphlops gadowi*—Hahn, 1980: 16; Casas-Andreu, 1982: 263.

*Leptotyphlops goudotii bakewelli*—Hahn, 1980: 15.

*Leptotyphlops phenops bakewelli*—Hahn, 1980: 16.

*Leptotyphlops pheonops* (sic)—Himmelstein, 1980: 33; Smith and Smith, 1993: 593.

*Leptotyphlops goudotii*—Hartshorn, 1984: 145; Campbell and Vannini, 1989: 12; Johnson, 1990: 278; Smith and Smith, 1993: 591; IICA, 1994: 184; Smith, 1994: 86; Frank and Ramus, 1995: 250 (part); Hedges, 1996: 111, 115 (part); Köhler, 1996b: 35, 2001a: 123 (part), 2001b: 12 (part), 2003a: 172, map (part), 2008: 183–184, map (part); Lee, 1996: 280–281, fig. 151A, map (part), 2000: 258–259, fig. 125A (part), 2002: 157; Campbell, 1998: 186–187 (part); Wallach, 1998a: 490 (part); McDiarmid et al., 1999: 30–31 (part); Sasa Marín, 2000: 150 (part); Stafford and Meyer, 2000: 173–174 (part); Dueñas et al., 2001: 96; Kley, 2001: 92, 2003: 375; Köhler, 2001b: 12, fig. 11B (part); Levell, 2001: 109; Asmundsson, 2003: 131; Casas-Andreu et al., 2004: 389; Vásquez-Marroquín, 2004: 19; Gallo, 2005: 89; Greenbaum and Komar, 2005: 2392, 2010: 444, 452; Gutiérrez-Espeleta and Van Gyseghem, 2005: 145; Henríquez and Herrera, 2005: 11–13, 19, 44; Köhler et al., 2005: 209–210, pl. 133, map 125 (part); Herrera et al., 2006: 43; García-Recinos, 2007: 32; Adalsteinsson, 2008: 6, 29, 41, 47, figs. 3.2, 3.5 (part); Flores-Benabib and Flores-Villela, 2008: 13–14; Henríquez and Ortez, 2008: 15; CONABIO, 2009: 17 (part); Henríquez and Henríquez, 2009: 119; Acevedo et al., 2010: 425; Anonymous, 2010a: 108; Johnson et al., 2010: 368; Marroquín-Eliás and López-Méndez, 2010: 5–6, 8–9, 19–20, 22, fig. 34; Mayén et al., 2010: 109; Pampa-Ramírez, 2010: 9–10; Stafford et al., 2010: 404; Tot et al., 2010: 109; Wilson and Johnson, 2010: 137, 233 (part); Wilson and Townsend, 2010: 811 (part); Illescas-Palomo et al., 2011: 231–232 (map); Wilson et al., 2013: 44 (part); Pyron et al., 2013: 24.

*Leptotyphlops goudotii* (sic)—Villa et al., 1988: 85 (part); Solís-Rivera et al., 1999: 37; Herrera et al., 2006: 41; Bastida-Zavala et al., 2013: 381.

*Leptotyphlops goudotii* (sic) *phenops*—Pérez-Higareda and Smith, 1991: 28–29 (part).

*Leptotyphlops gaudoti* (sic)—Casas-Andreu et al., 1996: 34 (part); Meerman, 2005: 3.

*Leptotyphlops* (sic) *goudotii* (sic)—UICN, 1999: 37.

*Leptotyphlops goudotii* (sic)—FUNDE, 2004: 8; Conrad, 2008: 35, 181.

*Epictia goudotii*—Adalsteinsson et al., 2009: 7, 10, 17, 31, 46, figs. 3A, 12 (part); Canseco-Márquez and Gutiérrez-Mayén, 2010: 252–253, fig. 169, pl. 175, map 108; Sánchez-Aguilar et al., 2011: 65; Guerra-Centeno et al., 2012: 152–153 (col. photo); Percino-Daniel et al., 2013: 943; Rioja-Paradela et al., 2013: 583; Hernández-Ordóñez et al., 2014: 6; Guerra-Centeno et al., 2014: 30; Guerra-Centeno et al., 2015: 19.

*Leptotyphlops goudotii pheops* (sic)—CONABIO, 2009: 17.

*Epictia phenops*—Pinto et al., 2010: 22; Wallach et al., 2014: 278 (part); McCranie, 2015: 379; Mata-Silva et al., 2015: 23, 41; Johnson et al., 2015a: 92, 2015b: 288, 304, 318; Mizuno and Kojima, 2015: 220; McCranie and Hedges, 2016: 4, 7, 9–13, figs. 2–4 (part); Schätti and Stutz, 2016: 4, 28, fig. 1 (2 col. photos); Wilson and Johnson, 2016: 38.

*Epictia goudotii phenops*—Pinto and Curcio, 2011: 61; Çinar, 2012: 121.

*Epictia goudoti*—CONABIO, 2012: 52 (part).

*Epictia* (*Leptotyphlops*) *goudotii* (*phenops*)—Rodríguez et al., 2013: 7.

**Lectotype:** USNM 30290, a 147 mm (LOA) specimen, from “Tehuantepec” [= Santo Domingo Tehuantepec, Oaxaca, Mexico, 16°19'28"N, 95°14'21"W, elev. 50 m asl], by lectotype designation of McCranie and Hedges (2016: 9, 12).

**Paralectotypes** (8): GUATEMALA: ALTA VERAPAZ: Cobán, collected by H. Hague ca. 1867, USNM 6760; MEXICO: OAXACA: Tehuantepec, collected by A.-L.-J. François Sumichrast between 1855 and 1869 (longest specimen is 156 mm LOA), USNM 12444, USNM 30289, USNM 30291–94, and USNM 30295 (field no. 238).

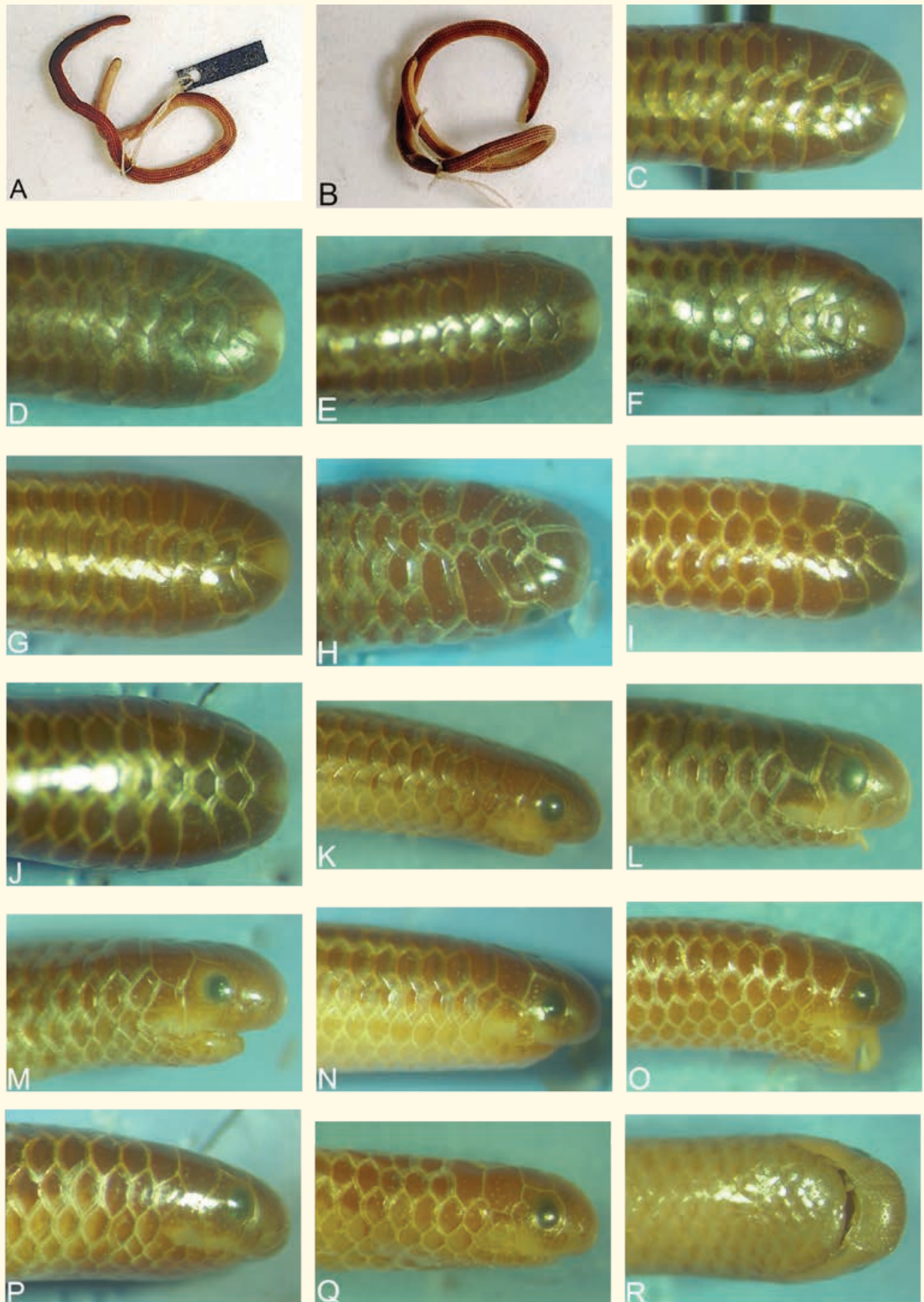


**Etymology:** The origin of the name for this species is derived from the Greek *phae*, meaning brown, and the Greek *nops*, meaning blind, referring to a brown blind snake.

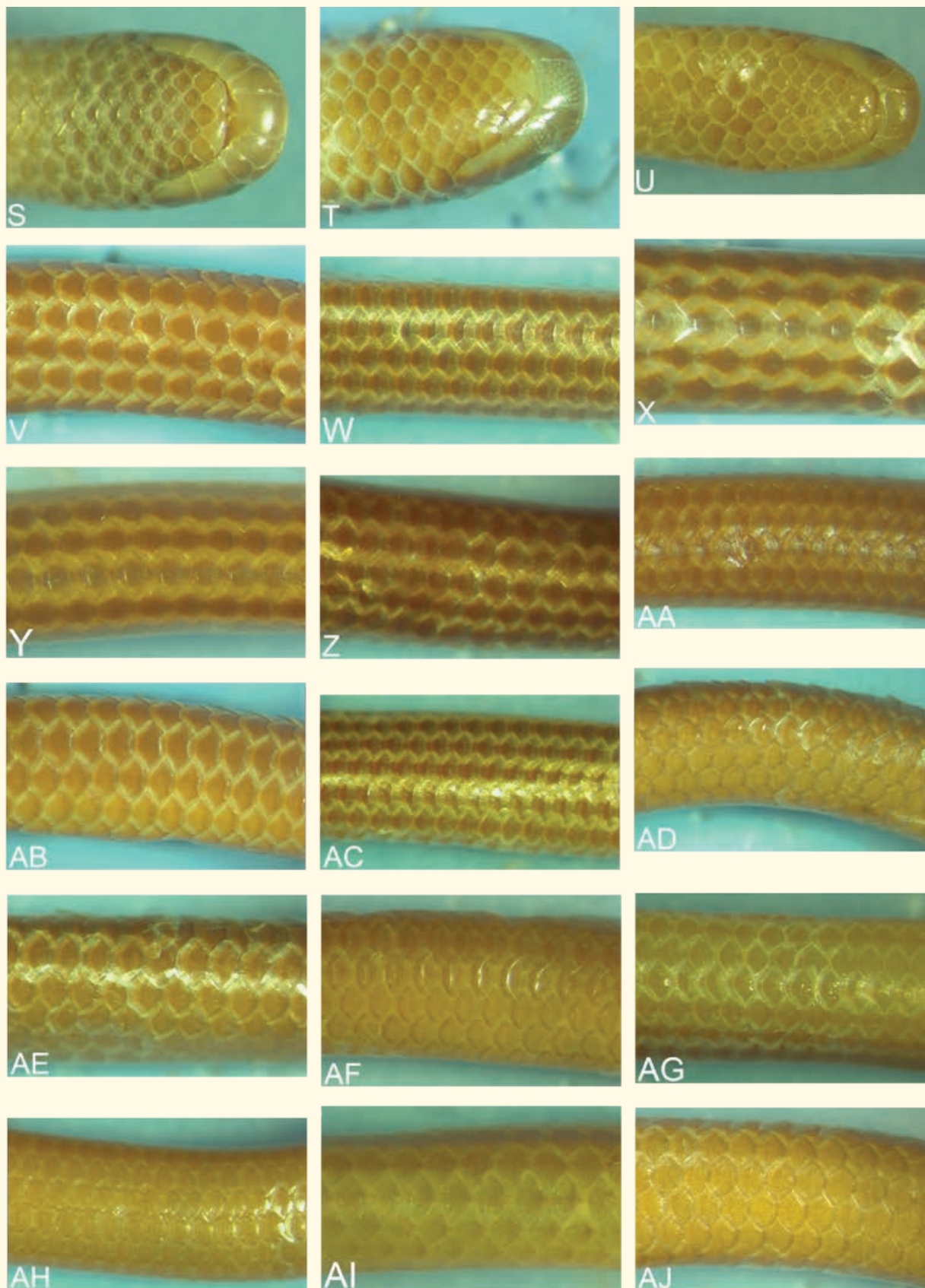
**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 53–195 ( $\bar{x}$  = 131.5) mm; (4) total middorsals = 216–277 ( $\bar{x}$  = 243.5); (5) subcaudals = 12–22 ( $\bar{x}$  = 16.3); (6) relative body proportion = 33–77 ( $\bar{x}$  = 56.9); (7) relative tail length = 3.5%–7.8% ( $\bar{x}$  = 5.5%); (8) relative tail width = 2.0–5.4 ( $\bar{x}$  = 3.5); (9) relative rostral width = 0.22–0.48 ( $\bar{x}$  = 0.37); (10) relative eye size = 0.34–0.46 ( $\bar{x}$  = 0.42); (10) rostral sagittate with truncated apex; (11) supralabials 2, moderate anterior supralabial reaching mid-eye level; (12) frontal hexagonal, as wide than long; (13) supraoculars large and pentagonal, twice as broad as deep, with posterior borders oblique to those of supranasals; (14) widest anteriormost vertebral scale 4<sup>th</sup>; (15) parietals and occipitals subequal, with transverse or oblique orientation; (16) infralabials 4; (17) cloacal shield semilunate in shape; (18) head brown, usually with a yellow spot covering entire rostral; (19) dorsum with 3 middorsal brown stripes of triangular-shaped spots bordered by 4 narrow to broad zigzag yellow stripes, 2 midlateral scale rows forming a solid brown stripe (= 5 dark stripes); (20) venter uniform pale brown; (21) midbody stripe formula (3 + 1/1 + 0) and middorsal pattern (3D + 4L); (22) tail with a pale terminal spot covering the 0–3.5 ( $\bar{x}$  = 1.2) dorsal scales and 0–13.5 ( $\bar{x}$  = 8.5) ventral scales (ventral/dorsal ratio 7.1); and (23) apical spine a small compressed spike.

**Description:** Head as wide as neck, dorsal profile rounded, all head shields with prominent sensory pits that appear as depressions in the scales; rostral sagittate with parallel anterior borders that taper to an oval apex (Fig. 5C); frontal hexagonal, longer than wide, smaller than all succeeding vertebrals; postfrontal 1½ times broader than deep, subhexagonal in shape with rounded posterior contours, interparietal and interoccipital distinctly wider than long; broadest anteriormost vertebral scale 4<sup>th</sup>; supraoculars large and pentagonal with oblique borders, twice as broad as deep; parietals longer than occipitals, both shields obliquely or transversely oriented; lateral head profile rounded; nasal completely divided, suture forming a deep V-shaped angle along anterior supralabial and infranasal, nostril oval and positioned nearer rostral than supralabial; infranasal twice as high as wide, narrowing toward lip; supralabials 2, anterior supralabial moderate in height with nearly parallel sides, reaching orbit and nearly extending to mid-eye level, its labial border usually twice as long as that of infranasal (Fig. 5S); ocular large, 1½ times tall as long, lower half with tapering sides (often concave posteriorly); eye moderate-sized and round, smaller in diameter than the lip-orbit gap (ED/OH = 0.34–0.46,  $\bar{x}$  = 0.42), protuberant but not visible in dorsal view; posterior supralabial longer than high, taller than anterior supralabial, with posterior border rounded; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 4, 1<sup>st</sup>, 2<sup>nd</sup>, and 3<sup>rd</sup> small and 4<sup>th</sup> elongated; costal scales rounded and imbricate, in 14 rows throughout; cloacal shield normally semilunate (Fig. 5AP), but subtriangular in some specimens from Mexico and El Salvador; Fig. 5AR); and termination of tail usually in form of a narrow horizontal or ventrally angled spike (Fig. 5AS), a horizontal thorn, or, less commonly, a compressed cone (Fig. 5AK).

Color pattern in life chocolate brown with pale yellow stripes, a small to moderate yellow rostral spot, and a large yellow subcaudal spot. Midbody color pattern in most preserved specimens consists of 3 brown to dark brown stripes, consisting of triangular-shaped spots, bordered by 4 moderate to narrow yellow zigzag stripes (Fig. 5V; middorsal pattern = 3D + 4L), a solid brown midlateral stripe 2 scales in width that lacks pale borders (Fig. 5AB; midbody stripe formula = 3 + 1/1 + 0), and 7 midventral scale rows of uniform pale brown pigmentation or occasionally with each scale faintly outlined in yellow. Head brown with a yellow spot covering most (rarely only part) of rostral; lateral head brown with a narrow short yellow bar restricted to lower half of posterior supralabial and ocular (Fig. 5K). Tail uniformly dark above and below, cloacal shield paler than surrounding cloaca, sometimes also with a pale ring, shield itself pale with brown vermiculations covering ½ of the scale; and yellow termination of tail highly asymmetrical with a short anterior spot averaging 1.2 dorsocaudals, and a very long ventral spot averaging 8.5 subcaudals, with a ventral/dorsal ratio of 7.1 (Fig. 5AL).











**Fig. 5.** Morphological variation in *Epictia phenops*. (A) dorsal view of lectotype of *E. phenops* (USNM 30290); (B) dorsal view of paralectotype (USNM 30289); (C, D, E, F, G, H, I, J) dorsal head (KU 43559, KU 183844, KU 183849, UCM 5281, UTEP 5980, MVZ 160487, UTEP 8312, UTEP 8313); (K, L, M, N, O, P, Q) lateral head (KU 43559, KU 183844, MVZ 160478, UTEP 5980, UTEP 8312, UTEP 8313, FMNH 111482); (R, S, T, U) ventral head (UMNH 2799, KU 183844, UTEP 8313); (V, W, X, Y, Z, AA) dorsal midbody (FMNH 105183, KU 87440, UCM 56664, UTEP 5981, KU 183849, UTEP 8312); (AB, AC, AD, AE, AF) lateral midbody (FMNH 105183, KU 87440, KU 183844, KU 183849, UTEP 8311); (AG, AH, AI, AJ) ventral midbody (KU 874440, UTEP 8312, UTEP 5981, KU 183849); (AK, AL, AM, AN) lateral tail (FMNH 111483, KU 183844, UMNH 2799, FMNH 105183); (AO, AP, AQ, AR) ventral tail (KU 87440, MVZ 88461, UTEP 8312, FMNH 105183); (AS, AT) lateral apical spine (UTEP 5980, KU 43559); and (AU, AV) lateral neck (KU 87440, FMNH 111483).

© USNM webpage (A, B), and remaining photos by Van Wallach

**Distribution:** The distribution of *Epictia phenops* extends from southern Mexico to western Honduras, including extreme southern Mexico (Oaxaca and Chiapas, elev. 40–1,670 m); Guatemala (Baja Verapaz, Escuintla, Guatemala, Izabal, Petén, and Zacapa, elev. 100–1,610 m); Belize (Corozal and Stann Creek, elev. NSL–50 m); El Salvador (Cuscatlán, La Libertad, Morazán, San Miguel, San Salvador, Santa Ana, San Vicente, and Sonsonate, elev. NSL–1,050 m); and Honduras (Copán and Lempira, elev. 50–700 m), overall elev. NSL–1,670 m (Map 5). In Chiapas this species occurs along the Pacific coastal plain and in the Sierra Madre de Chiapas, central depression, central plateau, and northern highlands (Johnson, 1984; Johnson et al., 2015). *Epictia phenops* inadvertently has been recorded from Panama (Smith, 1958b) and Trinidad (many authors, see Boos, 2001, for list).



**Map. 5.** Distribution of *Epictia phenops* in southern Mexico and upper Central America.

**Ecology:** This species inhabits lower montane rainforest, evergreen and semi-evergreen seasonal forest, tropical deciduous forest, short-tree savanna, and thorn woodland in Mexico (Johnson, 1984; Martín et al., 2011). It occurs in semi-evergreen seasonal forest and savanna in Belize (Stafford and Meyer, 2000). In Guatemala it is found in the Corozo Life Area, Coffee Life Area, and Pine Life Area (Stuart, 1950). *Epictia phenops* also inhabits tropical and subtropical dry forest, subtropical moist and wet forest, subtropical thorn-scrub forest, hardwood cloud forest, humid pine-oak forest, and subtropical lower montane wet forest (Campbell, 2001; Acevedo et al., 2010; Guerra-Centeno et al., 2014).

**Remarks:** Boulenger (1893) synonymized *Stenosoma phenops* Cope with *Stenosoma albifrons* Wagler, and it was Smith (1939, 1943) who first recognized *Epictia phenops* as distinct from *E. albifrons*, an idea also promoted by Taylor (1939). McCranie (2015) reported *E. phenops* from Honduras. Unverified records in Mexico are available for the states of Michoacán and Guerrero.

This species is most certainly polyphyletic as it ranges over a large geographic area with numerous habitats and exhibits an exceptionally broad range of middorsal counts (227–273), external characters, and visceral values. The visceral data ranges for nearly all the examined characters greatly exceeds the ranges for those of all of the other included species, suggesting a composite sample of more than one species. In addition, the molecular analysis of McCranie and Hedges (2016) identified *E. phenops* as being a composite taxon with at least three cryptic species. Particularly in Chiapas, Mexico, and Guatemala there are some specimens with purple heads and tails and a unique supralabial shape (as in *E. tenella*), in the form of an elongated diamond or trapezoid. Apparently, *E. phenops* and *E. bakewelli* are sympatric to the northwest of Acapulco, Guerrero, near Aguas Blancas, Mexico.



Clinal variation exists in the reduction of the middorsal scale counts from Oaxaca ( $\bar{x} = 250.7$ ) and Chiapas ( $\bar{x} = 244.7$ ), Mexico, through Guatemala ( $\bar{x} = 237.3$ ) and El Salvador ( $\bar{x} = 236.3$ ). Also, head width increases from 1.67 mm (Oaxaca), to 1.73 mm (Chiapas), 1.79 mm (Guatemala), and 1.81 mm (El Salvador). Interestingly, a number of characters follow a clinal trend from Oaxaca to Guatemala, but the material from El Salvador consistently reverses the trend, suggesting something else is occurring there. Data for the following characters are presented as means for Oaxaca, Chiapas, Guatemala, and El Salvador, respectively: subcaudals—17.0, 16.2, 14.7, 15.3; length/width ratio—60.8, 53.0, 52.0, 55.6; midtail width—1.9 mm, 2.2 mm, 2.4 mm, 2.1 mm; tail length/width ratio—3.6, 3.5, 3.1, 3.5; rostral width—0.64 mm, 0.61 mm, 0.59 mm, 0.64 mm; total length/rostral width—202.0, 226.4, 231.4, 203.2; and rostral width/head width ratio—0.39, 0.35, 0.33, 0.36.

I refer one specimen with a fused frontal-rostral (MCZ R-54331 from Tuxtla Gutierrez, Chiapas) to *E. phenops*, based upon the semilunate cloacal shield and color pattern. A distorted area between the rostral and frontal is present in this specimen, suggesting a scar rather than two fused scales. McCranie and Hedges (2016) reported length/width ratios of 48–120, dorsal caudal spots of 0–1, and ventral caudal spots of 7–15 in their sample of *E. phenops*. These data could not be incorporated into Table 2 because mean values were not provided for these characters.

***Epictia martinezi* sp. nov.**

Figs. 6A–I, 15K–N, 16S

*Glauconia albifrons*—Boulenger, 1893: 63 (part).

*Leptotyphlops albifrons*—Amaral, 1930: 138 (part).

*Leptotyphlops goudotii phenops*—Orejas-Miranda *In* Peters et al., 1970 and 1986: 170 (part); Hahn, 1980: 15–16 (part).

*Leptotyphlops phenops*—Wilson and Hahn, 1973: 120–123 (part).

*Leptotyphlops goudotii*—Wilson and Meyer, 1982: 23 (part); McDiarmid et al., 1999: 31–32 (part); Köhler, 2001b: 12, fig. 11b (part), 2003a: 171 (part), 2003b: 279 (part), 2008: 183–184, map (part); Wilson et al., 2001: 117, 124, 139, 141, 149, 152 (part); Wilson and McCranie, 2002: 92 (part), 2004: 21 (part); Casteñeda and Marineros, 2006: 10 (part); Townsend and Wilson, 2010a: 478, 2010b: 693, 698 (part); Wilson and Townsend, 2006: 96, 2010: 811 (part).

*Leptotyphlops goudoti*—Wilson, 1983: 125 (part); Wilson and McCranie, 1994: 148 (part), 1998: 18 (part); Marineros, 2000: 139 (part).

*Leptotyphlops goudotii* (sic)—Wilson and Meyer, 1985: 20–21, fig. 25 (part).

*Leptotyphlops goudoti ater*—Tipton, 2005: 24 (part).

*Leptotyphlops goudotii* (sic)—Alemán-Mejía, 2008: 101 (part).

*Epictia ater*—McCranie, 2009: 16, 2011: 43–47, pl. 4, fig. B, map 11, 2015: 378–379 (part); Wallach et al., 2014: 275–276 (part); Wilson and Johnson, 2016: 38.

*Epictia goudotii*—Wilson and Johnson, 2010: 101 (part).

*Epictia phenops*—McCranie and Hedges, 2016: 4, 7–8, fig. 2 (part).

**Holotype:** FMNH 283740 (field no. JRM 20118), a 153 mm (LOA) male collected by James R. McCranie on 18 June 2012, from between Río Lempa and Antigua, Departamento de Ocotepeque, Honduras, ca. 14°24.3"N, 89°12.2"W, elev. 730 m asl.

**Paratypes** (5): HONDURAS: OCOTEPEQUE: Río Lempa near Antigua, collected by James R. McCranie, 17 June 2012, FMNH 283735 (field no. JRM 20107), 283736 (field no. JRM 20108), 283737 (field no. JRM 20114); between Río Lempa and Antigua, collected by James R. McCranie, 18 June 2012, FMNH 283738–39 (field no. JRM 20116–17).

**Etymology:** This species is named in honor of Joe Martinez, Curatorial Assistant II, Department of Herpetology, Museum of Comparative Zoology, Harvard University (MCZ), and commemorates his 20 years of service to the museum. Joe is a great friend, an all-around herper, and my avid sports buddy.

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 71–169 ( $\bar{x} = 143.8$ ) mm; (4) total middorsals = 248–260 ( $\bar{x} = 256.3$ ); (5) subcaudals = 16–23 ( $\bar{x} = 19.8$ ); (6) relative body proportion = 39.4–50.4 ( $\bar{x} = 46.0$ ); (7) relative tail length = 5.5%–8.8% ( $\bar{x} = 7.4\%$ ); (8) relative tail width = 3.3–5.2

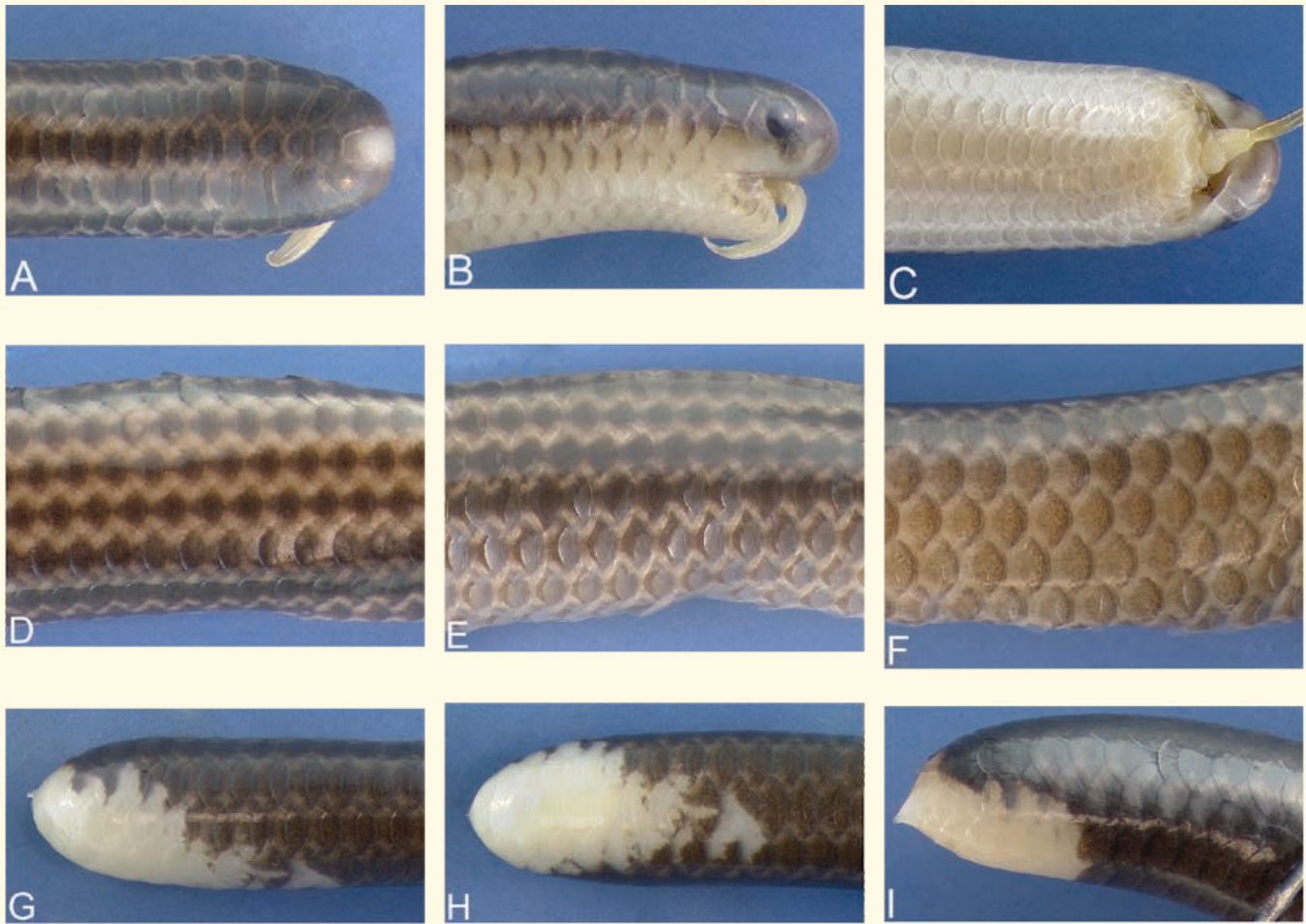


( $\bar{x}$  = 4.2); (9) relative rostral width = 0.37–0.51 ( $\bar{x}$  = 0.41); (10) relative eye size = 0.47–0.54 ( $\bar{x}$  = 0.50); (10) rostral parallel or barely tapering with a rounded or truncated apex extending to mid-eye level; (11) supralabials 2, moderate anterior supralabial reaching or nearly reaching mid-eye level; (12) frontal subhexagonal,  $1\frac{1}{4}$ – $1\frac{1}{2}$  times broader than deep; (13) supraoculars large and pentagonal with posterior borders oblique to posterior borders of supranasal,  $2\frac{1}{2}$  times as wide as long; (14) widest anteriormost vertebral scale 4<sup>th</sup>; (15) parietals deeper than occipitals, oriented obliquely; (16) infralabials 4; (17) cloacal shield semilunate shape; (18) head brown, with a moderate yellow spot covering most or all of the rostral; (19) dorsum with 3 dark brown middorsal stripes formed from diamond-shaped spots separated by 4 broad zigzag yellow lines and a pair of broader lateral dark brown stripes separated by a moderate yellow zigzag stripe (= 7 dark stripes); (20) venter pale brown, with each scale heavily stippled in brown with a narrow pale outline; (21) midbody stripe formula (3 + 2/2 + 0) and middorsal pattern (3D + 4L); (22) tail with a larger pale terminal spot ventrally, covering 5.5–9 ( $\bar{x}$  = 7.5) subcaudals, than dorsally, covering 1.5–3.5 ( $\bar{x}$  = 2.4) subcaudals, the ventral/dorsal ratio equals 3.1; and (23) apical spine a tiny spike.

**Description:** Holotype data include scale row formula = 14-14-14; midtail scale rows = 10; TMD = 248; SC = 20; LOA = 153.0 mm; TL = 13.0 mm; MBD = 3.4 mm; MTD = 2.8 mm; RW = 0.75 mm; HW = 2.1 mm; L/W = 45.0; TL/LOA = 8.5; TL/TW = 4.6; RW/HW = 0.51; and ED/OH = 0.47. Head barely distinguishable from neck, dorsal profile truncated, all head shields with prominent sensory pits that appear as depressions in the scales; rostral parallel anteriorly but slightly tapered posteriorly, with truncated apex (Fig. 6A); frontal hexagonal in shape,  $1\frac{1}{2}$  times as wide as deep; postfrontal larger than frontal, as wide as long; interparietal and interoccipital usually as broad as deep; broadest anteriormost vertebral scale 5<sup>th</sup> (Fig. 6A); supraoculars large, narrow and pentagonal,  $2\frac{1}{2}$  times as wide as long, posterior borders oblique to supranasal borders; parietals slightly longer than occipitals, both shields oblique in orientation; lateral head profile with rounded snout; nasal completely divided, suture forming a deep V-shaped angle (ca. 90°) along anterior supralabial and infranasal, nostril small and oval, positioned nearer the rostral than supralabial and entirely below the suture in the infranasal; infranasal as broad and as anterior supralabial, narrowing toward lip; supralabials 2, anterior supralabial moderate in height with nearly parallel sides, extending to mid-eye level, its labial border equal in length to that of infranasal; ocular large, twice as tall as broad, roughly pentagonal with a nearly straight anterior border; eye moderate with a distinct pupil and iris, slightly oval or elliptical in vertical plane, its height greater than the lip-orbit gap (ED/OH = 0.47–0.54,  $\bar{x}$  = 0.50), partially beneath supranasal (Fig. 6B), and barely visible in dorsal view; posterior supralabial taller than long, taller than anterior supralabial, with rounded posterior apex; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 4, first three infralabials short and last one elongated; costal scales rounded and imbricate in 14 rows throughout; cloacal shield semilunate; and tail terminates in a compressed thorn (Fig. 6I).

Coloration in life chocolate brown with pale stripes, a moderate yellow rostral spot, and a large yellow subcaudal spot. In preserved specimens, the midbody pattern consists of 3 dark brown middorsal stripes of contiguous diamonds separated by 4 broad pale zigzag stripes (Fig. 6D; middorsal pattern = 3D + 4L) and 2 broader lateral dark brown stripes separated by a moderate pale zigzag stripe (Fig. 6E); ventral 7 scale rows uniform pale brown to white, with heavy dark stippling on central portion of each scale (Fig. 6F; midbody stripe formula = 3 + 2/2 + 0). Head dark brown with a large posterior pale spot on lower half of posterior supralabial and ocular, a smaller pale preocular spot covering infranasal (with or without a narrow pale bar along suture to ocular shield, and a white labial border along entire upper lip (Fig. 6B); chin and throat white (Fig. 6C). Cloacal shield heavily stippled with brown but paler than ventral scales, a pale cloacal ring also present; tail uniform brown with caudal spot larger than dorsal spot, dorsal spot covering 1.5–3.5 dorsocaudals ( $\bar{x}$  = 2.4 scales), ventral spot covering 5.5–9 subcaudals ( $\bar{x}$  = 7.5 scales) (Fig. 6I), and ventral/dorsal ratio 3.1.

The hemipenis of FMNH 283740, from Ocotepeque, Honduras (Fig. 15K–L), is single with a simple sulcus spermaticus that curves around the lateral surface of the organ to terminate distally in the center of a depression surrounded by papillae. The organ, which is completely everted, is 4.7 mm in length, with a nude base 1.5 mm wide, a narrowed nude middle portion 1.5 mm long, and a distal, bulbous, calyculate head, 1.7 mm long and 2.6 mm wide. There are 5–6 rows of papillate calyces along sulcate surface and 6–7 rows of calyces on asulcate surface. Proximal to the calyces are 3 circular rows of small papillae; the distal surface of the organ, which is slightly concave, is covered with 3–4 circular rings of tiny papillae. The incompletely everted hemipenis of FMNH 283739, from Ocotepeque, Honduras (Fig. 15M–N), is 4.4 mm long with a naked base 1.6 mm wide, a nude neck region 1.2 mm wide, and a distal head with 4 exposed rows of calyces, each with a prominent papilla.



**Fig. 6.** Morphological variation in *Epictia martinezi* sp. nov. (A) dorsal head (FMNH 283737); (B) lateral head (FMNH 283737); (C) ventral head (FMNH 283739); (D) dorsal midbody (FMNH 283738); (E) lateral midbody (FMNH 283738); (F) ventral midbody (FMNH 283738); (G) lateral tail (FMNH 283738); (H) ventral tail (FMNH 283738); and (I) lateral apical spine (FMNH 283737).

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**Viscera:** (mean followed parenthetically by range,  $n = 2$ ). Posterior tip of sternohyoideus muscle = 13.7% (13.3–14.0%); sternohyoideus/snout–heart gap = 0.81 (0.80–0.83); heart length = 3.7% (3.2–4.4%) with midpoint at = 18.7% (18.2–19.2%); snout–heart interval = 20.7% (20.4–20.9%); heart–liver gap = 8.2% (7.9–8.4%) and interval = 48.3% (47.1–49.5%); heart–gall bladder gap 44.9% (44.2–45.6%); liver lobes multipartite; right liver length = 36.4% (36.0–36.8%) with midpoint at 47.0% (46.8–47.2%) and 36.5 (32–41) segments; left liver length = 26.7% (25.3–28.1%) with midpoint at 46.2% (45.3–47.0%) and 36.5 (34–39) segments; anterior liver extension = 0.11 (0.07–0.15) and posterior liver tail = 0.16 (0.15–0.16); left liver/right liver = 0.74 (0.69–0.78); liver–gall bladder gap = 0.4% (0.4–0.4%) and interval 38.2% (37.8–38.6%); gall bladder length = 1.4% (1.4–1.4%) with midpoint at 66.3% (65.8–66.7%); liver–kidney gap 16.0% (15.1–16.9%) and interval 60.6% (60.4–60.8%); gall bladder–gonad gap 6.2% (5.4–7.0%) and interval = 15.5% (14.7–16.2%); gall bladder–kidney gap = 14.2% (13.3–15.1%) and interval = 23.9% (23.2–24.5%); right gonad length = 4.3% (3.2–5.4%) with midpoint at 75.3% (74.6–76.0%); left gonad length = 3.8% (2.8–4.7%) with midpoint at 79.2% (79.0–79.3%); gonad–kidney gap = 0.2% (0–0.4%) and interval = 16.2% (14.7–17.6%); right adrenal midpoint = 76.8% (76.5–77.0%) and left adrenal midpoint = 78.9% (78.8–78.9%); right kidney length = 5.0% (4.9–5.0%) with midpoint at 83.7% (83.2–84.2%), and left kidney length = 5.0% (4.0–6.0%) with midpoint at 86.9% (86.1–87.6%); kidney overlap = 0.22 (0.14–0.29); kidney–vent gap = 10.7% (10.4–10.9%) and interval = 18.8% (18.3–19.3%); rectal caecum length = 1.1% (1.1–1.1%); and rectal



caecum–vent interval = 11.2% (10.4–11.9%). In the two male paratypes examined, 2 segments are present in each right testis and 1 or 2 ( $\bar{x} = 1.5$ ) in the left testes.

Respiratory system lacking tracheal lung and left lung complex; trachea length = 18.7% (18.0–19.3%) with midpoint at 11.3% (10.7–11.9%) and an estimated 162 (152–171) tracheal rings or 89.1 (88.0–90.2) rings/10% SVL; anterior lung tip = 18.7% (18.6–18.7%); tracheal entry terminal; cardiac lung length = 2.0% (1.8–2.2%); right lung length = 24.2% (23.7–24.6%) with midpoint at 32.7% (32.6–32.7%) with faveolar cephalad half and trabecular caudad half; posterior tip = 44.8% (44.6–44.9%); right bronchus length = 20.1% (18.7–21.4%) with posterior tip at 40.7% (39.6–41.7%); bronchus/right lung = 0.83 (0.79–0.87); trachea–bronchus length = 38.7% (36.7–40.7%) with midpoint at 21.3% (21.2–21.4%); trachea–bronchus/total lung length = 0.87 (0.82–0.91); and total lung length = 26.1% (25.9–26.3%), with midpoint at 31.8% (31.7–31.8%).

Visceral distance data include heart–right lung distance = 14.0% (13.5–14.4%); heart–liver distance = 28.3% (27.6–29.0%); trachea–liver distance = 35.7% (34.9–36.5%); liver–kidney distance = 38.3% (37.5–39.1%); trachea–bronchus–gall bladder distance = 45.0% (44.6–45.3%); right lung–adrenal distance = 45.2% (45.1–45.2%); heart–gonad distance = 56.6% (55.4–57.8%); trachea/bronchus–kidney distance = 64.0% (63.3–64.7%); trachea–adrenal distance = 66.5% (66.0–67.0%); and heart–kidney distance = 66.6% (66.5–66.7%).

**Distribution:** *Epictia martinezi* is known only from the type locality in western Honduras (near Antigua), known elev. 730 m (Map 6).



Map 6. Distribution of *Epictia martinezi* nov. sp. in western Honduras.



**Ecology:** The type locality of *Epictia martinezi* occurs in the Southern Cordillera of the Serranía region, specifically the Cordillera de Merendón, an area of subhumid valleys (McCranie, 2011) occupied by moist lower montane forest and pine-oak forest (Wilson and Meyer, 1985).

**Comparisons:** *Epictia martinezi* can be separated from *E. ater* by a mean middorsal count of 256.3 (vs. 237.3); a parallel rostral with a truncated apex (vs. waisted with triangular apex); a pale rostral spot covering most or all of rostral (vs. obscure or absent spot), and pale preocular spot present (vs. absent); a frontal shield is present (vs. absent); supraocular narrow and trapezoidal (vs. moderate and parallel-sided); parietals and occipitals oblique in orientation (vs. transverse); a semilunate cloacal shield (vs. subtriangular); a subcaudal pale spot averaging 7.5 scales (vs. 11.7 scales); 7 vivid midbody stripes (vs. uniformly dark); preocular pale spot present on infranasal (vs. absent); a shorter sternohyoideus length (11.4% vs. 13.7%); a shorter heart length ( $\leq 4.2\%$  vs.  $\geq 4.7\%$ ); a shorter snout–heart interval ( $\leq 20.9\%$  vs.  $\geq 21.4\%$ ); a more cranial right liver (47.0% vs. 49.9%), left liver (46.2% vs. 50.5%), and total liver midpoint (47.0% vs. 49.9%); a greater number of left liver ( $\geq 34$  vs.  $\leq 28$ ) and total liver segments (73.0 vs. 57.8); fewer right testis (2.0 vs. 5.3), left testis (1.5 vs. 5.3), and total testis segments (1.8 vs. 5.3); a more anterior right adrenal (76.8% vs. 80.2%), left adrenal (78.9% vs. 82.9%), and total adrenal midpoint (77.8% vs. 81.5%); a shorter rectal caecum (1.1% vs.  $\geq 1.1\%$ ); a shorter trachea length ( $\leq 19.3\%$  vs.  $\geq 20.3\%$ ) and cardiac lung length ( $\leq 2.2\%$  vs.  $\geq 2.7\%$ ); a more cranial right lung midpoint ( $\leq 32.7\%$  vs.  $\geq 34.7\%$ ) and lung posterior tip ( $\leq 44.9\%$  vs.  $\geq 46.3\%$ ); and fewer left testis (2.0 vs. 5.3), right testis (4.0 vs. 5.3), and total testis segments (3.0 vs. 5.3).

*Epictia martinezi* can be distinguished from *E. bakewelli* by a parallel rostral extending to mid-eye level (vs. waisted rostral, reaching post-eye level); a pale preocular spot (vs. lacking spot); a discrete frontal shield (vs. absent); oblique supranasal/supraocular borders (vs. parallel); a semilunate cloacal shield (vs. subtriangular); midbody color pattern of 7 diamond- or triangle-shaped dark stripes with zigzag borders (vs. 5 straight-sided dark stripes); 2 lateral dark stripes (vs. 1); a brown cloacal shield (vs. yellow shield); a longer heart–liver interval (48.3% vs. 46.1%); a greater number of left liver ( $\geq 34$  vs.  $\leq 32$ ) and total liver segments (73.0 vs. 70.5); a longer posterior liver tail ( $\geq 0.15$  vs.  $\leq 0.15$ ); a longer liver–gall bladder gap ( $\geq 0.40$  vs.  $\leq 0$ ); a shorter liver–kidney gap (16.0% vs. 20.8%) and interval ( $\leq 60.4\%$  vs.  $\geq 61.9\%$ ); a longer gall bladder length ( $\geq 1.4\%$  vs.  $\leq 1.2\%$ ) and more posterior midpoint (66.3% vs. 63.3%); a shorter gall bladder–gonad interval (15.5% vs. 18.3%); a shorter gall bladder–kidney gap (14.2% vs. 19.9%) and interval (23.9% vs. 27.0%); a more anterior right gonad midpoint (75.3% vs. 77.5%); fewer right testis (2.0 vs. 4.0), left testis (1.5 vs. 4.0), and total testis segments (1.8 vs. 4.0); a shorter gonad–kidney gap ( $\leq 0.4\%$  vs.  $\geq 0.4\%$ ) and longer interval (16.2% vs. 13.7%); a more cranial right adrenal midpoint (76.8% vs. 78.9%); a longer right kidney ( $\geq 4.9\%$  vs.  $\leq 3.3\%$ ), left kidney ( $\geq 4.0\%$  vs.  $\leq 3.7\%$ ), and total kidney length ( $\geq 9.0\%$  vs.  $\leq 7.0\%$ ); a longer kidney–vent interval ( $\geq 18.3\%$  vs.  $\leq 17.9\%$ ); a larger kidney–vent interval/right liver ratio (0.51 vs. 0.34); a shorter rectal caecum length ( $\leq 1.1\%$  vs.  $\geq 1.1\%$ ); a lesser rectal caecum/left kidney ratio ( $\leq 0.28$  vs.  $\geq 0.30$ ); fewer tracheal rings/10% SVL (88.0 vs. 100.2); a shorter right lung length (24.2% vs. 30.9%) and more cranial midpoint (32.7% vs. 35.9%); a more cranial right lung posterior tip (44.8% vs. 51.3%); a larger right lung/right bronchus ratio ( $\geq 0.79$  vs.  $\leq 0.70$ ); and a shorter heart–kidney distance ( $\leq 66.7\%$  vs.  $\geq 67.2\%$ ) and trachea/bronchus–kidney distance ( $\leq 64.7\%$  vs.  $\geq 65.0\%$ ).

*Epictia martinezi* is recognizable from *E. columbi* by a mean subcaudal number of 19.8 (vs. 23.7) and range  $\leq 23$  (vs.  $\geq 22$ ); a lower mean length/width ratio of 46.0% (vs. 58.3%) and actual range of  $\leq 51\%$  (vs.  $\geq 49\%$ ); a parallel rostral, extending to mid-eye level (vs. sagittate shield, not reaching eye level); a pale rostral and preocular spot (vs. absent); a supraocular width/length ratio of 2.5 (vs. 1.25); oblique supranasal/supraocular borders (vs. parallel); an oval eye, partly beneath the supranasal (vs. round eye, completely beneath ocular shield); an eye/ocular ratio  $\geq 0.47$  (vs.  $\leq 0.41$ ); lacking a preoral groove (vs. groove present); caudal pale spots present (vs. absent); an apical spine in form of spike (vs. cone with narrow blade); a vividly striped midbody color pattern (uniformly dark); dorso-caudal and subcaudal pale spots present (vs. absent); a longer sternohyoideus length ( $\geq 13.3\%$  vs. 11.7%); a greater sternohyoideus/snout–heart gap ratio ( $\geq 0.80$  vs. 0.75); a shorter heart length ( $\leq 4.2\%$  vs. 4.3%) and more caudad heart midpoint ( $\geq 18.2\%$  vs. 17.8%); a shorter heart–liver gap ( $\leq 8.4\%$  vs. 9.0%) and longer heart–gall bladder gap ( $\geq 44.2\%$  vs. 43.8%); a longer right liver ( $\geq 36.0\%$  vs. 34.4%), left liver ( $\geq 25.3\%$  vs. 24.6%), and total liver length ( $\geq 62.1\%$  vs. 59.0%); a more caudal right liver ( $\geq 46.8\%$  vs. 46.1%) and left liver midpoint ( $\geq 47.0\%$  vs. 47.5%); a shorter anterior liver extension ( $\leq 0.15$  vs. 0.18) and longer posterior liver tail ( $\geq 0.15$  vs. 0.10); a greater number of left liver ( $\geq 34$  vs. 28) and total liver segments ( $\geq 71$  vs. 63); a longer liver–gall bladder interval ( $\geq 37.8\%$  vs. 35.9%) and shorter gap ( $\leq 16.9\%$  vs. 20.3%); a longer gall bladder length ( $\geq 1.4\%$  vs. 1.2%) and more posterior

midpoint ( $\geq 65.8\%$  vs.  $64.3\%$ ); a shorter gall bladder–gonad gap ( $\leq 7.0\%$  vs.  $13.3\%$ ) and interval ( $15.5\%$  vs.  $18.4\%$ ); a shorter gall bladder–kidney gap ( $\leq 15.1\%$  vs.  $18.8\%$ ) and interval ( $\leq 24.5\%$  vs.  $27.7\%$ ); a more anterior right gonad ( $\leq 76.0\%$  vs.  $79.3\%$ ), left gonad ( $\leq 79.3\%$  vs.  $81.6\%$ ), and total gonad midpoint ( $\leq 77.7\%$  vs.  $80.5\%$ ); a more cranial right adrenal ( $\leq 77.0\%$  vs.  $80.7\%$ ), left adrenal ( $\leq 78.9\%$  vs.  $81.6\%$ ), and total adrenal midpoint ( $\leq 77.9\%$  vs.  $81.2\%$ ); a shorter gonad–kidney gap ( $\leq 0.4\%$  vs.  $1.6\%$ ) and longer interval ( $16.2\%$  vs.  $13.3\%$ ); a longer right kidney ( $\geq 4.9\%$  vs.  $3.9\%$ ), left kidney ( $\geq 4.0\%$  vs.  $3.9\%$ ), and total kidney length ( $\geq 9.0\%$  vs.  $7.8\%$ ); a more cranial right kidney ( $\leq 84.2\%$  vs.  $85.5\%$ ), left kidney ( $\leq 87.6\%$  vs.  $89.5\%$ ), and total kidney midpoint ( $\leq 85.9\%$  vs.  $87.5\%$ ); a larger kidney overlap ratio ( $\geq 0.14$  vs.  $0$ ); a longer kidney–vent gap ( $\geq 10.4\%$  vs.  $8.6\%$ ) and interval ( $\geq 18.3\%$  vs.  $16.4\%$ ); a shorter rectal caecum ( $1.1\%$  vs.  $2.0\%$ ); a smaller rectal caecum/left kidney ratio ( $\leq 0.28$  vs.  $0.51$ ); a shorter heart–right lung distance ( $\leq 14.4\%$  vs.  $15.4\%$ ), liver–kidney distance ( $\leq 39.1\%$  vs.  $41.4\%$ ), right lung–adrenal distance ( $\leq 45.2\%$  vs.  $48.0\%$ ), heart–gonad distance ( $\leq 57.8\%$  vs.  $61.5\%$ ), trachea/bronchus–kidney distance ( $\leq 64.7\%$  vs.  $67.2\%$ ), heart–kidney distance ( $\leq 66.7\%$  vs.  $69.7\%$ ), and trachea–adrenal distance ( $\leq 67.0$  vs.  $70.6\%$ ); and a longer trachea/bronchus–gall bladder distance ( $\geq 44.6\%$  vs.  $44.0\%$ ).

*Epicitia martinezi* can be differentiated from *E. magnamaculata* by a mean middorsal count of  $256.3$  (vs.  $238.7$ ); a parallel rostral, extending to mid-eye level (vs. sagittate, not reaching eye level); a moderate pale head spot, confined to rostral shield (vs. large, expanded onto adjacent shields); a pale preocular spot present (vs. absent); a supraocular width/length ratio of  $2.5$  (vs.  $1.5$ ); oblique supranasal/supraocular borders (vs. parallel); eye not beneath supralabial (vs. partly beneath anterior supralabial); a semilunate cloacal shield (vs. subtriangular); a subcaudal/dorsocaudal pale spot ratio of  $3.1$  (vs.  $0.9$ ); a mean subcaudal spot size of  $7.5$  scales (vs.  $3.9$  scales); a tiny apical spine (vs. broad compressed blade);  $7$  dark zigzag midbody stripes (vs.  $11$  dark straight-sided stripes); a pale venter  $7$  scale rows wide (vs.  $3$  scale rows in width); a shorter heart–gall bladder gap ( $44.9\%$  vs.  $49.4\%$ ); a shorter right liver ( $36.4\%$  vs.  $38.8\%$ ), left liver ( $26.7\%$  vs.  $29.9\%$ ), and total liver length ( $63.1\%$  vs.  $68.6\%$ ); a more cranial left liver midpoint ( $46.2\%$  vs.  $48.9\%$ ); a greater number of left liver segments ( $36.5$  vs.  $27.2$ ); a shorter liver–gall bladder gap ( $\leq 0.4\%$  vs.  $\geq 0.6\%$ ) and interval ( $38.2\%$  vs.  $42.7\%$ ); a more cranial gall bladder midpoint ( $66.3\%$  vs.  $71.1\%$ ); a longer gall bladder–kidney interval ( $23.9\%$  vs.  $19.4\%$ ); a more anterior right gonad ( $75.3\%$  vs.  $79.9\%$ ), left gonad ( $79.2\%$  vs.  $82.6\%$ ), and total gonad midpoint ( $77.2\%$  vs.  $81.2\%$ ); a greater number of right testis ( $2.0$  vs.  $4.0$ ), left testis ( $1.5$  vs.  $3.0$ ), and total testis segments ( $1.8$  vs.  $3.5$ ); a longer gonad–kidney interval ( $\geq 16.2\%$  vs.  $\leq 11.5\%$ ); a longer right kidney length ( $\geq 4.9\%$  vs.  $\leq 4.0\%$ ) and more cranial midpoint ( $83.7\%$  vs.  $85.8\%$ ); a longer total kidney length ( $\geq 9.0\%$  vs.  $\leq 8.5\%$ ); a longer kidney–vent interval ( $18.8\%$  vs.  $15.8\%$ ); a more caudal right adrenal ( $76.8\%$  vs.  $72.9\%$ ), left adrenal ( $78.9\%$  vs.  $74.7\%$ ), and total adrenal midpoint ( $77.8\%$  vs.  $73.8\%$ ); a shorter right lung length ( $24.2\%$  vs.  $28.9\%$ ), and more cranial midpoint ( $32.7\%$  vs.  $35.4\%$ ) and posterior tip ( $44.8\%$  vs.  $49.9\%$ ); a larger bronchus/right lung ratio ( $0.83$  vs.  $0.68$ ); and a shorter trachea/bronchus–gall bladder distance ( $\leq 45.3\%$  vs.  $\geq 45.3\%$ ) and trachea–adrenal distance ( $\leq 67.0\%$  vs.  $\geq 67.8\%$ ).

*Epicitia martinezi* is identifiable from *E. phenops* by a parallel rostral with a truncated apex (vs. sagittate with oval apex); a pale preocular spot (vs. spot absent); eye beneath supranasal (vs. entirely beneath ocular);  $7$  dark midbody stripes,  $3 + 2/2 + 0$  (vs.  $5$  dark stripes,  $3 + 1/1 + 0$ ); a subcaudal/dorsocaudal pale spot ratio of  $3.1$  (vs.  $7.1$ ); a shorter heart–liver interval ( $48.3\%$  vs.  $52.5\%$ ); a shorter heart–gall bladder gap ( $44.9\%$  vs.  $48.1\%$ ); a shorter right liver ( $36.4\%$  vs.  $40.0\%$ ), left liver ( $26.7\%$  vs.  $31.3\%$ ), and total liver length ( $63.1\%$  vs.  $71.3\%$ ); a shorter liver–gall bladder interval ( $38.2\%$  vs.  $41.6\%$ ); a more cranial gall bladder midpoint ( $66.3\%$  vs.  $69.7\%$ ); a longer gall bladder–kidney interval ( $23.9\%$  vs.  $21.8\%$ ); a more cranial right gonad ( $75.3\%$  vs.  $78.9\%$ ), left gonad ( $79.2\%$  vs.  $81.8\%$ ), and total gonad midpoint ( $77.2\%$  vs.  $80.4\%$ ); a lesser number of right testis ( $2.0$  vs.  $5.8$ ), left testis ( $1.5$  vs.  $4.8$ ), and total testis segments ( $1.8$  vs.  $5.3$ ); a longer gonad–kidney interval ( $16.2\%$  vs.  $14.1\%$ ); a greater kidney–vent interval/right liver ratio ( $0.51$  vs.  $0.25$ ); and a shorter heart–right lung distance ( $14.0\%$  vs.  $18.0\%$ ), trachea–liver distance ( $35.7\%$  vs.  $37.8\%$ ), trachea/bronchus–gall bladder distance ( $45.0\%$  vs.  $48.9\%$ ), heart–gonad distance ( $56.6\%$  vs.  $60.3\%$ ), trachea/bronchus–kidney distance ( $64.0\%$  vs.  $67.1\%$ ), heart–kidney distance ( $66.6\%$  vs.  $69.2\%$ ), and trachea–adrenal distance ( $66.5\%$  vs.  $71.2\%$ ).

*Epicitia martinezi* can be separated from *E. goudotii* by a subcaudal number of  $\geq 16$  (vs.  $\leq 16$ ); a parallel rostral, extending to mid-eye level (vs. triangular rostral, not reaching eye level); a moderate pale rostral spot covering entire shield (vs. indistinct, and small to absent); a pale preocular spot (vs. pale spot lacking); oblique supranasal/supraocular borders (vs. parallel); an oval eye with eye/ocular ratio of  $\geq 0.47$  (vs. round eye,  $\leq 0.46$ ); a moderate anterior supralabial, extending to mid-eye level (vs. small labial, not or just reaching lower edge of eye); lacking a

preoral groove (vs. groove present); a semilunate cloacal shield (vs. subtriangular); a subcaudal/dorsocaudal pale spot ratio of 3.1 (vs. 1.4); a subcaudal pale spot averaging  $\geq 5.5$  scales (vs.  $\leq 2.0$  scales); apical spine a spike (vs. cone); vividly striped color pattern (vs. uniformly dark); a shorter heart length ( $\leq 4.2\%$  vs.  $6.0\%$ ) and more craniad midpoint ( $\leq 19.2\%$  vs.  $19.7\%$ ); a shorter snout–heart interval ( $\leq 20.9\%$  vs.  $22.7\%$ ); a longer heart–liver gap ( $\geq 7.9\%$  vs.  $5.6\%$ ) and shorter interval ( $\leq 49.5\%$  vs.  $\geq 52.8\%$ ); a shorter heart–gall bladder gap ( $\leq 45.6\%$  vs.  $46.8\%$ ); a shorter right liver ( $\leq 36.8\%$  vs.  $41.2\%$ ), left liver ( $\leq 28.1\%$  vs.  $30.0\%$ ), and total liver length ( $\leq 64.1\%$  vs.  $71.2\%$ ); a more cranial right liver ( $\leq 47.2\%$  vs.  $48.9\%$ ) and left liver midpoint ( $\leq 47.0\%$  vs.  $48.1\%$ ); a more anterior total liver midpoint ( $47.0\%$  vs.  $48.9\%$ ); a shorter posterior liver tail ( $\leq 0.16$  vs.  $0.16$ ); a greater number of left liver ( $\geq 34$  vs.  $21$ ) and total liver segments ( $\geq 71$  vs.  $56$ ); a longer liver–gall bladder gap ( $\geq 0.4\%$  vs.  $0$ ) and shorter interval ( $\leq 38.6\%$  vs.  $43.3\%$ ); a shorter liver–kidney gap ( $\leq 16.9\%$  vs.  $17.2\%$ ) and interval ( $\leq 60.8\%$  vs.  $63.9\%$ ); a shorter gall bladder length ( $\leq 1.4\%$  vs.  $2.1\%$ ) and midpoint ( $\leq 66.7\%$  vs.  $70.6\%$ ); a shorter gall bladder–gonad gap ( $\leq 7.0\%$  vs.  $7.3\%$ ) and interval ( $\leq 16.2\%$  vs.  $19.3\%$ ); a longer gall bladder–kidney interval ( $\geq 23.2\%$  vs.  $22.7\%$ ); a longer right kidney ( $\geq 4.9\%$  vs.  $3.4\%$ ), left kidney ( $\geq 4.0\%$  vs.  $3.4\%$ ), and total kidney length ( $\geq 9.0\%$  vs.  $6.8\%$ ); a more cranial right gonad ( $\leq 76.0\%$  vs.  $81.8\%$ ), left gonad ( $\leq 79.3\%$  vs.  $86.5\%$ ), and total gonad midpoint ( $\leq 77.7\%$  vs.  $84.2\%$ ); a longer gonad–kidney gap ( $0.2\%$  vs.  $-2.1\%$ ) and interval ( $\geq 14.7\%$  vs.  $13.3\%$ ); a more craniad right adrenal ( $\leq 77.0\%$  vs.  $83.7\%$ ), left adrenal ( $\leq 78.9\%$  vs.  $88.0\%$ ), and total adrenal midpoint ( $\leq 77.9\%$  vs.  $85.9\%$ ); a longer gonad–kidney gap ( $\geq 0$  vs.  $-2.1\%$ ); a more anterior right kidney ( $\leq 84.2\%$  vs.  $88.4\%$ ), left kidney ( $\leq 87.6\%$  vs.  $90.6\%$ ), and total kidney midpoint ( $\leq 85.9\%$  vs.  $89.5\%$ ); a longer kidney–vent gap ( $\geq 10.4\%$  vs.  $7.7\%$ ) and interval ( $\geq 18.3\%$  vs.  $13.3\%$ ); a greater kidney–vent interval/right liver ratio ( $0.51$  vs.  $0.32$ ); a shorter rectal caecum length ( $\leq 1.1\%$  vs.  $1.3\%$ ); a longer rectal caecum–vent interval ( $\geq 10.4\%$  vs.  $8.6\%$ ); a shorter trachea length ( $18.7\%$  vs.  $21.0\%$ ); a shorter right lung length ( $24.2\%$  vs.  $27.9\%$ ) and more cranial midpoint ( $32.7\%$  vs.  $36.7\%$ ) and posterior tip ( $44.8\%$  vs.  $50.6\%$ ); a longer bronchus length ( $20.1\%$  vs.  $14.6\%$ ) and more craniad posterior tip ( $40.7\%$  vs.  $37.3\%$ ); a longer trachea–bronchus length ( $38.7\%$  vs.  $35.6\%$ ); a larger bronchus/right lung ratio ( $0.83$  vs.  $0.52$ ); and a shorter heart–right lung distance ( $\leq 14.4\%$  vs.  $17.0\%$ ), heart–liver distance ( $\leq 29.0\%$  vs.  $29.2\%$ ), trachea–liver distance ( $\leq 36.5\%$  vs.  $36.7\%$ ), liver–kidney distance ( $\leq 39.1\%$  vs.  $40.6\%$ ), trachea/bronchus–gall bladder distance ( $\leq 45.3\%$  vs.  $51.1\%$ ), right lung–adrenal distance ( $\leq 45.2\%$  vs.  $49.2\%$ ), heart–gonad distance ( $\leq 57.8\%$  vs.  $62.1\%$ ), trachea/bronchus–kidney distance ( $\leq 64.7\%$  vs.  $70.0\%$ ), heart–kidney distance ( $\leq 66.7\%$  vs.  $69.8\%$ ), and trachea–adrenal distance ( $\leq 67.0\%$  vs.  $73.7\%$ ).

*Epicitia martinezi* is diagnosable from *E. albifrons* by  $\geq 248$  middorsals (vs.  $\leq 218$ ) and  $\geq 16$  subcaudals (vs.  $\leq 15$ ); a mean tail length/width ratio and range of  $4.2$  and  $\geq 3.3$  (vs.  $2.7$  and  $\leq 3.6$ ); a parallel rostral, extending to mid-eye level (vs. sagittate shield, reaching to post-eye level); a relative rostral width ratio of  $\geq 0.37$  (vs.  $\leq 0.37$ ); a pale preocular spot (vs. spot absent); oblique supranasal/supraocular borders (vs. parallel); relative eye size  $\geq 0.47$  (vs.  $\leq 0.45$ ); eye not beneath supralabial (vs. partly beneath anterior supralabial); a subtriangular cloacal shield (vs. pyramidal, with truncated apex); a pale dorsocaudal spot of  $1.5$ – $3.5$  scales (vs.  $\leq 1.0$  scale); a pale subcaudal spot of  $\geq 5.5$  scales (vs.  $\leq 4$  scales); a midbody stripe formula of  $3 + 2/2 + 0$  (vs.  $7 + 0$ ); moderate to broad pale stripes (vs. narrow pale stripes); a lesser sternohyoideus/snout–heart gap ratio ( $\leq 0.83$  vs.  $\geq 0.85$ ); a shorter heart length ( $\leq 4.2\%$  vs.  $\geq 4.4\%$ ); a shorter heart–liver interval ( $48.3\%$  vs.  $51.7\%$ ); a shorter right liver ( $36.4\%$  vs.  $39.1\%$ ), left liver ( $26.7\%$  vs.  $29.6\%$ ), and total liver length ( $63.1\%$  vs.  $68.7\%$ ); a more cranial right liver midpoint ( $47.0\%$  vs.  $48.5\%$ ); a greater number of right liver ( $\geq 32$  vs.  $\leq 29$ ), left liver ( $\geq 34$  vs.  $\leq 23$ ), and total liver segments ( $\geq 71$  vs.  $\leq 52$ ); a longer anterior liver asymmetry ( $0.11$  vs.  $0.03$ ) and shorter posterior liver tail ( $\leq 0.16$  vs.  $\geq 0.17$ ); a shorter liver–gall bladder interval ( $\leq 38.6\%$  vs.  $\geq 39.1\%$ ); a shorter liver–kidney gap ( $16.0\%$  vs.  $19.8\%$ ) and interval ( $\leq 60.8\%$  vs.  $\geq 61.0\%$ ); a more anterior gall bladder midpoint ( $\leq 66.7\%$  vs.  $\geq 66.7\%$ ); a shorter gall bladder–gonad gap ( $\leq 7.0\%$  vs.  $\geq 7.9\%$ ) and interval ( $\leq 16.2\%$  vs.  $\geq 16.7\%$ ); a shorter gall bladder–kidney gap ( $\leq 15.1\%$  vs.  $\geq 15.1\%$ ) and interval ( $23.9\%$  vs.  $26.3\%$ ); a shorter gall bladder–gonad gap ( $6.2\%$  vs.  $8.9\%$ ); a more craniad right gonad ( $\leq 76.0\%$  vs.  $\geq 79.6\%$ ), left gonad ( $\leq 79.3\%$  vs.  $\geq 83.3\%$ ), and total gonad midpoint ( $\leq 77.7\%$  vs.  $\geq 81.5\%$ ); fewer left testis ( $1.5$  vs.  $5.0$ ) and total testis segments ( $1.8$  vs.  $4.0$ ); a longer gonad–kidney gap ( $0.2\%$  vs.  $-0.6\%$ ); a more cranial right adrenal ( $\leq 77.0\%$  vs.  $\geq 81.8\%$ ), left adrenal ( $\leq 78.9\%$  vs.  $\geq 83.6\%$ ), and total adrenal midpoint ( $\leq 77.9\%$  vs.  $\geq 82.7\%$ ); a more craniad right kidney ( $83.7\%$  vs.  $89.4\%$ ), left kidney ( $86.9\%$  vs.  $91.6\%$ ), and total kidney midpoint ( $85.3\%$  vs.  $90.5\%$ ); a longer kidney–vent gap ( $10.7\%$  vs.  $6.8\%$ ) and interval ( $18.8\%$  vs.  $12.2\%$ ); a larger kidney–vent interval/right liver ratio ( $0.51$  vs.  $0.25$ ); a longer rectal caecum–vent interval ( $11.2\%$  vs.  $7.4\%$ ); a smaller rectal caecum/heart length ratio ( $0.34$  vs.  $0.78$ ) and rectal caecum/left kidney ratio ( $0.23$  vs.  $0.99$ ); a shorter right lung length ( $24.2\%$



vs. 30.2%) and more cranial midpoint (32.7% vs. 36.0%) and posterior tip (44.8% vs. 51.1%); a greater bronchus/right lung ratio (0.83 vs. 0.66); and a shorter heart–right lung distance ( $\leq 14.4\%$  vs.  $\geq 16.9\%$ ), trachea/bronchus–gall bladder distance ( $\leq 45.3\%$  vs.  $\geq 46.0\%$ ), right lung–adrenal distance ( $\leq 45.2\%$  vs.  $\geq 47.2\%$ ), heart–gonad distance ( $\leq 57.8\%$  vs.  $\geq 61.0\%$ ), trachea/bronchus–kidney distance ( $\leq 64.7\%$  vs.  $\geq 66.3\%$ ), heart–kidney distance ( $\leq 66.7\%$  vs.  $\geq 68.8\%$ ), and trachea–adrenal distance ( $\leq 67.0\%$  vs.  $\geq 71.7\%$ ).

*Epictia martinezi* can be distinguished from *E. tenella* by middorsals  $\geq 248$  (vs.  $\leq 233$ ); a relative rostral width of  $\geq 0.37$  (vs.  $\leq 0.34$ ); a parallel rostral, extending to mid-eye level (vs. subtriangular shield, not reaching eye level); a moderate pale rostral spot, covering entire rostral (vs. large spot, extending onto adjacent shields); a pale preocular spot (vs. spot lacking); a pentagonal supraocular (vs. hexagonal) with a width/length ratio of 2.5 (vs. 3.0–4.0); a hexagonal ocular (vs. pentagonal); an oval eye, partly beneath supranasal (vs. round eye, entirely beneath ocular); an anterior supralabial separated from supraocular by supranasal (vs. in contact with supraocular); a semilunate cloacal shield (vs. subtriangular); an average dorsocaudal spot length of 2.4 scales (vs. 1.1 scales), subcaudal spot length of 7.5 (vs. 1.8), and subcaudal/dorsocaudal pale spot ratio of 3.1 (vs. 1.6); a midbody stripe formula of 3 + 2/2 + 0 (vs. 7 + 0); a shorter sternohyoideus length ( $\leq 14.0\%$  vs.  $\geq 14.8\%$ ); a smaller sternohyoideus/snout–heart gap ratio ( $\leq 0.83$  vs.  $\geq 0.87$ ); a shorter heart length ( $\leq 4.2\%$  vs.  $\geq 4.9\%$ ); a more cranial heart midpoint ( $\leq 19.2\%$  vs.  $\geq 19.4\%$ ); a shorter snout–heart interval ( $\leq 20.9\%$  vs.  $\geq 21.9\%$ ); a longer heart–liver gap (12.2% vs. 9.9%); a more anterior right liver ( $\leq 47.2\%$  vs.  $\geq 47.2\%$ ) and left liver midpoint ( $\leq 47.0\%$  vs.  $\geq 47.9\%$ ); a longer posterior liver tail ( $\geq 0.15$  vs.  $\leq 0.08$ ); a lesser left liver/right liver ratio ( $\leq 0.78$  vs.  $\geq 0.79$ ); a longer liver–kidney interval (60.6% vs. 57.0%); a longer gall bladder–kidney interval (23.9% vs. 20.5%); fewer left testis (1.5 vs. 3.0) and total testis segments (1.8 vs. 3.0); a more cranial right adrenal ( $\leq 77.0\%$  vs.  $\geq 79.7\%$ ), left adrenal ( $\leq 78.9\%$  vs.  $\geq 81.0\%$ ), and total adrenal midpoint ( $\leq 77.9\%$  vs.  $\geq 80.4\%$ ); a longer gonad–kidney gap ( $\geq 0$  vs.  $\leq 0$ ) and interval (16.2% vs. 13.0%); a longer right kidney ( $\geq 4.9\%$  vs.  $\leq 4.0\%$ ) and total kidney length ( $\geq 9.0\%$  vs.  $\leq 8.4\%$ ); a greater kidney overlap ratio ( $\geq 0.14$  vs.  $\leq 0.14$ ); a shorter rectal caecum length ( $\leq 1.1\%$  vs.  $\geq 1.7\%$ ); a smaller rectal caecum/heart length ratio (0.34 vs. 0.55); a lesser rectal caecum/left kidney ratio ( $\leq 0.28$  vs.  $\geq 0.41$ ); a shorter trachea length ( $\leq 19.3\%$  vs.  $\geq 20.8\%$ ); a shorter right lung length ( $\leq 24.6\%$  vs.  $\geq 24.8\%$ ) and more cranial midpoint ( $\leq 32.7\%$  vs.  $\geq 36.2\%$ ) and posterior tip ( $\leq 44.9\%$  vs.  $\geq 49.1\%$ ); a larger bronchus/right lung ratio ( $\geq 0.79$  vs.  $\leq 0.71$ ); and a shorter heart–right lung distance ( $\leq 14.4\%$  vs.  $\geq 15.2\%$ ) and trachea–adrenal distance ( $\leq 67.0\%$  vs.  $\geq 67.7\%$ ).

**Remarks:** *Epictia martinezi* represents the new species that was revealed by the molecular phylogeny of McCranie and Hedges (2016), referred to as *E. phenops-1* and *E. phenops-2* (based on mitochondrial genes from FMNH 283737 and 283735, respectively, described above) in their fig. 2.

### *Epictia pauldwyeri* sp. nov.

Figs. 7A–AA, 15O, 16T

*Stenostoma albifrons*—Cope, 1875: 44; 1887: 63.

*Leptotyphlops goudotii*—Swanson, 1945: 213 (part); Dunn, 1949: 47–48, 55 (part); Auth, 1994: 19; Hedges, 1996: 111, 115 (part); Pérez-Santos, 1999: 295 (part); Young et al., 1999: 37; UICN, 1999: 128; Ibáñez et al., 2001: 170; González-Muñoz, 2008: 2; Köhler, 2008: 183–184, map (part); Jaramillo et al., 2010: 623, 637.

*Leptotyphlops goudoti*—H. Smith, 1958: 223; Pérez-Santos et al., 1993: 115 (part).

*Leptotyphlops goudotii goudotii*—Orejas-Miranda In J. Peters et al., 1970 and 1986: 169 (part); Pérez-Santos, 1999: 296, map 44 (part).

*Leptotyphlops goudottii goudottii* (sic)—Pérez-Santos et al., 1993: 115 (part); Pérez-Santos, 1999: 295–296 (part).

*Leptotyphlops goudotti* (sic)—Neal, 2007: 106.

*Epictia goudotii*—Johnson et al., 2015: 92; Ray and Ruback, 2015: 171, fig. 4; McCranie and Hedges, 2016: 13–14, fig. 4.

**Holotype:** FMNH 130672, a 112 mm (LOA) female collected by N. Gale on 20 March 1961, at Curundú, Ciudad de Panama, Canal Zone, Provincia de Panamá, Panama, ca. 8°59'08"N, 79°32'26"W, elev. 35 m asl.

**Paratypes** (10): PANAMA: CANAL ZONE: Ancon, 500 m, collected by Charles W. Myers in 1959, KU 116897 (field no. CWM 9181); Curundú, collected by Charles W. Myers in April 1966, KU 116896 (field no. CWM 6438); Gamboa, collected by N. Gale on 16 February 1961, MVZ 78739; PANAMÁ: Panama city, collected 1977, UMMZ 167679; Tocúmen, collected by Charles W. Myers in April 1968, KU 125032 (field no. CWM 9395); Paso

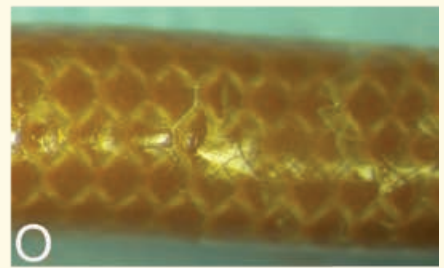
Blanco, between Pacora and Chepo, collected by Paul L. Swanson between August, 1942, and July, 1944, ANSP 25086; PANAMÁ OESTE: Bahía Serena, collected by Roberto Ibáñez on 21 Feb. 2002, CHP H-5379; Nueva Gorgona, collected by Charles W. Myers on 26 May 1963, KU 116898 (field no. CWM 7051); probably Panama, collected by Charles B. Adams on 23 August 1920, USNM 63110–11.

**Etymology:** This species is named in honor of Paul Dwyer, Mailroom Specialist, Museum of Comparative Zoology, Harvard University (MCZ), and commemorates his 42 years of service to the museum. Without Paul's daily endeavors in receiving, sorting, and delivering mail, posting letters and packages, sending and receiving loans, and mailing out *Breviora* and the *Bulletins*, research and education in the MCZ would come to a standstill.

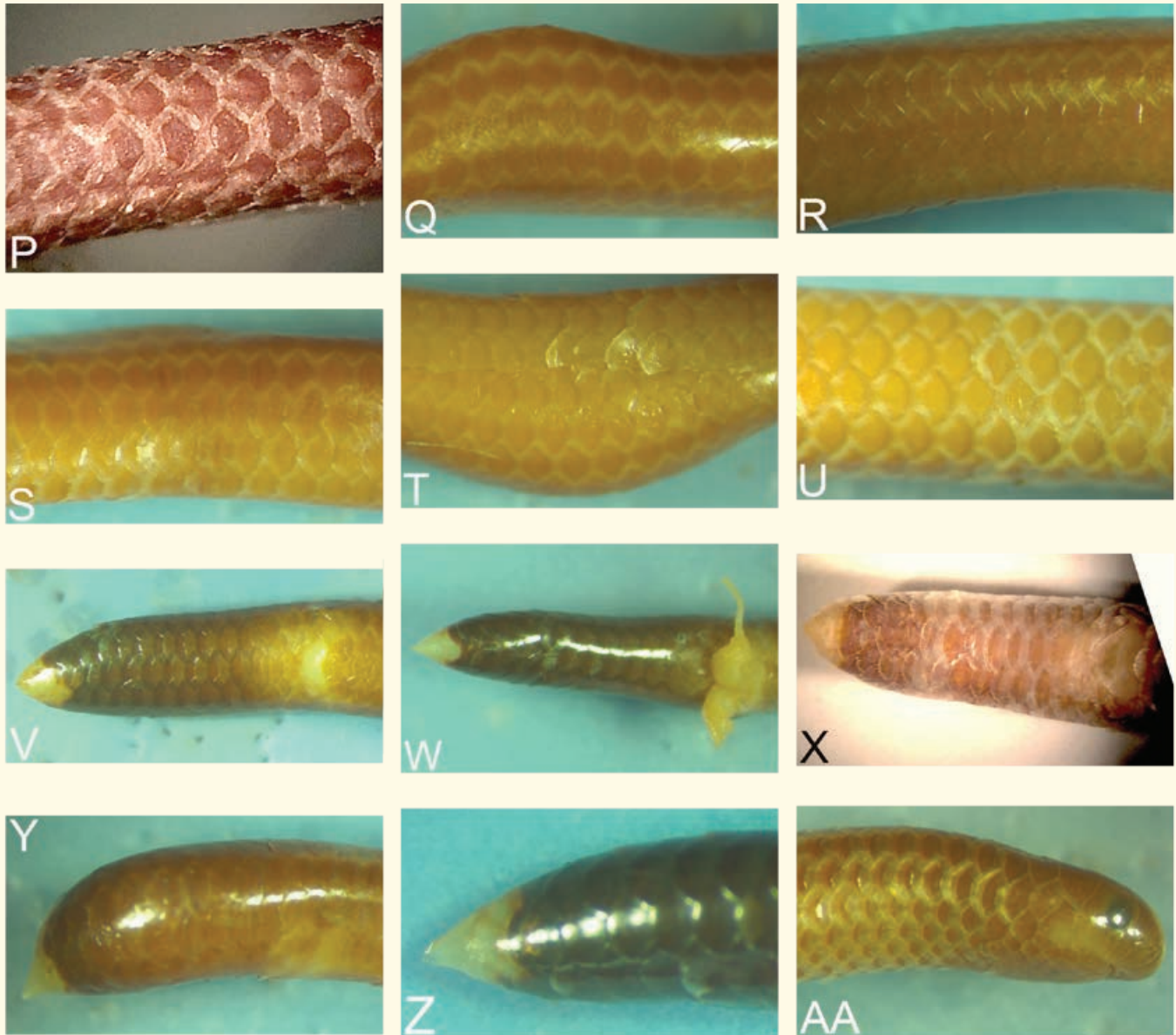
**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 67–129 ( $\bar{x}$  = 105.2) mm; (4) total middorsals = 202–226 ( $\bar{x}$  = 211.8); (5) subcaudals = 10–14 ( $\bar{x}$  = 12.7); (6) relative body proportion = 43–49 ( $\bar{x}$  = 45.7); (7) relative tail length = 3.6%–6.1% ( $\bar{x}$  = 4.8%); (8) relative tail width = 1.8–3.1 ( $\bar{x}$  = 2.5); (9) relative rostral width = 0.42–0.53 ( $\bar{x}$  = 0.47); (10) relative eye size = 0.39–0.48 ( $\bar{x}$  = 0.43); (10) rostral subtriangular with rounded apex extending to mid-eye level; (11) supralabials 2, short to moderate anterior supralabial reaching or nearly reaching mid-eye level; (12) frontal hexagonal, 1½ times broader than deep; (13) supraoculars large and rectangular with posterior borders parallel to posterior borders of supranasal, 1½ times as wide as long; (14) widest anteriormost vertebral scale 5<sup>th</sup>; (15) parietals deeper than occipitals, oriented transversely; (16) infralabials 4; (17) cloacal shield subtriangular in shape; (18) head brown, with a yellow spot covering the entire rostral; (19) dorsum with 7 brown stripes formed from diamond-shaped spots bordered by narrow zigzag yellow lines (= 7 dark stripes); (20) venter uniform pale brown, scales often outlined in yellow; (21) midbody stripe formula (7 + 0) and middorsal pattern (3); (22) tail with a larger pale terminal spot dorsally, covering 2–3.5 ( $\bar{x}$  = 2.3) dorsocaudals, than ventrally, covering 1–2.5 ( $\bar{x}$  = 1.8) subcaudals (ventral/dorsal ratio 0.8); and (23) apical spine a horizontally-compressed spike.

**Description:** Holotype data include scale row formula = 14-14-14; midtail scale rows = 10; TMD = 226; SC = 10; LOA = 112.0 mm; TL = 4.0 mm; MBD = 2.6 mm; MTD = 2.25 mm; RW = 0.8 mm; HW = 1.75 mm; L/W = 43.1; TL/LOA = 3.6; TL/TW = 1.8; RW/HW = 0.46; and ED/OH = 0.41. Head not distinguishable from neck (Fig. 7F), dorsal profile rounded, all head shields with prominent sensory pits that appear as depressions in the scales; rostral sagittate, subtriangular in shape with truncated apex (Fig. 7G), extending to anterior level of eye to mid-eye level; frontal hexagonal in shape, 1½ times as wide as deep; postfrontal larger than frontal, as wide as long; interparietal and interoccipital usually as broad as deep; broadest anteriormost vertebral scale 5<sup>th</sup>; supraoculars large and pentagonal, 1½ times as wide as long, posterior borders parallel to those of supranasals (Fig. 7G); parietals and occipitals subequal in length, parietal slightly longer than occipital, both shields transverse in orientation; lateral head profile with depressed and acuminate snout; nasal completely divided, suture forming a deep V-shaped angle along anterior supralabial and infranasal, nostril large and oval, positioned nearer the rostral than supralabial and entirely below the suture in the infranasal (Fig. 7L); infranasal twice as broad and twice the size of anterior supralabial, narrowing toward lip; supralabials 2, anterior supralabial moderate in height with nearly parallel sides, extending beyond lower level of orbit, its labial border usually 1½ times as long as that of infranasal; ocular large, twice as tall as broad, roughly pentagonal with a nearly straight anterior border; eye moderate with a distinct pupil and iris, slightly oval or elliptical in vertical plane, its height less than the lip-orbit gap (ED/OH = 0.39–0.48,  $\bar{x}$  = 0.43), not visible in dorsal view; posterior supralabial taller than long, taller than anterior supralabial, with rounded posterior apex; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 4, first three infralabials short and last one elongated; costal scales rounded and imbricate in 14 rows throughout; cloacal shield subtriangular (Fig. 7X); and tail terminating in a horizontally-compressed cone with a moderate spike (Fig. 7Z).

Overall coloration in life chocolate brown with pale stripes, a moderate yellow spot on the rostral, and a small caudal spot of equal size above and below. Midbody pattern of preserved specimens consists of 7 brown to dark brown stripes, formed by contiguous diamond-shaped spots, each bordered by a narrow pale zigzag stripe (Fig. 7Q, S; midbody stripe formula of 7 + 0); ventral 7 scale rows uniform pale brown, sometimes with light-bordered scales (middorsal pattern of 3 stripes). Head brown, with a pale bar on posterior upper lip (Fig. 7K, N). Cloacal shield yellow with a yellow cloacal ring; tail uniform brown with a small nearly symmetrical yellow tail tip, dorsal spot covering 2–3.5 dorsocaudals ( $\bar{x}$  = 2.3 scales), ventral spot covering 1–2.5 subcaudals ( $\bar{x}$  = 1.8 scales), and ventral/dorsal ratio 0.8 (Fig. 7Z).







**Fig. 7.** Morphological variation in *Epictia pauldwyeri* sp. nov. (A, B) dorsal and ventral views of holotype of *E. pauldwyeri* (FMNH 130672); (C, D) paratype of *E. pauldwyeri* (UMMZ 167679, ANSP 25086); (E, F, G, H) dorsal head (ANSP 25086, FMNH 130672, MVZ 78739, KU 125032); (I, J, K, L) lateral head (ANSP 25086, MVZ 78739, KU 125032, FMNH 130672); (M, N) ventral head (FMNH 130672, KU 125032); (O, P, Q) dorsal midbody (KU 116898, ANSP 25086, FMNH 130672); (R, S) lateral midbody (KU 116897, FMNH 130672); (T, U) ventral midbody (FMNH 130672, KU 116898); (V, W, X) ventral tail (KU 116896, KU 125032, ANSP 25086); (Y, Z) lateral apical spine (FMNH 130672, KU 125032); and (AA) lateral neck (KU 116897).

© Rachel Grill (A, B), Greg Schneider (C), Ned Gilmore (D, E, I, O, X), and remaining photos by Van Wallach

The hemipenis of KU 125032, from Tocúmen, Panama (Fig. 15O), is single with a simple sulcus spermaticus bordered by thick lips and a total length of 2.5 mm. The proximal 1.1 mm is a bulbous sphere 0.8 mm wide with about a dozen scattered papillae; otherwise the organ entirely nude. A pair of constrictions set off a small medial bulge 0.2 mm in length, followed by an attenuated distal arm 1.3 mm long and 0.15 mm in diameter throughout its entire length. With the exception of a larger bulbous base, organ similar in appearance to that of the African species *Leptotyphlops nigricans* and *L. scutifrons* (Branch, 1986).

**Viscera:** (mean value followed parenthetically by range,  $n = 3$ ). Posterior tip of sternohyoideus muscle = 14.7% (12.0–16.4%); sternohyoideus/snout–heart gap = 0.87 (0.76–0.97); heart length = 5.2% (5.1–5.4%) with midpoint at = 19.4% (18.3–20.5%); snout–heart interval = 22.0% (20.8–23.3%); heart–liver gap = 7.7% (7.4–8.4%) and interval = 49.0% (47.0–52.8%); heart–gall bladder gap = 42.9% (39.1–48.1%); liver lobes multipartite; right liver length = 36.0% (33.6–40.3%) with midpoint at 47.8% (47.2–48.4%) and 31.7 (26–41) segments; left liver length = 29.8% (26.2–35.6%) with midpoint at 47.9% (47.2–48.5%) and 25.3 (21–34) segments; anterior liver extension = 0.09 (0.05–0.12) and posterior liver tail = 0.08 (0.07–0.11); left liver/right liver = 0.82 (0.78–0.88); liver–gall bladder gap = –0.8% (–2.5 to 0.5%) and interval 36.9% (33.7–42.1%); liver–kidney gap = 14.2% (12.4–16.2%) and interval = 56.9% (53.5–62.0%); gall bladder length = 1.8% (1.4–2.0%) with midpoint at 65.9% (63.4–69.7%); gall bladder–gonad gap = 6.6% (2.8–9.7%) and interval = 15.5% (14.5–16.8%); gall bladder–kidney gap = 13.3% (12.6–14.4%) and interval = 21.7% (21.3–22.0%); right gonad length = 4.3% (3.2–5.1%) with midpoint at 75.5% (70.8–81.7%); left gonad length = 4.4% (3.7–5.6%) with midpoint at 78.3% (75.2–82.4%); gonad–kidney gap = –0.5% (–2.0 to 0.5%) and interval = 13.3% (10.2–17.3%); right adrenal midpoint = 78.6% (76.2–82.9%) and left adrenal midpoint = 81.3% (79.8–83.8%); right kidney length = 3.6% (3.5–3.7%) with midpoint at 81.8% (79.0–86.6%); left kidney length = 3.8% (3.0–4.2%) with midpoint at 84.8% (82.7–88.2%); kidney overlap = 0.14 (–0.07 to 0.42); kidney–vent gap = 13.3% (9.7–15.8%) and kidney–vent interval = 20.0% (15.3–22.8%); rectal caecum length = 1.6% (1.0–1.9%); and caecum–vent interval = 13.5% (11.1–15.8%). One developing egg plus 4 follicles present in right ovary, and 2 developing eggs and 3 follicles in left ovary of female holotype (SVL 108 mm). This suggests an assumed clutch size of three eggs. Four testis segments present in each of the right and left gonads of the two males examined.

Respiratory system lacking tracheal lung and left lung complex; trachea = 20.8% (19.4–22.3%) with midpoint at 11.6% (11.1–12.1%), with an estimated 159 (147–176) tracheal rings or 76.0 (74.1–78.5) rings/10% SVL; anterior lung tip = 19.5% (17.6–21.3%); tracheal entry terminal; cardiac lung = 2.5% (2.0–3.2%); right lung = 31.6% (29.2–33.3%) with midpoint at 37.8% (37.5–38.1%), with faveolar cranial half and trabecular caudal half; posterior tip = 53.6% (52.5–54.2%); right bronchus length = 21.9% (20.8–22.8%) with posterior tip at 43.9% (41.7–46.0%); bronchus/right lung length = 0.70 (0.63–0.78); trachea–bronchus length = 42.6% (40.3–45.0%) with midpoint at 22.5% (21.5–23.5%); trachea–bronchus/total lung length = 0.80 (0.74–0.86); and total lung length = 34.1% (31.2–36.6%) with midpoint at 36.6% (35.9–36.9%).

Visceral distance data include heart–right lung distance = 18.4% (17.4–19.2%); heart–liver distance = 28.4% (27.3–30.1%); liver–kidney distance = 35.5% (33.1–39.0%); trachea–liver distance = 36.2% (35.6–37.3%); right lung–adrenal distance = 42.1% (40.2–45.8%); trachea/bronchus–gall bladder distance = 43.3% (39.9–48.2%); heart–gonad distance = 56.1% (51.4–63.4%); trachea/bronchus–kidney distance = 60.8% (57.4–65.9%); heart–kidney distance = 63.9% (60.4–69.1%); and trachea–adrenal distance = 68.4% (66.1–72.2%).

**Distribution:** *Epictia pauldwyeri* is a Panamanian endemic that inhabits the Pacific coast of central Panama (Colon, Panamá, and Panamá Oeste), overall elev. NSL–250 m (Map 7).

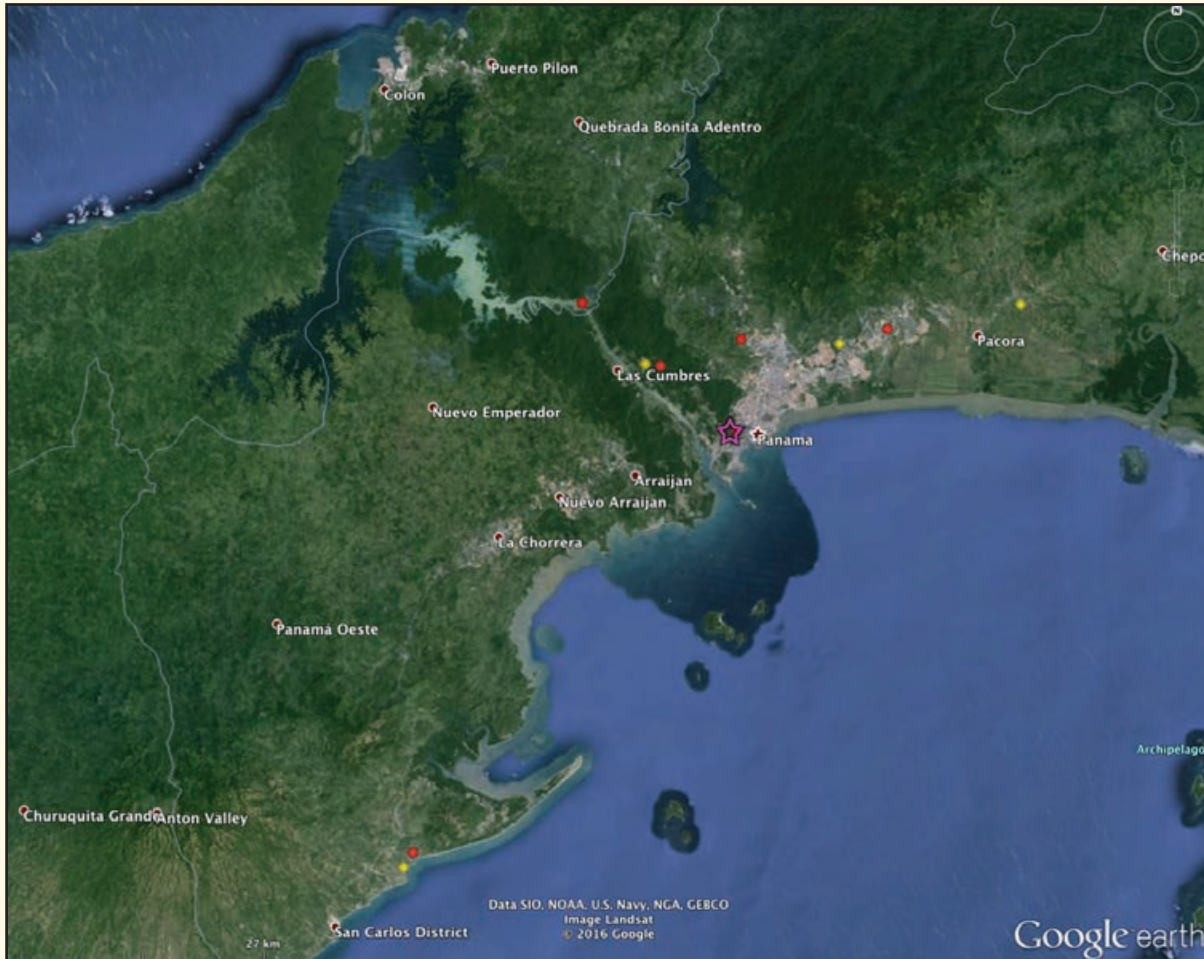
**Ecology:** This species occurs in wet tropical lowland rainforest in Panama (Jaramillo et al., 2010).

**Comparisons:** *Epictia pauldwyeri* can be distinguished from *E. ater* by a mean middorsal count of 211.8 (vs. 237.3); a mean subcaudal count of 12.7 (vs. 18.4); a subtriangular rostral with a rounded apex extending to mid-eye level (vs. waisted rostral with arrowhead apex extending beyond level of eyes); a distinct yellow spot covering the entire rostral (vs. an indistinct spot located at most in the central rostral region); a discrete frontal shield (vs. frontal fused with rostral); an eye partly beneath supranasal shield (vs. partly beneath supranasal and anterior supralabial); a dorsal/caudal tail spot ratio nearly equal at 0.8 (vs. 11.7); a midbody dorsal pattern with narrow, zigzag, pale-bordered, dark, diamond-shaped spots (vs. uniformly dark midbody dorsal pattern); a yellow cloacal shield (vs. brown shield); a longer heart length ( $\geq 5.1\%$  vs.  $\leq 5.1\%$ ); a shorter anterior liver asymmetry ( $\leq 0.12$  vs.  $\geq 0.12$ ); a smaller posterior liver tail/liver length ratio ( $\leq 0.11$  vs.  $\geq 0.11$ ); a larger left liver/right liver ratio ( $\geq 0.78$  vs.  $\leq 0.76$ ); and a shorter gonad–kidney interval (13.2% vs. 15.2%).

*Epictia pauldwyeri* is diagnosable from *E. bakewelli* by a middorsal count  $\leq 226$  (vs.  $\geq 245$ ), and a middorsal mean of 211.8 (vs. 253.3); a subcaudal range  $\leq 14$  (vs.  $\geq 16$ ) and mean of 12.7 (vs. 19.2); a subtriangular rostral with a rounded apex extending to mid-eye level (vs. waisted rostral with oval apex extending beyond level of eyes); a subtriangular cloacal shield (vs. semilunar); a discrete frontal shield (vs. frontal fused with rostral); a lower



subcaudal/dorsocaudal pale spot ratio of 0.8 (vs. 3.1); a pale, shorter, subcaudal spot of 1.8 scales (vs. 8.9 scales); midbody dorsal pattern with 7 narrow, zigzag, pale-bordered dark stripes formed from diamond-shaped spots (vs. 3 straight stripes composed of dark spots with moderate to broad pale straight borders and a broad midlateral dark stripe covering 2 scale rows); a longer heart ( $\geq 5.1\%$  vs.  $\leq 4.0\%$ ); a larger left liver/right liver ratio ( $\geq 0.78$  vs.  $\leq 0.78$ ); a shorter gall bladder–gonad interval (15.5% vs. 18.3%); a longer right kidney ( $\geq 3.7\%$  vs.  $\leq 3.5\%$ ); a more posterior trachea midpoint ( $\geq 11.1\%$  vs.  $\leq 11.1\%$ ); and fewer tracheal rings/10% SVL ( $\leq 78.5$  vs.  $\geq 81.0$ ).



**Map. 7.** Distribution of *Epictia pauldwyeri* nov. sp. in central Panama.

*Epictia pauldwyeri* can be differentiated from *E. columbi* by  $\leq 226$  midorsals (vs.  $\geq 240$ ) and  $\leq 14$  subcaudals (vs.  $\geq 22$ ); a tail length  $\leq 7$  mm (vs.  $\geq 9$  mm); a length/width ratio of  $\leq 49$  (vs.  $\geq 49$ ); a tail length/tail width ratio of  $\leq 3.1$  (vs.  $\geq 4.3$ ); a subtriangular rostral with a rounded apex (vs. sagittate with truncated apex); a pale rostral spot present (vs. absent); a large oval eye, partially beneath supranasal (vs. moderate round eye, entirely beneath ocular); lacking a preoral groove (vs. groove present); a subtriangular cloacal shield (vs. semilunate); pale dorsocaudal and subcaudal spots present (vs. absent); a striped dorsal pattern (vs. uniform); a yellow cloacal shield (vs. brown shield); a longer sternohyoideus (14.7% vs. 11.7%); a longer sternohyoideus/snout–heart gap (0.87 vs. 0.75); a more caudal heart midpoint (19.4% vs. 17.8%); a longer snout–heart interval (22.0% vs. 19.9%); a shorter heart–liver gap (7.7% vs. 9.0%) and heart–liver interval (10.9% vs. 15.2%); a longer right liver (36.0% vs. 34.4%) and left liver (29.8% vs. 24.6%) lobe; a more caudad right liver midpoint (47.8% vs. 46.1%); fewer right liver (31.7 vs. 35.0) and left liver (25.3 vs. 28.0) segments; a larger left liver/right liver ratio (0.82 vs. 0.72); a shorter anterior liver extension (0.09 vs. 0.18), a shorter liver–kidney gap (14.2% vs. 20.3%) and liver–kidney interval (56.9% vs. 62.5%); a shorter gall bladder–kidney gap (13.3% vs. 18.8%) and interval (21.7% vs. 27.7%); a shorter gall bladder–gonad gap (6.6%



vs. 13.3%) and interval (15.5% vs. 18.4%); longer right gonads (4.3% vs. 2.3%) and left gonads (4.4% vs. 0.8%); a more cranial right gonad (75.5% vs. 79.3%) and left gonad midpoint (78.3% vs. 81.6%); a more cranial right adrenal midpoint (78.6% vs. 80.7%); longer kidney overlap (0.14 vs. none); a more anterior right kidney (81.8% vs. 79.3%) and left kidney midpoint (84.8% vs. 89.5%); a shorter kidney–vent gap (13.3% vs. 16.4%), but longer kidney–vent interval (20.0% vs. 16.4%); a longer rectal caecum–vent interval (13.5% vs. 9.8%); fewer total tracheal rings (159 vs. 192) and rings/10% SVL (76.0 vs. 102.4); a longer right lung (31.6% vs. 26.6%) and bronchus (21.9% vs. 19.5%); a more caudal right lung (37.8% vs. 33.2%) and trachea-bronchus midpoint (22.5% vs. 20.3%); a more posterior lung tip (53.6% vs. 46.5%) and posterior bronchus tip (43.9% vs. 39.5%); a smaller caecum/heart ratio (0.19 vs. 0.48); a longer heart–lung distance (18.4% vs. 15.4%); a shorter liver–kidney distance (35.5% vs. 41.4%), lung–adrenal distance (42.1% vs. 48.0%), heart–gonad distance (56.1% vs. 61.5%), trachea/bronchus–kidney distance (60.8% vs. 67.2%), and heart–kidney distance (63.9% vs. 69.7%).

*Epictia pauldwyeri* can be separated from *E. magnamaculata* by a maximum length of 129 mm (vs. 220 mm); a mean middorsal count of 211.8 (vs. 238.7) and subcaudal count of 12.7 (vs. 17.3); a subtriangular rostral with a rounded apex extending to mid-eye level (vs. sagittate rostral with oval apex extending to anterior level of eyes); a distinct yellow spot covering the entire rostral (vs. an enlarged spot that extends beyond rostral border to edges of adjacent scales); frontal wider than long (vs. as long as wide); eye partly beneath supranasal shield (vs. partly beneath supranasal and anterior supralabial); tail terminating in a broad compressed blade (vs. apical spine); a midbody dorsal pattern with 7 dark stripes of diamond-shaped spots with pale, narrow, zigzag borders (vs. 11 dark stripes made of linear-shaped spots with pale, broad, straight borders); a yellow cloacal shield (vs. brown shield); and a shorter liver–gall bladder gap ( $\leq 0.5\%$  vs.  $\geq 0.6\%$ ).

*Epictia pauldwyeri* is identifiable from *E. martinezi* by  $\leq 226$  middorsals (vs.  $\geq 248$ ) and  $\leq 14$  subcaudals (vs.  $\geq 16$ ); a mean relative tail length of 4.8% (vs. 7.4%); a length/width tail ratio of  $\leq 3.1$  (vs.  $\geq 3.3$ ); a subtriangular rostral shape (vs. parallel); lacking a pale preocular spot (vs. present); a supraocular width/length ratio of 1.5 (vs. 2.5); parallel supranasal/supraocular borders (vs. oblique); a subtriangular cloacal shield (vs. semilunate); a subcaudal/dorsocaudal spot ratio of 0.8 (vs. 3.1); a mean subcaudal spot of  $\leq 2.5$  scales (vs.  $\geq 5.5$  scales); a 7 + 0 midbody stripe formula (vs. 3 + 2/2 + 0); a narrow pale stripe width (vs. moderate to broad); a yellow cloacal shield (vs. brown shield); a longer heart length ( $> 5.1\%$  vs.  $\leq 4.2\%$ ); a longer snout–heart interval (22.0% vs. 20.7%); a shorter heart–gall bladder gap (42.9% vs. 44.9%); a longer left liver length (29.8% vs. 26.7%) and total liver length (65.9% vs. 63.1%); a more posterior right liver midpoint ( $\geq 47.2\%$  vs.  $\leq 47.2\%$ ) and left liver midpoint ( $\geq 47.2\%$  vs.  $\leq 47.0\%$ ); fewer left liver segments ( $\leq 34$  vs.  $\geq 34$ ); a shorter posterior liver tail ( $\leq 0.11$  vs.  $\geq 0.15$ ); a larger left liver/right liver ratio ( $\geq 0.78$  vs.  $\leq 0.78$ ); a shorter liver–kidney interval (56.9% vs. 60.6%); a longer gall bladder length ( $\geq 1.4\%$  vs.  $\leq 1.4\%$ ); a shorter gall bladder–kidney interval ( $\leq 22.0\%$  vs.  $\geq 23.2\%$ ); a greater number of right testis (4.0 vs. 2.0), left testis (4.0 vs. 1.5), and total testis segments (4.0 vs. 1.8); a shorter gonad–kidney interval (13.3% vs. 16.2%); a shorter right kidney length ( $\leq 3.7\%$  vs.  $\geq 4.9\%$ ) and total kidney length ( $\leq 7.9\%$  vs.  $\geq 9.0\%$ ); a more cranial left kidney midpoint (84.8% vs. 86.9%); a more caudal left adrenal midpoint ( $\geq 79.8\%$  vs.  $\leq 78.9\%$ ); a longer kidney–vent gap (13.3% vs. 10.7%); a longer rectal caecum–vent interval (13.5% vs. 11.2%); a greater rectal caecum/left kidney ratio ( $\geq 0.33$  vs.  $\leq 0.28$ ); a longer trachea length ( $\geq 19.4\%$  vs.  $\leq 19.3\%$ ); a longer right lung length ( $\geq 29.2\%$  vs.  $\leq 24.3\%$ ) and more caudal midpoint ( $\geq 37.5\%$  vs.  $\leq 32.7\%$ ) and posterior tip ( $\geq 52.5\%$  vs.  $\leq 44.9\%$ ); a longer trachea-bronchus length (42.6% vs. 38.7%); a more caudal bronchus posterior tip ( $\geq 41.7\%$  vs.  $\leq 41.7\%$ ); a lesser bronchus/right lung ratio ( $\leq 0.78$  vs.  $\geq 0.79$ ); a more posterior trachea-bronchus midpoint ( $\geq 21.5\%$  vs.  $\leq 21.4\%$ ); and a longer heart–right lung distance ( $\geq 17.4\%$  vs.  $\leq 14.4\%$ ).

*Epictia pauldwyeri* can be differentiated from *E. phenops* by a mean middorsal count of 211.8 (vs. 243.5); a mean subcaudal count of 12.7 (vs. 16.3); a subtriangular rostral with a rounded apex (vs. sagittate rostral with oval apex); a distinct yellow spot covering the entire rostral (vs. an indistinct spot located at most in the central rostral region); frontal broader than deep (vs. as long as wide); supraoculars  $1\frac{1}{2}$  times as broad as deep (vs. twice as wide as long); posterior supranasal and supraocular borders parallel (vs. oblique); eye partly beneath supranasal shield (vs. entirely beneath ocular shield); a subtriangular cloacal shield (vs. semilunar); a dorsal spot larger than the caudal spot with a dorsal/caudal tail spot ratio of 0.8 (vs. 7.1); a midbody dorsal pattern with 7 dark stripes formed by diamond-shaped spots (vs. 3 stripes of triangular-shaped spots plus a midlateral dark stripe 2 rows wide); a yellow cloacal shield (vs. brown shield); and 4 testis segments (vs. 5 or 6).

*Epictia pauldwyeri* is recognizable from *E. goudotii* by a mean middorsal count of 211.8 (vs. 242.6) and mid-dorsal range  $\leq 226$  (vs.  $\geq 227$ ); a subtriangular rostral with a rounded apex extending to mid-eye level (vs. triangular rostral with rounded apex extending to anterior level of eyes); a rounded snout in dorsal and ventral profile (vs. obtuse profile); a distinct yellow spot covering entire rostral (vs. a small diffuse or absent spot); supraoculars 1½ times as broad as deep (vs. twice as wide as long); an oval eye (vs. round); lack of a preoral groove in ventral rostral (vs. distinct preoral groove); a yellow cloacal shield (vs. brown shield); a spine-like caudal termination (vs. compressed cone); a shorter heart ( $\leq 5.4\%$  vs.  $6.0\%$ ); a longer heart–liver gap ( $\geq 7.4\%$  vs.  $5.6\%$ ); a shorter right liver ( $\leq 40.3\%$  vs.  $41.2\%$ ); a more anterior right liver midpoint ( $\leq 48.4\%$  vs.  $48.9\%$ ); a smaller posterior liver tail/liver length ratio ( $\leq 0.11$  vs.  $0.16$ ); a larger left liver/right liver ratio ( $\geq 0.78$  vs.  $0.73$ ); a greater number of left liver segments ( $\geq 26$  vs.  $21$ ); a shorter liver–gall bladder interval ( $\leq 42.1\%$  vs.  $43.3\%$ ); a shorter liver–kidney gap ( $\leq 16.2\%$  vs.  $17.2\%$ ); a shorter liver–kidney interval ( $\leq 62.0\%$  vs.  $63.9\%$ ); a shorter gall bladder ( $\leq 1.4\%$  vs.  $2.1\%$ ); a more anterior gall bladder midpoint ( $\leq 69.7\%$  vs.  $70.6\%$ ); a shorter gall bladder–gonad interval ( $\leq 16.8\%$  vs.  $19.3\%$ ); a shorter gall bladder–kidney gap ( $\leq 14.4\%$  vs.  $15.0\%$ ) and gall bladder–kidney interval ( $\leq 22.0\%$  vs.  $22.7\%$ ); a more cranial right gonad midpoint ( $\leq 81.7\%$  vs.  $81.8\%$ ) and left gonad midpoint ( $\leq 82.4\%$  vs.  $86.5\%$ ); a higher number of testis segments ( $4$  vs.  $2$ ); a more anterior right adrenal midpoint ( $\leq 82.9\%$  vs.  $83.7\%$ ) and left adrenal midpoint ( $\leq 83.8\%$  vs.  $88.0\%$ ); a longer right kidney ( $\geq 3.7\%$  vs.  $3.4\%$ ); a more cranial right kidney midpoint ( $\leq 86.6\%$  vs.  $88.4\%$ ) and left kidney midpoint ( $\leq 88.2\%$  vs.  $90.6\%$ ); a longer kidney–vent gap ( $\geq 9.7\%$  vs.  $\leq 7.7\%$ ) and kidney–vent interval ( $\geq 15.3\%$  vs.  $13.3\%$ ); a longer gonad–kidney gap ( $\geq -2.0\%$  vs.  $-2.1\%$ ); a longer rectal caecum–vent interval ( $\geq 11.1\%$  vs.  $8.6\%$ ); a more anterior trachea midpoint ( $< 12.1\%$  vs.  $12.2\%$ ); fewer tracheal rings ( $\leq 176$  vs.  $176$ ) and fewer tracheal rings/10% SVL ( $\leq 78.5$  vs.  $85.4$ ); a longer right lung ( $\geq 29.2\%$  vs.  $27.9\%$ ); a more caudal right lung midpoint ( $\geq 37.5\%$  vs.  $36.7\%$ ); a longer intrapulmonary bronchus ( $\geq 20.8\%$  vs.  $14.6\%$ ); a more caudal bronchus posterior tip ( $\geq 41.7\%$  vs.  $37.3\%$ ); a larger bronchus/lung ratio ( $\geq 0.63$  vs.  $\leq 0.52$ ); a longer trachea-bronchus ( $\geq 40.3\%$  vs.  $35.6\%$ ); a more posterior trachea-bronchus midpoint ( $\geq 21.5\%$  vs.  $19.5\%$ ); a more caudal lung posterior tip ( $\geq 52.5\%$  vs.  $50.6\%$ ); a longer total lung ( $\geq 31.2\%$  vs.  $30.5\%$ ); a more posterior total lung midpoint ( $\geq 35.9\%$  vs.  $35.4\%$ ); a shorter trachea–adrenal distance ( $\leq 72.2\%$  vs.  $\geq 73.7\%$ ), liver–kidney distance ( $\leq 39.0\%$  vs.  $\geq 40.6\%$ ), trachea–kidney distance ( $\leq 65.9\%$  vs.  $70.0\%$ ), right lung–adrenal distance ( $\leq 45.8\%$  vs.  $49.2\%$ ), heart–kidney distance ( $\leq 69.1\%$  vs.  $69.8\%$ ), and trachea/bronchus–gall bladder distance ( $\leq 48.2\%$  vs.  $51.1\%$ ); and a longer heart–lung distance ( $\geq 17.4\%$  vs.  $17.0\%$ ).

*Epictia pauldwyeri* can be distinguished from *E. albifrons* by a relative rostral width of  $\geq 0.42$  (vs.  $\leq 0.37$ ); a subtriangular rostral with a rounded apex extending to mid-eye level (vs. sagittate rostral with rounded apex extending to anterior level of eyes); a distinct yellow spot covering the entire rostral (vs. an indistinct spot located at most in the central rostral region); supraoculars 1½ times as broad as deep (vs. twice as wide as long); and an oval eye (vs. round); a subtriangular cloacal shield (vs. pyramidal shield with truncated apex); a dorsal spot larger than the caudal spot with a dorsal/caudal tail spot ratio of  $0.8$  (vs.  $2.5$ ); a yellow cloacal shield (vs. brown shield); a longer heart ( $\geq 5.1\%$  vs.  $\leq 4.9\%$ ); a longer anterior liver asymmetry ( $\geq 0.05$  vs.  $\leq 0.05$ ); a lesser posterior liver tail/liver length ratio ( $\leq 0.11$  vs.  $\geq 0.17$ ); a larger left liver/right liver ratio ( $\geq 0.78$  vs.  $\leq 0.78$ ); a shorter gall bladder–kidney interval ( $\leq 22.0\%$  vs.  $\geq 22.0\%$ ); a shorter gall bladder–gonad interval ( $15.5\%$  vs.  $21.3\%$ ); a shorter gonad–kidney interval ( $13.2\%$  vs.  $15.9\%$ ); a more anterior left gonad midpoint ( $\leq 82.4\%$  vs.  $\geq 83.3\%$ ); greater number of testis segments ( $4$  vs.  $3$ ); a longer right kidney ( $\geq 3.7\%$  vs.  $\leq 3.5\%$ ); a more cranial left kidney midpoint ( $\leq 88.2\%$  vs.  $\geq 88.5\%$ ); a more anterior total kidney midpoint ( $\leq 87.4\%$  vs.  $\geq 87.4\%$ ); a longer kidney–vent gap ( $\geq 9.7\%$  vs.  $\leq 9.7\%$ ); a shorter rectal caecum ( $\leq 1.9\%$  vs.  $\geq 2.5\%$ ); a smaller rectal caecum/left kidney ratio ( $\leq 0.45$  vs.  $\geq 0.71$ ); a longer rectal caecum–vent interval ( $\geq 11.1\%$  vs.  $\leq 8.8\%$ ); a more posterior trachea midpoint ( $\geq 11.1\%$  vs.  $\leq 11.0\%$ ); a more posterior right lung midpoint ( $\geq 37.5\%$  vs.  $\leq 36.5\%$ ); a longer right bronchus ( $\geq 20.8\%$  vs.  $\leq 20.1\%$ ); a more caudal bronchus posterior tip ( $\geq 41.7\%$  vs.  $\leq 40.9\%$ ); a longer trachea-bronchus ( $\geq 40.3\%$  vs.  $\leq 39.8\%$ ), %); a more posterior trachea-bronchus midpoint ( $\geq 21.5\%$  vs.  $\leq 21.1\%$ ); a more caudal lung posterior tip ( $\geq 52.5\%$  vs.  $\leq 51.9\%$ ); a more posterior total lung midpoint ( $\geq 35.9\%$  vs.  $\leq 35.2\%$ ); and a shorter trachea–kidney distance ( $\leq 65.9\%$  vs.  $\geq 66.3\%$ ).

*Epictia pauldwyeri* can be separated from *E. tenella* by a maximum length of 142 mm (vs. 215 mm); a mean subcaudal count of 12.7 (vs. 17.2); eye a distinct yellow spot covering the entire rostral (vs. an enlarged spot that extends beyond rostral border to edges of adjacent scales); a relative rostral width of  $\geq 0.42$  (vs.  $\leq 0.34$ ); separation of supraocular from a short to moderately high anterior supralabial (vs. contact between supraocular and a tall supralabial); supraoculars pentagonal, 1½ times as broad as deep (vs. hexagonal and 3.0 times as wide as long);

posterior supranasal and supraocular borders parallel (vs. oblique); a pentagonal ocular in contact with four shields (vs. hexagonal ocular in contact with five shields); eye oval and partly beneath supranasal shield (vs. round and entirely beneath ocular shield); a midbody dorsal pattern with narrow, zigzag, pale-bordered, dark diamond-shaped spots (vs. dark stripes of oval-shaped spots with moderate to broad pale straight borders); a yellow cloacal shield (vs. brown shield); a larger posterior liver tail/liver length ratio ( $\geq 0.11$  vs.  $\geq 0.08$ ); and a greater number of testis segments (4 vs. 3).

**Remarks:** Surprisingly, Myers and Rand (1969) or Rand and Myers (1990) did not discover *Epictia goudotii* on Isla Barro Colorado, Panama, because the species occurs on both sides of the Panama Canal, but only on the Pacific versant. Swanson (1945) first recorded *Leptotyphlops goudotii* from Panama, and Smith (1958) referred to the species as *L. phenops* (“*albifrons*”). The records of Pérez-Santos et al. (1993) were based on specimens from the provinces of Colón and Panama, in Panama (Pérez-Santos, 1999). Young et al. (1999) listed *L. goudotii* from Panama.

Ray and Ruback (2015) listed only one known specimen of *E. goudotii* from Panama in their fig. 4, yet this species was listed in collections by ANSP (25086), FMNH (130672), KU (116896–98, 125032), MVZ (78739), STRI (CHP H-5379) and USNM (63110–11), all of which have proven to be the new species *E. pauldwyeri*. The only known Panamanian voucher specimen listed as *E. goudotii* I was unable to examine or for which no data are available is UAZ 27124 from 10 km NW Balboa, Canal Zone, which most likely represents *E. pauldwyeri*. If this specimen were to be confirmed as *E. goudotii*, it would be the only record of this species from Panama.

An interesting specimen, MCZ R-141087 (*Epictia* cf. *pauldwyeri*), from Loma Linda, Departamento del César, in northwestern Colombia shows a remarkable resemblance to *E. pauldwyeri* in external characters. Its internal anatomy is unknown, however, and without visceral data a reliable identification cannot be made. This specimen probably represents an undescribed species due to its geographic separation from Panama, which is approximately 700 airline km, although additional specimens or visceral data could answer the question of whether it is a cryptic mimic of, or conspecific with, *E. pauldwyeri*.

### *Epictia resetari* sp. nov.

Figs. 8A–R, 15P, 16U–W

*Stenostoma phaenops*—Ferrari-Pérez, 1886: 183; Smith and Smith, 1976: S-B-191 (part).

*Gluconia albifrons*—Boulenger, 1893: 63 (part); Taylor, 1939: 1, pl. 1, figs. 11–12 (part); Smith and Smith, 1976: S-B-97, S-B-127–128, S-F-47.

*Leptotyphlops phenops*—Klauber, 1940: 151 (part); Smith and Smith, 1976: S-F-47; Ramírez-Bautista and Moreno, 2006: 96 (part).

*Leptotyphlops phenops phenops*—Smith, 1943: 444–445 (part); Smith and Taylor, 1945: 24 (part); Smith et al., 1952: 257; Smith and Smith: 1976: S-B-130, S-F-19, S-F-47 (part); Guzmán-Guzmán, 1994: 35.

*Leptotyphlops goudotii phenops*—Peters et al., 1970 and 1986: 170 (part); Hahn, 1980: 16 (part).

*Leptotyphlops goudotii*—Greene, 1973: 150, 1994: 39, 151; Smith and Smith, 1976: S-B-129, S-F-47 (part); Hedges, 1996: 111, 115 (part); Campbell, 1998: 186–187 (part); García et al., 1998: 45; Kley, 2001: 90; Köhler, 2001b: 12, fig. 11B (part), 2008: 183–184, map (part); Adalsteinsson, 2008: 6, 29, 41, 47, figs. 3.2, 3.5 (part); CONABIO, 2009: 17 (part); Johnson et al., 2010: 368 (part); Pampa-Ramírez, 2010: 9–11, 20–23, 25–27, 29–32, 34–37, 40, 42, 48–49, figs. 9–11, 14; Pampa-Ramírez and Goyenechea, 2010: 366; Wilson and Mata-Silva, 2014: 51.

*Stenostoma phenops*—Smith and Smith, 1976: S-F-44.

*Leptotyphlops goudoti*—Smith and Smith, 1976: S-B-129, S-G-4 (part), 1993: 591, 709; Hahn, 1979: 230.2–3 (part); Flores-Villela et al., 1987: x; Flores-Villela, 1993: 35 (part); Ramírez-Bautista and Montes de Oca, 1997: 532; Vogt et al., 1997: 517, 532; Moreno-Casasola, 2003: 13.

*Leptotyphlops goudoti phenops*—Smith and Smith: 1976: S-B-130, S-B-191 (part); Pérez-Higareda, 1980: 23, 1986: 132; Pérez-Higareda et al., 1987: 15; Pérez-Higareda and Smith, 1991: fig. 1 (col. photo); Villafuerte and Flores-Villela, 1992: 53; Fox-Quesada, 2006: 263.

*Leptotyphlops goudotti phenops* (sic)—Smith, 1989: 51; Pérez-Higareda and Smith, 1991: 28–29, pl. 1; Villafuerte, 1991: 153, 171; Wilson et al., 2013: 44 (part).



*Leptotyphlops goudotii phenops* (sic)—Peters and Orejas-Miranda, 1970: 321–322, fig. 3; Branch, 1986: 293; Pérez-Higareda et al., 2007: 43–44, fig. 16, pl. 1 (col. photo).

*Epictia goudotii*—Adalsteinsson et al., 2009: 7, 10, 17, 31, 46, figs. 3A, 12 (part); Hernández-Salinas et al., 2010: 516; Wilson et al., 2013: 44 (part); Calderón-Alvarez, 2014: 44.

*Epictia phenops*—Wallach et al., 2014: 278 (part); McCranie and Hedges, 2016: 4, 7, fig. 2 (part); Terán-Juárez et al., 2016: 59, 74, 90.

**Holotype:** FMNH 178600 (field no. EHT 2194), a 116 mm (LOA) specimen collected by Edward H. Taylor on 17 July 1932, at Paso de Ovejas, Veracruz, Mexico, 19°17'00"N, 96°26'26"W, elev. 55 m asl.

**Paratypes** (7): MEXICO: VERACRUZ: 15.5 km SE Alvarado, collected by John R. Meyer on 17 August 1968, LACM 51798 (field no. JRM 3707); Cotaxtla, Cotaxtla Experimental Station, collected by David H. Janzen on 29 July 1962, LACM 28170; Finca Texquitipan, 6.4 km S Chote, collected by L. R. Cuesta on 30 May 1975, MVZ 128998; Río Blanco, 20 km WNW Piedras Negras, collected by unknown collector on 15 May 1946, KU 23252 (field no. WWD 5388); 33.0 km SE Veracruz, collected by A. R. Hardy on 19 August 1963, LACM 105291 (field no. AR 417; formerly LBSC 1311); and Laguna Catemaco, collected by Douglas C. Robinson on 16 July 1961, UMMZ 122826A–B (field no. EF 3442–43).

**Etymology:** This species is dedicated to Alan Resetar, Acting Divisional Manager and McCarter Collections Manager, Amphibian and Reptile Collection, Gantz Family Collections Center, Field Museum of Natural History (FMNH), and commemorates his 36 years of service to the museum. Alan has supported my research and made the FMNH collections available to me since 1982. His collection and departmental management, research, and hospitality to visiting researchers are most admirable and truly appreciated.

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 79–142 ( $\bar{x}$  = 122.7) mm; (4) total midodorsals = 238–258 ( $\bar{x}$  = 246.2); (5) subcaudals = 15–20 ( $\bar{x}$  = 17.7); (6) relative body proportion = 40–60 ( $\bar{x}$  = 54.1); (7) relative tail length = 4.9%–6.5% ( $\bar{x}$  = 6.0%); (8) relative tail width = 3.2–4.2 ( $\bar{x}$  = 3.6); (9) relative rostral width = 0.27–0.41 ( $\bar{x}$  = 0.35); (10) relative eye size = 0.45–0.47 ( $\bar{x}$  = 0.46); (10) rostral sagittate with an oval or truncated apex, extending to mid-eye level; (11) supralabials 2, moderate anterior supralabial reaching mid-eye level; (12) frontal present, hexagonal, as broad as deep; (13) supraoculars large, twice as broad as deep, posterior borders parallel to posterior supranasal borders; (14) widest anteriormost vertebral scale 3<sup>rd</sup>; (15) parietals and occipitals subequal, oriented transversely; (16) infralabials 4; (17) cloacal shield semilunate in shape; (18) head brown, with a small to moderate yellow spot covering most of or the entire rostral; (19) dorsum with 7 dark brown stripes consisting of diamond-shaped spots bordered by 8 moderate zigzag yellow stripes (= 7 dark stripes); (20) venter uniform brown with scales outlined in yellow; (21) midbody stripe formula (3 + 2/2 + 0) and middorsal pattern (3D + 4L); (22) tail with a pale terminal spot covering the 1–2 ( $\bar{x}$  = 1.3) dorsocaudals and 5½–9 ( $\bar{x}$  = 7.0) subcaudals (ventral/dorsal ratio 5.6); and (23) apical spine a stout compressed spike.

**Description:** Holotype data include scale row formula = 14-14-14; midtail scale rows = 10; TMD = 243; and SC = 20; LOA = 116.0 mm; TL = 7.5 mm; MBD = 2.1 mm; MTD = 1.9 mm; RW = 0.4 mm; HW = 1.5 mm; L/W = 55.2; TL/LOA = 6.5; TL/TW = 3.9; RW/HW = 0.27; and ED/OH = 0.46. Head wider than neck with rounded dorsal profile, all head shields with prominent sensory pits that appear as depressions in the scales; head tapered in dorsal profile with a truncated snout; rostral sagittate in shape with oval or truncated apex; frontal hexagonal, as broad as deep; postfrontal, interparietal and interoccipital hexagonal in shape, each larger than the preceding scale (Fig. 8D); broadest anteriormost vertebral scale 3<sup>rd</sup>; supraoculars large and pentagonal, twice as wide as long (Fig. 8D), with parallel posterior supranasal and supraocular borders; parietals slightly greater in length than occipitals, both shields oriented transversely; lateral head profile rounded; nasal completely divided, suture forming a shallow V-shaped angle along anterior supralabial and infranasal, nostril oval and positioned closer to the rostral than supralabial; infranasal twice as tall as long, narrowing toward lip, 1½ times broader than anterior supralabial; supralabials 2, anterior supralabial moderate in height with nearly parallel sides, not quite reaching center of eye, its labial border 1–1½ times as long as that of infranasal; ocular large, twice as high as wide, roughly rectangular with a nearly straight anterior border (but slightly concave border with supranasal) and only slightly pointed posterior border; eye large and round with small pupil, its diameter less than the lip-orbit gap (ED/OH = 0.45–0.47,  $\bar{x}$  = 0.46), partially beneath the supranasal (Fig. 8H), slightly protuberant but not visible in dorsal view; posterior supralabial longer than deep, taller than anterior supralabial, posterior border rounded; ventral rostral lacking a preoral groove;

mental butterfly-shaped; infralabials 4, the 4<sup>th</sup> the largest and longest, 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> each successively smaller in size; costal scales rounded and imbricate in 14 rows throughout; cloacal shield semilunate (Fig. 8R); and apical spine a compressed spike supported by a vertically compressed cone.

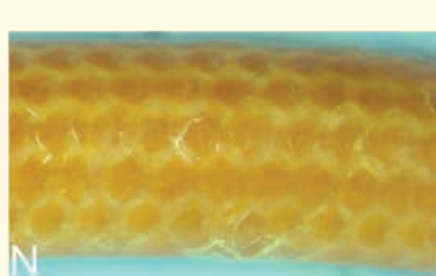
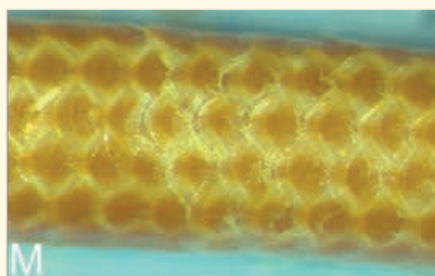
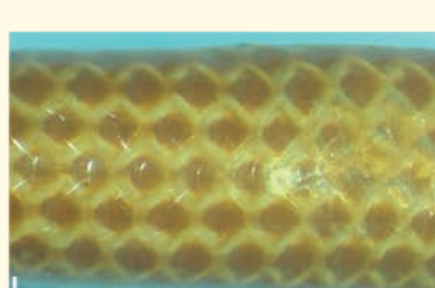
Coloration in life dark brown with yellow stripes, a yellow rostral spot of moderate size, and large yellow subcaudal spot (Fig. 16U–W). Midbody color pattern in preserved material consists of 7 dark brown to chocolate brown dorsal scale rows (forming stripes of connecting brown diamonds; Fig. 8L) bordered by 8 moderate yellow zigzag stripes and 7 ventral scale rows paler than dorsum, generally unicolored pale brown but often with each scale faintly outlined in yellow (midbody stripe formula = 7 + 0 and middorsal pattern = 3D + 4L). Head brown with an irregular pale yellow spot covering most of rostral; lateral head brown with a short, broad yellow bar along lower edge of posterior supralabial and ocular (Fig. 8K); and chin uniform pale brown. Tail uniform brown above and below, cloacal shield paler than surrounding cloaca and surrounded by a pale yellow ring, shield itself pale with brown vermiculations covering  $\frac{1}{2}$ – $\frac{3}{4}$  of the scale, with a yellow posterior border; yellow tail tip pattern consisting of a small dorsal spot covering 1–2 dorsocaudals ( $\bar{x}$  = 1.3 scales) and a moderate ventral spot covering  $5\frac{1}{2}$ –9 subcaudals ( $\bar{x}$  = 7.3 scales), with the ventral/dorsal ratio 5.6 (Fig. 8Q).

Peters and Orejas-Miranda (1970) described the hemipenis of UMMZ 122826A (field no. EF 3442, erroneously reported as UMMZ 122876; Fig. 15P) under the name *Leptotyphlops goudotii phenops*. This specimen originated from Lago Catemaco, Veracruz, so I refer it and UMMZ 122826B (field no. EF 3443) to *Epictia resetari*.

**Viscera:** (mean value followed parenthetically by range,  $n$  = 2). Posterior tip of sternohyoideus muscle = 12.75% (12.7–12.8%); sternohyoideus/snout–heart gap = 0.73 (0.71–0.76); heart length = 3.9% (3.7–4.0%) with midpoint at 19.4% (18.7–20.0%); snout–heart interval = 21.3% (20.6–22.0%); heart–liver gap = 7.0% (6.0–7.9%) and interval = 49.9% (49.2–50.6%); heart–gall bladder gap = 48.1% (46.0–50.2%); liver lobes multipartite; right liver length = 39.1% (39.0–39.2%) with midpoint at 47.75% (47.6–47.9%) and 30.5 (30–31) segments; left liver length = 28.1% (26.0–30.3%) with midpoint at 47.2% (47.0–47.4%) and 23.0 (20–26) segments; anterior liver extension = 0.13 (0.09–0.16) and posterior liver tail = 0.15 (0.13–0.17); left liver/right liver = 0.72 (0.66–0.78); liver–gall bladder gap = 2.1% (0.8–3.4%) and interval = 42.5% (41.6–43.4%); liver–kidney gap = 18.6% (18.0–19.1%) and interval = 62.9% (62.8–62.9%); gall bladder length = 1.4% (1.1–1.6%) with midpoint at 70.1% (68.8–71.3%); gall bladder–gonad gap = 6.3% (4.5–8.0%) and interval = 14.0% (12.7–15.2%); gall bladder–kidney gap = 15.1% (14.6–15.6%) and interval = 21.7% (20.6–22.8%); right gonad length = 4.6% (3.2–6.0%) with midpoint at 79.3% (79.2–79.4%); left gonad length = 2.5% (2.4–2.6%) with midpoint at 82.1% (82.0–82.2%); gonad–kidney gap = 2.5% (2.0–3.0%) and interval = 14.1% (13.2–15.0%); right adrenal midpoint = 82.0% (81.2–82.8%) and left adrenal midpoint = 83.55% (83.5–83.6%); gonad–kidney gap = 2.5% (2.0–3.0%) and interval = 14.1% (13.2–15.0%); right kidney length = 3.3% (3.0–3.6%) with midpoint at 87.5% (87.0–88.0%); left kidney length = 3.3% (3.0–3.6%) with midpoint at 89.5% (89.0–89.9%); kidney overlap = 0.26 (0.23–0.29); kidney–vent gap = 8.9% (8.6–9.2%) and interval = 14.2% (13.5–14.8%); rectal caecum length = 1.7% (1.2–2.2%); and caecum–vent interval = 8.9% (8.6–9.2%). One female (SVL 125 mm) contained 5 plus 6 follicles in the right ovary, and 2 developing eggs and 4 follicles in the left ovary; the other female (SVL 133.5 mm) had 5 eggs and 4 follicles in the right ovary, plus 3 eggs and 3 follicles in the left ovary. Based on these two specimens, the clutch size apparently is 7 to 8 eggs.

Respiratory system lacking tracheal lung and left lung complex; trachea length = 20.0% (19.5–20.4%) with midpoint at 11.4% (10.9–11.8%) and an estimated 185 (180–189) tracheal rings or 88.4 (83.3–93.5) rings/10% SVL; anterior lung tip = 19.6% (19.1–20.0%); tracheal entry terminal; cardiac lung length = 1.75% (1.5–2.0%); right lung length = 24.8% (24.3–25.2%) with midpoint at 33.7% (32.8–34.6%) and faveolar cranial half and trabecular caudal half; posterior lung tip = 46.1% (44.9–47.2%); right bronchus length = 17.3% (15.0–19.6%) with posterior tip at 38.6% (35.6–41.6%); bronchus/right lung = 0.70 (0.62–0.78); trachea–bronchus length = 37.3% (34.5–40.0%) with midpoint at 20.0% (18.4–21.6%); trachea–bronchus/total lung length = 0.81 (0.77–0.85); and total lung length = 26.5% (25.8–27.2%) with midpoint at 32.8% (32.0–33.6%).

Visceral distance data include heart–right lung distance = 14.4% (14.1–14.6%); heart–liver distance = 28.4% (27.6–29.2%); trachea–liver distance = 36.4% (35.8–37.0%); liver–kidney distance = 40.7% (40.4–41.1%); right lung–adrenal distance = 49.1% (47.8–50.3%); trachea/bronchus–gall bladder distance = 50.1% (47.2–52.9%); heart–gonad distance = 60.0% (59.2–60.7%); trachea/bronchus–kidney distance = 68.5% (66.4–70.6%); heart–kidney distance = 69.1% (68.0–70.3%); and trachea–adrenal distance = 71.4% (70.6–72.3%).

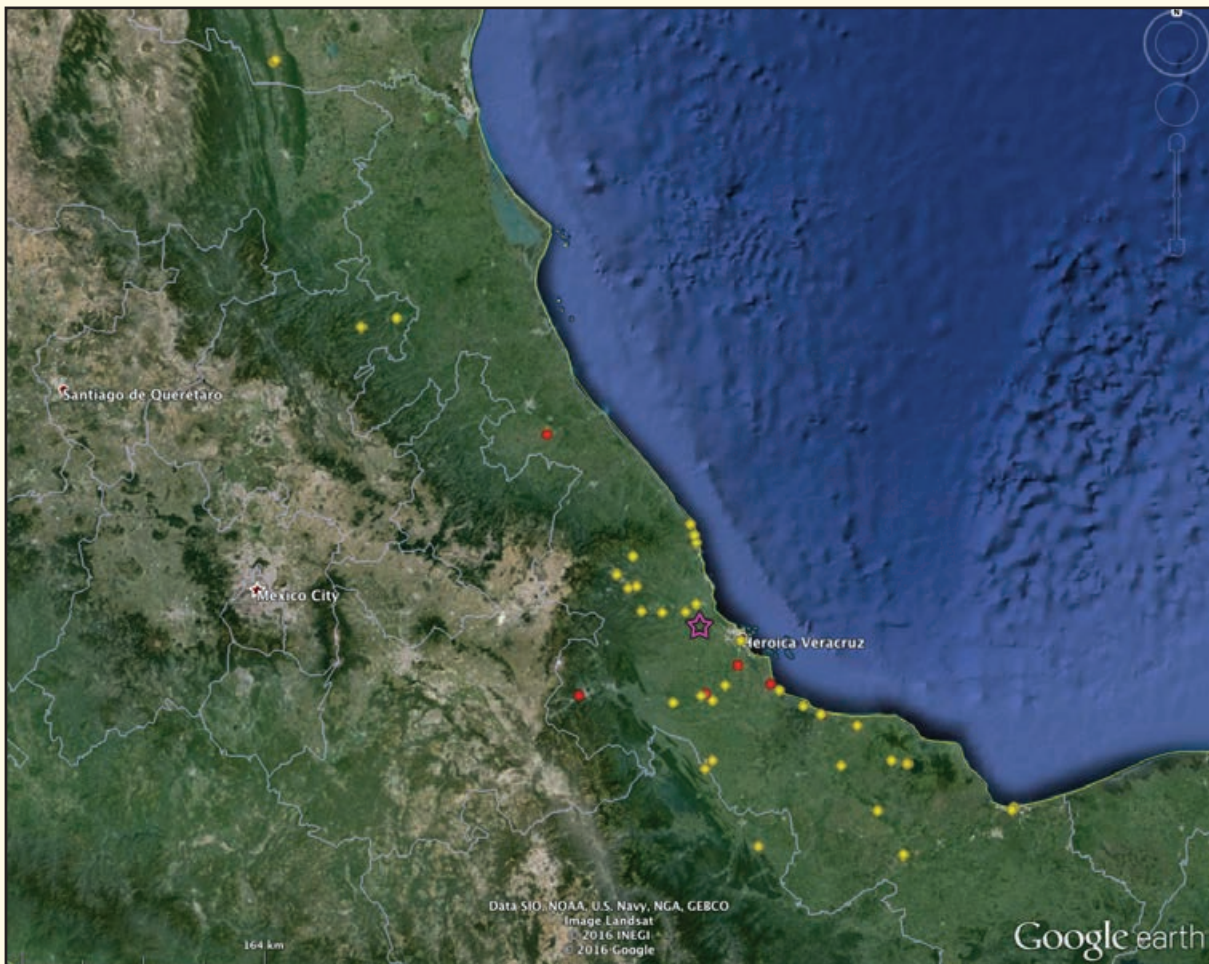






**Fig. 8.** Morphological variation in *Epictia resetari* sp. nov. (A, B) dorsal and ventral views of the holotype of *E. resetari* (FMNH 178600); (C) paratype of *E. resetari* (UMMZ 122826A); (D, E, F, G) dorsal head (LACM 51798, KU 23252, MVZ 128998, LACM105291); (H, I, J) lateral head (LACM 105291, LACM 51798, MVZ 128998); (K) ventral head (KU 23252); (L, M) dorsal midbody (LACM 51798, MVZ 128998); (N, O) lateral midbody (MVZ 128998, LACM 51798); (P) ventral midbody (MVZ 128998); (Q) lateral tail (LACM 51798); and (R) ventral tail (LACM 51798). © Rachel Grill (A, B), Mark O'Brien (C), and remaining photos by Van Wallach

**Distribution:** *Epictia resetari* is a Mexican endemic that inhabits the northeastern part of the country (S Tamaulipas, NE Hidalgo, and Veracruz), overall elev. NSL–900 m (Map 8).



**Map 8.** Distribution of *Epictia resetari* nov. sp. in eastern Mexico (Tamaulipas to Veracruz).

**Ecology:** This species has been found in bromeliads in open savanna (Smith, 1989), but mainly occurs in tropical evergreen and semi-deciduous forest (Vogt et al., 1997).

**Comparisons:** *Epictia resetari* can be differentiated from *E. ater* by a sagittate rostral with an oval apex that extends to mid-eye level (vs. a waisted rostral with arrowhead apex extending posterior to the eye level); a distinct pale spot that covers the entire rostral (vs. diffuse or indistinct spot centrally located); a discrete frontal shield (vs. frontal absent, fused to rostral); a supraocular twice as wide as long (vs. 1½ times as broad as deep); eye shape round (vs. oval); a semilunar cloacal shield (vs. subtriangular); a dorsal midbody pattern with dark stripes composed of diamond-shaped spots separated by moderate-sized, pale zigzag stripes (vs. uniformly dark); a shorter heart ( $\leq 4.0\%$  vs.  $\geq 4.7\%$ ); a longer liver–gall bladder gap ( $\geq 0.8\%$  vs.  $\leq 0.5\%$ ); a longer liver–kidney gap ( $\geq 18.0\%$  vs.  $\leq 16.7\%$ ) and liver–kidney interval ( $\geq 62.8\%$  vs.  $\leq 60.6\%$ ); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq 0.5\%$ ); a shorter rectal caecum–vent interval ( $\leq 9.2\%$  vs.  $\geq 9.6\%$ ); a shorter cardiac lung ( $\leq 2.0\%$  vs.  $\geq 2.7\%$ ); a more anterior right lung midpoint ( $\leq 34.6\%$  vs.  $\geq 34.7\%$ ); and a longer liver–kidney distance ( $\geq 40.4\%$  vs.  $\leq 37.6\%$ ).

*Epictia resetari* is identifiable from *E. bakewelli* by a sagittate rostral with an oval apex that extends to mid-eye level (vs. waisted rostral with oval apex extending posterior to the eye level); a discrete frontal shield (vs. frontal absent, fused to rostral); eye shape round (vs. oval); pale caudal spot more than 5 times larger ventrally than dorsally (vs. less than 3 times); a dorsal midbody pattern with 7 dark stripes composed of diamond-shaped spots separated by moderate-sized, pale zigzag stripes (vs. 3 dark stripes of linear-shaped spots bordered by moderate to broad, linear pale stripes and a midlateral dark stripe covering 2 scale rows); a brown cloacal shield (vs. yellow shield); a smaller sternohyoideus/snout–heart gap ( $\leq 0.76$  vs.  $\geq 0.77$ ); fewer right liver ( $\leq 31$  vs.  $\geq 40$ ), left liver ( $\leq 26$  vs.  $\geq 27$ ), and total liver segments ( $\leq 56$  vs.  $\geq 69$ ); a longer liver–gall bladder gap ( $\geq 0.8\%$  vs.  $\leq 0.7\%$ ); a longer liver–kidney interval ( $\geq 62.8\%$  vs.  $\leq 62.2\%$ ); a shorter gall bladder–gonad interval (14.0% vs. 18.3%); a greater kidney overlap ratio ( $\geq 0.23$  vs.  $\leq 0.21$ ); a more caudal right kidney midpoint ( $\geq 87.0\%$  vs.  $\leq 86.9\%$ ); a shorter caecum–vent interval ( $\leq 9.2\%$  vs.  $\geq 9.6\%$ ); and a longer lung–adrenal distance ( $\geq 47.8\%$  vs.  $\leq 45.4\%$ ).

*Epictia resetari* can be separated from *E. columbi* by subcaudals  $\leq 20$  (vs.  $\geq 22$ ); rostral extending to mid-eye level (vs. post-eye level); pale rostral and caudal spots present (vs. absent); supraocular proportion twice as broad as deep (vs. barely broader than deep); anterior edge of eye beneath supranasal (vs. beneath ocular); lacking a preoral rostral groove (vs. present); tail terminus a spike (vs. cone with narrow blade); midbody dorsal pattern of 7 dark stripes (vs. uniformly dark); a shorter heart ( $\leq 4.0\%$  vs. 4.3%); a longer snout–heart interval ( $\geq 20.6\%$  vs. 19.9%); a shorter heart–liver gap ( $\leq 7.9\%$  vs. 9.0%), but longer heart–liver interval ( $\geq 49.2\%$  vs. 47.7%); a longer heart–gall bladder gap ( $\geq 46.0\%$  vs. 43.8%); a longer right liver ( $\geq 39.0\%$  vs. 34.4%) and left liver ( $\geq 26.0\%$  vs. 24.6%); a more posterior right liver midpoint ( $\geq 47.6\%$  vs. 46.1%) and more cranial left liver midpoint ( $\leq 47.4\%$  vs. 47.5%); a shorter anterior liver extension ( $\leq 0.16$  vs. 0.18) and longer posterior liver tail ( $\geq 0.13$  vs. 0.10); fewer right liver segments ( $\leq 31$  vs. 35) and left liver segments ( $\leq 26$  vs. 28); a longer liver–gall bladder gap ( $\geq 0.8\%$  vs. 0.4%) and liver–gall bladder interval ( $\geq 41.6\%$  vs. 35.9%); a more caudal gall bladder midpoint ( $\geq 68.8\%$  vs. 64.3%); a shorter gall bladder–gonad gap ( $\leq 6.3\%$  vs. 13.3%) and interval ( $\leq 14.0\%$  vs. 18.4%); a shorter gall bladder–kidney gap ( $\leq 15.6\%$  vs. 18.8%) and gall bladder–kidney interval ( $\leq 22.8\%$  vs. 27.7%); a shorter liver–kidney gap ( $\leq 19.1\%$  vs. 20.3%), but longer liver–kidney interval ( $\geq 62.8\%$  vs. 62.5%); a longer right gonad ( $\geq 3.2\%$  vs. 2.3%) and left gonad ( $\geq 2.4\%$  vs. 0.8%); a more caudal left gonad midpoint ( $\geq 82.0\%$  vs. 81.6%); a longer gonad–kidney gap ( $\geq 2.0\%$  vs. 1.6%); a more caudal right adrenal ( $\geq 81.2\%$  vs. 80.7%) and left adrenal midpoint ( $\geq 83.5\%$  vs. 81.6%); a shorter right kidney ( $\leq 3.6\%$  vs. 3.9%) and left kidney ( $\leq 3.6\%$  vs. 3.9%); kidney overlap ( $\geq 0.23$  vs. none); a more posterior right kidney midpoint ( $\geq 87.0\%$  vs. 85.5%); a longer kidney–vent gap ( $\geq 8.6\%$  vs. 8.6%) and shorter kidney–vent interval ( $\leq 14.8\%$  vs. 16.4%); a shorter rectal caecum–vent interval ( $\leq 9.2\%$  vs. 9.8%); a longer trachea ( $\geq 19.5\%$  vs. 18.8%) and more caudal trachea midpoint ( $\geq 10.9\%$  vs. 10.5%); fewer tracheal rings ( $\leq 189$  vs. 192) and fewer rings/10% SVL ( $\leq 93.5\%$  vs. 102.4%); a more caudal anterior lung tip ( $\geq 19.1\%$  vs. 18.4%); a shorter right lung ( $\leq 25.2\%$  vs. 26.6%); a shorter heart–right lung distance ( $\leq 14.6\%$  vs. 15.4%); liver–kidney distance ( $\leq 41.1\%$  vs. 41.4%), and heart–gonad distance ( $\leq 60.7\%$  vs. 61.5%); and a longer trachea–liver distance ( $\geq 35.8\%$  vs. 35.6%) and trachea/bronchus–gall bladder distance ( $\geq 47.2\%$  vs. 44.0%).

*Epictia resetari* is diagnosable from *E. magnamaculata* by a maximum length of 142 mm (vs. 220 mm); a rostral that extends to mid-eye level (vs. not reaching the eye level); a pale spot that covers entire rostral (vs. large spot extending beyond rostral border); a supraocular twice as wide as long (vs. 1½ times as wide as long); eye round (vs.



oval); a semilunate cloacal shield (vs. subtriangular); a pale caudal spot more than 5 times larger ventrally than dorsally (vs. larger dorsally than ventrally); tail ending in a broad compressed blade (vs. apical spine); a dorsal midbody pattern with 7 dark stripes composed of diamond-shaped spots separated by moderate-sized, pale zigzag stripes (vs. 11 dark stripes of linear-shaped spots bordered by broad, pale linear stripes); fewer right liver segments ( $\leq 31$  vs.  $\geq 32$ ); a longer liver–kidney gap (18.6% vs. 16.2%) and interval (62.9% vs. 60.5%); a longer gall bladder–kidney gap (15.1% vs. 12.3%) and interval (21.7% vs. 19.4%); a longer gonad–kidney gap (2.5% vs. 0.2%) and interval (14.1% vs. 11.5%); a shorter right lung length (24.8% vs. 28.9%) and posterior tip (46.1% vs. 49.9%); a shorter heart–right lung distance (14.4% vs. 16.7%); a longer liver–kidney distance (40.7% vs. 38.4%), right lung–adrenal distance (49.1% vs. 46.9%), and trachea/bronchus–kidney distance (68.5% vs. 66.5%).

*Epictia resetari* can be distinguished from *E. martinezi* by sagittate rostral shape (vs. parallel); lacking a pale preocular spot (vs. present); parallel supranasal/supraocular borders (vs. oblique); a round eye shape and eye/ocular ratio of  $\leq 0.47$  (vs. oval eye,  $\geq 0.47$ ); mean subcaudal/dorsocaudal spot ratio of 5.6 (vs. 3.1); mean dorsocaudal spot size of 1.3 scales (vs. 2.4 scales); a shorter sternohyoideus length ( $\leq 12.8\%$  vs.  $\geq 13.3\%$ ); a lesser sternohyoideus/snout–heart gap ratio ( $\leq 0.76$  vs.  $\geq 0.81$ ); a longer heart–gall bladder gap ( $\geq 46.0\%$  vs.  $\leq 45.6\%$ ); a longer right liver length ( $\geq 39.0\%$  vs.  $\leq 36.8\%$ ) and total liver length ( $\geq 65.2\%$  vs.  $\leq 64.1\%$ ); a more caudad right liver ( $\geq 47.6\%$  vs.  $\leq 47.2\%$ ) and left liver midpoint ( $\geq 47.0\%$  vs.  $\leq 47.0\%$ ); fewer right liver ( $\leq 31$  vs.  $\geq 32$ ), left liver ( $\leq 26$  vs.  $\geq 34$ ), and total liver segments ( $\leq 56$  vs.  $\geq 71$ ); a longer liver–gall bladder gap ( $\geq 0.8\%$  vs.  $\leq 0.4\%$ ) and interval ( $\geq 41.6\%$  vs.  $\leq 38.6\%$ ); a longer liver–kidney gap ( $\geq 18.0\%$  vs.  $\leq 16.9\%$ ) and interval ( $\geq 62.8\%$  vs.  $\leq 60.8\%$ ); a longer liver–gall bladder interval (42.5% vs. 38.2%); a longer liver–kidney gap (18.6% vs. 16.0%) and interval (62.9% vs. 60.6%); a more posterior gall bladder midpoint ( $\geq 68.8\%$  vs.  $\leq 66.7\%$ ); a shorter gall bladder–kidney interval ( $\leq 22.8\%$  vs.  $\geq 23.2\%$ ); a more caudal right gonad ( $\geq 79.2\%$  vs.  $\leq 76.0\%$ ), left gonad ( $\geq 82.0\%$  vs.  $\leq 79.3\%$ ), and total gonad midpoint ( $\geq 80.6\%$  vs.  $\leq 77.7\%$ ); a more caudad right adrenal ( $\geq 81.2\%$  vs.  $\leq 77.0\%$ ), left adrenal ( $\geq 83.5\%$  vs.  $\leq 78.9\%$ ), and total adrenal midpoint ( $\geq 82.4\%$  vs.  $\leq 77.9\%$ ); a longer gonad–kidney gap (2.5% vs. 0.2%) and shorter interval (14.1% vs. 16.2%); a shorter right kidney ( $\leq 3.6\%$  vs.  $\geq 4.9\%$ ), left kidney ( $\leq 3.6\%$  vs.  $\geq 4.0\%$ ), and total kidney length ( $\leq 7.2\%$  vs.  $\geq 9.0\%$ ); a more caudal right kidney ( $\geq 87.0\%$  vs.  $\leq 84.2\%$ ), left kidney ( $\geq 89.0\%$  vs.  $\leq 87.6\%$ ), and total kidney midpoint ( $\geq 88.0\%$  vs.  $\leq 84.7\%$ ); a shorter kidney–vent gap ( $\leq 9.2\%$  vs.  $\geq 10.4\%$ ) and interval ( $\leq 14.8\%$  vs.  $\geq 18.3\%$ ); a lesser kidney–vent interval/right liver ratio (0.38 vs. 0.51); a larger rectal caecum/left kidney ratio (0.53 vs. 0.23); a shorter rectal caecum–vent interval (8.9% vs. 11.2%); a shorter bronchus length (17.3% vs. 20.1%) and more cranial posterior tip (37.3% vs. 40.7%); a longer liver–kidney distance ( $\geq 40.4\%$  vs.  $\leq 39.1\%$ ); and a longer trachea/bronchus–gall bladder distance ( $\geq 47.2\%$  vs.  $\leq 45.3\%$ ), right lung–adrenal distance ( $\geq 47.8\%$  vs.  $\leq 45.2\%$ ), heart–gonad distance ( $\geq 59.2\%$  vs.  $\leq 57.8\%$ ), trachea/bronchus–kidney distance ( $\geq 66.4\%$  vs.  $\leq 64.7\%$ ), heart–kidney distance ( $\geq 68.0\%$  vs.  $\leq 66.7\%$ ), and trachea–adrenal distance ( $\geq 70.6\%$  vs.  $\leq 67.0\%$ ).

*Epictia resetari* is recognizable from *E. pauldwyeri* by a middorsal scale count of  $\geq 238$  (vs.  $\leq 226$ ) and subcaudals from  $\geq 15$  (vs.  $\leq 14$ ); a relative rostral width of  $\leq 0.41$  (vs.  $\geq 0.42$ ); a sagittate rostral with an oval apex that extends to mid-eye level (vs. subtriangular rostral with rounded apex that extending to anterior level of eye); a frontal shield as broad as deep (vs.  $1\frac{1}{2}$  times broader than deep); a supraocular twice as broad as deep (vs.  $1\frac{1}{2}$  times as broad as deep); eye shape round (vs. oval); a semilunate cloacal shield (vs. subtriangular); a pale caudal spot more than 5 times larger ventrally than dorsally (vs. larger dorsally than ventrally); a brown cloacal shield (vs. yellow shield); a shorter sternohyoideus/snout–heart gap ( $\leq 0.76$  vs.  $\geq 0.76$ ); a shorter heart ( $\leq 4.0\%$  vs.  $\geq 5.1\%$ ); a longer posterior liver tail ( $\geq 0.13$  vs.  $\leq 0.11$ ); a smaller left liver/right liver ratio ( $\leq 0.78$  vs.  $\geq 0.78$ ); a longer liver–gall bladder gap ( $\geq 0.8\%$  vs.  $\leq 0.5\%$ ); a longer liver–kidney gap ( $\geq 18.0\%$  vs.  $\leq 16.2\%$ ) and longer liver–kidney interval ( $\geq 62.8\%$  vs.  $\leq 62.0\%$ ); a longer gall bladder–kidney gap ( $\geq 14.6\%$  vs.  $\leq 14.4\%$ ); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq 0.5\%$ ); a more posterior right kidney midpoint ( $\geq 87.0\%$  vs.  $\leq 86.6\%$ ), left kidney midpoint ( $\geq 89.0\%$  vs.  $\leq 88.2\%$ ), and total kidney midpoint ( $\geq 88.0\%$  vs.  $\leq 87.4\%$ ); a shorter kidney–vent gap ( $\leq 9.2\%$  vs.  $\geq 9.7\%$ ) and kidney–vent interval ( $\leq 14.8\%$  vs.  $\geq 15.3\%$ ); a shorter rectal caecum–vent interval ( $\leq 9.2\%$  vs.  $\geq 11.1\%$ ); more tracheal rings ( $\geq 180$  vs.  $\leq 176$ ); more tracheal rings/10% SVL ( $\geq 83.3$  vs.  $\leq 78.5$ ); a shorter cardiac lung ( $\leq 2.0\%$  vs.  $\geq 2.0\%$ ); a shorter right lung ( $\leq 25.2\%$  vs.  $\geq 29.2\%$ ); a more cranial right lung midpoint ( $\leq 34.6\%$  vs.  $\geq 37.5\%$ ); a shorter intrapulmonary bronchus ( $\leq 19.6\%$  vs.  $\geq 20.8\%$ ); a more cranial bronchus posterior tip ( $\leq 41.6\%$  vs.  $\geq 41.7\%$ ); a shorter trachea–bronchus ( $\leq 40.0\%$  vs.  $\geq 40.3\%$ ); a more cranial lung posterior tip ( $\leq 47.2\%$  vs.  $\geq 52.5\%$ ); a shorter total lung ( $\leq 27.2\%$  vs.  $\geq 31.2\%$ ); a more anterior total lung midpoint ( $\leq 33.6\%$  vs.  $\geq 35.9\%$ ); a



shorter heart–lung distance ( $\leq 14.6\%$  vs.  $\geq 17.4\%$ ); and a longer liver–kidney distance ( $\geq 40.4\%$  vs.  $\leq 39.0\%$ ), right lung–adrenal distance ( $\geq 47.8\%$  vs.  $\leq 45.8\%$ ), and trachea–kidney distance ( $\geq 66.4\%$  vs.  $\leq 65.9\%$ ).

*Epictia resetari* can be separated from *E. phenops* by supraoculars with posterior borders parallel to posterior borders of supranasal (vs. oblique); a round eye partly beneath supranasal shield (vs. oval eye entirely beneath ocular); a pale caudal spot 5 times larger ventrally than dorsally (vs. 7 times larger ventrally than dorsally); a dorsal midbody pattern with 7 dark stripes composed of diamond-shaped spots (vs. 3 dark stripes of triangular-shaped spots and a dark midlateral stripe covering 2 scale rows); and a longer sternohyoideus/snout–heart gap ( $\geq 0.76$  vs.  $\leq 0.76$ ); a shorter heart–liver interval (49.9% vs. 52.5%); a shorter left liver (28.2% vs. 31.3%) and total liver length (67.3% vs. 71.3%); a longer liver–kidney gap (18.6% vs. 16.0%); a shorter right lung length (24.8% vs. 31.4%), midpoint (33.7% vs. 36.6%), and posterior tip (46.1% vs. 52.3%); a shorter bronchus length (17.3% vs. 19.4%); a shorter heart–right lung distance (14.4% vs. 18.0%); and a longer right lung–adrenal distance (49.1% vs. 45.6%).

*Epictia resetari* can be differentiated from *E. goudotii* by a relative rostral width of  $\leq 0.41$  (vs.  $\geq 0.42$ ); a sagittate rostral with an oval apex that extends to mid-eye level (vs. triangular rostral with rounded apex extending to anterior level of eye); a distinct pale rostral spot (vs. weak or absent spot); a frontal shield as broad as deep (vs.  $1\frac{1}{2}$  times broader than deep); anterior supralabial moderate in height, reaching mid-eye level (vs. short, not or barely reaching eye level); a rounded snout in dorsal and ventral profile (vs. obtuse profile); a semilunate cloacal shield (vs. subtriangular); pale caudal spot more than 5 times larger ventrally than dorsally (vs. slightly larger ventrally than dorsally); lack of a preoral groove in ventral rostral (vs. distinct preoral groove); a spine-like caudal termination (vs. compressed cone); a dorsal midbody pattern with moderate-sized, distinct pale stripes (vs. narrow and pale stripes); a shorter sternohyoideus length ( $\leq 12.8\%$  vs.  $13.7\%$ ); a smaller sternohyoideus/snout–heart gap ratio ( $\leq 0.76$  vs.  $0.82$ ); a shorter heart length ( $\leq 4.0\%$  vs.  $6.0\%$ ); a shorter snout–heart interval ( $\leq 22.0\%$  vs.  $22.7\%$ ); a longer heart–liver gap ( $\geq 6.0\%$  vs.  $5.6\%$ ); a shorter heart–liver interval ( $\leq 50.6\%$  vs.  $52.8\%$ ); a shorter right liver ( $\leq 39.2\%$  vs.  $41.2\%$ ) and total liver length ( $\leq 69.3\%$  vs.  $71.2\%$ ); a more cranial right liver ( $\leq 47.9\%$  vs.  $48.9\%$ ) and left liver midpoint ( $\leq 47.4\%$  vs.  $48.1\%$ ); fewer right liver ( $\leq 31$  vs.  $35$ ) and total liver segments ( $\leq 56$  vs.  $56$ ); a longer liver–kidney gap ( $\geq 18.0\%$  vs.  $17.2\%$ ) and shorter liver–kidney interval ( $\geq 62.8\%$  vs.  $63.9\%$ ); a shorter gall bladder length ( $\leq 1.6\%$  vs.  $2.1\%$ ); a shorter gall bladder–gonad interval ( $\leq 15.2\%$  vs.  $19.3\%$ ); a more anterior right gonad ( $\leq 79.4\%$  vs.  $81.8\%$ ) and left gonad midpoint ( $\leq 82.2\%$  vs.  $86.5\%$ ); a more cranial right adrenal ( $\leq 82.8\%$  vs.  $83.7\%$ ) and left adrenal midpoint ( $\leq 83.6\%$  vs.  $88.0\%$ ); a more anterior right kidney ( $\leq 88.0\%$  vs.  $88.4\%$ ), left kidney midpoint ( $\leq 89.9\%$  vs.  $90.6\%$ ); a greater kidney overlap ratio ( $\geq 0.23$  vs.  $0.23$ ); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $-2.1\%$ ); a longer kidney–vent gap ( $\geq 8.6\%$  vs.  $7.7\%$ ) and interval ( $\geq 13.5\%$  vs.  $13.3\%$ ); a longer rectal caecum–vent interval ( $\geq 8.6\%$  vs.  $8.6\%$ ); a shorter trachea ( $\leq 20.4\%$  vs.  $21.0\%$ ); a more anterior trachea midpoint ( $\leq 11.8\%$  vs.  $12.2\%$ ); more tracheal rings ( $\geq 180$  vs.  $176$ ); a more cranial anterior lung tip ( $\leq 20.0\%$  vs.  $20.2\%$ ); a shorter cardiac lung ( $\leq 2.0\%$  vs.  $2.6\%$ ); a shorter right lung ( $\leq 25.2\%$  vs.  $27.9\%$ ); a more anterior right lung midpoint ( $\leq 34.6\%$  vs.  $36.7\%$ ); a longer right bronchus ( $\geq 15.0\%$  vs.  $14.6\%$ ); a larger bronchus/lung ratio ( $\geq 0.62$  vs.  $0.52$ ); a more cranial posterior lung tip ( $\leq 47.2\%$  vs.  $50.6\%$ ); a shorter total lung ( $\leq 27.2\%$  vs.  $30.5\%$ ); a more anterior total lung midpoint ( $\leq 33.6\%$  vs.  $35.4\%$ ); and a shorter heart–lung distance ( $\leq 14.6\%$  vs.  $17.0\%$ ), heart–liver distance ( $\leq 29.2\%$  vs.  $29.2\%$ ), heart–gonad distance ( $\leq 60.7\%$  vs.  $62.1\%$ ), and trachea–adrenal distance ( $\leq 72.2\%$  vs.  $73.7\%$ ).

*Epictia resetari* is identifiable from *E. albifrons* by middorsal scales  $\geq 238$  (vs.  $\leq 218$ ) and subcaudals  $\geq 15$  (vs.  $\leq 15$ ); a rostral extending to mid-eye level (vs. extending to anterior level of eye); a distinct pale spot that covers entire rostral (vs. diffuse or indistinct spot centrally located); a frontal shield as wide as long (vs.  $1\frac{1}{2}$  times broader than deep); eye shape round (vs. oval); a semilunate cloacal shield (vs. pyramidal, with truncated apex); a pale caudal spot more than 5 times larger ventrally than dorsally (vs.  $2\frac{1}{2}$  times larger ventrally than dorsally); a shorter sternohyoideus ( $\leq 12.8\%$  vs.  $\geq 13.8\%$ ); a smaller sternohyoideus/snout–heart gap ratio ( $\leq 0.76$  vs.  $\geq 0.85$ ); a shorter heart length ( $\leq 4.0\%$  vs.  $\geq 4.4\%$ ); a longer heart–gall bladder gap (48.1% vs. 46.1%); a more posterior left liver midpoint ( $\geq 47.0\%$  vs.  $\leq 45.0\%$ ); a longer anterior liver extension ( $\geq 0.09$  vs.  $\leq 0.05$ ); a shorter posterior liver tail ( $\leq 0.17$  vs.  $\geq 0.17$ ); a greater number of right liver segments ( $\geq 30$  vs.  $\leq 29$ ); a longer liver–gall bladder interval ( $\geq 41.6\%$  vs.  $\leq 40.3\%$ ); a more posterior gall bladder midpoint (70.1% vs. 67.8%); a shorter gall bladder–gonad gap (6.3% vs. 8.9%) and interval ( $\leq 15.2\%$  vs.  $\geq 16.7\%$ ); a shorter gall bladder–kidney gap (15.1% vs. 19.2%) and interval (21.7% vs. 26.3%); a shorter left gonad (2.5% vs. 4.8%) and total gonad length (7.1% vs. 11.1%); a more anterior right gonad ( $\leq 79.4\%$  vs.  $\geq 79.6\%$ ), left gonad ( $\leq 82.0\%$  vs.  $\geq 83.3\%$ ) and total gonad midpoint ( $\leq 80.6\%$  vs.  $\geq 81.5\%$ ); a more anterior left adrenal ( $\leq 83.6\%$  vs.  $\geq 83.6\%$ ) and total adrenal midpoint (82.8% vs. 85.0%); a

larger kidney overlap ratio ( $\geq 0.23$  vs.  $\leq 0.22$ ); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq -0.3\%$ ); a more craniad left kidney (89.5% vs. 91.6%) and total kidney midpoint (88.5% vs. 90.5%); a longer kidney–vent gap (8.9% vs. 6.8%) and interval (14.2% vs. 12.2%); a shorter rectal caecum length ( $\leq 2.2\%$  vs.  $\geq 2.5\%$ ); a longer rectal caecum–vent interval (8.9% vs. 7.4%); a smaller rectal caecum/left kidney ratio (0.53 vs. 0.99); more numerous tracheal rings ( $\geq 180$  vs.  $\leq 153$ ); a greater number of tracheal rings/10% SVL ( $\geq 83.3$  vs.  $\leq 79.5$ ); a shorter right lung length ( $\leq 25.2\%$  vs.  $\geq 29.6\%$ ); a more cranial right lung midpoint ( $\leq 34.6\%$  vs.  $\geq 35.5\%$ ) and posterior lung tip ( $\leq 47.2\%$  vs.  $\geq 50.3\%$ ); a shorter bronchus (17.3% vs. 19.8%) and trachea–bronchus length (37.3% vs. 39.7%); a more craniad bronchus posterior tip (38.6% vs. 40.7%); a shorter total lung length ( $\leq 27.2\%$  vs.  $\geq 30.8\%$ ) and total lung midpoint ( $\leq 33.6\%$  vs.  $\geq 34.9\%$ ); and a shorter heart–lung distance ( $\leq 14.6\%$  vs.  $\geq 16.9\%$ ) and heart–gonad distance ( $\leq 60.7\%$  vs.  $\geq 61.0\%$ ).

*Epictia resetari* can be distinguished from *E. tenella* by a maximum length of 142 mm (vs. 215 mm); a mid-dorsal scale count  $\geq 238$  (vs.  $\leq 233$ ); a sagittate rostral that extends to mid-eye level (vs. subtriangular rostral that does not reach anterior level of eye); a pale spot that covers entire rostral (vs. large spot extending beyond rostral border); a frontal shield as wide as long (vs. 1½ times wider than long); supraocular elongate and hexagonal with posterior borders parallel to posterior borders of supranasal (vs. short and pentagonal with oblique borders); ocular shield hexagonal, in contact with 5 scales (vs. pentagonal, in contact with 4 scales); eye partially beneath supranasal (vs. entirely beneath ocular); anterior supralabial moderate in height, separated from supraocular (vs. tall in height and contacting supraocular); a semilunate cloacal shield (vs. subtriangular); a pale caudal spot more than 5 times larger ventrally than dorsally (vs. slightly larger ventrally than dorsally); a dorsal midbody pattern with dark stripes composed of diamond-shaped spots separated by moderate-sized, pale zigzag stripes (vs. oval blotched dark stripes bordered by moderate to broad, straight pale stripes); a shorter sternohyoideus length ( $\leq 12.8\%$  vs.  $\geq 14.8\%$ ); a smaller sternohyoideus/snout–heart gap ratio ( $\leq 0.76$  vs.  $\geq 0.87$ ); a shorter heart length ( $\leq 4.0\%$  vs.  $\geq 4.9\%$ ); a longer heart–gall bladder gap (48.1% vs. 43.9%); a longer right liver length ( $\geq 39.0\%$  vs.  $\leq 38.3\%$ ), but shorter left liver length (28.2% vs. 31.2%); a more anterior left liver midpoint ( $\leq 47.4\%$  vs.  $\geq 47.9\%$ ); a larger posterior liver tail/liver length ratio ( $\geq 0.13$  vs.  $\leq 0.08$ ); a smaller left liver/right liver ratio ( $\leq 0.78$  vs.  $\geq 0.79$ ); fewer right liver ( $\leq 31$  vs.  $\geq 38$ ) and left liver segments ( $\leq 26$  vs.  $\geq 38$ ); a more posterior gall bladder midpoint (70.1% vs. 67.9%); a longer liver–gall bladder interval (42.5% vs. 38.2%); a longer gall bladder–kidney gap (15.1% vs. 12.3%); a longer liver–kidney gap (18.6% vs. 14.7%) and interval ( $\geq 62.8\%$  vs.  $\leq 60.5\%$ ); a more posterior right gonad midpoint ( $\geq 79.2$  vs.  $\leq 78.5\%$ ); a more posterior right adrenal ( $\geq 82.8\%$  vs.  $\leq 80.6\%$ ) and left adrenal midpoint ( $\geq 83.5\%$  vs.  $\leq 83.1\%$ ); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq 0$ ); a more caudad right kidney (87.5% vs. 82.9%), left kidney (89.5% vs. 85.9%), and total kidney midpoint (88.5% vs. 84.4%); a more posterior right kidney ( $\geq 87.0\%$  vs.  $\leq 86.5\%$ ) and left kidney midpoint ( $\geq 89.9\%$  vs.  $\leq 89.0\%$ ); a greater kidney overlap ratio ( $\geq 0.23$  vs.  $\leq 0.14$ ); a shorter kidney–vent gap ( $\leq 9.2\%$  vs.  $\geq 9.7\%$ ) and kidney–vent interval ( $\leq 14.8\%$  vs.  $\geq 15.5\%$ ); a shorter trachea ( $\leq 20.4\%$  vs.  $\geq 20.8\%$ ); a shorter right lung (24.8% vs. 32.4%); a more cranial right lung midpoint ( $\leq 34.6\%$  vs.  $\geq 36.2\%$ ), posterior tip ( $\leq 47.2\%$  vs.  $\geq 49.1\%$ ), and total lung midpoint ( $\leq 33.6\%$  vs.  $\geq 34.8\%$ ); a shorter trachea–bronchus length (37.3% vs. 41.5%) and a more caudal posterior tip (38.6% vs. 42.4%); a shorter heart–right lung distance ( $\leq 14.6\%$  vs.  $\geq 15.2\%$ ); and a longer liver–kidney distance (40.7% vs. 35.9%), right lung–adrenal distance ( $\geq 47.8\%$  vs.  $\leq 45.5\%$ ), trachea/bronchus–gall bladder distance (50.1% vs. 46.3%), heart–gonad distance ( $\geq 59.2\%$  vs.  $\leq 58.1\%$ ), heart–kidney distance ( $\geq 68.0\%$  vs.  $\leq 67.3\%$ ), trachea/bronchus–kidney distance (68.5% vs. 62.7%), and trachea–adrenal distance ( $\geq 70.6\%$  vs.  $\leq 69.8\%$ ).

**Remarks:** *Epictia resetari* represents a new species revealed by the molecular phylogeny of McCranie and Hedges (2016), referred to as *E. phenops*-3 (voucher specimen unknown) and *E. phenops*-4 (based on mitochondrial genes from UTA 52658 from “near La Victoria, Catemaco, Veracruz”) in their fig. 2. *Epictia resetari* closely resembles *E. vindumi*, but the populations are separated by 1,000 km and therefore recognizable under the concept of allopatric speciation. Separation and speciation probably is due to the Pleistocene glaciation (Martin, 1958; Lee, 1980).

### *Epictia schneideri* sp. nov.

Figs. 9A–O, 16X–Y

*Leptotyphlops albifrons*—Amaral, 1930b: 138 (part).

- Leptotyphlops bakewelli*—Smith and Taylor, 1945: 24 (part); Smith and Smith, 1976: S-B-128, S-C-37, S-D-4, S-F-17, S-F-30 (part), 1993: 590 (part).
- Leptotyphlops phenops bakewelli*—Smith and Taylor, 1945: 24, 1950: 328 (part); Davis and Dixon, 1959: 81; Holman, 1964: 49; Smith and Smith, 1976: S-B-130, S-C-37, S-D-30, S-F-17, S-F-30 (part).
- Leptotyphlops goudotii bakewelli*—Smith and Smith, 1976: S-B-129, S-C-37, S-D-18 (part); Orejas-Miranda *In* Peters et al., 1970 and 1986: 169 (part); Liner, 1994: 90, 2007: 54 (part); Wallach, 1998a: 490 (part); Liner and Casas-Andreu, 2008: 122 (part).
- Leptotyphlops phenops phenops*—Smith and Smith, 1976: S-B-130 (part).
- Leptotyphlops goudoti*—Smith and Smith, 1976: S-B-129, S-C-37, S-D-18, 1993: 591, 709 (part); Hahn, 1979: 230.2–3 (part); Flores-Villela, 1993: 35 (part).
- Leptotyphlops goudoti bakewelli*—Smith and Smith, 1976: S-B-128–130, S-C-37, S-G-4, 1993: 590–591, 593, 709 (part); Saldaña de la Riva, 1987: 39, 251–252 (part); Pérez-Ramos et al., 2000: 32 (part); Tipton, 2005: 24 (part); Varin, 2008: 122 (part).
- Leptotyphlops goudotii*—Smith and Smith, 1976: S-B-129, S-C-37, S-D-18, S-F-12 (part); Frank and Ramus, 1995: 250 (part); Hedges, 1996: 111, 115 (part); McDiarmid et al., 1999: 31 (part); Köhler, 2001a: 123 (part), 2001b: 12, fig. 11B (part); 2008: 183–184, map (part); Casas-Andreu et al., 2004: 389 (part); Adalsteinsson, 2008: 6, 29, 41, 47, figs. 3.2, 3.5 (part); Anonymous, 2009: 69 (part); CONABIO, 2009: 17 (part); Wilson and Johnson, 2010: 137, 233 (part); Wilson and Townsend, 2010: 811 (part); Wilson et al., 2013: 44 (part).
- Leptotyphlops goudotii phenops*—Hahn, 1980: 15–16 (part).
- Leptotyphlops goudotii bakewelli* (sic)—Pérez-Higareda and Smith, 1991: 29 (part).
- Leptotyphlops gaudoti* (sic)—Casas-Andreu et al., 1996: 34 (part).
- Epictia goudotii*—Adalsteinsson et al., 2009: 7, 10, 17, 31, 46, figs. 3A, 12 (part).
- Epictia goudoti*—CONABIO, 2012: 52 (part).
- Epictia bakewelli*—Wallach et al., 2014: 276 (part); Mata-Silva et al., 2015: 23, 41 (part); McCranie and Hedges, 2016: 4, 6, 18–20, figs. 2, 4 (part); Wilson and Johnson, 2016: 38 (part).

**Holotype:** TCWC 9450 (field no. RWA 543), a 141 mm (LOA) specimen collected by Roy W. Axtell on 23 June 1953, from 1.7 km SW Colotlipa, Guerrero, Mexico, 17°23'46"N, 99°10'48"W, elev. 825 m asl.

**Paratypes** (11): MEXICO: GUERRERO: Acahuizotla, 850 m, collected by Ralph W. Axtell on 14 June 1952, TCWC 7502 (field no. RWA 168); 1.7 km W Acahuizotla, collected by John E. Winbery on 11 June 1952, TCWC 7411 (field no. JEW 543); 1.7 km SW Colotlipa, 825 m, collected by D. K. Richards on 2 July 1953, TCWC 9451 (field no. DKR 112); 1.7 km SW Colotlipa, 825 m, collected by D. W. Morris on 29 June 1953, TCWC 9451 (field no. DWM 114); Chilpancingo, 1,290 m, collected by Wilmot W. Brown, Jr., on 15 May 1937, MCZ R-43278. OAXACA: Distrito Putla, 11.7 km S Putla, 760 m, UTEP 5981; Distrito Miahuatlán, San José Lachiguiri, 1,675 m, collected by Thomas B. MacDougall on 3 November 1971, UCM 52580 (field no. TBM 97). No specific locality, collected by Edward H. Taylor, FMNH 99676 (field no. EHT 15935/1015), FMNH 99677 (field no. EHT 15937/1016), FMNH 99678 (field no. EHT 15934/1018), and FMNH 99679 (field no. EHT 15938/1148).

**Etymology:** This species is named in honor of Greg Schneider, Collections Manager, Division of Reptiles and Amphibians, Museum of Zoology, University of Michigan (UMMZ), and commemorates his 30 years of service to the museum. Greg facilitated my work in Ann Arbor in 1986, and has provided loans, data, and photos on scoleophidians in the UMMZ collections since that time.

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 83–181 ( $\bar{x}$  = 123.6) mm; (4) total midodorsals = 243–265 ( $\bar{x}$  = 246.8); (5) subcaudals = 13–22 ( $\bar{x}$  = 18.2); (6) relative body proportion = 42–64 ( $\bar{x}$  = 53.3); (7) relative tail length = 4.5%–8.7% ( $\bar{x}$  = 6.6%); (8) relative tail width = 3.3–5.3 ( $\bar{x}$  = 4.2); (9) relative rostral width = 0.23–0.47 ( $\bar{x}$  = 0.37); (10) relative eye size = 0.44–0.45 ( $\bar{x}$  = 0.45); (10) rostral waisted with a posterior constriction, apex truncated, extending beyond eye level; (11) supralabials 2, moderate anterior supralabial reaching mid-eye level but not in contact with supraocular; (12) frontal fused with rostral; (13) supraoculars large and blocky, twice as broad as deep, with posterior borders parallel to those of supranasals; (14) widest anteriormost vertebral scale 2<sup>nd</sup>; (15) parietals and occipitals subequal, oriented transversely; (16) infralabials 4;

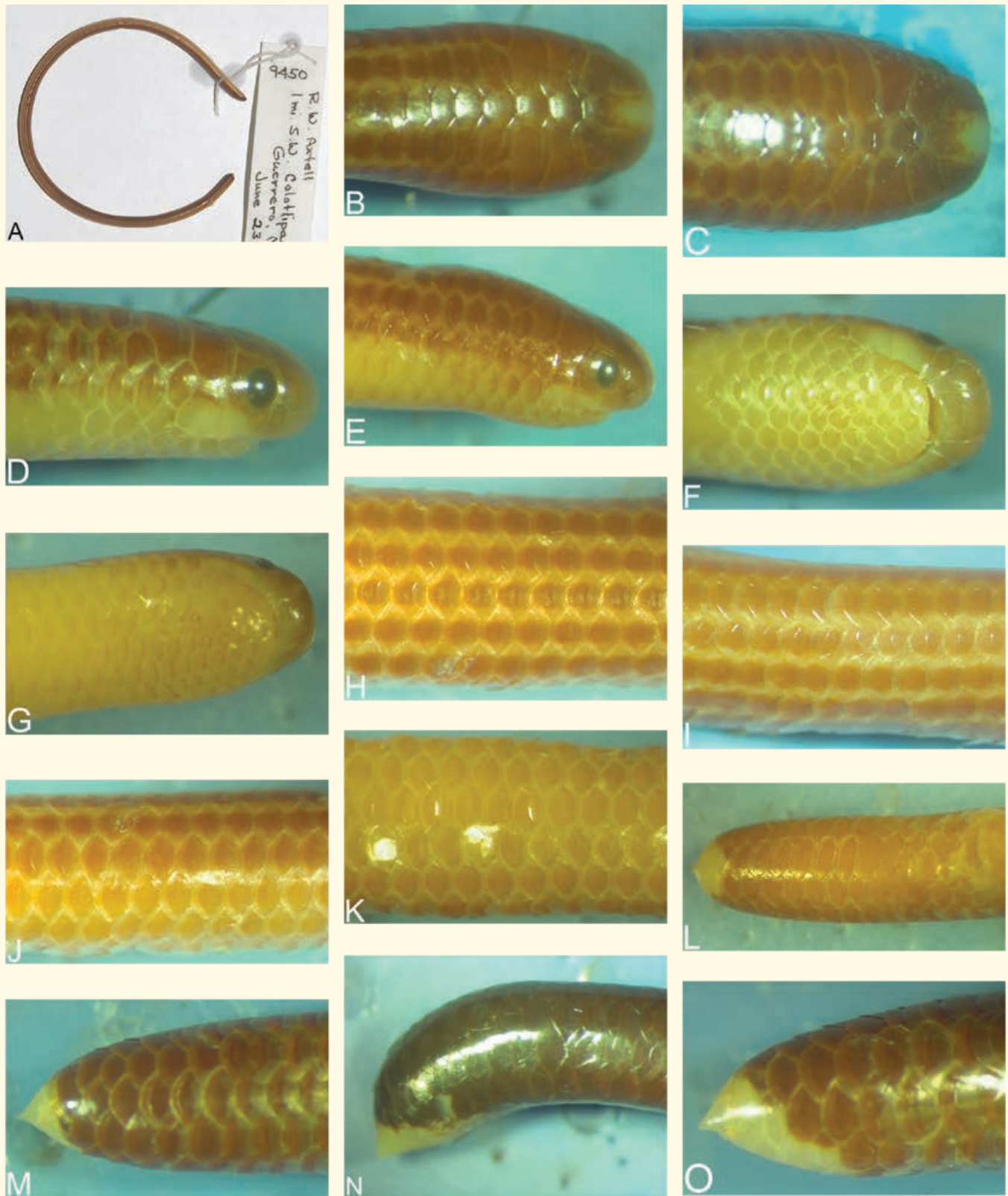


(17) cloacal shield semilunate in shape; (18) head brown with a pale spot on upper rostral; (19) dorsum with 3 brown middorsal linear stripes of rectangular-shaped spots bordered by moderate straight yellow lines and a solid brown midlateral stripe covering 2 scales (= 5 dark stripes); (20) venter uniform pale yellow with diffuse brown vermiculations on each scale; (21) midbody stripe formula (3 + 1/1 + 0), and middorsal pattern (3D + 4L); (22) tail with a pale terminal spot covering the 0.5–2 ( $\bar{x}$  = 1.8) dorsocaudals and 2–7 ( $\bar{x}$  = 5.2) subcaudals (ventral/dorsal ratio 1.8); and (23) apical spine a small spike.

**Description:** Holotype data include scale row formula = 14-14-14; midtail scale rows = 10; TMD = 259; SC = 16; LOA = 141.0 mm; TL = 8.5 mm; MBD = 3.0 mm; MTD = 2.6 mm; RW = 0.75 mm; HW = 1.9 mm; L/W = 47.8; TL/LOA = 6.0; TL/TW = 3.3; RW/HW = 0.39; and ED/OH = 0.45. Head broader than neck, all head shields with prominent sensory pits that appear as depressions in the scales; head tapered in dorsal profile with a rounded snout (Fig. 9B); rostral waisted posteriorly at site of fusion with frontal shield, parallel-sided anteriorly and tapering posteriorly with truncated apex (= fused frontal) extending beyond interocular level and in contact with supraoculars; postfrontal enlarged, slightly broader than deep (or as wide as long), subhexagonal in shape with rounded posterior contours, more than 1/2 of the size of the supraoculars, interparietal and interoccipital distinctly broader than deep; broadest anteriormost vertebral scale 2<sup>nd</sup>; supraoculars large and squarish or quadrangular with borders parallel to those of supranasals, twice as broad as deep; parietals slightly longer than occipitals, both shields oriented transversely; lateral head profile rounded; nasal completely divided, suture forming a shallow V-shaped angle along anterior supralabial and infranasal, nostril slit-like and positioned close to the rostral border; infranasal twice as tall as wide, narrowing toward lip; supralabials 2, anterior supralabial moderate in height with nearly parallel sides, reaching orbit and extending approximately to mid-eye level, its labial border equal to that of infranasal; ocular large, twice as tall as broad, roughly hexagonal with nasal and labial borders equal in length, slightly concave border with supranasal; eye large with distinct pupil and iris, distinctly oval or elliptical in vertical plane (Fig. 9D), equal to or slightly less than the lip-orbit gap (ED/OH = 0.44–0.45,  $\bar{x}$  = 0.45), slightly protuberant and barely visible in dorsal view; posterior supralabial as long as deep or slightly broader than deep, taller than anterior supralabial, posterior border rounded; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 4, 1<sup>st</sup> to 3<sup>rd</sup> small and 4<sup>th</sup> elongated; costal scales rounded and imbricate in 14 rows throughout; cloacal shield semilunate; and apical spine a small, horizontally-compressed spike supported on a conical base (Fig. 9L).

Overall coloration in life chocolate brown with yellow stripes, with a small, yellow, rostral spot and a moderate, yellow, caudal spot (Fig. 16X–AA). Preserved specimens golden brown to brown with 4 broad straight-sided yellow stripes that separate the 3 brown middorsal stripes at midbody (middorsal pattern of 3D + 4L), which appear as a connected string of rectangular-shaped spots; 2 brown midlateral scale rows (Fig. 9J), lacking yellow borders, form a single wide stripe (= 5 dark stripes) and separate the dorsal and ventral color patterns (midbody stripe formula = 3 + 1/1 + 0). Venter pale yellowish-tan, with faint brown diffusion (Fig. 9K). Head dorsum darker brown than body, with a moderate yellow spot on central portion of anterior part of rostral; lateral head brown with large yellow spot on lower half of the posterior supralabial and ocular (Fig. 9D), each shield with a yellow triangle rather than a horizontal bar. Chin immaculate yellow (Fig. 9F). Cloacal shield yellow with heavy brown vermiculations covering 1/3–1/2 of surface, cloaca with a pale yellow ring around cloacal shield. Tail brown with its apex covered by a small yellow spot, 1.8 times as long ventrally ( $\bar{x}$  = 5.2 subcaudals) as dorsally ( $\bar{x}$  = 1.8 dorsocaudals) (Fig. 9O).

**Viscera:** (mean value followed parenthetically by range,  $n$  = 3). Posterior tip of sternohyoideus muscle = 12.7% (12.3–13.4%); sternohyoideus/snout–heart gap = 0.83 (0.79–0.89); heart length = 3.9% (3.8–4.0%) with midpoint at = 17.2% (17.1–17.4%); snout–heart interval = 19.2% (19.1–19.3%); heart–liver gap = 8.7% (7.9–9.1%) and interval = 49.2% (48.2–49.7%); heart–gall bladder gap = 45.6% (44.2–46.3%); liver lobes multipartite; right liver length = 36.6% (36.5–36.6%) with midpoint at 46.2% (45.5–46.5%) and 43.7 (43–44) segments; left liver length = 27.2% (26.6–27.5%) with midpoint at 44.9% (43.4–45.6%) and 29.0 (27–30) segments; anterior liver extension = 0.09 (0.08–0.10) and posterior liver tail = 0.16 (0.15–0.19); left liver/right liver = 0.74 (0.73–0.75); liver–gall bladder gap = 0.4% (–0.3 to 0.7%) and interval = 38.5% (37.7–38.9%); liver–kidney gap = 17.2% (17.1–17.5%) and interval = 59.2% (58.4–60.8%); gall bladder length = 1.6% (1.5–1.7%) with midpoint at 65.6% (64.2–66.3%); gall bladder–gonad gap = 7.0% (5.3–8.1%) and interval = 14.3% (14.1–14.4%); gall bladder–kidney gap = 15.3% (14.8–16.4%) and interval = 22.3% (21.1–24.6%); right gonad length = 3.4% (2.7–4.7%) with midpoint at 75.1% (72.5–76.5%); left gonad length = 2.8% (2.7–2.9%) with midpoint at 77.7% (76.3–78.5%); gonad–kidney gap = 2.6% (2.0–3.5%) and interval = 13.6% (11.4–17.8%); right adrenal midpoint = 78.1% (76.5–78.9%) and left adrenal



**Fig. 9.** Morphological variation in *Epictia schneideri* sp. nov. (A) holotype of *E. schneideri* (TCWC 9450); (B, C) dorsal head (TCWC 9451, TCWC 7502); (D, E) lateral head (TCWC 9451, TCWC 7502); (F, G) ventral head (TCWC 9451, TCWC 7502); (H, I) dorsal midbody (TCWC 7502, TCWC 9451); (J) lateral midbody (TCWC 7502); (K) ventral midbody (TCWC 7502); (L) dorsal tail (TCWC 9451); (M) ventral tail (TCWC 7502); (N) lateral tail (UCM 52580); and (O) lateral apical spine (TCWC 9451).

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midpoint = 80.1% (78.9–80.9%); right kidney length = 3.0% (2.7–3.5%) with midpoint at 83.1% (83.0–83.2%); left kidney length = 3.0% (2.7–3.2%) with midpoint at 85.6% (85.1–86.4%); kidney overlap = 0.12 (0 to 0.21); kidney–vent gap = 12.9% (12.0–13.4%) and kidney–vent interval = 18.3% (18.1–18.7%); rectal caecum length = 0.7% (0.3–1.2%); and caecum–vent interval = 12.9% (12.0–13.4%). The three females contained 1 to 3 ( $\bar{x}$  = 1.7) developing eggs plus 4 or 5 ( $\bar{x}$  = 4.7) follicles in the right ovary, and 1 to 3 ( $\bar{x}$  = 1.7) developing eggs and 6 or 7 ( $\bar{x}$  = 6.7) follicles in the left ovary, for an assumed clutch size of 1 to 3 eggs ( $\bar{x}$  = 1.7).

Respiratory system lacking tracheal lung and left lung complex; trachea length = 17.7% (17.5–17.8%) with midpoint at 10.3% (10.2–10.5%) with an estimated 180 (170–184) tracheal rings or 100.2 (96.9–101.8) rings/10% SVL; anterior lung tip = 17.0% (16.8–17.5%); tracheal entry terminal; cardiac lung length = 2.1% (1.8–2.3%); right lung length = 32.2% (26.9–34.9%) with midpoint at 35.3% (32.7–36.6%) with faveolar cranial half and trabecular caudal half; posterior tip = 51.4% (46.2–54.0%); right bronchus length = 20.0% (17.0–21.5%); posterior tip of bronchus = 39.2% (36.3–40.6%); bronchus/right lung = 0.62 (0.62–0.63); trachea–bronchus length = 37.7% (34.5–39.3%) with midpoint at 20.3% (19.0–20.0%); trachea–bronchus/total lung length = 0.74 (0.73–0.75); and total lung length = 34.4% (28.7–37.2%) with midpoint at 34.2% (31.9–35.4%).

Visceral distance data include heart–right lung distance = 18.1% (15.3–19.5%); heart–liver distance = 29.0% (28.1–29.4%); trachea–liver distance = 35.9% (35.0–36.3%); liver–kidney distance = 38.2% (37.7–39.2%); right lung–adrenal distance = 43.8% (43.1–45.0%); trachea/bronchus–gall bladder distance = 45.3% (45.2–45.3%); heart–gonad distance = 57.9% (55.1–59.4%); trachea/bronchus–kidney distance = 64.0% (63.2–65.7%); heart–kidney distance = 67.2% (67.0–67.3%); and trachea–adrenal distance = 68.8% (67.2–69.7%).



**Map 9.** Distribution of *Epictia schneideri* nov. sp. in southern Mexico (Guerrero and Oaxaca).



**Distribution:** *Epictia schneideri* is a Mexican endemic known to occur in the Sierra Madre del Sur of southern Mexico (Guerrero, including Isla Ixtapa, and Oaxaca), overall elev. 825–1,675 m (Map 9).

**Ecology:** This species occurs in pine-oak, deciduous, and semi-evergreen forests (Casas-Andreu et al., 1996).

**Comparisons:** *Epictia schneideri* can be differentiated from *E. ater* by a truncated rostral apex (vs. triangular); a semilunate cloacal shield (vs. subtriangular); a pale subcaudal spot  $\leq 7$  scales (vs.  $\geq 6.5$  scales); a pale dorsocaudal/subcaudal spot ratio of 1.8 (vs. 5.1); a distinctly striped brown and yellow dorsal color pattern (vs. unicolored brown or black); a shorter heart length ( $\leq 4.0\%$  vs.  $\geq 4.7\%$ ) and more craniad midpoint ( $\leq 17.4\%$  vs.  $\geq 19.0\%$ ); a shorter snout–heart interval ( $\leq 19.1\%$  vs.  $\geq 21.4\%$ ); a more cranial right liver ( $\leq 46.5\%$  vs.  $\geq 46.6\%$ ), left liver ( $\leq 45.6\%$  vs.  $\geq 45.6\%$ ), and total liver midpoint (46.2% vs. 49.9%); a greater number of right liver (43.7 vs. 32.5) and total liver segments (72.7 vs. 57.8); a shorter anterior liver extension ( $\leq 0.10$  vs.  $\geq 0.12$ ); a longer liver–kidney gap ( $\geq 17.1\%$  vs.  $\leq 16.7\%$ ); a more anterior gall bladder midpoint (65.6% vs. 68.6%); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq 0.5\%$ ); a more cranial right adrenal (78.1% vs. 80.2%), left adrenal (80.1% vs. 82.9%), and total adrenal midpoint (79.1% vs. 81.5%); a shorter left kidney length ( $\leq 3.2\%$  vs.  $\geq 3.2\%$ ); a shorter trachea length ( $\leq 17.8\%$  vs.  $\geq 20.3\%$ ) and more anterior midpoint ( $\leq 10.5\%$  vs.  $\geq 11.2\%$ ); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs.  $\geq 18.5\%$ ); a shorter cardiac lung ( $\leq 2.3\%$  vs.  $\geq 2.7\%$ ), right lung (32.2% vs. 27.8%) and bronchus length (20.0% vs. 17.7%); a longer liver–kidney distance ( $\geq 37.7\%$  vs.  $\leq 37.6\%$ ); and a shorter trachea–liver distance (35.9% vs. 38.2%) and trachea/bronchus–gall bladder distance (45.3% vs. 48.1%).

*Epictia schneideri* is recognizable from *E. bakewelli* by a truncated rostral apex (vs. rounded); a small, indistinct pale rostral spot centered on the shield (vs. moderate, bold, and covering entire shield); a supraocular width/length ratio of 2.0 (vs. 1.5); a midbody stripe pattern of 5 dark stripes with 3 + 1/1 + 0 formula (vs. 7 dark stripes with 3 + 2/2 + 0 formula); a single midlateral dark stripes 2 scales wide (vs. 2 stripes, each a single scale wide); a semilunate cloacal shield (vs. subtriangular); a pale dorsocaudal spot  $\leq 2$  scales (vs.  $\geq 3$  scales); a pale subcaudal spot 5.2 scales long (vs. 8.9 scales); a pale subcaudal/dorsocaudal spot ratio of 1.8 (vs. 3.1); a brown cloacal shield (vs. yellow shield); a longer heart length ( $\geq 3.8\%$  vs.  $\leq 3.7\%$ ) and more anterior midpoint ( $\leq 17.4\%$  vs.  $\geq 17.9\%$ ); a shorter snout–heart interval ( $\leq 19.3\%$  vs.  $\geq 19.6\%$ ); a longer heart–liver gap ( $\geq 7.9\%$  vs.  $\leq 7.8\%$ ) and interval (49.2% vs. 46.1%); a longer heart–gall bladder gap (45.6% vs. 42.3%); a longer total liver length (63.8% vs. 61.6%); a greater number of right liver segments ( $\geq 43$  vs.  $\leq 41$ ); a longer posterior liver tail ( $\geq 0.15$  vs.  $\leq 0.15$ ); a shorter liver–kidney gap (17.2% vs. 20.8%) and interval ( $\leq 60.8\%$  vs.  $\geq 61.9\%$ ); a longer liver–gall bladder interval (38.5% vs. 36.2%); a longer gall bladder length ( $\geq 1.5\%$  vs.  $\leq 1.2\%$ ); a more caudal gall bladder midpoint (65.6% vs. 63.3%); a shorter gall bladder–kidney gap (15.3% vs. 19.9%) and interval (22.3% vs. 27.0%); a shorter gall bladder–gonad gap (7.0% vs. 12.2%) and interval (14.3% vs. 18.3%); a more craniad right gonad (75.1% vs. 77.5%), left gonad (77.7% vs. 79.6%), and total gonad midpoint (76.4% vs. 78.6%); a shorter left kidney ( $\leq 3.2\%$  vs.  $\geq 3.5\%$ ) and total kidney length ( $\leq 6.7\%$  vs.  $\geq 6.7\%$ ); a more cranial right kidney ( $\leq 83.2\%$  vs.  $\geq 83.7\%$ ), left kidney ( $\leq 86.4\%$  vs.  $\geq 86.5\%$ ), and total kidney midpoint ( $\leq 84.7\%$  vs.  $\geq 85.1\%$ ); a longer kidney–vent gap ( $\geq 12.0\%$  vs.  $\leq 11.7\%$ ) and interval ( $\geq 18.1\%$  vs.  $\leq 17.9\%$ ); a shorter trachea length ( $\leq 17.8\%$  vs.  $\geq 18.5\%$ ); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs.  $\geq 17.6\%$ ); a shorter liver–kidney distance (38.2% vs. 41.4%) and trachea/bronchus–kidney distance (64.0% vs. 66.1%); and a longer heart–liver distance (29.0% vs. 26.6%) and trachea/bronchus–gall bladder distance (45.3% vs. 42.8%).

*Epictia schneideri* can be separated from *E. columbi* by subcaudals  $\leq 22$  (vs.  $\geq 22$ ); a waisted rostral shape, extending posterior to eye level (vs. sagittate, not reaching eye level); a pale rostral spot present (vs. absent); lacking a discrete frontal (vs. frontal present); a supraocular width/length ratio twice as broad as deep (vs. barely wider than long); an oval eye shape,  $\geq 0.45$  ocular height, partially beneath supranasal and anterior supralabial (vs. round,  $\leq 0.41$  ocular height, completely beneath ocular); lacking a preoral groove (vs. present); a bicolored pattern with a single lateral and 3 dark dorsal stripes (vs. lacking stripes, uniformly dark); a longer sternohyoideus length ( $\geq 12.3\%$  vs. 11.7%); a larger sternohyoideus/snout–heart gap ratio ( $\geq 0.83$  vs. 0.75); a shorter heart length ( $\leq 4.0\%$  vs. 4.3%) and more craniad midpoint ( $\leq 17.4\%$  vs. 17.8%); a shorter snout–heart interval ( $\leq 19.3\%$  vs. 19.9%); a shorter heart–liver gap (12.1% vs. 15.2%) and longer interval ( $\geq 48.2\%$  vs. 47.7%); a longer heart–gall bladder gap ( $\geq 44.2\%$  vs. 43.8%); a longer right liver ( $\geq 36.5\%$  vs. 34.4%), left liver ( $\geq 26.6\%$  vs. 24.6%), and total liver length ( $\geq 63.1\%$  vs. 59.0%); a more anterior left liver midpoint ( $\leq 45.6\%$  vs. 47.5%); a shorter anterior liver extension ( $\leq 0.10$  vs. 0.18)

and longer posterior liver tail ( $\geq 0.15$  vs. 0.10); a greater left liver/right liver ratio ( $\geq 0.73$  vs. 0.72); a greater number of right liver ( $\geq 43$  vs. 35) and total liver segments ( $\geq 70$  vs. 63); a longer liver–gall bladder interval ( $\geq 37.7\%$  vs. 35.9%); a shorter liver–kidney gap ( $\leq 17.5\%$  vs. 20.3%) and interval ( $\leq 60.8\%$  vs. 62.5%); a longer gall bladder length ( $\geq 1.5\%$  vs. 1.2%); a shorter gall bladder–gonad gap ( $\leq 8.1\%$  vs. 13.3%); a shorter gall bladder–kidney gap ( $\leq 16.4\%$  vs. 18.8%) and interval ( $\leq 24.6\%$  vs. 27.7%); a longer total gonad length (6.1% vs. 3.1%); a more cranial right gonad ( $\leq 76.5\%$  vs. 79.3%), left gonad ( $\leq 78.5\%$  vs. 81.6%), and total gonad midpoint ( $\leq 77.5\%$  vs. 80.5%); a more cranial right adrenal ( $\leq 78.9\%$  vs. 80.7%), left adrenal ( $\leq 80.9\%$  vs. 81.6%), and total adrenal midpoint ( $\leq 79.9\%$  vs. 81.2%); a longer gonad–kidney gap ( $\geq 2.0\%$  vs. 1.6%); a shorter right kidney ( $\leq 3.5\%$  vs. 3.9%), left kidney ( $\leq 3.2\%$  vs. 3.9%), and total kidney length ( $\leq 6.7\%$  vs. 7.8%); a more anterior right kidney ( $\leq 83.2\%$  vs. 85.5%), left kidney ( $\leq 86.4\%$  vs. 89.5%), and total kidney midpoint ( $\leq 84.7\%$  vs. 87.5%); a greater kidney overlap ( $\geq 0$  vs. 0); a longer kidney–vent gap ( $\geq 12.0\%$  vs. 8.6%) and interval ( $\geq 18.1\%$  vs. 16.4%); a shorter rectal caecum length ( $\leq 1.2\%$  vs. 2.0%); a longer rectal caecum–vent interval ( $\geq 12.0\%$  vs. 9.8%); a smaller rectal caecum/left kidney ratio ( $\leq 0.38$  vs. 0.51); a shorter trachea length ( $\leq 17.8\%$  vs. 18.8%) and more cranial midpoint ( $\leq 10.5\%$  vs. 10.5%); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs. 18.4%); a longer cardiac lung ( $\geq 1.8\%$  vs. 1.6%), right lung ( $\geq 26.9\%$  vs. 26.6%), and total lung length ( $\geq 28.7\%$  vs. 28.1%); a more caudad posterior tip of lung (51.4% vs. 46.5%); a smaller bronchus/right lung ratio ( $\leq 0.63$  vs. 0.74); a smaller trachea-bronchus/total lung ratio ( $\leq 0.75$  vs. 0.82); a shorter right lung–adrenal distance ( $\leq 45.0\%$  vs. 48.0%), liver–kidney distance ( $\leq 39.2\%$  vs. 41.4%), heart–gonad distance ( $\leq 59.4\%$  vs. 61.5%), trachea/bronchus–kidney distance ( $\leq 65.7\%$  vs. 67.2%), and trachea–adrenal distance ( $\leq 69.7\%$  vs. 70.6%); and a longer trachea/bronchus–gall bladder distance ( $\geq 45.2\%$  vs. 44.0%).

*Epictia schneideri* can be distinguished from *E. magnamaculata* by a waisted rostral shape with a truncated apex extending beyond eye level (vs. sagittate with oval apex not reaching eye level); a small, indistinct, pale rostral spot centered on shield (vs. large, bold, and extending beyond rostral border onto at least the supranasals and frontal); pale paravertebral stripes not bordering occipitals and parietals and contacting rostral spot (vs. contacting occipitals, parietals, and rostral spot); lacking a discrete frontal (vs. frontal present); semilunate cloacal shield (vs. subtriangular); a pale subcaudal spot 1.8 scales long (vs. 4.2 scales); pale subcaudal/dorsocaudal spot ratio 1.8 (vs. 0.9); midbody stripe pattern of 5 dark stripes, 3 + 1/1 + 0 (vs. 11 dark stripes, 3 + 3/ 3 + 1/1); 1 midlateral dark stripe, 2 scales wide (vs. 3 stripes, each a single scale wide); unicolored midbody venter 7 rows wide (vs. 3 rows wide); a more anterior heart midpoint ( $\leq 17.4\%$  vs.  $\geq 17.5\%$ ); a shorter snout–heart interval ( $\leq 19.3\%$  vs.  $\geq 19.4\%$ ); a shorter heart–liver interval (49.2% vs. 51.6%); a shorter heart–gall bladder gap (45.6% vs. 49.4%); a shorter right liver (36.6% vs. 38.8%), left liver (27.2% vs. 29.9%), and total liver length (63.8% vs. 68.6%); a more cranial right liver (46.2% vs. 48.6%), left liver (44.9% vs. 48.9%), and total liver midpoint (46.2% vs. 48.6%); a more cranial left gonad midpoint ( $\leq 78.5\%$  vs.  $\geq 78.7\%$ ); a shorter liver–gall bladder gap (0.4% vs. 2.4%) and interval (38.5% vs. 42.7%); a more anterior gall bladder midpoint (65.6% vs. 71.1%); a longer gall bladder–kidney gap (15.3% vs. 12.3%) and interval (22.3% vs. 19.4%); a more cephalad right gonad (75.1% vs. 79.9%), left gonad (77.7% vs. 82.6%), and total gonad midpoint (76.4% vs. 81.2%); a longer gonad–kidney gap (2.6% vs. 0.2%); a more cranial right kidney (83.1% vs. 85.8%), left kidney (85.6% vs. 88.1%), and total kidney midpoint (84.4% vs. 86.9%); a more cranial right adrenal (78.1% vs. 72.9%), left adrenal (80.1% vs. 74.7%), and total adrenal midpoint (79.1% vs. 73.8%); a longer kidney–vent gap (12.9% vs. 10.3%) and interval (18.3% vs. 15.8%); a shorter trachea length ( $\leq 17.8\%$  vs.  $\geq 18.3\%$ ); a longer rectal caecum–vent interval (12.9% vs. 10.0%); a shorter trachea length (17.7% vs. 19.8%); a shorter right lung length (32.2% vs. 35.4%); a shorter trachea–liver distance (35.9% vs. 37.5%), trachea/bronchus–gall bladder distance (45.3% vs. 50.7%), heart–gonad distance (57.9% vs. 61.2%), and trachea/bronchus–kidney distance (64.0% vs. 66.5%); and a longer right lung–adrenal distance (43.8% vs. 38.4%) and trachea–adrenal distance (68.8% vs. 62.7%).

*Epictia schneideri* is diagnosable from *E. martinezi* by a waister rostral shape extending past eye level (vs. parallel, extending to mid-eye level); a small, indistinct, pale rostral spot not completely covering shield (vs. moderate, distinct spot completely covering shield); lacking a pale preocular spot and discrete frontal (vs. present); an eye size  $\leq 0.46$  ocular height (vs.  $\geq 0.47$  ocular height); a pale subcaudal/dorsocaudal spot ratio of 1.8 (vs. 3.1); 5 midbody stripes with straight borders, 3 + 1/1 + 0 (vs. 7 stripes with zigzag borders, 3 + 2/2 + 0); 1 midlateral dark stripe, 2 scales wide (vs. 2 stripes, each 1 scale wide); a more anterior heart midpoint ( $\leq 17.4\%$  vs.  $\geq 18.2\%$ ); a shorter snout–heart interval ( $\leq 19.3\%$  vs.  $\geq 20.4\%$ ); a more cranial right liver midpoint ( $\leq 46.5\%$  vs.  $\geq 46.8\%$ ); a greater number of right liver ( $\geq 43$  vs.  $\leq 41$ ) and left liver segments ( $\leq 30$  vs.  $\geq 32$ ); a longer liver–kidney gap ( $\geq$

17.1% vs.  $\leq 16.9\%$ ); a longer gall bladder length ( $\geq 1.5\%$  vs.  $\leq 1.4\%$ ); a more cranial left gonad midpoint ( $\leq 78.5\%$  vs.  $\geq 79.0\%$ ) and posterior left adrenal midpoint ( $\geq 78.9\%$  vs.  $\leq 78.9\%$ ); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq 0.4\%$ ); a shorter right kidney ( $\leq 3.5\%$  vs.  $\geq 4.9\%$ ), left kidney ( $\leq 3.2\%$  vs.  $\geq 4.0\%$ ), and total kidney length ( $\leq 6.7\%$  vs.  $\geq 9.0\%$ ); a more cranial right kidney midpoint ( $\leq 83.2\%$  vs.  $\geq 83.2\%$ ); a longer kidney–vent gap ( $\geq 12.0\%$  vs.  $\leq 10.9\%$ ); a longer rectal caecum–vent interval ( $\geq 12.0\%$  vs.  $\leq 11.9\%$ ); a shorter trachea length ( $\leq 17.8\%$  vs.  $\geq 18.0\%$ ) and more cranial midpoint ( $\leq 10.5\%$  vs.  $\geq 10.7\%$ ); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs.  $\geq 18.6\%$ ); a longer right lung length ( $\geq 26.9\%$  vs.  $\leq 24.6\%$ ) and more caudal midpoint ( $\geq 32.7\%$  vs.  $\leq 32.7\%$ ) and posterior tip ( $\geq 46.2\%$  vs.  $\leq 44.9\%$ ); a smaller bronchus/right lung ratio ( $\leq 0.63$  vs.  $\geq 0.79$ ); a more anterior trachea-bronchus midpoint ( $\leq 21.0\%$  vs.  $\geq 21.2\%$ ); a longer total lung length ( $\geq 28.7\%$  vs.  $\leq 26.3\%$ ); a smaller trachea-bronchus/total lung ratio ( $\leq 0.75$  vs.  $\geq 0.82$ ); a shorter right lung–adrenal distance ( $\leq 45.0\%$  vs.  $\geq 45.1\%$ ); and a longer heart–right lung distance ( $\geq 15.3\%$  vs.  $\leq 14.4\%$ ), heart–kidney distance ( $\geq 67.1\%$  vs.  $\leq 66.7\%$ ), and trachea–adrenal distance ( $\geq 67.2\%$  vs.  $\leq 67.0\%$ ).

*Epictia schneideri* can be differentiated from *E. pauldwyeri* by  $\geq 243$  total middorsals (vs.  $\leq 226$ ); a mean subcaudal count of 18.2 (vs. 12.7) and range of  $\geq 13$  (vs.  $\leq 14$ ); a tail length/width ratio  $\geq 3.3$  (vs.  $\leq 3.1$ ); a waister rostral shape, extending posterior to eye (vs. subtriangular shape, extending to mid-eye level); a small, indistinct rostral spot, covering center of shield (vs. moderate, distinct spot, covering entire shield); lacking a discrete frontal (vs. present); a semilunate cloacal shield (vs. subtriangular); a subcaudal/dorsocaudal ratio of 1.8 (vs. 0.9); 3 midbody dark dorsal stripes and 1 broad lateral stripe with connected rectangles and straight borders, 3 + 1/1 + 0 (vs. 7 stripes of connected diamonds with zigzag borders, 7 + 0); a single midlateral dark stripe, 2 scales wide (vs. 2 stripes, a single scale wide each); a brown cloacal shield (vs. yellow shield); a shorter heart length ( $\leq 4.0\%$  vs.  $\geq 5.1\%$ ) and more cranial midpoint ( $\leq 17.4\%$  vs.  $\geq 18.3\%$ ); a shorter snout–heart interval ( $\leq 19.3\%$  vs.  $\geq 20.8\%$ ); a more cranial right liver ( $\leq 46.5\%$  vs.  $\geq 47.2\%$ ) and left liver midpoint ( $\leq 45.6\%$  vs.  $\geq 47.2\%$ ); a longer posterior liver tail ( $\geq 0.15$  vs.  $\leq 0.11$ ); a smaller left liver/right liver ratio ( $\leq 0.75$  vs.  $\geq 0.78$ ); a greater number of right liver segments ( $\geq 43$  vs.  $\leq 41$ ); a longer liver–kidney gap ( $\geq 17.1\%$  vs.  $\leq 16.2\%$ ) and interval (59.2% vs. 56.9%); a longer gall bladder–kidney gap ( $\geq 14.8\%$  vs.  $\leq 14.4\%$ ); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq 0.5\%$ ); a shorter right kidney length ( $\leq 3.5\%$  vs.  $\geq 3.5\%$ ); a lesser rectal caecum/left kidney ratio (0.24 vs. 0.41); a longer trachea length ( $\leq 17.8\%$  vs.  $\geq 19.4\%$ ) and more anterior midpoint ( $\leq 10.5\%$  vs.  $\geq 11.1\%$ ); a greater number of tracheal rings/10% SVL ( $\geq 96.9$  vs.  $\leq 78.5$ ); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs.  $\geq 17.6\%$ ); a more cranial right lung midpoint ( $\leq 36.6\%$  vs.  $\geq 37.5\%$ ) and posterior tip (51.4% vs. 53.6%); a more cranial bronchus posterior tip ( $\leq 40.6\%$  vs.  $\geq 41.7\%$ ); a smaller bronchus/right lung ratio ( $\leq 0.63$  vs.  $\geq 0.63$ ); a shorter trachea-bronchus length ( $\leq 39.3\%$  vs.  $\geq 40.3\%$ ) and more anterior midpoint ( $\leq 21.0\%$  vs.  $\geq 21.5\%$ ); and a longer liver–kidney distance (38.2% vs. 35.5%), trachea/bronchus–gall bladder distance (45.3% vs. 43.3%), trachea/bronchus–kidney distance (64.0% vs. 60.8%), and heart–kidney distance (67.2% vs. 63.9%).

*Epictia schneideri* is identifiable from *E. phenops* by a waister rostral shape with a truncated apex, extending posterior to the eye (vs. sagittate with oval apex, extending to mid-eye level); lacking a discrete frontal (vs. present); an eye partly beneath supranasal and anterior supralabial (vs. completely beneath ocular); a subcaudal/dorsocaudal ratio of 1.8 (vs. 7.1); midbody dark stripes of connected rectangles with straight borders (vs. connected triangles with zigzag borders); a shorter heart–liver interval (49.2% vs. 52.5%); a shorter heart–gall bladder gap (45.6% vs. 48.1%); a shorter right liver (36.6% vs. 40.0%), left liver (27.2% vs. 31.3%), and total liver length (63.8% vs. 71.3%); a more cranial right liver (46.2% vs. 48.8%), left liver (44.9% vs. 47.5%), and total liver midpoint (46.2% vs. 48.8%); a shorter liver–gall bladder interval (38.5% vs. 41.6%); a shorter liver–kidney interval (59.2% vs. 62.1%); a more cranial gall bladder midpoint (65.6% vs. 69.7%); a more cranial right gonad (75.1% vs. 78.9%), left gonad (77.7% vs. 81.8%), and total gonad midpoint (76.4% vs. 80.4%); a more anterior right adrenal (78.1% vs. 81.2%), left adrenal (80.1% vs. 83.2%), and total adrenal midpoint (79.1% vs. 82.2%); a more caudal right kidney (83.1% vs. 86.7%), left kidney (85.6% vs. 88.9%), and total kidney midpoint (84.4% vs. 87.8%); a lesser kidney overlap ratio (0.12 vs. 0.26); a longer kidney–vent gap (12.9% vs. 9.2%) and interval (18.3% vs. 15.2%); a greater kidney–vent interval/right liver ratio (0.49 vs. 0.25); a longer rectal caecum–vent interval (12.9% vs. 9.7%); a shorter trachea length ( $\leq 17.8\%$  vs.  $\geq 18.1\%$ ); a shorter trachea–liver distance (35.9% vs. 37.8%); a shorter right lung–adrenal distance (43.8% vs. 45.6%); a shorter trachea/bronchus–gall bladder distance (45.3% vs. 48.9%); a shorter heart–gonad distance (57.9% vs. 60.3%); a shorter trachea–adrenal distance (68.8% vs. 71.2%) and heart–kidney distance (67.2% vs. 69.2%); and a longer trachea/bronchus–kidney distance (64.0% vs. 67.1%).



*Epictia schneideri* can be separated from *E. resetari* by a waisted rostral with a truncated apex, extending to post-eye level (vs. sagittate with oval apex, extending to mid-eye level); a small rostral, not completely covering rostral (vs. moderate, completely covering rostral); lacking a discrete frontal (vs. frontal present); an oval eye, partly beneath anterior supranasal (vs. round, eye, not beneath anterior supralabial); a subcaudal/dorsocaudal ratio of 1.8 (vs. 5.6); 5 midbody dark stripes with straight-sided rectangles, 3 + 1/1 + 0 (vs. 7 stripes with zigzag-bordered diamonds, 3 + 2/2 + 0); 1 midlateral dark stripe, 2 scales wide (vs. 2 stripes, each 1 scale wide); a sternohyoideus/snout–heart gap ratio  $\geq 0.83$  (vs.  $\leq 0.74$ ); a more cranial heart midpoint ( $\leq 17.4\%$  vs.  $\geq 18.7\%$ ); a shorter snout–heart interval ( $\leq 19.3\%$  vs.  $\geq 20.6\%$ ); a longer heart–liver gap ( $\geq 7.9\%$  vs.  $\leq 7.9\%$ ); a shorter heart–gall bladder gap (45.6% vs. 48.1%); a shorter right liver ( $\leq 36.6\%$  vs.  $\geq 39.0\%$ ) and total liver length ( $\leq 64.1\%$  vs.  $\geq 65.2\%$ ); a more cranial right liver ( $\leq 46.5\%$  vs.  $\geq 47.6\%$ ) and left liver midpoint ( $\leq 45.6\%$  vs.  $\geq 47.0\%$ ); a greater number of right liver ( $\geq 43$  vs.  $\leq 31$ ), left liver ( $\geq 27$  vs.  $\leq 26$ ), and total liver segments ( $\geq 70$  vs.  $\leq 56$ ); a shorter liver–kidney interval (59.2% vs. 62.9%); a shorter liver–gall bladder gap ( $\leq 0.7\%$  vs.  $\geq 0.8\%$ ) and interval ( $\leq 38.9\%$  vs.  $\geq 41.6\%$ ); a shorter liver–kidney gap ( $\leq 17.5\%$  vs.  $\geq 18.0\%$ ); a more anterior gall bladder midpoint ( $\leq 66.3\%$  vs.  $\geq 68.8\%$ ); a more cranial right gonad ( $\leq 76.5\%$  vs.  $\geq 79.2\%$ ), left gonad ( $\leq 78.5\%$  vs.  $\geq 82.0\%$ ), and total gonad midpoint ( $\leq 77.5\%$  vs.  $\geq 80.6\%$ ); a more cranial right adrenal ( $\leq 78.9\%$  vs.  $\geq 81.2\%$ ), left adrenal ( $\leq 80.9\%$  vs.  $\geq 83.5\%$ ), and total adrenal midpoint ( $\leq 79.9\%$  vs.  $\geq 82.4\%$ ); a more anterior right kidney ( $\leq 83.2\%$  vs.  $\geq 87.0\%$ ), left kidney ( $\leq 86.4\%$  vs.  $\geq 89.0\%$ ), and total kidney midpoint ( $\leq 84.7\%$  vs.  $\geq 88.0\%$ ); a smaller kidney overlap ratio ( $\leq 0.21$  vs.  $\geq 0.23$ ); a longer kidney–vent gap ( $\geq 12.0\%$  vs.  $\leq 9.2\%$ ) and interval ( $\geq 18.1\%$  vs.  $\leq 14.8\%$ ); a shorter rectal caecum length ( $\leq 1.2\%$  vs.  $\geq 1.2\%$ ); a longer rectal caecum–vent interval ( $\geq 12.0\%$  vs.  $\leq 9.2\%$ ); a lesser rectal caecum/left kidney ratio (0.24 vs. 0.53); a shorter trachea length ( $\leq 17.8\%$  vs.  $\geq 19.5\%$ ) and more cranial midpoint ( $\leq 10.5\%$  vs.  $\geq 10.9\%$ ); a greater number of tracheal rings/10% SVL ( $\geq 96.9$  vs.  $\leq 93.5$ ); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs.  $\geq 19.1\%$ ); a longer right lung length ( $\geq 26.9\%$  vs.  $\leq 25.2\%$ ); a more caudad right lung posterior tip (51.4% vs. 46.1%); a longer total lung length ( $\geq 28.7\%$  vs.  $\leq 27.2\%$ ); a smaller trachea-bronchus/total lung ratio ( $\leq 0.75$  vs.  $\geq 0.77$ ); a longer heart–right lung distance ( $\geq 15.3\%$  vs.  $\leq 14.6\%$ ); a shorter liver–kidney distance ( $\leq 39.2\%$  vs.  $\geq 40.4\%$ ), trachea/bronchus–gall bladder distance ( $\leq 45.3\%$  vs.  $\geq 47.2\%$ ), right lung–adrenal distance ( $\leq 45.0\%$  vs.  $\geq 47.8\%$ ), heart–gonad distance (57.9% vs.  $\geq 60.0\%$ ), trachea/bronchus–kidney distance ( $\leq 65.7\%$  vs.  $\geq 66.4\%$ ), and trachea–adrenal distance ( $\leq 69.7\%$  vs.  $\geq 70.6\%$ ); and a shorter heart–kidney distance ( $\leq 67.3\%$  vs.  $\geq 68.0\%$ ).

*Epictia schneideri* can be distinguished from *E. goudotii* by a waisted rostral with a truncated apex, extending posterior to eye (vs. triangular with rounded apex, not reaching eye); a small, indistinct, rostral spot covering central shield (vs. usually absent); lacking a discrete frontal (vs. present); an oval eye shape (vs. round); an eye partly beneath anterior supralabial (vs. not beneath supralabial); a moderately tall anterior supralabial, reaching mid-eye level (vs. short, not or barely reaching lower eye level); lacking a preoral groove (vs. present); a semilunate cloacal shield (vs. subtriangular shield); a pale dorsocaudal spot of 1.8 (vs. 0.5); a pale dorsocaudal/subcaudal spot ratio of 5.2 scales (vs. 0.7 scales) and subcaudal spot length  $\geq 2$  scales (vs.  $\leq 2$  scales); caudal termination a tiny spike (vs. spineless cone); a vividly striped middorsal pattern (vs. uniform brown with at most pale scale edges); a shorter sternohyoideus length ( $\leq 13.4\%$  vs. 13.7%); a shorter heart length ( $\leq 4.0\%$  vs. 6.0%) and more anterior midpoint ( $\leq 17.4\%$  vs. 19.7%); a shorter snout–heart interval ( $\leq 19.3\%$  vs. 22.7%); a longer heart–liver gap ( $\geq 7.9\%$  vs. 5.6%) and shorter interval ( $\leq 49.7\%$  vs. 52.8%); a shorter heart–gall bladder gap ( $\leq 46.3\%$  vs. 46.8%); a longer right liver ( $\leq 36.6\%$  vs. 41.2%), left liver ( $\leq 27.5\%$  vs. 30.0%), and total liver length ( $\leq 64.1\%$  vs. 71.2%); a more cranial right liver ( $\leq 46.5\%$  vs. 48.9%) and left liver midpoint ( $\leq 45.6\%$  vs. 48.1%); a shorter anterior liver extension ( $\leq 0.10$  vs. 0.11); a left liver/right liver ratio of  $\geq 0.73$  (vs. 0.73); a greater number of right liver ( $\geq 43$  vs. 35), left liver ( $\geq 27$  vs. 21), and total liver segments ( $\geq 70$  vs. 56); a shorter liver–gall bladder interval ( $\leq 38.9\%$  vs. 43.3%); a shorter liver–kidney interval ( $\leq 60.8\%$  vs. 63.9%); a shorter gall bladder length ( $\leq 1.7\%$  vs. 2.1%) and more cranial midpoint ( $\leq 66.3\%$  vs. 70.6%); a more cranial right gonad ( $\leq 76.5\%$  vs. 81.8%), left gonad ( $\leq 78.5\%$  vs. 86.5%), and total gonad midpoint ( $\leq 77.5\%$  vs. 84.2%); a more cranial right adrenal ( $\leq 78.9\%$  vs. 83.7%), left adrenal ( $\leq 80.9\%$  vs. 88.0%), and total adrenal midpoint ( $\leq 79.9\%$  vs. 85.9%); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $-2/1\%$ ); a shorter left kidney ( $\leq 3.2\%$  vs. 3.4%) and total kidney length ( $\leq 6.7\%$  vs. 6.8%); a more cranial right kidney ( $\leq 83.2\%$  vs. 88.4%), left kidney ( $\leq 86.4\%$  vs. 90.6%), and total kidney midpoint ( $\leq 84.7\%$  vs. 89.5%); a lesser kidney overlap ratio ( $\leq 0.21$  vs. 0.23); a longer kidney–vent gap ( $\geq 12.0\%$  vs. 7.7%) and interval ( $\geq 18.1\%$  vs. 13.3%); a shorter rectal caecum length ( $\leq 1.2\%$  vs. 1.3%); a smaller rectal caecum/left kidney ratio ( $\leq 0.38$  vs. 0.38); a longer rectal caecum–vent interval ( $\geq 12.0\%$  vs. 8.6%); a shorter trachea length ( $\leq 17.8\%$  vs. 21.0%) and more anterior midpoint

( $\leq 10.5\%$  vs.  $12.2\%$ ); a greater number of tracheal rings/10% SVL ( $\geq 96.9$  vs.  $85.4$ ); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs.  $20.2\%$ ); a shorter cardiac lung length ( $\leq 2.3\%$  vs.  $2.6\%$ ); a longer right lung length ( $32.2\%$  vs.  $27.9\%$ ) and more cranial midpoint ( $\leq 36.6\%$  vs.  $36.7\%$ ); a longer bronchus ( $\geq 17.0\%$  vs.  $14.6\%$ ) and trachea-bronchus length ( $37.7\%$  vs.  $35.6\%$ ); a greater bronchus/right lung ratio ( $\geq 0.62$  vs.  $0.52$ ); and a longer trachea-bronchus/total lung ( $\geq 0.73$  vs.  $0.70$ ); a shorter trachea–liver distance ( $\leq 36.3\%$  vs.  $36.7\%$ ), liver–kidney distance ( $\leq 39.2\%$  vs.  $40.6\%$ ), right lung–adrenal distance ( $\leq 45.0\%$  vs.  $49.2\%$ ), trachea/bronchus–gall bladder distance ( $\leq 45.3\%$  vs.  $51.1\%$ ), heart–gonad distance ( $\leq 59.4\%$  vs.  $62.1\%$ ), trachea/bronchus–kidney distance ( $\leq 65.7\%$  vs.  $70.0\%$ ), heart–kidney distance ( $\leq 67.3\%$  vs.  $69.8\%$ ), and trachea–adrenal distance ( $\leq 69.7\%$  vs.  $73.7\%$ ).

*Epictia schneideri* is identifiable from *E. albifrons* by total middorsals  $\geq 243$  (vs.  $\leq 218$ ); a subcaudal mean of  $18.2$  (vs.  $13.1$ ); a mean length/width ratio of  $53.3$  (vs.  $40.0$ ) and range  $\geq 42$  (vs.  $\leq 49$ ); a waisted rostral shape (vs. sagittate); a small, indistinct rostral spot, not completely covering shield (vs. moderate, distinct spot, completely covering shield); lacking a discrete frontal (vs. frontal present); a subtriangular cloacal shield (vs. pyramidal, with truncated apex); a pale subcaudal spot averaging  $5.2$  scales (vs.  $2.5$  scales);  $5$  midbody dark stripes, with straight-side connected rectangles,  $3 + 1/1 + 0$  (vs.  $7$  with zigzag-bordered triangles,  $7 + 0$ ); a single midlateral dark stripe,  $2$  scales wide (vs. double stripes, each  $1$  scale in width); a shorter sternohyoideus length ( $\leq 13.4\%$  vs.  $\geq 13.8\%$ ); a shorter heart length ( $\leq 4.0\%$  vs.  $\geq 4.4\%$ ) and more cranial midpoint ( $\leq 17.4\%$  vs.  $\geq 18.6\%$ ); a shorter snout–heart interval ( $\leq 19.3\%$  vs.  $\geq 20.8\%$ ); a longer heart–liver gap ( $12.1\%$  vs.  $9.0\%$ ); a shorter right liver ( $36.6\%$  vs.  $39.1\%$ ), left liver ( $\leq 27.5\%$  vs.  $\geq 27.8\%$ ), and total liver length ( $63.8\%$  vs.  $68.7\%$ ); a longer anterior liver extension ( $\geq 0.08$  vs.  $\leq 0.05$ ); a greater number of right liver ( $\geq 43$  vs.  $\leq 29$ ), left liver ( $\geq 27$  vs.  $\leq 23$ ), and total liver segments ( $\geq 70$  vs.  $\leq 52$ ); a shorter liver–gall bladder interval ( $\leq 38.9\%$  vs.  $\geq 39.1\%$ ); a shorter liver–kidney gap ( $17.2\%$  vs.  $19.8\%$ ) and interval ( $\leq 60.8\%$  vs.  $\geq 61.0\%$ ); a more anterior gall bladder midpoint ( $\leq 66.3\%$  vs.  $\geq 66.7\%$ ); a shorter gall bladder–kidney gap ( $15.3\%$  vs.  $19.2\%$ ) and interval ( $22.3\%$  vs.  $26.3\%$ ); a shorter right gonad ( $3.4\%$  vs.  $6.4\%$ ), left gonad ( $2.8\%$  vs.  $4.8\%$ ), and total gonad length ( $6.1\%$  vs.  $11.1\%$ ); a more cranial right gonad ( $\leq 76.5\%$  vs.  $79.6\%$ ), left gonad ( $\leq 78.5\%$  vs.  $83.3\%$ ), and total gonad midpoint ( $\leq 77.5\%$  vs.  $81.5\%$ ); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq -0.3\%$ ); a more cranial right adrenal ( $\leq 78.9\%$  vs.  $81.8\%$ ), left adrenal ( $\leq 80.9\%$  vs.  $83.6\%$ ), and total adrenal midpoint ( $\leq 79.9\%$  vs.  $82.7\%$ ); a more cranial right kidney ( $\leq 83.2\%$  vs.  $86.3\%$ ), left kidney ( $\leq 86.4\%$  vs.  $88.5\%$ ), and total kidney midpoint ( $\leq 84.7\%$  vs.  $87.4\%$ ); a longer kidney–vent gap ( $\geq 12.0\%$  vs.  $\leq 9.7\%$ ) and interval ( $\geq 18.1\%$  vs.  $\leq 15.4\%$ ); a greater kidney–vent interval/right liver ratio ( $0.49$  vs.  $0.25$ ); a shorter rectal caecum length ( $\leq 1.2\%$  vs.  $\geq 2.5\%$ ); a longer rectal caecum–vent interval ( $\geq 12.0\%$  vs.  $\leq 8.8\%$ ); a lesser rectal caecum/heart ratio ( $0.18$  vs.  $0.78$ ) and rectal caecum/left kidney ratio ( $\leq 0.38$  vs.  $\geq 0.71$ ); a shorter trachea length ( $\leq 17.8\%$  vs.  $\geq 19.5\%$ ) and more cranial midpoint ( $\leq 10.5\%$  vs.  $\geq 10.9\%$ ); a greater number tracheal rings/10% SVL ( $\geq 96.9$  vs.  $\leq 79.5$ ); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs.  $\geq 18.4\%$ ) and bronchus posterior tip ( $\leq 40.6\%$  vs.  $\geq 40.6\%$ ); a smaller bronchus/right lung ratio ( $\leq 0.63$  vs.  $\geq 0.63$ ); and a shorter liver–kidney distance ( $38.2\%$  vs.  $42.1\%$ ), trachea-bronchus length ( $\leq 39.3\%$  vs.  $\geq 39.6\%$ ), right lung–adrenal distance ( $\leq 45.0\%$  vs.  $\geq 47.2\%$ ), trachea/bronchus–gall bladder distance ( $\leq 45.3\%$  vs.  $\geq 46.0\%$ ), heart–gonad distance ( $\leq 59.4\%$  vs.  $\geq 61.0\%$ ), trachea/bronchus–kidney distance ( $\leq 65.7\%$  vs.  $\geq 66.3\%$ ), heart–kidney distance ( $\leq 67.3\%$  vs.  $\geq 68.8\%$ ), and trachea–adrenal distance ( $\leq 69.7\%$  vs.  $\geq 71.7\%$ ).

*Epictia schneideri* can be separated from *E. tenella* by total middorsals  $\geq 243$  (vs.  $\leq 233$ ); a waisted rostral shape, extending beyond eye level (vs. subtriangular, not reaching eye level); a small, indistinct, pale rostral spot not covering entire shield (vs. large, distinct, spot extending beyond rostral border); lacking a discrete frontal (vs. frontal present); supraocular pentagonal, twice as broad as deep (vs. hexagonal, more than three times broader than deep); parallel supranasal–supraocular borders (vs. oblique); ocular hexagonal, contacting  $5$  shields (vs. pentagonal, contacting  $4$  shields); eye oval, partly beneath supranasal and anterior supralabial (vs. round eye, completely beneath ocular); anterior supralabial moderate in height, not contacting supraocular (vs. tall, contacting supraocular); a semilunate cloacal shield (vs. subtriangular shield); a pale dorsocaudal/subcaudal spot ratio of  $5.2$  (vs.  $1.8$ );  $5$  midbody dark stripes with straight-sided conjoined rectangles,  $3 + 1/1 + 0$  (vs.  $7$  stripes, with zigzag-bordered ovals or diamonds,  $7 + 0$ ); a single midlateral dark stripe,  $2$  scales wide (vs.  $2$  stripes, each  $1$  scale wide); a shorter sternohyoideus length ( $\leq 13.4\%$  vs.  $\geq 14.8\%$ ); a greater sternohyoideus/snout–heart gap ratio ( $0.83$  vs.  $0.57$ ); a shorter heart length ( $\leq 4.0\%$  vs.  $\geq 4.9\%$ ) and more cranial midpoint ( $\leq 17.4\%$  vs.  $\geq 19.4\%$ ); a shorter snout–heart interval ( $\leq 19.3\%$  vs.  $\geq 21.9\%$ ); a longer heart–liver gap ( $12.1\%$  vs.  $9.9\%$ ); a longer left liver ( $\leq 27.5\%$  vs.  $\geq 27.6\%$ ) and total liver length ( $63.8\%$  vs.  $66.9\%$ ); a more anterior right liver ( $46.5\%$  vs.  $\geq 47.2\%$ ), left liver ( $\leq 45.6\%$  vs.  $\geq 47.9\%$ ), and

total liver midpoint (46.2% vs. 48.4%); a longer posterior liver tail ( $\geq 0.15$  vs.  $\leq 0.08$ ); a lesser left liver/right liver ratio ( $\leq 0.75$  vs.  $\geq 0.79$ ); a greater number of right liver ( $\geq 43$  vs.  $\leq 43$ ) and left liver segments ( $\leq 30$  vs.  $\geq 31$ ); a longer liver–kidney gap (17.2% vs. 14.7%) and interval (59.2% vs. 57.0%); a longer gall bladder–kidney gap (15.3% vs. 12.3%); a more cranial left gonad midpoint ( $\leq 78.5\%$  vs.  $\geq 79.0\%$ ); a more cranial right adrenal ( $\leq 78.9\%$  vs. 79.7%), left adrenal ( $\leq 80.9\%$  vs. 81.0%), and total adrenal midpoint ( $\leq 79.9\%$  vs. 80.4%); a longer gonad–kidney gap ( $\geq 2.0\%$  vs.  $\leq 0$ ); a shorter rectal caecum length ( $\leq 1.2\%$  vs.  $\geq 1.7\%$ ); a smaller rectal caecum/heart ratio (0.18 vs. 0.55); a lesser rectal caecum/left kidney ratio ( $\leq 0.38$  vs.  $\geq 0.41$ ); a shorter tracheal length ( $\leq 17.8\%$  vs.  $\geq 20.8\%$ ) and more anterior midpoint ( $\leq 10.5\%$  vs.  $\geq 11.5\%$ ); a greater number of tracheal rings/10% SVL ( $\geq 96.9$  vs.  $\leq 90.4$ ); a more cranial anterior tip of lung ( $\leq 17.5\%$  vs.  $\geq 19.3\%$ ); a more cranial right lung midpoint (35.3% vs. 39.4%), bronchus posterior tip (39.2% vs. 42.4%) and posterior tip of lung (51.4% vs. 55.6%); a shorter trachea-bronchus length ( $\leq 39.3\%$  vs.  $\geq 39.8\%$ ); and a longer liver–kidney distance (38.2% vs. 35.9%), right lung–adrenal distance (43.8% vs. 41.6%), and heart–kidney distance (67.2% vs. 63.9%).

**Remarks:** *Epictia schneideri* presumably represents the new species revealed by the molecular phylogeny of McCranie and Hedges (2016), referred to as *E. bakewelli*-4 (voucher specimen unknown) in their fig. 2, or an entirely separate discovery if that specimen did not originate from the Sierra Madre del Sur. The two other apparently undescribed species, represented as *bakewelli*-1 (based on mitochondrial genes from UTA 57498 from “between Puerto Escondido and Puerto Angel”) and *bakewelli*-3 (based on UTA 53657 from “between Mazunte and Piontepanoc”) in fig. 2, originate from coastal localities in Oaxaca.

I refer two specimens from Oaxaca (UTEP 5981 from near Putla, and UCM 52580 from San José Lachiguiri) as *E. schneideri* based on the unique color pattern of the species, in which 4 broad yellow middorsal stripes are as wide as or wider than the 3 enclosed brown stripes, the latter either composed of a brown stripe or segmented rectangles; laterally, 2 broader brown stripes are bordered by narrower yellow stripes; the midventral 7 scale rows are uniform pale yellow, but sometimes with a little brown infusion or pale brown. Several character differences are present in specimens from Oaxaca and those examined from Guerrero and Colima (supraoculars and cloacal shield). The pale caudal spots also differ in the three populations as follows (mean data for Colima ( $n = 3$ ), Guerrero ( $n = 6$ ), and Oaxaca ( $n = 2$ ), respectively): subcaudal spot—9.3, 3.6, 6.0; dorsocaudal spot—3.3, 1.4, 1.0, and subcaudal/dorsocaudal ratio—2.8, 2.6, 6.0. The midbody stripe formula is 3 + 1/1 + 0 in Colima material, but 3 + 2/2 + 0 in Guerrero and Oaxaca specimens.

### *Epictia vindumi* sp. nov.

Figs. 10A–O, 16Z

*Glauconia albifrons*—Barbour and Cole, 1906: 150; Fowler, 1913: 173; Werner, 1917: 203 (part); Haas, 1930: 59, 73, figs. 90–92 (part), 1931: 127 (part); Shattuck, 1933: 576; Dunn, 1944: 80; Smith and Smith, 1976: S-B-97, S-F-50.

*Stenostoma albifrons*—Schmidt, 1936: 168.

*Leptotyphlops albifrons*—Gäige, 1936: 298; 1938: 297; Schmidt, 1936: 168–169, 183; Schmidt and Andrews, 1936: 168–169, 183; Barrera, 1962: 9, 1963: 86; Smith and Smith, 1976: S-B-127–128, S-F-50.

*Leptotyphlops goudoti phenops*—Smith and Smith, 1976: S-B-129–130 (part); CONANP, 2012: 155.

*Leptotyphlops goudotii phenops*—Orejas-Miranda *In* Peters et al., 1970 and 1986: 170 (part); Smith and Smith, 1976: S-B-129–130, S-F-51; Hahn, 1980: 16 (part); Lee, 2000: 259.

*Leptotyphlops phenops*—Smith, 1939: 28; Klauber, 1940: 151 (part); Martin del Campo *In* Pearse, 1945: 225; List, 1966: 90–91, 107, pl. 16, fig. 7; Langebartel, 1968: 110–111, fig. 2K, 152; Smith and Smith, 1976: S-B-130, S-F-51 (part); Lee, 1977: 146, 177, fig. 43 (lower right), 1980: 11, 48, 63, pl. 15; Ferri, 2000: 105 (part).

*Leptotyphlops phenops phenops*—Smith and Taylor, 1945: 24 (part); Smith and Smith, 1976: S-B-130, S-F-51 (part).

*Leptotyphlops goudoti*—Hahn, 1979: 230.2–3 (part); Flores-Villela, 1993: 35 (part); Wilson and McCranie, 1998: 18, 31, 35 (part).

*Leptotyphlops goudotii* (sic)—Villa et al., 1988: 85 (part).

*Leptotyphlops goudotii*—Lazcano-Barrero et al., 1992: 36; Hedges, 1996: 111, 115 (part); Lee, 1996: 280–281, fig. 151A, map (part), 2000: 258–259, fig. 125A, col. fig. 306, map (part); Campbell, 1998: 186–187 (part); Wallach, 1998a: 490 (part); Cundall and Irish, 1998: 597; Lee, 2000: 258–259, fig. 125A, col. fig. 306, map 101; Sasa Marin, 2000: 150 (part); Köhler, 2001b: 12, fig. 11B (part), 2008: 183–184, map (part); Kearney, 2002: 735; García-Gil, 2006a: 220, 2006b: 209;



González-Baca, 2006: 13; Merediz-Alonso et al., 2007: 89; Elvira-Quesada et al., 2007: 37, 89; CONABIO, 2009: 17 (part); Anonymous, 2010b: 38; Chablé-Santos, 2010: 261, Anexo XV; Johnson et al., 2010: 368 (part); Wilson et al., 2013: 44 (part); Guerrero-González, 2014: 2.

*Epictia goudotii*—Canseco-Márquez and Gutiérrez-Mayén, 2010: 252 (part).

*Epictia phenops*—Wallach et al., 2014: 278 (part).

**Holotype:** FMNH 153536 (field number EWA 79), a 153 mm (LOA) specimen collected by E. Wyllis Andrews in February of 1959, from Chichén Itza, Yucatán, Mexico, 20°41'03"N, 88°34'06"W, elev. 35 m asl.

**Paratypes** (45): MEXICO: YUCATÁN: Chichén Itza: collected by Leon J. Cole between 13 February and 9 April 1904, MCZ R-7113; collected by Oliver G. Ricketson, Jr., in 1925, MCZ R-22060–62; collected by Joseph C. Bequaert in June of 1929, MCZ R-28747; collected by E. Wyllis Andrews on 2 April 1934, FMNH 20616–17; collected by E. Wyllis Andrews on 5 April 1934, FMNH 20618; collected by E. Wyllis Andrews on 2 April 1939, FMNH 36337 (field no. EWA 610); collected by E. Wyllis Andrews on 1 October 1939, FMNH 36338 (field no. EWA 15), FMNH 36343 (field no. EWA 7); collected by E. Wyllis Andrews on 5 October 1939, FMNH 36344 (field no. EWA 53); collected by E. Wyllis Andrews on 17 October 1939, FMNH 36339 (field no. EWA 210); collected by E. Wyllis Andrews on 7 November 1939, FMNH 36340 (field no. EWA 494); collected by E. Wyllis Andrews on 18 November 1939, FMNH 36336 (field no. EWA 522); collected by E. Wyllis Andrews on 15 March 1940, FMNH 36332 (field no. EWA 1322); collected by E. Wyllis Andrews, date unknown, FMNH 36334 (field no. EWA 1295), FMNH 36335 (field no. EWA 1292). Dzibilchaltun: collected by E. Wyllis Andrews in December of 1958, FMNH 153532 (field no. EWA 33), FMNH 153533 (field no. EWA 33), FMNH 153535 (field no. EWA 46); collected by E. Wyllis Andrews in January of 1959, FMNH 153542 (field no. EWA 58), FMNH 153546 (field no. EWA 184); collected by E. Wyllis Andrews in February of 1959, FMNH 153543 (field no. EWA 74); collected by E. Wyllis Andrews in September of 1959, FMNH 153545 (field no. EWA 100); collected by E. Wyllis Andrews in April of 1960, FMNH 153501 (field no. EWA 139), FMNH 153537 (field no. EWA 135), FMNH 153544 (field no. EWA 137), FMNH 153596 (field no. EWA 138); collected by E. Wyllis Andrews in November of 1961, FMNH 153586 (field no. EWA 165); collected by E. Wyllis Andrews in January of 1962, FMNH 153538 (field no. EWA 192); collected by E. Wyllis Andrews in November of 1963, FMNH 153587 (field no. EWA 229), FMNH 153588 (field no. EWA 230), FMNH 153589 (field no. EWA 231). Kantunil: collected by E. Wyllis Andrews on 7 November 1939, FMNH 36341 (field no. EWA 496), FMNH 36342 (field no. EWA 495). Merida: Had Chenku: collected by E. Wyllis Andrews on 7 January 1942, FMNH 40724, collected by E. Wyllis Andrews on 20 January 1942, FMNH 40725; collected by Eduardo C. Welling on 10 March 1965, UCM 29978. Piste: collected by Eduardo C. Welling on 8 August 1967, CM 49549; collected by Eduardo C. Welling on 20 August 1967, CM 49550; collected by Eduardo C. Welling on 3 September 1967, CM 49551–52; collected by Eduardo C. Welling on 16 September 1967, CM 49553; collected by Eduardo C. Welling on 22 September 1967, CM 49554.

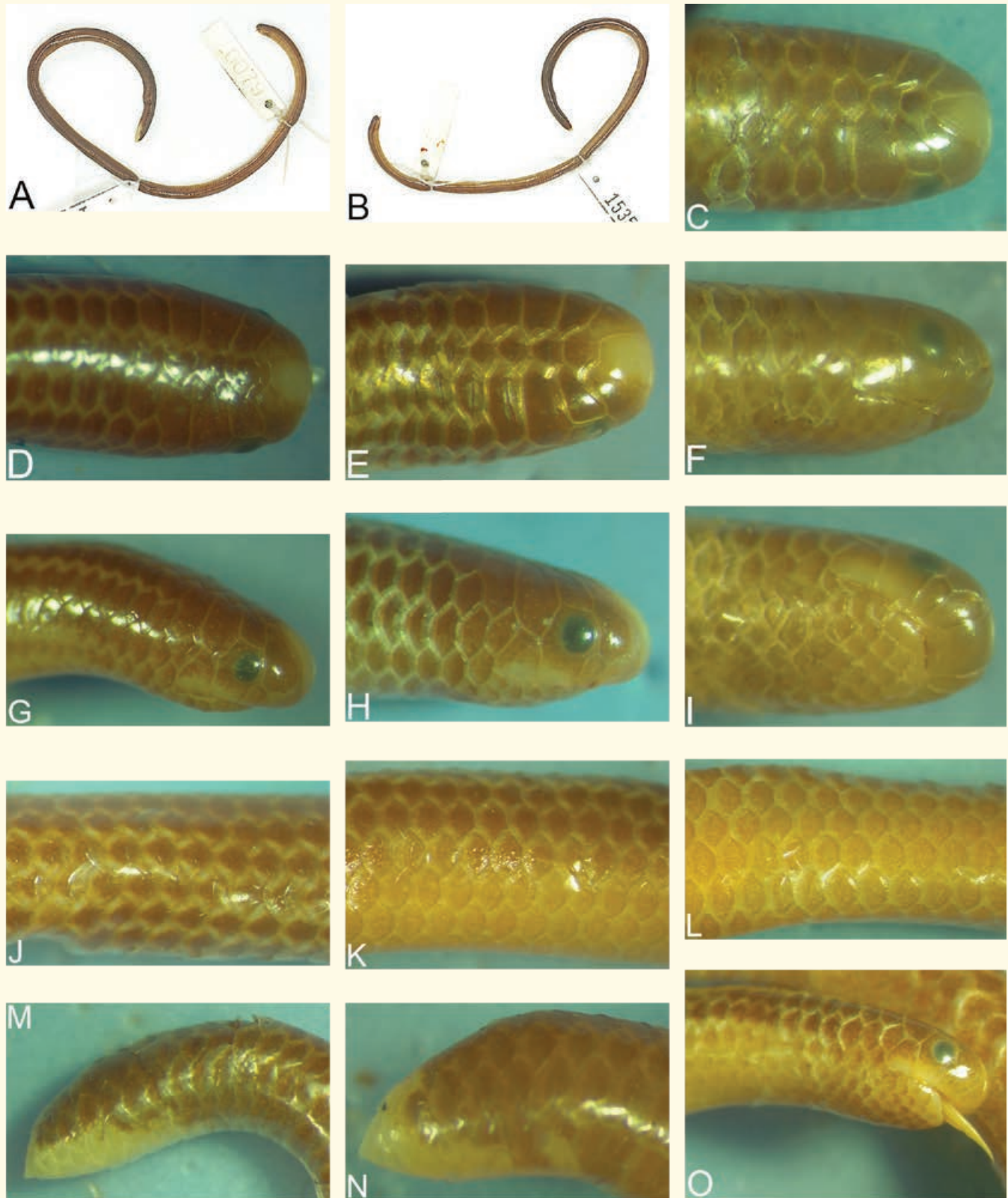
**Etymology:** This species is named in honor of Jens Vindum, Senior Collection Manager, Department of Herpetology, California Academy of Sciences (CAS), and commemorates his 35 years of service to the museum. During my early visits to the Academy from 1983 to 1985, to examine snake viscera, Jens was a most accommodating host during my stay, and since then always has lent material and shared data for my research.

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 72–163 ( $\bar{x}$  = 142.8) mm; (4) total midodorsals = 230–253 ( $\bar{x}$  = 243.6); (5) subcaudals = 15–23 ( $\bar{x}$  = 17.8); (6) relative body proportion = 40–70 ( $\bar{x}$  = 53.6); (7) relative tail length = 5.1%–9.0% ( $\bar{x}$  = 6.5%); (8) relative tail width = 2.8–5.7 ( $\bar{x}$  = 3.8); (9) relative rostral width = 0.24–0.44 ( $\bar{x}$  = 0.37); (10) relative eye size = 0.43–0.53 ( $\bar{x}$  = 0.48); (10) rostral parallel with a rounded apex, extending beyond the eye level; (11) supralabials 2, moderate anterior supralabial reaching mid-eye level; (12) frontal hexagonal, as broad as deep; (13) supraoculars large and pentagonal, twice as broad as deep, posterior border sloblique to supranasal borders; (14) widest anteriormost vertebral scale 3<sup>rd</sup>; (15) parietals and occipitals subequal, oriented transversely; (16) infralabials 4; (17) cloacal shield semilunate in shape; (18) head brown, with a yellow spot covering entire rostral; (19) dorsum with 7–9 dark brown stripes of diamond-shaped spots, bordered by moderate zigzag yellow stripes (= 7–9 dark stripes); (20) venter pale brown, many scales outlined in yellow; (21) midbody stripe formula (7–9 + 0) and middorsal pattern (3); (22) tail with a pale terminal spot covering dorsal scales 1–3 ( $\bar{x}$  = 1.7) and ventral scales 8–13 ( $\bar{x}$  = 9.8) (ventral/dorsal ratio 5.8); and (23) apical spine a small compressed spike.

**Description:** Holotype data include scale row formula = 14-14-14; midtail scale rows = 10; TMD = 249; SC = 18; LOA = 153.0 mm; TL = 9.5 mm; MBD = 3.05 mm; MTD = 2.45 mm; RW = 0.75 mm; HW = 2.0 mm; L/W = 50.2; TL/LOA = 56.2; TL/TW = 3.9; RW/HW = 0.375; and ED/OH = 0.47. Head slightly wider than neck, tapered in dorsal profile with a truncated snout, all head shields with prominent sensory pits that appear as depressions in the scales; rostral sagittate with parallel sides anteriorly, tapering posteriorly with truncated apex, extending beyond eye level (Fig. 10E); frontal hexagonal, as wide as deep, larger than next three scales (Fig. 10E); postfrontal, interparietal, and interoccipital subhexagonal in shape, with rounded edges; broadest anteriormost vertebral scale 3<sup>rd</sup>; supraoculars pentagonal, two to three times as wide as long, posterior border obliquely oriented to supranasal border (Fig. 10C); parietals and occipitals subequal in length, both shields transversely oriented; lateral head profile rounded; nasal completely divided, suture forming a shallow V-shaped angle along anterior supralabial and infranasal, nostril oval and positioned nearer the rostral than supralabial; infranasal twice as tall as long, narrowing toward lip; supralabials 2, anterior supralabial moderate in height with nearly parallel sides, not quite reaching center of eye, its labial border 1–1½ times as long as that of infranasal; ocular large, twice as high as wide, with a convex border with supranasal; eye large and elliptical, its diameter equal to distance between lip and orbit (ED/OH = 0.43–0.53,  $\bar{x}$  = 0.48), anterior edge partially beneath supranasal, slightly protuberant and visible in dorsal view; posterior supralabial taller than long, taller than anterior supralabial, with rounded posterior border; ventral rostral lacking a preoral groove (Fig. 10I); mental butterfly-shaped, infralabials 4, 4<sup>th</sup> the largest and longest, 2<sup>nd</sup> infralabial next largest, larger than 1<sup>st</sup> and 3<sup>rd</sup>; costal scales rounded and imbricate in 14 rows throughout; cloacal shield semi-lunate; and apical spine a compressed spike supported by a vertically compressed cone.

Overall color in life brown with yellow stripes, a moderate yellow rostral spot, and large yellow subcaudal spot. Midbody color pattern consists of 7–9 dark brown dorsal scale rows (forming stripes consisting of strings of diamond-shaped spots; Fig. 10J) bordered by 4 moderate yellow zigzag stripes, 2–3 midlateral brown stripes, each a single row in width, and 5–7 unicolored pale brown ventral scale rows (midbody stripe formula = 7–9 + 0 and middorsal pattern = 3). Head brown with an irregular pale yellow spot covering most of rostral; lateral head brown with a short yellow bar along lower edge of posterior supralabial and ocular (Fig. 10H); throat pale brown. Tail uniform brown above and below, cloacal shield paler than surrounding cloaca; yellow tail tip pattern consists of a small dorsal spot covering 1–3 dorsocaudals (average 1.7 scales) and a large ventral spot covering 8–13 subcaudals (average 9.8 scales), with the ventral/dorsal ratio 5.8.

**Viscera:** (mean value followed parenthetically by range,  $n$  = 5). Posterior tip of sternohyoideus muscle = 13.3% (11.8–14.8%); sternohyoideus/snout–heart gap = 0.87 (0.81–0.90); heart length = 4.4% (4.1–4.9%) with midpoint at 17.5% (15.6–18.9%); snout–heart interval = 19.7% (17.8–21.4%); heart–liver gap = 7.6% (6.6–9.0%) and interval = 49.5% (47.0–52.7%); heart–gall bladder gap = 46.7% (43.8–49.0%); liver lobes multipartite; right liver length = 37.5% (36.2–39.5%) with midpoint at 46.1% (42.4–49.4%) and 35.4 (26–42) segments; left liver length = 27.8% (23.7–31.8%) with midpoint at 45.6% (41.1–48.2%) and 25.6 (17–33) segments; anterior liver extension = 0.12 (0.07–0.18) and posterior liver tail = 0.14 (0.11–0.17); left liver/right liver = 0.74 (0.65–0.82); liver–gall bladder gap = 1.6% (0.7–4.3%) and interval = 40.6% (38.3–42.8%); gall bladder length = 1.5% (1.2–1.9%) with midpoint at 67.2% (62.3–71.0%); gall bladder–gonad gap = 8.9% (6.1–12.5%) and interval = 15.4% (12.8–18.4%); gall bladder–kidney gap = 16.6% (11.8–21.7%) and interval = 24.3% (20.0–29.3%); right gonad length = 3.1% (2.5–3.9%) with midpoint at 78.4% (73.7–82.7%); left gonad length = 2.6% (1.9–3.3%) with midpoint at 80.9% (78.5–85.2%); gonad–kidney gap = 2.5% (0–4.9%) and interval = 13.8% (10.7–19.1%); right adrenal midpoint = 80.5% (76.6–84.4%) and left adrenal midpoint = 82.4% (79.6–86.0%); right kidney length = 3.8% (3.1–4.3%) with midpoint at 86.5% (84.5–88.3%); left kidney length = 4.0% (3.9–4.2%) with midpoint at 88.7% (86.9–90.1%); kidney overlap = 0.28 (0.20–0.39); kidney–vent gap = 9.3% (7.8–11.0%) and kidney–vent interval = 15.4% (13.6–17.6%); rectal caecum length = 1.2% (1.0–1.3%); caecum–vent interval = 10.4% (8.7–12.5%). The smallest female (SVL 121 mm) contained 2 developing eggs and no follicles in the right ovary, and 1 developing egg and no follicles in the left ovary; another female (SVL 143.5 mm) contained 4 eggs and 3 follicles in the right ovary, and 4 eggs plus 5 follicles in the left ovary; and the largest female (SVL 152 mm) contained 7 eggs plus 7 follicles in the right ovary, and 6 eggs plus 4 follicles in the left ovary. Based upon this sample of three specimens, clutch size appears to be from 3 to 11 eggs. Two testis segments were present in the right testis and 4 segments in the left testis in the one male I examined.



**Fig. 10.** Morphological variation in *Epictia vindumi* sp. nov. (A, B) dorsal and ventral view of holotype of *E. vindumi* (FMNH 153536); (C, D, E) dorsal head (FMNH 153537, FMNH 153543, FMNH 153588); (F, G, H) lateral head (FMNH 153537, FMNH 153538, FMNH 153543); (I) ventral head (FMNH 153537); (J) dorsal midbody (FMNH 153538); (K) lateral midbody (FMNH 153538); (L) ventral midbody (FMNH 153538); (M) lateral tail (FMNH 153538); (N) lateral apical spine (FMNH 153537); and (O) lateral neck (FMNH 153586).

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Respiratory system lacking tracheal lung and left lung complex, trachea length = 18.6% (16.8–20.2%) with midpoint at 10.4% (9.4–11.3%) with an estimated 182 (168–207) tracheal rings or 96.5 (85.1–116.5) rings/10% SVL; anterior lung tip = 17.8% (15.8–19.2%); tracheal entry terminal; cardiac lung length = 1.9% (1.2–2.5%); right lung length = 25.8% (19.5–32.9%) with midpoint at 32.6% (28.3–37.9%) with faveolar cranial half and trabecular caudal half; right lung posterior tip = 45.5% (38.3–54.3%); right bronchus length = 17.7% (15.3–20.8%); posterior tip of bronchus = 37.5% (33.6–41.2%); bronchus/right lung = 0.70 (0.58–0.79); trachea-bronchus length = 36.4% (32.6–40.0%) with midpoint at 19.3% (17.34–21.2%); trachea-bronchus/total lung length = 0.80 (0.72–0.86); and total lung length = 27.7% (20.9–35.4%) with midpoint at 31.7% (27.3–36.6%).

Visceral distance data include heart–right lung distance = 15.1% (11.9–19.0%); heart–liver distance = 28.6% (26.8–30.5%); trachea–liver distance = 35.7% (33.0–38.1%); liver–kidney distance = 41.5% (36.9–45.5%); trachea/bronchus–gall bladder distance = 47.9% (45.0–50.2%); right lung–adrenal distance = 48.8% (45.3–52.3%); heart–gonad distance = 60.9% (58.1–63.8%); trachea/bronchus–kidney distance = 68.3% (64.5–70.6%); heart–kidney



**Map. 10.** Distribution of *Epictia vindumi* nov. sp. in southeastern Mexico (Yucatán and Quintana Roo).

distance = 70.1% (67.3–72.3%); and trachea–adrenal distance = 71.0% (68.7–73.9%).

**Distribution:** *Epictia vindumi* is a Mexican endemic with a distribution restricted to the northern portion of the Yucatan Peninsula (Quintana Roo and Yucatán), overall elev. NSL–30 m (Map 10).

**Ecology:** This species occurs in low scrubby deciduous thorn forest, ranging in height from three to seven meters and dominated by deciduous legumes (Lee, 1977).

**Comparisons:** *Epictia vindumi* can be differentiated from *E. ater* by a sagittate rostral with a truncated apex that extends to posterior eye level (vs. waisted rostral with arrowhead apex extending nearly to posterior border of ocular); a distinct rostral spot covering entire shield (vs. indistinct spot restricted to central region); a discrete frontal (vs. frontal fused with rostral); an elongate supraocular, twice as broad as deep, with posterior border oblique to supranasal posterior border (vs. blocky supraocular, 1½ times as wide as long, with posterior border parallel to that of supranasal); a round eye partly beneath supranasal shield (vs. oval eye partly beneath supranasal and anterior supralabial); a semilunate cloacal shield (vs. subtriangular shield); a midbody dorsal pattern consisting of brown diamond-shaped spots bordered by moderate, pale zigzag stripes (vs. uniformly dark); a more anterior heart midpoint ( $\leq 18.9\%$  vs.  $\geq 19.0\%$ ); a shorter snout–heart interval ( $\leq 21.4\%$  vs.  $\geq 21.4\%$ ); a more cranial right liver (46.1% vs. 49.9%), left liver (45.6% vs. 50.5%), and total liver midpoint (46.1% vs. 49.9%); a longer liver–gall bladder gap ( $\geq 0.7\%$  vs.  $\leq 0.5\%$ ) and interval (40.6% vs. 37.6%); a longer liver–kidney gap (19.8% vs. 15.3%) and interval (63.4% vs. 58.2%); a longer gall bladder–kidney gap (16.6% vs. 13.9%) and interval (24.3% vs. 22.3%); a longer gall bladder–gonad gap (8.9% vs. 5.3%); a shorter total gonad length (5.7% vs. 9.4%); a more posterior right gonad midpoint (78.4% vs. 76.4%); fewer right testis (2.0 vs. 5.3) and total testis segments (3.0 vs. 5.3); a longer gonad–kidney gap (2.5% vs. 0.2%); a more posterior right kidney (86.5% vs. 83.9%) and total kidney midpoint (87.6% vs. 85.5%); a shorter kidney–vent interval (15.4% vs. 18.1%); a shorter trachea ( $\leq 20.2\%$  vs.  $\geq 20.3\%$ ); a shorter cardiac lung length ( $\leq 2.5\%$  vs.  $\geq 2.7\%$ ); a more cranial right lung midpoint (33.5% vs. 36.3%), posterior lung tip (47.2% vs. 50.1%), and bronchus posterior tip (37.5% vs. 40.0%); a shorter trachea–bronchus length (36.4% vs. 39.1%) and trachea–liver distance (35.7% vs. 38.2%); and a longer liver–kidney distance (41.5% vs. 36.7%), liver–kidney distance (48.0% vs. 36.7%), heart–gonad distance (60.9% vs. 56.2%), trachea/bronchus–kidney distance (68.3% vs. 64.0%), and heart–kidney distance (70.1% vs. 65.4%).

*Epictia vindumi* is recognizable from *E. bakewelli* by a sagittate rostral with a truncated apex that extends to posterior of eye level (vs. waisted rostral with rounded apex extending nearly to posterior border of ocular); frontal shield present (vs. frontal absent, fused to rostral); posterior borders of supraocular and supranasal oblique (vs. parallel); a round eye (vs. oval eye); pale caudal spot 6 times longer ventrally than dorsally (vs. 3 times longer ventrally); a midbody dorsal pattern consisting of 7–9 brown diamond-shaped spots bordered by pale zigzag stripes (vs. 3 dark stripes of rectangular-shaped spots separated by 4 straight pale stripes, 3D + 4L, midlateral 2 scale rows forming a solid brown stripe); a brown cloacal shield (vs. yellow shield); a longer heart ( $\geq 4.1\%$  vs.  $\leq 4.0\%$ ); a longer heart–liver interval (49.5% vs. 46.1%); a longer heart–gall bladder gap (46.7% vs. 42.3%); a longer right liver (37.5% vs. 35.2%) and total liver length (65.2% vs. 61.6%); a longer liver–gall bladder gap ( $\geq 0.7\%$  vs.  $\leq 0.7\%$ ) and interval (40.6% vs. 36.2%); a more caudad gall bladder midpoint (67.2% vs. 63.3%); a shorter gall bladder–gonad gap (8.9% vs. 12.2%) and interval (15.4% vs. 18.3%); a shorter gall bladder–kidney gap (16.6% vs. 19.9%) and interval (24.3% vs. 27.0%); fewer right testis segments (2 vs. 4); a more posterior left adrenal midpoint (82.4% vs. 80.3%); a longer left kidney ( $\geq 3.9\%$  vs.  $\leq 3.7\%$ ); a longer total kidney length ( $\geq 7.0\%$  vs.  $\leq 7.0\%$ ); a shorter right lung (27.5% vs. 30.9%), midpoint (33.5% vs. 35.9%), and posterior tip (47.2% vs. 51.3%); a more caudal bronchus posterior tip (37.5% vs. 39.9%); a longer heart–liver distance (28.6% vs. 26.6%); a shorter trachea–bronchus length (36.4% vs. 38.8%); and a longer trachea/bronchus–gall bladder distance (47.9% vs. 42.8%), right lung–adrenal distance (48.0% vs. 43.7%), heart–gonad distance (60.9% vs. 58.9%), trachea/bronchus–kidney distance (68.3% vs. 66.1%), heart–kidney distance (70.1% vs. 68.0%), and trachea–adrenal distance (71.0% vs. 68.8%).

*Epictia vindumi* can be separated from *E. columbi* by the rostral extending beyond eye level (vs. not reaching eye level); pale rostral and caudal spots present (vs. absent); oblique supranasal/supraocular borders (vs. parallel); eye partially beneath supranasal (vs. entirely beneath ocular shield); preoral rostral groove absent (vs. present); tail terminus (small spine vs. cone with narrow blade); a longer sternohyoideus ( $\geq 11.8\%$  vs. 11.7%); a larger sternohyoideus/snout–heart gap ratio ( $\geq 0.81$  vs. 0.75); a shorter heart–liver gap ( $\leq 9.0\%$  vs. 9.0%), but longer heart–liver interval ( $\geq 47.0\%$  vs. 47.0%); a longer heart–gall bladder gap ( $\geq 43.8\%$  vs. 43.8%); a longer right liver ( $\geq 36.2\%$  vs. 34.4%), left liver (27.8% vs. 24.6%), and total liver length (65.2% vs. 59.05); a shorter anterior liver extension ( $\leq 0.18$  vs. 0.18), but longer posterior liver tail ( $\geq 0.11$  vs. 0.10); a longer liver–gall bladder interval ( $\geq 38.3\%$  vs. 35.9%); a longer gall bladder length ( $\geq 1.2\%$  vs. 1.2%); a more caudad gall bladder midpoint (67.2% vs. 64.3%); a shorter gall bladder–kidney gap (16.6% vs. 18.8%) and interval (24.3% vs. 27.7%); a shorter gall bladder–gonad gap ( $\leq 12.5\%$  vs. 13.3%) and interval (15.4% vs. 18.4%); a longer right gonad ( $\geq 2.5\%$  vs. 2.3%) and left gonad length ( $\geq 1.9\%$  vs. 0.8%); a greater kidney overlap ( $\geq 0.20$  vs. none); a shorter rectal caecum length ( $\leq 1.3\%$  vs.

2.0%) and rectal caecum/left kidney ratio ( $\leq 0.33$  vs. 0.51); a longer left kidney length ( $\geq 3.9\%$  vs. 3.9%); a more cranial bronchus posterior tip (37.5% vs. 39.5%); and a longer trachea/bronchus–gall bladder distance ( $\geq 45.0\%$  vs. 44.0%), and trachea/bronchus–gall bladder distance (47.9% vs. 44.0%).

*Epictia vindumi* can be distinguished from *E. magnamaculata* by a maximum length of 163 mm (vs. 220 mm); a rostral with a truncated apex that extends to posterior level of eye (vs. rostral with oval apex reaching anterior level of eye); a moderate rostral spot covering entire shield (vs. enlarged spot extending onto adjacent scale borders); a frontal as broad as deep (vs.  $1\frac{1}{2}$  times wider than long); an elongate supraocular, twice as broad as deep, with posterior border oblique to supranasal posterior border (vs. blocky supraocular,  $1\frac{1}{2}$  times as wide as long, with posterior border parallel to that of supranasal); a round eye partly under supranasal (vs. oval eye partly beneath supranasal and anterior supralabial); a semilunate cloacal shield (vs. subtriangular shield); a pale caudal spot 6 times longer ventrally than dorsally (vs. approximately equal above and below); tail terminating in a broad compressed blade (vs. apical spine); parietals and occipitals subequal and oblique in orientation (vs. parietals deeper than occipitals and oriented transversely); midbody dorsal pattern consisting of 7 brown stripes with diamond-shaped spots bordered by moderate, pale zigzag stripes (vs. 11 brown linear-blotched stripes separated by broad straight stripes); fewer right testis segments (2 vs. 4); a shorter heart–liver interval (49.5% vs. 51.6%); a shorter heart–gall bladder gap (46.7% vs. 49.4%); a shorter left liver (27.8% vs. 29.9%) and total liver length (65.2% vs. 68.6%); a more anterior right liver (46.1% vs. 48.6%), left liver (45.6% vs. 48.9%), and total liver midpoint (46.1% vs. 48.6%); a shorter liver–gall bladder interval (40.6% vs. 42.7%); a longer liver–kidney gap (19.8% vs. 16.2%) and interval (63.4% vs. 60.5%); a more cranial gall bladder midpoint (67.2% vs. 71.1%); a longer gall bladder–kidney gap (16.6% vs. 12.3%) and interval (24.3% vs. 19.4%); a longer gonad–kidney interval (13.8% vs. 11.5%); a more cranial right lung (47.2% vs. 49.9%) and bronchus posterior tip (37.5% vs. 39.6%); a longer trachea–bronchus length (36.4% vs. 38.5%); a shorter trachea/bronchus–gall bladder distance (47.9% vs. 50.7%); and a longer liver–kidney distance (41.5% vs. 38.4%) and trachea–adrenal distance (71.0% vs. 62.7%).

*Epictia vindumi* is diagnosable from *E. martinezi* by a sagittate rostral extending to post-eye level (vs. parallel rostral, extending to mid-eye level); lacking a pale preocular spot (vs. present); a round eye shape (vs. oval); a mean dorsocaudal spot length of 1.7 scales (vs. 2.4 scales); a mean subcaudal/dorsocaudal spot ratio of 5.8 (vs. 3.1); midbody stripe formula  $7 + 0$ , with all stripes equal in width (vs.  $3 + 2/2 + 0$  formula, with lateral stripes broader than middorsal stripes); a longer total liver length (65.2% vs. 63.1%); fewer left liver segments ( $\leq 33$  vs.  $\geq 34$ ); a longer liver–gall bladder interval (40.6% vs. 38.2%); a longer liver–kidney gap (19.8% vs. 16.0%) and interval (63.4% vs. 60.6%); a longer gall bladder–kidney gap (16.6% vs. 14.2%) and gall bladder–gonad gap (8.9% vs. 6.2%); a more caudal right gonad (78.4% vs. 75.3%) and total gonad midpoint (79.7% vs. 77.2%); a longer gonad–kidney gap (2.5% vs. 0.2%) and shorter interval (13.8% vs. 16.2%); a shorter right kidney ( $\leq 4.3\%$  vs.  $\geq 4.9\%$ ) and total kidney length ( $\leq 8.2\%$  vs.  $\geq 9.0\%$ ); a more posterior right kidney ( $\geq 84.5\%$  vs.  $\leq 84.2\%$ ) and total kidney midpoint (87.6% vs. 85.3%); a more caudal right adrenal (80.5% vs. 76.8%), left adrenal (82.4% vs. 78.9%), and total adrenal midpoint (81.4% vs. 77.8%); a shorter kidney–vent interval ( $\leq 17.6\%$  vs.  $\geq 18.3\%$ ); a greater number of left testis (4.0 vs. 1.5) and total testis segments (3.0 vs. 1.8); a longer right lung length (27.5% vs. 24.2%) and more caudal posterior tip (47.2% vs. 44.8%); a shorter bronchus length (17.7% vs. 20.1%) and more cranial posterior tip (37.5% vs. 40.7%); a lesser bronchus/right lung ratio ( $\leq 0.79$  vs.  $\geq 0.79$ ); a shorter trachea–bronchus length (36.4% vs. 38.7%) and more cranial midpoint ( $\leq 21.2\%$  vs.  $\geq 21.2\%$ ); and a longer heart–right lung distance (16.0% vs. 14.0%), liver–kidney distance (41.5% vs. 38.3%), right lung–adrenal distance ( $\geq 45.3\%$  vs.  $\leq 45.2\%$ ), trachea/bronchus–gall bladder distance (47.9% vs. 45.0%), heart–gonad distance ( $\geq 58.1\%$  vs.  $\leq 57.8\%$ ), trachea/bronchus–kidney distance (68.3% vs. 64.0%), heart–kidney distance ( $\geq 67.3\%$  vs.  $\leq 66.7\%$ ), and trachea–adrenal distance ( $\geq 68.7\%$  vs.  $\leq 67.0\%$ ).

*Epictia vindumi* can be separated from *E. pauldwyeri* by middorsals  $\geq 230$  (vs.  $\leq 226$ ); subcaudals  $\geq 15$  (vs.  $\leq 14$ ); relative rostral width of  $\leq 0.44$  (vs.  $\geq 0.42$ ); a sagittate rostral with truncated apex that extends to posterior eye level (vs. subtriangular rostral with rounded apex reaching mid-eye level); a frontal as wide as long (vs.  $1\frac{1}{2}$  times broader than deep); an elongate supraocular, twice as broad as deep, with posterior border oblique to supranasal posterior border (vs. blocky supraocular,  $1\frac{1}{2}$  times as wide as long, with posterior border parallel to that of supranasal); a round eye (vs. oval eye); a semilunate cloacal shield (vs. subtriangular shield); a pale caudal spot 6 times longer ventrally than dorsally (vs. subequal above and below); a brown cloacal shield (vs. yellow shield); a shorter heart length ( $\leq 4.9\%$  vs.  $\geq 5.1\%$ ); a longer heart–gall bladder gap (46.7% vs. 42.9%); a shorter left liver



length (27.8% vs. 29.8%) and more cranial midpoint (45.6% vs. 47.9%); a longer posterior liver tail ( $\geq 0.11$  vs.  $\leq 0.11$ ); a longer liver–gall bladder gap ( $\geq 0.7\%$  vs.  $\leq 0.5\%$ ) and interval (40.6% vs. 36.9%); a longer liver–kidney gap (19.8% vs. 14.2%) and interval (63.4% vs. 56.9%); a longer gall bladder–kidney gap (16.6% vs. 13.3%) and interval (24.3% vs. 21.7%); a longer gall bladder–gonad gap (8.9% vs. 6.6%); a more caudad right gonad (78.4% vs. 75.5%), left gonad (80.9% vs. 78.3%), and total gonad midpoint (79.7% vs. 76.9%); fewer right testis segments (2 vs. 4); a longer gonad–kidney gap (2.5% vs.  $-0.5\%$ ); a more caudal right kidney (86.5% vs. 81.8%), left kidney (88.7% vs. 84.8%), and total kidney midpoint (87.6% vs. 83.3%); a larger kidney overlap (0.28 vs. 0.14); a shorter kidney–vent gap (9.3% vs. 13.3%) and interval (15.4% vs. 20.0%); a smaller kidney–vent interval/right liver ratio (0.45 vs. 0.67); a shorter rectal caecum–vent interval (10.4% vs. 13.5%); a larger rectal caecum/heart ratio (0.29 vs. 0.19); a smaller rectal caecum/left kidney ratio ( $\leq 0.24$  vs.  $\geq 0.33$ ); a shorter trachea length (18.6% vs. 20.8%); more tracheal rings/10% SVL ( $\geq 85.1$  vs.  $\leq 78.5$ ); a shorter right lung length (27.5% vs. 31.6%); a more anterior right lung midpoint (33.5% vs. 37.8%) and posterior tip (47.2% vs. 53.6%); a shorter bronchus length ( $\leq 20.8\%$  vs.  $\geq 20.8\%$ ) and trachea–bronchus length ( $\leq 40.0\%$  vs.  $\geq 40.3\%$ ); a more cranial trachea–bronchus midpoint (19.3% vs. 22.5%) a more cranial bronchus midpoint (37.5% vs. 43.9%) and posterior tip ( $\leq 41.2\%$  vs.  $\geq 41.7\%$ ); a more anterior trachea–bronchus midpoint ( $\leq 21.2\%$  vs.  $\geq 21.5\%$ ); a shorter heart–right lung distance (16.0% vs. 18.4%); and a longer liver–kidney distance (41.5% vs. 35.5%), trachea/bronchus–gall bladder distance (47.9% vs. 43.3%), right lung–adrenal distance (48.0% vs. 42.1%), heart–gonad distance (60.9% vs. 56.1%), trachea/bronchus–kidney distance (68.3% vs. 60.8%), heart–kidney distance (70.1% vs. 63.9%), and trachea–adrenal distance (71.0% vs. 68.4%).

*Epicitia vindumi* is identifiable from *E. phenops* by a rostral with a truncated apex extending to posterior level of eye (vs. oval apex that extends to mid-eye level); a round eye partly beneath supranasal shield (vs. oval eye entirely beneath ocular); a midbody dorsal pattern with 7–9 brown stripes (vs. 3 brown stripes and a solid midlateral brown stripe 2 scales wide); a shorter heart–liver interval (49.5% vs. 52.5%); a shorter right liver (37.5% vs. 40.0%), left liver (27.8% vs. 31.3%), and total liver length (65.2% vs. 71.3%); a more cranial right liver (46.1% vs. 48.8%) and total liver midpoint (46.1% vs. 48.8%); a longer liver–kidney gap (19.8% vs. 16.0%); a more anterior gall bladder midpoint (67.2% vs. 69.7%); a longer gall bladder–kidney gap (16.6% vs. 14.4%) and interval (24.3% vs. 21.8%); a longer gall bladder–gonad gap (8.9% vs. 6.3%); fewer right testis (2.0 vs. 5.8) and total testis segments (3.0 vs. 5.3); a larger kidney–vent interval/right liver ratio (0.45 vs. 0.25); a shorter right lung length (27.5% vs. 31.4%); a more cranial right lung midpoint (33.5% vs. 36.6%) and posterior tip (47.2% vs. 52.3%); a more cranial bronchus posterior tip (37.5% vs. 40.3%); a longer trachea–bronchus length (36.4% vs. 39.1%); a shorter heart–right lung distance (16.0% vs. 18.0%) and trachea–liver distance (35.7% vs. 37.8%); and a longer liver–kidney distance (41.5% vs. 39.0%) and right lung–adrenal distance (48.0% vs. 45.6%).

*Epicitia vindumi* can be differentiated from *E. resetari* by a rostral with a truncated apex that extends to posterior eye level (vs. rostral with oval apex reaching mid-eye level); posterior borders of supraocular and supranasal oblique (vs. parallel); parietals equal in length to occipitals (vs. longer than occipitals); parietals and occipitals obliquely oriented (vs. transversely oriented); by a uniform brown cloacal region (vs. pale ring around cloacal shield); a larger sternohyoideus/snout–heart gap ratio ( $\geq 0.81$  vs.  $\leq 0.76$ ); a longer heart ( $\geq 4.1\%$  vs.  $\leq 4.0\%$ ); a shorter total liver length (65.2% vs. 67.3%); a more cranial gall bladder midpoint (67.2% vs. 70.1%); a longer gall bladder–kidney interval (24.3% vs. 21.7%); a longer gall bladder–gonad gap (8.9% vs. 6.3%); a longer left kidney ( $\geq 3.9\%$  vs.  $\leq 3.6\%$ ); a smaller rectal caecum/left kidney ratio ( $\leq 0.33$  vs.  $\geq 0.33$ ); a longer right lung (27.5% vs. 24.8%); and a shorter trachea/bronchus–gall bladder distance (47.9% vs. 50.1%).

*Epicitia vindumi* is recognizable from *E. schneideri* by a sagittate rostral (vs. waisted); a moderate, distinct, pale rostral spot completely covering rostral (vs. small, indistinct, spot not extending to rostral edges); a discrete frontal (vs. absent); a round eye (vs. oval); an eye partly beneath anterior supralabial (vs. not beneath supralabial); a mean, pale subcaudal spot of 9.8 scales (vs. 1.8 scales); a mean, pale subcaudal/dorsocaudal spot ratio of 5.8 (vs. 1.8); a midbody stripe pattern of 7–9 + 0 (vs. 3 + 1/1 + 0); 7–9 dark midbody stripes with zigzag-bordered diamonds (vs. 5 stripes with straight-sided rectangles); a pair of dark lateral stripes, 1 scale row in width (vs. a single dark stripe, 2 scale rows wide); a longer heart length ( $\geq 4.1\%$  vs.  $\leq 4.0\%$ ); fewer right liver segments ( $\leq 42$  vs.  $\geq 43$ ); a longer liver–gall bladder gap ( $\geq 0.7\%$  vs.  $\leq 0.7\%$ ) and interval (40.6% vs. 38.5%); a longer liver–kidney gap (19.8% vs. 17.2%) and interval (63.4% vs. 59.2%); a longer gall bladder–kidney interval (24.3% vs. 22.3%); a more posterior right gonad (78.4% vs. 75.1%), left gonad (80.9% vs. 77.7%), and total gonad midpoint (79.7% vs. 76.4%);

a more caudal right adrenal (80.5% vs. 78.1%), left adrenal (82.4% vs. 80.1%), and total adrenal midpoint (81.4% vs. 79.1%); a longer left kidney ( $\geq 3.9\%$  vs.  $\leq 3.2\%$ ) and total kidney length ( $\geq 7.0\%$  vs.  $\leq 6.7\%$ ); a more caudad right kidney ( $\geq 84.5\%$  vs.  $\leq 83.2\%$ ), left kidney ( $\geq 86.9\%$  vs.  $\leq 86.4\%$ ), and total kidney midpoint ( $\geq 85.7\%$  vs.  $\leq 84.7\%$ ); a greater kidney overlap ratio (0.28 vs. 0.12); a shorter kidney–vent gap ( $\leq 11.0\%$  vs.  $\geq 12.0\%$ ) and interval ( $\leq 17.6\%$  vs.  $\geq 18.1\%$ ); a shorter rectal caecum–vent interval (10.4% vs. 12.9%); a shorter right lung length (27.5% vs. 32.2%) and more cranial posterior tip (47.2% vs. 51.4%); a shorter bronchus length (17.7% vs. 20.0%); a shorter heart–right lung distance (16.0% vs. 18.1%); and a longer liver–kidney distance (41.5% vs. 38.2%), right lung–adrenal distance ( $\geq 45.3\%$  vs.  $\leq 45.0\%$ ), trachea/bronchus–gall bladder distance (47.9% vs. 45.3%), heart–gonad distance (60.9% vs. 57.9%), trachea/bronchus–kidney distance (68.3% vs. 64.0%), heart–kidney distance ( $\geq 67.3\%$  vs.  $\leq 67.3\%$ ), and trachea–adrenal distance (71.0% vs. 68.8%).

*Epictia vindumi* can be distinguished from *E. goudotii* by a relative rostral width of  $\leq 0.44$  (vs.  $\geq 0.42$ ); a sagittate rostral with a truncated apex that extends to posterior eye level (vs. triangular rostral with rounded apex reaching anterior eye level); a rounded snout in dorsal and ventral profile (vs. obtuse profile); posterior borders of supraocular and supranasal oblique (vs. parallel); a moderate anterior supralabial reaching mid-eye level (vs. a short anterior supralabial not or barely reaching lower border of eye); a semilunate cloacal shield (vs. subtriangular shield); a distinct yellow spot covering entire rostral (vs. indistinct or diffuse spot not covering entire rostral or absent); a pale caudal spot 6 times longer ventrally than dorsally (vs. barely longer ventrally than dorsally); lack of a preoral groove in ventral rostral (vs. distinct preoral groove); a spine-like caudal termination (vs. compressed cone); a midbody pattern with moderate, pale stripes (vs. narrow, pale scale borders); a shorter heart length ( $\leq 4.9\%$  vs.  $6.0\%$ ); a more cranial heart midpoint ( $\leq 18.9\%$  vs.  $19.7\%$ ); a shorter snout–heart interval ( $\leq 21.4\%$  vs.  $22.7\%$ ); a longer heart–liver gap ( $\geq 6.6\%$  vs.  $5.6\%$ ), but shorter heart–liver interval ( $\leq 52.7\%$  vs.  $52.8\%$ ); a shorter right liver ( $\leq 39.5\%$  vs.  $41.2\%$ ), left liver (27.8% vs. 30.0%), and total liver length ( $\leq 70.6\%$  vs.  $71.2\%$ ); a more anterior right liver (46.1% vs. 48.9%), left liver (45.6% vs. 48.1%), and total liver midpoint (46.1% vs. 48.9%); a longer liver–gall bladder gap ( $\geq 0.7\%$  vs. 0); a shorter liver–gall bladder interval ( $\leq 42.8\%$  vs.  $43.3\%$ ); a longer liver–kidney gap (19.8% vs. 17.2%); a shorter gall bladder length ( $\leq 1.9\%$  vs.  $2.1\%$ ) and more cranial midpoint (67.2% vs. 70.6%); a shorter gall bladder–gonad interval (15.4% vs. 19.3%); a longer gall bladder–kidney interval (24.3% vs. 22.7%); a more anterior left gonad ( $\leq 85.2\%$  vs.  $86.5\%$ ) and total gonad midpoint ( $\leq 83.9\%$  vs.  $84.2\%$ ); a more anterior left adrenal ( $\leq 86.0\%$  vs.  $88.0\%$ ) and total adrenal midpoint ( $\leq 85.2\%$  vs.  $85.9\%$ ); a longer gonad–kidney gap ( $\geq 0$  vs.  $-2.1\%$ ); a shorter right kidney ( $\leq 88.3\%$  vs.  $88.4\%$ ) and left kidney midpoint ( $\leq 90.1\%$  vs.  $90.6\%$ ); a longer kidney–vent gap ( $\geq 7.8\%$  vs.  $7.7\%$ ) and interval ( $\geq 13.6\%$  vs.  $13.3\%$ ); a shorter rectal caecum length ( $\leq 1.3\%$  vs.  $1.3\%$ ); a smaller caecum/left kidney ratio ( $\leq 0.33$  vs.  $0.38$ ); a longer caecum–vent interval ( $\geq 8.7\%$  vs.  $8.6\%$ ); a shorter trachea length ( $\leq 20.2\%$  vs.  $21.0\%$ ); a more anterior trachea midpoint ( $\leq 11.3\%$  vs.  $12.2\%$ ); a more cranial anterior lung tip ( $\leq 19.2\%$  vs.  $20.2\%$ ), and right lung midpoint (33.5% vs. 36.7%), and posterior tip (47.2% vs. 50.6%); a shorter cardiac lung length ( $\leq 2.5\%$  vs.  $2.6\%$ ); a longer bronchus length ( $\geq 15.3\%$  vs.  $14.6\%$ ); a greater bronchus/right lung ratio ( $\geq 0.58$  vs.  $0.52$ ); and a shorter trachea/bronchus–gall bladder distance ( $\leq 50.2\%$  vs.  $51.1\%$ ) and trachea–adrenal distance (71.0% vs. 73.7%).

*Epictia vindumi* is diagnosable from *E. albifrons* by the total middorsals  $\geq 230$  (vs.  $\leq 218$ ) and subcaudals  $\geq 15$  (vs.  $\leq 15$ ); a rostral with a truncated apex that extends to posterior eye level (vs. rostral with rounded apex reaching anterior level of eye); a distinct rostral spot covering entire shield (vs. indistinct spot restricted to central region); posterior borders of supraocular and supranasal oblique (vs. parallel); a round eye (vs. oval eye); a semilunate cloacal shield (vs. pyramidal shield with truncated apex); a pale caudal spot 6 times longer ventrally than dorsally (vs.  $2\frac{1}{2}$  times longer ventrally than dorsally); a longer heart–liver gap (12.0% vs. 9.0%); a longer total liver length (65.2% vs. 68.7%); a more cranial right liver midpoint (46.1% vs. 48.5%); a longer anterior liver extension ( $\geq 0.07$  vs.  $\leq 0.05$ ) and shorter posterior liver tail ( $\leq 0.17$  vs.  $\geq 0.17$ ); a shorter gall bladder–kidney gap (16.6% vs. 19.2%) and interval (24.3% vs. 26.3%); a shorter gall bladder–gonad interval (15.4% vs. 21.3%); a shorter right gonad (3.1% vs. 6.4%) and total gonad length (5.7% vs. 11.1%); a more cranial right gonad (78.4% vs. 80.6%), left gonad (80.9% vs. 85.9%), and total gonad midpoint (79.7% vs. 83.3%); a more anterior right adrenal (80.5% vs. 83.6%), left adrenal (82.4% vs. 86.4%), and total adrenal midpoint (81.4% vs. 85.0%); a longer gonad–kidney gap (2.5% vs.  $-0.6\%$ ), but shorter interval (13.8% vs. 15.9%); a more anterior right kidney (86.5% vs. 89.4%), left kidney (88.7% vs. 91.6%), and total kidney midpoint (87.6% vs. 90.5%); a larger kidney overlap (0.28 vs. 0.18); a longer kidney–vent gap (9.3% vs. 6.8%) and interval (15.4% vs. 12.2%); a larger kidney–vent interval/right liver

ratio (0.45 vs. 0.25); a shorter rectal caecum length ( $\leq 1.3\%$  vs.  $\geq 2.5\%$ ); a smaller rectal caecum/heart (0.29 vs. 0.78) and rectal caecum/left kidney ratio (0.29 vs. 0.99); a longer rectal caecum–vent interval (10.4% vs. 7.4%); more tracheal rings ( $\geq 168$  vs.  $\leq 153$ ); a greater number of tracheal rings/10% SVL ( $\geq 85.1$  vs.  $\leq 79.5$ ); a shorter right lung (27.5% vs. 30.2%), bronchus (17.7% vs. 19.8%), and trachea-bronchus length (36.4% vs. 39.7%); a more cranial right lung midpoint (33.5% vs. 36.0%), right lung posterior tip (47.2% vs. 51.1%), and bronchus posterior tip (37.5% vs. 40.7%); and a shorter trachea–adrenal distance (71.0% vs. 74.0%).

*Epictia vindumi* can be separated from *E. tenella* by a shorter maximum length of 163 mm (vs. 215 mm); a middorsals count of  $\geq 230$  (vs.  $\leq 233$ ); a sagittate rostral that extends to posterior eye level (vs. subtriangular rostral that does not reach eye level); a moderate rostral spot covering entire shield (vs. enlarged spot extending onto adjacent scales); a frontal as long as wide (vs. three times broader than deep); a pentagonal supraocular twice as broad as deep (vs. hexagonal supraocular, three times as wide as long); a hexagonal ocular in contact with 5 scales (vs. pentagonal ocular contacting 4 scales); an eye partly beneath supranasal shield (vs. eye completely under ocular); an anterior supralabial of moderate height not contacting supraocular (vs. a tall supralabial in contact with supraocular); a semilunar cloacal shield (vs. subtriangular shield); a pale caudal spot 6 times longer ventrally than dorsally (vs. barely longer below than above); a midbody dorsal pattern consisting of brown diamond-shaped spots bordered by pale zigzag stripes (vs. oval-shaped spots separated by pale straight stripes); a shorter sternohyoideus ( $\leq 14.8\%$  vs.  $\geq 14.8\%$ ); a shorter heart length ( $\leq 4.9\%$  vs.  $\geq 4.9\%$ ); a more anterior heart midpoint ( $\leq 18.9\%$  vs.  $\geq 19.4\%$ ); a shorter snout–heart interval ( $\leq 21.4\%$  vs.  $\geq 21.9\%$ ); a longer heart–liver gap (12.0% vs. 9.9%); a longer heart–gall bladder gap (46.7% vs. 43.9%); a shorter left liver length (27.8% vs. 31.2%); a more cranial right liver (46.1% vs. 48.5%), left liver (45.6% vs. 48.7%), and total liver midpoint (46.1% vs. 48.4%); a longer posterior liver tail ( $\geq 0.11$  vs.  $\leq 0.08$ ); a longer liver–gall bladder interval (40.6% vs. 38.2%); a longer liver–kidney gap (19.8% vs. 14.7%) and interval (63.4% vs. 57.0%); a longer gall bladder–kidney gap (16.6% vs. 12.3%) and interval (24.3% vs. 20.5%); a longer gall bladder–gonad gap (8.9% vs. 5.8%); a longer gonad–kidney gap ( $\geq 0$  vs.  $\leq 0$ ); a more caudal right kidney (86.5% vs. 82.9%), left kidney (88.7% vs. 85.9%), and total kidney midpoint (87.6% vs. 84.4%); a greater kidney overlap ratio ( $\geq 0.20$  vs.  $\leq 0.14$ ); a shorter kidney–vent gap (9.3% vs. 12.4%) and interval (15.4% vs. 19.0%); a shorter rectal caecum length ( $\leq 1.3\%$  vs.  $\geq 1.7\%$ ); a smaller rectal caecum/heart (0.29 vs. 0.55) and rectal caecum/left kidney ratio ( $\leq 0.33$  vs.  $\geq 0.41$ ); a shorter trachea length ( $\leq 20.2\%$  vs.  $\geq 20.8\%$ ); a more anterior trachea midpoint ( $\leq 11.3\%$  vs.  $\geq 11.5\%$ ); a more cranial anterior lung tip ( $\leq 19.2\%$  vs.  $\geq 19.3\%$ ); a shorter right lung (27.5% vs. 32.4%) and trachea bronchus length (36.4% vs. 41.5%); a more posterior right lung midpoint (33.5% vs. 39.4%), trachea-bronchus midpoint (19.3% vs. 21.7%), bronchus posterior tip (37.5% vs. 42.4%), and posterior lung tip (47.2% vs. 55.6%); a shorter heart–right lung distance (16.0% vs. 18.9%); and a longer liver–kidney distance (41.5% vs. 35.9%), right lung–adrenal distance (48.0% vs. 41.6%), heart–gonad distance ( $\geq 58.1\%$  vs.  $\leq 58.1\%$ ), heart–gonad distance (60.9% vs. 56.7%), heart–kidney distance ( $\geq 67.3\%$  vs.  $\leq 67.3\%$ ), trachea/bronchus–kidney distance (68.3% vs. 62.7%), heart–kidney distance (70.1% vs. 63.9%), and trachea–adrenal distance (71.0% vs. 68.9%).

**Remarks:** *Epictia vindumi* is an isolated and allopatric population, closely related to the Gulf Coast population (*E. resetari*), and separated by a distance of more than 1,000 km. Both Martin (1958) and Lee (1980) pointed out a Yucatán–East Mexico disjunct pattern of species due to Pleistocene glaciation events.

The anterior supralabial is fused with the ocular on both sides in FMNH 20618, from Chichen Itza.

### *Epictia wynni* sp. nov.

Figs. 11A–U, 15Q–R

*Leptotyphlops phenops*—Klauber, 1940: 151 (part); Dixon et al., 1972: 229; Smith and Smith, 1976: S-B-130 (part), S-F-34; Carabias-Lillo et al., 1999: 118.

*Leptotyphlops phenops phenops*—Smith and Taylor, 1945: 24 (part); Smith and Smith, 1976: S-B-130 (part), S-F-34; Yescas-Laguna, 2007: 149.

*Leptotyphlops goudotii phenops*—Orejas-Miranda In Peters et al., 1970 and 1986: 170 (part); Hahn, 1980: 16 (part).

*Leptotyphlops goudoti*—Smith and Smith, 1976: S-B-129–130 (part); Hahn, 1979: 230.2–3 (part); Montes de Oca and Pérez-Ramos, 1998: 90–91, 165 (map), 172; Carabias-Lillo et al., 1999: 118.

*Leptotyphlops goudoti phenops*—Smith and Smith, 1976: S-B-130 (part).



*Leptotyphlops goudotii*—Hedges, 1996: 111, 115 (part); Köhler, 2001b: 12, fig. 11B (part), 2008: 183–184, map (part); Tinoco-Navarro, 2005: 24, 27, 29–31, 33, 36, 46, 58, 77, 79, 81, 83, 85, 88, 90, 92; CONABIO, 2009: 17 (part); Dixon and Lemos-Espinal, 2010: 286–287, 428, map 71; Hernández-Salinas and Ramírez-Bautista, 2013: 10, fig. 5B.

*Leptotyphlops a[lbifrons] phenops*—Villavicencio, 2001: 131.

*Leptotyphlops goudotti* (sic)—Huitzil-Mendoza, 2007: 91.

*Epictia goudotii*—Ramírez-Bautista et al., 2010: 83, fig. 122, pl. 83, 2014: 200–201, col. photo 223; Wilson et al., 2013: 44 (part); Lemos-Espinal and Smith, 2015: 7.

*Epictia phenops*—Wallach et al., 2014: 278 (part).

**Holotype:** TCWC 32899 (field no. RLB 137), a 163 mm (LOA) specimen collected by R. L. Beck on 7 June 1970, from Río Ayutla, 30 km north of Jalpan de Serra, Querétaro, Mexico, 21°25'01"N, 99°36'15"W, elev. 575 m asl.

**Paratypes** (15): MEXICO: QUERÉTARO: Arroyo Seco, ca. 2 mi S Conca, between Hacienda X-Conca and Río Santa Maria, collected by Carl S. Lieb on 6 June 1979, UTEP H-20217 (field no. CSL 5708); 2.5 km NW Hacienda Conca, collected by Carl S. Lieb on 30 December 1971, TCWC H-37722 (field no. CSL 1201); nr. Río Santa Maria, W of Hacienda Conca, collected by Carl S. Lieb on 1 January 1972, TCWC H-37723 (field no. CSL 1223); Hacienda Conca, collected by Robert A. Thomas on 6 January 1974, TCWC H-45539 (field no. RAT 4892); Hacienda Conca, collected by Robert A. Thomas on 7 January 1974, H-45542 (field no. RAT 4895), H-45544 (field no. RAT 4897); Hacienda Conca, collected by Robert A. Thomas on 8 January 1974, H-45547 (field no. RAT 4912); El Trapiche, collected by S. Hayes on 4 January 1974, TCWC H-45525 (field no. RAT 4852); El Trapiche, collected by Robert A. Thomas on 5 January 1974, TCWC H-45526 (field no. RAT 4860), H-45528 (field no. RAT 4864), H-45530 (field no. RAT 4866), and H-45532–35 (field no. RAT 4868–71).

**Etymology:** This species is dedicated to Addison H. Wynn, Museum Specialist (Collections Manager), Division of Amphibians and Reptiles, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution (USNM), and commemorates his 35 years of service to the museum. Addison is an excellent researcher who works diligently on scolecophidians, and always has assisted me as a source of specimens, data, and ideas.

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 125–163 ( $\bar{x}$  = 147.2) mm; (4) total midodorsals = 242–260 ( $\bar{x}$  = 249.8); (5) subcaudals = 14–20 ( $\bar{x}$  = 16.3); (6) relative body proportion = 43–58 ( $\bar{x}$  = 47.8); (7) relative tail length = 4.4%–6.9% ( $\bar{x}$  = 5.7%); (8) relative tail width = 2.5–4.3 ( $\bar{x}$  = 3.3); (9) relative rostral width = 0.29–0.42 ( $\bar{x}$  = 0.36); (10) relative eye size = 0.36–0.44 ( $\bar{x}$  = 0.41); (10) rostral subtriangular with truncated apex, not or just reaching eye level; (11) supralabials 2, moderate anterior supralabial reaching mid-eye level; (12) frontal hexagonal, as wide than long; (13) supraoculars large, twice as broad as deep, posterior borders parallel to supranasal borders; (14) widest anteriormost vertebral scale 5<sup>th</sup>; (15) parietals deeper than occipitals, oriented transversely; (16) infralabials 3; (17) cloacal shield subtriangular; (18) head brown, with a small yellow spot on rostral; (19) dorsum with 7 dark brown to black stripes composed of contiguous strings of triangular- or diamond-shaped spots bordered by moderate to broad zigzag yellow stripes (= 7 dark stripes); (20) venter uniform brown; (21) midbody stripe formula (7 + 0) and middorsal pattern (3D + 4L); (22) tail with a pale terminal spot covering the 0–1 ( $\bar{x}$  = 0.4) dorsal scales and 0–8 ( $\bar{x}$  = 4.0) ventral scales (ventral/dorsal ratio 10.0); and (23) apical spine a small thin spike.

**Description:** Holotype data include scale row formula = 14-14-14; midtail scale rows = 10; TMD = 256; SC = 15; LOA = 163.0 mm; TL = 9.0 mm; MBD = 3.45 mm; MTD = 2.65 mm; RW = 0.75 mm; HW = 1.8 mm; L/W = 47.2; TL/LOA = 5.5; TL/TW = 3.4; RW/HW = 0.42; and ED/OH = 0.40. Head as broad as neck, all head shields with prominent sensory pits that appear as depressions in the scales; head tapered in dorsal profile with a rounded snout; rostral subtriangular in shape, apex usually truncated (occasionally rounded), not or just reaching the eye level; frontal and postfrontal broader than deep, subhexagonal in shape with rounded posterior contours (Fig. 11D); interparietal and interoccipital twice as broad as deep; broadest anteriormost vertebral scale 5<sup>th</sup>; supraoculars large and pentagonal with posterior borders parallel to supranasal borders, twice as wide as long; parietals and occipitals equal in length, both shields transverse in orientation; lateral head profile bluntly rounded with a slightly domed snout (Fig. 11F); nasal completely divided, suture forming a deep V-shaped angle (nearly 90°) along anterior supralabial and infranasal, nostril oval and positioned nearer the rostral than supralabial, located below suture in infranasal; infranasal twice as tall as long, narrowing toward lip; supralabials 2, anterior supralabial moderate in height

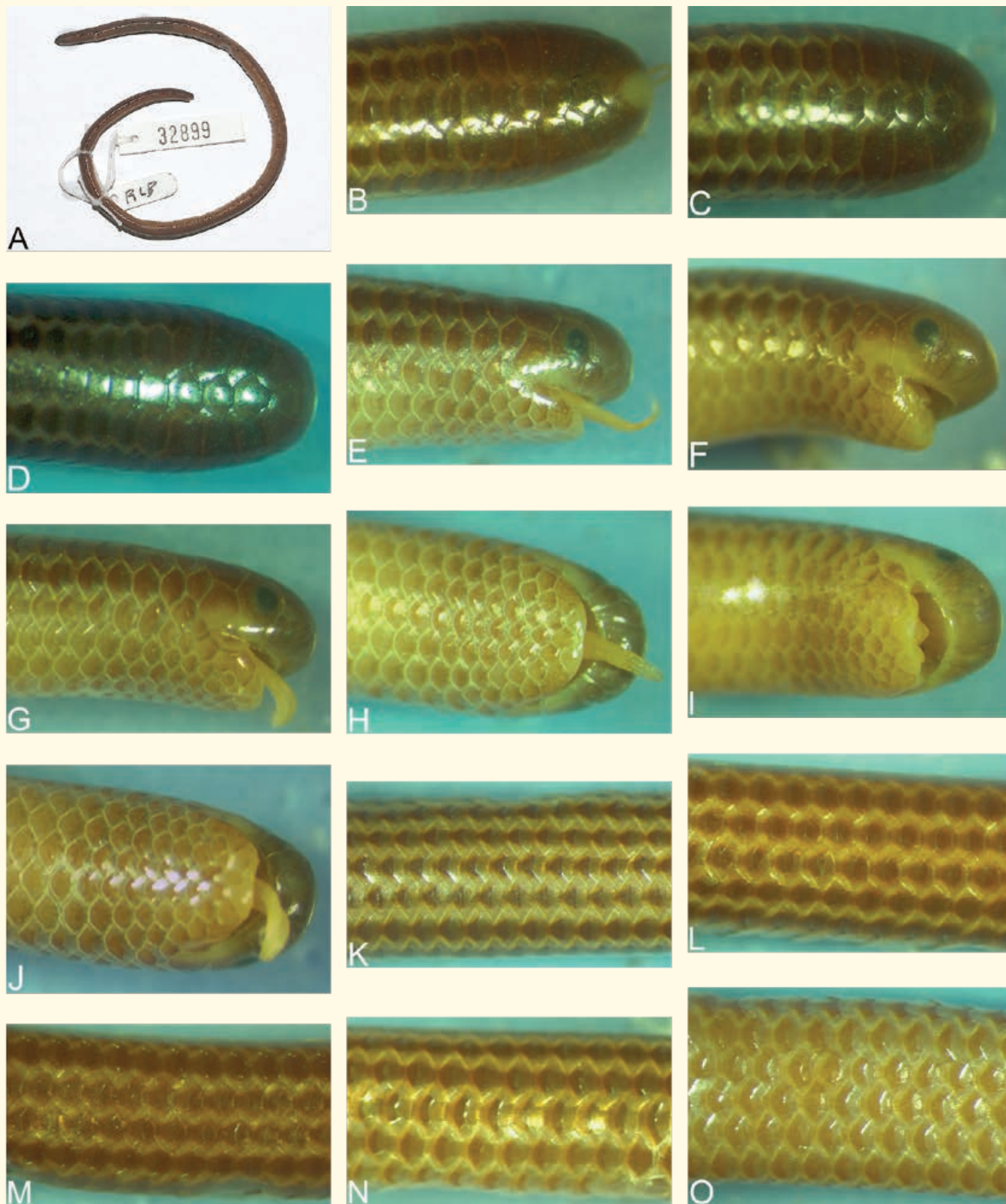
with nearly parallel sides, just reaching lower level of orbit, its labial border usually  $1\frac{1}{2}$  times as long as that of infranasal (rarely 1–2 times); ocular large, twice as tall as broad, roughly pentagonal with a nearly straight anterior border (but slightly concave border with supranasal); eye moderate-sized with distinct pupil and iris, slightly oval or elliptical in vertical plane, equal in depth to lip-orbit gap ( $ED/OH = 0.36\text{--}0.44$ ,  $\bar{x} = 0.41$ ), protuberant but not visible in dorsal view; posterior supralabial slightly taller than long, taller than anterior supralabial, posterior border rounded; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 3, 1<sup>st</sup> twice as broad as long, the normal 2<sup>nd</sup> and 3<sup>rd</sup> infralabials fused into single scale,  $1\frac{1}{4}$  times as broad as long, with scalloped posterior border (Fig. 11F–H), 3<sup>rd</sup> hidden beneath upper lip when mouth closed, 3 times as long as broad; costal scales roughly hexagonal in shape with rounded posterior edges and imbricate in 14 rows throughout; cloacal shield sub triangular (Fig. 11S); and apical spine a small thorn (Fig. 11T), horizontal or angled downward, projecting from a vertically compressed cone.

Overall coloration in life chocolate brown with bold yellow stripes, a small yellow rostral spot, and a moderate yellow caudal spot. The midbody region in preserved specimens contains 7 brown stripes composed of strings of interconnected diamond-shaped spots, 3 middorsal stripes bordered by broad, yellow, zigzag stripes (Fig. 11K) and 2 broader, dark, lateral stripes separated by moderate, yellow, zigzag stripes (Fig. 11U; middorsal pattern = 3D + 4L); ventral 7 scale rows paler than dorsum, generally unicolored pale brown but often with each scale faintly outlined in yellow (Fig. 11P, Q; midbody stripe formula = 3 + 2/2 + 0). Head dark brown with an irregular pale yellow spot covering most of upper rostral; lateral head with a broad, but short yellow spot bar along lower edge of posterior supralabial and ocular; throat pale brown (Fig. 11J). Tail uniform brown above and below, cloacal shield paler than surrounding cloaca, sometimes with a pale yellow ring, shield itself pale with brown vermiculations covering  $\frac{1}{2}\text{--}\frac{3}{4}$  of the scale; tail with a distinctive yellow tip pattern consisting of a very small dorsal spot covering not more than one dorsocaudal and a moderate ventral spot (averaging 4.0 subcaudals), the ventral/dorsal ratio being 10.0 (Fig. 11C); and tail terminates in a vertically compressed horizontally directed spike.

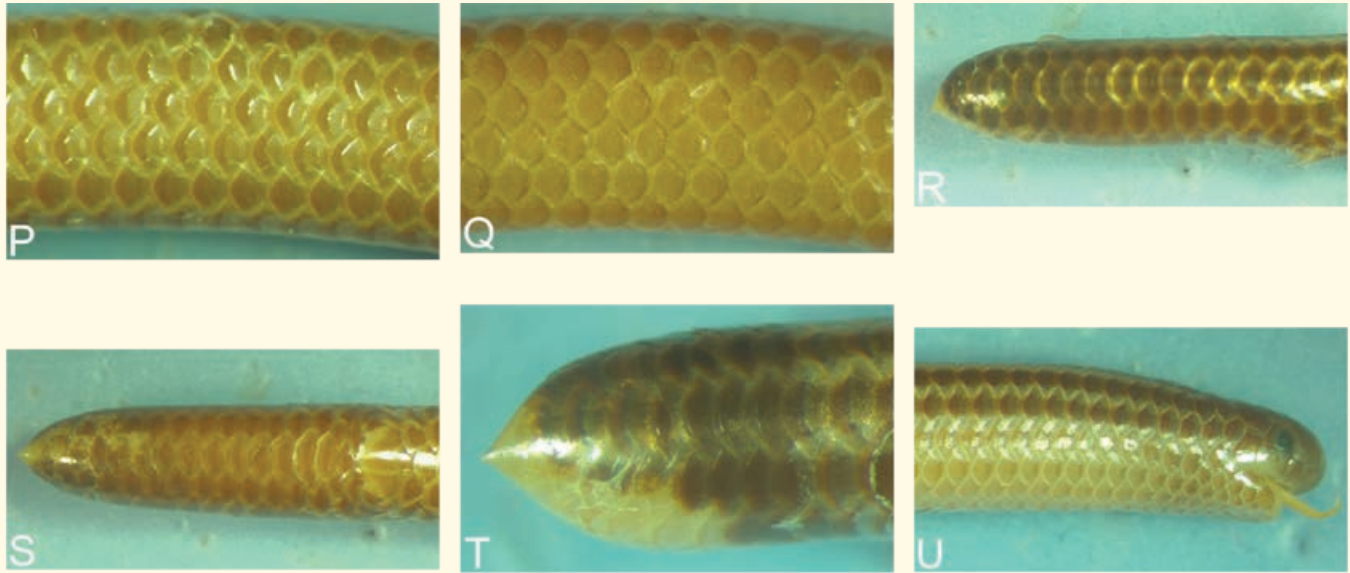
The hemipenis of TCWC 45525, from Querétaro, Mexico (Fig. 15Q–R), is a simple organ 3.0 mm in length with a single sulcus spermaticus that curves clockwise around the organ. The basal half is entirely naked and bulbous, measuring 1.5 mm in length and 1.0 mm in width; the distal neck, also 1.5 mm long, is ornamented on the asulcate side with numerous rugae and papillae. The proximal neck supports 7 circular folds of transverse rugae, and the distal neck is covered with six columns of papillae arranged in 5 transverse rows.

**Viscera:** (mean value followed parenthetically by range,  $n = 3$ ). Posterior tip of sternohyoideus muscle = 14.0% (12.1–15.5%); sternohyoideus/snout–heart gap = 0.84 (0.74–0.93); heart length = 4.2% (3.9–4.7%) with midpoint at 18.6% (18.2–19.1%); snout–heart interval = 20.7% (20.2–21.5%); heart–liver gap = 8.4% (6.8–9.8%) and interval = 53.3% (52.7–53.9%); heart–gall bladder gap = 49.3% (48.4–50.4%); liver lobes multipartite, right liver length = 40.8% (38.3–42.7%) with midpoint at 49.5% (48.4–50.4%) and 33.0 (28–38) segments; left liver length = 32.6% (26.2–36.8%) with midpoint at 48.3% (45.8–51.4%) and 29.0 (23–34) segments; anterior liver extension = 0.07 (0.01–0.18) and posterior liver tail = 0.13 (0.13–0.13); left liver/right liver = 0.79 (0.68–0.86); liver–gall bladder gap = 0.2% (–0.3 to 4.0%) and interval = 42.0% (39.8–43.3%); gall bladder length = 1.1% (1.0–1.2%) with midpoint at 70.6% (69.9–71.5%); gall bladder–kidney gap = 13.6% (11.6–15.0%) and interval = 20.2% (18.6–21.1%); gall bladder–gonad gap = 6.3% (5.5–7.2%) and interval = 13.7% (12.8–14.5%); right gonad length = 3.8% (3.3–4.7%) with midpoint at 79.4% (78.9–80.0%); left gonad length = 2.7% (1.6–3.9%) with midpoint at 82.3% (82.2–82.4%); gonad–kidney gap = 1.0% (0–2.3%) and interval = 12.8% (11.2–14.5%); right adrenal midpoint = 81.2% (80.6–81.8%) and left adrenal midpoint = 83.6% (83.3–84.0%); right kidney length = 3.6% (3.3–3.9%) with midpoint at 86.5% (85.7–87.0%); left kidney length = 3.7% (3.5–3.9%) with midpoint at 88.4% (87.8–89.1%); kidney overlap = 0.31 (0.27–0.40); kidney–vent gap = 9.8% (9.0–10.5%), and kidney–vent interval = 15.3% (14.7–16.3%); rectal caecum length = 1.7% (1.6–1.9%); and rectal caecum–vent interval = 11.3% (10.5–11.7%). The smallest female (SVL 129 mm) had 3 developing eggs plus 7 follicles in the right ovary and 3 developing egg and 5 follicles in the left ovary, and the largest female (SVL 153.5 mm) had 6 eggs plus 8 follicles in the right ovary and 4 eggs and 5 follicles in the left ovary. The clutch size, therefore, appears to be 6 to 10 eggs. Five testis segments were present in both the right and left testes in the single male I examined.

Respiratory system lacking tracheal lung and left lung complex; trachea length = 19.6% (19.2–20.3%) with midpoint at 10.9% (10.6–11.3%) and an estimated 187 (152–220) tracheal rings or 94.6 (81.7–112.6) rings/10% SVL; anterior lung tip = 19.0% (18.2–19.5%); tracheal entry terminal; cardiac lung length = 1.7% (1.2–2.0%);







**Fig. 11.** Morphological variation in *Epictia wyzni* sp. nov. (A) holotype of *E. wyzni* (TCWC 32899); (B, C, D) dorsal head (TCWC 45528, TCWC 45547, TCWC 45530); (E, F, G) lateral head (TCWC 45528, TCWC 45547, TCWC 45530); (H, I, J) ventral head (TCWC 45528, TCWC 45547, TCWC 45530); (K, L, M) dorsal midbody (TCWC 45528, TCWC 45547, TCWC 45530); (N) lateral midbody (TCWC 45547); (O, P, Q) ventral midbody (TCWC 45528, TCWC 45547, TCWC 45530); (R) lateral tail (TCWC 45547); (S) ventral tail (TCWC 45547); (T) lateral apical spine (TCWC 45528); and (U) lateral neck (TCWC 45528).

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right lung length = 33.8% (26.7–37.6%) with midpoint at 37.6% (33.6–40.0%), with faveolar cranial half and trabecular caudal half; posterior tip = 54.5% (46.9–58.6%); right bronchus length = 20.8% (18.6–23.6%); posterior tip of bronchus = 41.6% (38.8–44.2%); bronchus/right lung = 0.63 (0.55–0.70); trachea-bronchus length = 40.5% (37.8–43.0%) with midpoint at 21.4% (19.9–22.7%); trachea-bronchus/total lung length = 0.75 (0.69–0.81); and total lung length = 35.5% (28.7–39.1%) with midpoint at 36.8% (32.6–39.1%).

Visceral distance data include the heart–right lung distance = 19.0% (15.4–20.9%); heart–liver distance = 30.9% (30.2–31.3%); liver–kidney distance = 38.0% (37.0–39.3%); trachea–liver distance = 38.6% (37.8–39.1%); right lung–adrenal distance = 44.8% (42.5–49.3%); trachea/bronchus–gall bladder distance = 49.3% (48.8–50.0%); heart–gonad distance = 60.7% (59.8–61.4%); trachea/bronchus–kidney distance = 66.1% (64.1–67.8%); heart–kidney distance = 68.9% (68.2–69.5%); and trachea–adrenal distance = 71.5% (71.0–72.3%).

**Distribution:** *Epictia wyzni* is a Mexican endemic known to inhabit the Sierra Madre Oriental in northeastern Mexico (N Querétaro and NW Hidalgo), overall elev. 315–2,500 m (Map 11).

**Ecology:** This species inhabits agricultural and cultivated areas, tropical deciduous and evergreen forest, and pine-oak forest (Montes de Oca and Pérez-Ramos, 1998; Hernández-Salinas and Ramírez-Bautista, 2013), as well as thorn-scrub regions with abundant acacia with scattered cacti and non-thorny shrubs (Dixon et al., 1972). UTEP H-20217 was found under a stone in an open pasture.

**Comparisons:** *Epictia wyzni* is identifiable from all other Mesoamerican species (plus *E. albifrons*, *E. goudotii*, and *E. tenella*) by the presence of only 3 infralabials, resulting from the fusion of the normal 2<sup>nd</sup> and 3<sup>rd</sup> infralabials. Instead of being twice as long as wide, the 2<sup>nd</sup> infralabial in *E. wyzni* is broader than long, with a slightly concave posterior border.

*Epictia wyzni* is identifiable from *E. ater* by a subtriangular and truncated rostral that reaches anterior eye level (vs. waisted rostral with arrowhead apex extending nearly to posterior border of ocular); a discrete frontal (vs. frontal absent, fused with rostral); an elongate supraocular twice as wide as long (vs. blocky supraocular 1½ times

as wide as deep); eye round and completely beneath ocular shield (vs. oval and partly beneath supranasal and anterior supralabial); infralabials 3 (vs. 4); pale caudal spot 10 times longer ventrally than dorsally (vs. 5 times); a dorsal midbody pattern of dark stripes consisting of triangular and diamond-shaped spots bordered by moderate to broad, linear pale stripes (vs. uniformly dark, lacking stripes); a shorter heart length ( $\leq 4.7\%$  vs.  $4.7\%$ ) and snout–heart interval ( $\leq 21.4\%$  vs.  $\geq 21.4\%$ ); a shorter heart–liver gap ( $11.2\%$  vs.  $13.8\%$ ) but longer interval ( $53.3\%$  vs.  $50.4\%$ ); a longer heart–gall bladder gap ( $49.3\%$  vs.  $45.6\%$ ); a longer right liver ( $40.8\%$  vs.  $36.5\%$ ), left liver ( $32.6\%$  vs.  $28.6\%$ ), and total liver length ( $73.5\%$  vs.  $65.0\%$ ); a more cranial left liver midpoint ( $48.3\%$  vs.  $50.5\%$ ); a shorter liver–gall bladder interval ( $42.0\%$  vs.  $37.6\%$ ); a longer liver–kidney interval ( $61.2\%$  vs.  $58.2\%$ ); a shorter gall bladder length ( $\leq 1.2\%$  vs.  $\geq 1.2\%$ ); a more caudal gall bladder midpoint ( $70.6\%$  vs.  $68.6\%$ ); a shorter gall bladder–kidney interval ( $20.2\%$  vs.  $22.3\%$ ); a more caudal right gonad ( $79.4\%$  vs.  $76.4\%$ ), left gonad ( $82.3\%$  vs.  $79.6\%$ ), and total gonad midpoint ( $80.9\%$  vs.  $78.0\%$ ); a shorter gonad–kidney interval ( $12.8\%$  vs.  $15.2\%$ ); a more posterior right kidney ( $86.5\%$  vs.  $83.9\%$ ) and total kidney midpoint ( $87.5\%$  vs.  $85.5\%$ ); a greater kidney overlap ( $\geq 0.27$  vs.  $\leq 0.24$ ); a shorter kidney–vent interval ( $15.3\%$  vs.  $18.1\%$ ); a smaller kidney–vent interval/right liver ratio ( $0.39$  vs.



**Map 11.** Distribution of *Epictia wynnii* nov. sp. in northeastern Mexico (Querétaro and Hidalgo).

0.50); a larger rectal caecum/heart ratio ( $0.34$  vs.  $0.23$ ); a larger rectal caecum/left kidney ratio ( $0.47$  vs.  $0.37$ ); a shorter trachea length ( $\leq 20.3\%$  vs.  $\geq 20.3\%$ ); a longer right lung ( $33.8\%$  vs.  $27.8\%$ ) and bronchus length ( $20.8\%$  vs.  $17.7\%$ ); a more caudal posterior lung tip ( $54.5\%$  vs.  $50.1\%$ ); and a longer heart–right lung distance ( $19.0\%$  vs.  $16.2\%$ ), heart–gonad distance ( $60.7\%$  vs.  $56.2\%$ ), trachea–bronchus distance ( $66.1\%$  vs.  $64.0\%$ ), and heart–kidney distance ( $68.9\%$  vs.  $65.4\%$ ).



*Epictia wynni* can be differentiated from *E. bakewelli* by a subtriangular rostral with a truncated apex that reaches anterior eye level (vs. waisted rostral with rounded apex extending beyond posterior level of the eye); a somewhat distinct rostral spot that does not cover entire rostral (vs. distinct spot covering entire rostral); a discrete frontal (vs. frontal absent, fused with rostral); eye round (vs. oval and partly beneath supranasal); infralabials 3 (vs. 4); cloacal shield subtriangular (vs. semilunate); a pale caudal spot 10 times longer ventrally than dorsally (vs. 3 times); a dorsal midbody pattern of 7 dark stripes consisting of triangle- and diamond-shaped spots (vs. 3 dark linear stripes of rectangular spots and a dark midlateral stripe covering 2 scale rows); a brown cloacal shield (vs. yellow shield); a longer heart–liver interval (53.3% vs. 46.1%); a longer heart–gall bladder gap (49.3% vs. 42.3%); a longer right liver (40.8% vs. 35.2%), left liver (32.6% vs. 26.4%), and total liver length (73.5% vs. 61.6%); a more caudad right liver (49.5% vs. 45.2%), left liver (48.3% vs. 45.4%), and total liver midpoint (49.5% vs. 45.2%); fewer right liver segments ( $\leq 38$  vs.  $\geq 40$ ); a longer liver–gall bladder interval (42.0% vs. 36.2%); a shorter liver–kidney gap (14.8% vs. 20.8%); a more caudal gall bladder midpoint (70.6% vs. 63.3%); a shorter gall bladder–kidney gap (13.6% vs. 19.9%) and interval (20.2% vs. 27.0%); a shorter gall bladder–gonad gap (6.3% vs. 12.2%); a more posterior left gonad (82.3% vs. 79.6%) and total gonad midpoint (80.9% vs. 78.6%); a more caudal right adrenal (81.2% vs. 78.9%), left adrenal ( $\geq 83.3\%$  vs.  $\leq 83.1\%$ ), and total adrenal midpoint (82.4% vs. 79.6%); a shorter gall bladder–gonad interval (13.7% vs. 18.3%); greater kidney overlap ( $\geq 0.27$  vs.  $\leq 0.21$ ); a longer rectal caecum length ( $\geq 1.6\%$  vs.  $\leq 1/5\%$ ); a larger rectal caecum/left kidney ratio ( $\geq 0.42$  vs.  $\leq 0.42$ ); a longer right lung length (33.8% vs. 30.9%); a more caudad posterior lung tip (54.5% vs. 51.3%); a shorter liver–kidney distance (38.0% vs. 41.4%); and a longer heart–liver distance (30.9% vs. 26.6%), trachea–liver distance (38.6% vs. 34.5%), trachea/bronchus–gall bladder distance (49.3% vs. 42.8%), and trachea–adrenal distance (71.5% vs. 68.8%).

*Epictia wynni* can be separated from *E. columbi* by the number of subcaudals  $\leq 20$  (vs.  $\geq 22$ ); a relative tail width  $\leq 4.3\%$  (vs.  $\geq 4.3\%$ ); a subtriangular rostral shape (vs. sagittate); pale rostral and caudal spots present (vs. absent); supraoculars twice as wide as long (vs. barely wider than long); lacking a preoral groove (vs. groove present); infralabials 3 (vs. 4); a subtriangular cloacal shield (vs. semilunate); tail terminus a thorn (vs. compressed cone); a longer sternohyoideus length ( $\geq 12.1\%$  vs. 11.7%); a more posterior heart midpoint ( $\geq 18.2\%$  vs. 17.8%) and longer snout–heart interval ( $\geq 20.2\%$  vs. 19.9%); a shorter heart–liver gap (11.2% vs. 15.2%) but longer heart–liver interval ( $\geq 52.7\%$  vs. 47.7%) and heart–gall bladder gap ( $\geq 48.4\%$  vs. 43.8%); a longer right liver ( $\geq 38.3\%$  vs. 34.4%), left liver ( $\geq 26.2\%$  vs. 24.6%), and total liver length (73.5% vs. 59.0%); a more caudad right liver ( $\geq 48.4\%$  vs. 46.1%) and total liver midpoint (49.5% vs. 46.1%); a shorter anterior liver extension ( $\leq 0.18$  vs. 0.18), but longer posterior liver tail ( $\geq 0.13$  vs. 0.10); a shorter liver–gall bladder gap ( $\leq 0.40$  vs. 0.40), but longer interval ( $\geq 39.8\%$  vs. 35.9%); a shorter liver–kidney gap ( $\leq 15.6\%$  vs. 20.3%); a shorter gall bladder length ( $\leq 1.2\%$  vs. 1.2%) and more posterior midpoint ( $\geq 69.9\%$  vs. 64.3%); a shorter gall bladder–gonad gap ( $\leq 7.2\%$  vs. 13.3%); a shorter gall bladder–kidney gap ( $\leq 15.0\%$  vs. 18.8%) and interval ( $\leq 21.1\%$  vs. 27.7%); a more caudal left gonad midpoint ( $\geq 82.2\%$  vs. 81.6%); a more caudal left adrenal midpoint ( $\geq 83.3\%$  vs. 81.6%); a shorter right kidney ( $\leq 3.9\%$  vs. 3.9%) and left kidney length ( $\leq 3.9\%$  vs. 3.9%); a more posterior right kidney midpoint ( $\geq 85.7\%$  vs. 85.5%), but more anterior left kidney midpoint ( $\leq 89.1\%$  vs. 89.5%); greater kidney overlap ( $\geq 0.27$  vs. none); a longer kidney–vent gap ( $\geq 9.0\%$  vs. 8.6%), but shorter interval ( $\leq 16.3\%$  vs. 16.4%); a shorter rectal caecum length ( $\leq 1.9\%$  vs. 2.0%); a longer rectal caecum–vent interval ( $\geq 10.5\%$  vs. 9.8%); a longer trachea length ( $\geq 19.2\%$  vs. 18.8%) and more caudad midpoint ( $\geq 10.6\%$  vs. 10.5%); a longer right lung ( $\geq 26.7\%$  vs. 26.6%) and trachea–bronchus length (40.5% vs. 38.3%); a more caudad right lung midpoint ( $\geq 33.6\%$  vs. 33.2%); a smaller bronchus/right lung ratio ( $\leq 0.70$  vs. 0.74); a more caudad right lung ( $\geq 46.9\%$  vs. 46.5%) and bronchus posterior tip (41.6% vs. 39.5%); a longer heart–right lung distance ( $\geq 15.4\%$  vs. 15.4%), heart–liver distance ( $\geq 30.2\%$  vs. 28.3%), trachea–liver distance ( $\geq 37.8\%$  vs. 35.6%), trachea/bronchus–gall bladder distance ( $\geq 48.8\%$  vs. 44.0%), and trachea–adrenal distance ( $\geq 71.1\%$  vs. 70.6%); and a shorter liver–kidney distance ( $\leq 39.3\%$  vs. 41.4%), right lung–adrenal distance (44.8% vs. 48.0%), heart–gonad distance ( $\leq 61.4\%$  vs. 61.5%), and heart–kidney distance ( $\leq 69.5\%$  vs. 69.7%).

*Epictia wynni* is diagnosable from *E. magnamaculata* by a maximum length of 163 mm (vs. 220 mm); a subtriangular rostral with a truncated apex that reaches anterior eye level (vs. sagittate rostral with oval apex that reaches anterior level of the eye); a somewhat distinct rostral spot that does not cover entire rostral (vs. large distinct spot covering rostral and adjacent scales); a frontal as long as wide (vs. 1½ times as wide as long); an elongate supraocular twice as wide as long (vs. blocky supraocular 1½ times as wide as deep); eye round and entirely beneath ocular (vs. oval and partly beneath supranasal and anterior supralabial); infralabials 3 (vs. 4); pale caudal



spot much longer ventrally than dorsally (vs. longer barely dorsally than ventrally); terminal tail supporting a broad compressed blade (vs. apical spine); a dorsal midbody pattern of 7 dark zigzag stripes consisting of triangle- and diamond-shaped spots (vs. 11 straight-sided dark stripes); a longer right liver (40.8% vs. 38.8%), left liver (32.6% vs. 29.9%), and total liver length (73.5% vs. 68.6%); a shorter liver–gall bladder gap ( $\leq 0.4\%$  vs.  $\geq 0.6\%$ ); a shorter gall bladder length ( $\leq 1.2\%$  vs.  $\geq 1.2\%$ ); a greater number of left testis (5.0 vs. 3.0) and total testis segments (5.0 vs. 3.5); a longer right lung (33.8% vs. 28.9%), bronchus (20.8% vs. 18.7%), and trachea-bronchus length (40.5% vs. 38.5%); a more caudal right lung midpoint (37.6% vs. 35.4%), bronchus posterior tip (41.6% vs. 39.6%), and right lung posterior tip (54.5% vs. 49.9%); a shorter right lung–adrenal distance (44.8% vs. 46.9%); and a longer heart–right lung distance (19.0% vs. 16.7%) and trachea–adrenal distance (71.5% vs. 62.7%).

*Epicidia wynni* can be distinguished from *E. martinezi* by a subtriangular rostral, not reaching the eye level (vs. parallel rostral, extending to mid-eye level); a small pale rostral spot, not covering entire shield (vs. moderate spot, covering entire shield); lacking a pale preocular spot (vs. present); parallel supranasal/supraocular borders (vs. oblique); a round eye, 0.42 ocular height, entirely beneath ocular (vs. oval eye, 0.50 ocular height, partially beneath supranasal); infralabials 3 (vs. 4); a subtriangular cloacal shield (vs. semilunate); a pale subcaudal/dorsocaudal spot ratio of 10.0 (vs. 3.1); a pale dorsal spot 1 scale long (vs. 1.5–3.5 scales); a midbody stripe formula of 7 + 0 (vs. 3 + 2/2 + 0 formula); straight dorsal stripe borders (vs. zigzag); a longer heart–liver interval ( $\geq 52.7\%$  vs.  $\leq 49.5\%$ ); a longer heart–gall bladder gap ( $\geq 48.4\%$  vs.  $\leq 45.6\%$ ); a longer right liver ( $\geq 38.3\%$  vs.  $\leq 36.8\%$ ) and total liver length ( $\geq 64.5\%$  vs.  $\leq 64.1\%$ ); a more posterior right liver midpoint ( $\geq 48.4\%$  vs.  $\leq 47.2\%$ ); a more caudal left liver (48.3% vs. 46.2%) and total liver midpoint (49.5% vs. 47.0%); a shorter posterior liver tail ( $\leq 0.13$  vs.  $\geq 0.15$ ); a longer left liver length (32.6% vs. 26.7%); a shorter liver–gall bladder gap ( $\leq 0.40$  vs.  $\geq 0.40$ ) and longer interval ( $\geq 39.8\%$  vs.  $\leq 38.6\%$ ); a shorter gall bladder length ( $\leq 1.2\%$  vs.  $\geq 1.4\%$ ) and more caudad midpoint ( $\geq 69.9\%$  vs.  $\leq 66.7\%$ ); a shorter gall bladder–gonad interval ( $\leq 14.5\%$  vs.  $\geq 14.7\%$ ); a shorter gall bladder–kidney interval ( $\leq 21.1\%$  vs.  $\geq 23.2\%$ ); a more caudal right gonad ( $\geq 78.9\%$  vs.  $\leq 76.0\%$ ), left gonad ( $\geq 82.2\%$  vs.  $\leq 79.3\%$ ), and total gonad midpoint ( $\geq 80.7\%$  vs.  $\leq 77.7\%$ ); a greater number of right testis (5.0 vs. 2.0), left testis (5.0 vs. 1.5), and total testis segments (5.0 vs. 1.8); a shorter gonad–kidney interval (12.8% vs. 16.2%); a more caudad right adrenal ( $\geq 80.6\%$  vs.  $\leq 77.0\%$ ), left adrenal ( $\geq 83.3\%$  vs.  $\leq 78.9\%$ ), and total adrenal midpoint ( $\geq 82.0\%$  vs.  $\leq 77.9\%$ ); a shorter right kidney ( $\leq 3.9\%$  vs.  $\geq 4.9\%$ ), left kidney ( $\leq 3.9\%$  vs.  $\geq 4.0\%$ ), and total kidney length ( $\leq 7.4\%$  vs.  $\geq 9.0\%$ ); a more posterior right kidney ( $\geq 85.7\%$  vs.  $\leq 82.4\%$ ), left kidney ( $\geq 87.8\%$  vs.  $\leq 87.6\%$ ), and total kidney midpoint ( $\geq 86.8\%$  vs.  $\leq 85.9\%$ ); a shorter kidney–vent interval ( $\leq 16.3\%$  vs.  $\geq 18.3\%$ ); a longer rectal caecum length ( $\geq 1.6\%$  vs.  $\leq 1.1\%$ ); a greater rectal caecum/left kidney ratio ( $\geq 0.41$  vs.  $\leq 0.28$ ); a longer right lung length ( $\geq 26.7\%$  vs.  $\leq 24.6\%$ ) and more caudad midpoint ( $\geq 33.6\%$  vs.  $\leq 32.7\%$ ) and posterior tip ( $\geq 46.9\%$  vs.  $\leq 44.9\%$ ); a lesser bronchus/right lung ratio ( $\leq 0.70$  vs.  $\geq 0.79$ ); and a longer heart–right lung distance ( $\geq 15.4\%$  vs.  $\leq 14.4\%$ ), heart–liver distance ( $\geq 30.2\%$  vs.  $\leq 29.0\%$ ), trachea–liver distance ( $\geq 37.8\%$  vs.  $\leq 36.5\%$ ), trachea/bronchus–gall bladder distance ( $\geq 48.8\%$  vs.  $\leq 45.3\%$ ), heart–gonad distance ( $\geq 59.8\%$  vs.  $\leq 57.8\%$ ), trachea/bronchus–kidney distance (66.1% vs. 64.0%), heart–kidney distance ( $\geq 68.2\%$  vs.  $\leq 66.7\%$ ), and trachea–adrenal distance (71.1% vs.  $\leq 67.0\%$ ).

*Epicidia wynni* is recognizable from *E. pauldwyeri* by a middorsal count  $\geq 242$  (vs.  $\leq 226$ ) and subcaudal count  $\geq 14$  (vs.  $\leq 14$ ); a truncated rostral that reaches anterior eye level (vs. rostral with rounded apex that reaches mid-eye level); a somewhat distinct rostral spot that does not cover entire rostral (vs. distinct spot covering entire rostral); a frontal as long as wide (vs. 1½ times as broad as deep); an elongate supraocular twice as wide as long (vs. blocky supraocular 1½ times as wide as deep); eye round and entirely beneath ocular (vs. oval and partly beneath supranasal); infralabials 3 (vs. 4); a pale caudal spot averaging 10 times longer ventrally than dorsally (vs. slightly longer dorsally than ventrally); a dorsal midbody pattern of moderate to broad, straight pale stripes (vs. narrow, zigzag pale stripes); a brown cloacal shield (vs. yellow shield); a shorter heart length ( $\leq 4.7\%$  vs.  $\geq 5.1\%$ ); a longer heart–liver interval ( $\geq 52.7\%$  vs.  $\leq 52.7\%$ ); a longer heart–gall bladder gap ( $\geq 48.4\%$  vs.  $\leq 48.1\%$ ); a longer right liver (40.8% vs. 36.0%), left liver (32.6% vs. 29.8%), and total liver length (73.5% vs. 65.9%); a longer posterior liver tail ( $\geq 0.13$  vs.  $\leq 0.11$ ); a longer liver–gall bladder interval (42.0% vs. 36.9%); a longer liver–kidney interval (61.2% vs. 56.9%); a shorter gall bladder length ( $\leq 1.2\%$  vs.  $\geq 1.4\%$ ) and more caudad midpoint ( $\geq 69.9\%$  vs.  $\leq 69.7\%$ ); a shorter gall bladder–kidney interval ( $\leq 21.1\%$  vs.  $\geq 21.3\%$ ); a more posterior right gonad (79.4% vs. 75.5%), left gonad (82.3% vs. 78.3%), and total gonad midpoint (80.9% vs. 76.9%); a more caudad right adrenal (81.2% vs. 78.6%), left adrenal (83.6% vs. 81.3%), and total adrenal midpoint (82.4% vs. 80.0%); a more caudal right kidney (86.5% vs. 81.8%), left kidney (88.4% vs. 84.8%), and total kidney midpoint (87.5% vs. 83.3%); greater kidney overlap (0.31

vs. 0.14); a shorter kidney–vent gap (9.8% vs. 13.3%) and interval (15.3% vs. 20.0%); a smaller kidney–vent interval/right liver ratio (0.39 vs. 0.67); a shorter rectal caecum–vent interval (11.3% vs. 13.5%); a larger rectal caecum/heart ratio (0.34 vs. 0.19); a longer right lung (33.8% vs. 31.6%) and trachea–bronchus length (40.5% vs. 42.6%); a more cranial bronchus posterior tip (41.6% vs. 43.9%); and a longer heart–liver distance ( $\geq 30.2\%$  vs.  $\leq 30.1\%$ ), trachea–liver distance ( $\geq 37.8\%$  vs.  $\leq 37.3\%$ ), liver–kidney distance (38.0% vs. 35.5%), right lung–adrenal distance (44.8% vs. 42.1%), trachea/bronchus–gall bladder distance ( $\geq 48.8\%$  vs.  $\leq 48.2\%$ ), heart–gonad distance (60.7% vs. 56.1%), trachea/bronchus–kidney distance (66.1% vs. 60.8%), heart–kidney distance (68.9% vs. 63.9%), and trachea–adrenal distance (71.5% vs. 68.4%).

*Epictia wynni* can be separated from *E. phenops* by a subtriangular rostral with a truncated apex that does not reach anterior level of eye (vs. sagittate rostral with oval apex that reaches mid-eye level); posterior borders of supraocular and supranasal parallel (vs. oblique); eye round (vs. oval); infralabials 3 (vs. 4); cloacal shield subtriangular (vs. semilunate); a dorsal midbody pattern of 8 straight pale stripes bordering 7 dark stripes (vs. 4 pale zigzag stripes bordering 3 dark stripes, the midlateral 2 scale rows forming a solid brown stripe); a pale dorsocaudal spot that averages 0.4 scale in length (vs. 1.2 scales); a pale subcaudal spot averaging 4.0 scales long (vs. 8.5 scales); a longer right lung length (33.8% vs. 31.4%); and a more caudal posterior tip of right lung (54.5% vs. 52.3%).

*Epictia wynni* can be distinguished from *E. resetari* by a subtriangular rostral with a truncated apex that reaches anterior eye level (vs. sagittate rostral with oval apex that reaches mid-eye level); a somewhat distinct rostral spot that does not cover entire rostral (vs. distinct spot covering entire rostral); eye beneath ocular (vs. partly beneath supranasal); infralabials 3 (vs. 4); cloacal shield subtriangular (vs. semilunate); a pale caudal spot 10 times longer ventrally than dorsally (vs. 5 times); a dorsal midbody pattern of straight pale stripes (vs. pale zigzag stripes); a longer heart–liver interval ( $\geq 52.7\%$  vs.  $\leq 50.6\%$ ); a longer left liver (32.6% vs. 28.2%) and total liver length (73.5% vs. 67.3%); a more caudal right liver midpoint ( $\geq 48.4\%$  vs.  $\leq 47.9\%$ ); a shorter posterior liver tail ( $\leq 0.13$  vs.  $\geq 0.13$ ); a shorter liver–gall bladder gap ( $\leq 0.4\%$  vs.  $\geq 0.8\%$ ); a shorter liver–kidney gap ( $\leq 15.6\%$  vs.  $\geq 18.0\%$ ); a more cranial right kidney ( $\leq 87.0\%$  vs.  $\geq 87.0\%$ ) and total kidney midpoint ( $\leq 88.0\%$  vs.  $\geq 88.0\%$ ); a longer rectal caecum–vent interval ( $\geq 10.5\%$  vs.  $\leq 9.2\%$ ); a longer right lung length ( $\geq 26.7\%$  vs.  $\leq 25.2\%$ ) and more caudal midpoint (37.6% vs. 33.7%); a more caudal right lung posterior tip (54.5% vs. 46.1%); a shorter trachea–bronchus length (40.5% vs. 37.3%); a longer bronchus length (20.8% vs. 17.3%) and posterior tip (41.6% vs. 38.6%); a shorter liver–kidney distance ( $\leq 39.3\%$  vs.  $\geq 40.4\%$ ); and a longer heart–lung distance ( $\geq 15.4\%$  vs.  $\leq 14.6\%$ ), heart–liver distance ( $\geq 30.2\%$  vs.  $\leq 29.2\%$ ), and trachea–liver distance ( $\geq 37.8\%$  vs.  $\leq 37.0\%$ ).

*Epictia wynni* is recognizable from *E. schneideri* by a subtriangular rostral, not reaching eye (vs. waisted rostral, extending past eye); a discrete frontal present (vs. absent); a round eye, completely beneath ocular (vs. oval, partly beneath supranasal and anterior supralabial); infralabials 3 (vs. 4); a subtriangular cloacal shield (vs. semilunate); a pale subcaudal spot 0.4 scales in length (vs. 1.8 scales long); a pale subcaudal/dorsocaudal spot ratio of 10.0 (vs. 1.8); a midbody stripe formula of 7 + 0 (vs. 3 + 1/1 + 0); 7 dark midbody stripes with zigzag-borders (vs. 5 stripes, with straight-sided borders); a pair of dark lateral stripes, a single scale row in width (vs. a single dark stripe, 2 scale rows wide); a longer heart midpoint ( $\geq 18.2\%$  vs.  $\leq 17.4\%$ ); a longer snout–heart interval ( $\geq 20.2\%$  vs.  $\leq 19.3\%$ ); a longer heart–liver interval ( $\geq 52.7\%$  vs.  $\leq 49.7\%$ ); a longer heart–gall bladder gap ( $\geq 48.4\%$  vs.  $\leq 46.3\%$ ); a longer right liver ( $\geq 38.3\%$  vs.  $\leq 36.6\%$ ), left liver (32.6% vs. 27.2%), and total liver length ( $\geq 64.5\%$  vs.  $\leq 64.1\%$ ); a more caudal right liver ( $\geq 48.4\%$  vs.  $\leq 46.5\%$ ), left liver ( $\geq 45.8\%$  vs.  $\leq 45.6\%$ ), and total liver midpoint (49.5% vs. 46.2%); a shorter posterior liver tail ( $\leq 0.13$  vs.  $\geq 0.15$ ); fewer right liver segments ( $\leq 38$  vs.  $\geq 43$ ); a longer liver–gall bladder interval ( $\geq 39.8\%$  vs.  $\leq 38.9\%$ ); a shorter liver–kidney gap ( $\leq 15.6\%$  vs.  $\geq 17.1\%$ ) and longer interval (61.2% vs. 59.2%); a shorter gall bladder length ( $\leq 1.2\%$  vs.  $\geq 1.5\%$ ) and more posterior midpoint ( $\geq 69.9\%$  vs.  $\leq 66.3\%$ ); a shorter gall bladder–kidney interval ( $\leq 21.1\%$  vs.  $\geq 21.1\%$ ); a more caudal right gonad ( $\geq 78.9\%$  vs.  $\leq 76.5\%$ ), left gonad ( $\geq 82.2\%$  vs.  $\leq 78.5\%$ ), and total gonad midpoint ( $\geq 80.7\%$  vs.  $\leq 77.5\%$ ); a more caudal right adrenal ( $\geq 80.6\%$  vs.  $\leq 78.9\%$ ), left adrenal ( $\geq 83.3\%$  vs.  $\leq 80.9\%$ ), and total adrenal midpoint ( $\geq 82.0\%$  vs.  $\leq 79.9\%$ ); a longer left kidney ( $\geq 3.5\%$  vs.  $\leq 3.2\%$ ) and total kidney length ( $\geq 6.9\%$  vs.  $\leq 6.7\%$ ); a more caudal right kidney ( $\geq 85.7\%$  vs.  $\leq 83.2\%$ ), left kidney ( $\geq 87.8\%$  vs.  $\leq 86.4\%$ ), and total kidney midpoint ( $\geq 86.8\%$  vs.  $\leq 84.7\%$ ); a greater kidney overlap ratio ( $\geq 0.27$  vs.  $\leq 0.21$ ); a shorter kidney–vent gap ( $\leq 10.5\%$  vs.  $\geq 12.0\%$ ) and interval ( $\leq 16.3\%$  vs.  $\geq 18.1\%$ ); a longer rectal caecum length ( $\geq 1.6\%$  vs.  $\leq 1.2\%$ ); a shorter rectal caecum–vent interval ( $\leq 11.7\%$  vs.  $\geq 12.0\%$ ); a larger rectal caecum/left kidney ratio ( $\geq 0.41$  vs.  $\leq 0.38$ ); a longer trachea length ( $\geq 19.2\%$  vs.  $\leq 17.8\%$ ) and more posterior midpoint ( $\geq 10.6\%$  vs.  $\leq 10.5\%$ ); a more caudal anterior tip of lung ( $\geq 18.2\%$

vs.  $\leq 17.5\%$ ); a more caudad right lung midpoint (37.6% vs. 35.3%), bronchus posterior tip (41.6% vs. 39.2%), and right lung posterior tip (54.5% vs. 51.4%); a longer trachea-bronchus length (40.5% vs. 37.7%); and a longer heart–liver distance ( $\geq 30.2\%$  vs.  $\leq 29.4\%$ ), trachea–liver distance ( $\geq 37.8\%$  vs.  $\leq 36.3\%$ ), trachea/bronchus–gall bladder distance ( $\geq 48.8\%$  vs.  $\leq 45.3\%$ ), heart–gonad distance ( $\geq 59.8\%$  vs.  $\leq 59.4\%$ ), trachea/bronchus–kidney distance (66.1% vs. 64.0%), heart–kidney distance ( $\geq 68.2\%$  vs.  $\leq 67.3\%$ ), and trachea–adrenal distance ( $\geq 71.1\%$  vs.  $\leq 69.7\%$ ).

*Epictia wynni* can be differentiated from *E. vindumi* by a subtriangular rostral with a truncated apex that reaches anterior eye level (vs. sagittate rostral with truncated apex that reaches posterior level of eye); a somewhat distinct rostral spot that does not cover entire rostral (vs. distinct spot covering entire rostral); posterior borders of supraocular and supranasal parallel (vs. oblique); eye beneath ocular (vs. partly beneath supranasal); infralabials 3 (vs. 4); cloacal shield subtriangular (vs. semilunate); a pale caudal spot 10 times longer ventrally than dorsally (vs. six times); a dorsal midbody pattern of straight pale stripes (vs. pale zigzag stripes); a longer heart–liver interval ( $\geq 52.7\%$  vs.  $\leq 52.7\%$ ); a longer right liver (40.8% vs. 37.5%), left liver (32.6% vs. 27.8%), and total liver length (73.5% vs. 65.2%); a more caudal right liver (49.5% vs. 46.1%), left liver (48.3% vs. 45.6%), and total liver midpoint (49.5% vs. 46.1%); a longer heart–gall bladder gap (53.3% vs. 49.5%) and shorter liver–gall bladder gap ( $\leq 0.4\%$  vs.  $\geq 0.7\%$ ); a shorter liver–kidney gap (14.8% vs. 19.8%) and interval (61.2% vs. 63.4%); a shorter gall bladder length ( $\leq 1.2\%$  vs.  $\geq 1.2\%$ ) and more caudal midpoint (70.6% vs. 67.2%); a shorter gall bladder–kidney gap (13.6% vs. 16.6%) and interval (20.2% vs. 24.3%); a shorter gall bladder–gonad gap (6.3% vs. 8.9%); a greater number of right testis (5.0 vs. 2.0) and total testis segments (5.0 vs. 3.0); a longer rectal caecum length ( $\geq 1.6\%$  vs.  $\leq 1.3\%$ ); a larger rectal caecum/left kidney ratio ( $\geq 0.41$  vs.  $\leq 0.33$ ); a longer right lung (33.8% vs. 27.5%), bronchus (20.8% vs. 17.7%) and trachea-bronchus length (40.5% vs. 36.4%); a more posterior right lung midpoint (37.6% vs. 33.5%), right lung posterior tip (54.5% vs. 47.2%), trachea-bronchus midpoint (21.4% vs. 19.3%), and bronchus posterior tip (41.6% vs. 37.5%); a longer heart–right lung distance (19.0% vs. 16.0%), heart–liver distance (30.9% vs. 28.6%), and trachea–liver distance (38.6% vs. 35.7%); and a shorter liver–kidney distance (38.0% vs. 41.5%), right lung–adrenal distance (44.8% vs. 48.0%), and trachea/bronchus–kidney distance (66.1% vs. 68.3%).

*Epictia wynni* is diagnosable from *E. goudotii* by a relative rostral width of  $\leq 0.42$  (vs. 0.42 HW); a subtriangular rostral with a truncated apex that reaches anterior eye level (vs. triangular rostral with rounded apex that reaches anterior level of eye); a rounded snout in dorsal and ventral profile (vs. obtuse profile); a frontal as deep as broad (vs.  $1\frac{1}{2}$  times as broad as deep); eye entirely beneath ocular (vs. partly beneath supranasal); anterior supralabial moderately high, extending to mid-eye level (vs. short, not or barely reaching lower level of eye); infralabials 3 (vs. 4); a pale caudal spot 10 times longer ventrally than dorsally (vs.  $1\frac{1}{2}$  times); lack of a preoral groove in ventral rostral (vs. distinct preoral groove); a spine-like caudal termination (vs. compressed cone); a dorsal midbody pattern of pale straight stripes (vs. pale zigzag stripes); a shorter heart length ( $\leq 4.7\%$  vs. 6.0%); a shorter snout–heart interval ( $\leq 21.5\%$  vs. 22.7%); a longer heart–liver gap ( $\geq 6.8\%$  vs. 5.6%); a longer heart–gall bladder gap ( $\geq 48.4\%$  vs. 46.8%); a longer left liver (32.6% vs. 30.0%) and total liver length (73.5% vs. 71.2%); a shorter posterior liver tail ( $\leq 0.13$  vs. 0.16); more left liver segments ( $\geq 23$  vs. 21); a shorter liver–gall bladder interval ( $\leq 43.3\%$  vs. 43.3%); a shorter liver–kidney gap ( $\leq 15.6\%$  vs. 17.2%) and interval ( $\leq 63.2\%$  vs.  $\geq 63.9\%$ ); a shorter gall bladder length ( $\leq 1.2\%$  vs. 2.1%); a shorter gall bladder–gonad gap ( $\leq 7.2\%$  vs. 7.3%) and interval (13.7% vs. 19.3%); a shorter gall bladder–kidney gap ( $\leq 15.0\%$  vs. 15.0%) and interval ( $\leq 21.1\%$  vs. 22.7%); a more anterior right gonad ( $\leq 80.0\%$  vs. 81.8%), left gonad ( $\leq 82.4\%$  vs. 86.5%), and total gonad midpoint (80.9% vs. 84.2%); a greater number of right (5.0 vs. 2.0) and total testis segments (5.0 vs. 3.5); a more anterior right adrenal ( $\leq 81.8\%$  vs.  $\geq 83.7\%$ ), left adrenal ( $\leq 84.0\%$  vs. 88.0%), and total adrenal midpoint (82.4% vs. 85.9%); a longer gonad–kidney gap ( $\geq 0$  vs.  $-2.1\%$ ); a longer left kidney ( $\geq 3.5\%$  vs. 3.4%); a more cranial right kidney ( $\leq 87.0\%$  vs. = 88.4%), left kidney ( $\leq 89.1\%$  vs. 90.6%), and total kidney midpoint (87.5% vs. 89.5%); a greater kidney overlap ( $\geq 0.27$  vs. 0.23); a longer kidney–vent gap ( $\geq 9.0\%$  vs. 7.7%) and interval ( $\geq 14.7\%$  vs. 13.3%); a longer rectal caecum ( $\geq 1.6\%$  vs. 1.3%); a greater rectal caecum/left kidney ratio ( $\geq 0.41$  vs. 0.38); a longer rectal caecum–vent interval ( $\geq 10.5\%$  vs. 8.6%); a shorter trachea length ( $\leq 20.3\%$  vs. 21.0%); a more cranial trachea midpoint ( $\leq 11.3\%$  vs. 12.2%) and anterior lung tip ( $\leq 19.5\%$  vs. 20.2%); a longer right lung (33.8% vs. 27.9%), bronchus length ( $\geq 18.6\%$  vs. 14.6%), and trachea-bronchus length (40.5% vs. 35.6%); a more caudal trachea-bronchus midpoint ( $\geq 19.9\%$  vs. 19.5%), posterior tip (41.6% vs. 37.3%), and right lung posterior lung tip (54.5% vs. 50.6%); a longer heart–right lung distance (19.0% vs. 17.0%), heart–liver distance ( $\geq 30.2\%$  vs. 29.2%), and trachea–liver distance ( $\geq 37.8\%$  vs.



36.7%); and a shorter liver–kidney distance ( $\leq 39.3\%$  vs.  $40.6\%$ ), right lung–adrenal distance ( $44.8\%$  vs.  $49.2\%$ ), trachea/bronchus–gall bladder distance ( $\leq 50.0\%$  vs.  $51.1\%$ ), heart–gonad distance ( $\leq 61.4\%$  vs.  $62.1\%$ ), trachea/bronchus–kidney distance ( $\leq 67.8\%$  vs.  $70.0\%$ ), heart–kidney distance ( $\leq 69.5\%$  vs.  $69.8\%$ ), and trachea–adrenal distance ( $\leq 72.3\%$  vs.  $73.7\%$ ).

*Epictia wynni* can be separated from *E. albifrons* by a middorsal count of  $\geq 242$  (vs.  $\leq 218$ ); a subtriangular rostral with a truncated apex that reaches anterior eye level (vs. sagittate rostral with rounded apex that reaches anterior level of eye); a frontal as long as wide (vs.  $1\frac{1}{2}$  times as long as wide; round (vs. oval); eye round and entirely beneath ocular (vs. oval and partly beneath supranasal); infralabials 3 (vs. 4); cloaca shield subtriangular (vs. pyramidal with truncated apex); a pale caudal spot averaging 10 times longer ventrally than dorsally (vs.  $2\frac{1}{2}$  times); a dorsal midbody pattern of pale straight stripes (vs. pale zigzag stripes); a longer heart–liver gap ( $11.2\%$  vs.  $9.0\%$ ) and heart–gall bladder gap ( $\geq 48.4\%$  vs.  $\leq 47.5\%$ ); a longer left liver ( $32.6\%$  vs.  $29.6\%$ ) and total liver length ( $73.5\%$  vs.  $68.7\%$ ); a more caudal left liver midpoint ( $\geq 45.8\%$  vs.  $\leq 45.0\%$ ); a shorter posterior liver tail ( $\leq 0.13$  vs.  $\geq 0.18$ ); a longer liver–gall bladder interval ( $42.0\%$  vs.  $39.7\%$ ); a shorter liver–kidney gap ( $14.8\%$  vs.  $19.8\%$ ) and interval ( $61.2\%$  vs.  $64.4\%$ ); a shorter gall bladder length ( $\leq 1.2\%$  vs.  $\geq 1.3\%$ ); a more posterior gall bladder midpoint ( $\geq 69.9\%$  vs.  $\leq 68.9\%$ ); a shorter gall bladder–gonad gap ( $\leq 7.2\%$  vs.  $\geq 7.9\%$ ), gall bladder–gonad interval ( $13.7\%$  vs.  $21.3\%$ ), gall bladder–kidney gap ( $\leq 15.0\%$  vs.  $\geq 15.1\%$ ), and gall bladder–kidney interval ( $\leq 21.1\%$  vs.  $\geq 22.0\%$ ); a more cranial left gonad ( $\leq 82.4\%$  vs.  $\geq 83.3\%$ ) and total gonad midpoint ( $80.9\%$  vs.  $83.3\%$ ); a greater number of right testis segments (5.0 vs. 3.0); a more anterior right adrenal ( $\leq 81.8\%$  vs.  $\geq 81.8\%$ ), left adrenal ( $83.6\%$  vs.  $86.4\%$ ), and total adrenal midpoint ( $82.4\%$  vs.  $85.0\%$ ); a shorter gonad–kidney interval ( $12.8\%$  vs.  $15.9\%$ ); a longer left kidney length ( $\geq 3.5\%$  vs.  $\leq 3.5\%$ ); a more cranial right kidney ( $86.5\%$  vs.  $89.4\%$ ), left kidney ( $88.4\%$  vs.  $91.6\%$ ), and total kidney midpoint ( $87.5\%$  vs.  $90.5\%$ ); a larger kidney overlap ( $\geq 0.27$  vs.  $\leq 0.22$ ); a longer kidney–vent gap ( $9.8\%$  vs.  $6.8\%$ ) and interval ( $15.3\%$  vs.  $12.2\%$ ); a shorter rectal caecum length ( $\leq 1.9\%$  vs.  $\geq 2.5\%$ ); a smaller rectal caecum/left kidney ratio ( $\leq 0.54$  vs.  $\geq 0.71$ ); a longer rectal caecum–vent interval ( $\geq 10.5\%$  vs.  $\leq 8.8\%$ ); a greater number of tracheal rings/10% SVL ( $\geq 81.7$  vs.  $\leq 79.5$ ); a longer right lung ( $33.8\%$  vs.  $30.2\%$ ); a more caudad posterior lung tip ( $54.5\%$  vs.  $51.1\%$ ); a longer trachea/bronchus–gall bladder distance ( $\geq 48.8\%$  vs.  $\leq 47.8\%$ ); and a shorter liver–kidney distance ( $38.0\%$  vs.  $42.1\%$ ), right lung–adrenal distance ( $44.8\%$  vs.  $49.0\%$ ), trachea/bronchus–kidney distance ( $66.1\%$  vs.  $69.6\%$ ), heart–kidney distance ( $68.9\%$  vs.  $71.9\%$ ), and trachea–adrenal distance ( $71.5\%$  vs.  $74.0\%$ ).

*Epictia wynni* is identifiable from *E. tenella* by a total middorsals  $\geq 242$  (vs.  $\leq 233$ ); a rostral that extends to anterior eye level (vs. rostral that does not reach eye level); a somewhat distinct rostral spot that does not cover entire rostral (vs. large distinct spot covering rostral and adjacent scales); a frontal as long as wide (vs.  $1\frac{1}{2}$  times as broad as deep); a pentagonal supraocular twice as wide as long (vs. hexagonal supraocular three times as broad as deep); supraocular and supranasal posterior borders parallel (vs. oblique); ocular hexagonal, in contact with 5 scales (vs. pentagonal, in contact with 4 scales); anterior supralabial moderate in height, reaching mid-eye level but not contacting supraocular (vs. tall and in contact with supraocular); infralabials 3 (vs. 4); a pale caudal spot 10 times longer ventrally than dorsally (vs.  $1\frac{1}{2}$  times); a dorsal midbody pattern of dark stripes composed of triangle- and diamond-shaped spots (vs. dark stripes of oval-shaped spots); a longer sternohyoideus length ( $14.0\%$  vs.  $11.8\%$ ); a shorter heart length ( $\leq 4.7\%$  vs.  $\geq 4.9\%$ ); a more anterior heart midpoint ( $\leq 19.1\%$  vs.  $\geq 19.4\%$ ) and snout–heart interval ( $\leq 21.5\%$  vs.  $\geq 21.9\%$ ); a longer heart–liver interval ( $53.3\%$  vs.  $48.6\%$ ) and heart–gall bladder gap ( $\geq 48.4\%$  vs.  $\leq 48.1\%$ ); a longer right liver ( $\geq 38.3\%$  vs.  $\leq 38.3\%$ ) and total liver length ( $73.5\%$  vs.  $66.9\%$ ); a longer posterior liver tail ( $\geq 0.13$  vs.  $\leq 0.08$ ); fewer right liver segments ( $\leq 38$  vs.  $\geq 38$ ); a longer liver–gall bladder ( $42.0\%$  vs.  $38.2\%$ ) and liver–kidney interval ( $61.2\%$  vs.  $57.0\%$ ); a shorter gall bladder length ( $\leq 1.2\%$  vs.  $\geq 1.3\%$ ); a more caudal right gonad ( $\geq 78.9\%$  vs.  $\leq 78.5\%$ ) and total gonad midpoint ( $80.9\%$  vs.  $78.8\%$ ); a greater number of right (5.0 vs. 3.0), left (5.0 vs. 4.0) and total testis segments (5.0 vs. 3.5); a more posterior right adrenal ( $\geq 80.6\%$  vs.  $\leq 80.6\%$ ) and left adrenal midpoint ( $\geq 83.3\%$  vs.  $\leq 83.1\%$ ); a longer gonad–kidney gap ( $1.0\%$  vs.  $-1.6\%$ ); a more posterior right kidney ( $86.5\%$  vs.  $82.9\%$ ), left kidney ( $88.4\%$  vs.  $85.9\%$ ), and total kidney midpoint ( $87.5\%$  vs.  $84.4\%$ ); a larger kidney overlap ( $\geq 0.27$  vs.  $\leq 0.14$ ); a longer gonad–kidney gap ( $\geq 0$  vs.  $\leq 0$ ); a shorter kidney–vent gap ( $9.8\%$  vs.  $12.4\%$ ) and interval ( $15.3\%$  vs.  $19.0\%$ ); a smaller rectal caecum/heart ratio (0.34 vs. 0.55); a smaller kidney–vent interval/right liver ratio (0.39 vs. 0.50); a shorter trachea length ( $\leq 20.3\%$  vs.  $\geq 20.8\%$ ) and more cranial midpoint ( $\leq 11.3\%$  vs.  $\geq 11.5\%$ ); and a longer heart–liver distance ( $30.9\%$  vs.  $28.0\%$ ), trachea–liver distance ( $38.6\%$  vs.  $36.4\%$ ), liver–kidney distance ( $38.0\%$  vs.  $35.9\%$ ), right lung–adrenal distance ( $44.8\%$  vs.  $41.6\%$ ), trachea/bronchus–gall

bladder distance ( $\geq 48.8\%$  vs.  $\leq 48.7\%$ ), heart–gonad distance ( $\geq 59.8\%$  vs.  $\leq 58.1\%$ ), trachea/bronchus–kidney distance ( $66.1\%$  vs.  $62.7\%$ ), heart–kidney distance ( $\geq 68.2\%$  vs.  $\leq 67.3\%$ ), and trachea–adrenal distance ( $\geq 71.1\%$  vs.  $\leq 69.8\%$ ).

**Remarks:** This population is distinguished from all other Mesoamerican *Epictia* by the presence of only 3 infralabials, with the normal 2<sup>nd</sup> and 3<sup>rd</sup> fused to form an elongate shield resembling the last infralabial, but with a concave posterior border. Only 3 infralabials are present in the South American *E. australis*, *E. borapeliotes*, *E. diaplocia* and *E. munoai*, but this condition is unique among the Mesoamerican species.

The correct identification of the *Epictia* reported for Hidalgo is uncertain (Ramirez-Bautista et al., 2014), but provisionally I refer to them as *E. wynni* based on the geographical proximity to the Querétaro population, the apparent straight yellow stripes (Ramirez-Bautista et al., 2014: photo 223), and the small dorsal caudal spot (Hernández-Salinas and Ramírez-Bautista, 2013: fig. 5B).

### ***Epictia goudotii* (Duméril & Bibron, 1844)**

Figs. 12A–X, 16AA–AB

*Stenostoma goudotii* Duméril & Bibron, 1844: 330; d'Orbigny, 1848: 749, 1867: 174; Buffon and Monlau, 1854: 421–422; Sherborn, 1925: 2765; Nicéforo-María, 1942: 86; Daniel, 1955: 54; Hahn, 1980: 14; Schwartz and Henderson, 1988: 223; McDiarmid et al., 1999: 30; Illescas-Palomo et al., 2011: 231.

*Stenostomati goudoti*—Tschudi, 1845: 163.

*Stenostoma goudoti*—Tschudi, 1846: 47.

*Stenostoma fallax* Peters, 1857: 402, 1862: 36; Günther, 1866: 25, 1885–1902: 85; Orejas-Miranda In Peters et al., 1970 and 1986: 169; Vanzolini, 1977: 83; Hahn, 1980: 15; Bauer et al., 1995a: 24, 1995b: 77, 2002: 159; Wallach, 1998a: 552; McDiarmid et al., 1999: 30; Illescas-Palomo et al., 2011: 231; Wallach et al., 2014: 277.

*Stenostoma godouti* (sic)—Jan, 1861: 188, 1863: 15, 1864: 35–36; Jan and Sordelli, 1861 In 1860–1881: 2, livr. 2, pl. 5, fig. 2, pl. 6, fig. 2.

*Stenostoma goudotii* (sic)—Cope, 1875: 129; Hahn, 1980: 15; McDiarmid et al., 1999: 31; Illescas-Palomo et al., 2011: 231; Wallach et al., 2014: 277.

*Glauconia albifrons*—Boulenger, 1893: 63 (part); Günther, 1893 In 1885–1902: 85 (part).

*Glauconia goudotii*—Boulenger, 1893: 64; Dunn, 1949: 44, 47–48, 55; Emsley, 1977: 234; Kornacker, 1999: 47 (part); McDiarmid et al., 1999: 31; Illescas-Palomo et al., 2011: 231.

*Glauconia goudoti*—Werner, 1917: 203.

*Leptotyphlops goudotii*—Amaral, 1930: 139, 1931: 90; Dunn, 1944a: 53, 1944b: 28, 1949: 44 (part); Swanson, 1945: 213 (part); Daniel, 1949: 303, 1955: 54; Schwartz and Thomas, 1975: 189 (part); Vanzolini, 1977: 83; Hahn, 1980: 14–15; Pérez-Santos, 1986: 74, 83, figs. 27, 31 (part); Castro and Restrepo, 1987: 31; Sokolov, 1988: 355; Auth, 1994: 19 (part); Frank and Ramus, 1995: 250 (part); Hedges, 1996: 111, 115 (part); Wallach, 1998a: 490 (part), 552, 1998b: 184; Crother, 1999: 320; Kornacker, 1999: 47, 220; Mattison, 1999: 146; McDiarmid et al., 1999: 30–32 (part); Solís-Rivera et al., 1999: 128; Oliveros et al., 2000: 104–107; Ibáñez et al., 2001: 170; Köhler, 2001b: 12, fig. 11b (part), 2003a: 172, map (part); 2008: 183–184, map (part); Bauer et al., 2002: 159; Sasa and Bolaños, 2004: 183; Solórzano, 2004: 124–125; Navarrete et al., 2006: 43, 2009: 56; Anonymous, 2007a: 150; Adalsteinsson, 2008: 6; Cundall and Irish, 2008: 597; Acosta-Galvis et al., 2010: 601; Jaramillo et al., 2010: 623, 637 (part); Méndez-Vergara et al., 2010: 230; Wilson and Johnson, 2010: 137, 233 (part); Wilson and Townsend, 2010: 811 (part); Beolens et al., 2011: 104; Gallo-Delgado, 2011: 158; Illescas-Palomo et al., 2011: 231; Rodríguez et al., 2011: 14; EOL, 2015: 457414.

*Leptotyphlops albifrons*—Brongersma, 1940: 117, 1959a: 120, 123, 126, 1959b: 52; Hummelinck, 1940: 114, pl. 13 (lower); Nicéforo-María, 1942: 86; Marcuzzi, 1950: 3, 1954: 249; Daniel, 1955: 54; Müller, 1973: 60; Pérez-Santos, 1983: 82, 1986: 72–73 (part); Pérez-Santos and Moreno, 1986: 20, 1988: 417; Buurt, 2001: 90–91, figs. 55, 66, 2005: 107–108, pls. 63–64, 2006: 313, 2011: 151; Markezich, 2002: 72; Suárez et al., 2000: 67, 71–72; Ayerbe-González et al., 2007: 58; Kraus, 2009: 297; Vargas-Suárez et al., 2015: 4.

*Leptotyphlops goudoti*—Taylor, 1940: 540; Dunn, 1946: 122; Smith, 1958: 223; Medem, 1969: 179; Scott, 1969: 72; Hardy, 1975: 80; Schwartz and Thomas, 1975: 189 (part); Smith and Smith, 1976: S-B-128; Pérez-Santos, 1983: 82; Schwartz and Henderson, 1988: 223 (part); Schwartz and Henderson, 1991: 619–620 (part); Flores-Villela et al., 1995: 262; Wrobel, 2004: 286; Varin, 2008: 122; Illescas-Palomo et al., 2011: 231.

- Leptotyphlops albifrons albifrons*—Roze, 1952: 156–157, 1970: 68–70.
- Leptotyphlops albifrons goudotti* (sic)—Roze, 1952: 156.
- Leptotyphlops albifrons margaritae*—Roze, 1952: 154–156, figs. 6, 7, 1964: 218, 1966: 42–43, map 4, 1970: 69–70; Orejas-Miranda *In* Peters et al., 1970 and 1986: 169; Hahn, 1980: 15; Miller et al., 1982: 399; Wallach, 1998a: 552; McDiarmid et al., 1999: 31; Bisbal, 2001: 20; Sanz, 2007: 117, 119; Illescas-Palomo et al., 2011: 231.
- Leptotyphlops albifrons* ssp.—Roze, 1957: 180–181, 1958: 257–258; 1966: 41–42, map 4.
- Leptotyphlops goudotii goudotii*—Orejas-Miranda *In* Peters et al., 1970 and 1986: 169; Boos, 1975: 22; Serna, 1977: 101; Hahn, 1980: 15; Freiberg, 1982: 118; Boos, 1984: 20; Smith, 1987: xxxiii; Pérez-Santos and Moreno, 1988: 419, map 27 (part); Lancini and Kornacker, 1989: 104 (part); Rivas-Fuenmayor and Oliveros, 1997: 78; Kornacker, 1999: 47, 220; Mijares-Urrutia and Arends, 2000: 25 (part); Börschig, 2007: 167; Illescas-Palomo et al., 2011: 231; EOL, 2015: 1294339.
- Stenostoma albifrons*—Savage, 1970: 279.
- Leptotyphlops goudotti goudotti* (sic)—Lancini, 1979: 170, 1986: 170; Péfaur, 1992: 12; Rivas-Fuenmayor and Oliveros, 1997: 73.
- Leptotyphlops margaritae*—Huber et al., 1986: 7–8.
- Leptotyphlops goudotti* (sic)—Villa et al., 1988: 85 (part); La Marca, 1997: 142; Péfaur, 2000: 66; Rivero and Manzanilla, 2006: 85; Lotzkat, 2007: 124; Rivas-Fuenmayor et al., 2005: 351, 2012: 27.
- Leptotyphlops goudotii goudotii* (sic)—Pérez-Santos et al., 1993: 115.
- Leptotyphlops goudoti goudoti*—Smith and Smith, 1993: 591; Sánchez et al., 1995: 317; Tipton, 2005: 24; Varin, 2008: 122.
- Stenostoma phenops*—McDiarmid et al., 1999: 30–31.
- Leptotyphlops albifrons magnamaculata*—McDiarmid et al., 1999: 31.
- Leptotyphlops albifrons ater*—McDiarmid et al., 1999: 31.
- Leptotyphlops ater*—McDiarmid et al., 1999: 31.
- Leptotyphlops bakewelli*—McDiarmid et al., 1999: 31.
- Leptotyphlops gadowi*—McDiarmid et al., 1999: 31.
- Leptotyphlops goudotii ater*—McDiarmid et al., 1999: 31.
- Leptotyphlops goudotii bakewelli*—McDiarmid et al., 1999: 31.
- Leptotyphlops goudotii goudotii*—McDiarmid et al., 1999: 31.
- Leptotyphlops goudotii magnamaculatus*—McDiarmid et al., 1999: 31.
- Leptotyphlops goudotii phenops*—McDiarmid et al., 1999: 31.
- Leptotyphlops magnamaculata*—McDiarmid et al., 1999: 31.
- Leptotyphlops phenops*—McDiarmid et al., 1999: 31; Gutiérrez-Espeleta and Van Gyseghem, 2005: 141.
- Leptotyphlops phenops bakewelli*—McDiarmid et al., 1999: 31.
- Leptotyphlops phenops phenops*—McDiarmid et al., 1999: 31.
- Epictia goudotii*—Adalsteinsson et al., 2009: 10, 17, 46, figs. 3A, 12 (part); Pinto et al., 2010: 19–22, 28, fig. 12A–C; Arredondo and Zaher, 2010: 191, 197; Canseco-Márquez and Gutiérrez-Mayén, 2010: 252 (part); Ugueto and Rivas, 2010: 216–219, figs. 85A, E, 87, 88, map 25; Çinar, 2012: 121; Wallach et al., 2014: 277 (part); Cortes-Ávila and Toledo, 2013: 192; Pantoja-Leite, 2013: 200; Vargas-Suárez et al., 2013: 48; Angarita et al., 2015: 36; Arévalo-Páez et al., 2015: 40, fig. 1B; Mumaw et al., 2015: 294–295, 423, 431–433, figs. 373–375, 377, map 59; Pérez-González et al., 2015: 4, col. photo 62; Wilson and Johnson, 2016: 38.
- Epictia goudotti* (sic)—Ugueto and Rivas, 2010: 333, pl. 7.1 (2 figs.); Pinto and Curcio, 2011: 61; Pinto and Fernandes, 2012: 46.
- Tricheilostoma goudotii*—Medina-Rangel, 2011: 963.
- Epictia albifrons*—Powell et al., 2011: 83.
- Leptotyphlops* (sic) sp.—Romero-Pérez, 2011: 126 (two col. photos).
- Epictia goudotii goudotii*—Çinar, 2012: 121; Valencia, 2012: 8.



*Crishagenus goudotii*—Hoser, 2012: 34.

*Epictia goudoti*—Mumaw et al., 2015: 294; Blanco-Torres et al., 2013: 117; Blanco-Torres and Renjifo, 2014: 162.

*Epictia albifrons*—Barrio-Amorós and Ortiz, 2015: 88.

*Epictia* cf. *goudoti*—Montero-Arias and Quintero-Corzo, 2015: 187.

**Holotype:** MNHN 1068, a 148–151 mm (LOA) male collected by Justin P. Goudot between 1822 and 1826 or 1837 and 1842, from “la vallée de la Magdeleine, à la Nouvelle-Grenade” [= lower Río Magdalena Valley, Departamento de Magdalena, Colombia, ca. 9–11°N, 74–75°W, elev. ca. 25–100 m asl].

**Etymology:** This patronym is named after the French explorer and naturalist Justin-Marie Goudot, who collected the holotype. From 1822 to 1842, he was a collector in Colombia (at that time known as New Granada) for the Paris Natural History Museum (MNHN).

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 73–164 ( $\bar{x}$  = 110.2) mm, (4) total middorsals = 227–260 ( $\bar{x}$  = 247.8); (5) subcaudals = 11–16 ( $\bar{x}$  = 13.8); (6) relative body proportion = 48–76 ( $\bar{x}$  = 59.8); (7) relative tail length = 3.5%–6.6% ( $\bar{x}$  = 4.7%); (8) relative tail width = 2.0–3.9 ( $\bar{x}$  = 3.3); (9) relative rostral width = 0.42–0.60 ( $\bar{x}$  = 0.50); (10) relative eye size = 0.36–0.44 ( $\bar{x}$  = 0.39); (10) rostral triangular with rounded apex; (11) supralabials 2, small anterior supralabial not or barely reaching lower level of eye; (12) frontal discrete, separate from rostral, subhexagonal in shape; (13) supraoculars large and pentagonal, twice as broad as deep, with posterior borders parallel to those of supranasals; (14) widest anteriormost vertebral scale 5<sup>th</sup>; (15) parietals deeper than occipitals, oriented transversely; (16) infralabials 4; (17) cloacal shield subtriangular in shape; (18) head brown, lacking a pale rostral spot; (19) dorsum uniform brown, sometimes with narrow, pale scale edges (no stripes); (20) venter uniform pale yellow with diffuse brown vermiculations on each scale; (21) midbody stripe formula (U or O) and middorsal pattern (U or O); (22) tail with a pale terminal spot covering the 0–3 ( $\bar{x}$  = 0.5) dorsal scales and 0–2 ( $\bar{x}$  = 0.7) ventral scales (ventral/dorsal ratio 1.4); and (23) caudal termination a compressed cone.

**Description:** Head as broad as neck, tapered with an obtuse snout profile; rostral triangular in shape with rounded or truncated apex (Fig. 12H); frontal longer than wide and subtriangular in shape with rounded apex; postfrontal, interparietal and interoccipital subhexagonal slightly longer than broad; supraoculars large and quadrangular with parallel sides, 1½–2 times as broad as deep; parietals longer than occipitals, both shields oriented transversely; broadest anteriormost vertebral scale 5<sup>th</sup>; head depressed in lateral view with elongated, projecting snout; nasal completely divided, suture forming a shallow V-shaped angle along anterior supralabial and infranasal, nostril oval and positioned nearer the rostral than supralabial; infranasal 1½ times as tall as wide, narrowing toward lip, just barely taller than adjacent supralabial; supralabials 2, anterior supralabial short, not or just reaching lower level of orbit (Fig. 12K), its labial border equal in length to that of infranasal; ocular large, hexagonal, 1½ times as tall as broad, with a slightly curved anterior border; eye small, usually lacking a distinct pupil and iris, slightly oval or elliptical in vertical plane, less than the lip-orbit gap ( $ED/OH$  = 0.36–0.44,  $\bar{x}$  = 0.39), partially beneath the supranasal, barely protuberant but not visible in dorsal view; posterior supralabial longer than deep, much taller than anterior supralabial, posterior border rounded; ventral rostral slightly bulbous anteriorly with a distinct preoral groove (Fig. 12N); mental butterfly-shaped, infralabials 4, first 3 pairs small and 4<sup>th</sup> elongate; costal scales rounded and imbricate in 14 rows throughout; cloacal shield triangular; and tail terminating in a compressed cone-like base lacking a spine (Fig. 12Q, R).

Coloration in life uniform dark brown to black, usually lacking a pale rostral spot and caudal spot reduced to < 1 scale above and below (Fig. 16K, L; midbody pattern = U). Preserved specimens brown (Fig. 12O), occasionally





**Fig. 12.** Morphological variation in *Epictia goudotii*. (A) dorsal head of holotype of *E. goudotii* (MNHN 1068); (B) lateral head of holotype of *E. goudotii* (MNHN 1068); (C) ventral head of holotype of *E. goudotii* (MNHN 1068); (D) lateral tail of holotype of *E. goudotii* (MNHN 1068); (E) dorsal head of holotype of *S. fallax* (ZMB 33928); (F) lateral head of holotype of *S. fallax* (ZMB 33928); (G) ventral head of holotype of *S. fallax* (ZMB 33928); (H, I, J) dorsal head (MCZ R-33928, MCZ R-92795, MCZ R-92796); (K, L, M) lateral head (MCZ R-33928, KU 116942, MCZ R-92797); (N) ventral head (MCZ R-33928); (O) dorsal midbody (MCZ R-33928); (P) ventral midbody (MCZ R-33928); (Q) lateral tail (MCZ R-33928); and (R) ventral tail (MCZ R-33928).

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with pale zigzag borders along the dorsal scale rows forming 4–8 thin lines (middorsal pattern = O); venter uniform pale brown, individual scales pale with an infusion of brown speckling (Fig. 12P); head brown, the rostral with or without an indistinct pale spot; cloacal shield and cloacal region brown; and tail brown with symmetrically reduced or absent pale spot, dorsal spot covering 0–3 dorsocaudals ( $\bar{x}$  = 0.5 scale), ventral spot covering 0–2 subcaudals ( $\bar{x}$  = 0.7 scale), and ventral/dorsal spot ratio 1.4.

**Distribution:** *Epictia goudotii* is restricted to northern South America, including northern and western Colombia (Atlántico, Cesar, Cundinamarca, La Guajira, Magdalena, Meta, Santander, Tolima, and Isla Salamanca, elev. NSL–1,280 m); northern Venezuela (Anzoátegui, Aragua, Carabobo, Distrito Federal, Falcón, Lara, Monagas, Nueva Esparta: Isla Margarita, Portuguesa, Sucre, Vargas, and Yaracuy, elev. NSL–800 m); and the Netherlands Antilles (Bonaire, elev. NSL–240 m), overall elev. NSL–1,280 m (Map 12). See Remarks for a different taxonomic arrangement.

*Epictia goudotii* previously was considered to inhabit southern Mexico; Central America, including Panama (Smith, 1958b); northern South America, including Colombia, Venezuela, and Trinidad; the offshore islands of Cozumel (Mexico); the Bay Islands [Barbareta, Guanaja, Roatán, and Utila], Cayos Cochinos [Cayo Cochino Grande, Cayo Cochino Pequeño], and Swan Islands [Cisne] (Honduras); Bonaire (Netherlands Antilles); San Andrés and Providencia (Colombia); and Margarita (Venezuela) (Peters et al., 1970; Hahn, 1980; McDiarmid et al., 1999). This species also was reported from Antigua, Grenada, and Watling’s Island in the Caribbean (Barbour, 1930), but these records have been discounted (Powell and Henderson, 2012), and a record for the Suma Islands (Hahn, 1980; McDiarmid et al., 1999) that likely refers to the Exuma Islands in the Bahamas, as once they were called Yumey and Suma ([www.bahamas.com/islands/exumas](http://www.bahamas.com/islands/exumas)), also is not substantiated. Whether the range of *E. goudotii* extends to include Trinidad remains to be seen (Murphy, 1997; Boos, 2001), but considering the proximity to the mainland and the short time span since the sea level rise separated Trinidad from Venezuela, *E. goudotii* conceivably could be present.

**Ecology:** In Colombia, *Epictia goudotii* occurs in shrubland and riverside woodland (Montero-Arias and Quintero-Corzo, 2015). In Venezuela, it inhabits tropical thorny mountains (Rivas-Fuenmayor and Oliveros, 1997), pine savanna (Suárez et al., 2002), and deciduous and semi-deciduous forests on Isla de Margarita (Rivas-Fuenmayor et al., 2005).

**Remarks:** The epithet *goudotii* has been misapplied to most of the species of *Epictia* in Mesoamerica (Peters et al., 1970; Hahn, 1980; McDiarmid et al., 1999) when, in fact, it does not occur anywhere from Mexico to Panama. I examined the type specimen of *E. goudotii*, as did Pinto et al. (2010), who provided the first accurate description of the species.



*Epictia goudotii* differs substantially from most other Mesoamerican *Epictia* in the following characters: (1) head and tail uniform brown, rarely with a pale rostral spot and/or one pale subcaudal or dorsocaudal (vs. distinct yellow spot rostral spot and yellow subcaudals and dorsocaudals); (2) dorsum superficially brown with, at most, only pale edges to the scale rows (vs. boldly striped in yellow and brown); (3) anterior supralabial short, not or just reaching lower level of eye (vs. tall, extending to mid-eye level); (4) head depressed (vs. normal); (5) lateral snout profile acuminate (vs. rounded); (6) eye round and small (vs. large and vertically elliptical); (7) rostral triangular



**Map. 12.** Distribution of *Epictia goudotii* in northwestern South America.

(vs. parallel, waisted, sagittate, or subtriangular); (8) ocular shield with broader ventral border than dorsal border (vs. broader dorsal border than ventral border); (9) preoral groove in ventral rostral (vs. absent); (10) tail lacking an apical spine (vs. distinct spine or blade present); and (11) sensory pits indistinct (vs. large and prominent). Therefore, I delete *E. goudotii* from the faunal list of Panama, and term the Mesoamerican species the “*Epictia phenops* species group.”

Boulenger (1893) separated *E. goudotii* from *E. albifrons* by an erroneous character, as he believed that an incompletely divided nasal shield was present in *E. goudotii*, whereas completely divided nasals are present in all species of the Leptotyphlopidae. This error probably was due to the small size of *E. goudotii* (< 135 mm), the poor optics available in the 1890s, and likely a poorly preserved specimen (see Figs. 12A–F for condition of type specimens described in 1844 and 1857).

The supraocular is fused with the ocular on the right side in KU 116942, an aberrant condition also present in the holotype of *E. nasalis*. Pinto et al. (2010) summarized data on seven *E. goudotii* thusly: LOA = 83–135 mm

( $\bar{x}$  = 112 mm); TMD = 227–260 ( $\bar{x}$  = 238.1); SC = 12–16 ( $\bar{x}$  = 15.1); LOA/MBD = 53–64 ( $\bar{x}$  = 58.2); TL/LOA = 4.4%–6.6% ( $\bar{x}$  = 5.2%); TL/TW = 2.9–3.9 ( $\bar{x}$  = 3.5); and RW/HW = 0.4–0.6 ( $\bar{x}$  = 0.5).

The taxon that Roze (1952, 1964, 1966) described from Isla de Margarita, Venezuela (*Leptotyphlops albifrons margaritae*), appears to differ from typical *E. goudotii* in a few characters, as follows (*E. goudotii* data in parentheses): (1) infralabials 6 (vs. 4 infralabials); (2) rounded lateral snout profile (vs. depressed and projecting); (3) anterior supralabial moderate in height (vs. short anterior supralabial); (4) scale row formula of 14–14–12 (vs. 14–14–14); (5) rostral and tail tip with yellow spots (vs. lacking rostral and tail tip spots); and (6) total length 135.5–160 mm with of 147.8 mm (vs. 83–135 mm with of 110.2 mm). The holotype (MHNLS 4515) and paratype (MBUCV 1195) should be re-examined to determine their affinity and taxonomic status as they might represent a valid insular species (Ugueto and Rivas, 2010).

Mumaw et al. (2016) removed *Stenostoma fallax* Peters from the synonymy of *E. goudotii* and recognized *E. fallax* as the name for the population occurring in northern Venezuela. They separated the two species based on the following characters (*E. fallax* characters first, followed by *E. goudotii* characters): (1) anterior supralabial (moderately high, reaching mid-eye level vs. short, not reaching eye level); (2) rostral apex (rounded vs. subacuminate); (3) pale rostral and caudal spots (present vs. absent or faintly visible); (4) pale rostral spot (extending onto frontal vs. restricted to center of rostral, if visible); (5) dorsal view of snout (short and rounded vs. elongated and truncated); (6) pale posterior upper lip spot (half-moon shaped and distinct vs. irregular and indistinct); (7) pale paravertebral stripes (prominent, extending to parietals and occipitals vs. diffuse at most, not reaching occipitals); (8) pale mid-body zigzag stripes (present vs. absent); and (9) rostral shape and length (subtriangular, short in length, not reaching eye level vs. triangular, moderate in length, extending to mid-eye level). I examined only a single specimen from Venezuela (KU 116942) and it differs from typical *E. goudotii* in these characters: (1) pale dorsocaudal spot 3 scales long (vs. 0); (2) dorsal tail spot larger than ventral spot (ventral spot larger than dorsal spot, which is lacking); (3) apical spine present (vs. cone); (4) dorsal head profile truncated (vs. tapered); (5) pale rostral spot (present vs. absent); (6) parietals equal to occipitals in depth (vs. parietals deeper than occipitals); (7) pale border on lower lip present (vs. absent); (8) eye large, eye height/lip-orbit gap > 1.0 (vs. moderate, eye height/lip-orbit gap ≤ 1.0); and (9) anterior supralabial moderately tall (vs. short). The assessment of these two taxa is beyond the scope of this paper, but the above evidence suggests that two species are present. If so, then *E. goudotii* would be restricted to northern and western Colombia and the Netherlands Antilles, and *E. fallax* would be endemic to northern Venezuela as proposed by Mumaw et al. (2016). Such a situation might call into question the identity of the population on the Netherlands Antilles, since those islands are closer to Venezuela than Colombia, but the small sample I examined ( $n$  = 2 Colombia,  $n$  = 3 Bonaire) revealed no external differences between the specimens.

### ***Epictia albifrons* (Wagler In Spix and Wagler, 1824)**

Figs. 13A–AS

*Stenostoma albifrons* Wagler In Spix and Wagler, 1824: 68–69, pl. 25, fig. 3; Fitzinger, 1826: 907, 1843: 24; Spix, 1828: 87; Wagler, 1830: 195; Gray, 1845: 140; d'Orbigny, 1848: 749, 1867: 174; Buffon and Monlau, 1854: 421–422 (part); Jan, 1857: 43, 1859: 275; Hoeven, 1858: 280 (part); Giebel, 1861: 94; Cope, 1887: 63 (part); Peters, 1881: 71; Bocourt, 1882 In Duméril et al., 1870–1890: 505 (part); Schumacher, 1886: 31; Boettger, 1888: 192, 198; Berg, 1889: 146; Sherborn, 1922: 176; Loveridge, 1957: 245; Hahn, 1980: 5–6; Vanzolini, 1981: xxv; Hoogmoed and Gruber, 1983: 339; Pérez-Santos, 1983: 82; Williams and Wallach, 1989: 140; McDiarmid et al., 1999: 19–20; Franzen and Glaw, 2007: 261; Mumaw et al., 2015: 288–291, map 59.

*Typhlops albifrons*—Wagler, 1830: 195; Gray, 1831: 77.

*Epictia albifrons*—Gray, 1845: 140; Hoser, 2012: 33; Rivas-Fuenmayor et al., 2012: 27; Wallach et al., 2014: 275 (part); Mumaw et al., 2015: 291, figs. 346–351; McCranie and Hedges, 2016: 20–21.

*Glauconia albifrons*—Boulenger, 1893: 63 (part), 1898: 129; Günther, 1893 In 1885–1902: 85 (part); Butler, 1895: 704; Boettger, 1898: 6 (part); Werner, 1901: 1, 6 (part), 1915: 309 (part); Ihering, 1911: 308–309 (part); Brehm, 1913: 264 (part); Perrier, 1928: 3, 102; McDiarmid et al., 1999: 19.

*Leptotyphlops albifrons*—Amaral, 1925: 3 (part), 1930a: 76 (part), 1930b: 138 (part), 1931: 90, 1935: 227 (part), 1937a: 95 (part), 1937b: 1,745 (part), 1949: 151, 1977 and 1978: 28, figs. 1–3; Nicéforo-María, 1942: 86 (part); Smith and List, 1958: 271; Orejas-Miranda, 1967: 438–439, fig. 2; Freiberg, 1970: 22, photo, 1982: 117; Haas, 1973: 480; Wilson and Hahn, 1973: 120–121; Vanzolini, 1977: 56, 1981: xviii; Cunha and Nascimento, 1978: 40, 1993: 11; Hahn, 1980: 6; Vanzolini,

1981: xviii; Hoogmoed and Gruber, 1983: 339–340; Pérez-Sanrtos, 1983: 82, 1986a: 72–73, 80, fig. 28; Smith, 1987: xxxiii; Sokolov, 1988: 355; Welch, 1994: 27 (part); Freitas, 1999: 76, 2003: 23–24, fig. 9; Kornacker, 1999: 46, 220 (part); Mattison, 1999: 146; McDiarmid et al., 1999: 19–20 (part); Giraud, 2002: 211; Wrobel, 2004: 284; Tipton, 2005: 20–21; Börschig, 2007: 229–230 (part); Franzen and Glaw, 2007: 261; Adalsteinsson, 2008: 3, 6; Varin, 2008: 122; Silveira-Bérnils, 2008: 9; Delhay, 2009: 180 (part); Ávila-Pires et al., 2010: 70, 97 (part); Beolens et al., 2011: 278.

*Leptotyphlops tenella*—Orejas-Miranda In Peters et al., 1970: 167; Roze, 1970: 70; Freiberg, 1982: 118; Vanzolini, 1986: 10.

**Holotype:** The holotype of *Stenostoma albifrons* (ZSM 1348/0) was a 183 mm (LOA) specimen collected by J. B. von Spix and K. F. P. von Martius from 25 July to 21 August 1819 or 16 April to 12 June 1820, from “in adjacentibus urbis Para” [= Santa Maria de Belém do Grão Pará *fide* Vanzolini, 1981: xxv, which is near Belém, state of Pará, in northeastern Brazil, 01°27'S, 48°30'W, elev. NSL]. The type specimen now is lost (Franzen and Glaw, 2007).

**Neotype:** I reject the neotype designation of MCZ R-2885 suggested by Mumaw et al. (2015) under Art. 75.3.3, Art. 75.3.6, and Recommendation 75B of the Code (see Remarks below for discussion). Instead, I hereby designate BYU 11490, a 154 mm (LOA) female topotype collected by Mormon missionaries between 1946 and 1953 in the vicinity of Belém, state of Pará, Brazil, as the neotype of *Stenostoma albifrons*.

**Topotypes:** Nine adult males (BYU 11487, 11489, 11491, 11493–94, 11497–500), two adult females (BYU 11490, 11492), and three juvenile females (BYU 11488, 11501–02), all from the type locality (Table 5). Mormon missionaries attached to the Brazil North Central Mission in Belém, Pará, Brazil collected this series of 14 specimens between 1946 and 1953. Two additional specimens from the original series of 16 specimens (BYU 11495–96) were lent to Edward H. Taylor at KU on 21 January 1954 and 30 January 1959, respectively, and now are presumed lost. A search of collections containing Taylor material (CAS, CM, FMNH, KU, and MCZ) and the VertNet online database failed to find either of these specimens or any other leptotyphloid specimens from Belém, Brazil.

**Table 5.** Morphometrics of the topotype series of *Epictia albifrons*. BYU = BYU catalogue number; Type = NT (neotype), TT (topotype); A/S (age/sex) = J (juvenile), A (adult), F (female), M (male); LOA = overall or total length; TL = tail length; RTL = relative tail length (TL/LOA); MBD = midbody diameter; L/W = relative body thickness (LOA/MBD); MTD = midtail diameter; RTW = relative tail width (TL/TW); RRW = relative rostral width (RW/HW); TMD = total middorsals; SC = subcaudals; LTS = left testis segments; and RTS = right testis segments.

BYU	Type	S/A	LOA	SVL	TL	RTL	MBD	L/W	MTD	RTW	RW	TMD	SC	LTS	RTS
11501	TT	J/F	63.0	60.0	3.0	4.76	1.4	45.0	1.3	2.3	0.33	211	15	—	—
11488	TT	J/F	69.0	66.0	3.0	4.35	1.4	49.3	1.2	2.5	0.28	215	12	—	—
11502	TF	J/F	69.0	65.5	3.5	5.07	1.7	40.6	1.4	2.5	0.25	210	14	—	—
11497	TT	A/M	103.0	97.0	6.0	5.83	2.9	35.5	2.4	2.5	0.31	208	12	5	6
11499	TT	A/M	117.0	109.5	7.5	6.41	3.0	39.0	2.1	3.6	0.32	212	15	—	—
11494	TT	A/M	126.5	120.5	6.0	4.74	3.5	36.1	3.5	2.1	0.30	206	11	7	4
11491	TT	A/M	127.0	119.5	7.5	5.91	3.6	35.3	2.2	3.4	0.33	218	13	5	5
11487	TT	A/M	130.0	122.0	8.0	6.15	3.5	37.1	2.8	2.9	0.37	208	12	5	6
11493	TT	A/M	143.0	134.0	9.0	6.29	3.8	37.6	3.2	2.8	0.32	217	14	9	10
11500	TT	A/M	136.0	128.0	8.0	5.88	3.4	40.0	2.8	2.9	0.37	216	13	5	5
11489	TT	A/M	140.0	133.0	7.0	5.00	3.4	41.2	2.7	2.6	0.37	218	15	5	3
11498	TT	A/M	148.0	141.5	6.5	4.39	3.4	43.5	2.6	2.5	0.28	211	13	7	5
11490	NT	A/F	154.0	145.5	8.5	5.52	3.7	41.6	3.0	2.8	0.30	215	11	—	—
11492	TT	A/F	168.0	159.0	9.0	5.36	4.4	38.2	3.0	3.0	0.26	212	11	—	—

**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length = 63–168 ( $\bar{x}$  = 121.0) mm; (4) total middorsals = 206–218 ( $\bar{x}$  = 212.6); (5) subcaudals = 11–15 ( $\bar{x}$  = 13.1); (6) relative body proportion = 35–49 ( $\bar{x}$  = 40.0); (7) relative tail length = 4.3%–6.4% ( $\bar{x}$  = 5.4%); (8) relative tail width = 2.1–3.6 ( $\bar{x}$  = 2.7); (9) relative rostral width = 0.25–0.37 ( $\bar{x}$  = 0.31); (10) relative eye size = 0.35–0.37 ( $\bar{x}$  = 0.42); (10) rostral sagittate

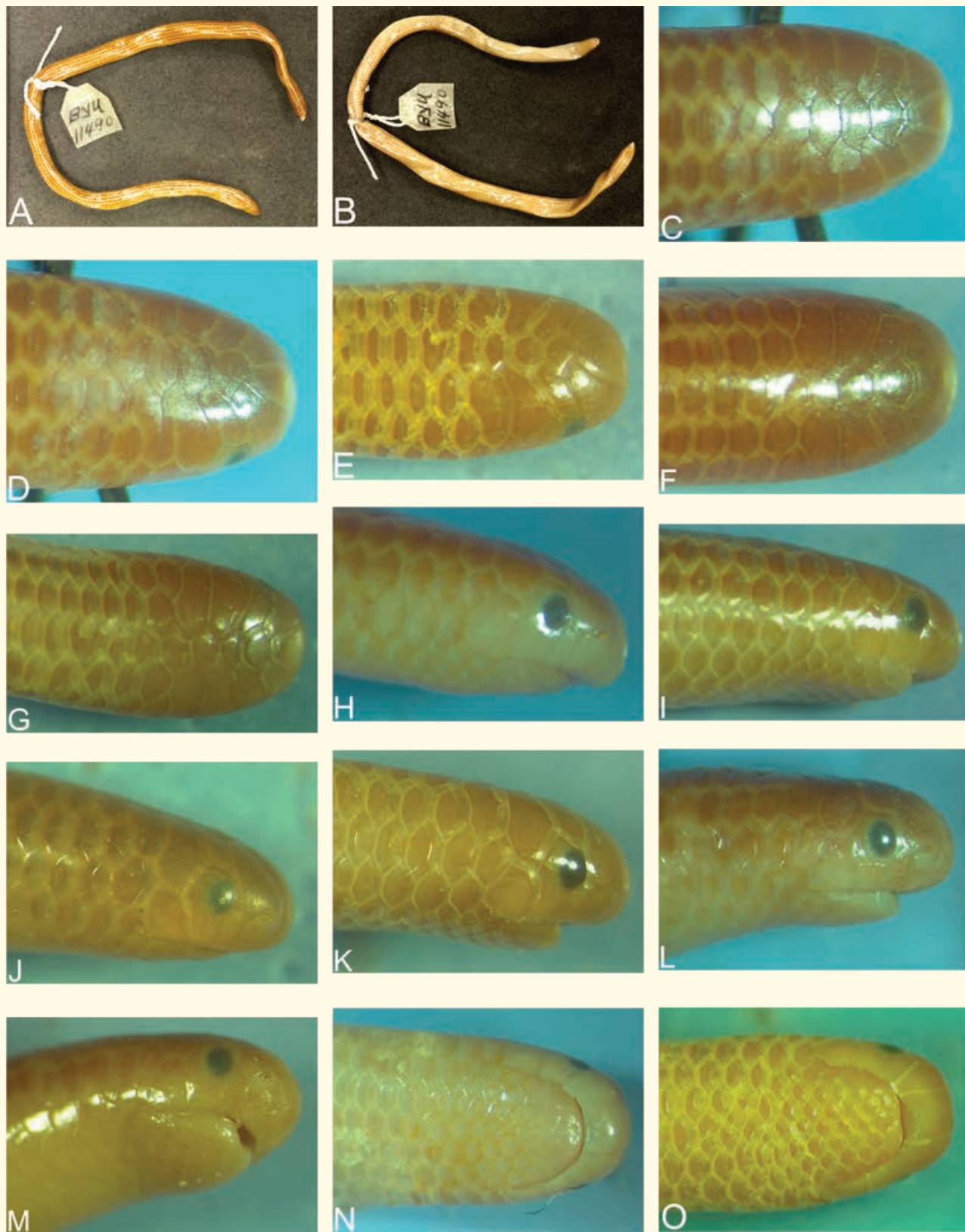


with truncated apex; (11) supralabials 2, anterior supralabial reaching eye level but not in contact with supraocular; (12) frontal separate from rostral; (13) supraoculars large and pentagonal, twice as broad as deep, with posterior border parallel to that of supranasal; (14) frontal, interparietal, and interoccipital hexagonal in shape, broader than deep; (15) parietals slightly longer than occipitals, oriented obliquely; (16) infralabials 4; (17) cloacal shield semilunate in shape; (18) head brown with a moderate pale spot on rostral; (19) dorsum with 7 dark brown stripes, formed from connected diamond-shaped spots, separated by 6 moderate to broad yellow zigzag stripes (= 7 dark stripes); (20) venter pale brown, each scale outlined in yellow; (21) midbody stripe formula (7 + 0) and middorsal pattern (3); (22) tail brown, above and below, with a small, pale terminal spot covering the last 0–1 ( $\bar{x}$  = 1.0) dorsal scales and 1–4 ( $\bar{x}$  = 2.5) ventral scales (subcaudal/dorsocaudal ratio 2.5); and (23) apical spine a horizontal thorn with minute point.

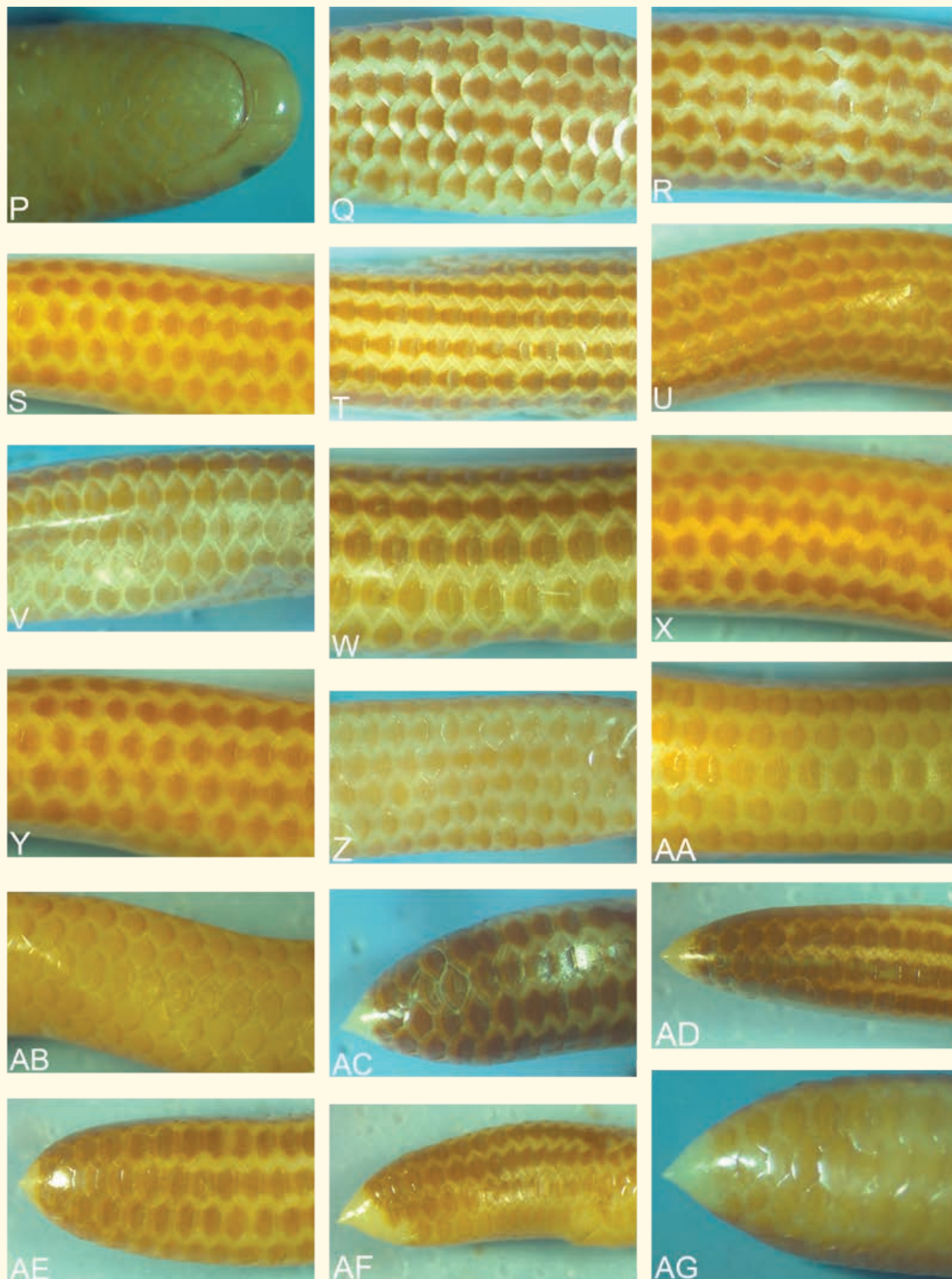
**Description:** The neotype of *Epictia albifrons* is an adult female with scale row formula = 14-14-14; midtail scale rows = 10; LOA = 154 mm; SVL = 145.5 mm; TL = 8.5 mm; T/LOA = 5.5%; MBD = 3.7 mm; L/W ratio = 41.6; L/H ratio = 77.0; MTD = 3.0 mm; TL/W ratio = 2.8; TMD 208; SC 13; DC = 12; RW = 0.6 mm; HW = 2.0 mm; RW/HW ratio = 0.30; and ED/OH = 0.42. Head narrower than neck and body, smoothly tapering to the snout, which is rounded in dorsal and lateral aspect; dorsal rostral sagittate in shape with a truncated posterior border that extends just beyond the posterior border of the eyes; ventral rostral broad,  $\frac{1}{5}$  of head width, with a preoral ridge (Fig. 13P); supraoculars large, oblique, and pentagonal, 2–2½ as wide as deep, with parallel borders and a horizontal suture with the ocular; frontal hexagonal in shape and twice as broad as long (Fig. 13C); succeeding three vertebral scales (postfrontal, interparietal, interoccipital) all broader than long and hexagonal in shape; parietals and occipitals large and obliquely oriented to body axis, with the parietals 1½ times the depth of the occipitals; nasal completely divided by an obliquely oriented anterodorsal suture, with the elliptical nostril placed near the rostral border ( $\frac{3}{4}$  of labial-rostral distance) and directed anterolaterally; supranasal separated from anterior supralabial and infranasal by a shallow V-shaped suture (Fig. 13K); infranasal taller than both supralabials, its ventral border narrower than that of anterior supralabial; supralabials 2, anterior supralabial moderate, reaching the mid-eye level of the pupil; ocular pentagonal, its width 0.7 times its height; eye large and vertically elliptical with a barely discernible pupil, its height 1½ times its width, less than its lip-orbit gap (ED/OH = 0.42–0.59,  $\bar{x}$  = 0.42), anterior edge partly beneath the supranasal and anterior supralabial, not visible in dorsal view; posterior supralabial taller than anterior supralabial, extending to the mid-eye level, contacting the parietal and excluding the postocular (or temporal) from the ocular; infralabials 4; cloacal shield pyramidal (Fig. 13AL), triangular in shape with a truncated apex, about as long as broad, bordered anteriorly by three scales; and apical spine in the form of a horizontally-directed thorn (Fig. 13AG–AI).

Color in life unknown, but based upon preserved material and other members of *Epictia*, I assume the pattern to be of dark brown and yellow stripes dorsally, with a yellow rostral spot of moderate size and a small yellow caudal spot. Dorsal midbody pattern in preserved specimens consists of 7 dark brown stripes of equal width in the form of strings of connected diamond-shaped spots (middorsal pattern = 3), separated by 6 moderate to broad yellow zigzag stripes at least  $\frac{1}{2}$  the width of the brown stripes (Fig. 13R–S, 13U); brown stripes fade midlaterally, so lowermost dark stripe paler than the middorsal stripes (Fig. 13W); midbody stripe pattern = 7 + 0. Venter pale brown, with each scale completely outlined in yellow (Fig. 13Z–AA). Head dorsum brown with a pale spot on anterior portion of the rostral; lower half of lateral head (prenasal, anterior supralabial, ocular, and posterior supralabial), throat (Fig. 13O), and anterior venter are immaculate cream. Venter darkens toward midbody (with increased pigmentation) and is pale brown posteriorly; cloacal shield pale brown; tail brown with yellow zigzag stripes; tip of tail pale (including spine and the last caudal scale rows above and below), terminal spot covering 0–1 ( $\bar{x}$  = 1.0) dorsocaudals and 1–4 ( $\bar{x}$  = 2.5) subcaudals for a subcaudal/dorsocaudal ratio of 2.5. Color pattern might be ontogenetic in nature, as the juveniles are uniform brown and lack the characteristic pale head and tail spots and dorsal stripes (Fig. 13AO–AS).

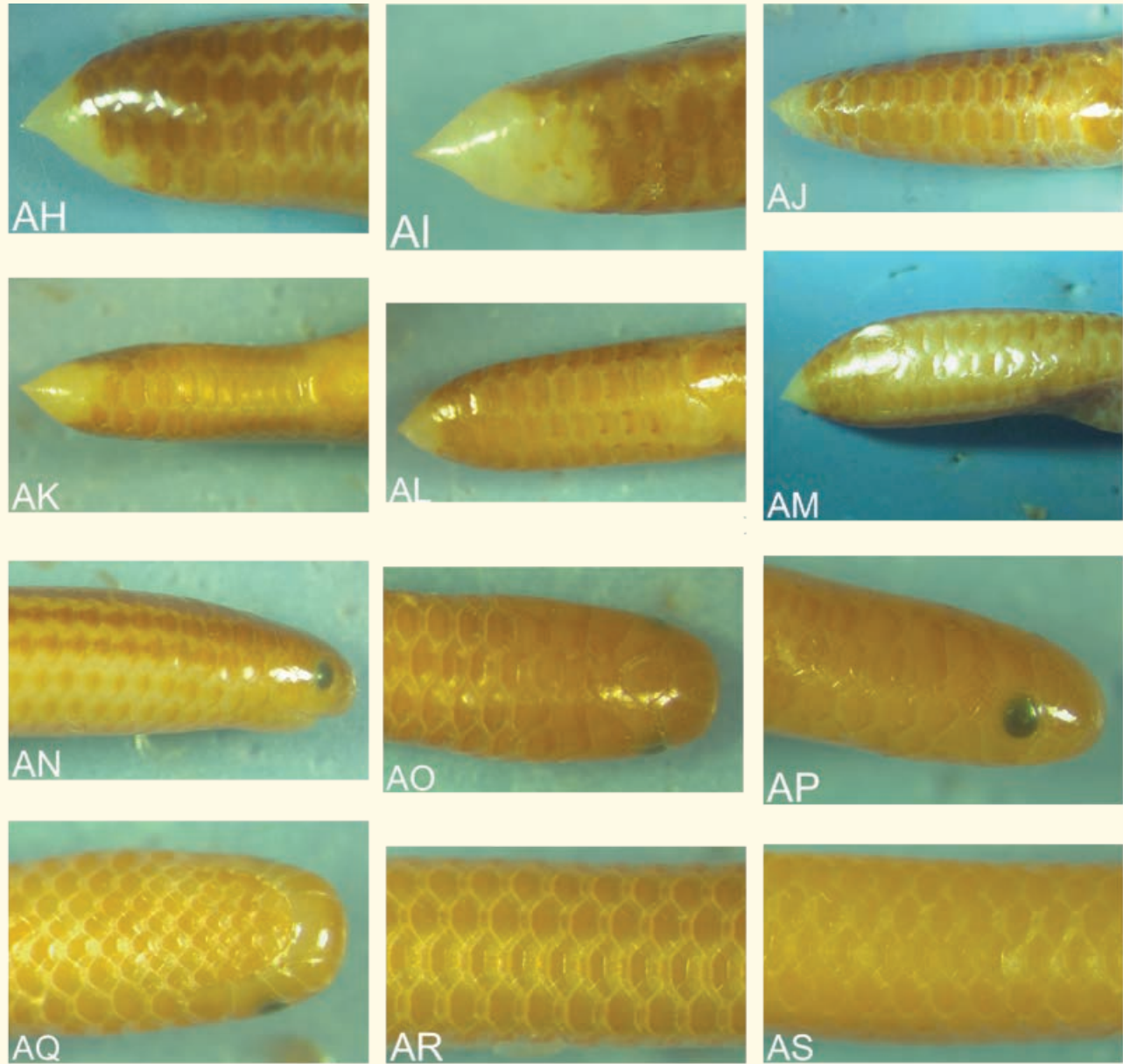
**Variation:** Intraspecific variation among the topotype series is summarized in Table 6. SRF = 14-14-14; TSR = 10; TMD = 206–218 ( $\bar{x}$  = 212.6 ± 3.91)  $n$  = 14; SC = 11–15 ( $\bar{x}$  = 13.1 ± 1.39)  $n$  = 14; LOA = 63–168 mm (males 103–148 mm, females 60–168 mm, juveniles 60–63 mm, and adults 103–168 mm); SVL = 60–159 mm (males 97.0–141.5 mm; females 60.0–159.0 mm); TL = 3.0–9.0 mm (males 6.0–9.0 mm, females 3.0–9.0 mm); MBD = 1.4–4.4 mm; MTD = 1.2–3.2 mm; RW = 0.3–0.7 mm; HW = 1.1–2.3 mm; LOA/MBD = 35.3–49.3 ( $\bar{x}$  = 40.0 ± 3.96)  $n$  = 14; TL/LOA = 4.3–6.4% ( $\bar{x}$  = 5.4 ± 0.70)  $n$  = 14; TL/TW = 2.1–3.6 ( $\bar{x}$  = 2.7 ± 0.41)  $n$  = 14; RW/HW = 0.25–0.37 ( $\bar{x}$  = 0.31 ± 0.04)  $n$  = 14; and LOA/HW = 55.2–82.2 ( $\bar{x}$  = 67.4 ± 7.74)  $n$  = 14.












**Fig. 13.** Morphological variation in *Epictia albifrons*. (A, B) dorsal and ventral views of neotype (BYU 11490); (C, D, E, F, G) dorsal head (BYU 11490, BYU 11490, BYU 11499, BYU 11487, BYU 11491); (H, I, J, K, L, M) lateral head (BYU 11490, BYU 11487, BYU 11498, BYU 11491, BYU 11492, BYU 11492); (N, O, P) ventral head (BYU 11490, BYU 11499, BYU 11490); (Q) anterior dorsal midbody (BYU 11490); (R, S, T, U) dorsal midbody (BYU 11490, BYU 11492, BYU 11487, BYU 11499); (V, W, X, Y) lateral midbody (BYU 11490, BYU 11487, BYU 11492, BYU 11499); (Z, AA, AB) ventral midbody (BYU 11490, BYU 11487, BYU 11499); (AC, AD, AE) dorsal tail (BYU 11490, BYU 11487, BYU 11492); (AF) lateral tail (BYU 11491); (AG, AH, AI) lateral apical spine (BYU 11490, BYU 11491, BYU 11499); (AJ, AK) ventral tail (BYU 11487, BYU 11491); (AL) cloacal shield (BYU 11987); (AM, AN) lateral neck (BYU 11490, BYU 11487); (AO) dorsal head of juvenile (BYU 11501); (AP) lateral head of juvenile (BYU 11501); (AQ) ventral head of juvenile (BYU 11501); (AR) dorsal midbody of juvenile (BYU 11501); and (AS) ventral midbody of juvenile (BYU 11501).  © Van Wallach

**Table 6.** Variation in morphometrics of *Epictia albifrons* topotypes. See Table 5 for character abbreviations. Data presented as  $\bar{x} \pm SD$  (range) *n*.

Character	Males	Females	Total Sample
TMD	212.7 ± 4.717 (206–218) 9	212.6 ± 2.302 (210–215) 5	212.6 ± 3.915 (206–218) 14
SC	13.1 ± 1.364 (11–15) 9	13.0 ± 1.581 (11–15) 5	13.1 ± 1.385 (11–15) 14
LOA	130.1 ± 13.910 (103–148) 9	161.0 (154–168) 2	135.7 ± 17.930 (103–168) 11
TL	7.3 ± 1.003 (6.0–9.0) 9	8.8 (8.5–9.0) 2	7.5 ± 1.083 (6.0–9.0) 11
RTL	5.6 ± 0.726 (4.4–6.4) 9	5.0 ± 0.470 (4.3–5.4) 5	5.4 ± 0.696 (4.3–6.4) 14
MBD	3.4 ± 0.280 (2.9–3.8) 9	4.1 (3.7–4.4) 2	3.1 ± 0.927 (1.4–3.6) 14
LOA/MBD	38.8 ± 2.790 (35.3–43.5) 9	9.9 (38.2–41.6) 2	40.0 ± 3.955 (35.3–49.3) 14
LOA/HW	68.9 ± 6.439 (61.6–73.7) 9	64.5 ± 9.810 (55.2–77.0) 5	67.4 ± 7.742 (55.2–82.2) 14
MTD	2.6 ± 0.350 (2.1–3.2) 9	3.0 (3.0–3.0) 2	2.4 ± 0.670 (1.2–2.3) 14
RTW	2.8 ± 0.465 (2.1–3.6) 9	2.6 ± 0.281 (2.3–3.0) 5	2.7 ± 0.406 (2.1–3.6) 14
RW	0.6 ± 0.083 (0.5–0.7) 9	0.6 (0.6–0.6) 2	0.56 ± 0.139 (0.3–0.7) 14
HW	1.9 ± 0.162 (1.6–2.0) 9	2.2 (2.0–2.3) 2	1.77 ± 0.370 (1.1–2.3) 14
RRW	0.33 ± 0.033 (0.28–0.37) 9	0.28 ± 0.033 (0.25–0.33) 5	0.31 ± 0.039 (0.25–0.37) 14

Although the sample is small, adult females appear to be somewhat longer than males. The two females (154 and 168 mm (LOA),  $\bar{x} = 161$  mm) were longer than any of the nine males (103–148 mm (LOA),  $\bar{x} = 130$  mm). Sexual dimorphism is lacking in ventrals (210–215,  $\bar{x} = 212.6$ , in females; 208–218,  $\bar{x} = 212.7$ , in males), subcaudals (11–15,  $\bar{x} = 13.0$ , in females, 11–15,  $\bar{x} = 13.1$ , in males), and relative tail thickness (TL/MTD 2.6 in females and 2.8 in males). A slightly broader rostral is present in males (RW/HW:  $\bar{x} = 0.33$  in males,  $\bar{x} = 0.28$  in females), as well as a somewhat longer proportioned tail (TL/LOA:  $\bar{x} = 5.6$  in males,  $\bar{x} = 5.0$  in females) and a slightly more robust body (L/W:  $\bar{x} = 38.8$  in males,  $\bar{x} = 42.9$  in females).

Even though several authors concluded that the ratio of head width to body length is more reliable than midbody width to body length (Schmidt, 1977; Laurent, 1964), in this particular case, albeit with a small sample size, the midbody diameter/total length ratio was less variable than the interocular head width/total length ratio: relative body width ratio  $\bar{x} = 40.0 \pm 3.96$  (range = 35.3–49.3) *n* = 14, CV = 0.099 vs. relative head width ratio  $\bar{x} = 67.4 \pm 7.74$  (range = 55.2–82.2) *n* = 14, CV = 0.115.

**Viscera:** A single male (BYU 11489) and female (BYU 11492) form the basis of this description, with data presented as the mean (followed parenthetically by male and female values, respectively). When male and female data are identical, only a single value is listed. Sternohyoideus posterior tip = 14.1% (14.3%, 13.8%); sternohyoideus/snout–heart gap = 0.86 (0.85–0.88); heart length = 4.7% (4.9%, 4.4%) with midpoint at 18.6%; snout–heart interval = 21% (21.1%, 20.8%); heart–liver gap = 8.0% (7.5%, 8.5%) and interval = 51.7% (48.1%, 55.3%); heart–gall bladder gap = 46.1% (44.7%, 47.5%); liver lobes multipartite; right liver length = 39.1% (35.7%, 42.5%) with midpoint at 48.4% (46.4%, 50.5%) and 28.0 (29, 27) segments; left liver length = 29.6% (27.8%, 31.4%) with midpoint at 44.7% (44.4%, 45.0%) and 21.5 (23, 20) segments; anterior liver extension = 0.02 (0.05, 0) and posterior liver tail = 0.10 (0.06, 0.13); left liver/right liver = 0.76 (0.78, 0.74); liver–gall bladder gap = –1.0% (–3.5%, 1.5%) and interval = 39.7% (39.1%, 40.3%); liver–kidney gap 19.8% (26.7%, 12.9%) and interval = 64.4% (67.7%, 61%); gall bladder length = 1.6% (1.9%, 1.3%) with midpoint at 67.8% (66.7%, 68.9%); gall bladder–gonad gap = 8.9% (9.8%, 7.9%) and interval = 21.3% (25.9%, 16.7%); gall bladder–kidney gap = 19.2% (23.3%, 15.1%) and interval = 26.3% (30.5%, 22.0%); right gonad length = 6.4% (8.3%, 4.4%) with midpoint at 80.6% (81.6%, 79.6%); left gonad length = 4.8% (6.4%, 3.1%) with midpoint at 85.9% (88.5%, 83.3%); right adrenal midpoint = 83.6% (85.3%, 81.8%) and left adrenal midpoint = 86.4% (89.1%, 83.6%); gonad–kidney gap = –0.6% (–0.3%, –0.8%) and interval = 15.9% (17.9%, 12.2%); right kidney length = 3.3% (3.0%, 3.5%) with midpoint at 89.4% (92.5%, 86.3%); left kidney length = 3.3% (3.0%, 3.5%) with midpoint at 91.6% (94.7%, 88.5%); kidney overlap = 0.18 (0.14, 0.22); kidney–vent gap = 6.8% (3.8%, 9.7%) and interval = 12.2% (9.0%, 15.4%); rectal caecum bulbous = 3.2% (3.8%, 2.5%), three to four times the width of ileum; and caecum–vent interval = 7.4% (6.0%, 8.8%).

I examined the testes of eight males, which are multipartite and varied as follows: left testis with 5–9 ( $\bar{x}$  = 6.0) segments, right testis with 3–10 ( $\bar{x}$  = 5.5) segments, and total testis segments 8–19 ( $\bar{x}$  = 11.5). The right ovary of the single female had 6 large ova (measuring  $3.0 \times 1.0$  mm to  $2.0 \times 0.75$  mm) and 4 small follicles (measuring  $1.5 \times 0.75$  mm to  $1.0 \times 0.5$  mm). The left gonad contained 7 large ova (from  $3.0 \times 1.0$  mm to  $2.0 \times 0.75$  mm) and 4 follicles ( $1.5 \times 0.75$  mm to  $1.0 \times 0.5$  mm). Thirteen developing ova and 7 follicles were present in the ovaries, suggesting a relatively large clutch size of 13. Estimated clutch size in other *Epictia* range from 1 (*E. columbi*) to 5 (*E. tenella*) (Wallach, 1998a).

Respiratory system lacking tracheal lung and left lung complex; trachea length = 19.9% (19.5%, 20.3%) with midpoint at 11.0% (10.9%, 11%) and an estimated 151.5 (153, 150) tracheal rings or 77.4 (75.4, 79.5) rings/10% SVL; anterior tip of lung = 19.0% (18.4%, 19.5%); tracheal entry into right lung terminal; cardiac lung length = 2.0% (2.6%, 1.3%); right lung length = 30.2% (30.8%, 29.6%) with midpoint at 36.0% (36.5%, 35.5%), cranial portion of lung faveolar and caudal portion trabecular; right lung posterior tip = 51.1% (51.9%, 50.3%); intrapulmonary or right bronchus length = 19.8% (19.5%, 20.1%) with posterior tip at 40.7% (40.6%, 40.9%); bronchus/right lung = 0.66 (0.68, 0.63); trachea-bronchus length = 39.7% (39.8%, 39.6%) with midpoint at 20.9% (20.7%, 21.1%); bronchus/right lung = 0.65 (0.63, 0.68); trachea-bronchus/total lung length = 0.78 (0.79, 0.77); and total lung length = 32.2% (33.5%, 30.8%) with midpoint at 35.1% (35.2%, 34.9%).

Visceral distance data include heart–right lung distance = 17.4% (17.9%, 16.9%); heart–liver distance = 29.9% (27.8%, 31.9%); liver–kidney distance = 42.1% (47.2%, 36.9%); trachea–liver distance = 37.5% (35.5%, 39.5%); right lung–adrenal distance = 49.0% (50.7%, 47.2%); trachea–gall bladder distance = 46.9% (46.0%, 47.8%); heart–gonad distance = 62.0% (63.0%, 61.0%); trachea/bronchus–kidney distance = 69.6% (72.9%, 66.3%); heart–kidney distance 71.9% (75.0%, 68.8%); and trachea–adrenal distance = 74.0% (76.3%, 71.7%).

**Distribution:** *Epictia albifrons* presently is a Brazilian endemic, known with certainty only from the type locality in northern Brazil (Pará), elev. NSL (Map 13).

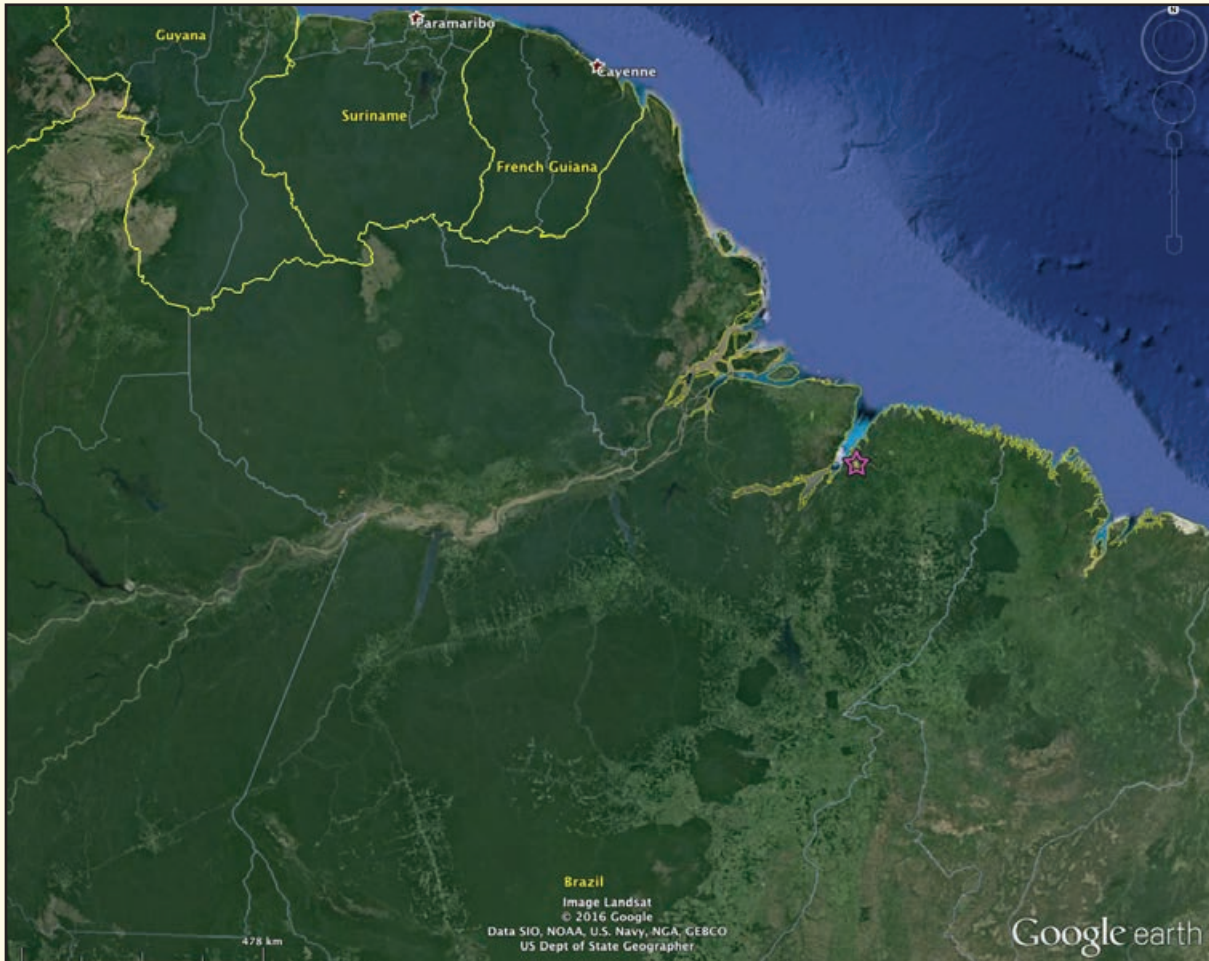
Some authors included the following countries as part of the distribution of *E. albifrons*: Ecuador (Peters, 1960; Miyata, 1982; Almendariz, 1991, but see Purtschert, 2007, and Cisneros-Heredia, 2008, for rebuttal), Peru (Carrillo de Espinoza and Icochea, 1995; Lehr, 2002, but see Lamar, 1997, for rebuttal), Bolivia (Fugler and Riva, 1990, and Fugler et al., 1995, but see Börschig, 2007, and Embert, 2007, for rebuttal), Paraguay (Serié, 1915, but see Aquino et al., 1996, for rebuttal), Uruguay (Vaz-Ferreira and Soriano, 1960, but see Carreira et al., 2005, for rebuttal), and Argentina (Abalos and Mischis, 1975; Di Fonzo de Abalos and Bucher, 1981; Cei, 1986, 1994; Williams and Francini, 1991; McDiarmid et al., 1999; but see Giraudo, 2002 and Giraudo and Scrocchi, 2002 for rebuttal).

**Habitat:** This species inhabits lowland tropical rainforest (Cunha and Nascimento, 1978).

**Comparisons:** In addition to all Brazilian species, I compared all the known species of *Epictia* occurring in Colombia, French Guiana, Guyana, Surinam, and Venezuela, essentially the Amazon and Orinoco basins east of the Andes: *E. albipuncta* (Burmeister, 1861), *E. australis* (Freiberg and Orejas-Miranda, 1968), *E. borapeliotes* (Vanzolini, 1996), *E. clinorostris* Arredondo and Zaher, 2010, *E. collaris* (Hoogmoed, 1977), *E. diaplocia* (Orejas-Miranda, 1969), *E. munoai* (Orejas-Miranda, 1961), *E. signata* (Jan, 1861), *E. tenella* (Klauber, 1939), and *E. unicolor* (Werner, 1913).

*Epictia albifrons* can be separated from *E. albipuncta* by a lower number of middorsals ( $\leq 218$  vs.  $\geq 246$ ) and by fewer midtail scale rows (10 vs. 12). *Epictia albifrons* is distinguishable from *E. australis* by the presence of fewer middorsals ( $\leq 218$  vs.  $\geq 233$ ); a narrower rostral ( $\leq 0.37$  HW vs.  $\geq 0.38$  HW); more infralabials (4 vs. 3); and a different color pattern (striped dorsum vs. two black gular and one caudal ring). *Epictia albifrons* is recognizable from *E. borapeliotes* by the presence of fewer middorsals ( $\leq 218$  vs.  $\geq 256$ ); a broader rostral ( $\geq 0.25$  HW vs.  $\leq 0.25$  HW); and more infralabials (4 vs. 3). *Epictia albifrons* can be differentiated from *E. clinorostris* by the presence of a rounded snout in lateral view (vs. depressed snout); by the presence of fewer middorsals ( $\leq 218$  vs.  $\geq 240$ ); the dorsal rostral long, extending past posterior eye level; with a truncated apex (vs. short, not reaching anterior level of eyes, with a rounded apex); by fewer infralabials (4 vs. 5); a dark dorsal pattern (triangular or diamond-shaped spots vs. rectangular spots); and a semilunate cloacal shield (vs. triangular). *Epictia albifrons* is discernible from *E. collaris* by the presence of fewer middorsals ( $\leq 218$  vs.  $\geq 155$ ); more infralabials (4 vs. 3); a longer dorsal rostral (extending past posterior border of eyes vs. reaching anterior eye level); larger eyes ( $2/5$ – $1/2$  of ocular shield height





**Map. 13.** Distribution of *Epictia albifrons* in northeastern Brazil.

vs.  $\frac{1}{3}$  of ocular height); dorsal color pattern (striped vs. not striped); lack of a pale nuchal spots (vs. 2 present); and a pale caudal spot larger ventrally than dorsally (vs. equal above and below). *Epictia albifrons* can be diagnosed from *E. diaplocia* by the presence of fewer subcaudals ( $\leq 15$  vs.  $\geq 14$ ); a truncated, sagittate rostral (vs. rounded apex); elongate pentagonal supraoculars that are twice as broad as deep (vs. short rectangular supraoculars  $1\frac{1}{2}$  times as broad as deep); and an enlarged frontal (wider than long vs. longer than wide). *Epictia albifrons* is identifiable from *E. munoai* by the presence of a sagittate rostral with a truncated apex (vs. subtriangular rostral with rounded apex); a greater number of infralabials (4 vs. 3); and the numerous visceral differences listed in Table 7. *Epictia albifrons* can be differentiated from *E. signata* by the dorsal pattern (striped vs. uniform); rostral shield (sagittate with truncated apex vs. triangular with rounded apex); and frontal (large with rounded borders vs. small and hexagonal). *Epictia albifrons* is discriminated from *E. tenella* by the supraocular-supralabial condition (absent vs. present). See *E. tenella* account for further comparisons. *Epictia albifrons* differs from *E. unicolor* by the presence of fewer middorsals ( $\leq 218$  vs. 246); fewer supralabials (2 vs. 3) and infralabials (4 vs. 5); fewer midtail scale rows (10 vs. 12); and the subocular condition (absent vs. present).

**Table 7.** Comparison of visceral characters (as % SVL or ratio) of *Epictia albifrons* with *E. munoai*.

Character	Males		Females		Both Sexes	
	<i>E. munoai</i>	<i>E. albifrons</i>	<i>E. munoai</i>	<i>E. albifrons</i>	<i>E. munoai</i>	<i>E. albifrons</i>
	<i>n</i> = 3	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 4	<i>n</i> = 2
Heart-liver interval	43.7	48.1	44.5	55.3	43.9	51.7
Heart-liver gap	6.2	7.5	7.5	8.5	6.6	8.0
Heart-gall bladder gap	38.7	44.7	38.5	47.5	38.7	46.1
Right liver length	32.6	35.7	32.1	42.5	32.5	39.1
Left + right liver length	59.1	63.5	54.0	73.9	57.8	68.7
Right liver midpoint	44.4	46.4	46.2	50.5	44.8	48.5
Left liver midpoint	42.3	44.4	44.9	45.0	43.0	44.7
Liver-gall bladder interval	34.2	39.1	32.5	40.3	33.8	39.7
Gall bladder midpoint	61.3	66.7	61.9	68.9	61.5	67.8
Gall bladder-gonad gap	7.5	9.8	6.0	7.9	7.1	8.9
Right gonad midpoint	72.9	81.6	72.8	79.6	72.9	80.6
Left gonad midpoint	76.7	88.5	77.2	83.3	76.8	85.9
Right adrenal midpoint	77.0	85.3	75.8	81.8	76.6	83.6
Left adrenal midpoint	80.4	89.1	78.1	83.6	79.6	86.4
Right kidney midpoint	83.0	92.5	79.6	86.3	82.1	89.4
Left kidney midpoint	86.4	94.7	84.0	88.5	85.8	91.6
Kidney overlap	0.05	0.14	0	0.22	0.04	0.18
Kidney-vent gap	11.6	3.8	13.6	9.7	12.1	6.8
Kidney-vent interval	19.0	9.0	22.3	15.4	19.8	12.2
Rectal caecum-vent interval	10.5	6.0	14.3	8.8	11.4	7.4
Rectal caecum/left kidney	0.46	1.27	0.53	0.71	0.48	0.99
Right lung length	28.4	30.8	24.9	29.6	27.5	30.2
Right bronchus length	16.4	19.5	17.4	20.1	16.7	19.8
Trachea-bronchus length	36.8	39.8	38.1	39.6	37.1	39.7
Heart–liver distance	25.0	27.8	26.0	31.9	25.3	29.9
Trachea–liver distance	32.8	35.5	33.9	39.5	33.1	37.5
Trachea/bronchus–GB distance	41.6	46.0	41.0	47.8	41.4	46.9
Right lung–adrenal distance	43.8	50.7	41.9	47.2	43.1	49.0
Heart–gonad distance	53.5	63.0	52.6	61.0	53.3	62.0
Heart–kidney distance	65.3	75.0	64.7	71.7	64.4	71.9
Trachea–adrenal distance	66.8	76.3	64.7	71.7	66.1	74.0

**Remarks:** Confusion among *Epictia albifrons*, *E. goudotii*, and *E. phenops* long has existed. Jan (1864) noted the resemblance of *E. goudotii* to *E. albifrons*, but separated *E. goudotii* by the lack of pale spots on the snout and tail and the anterior supralabial not in contact with the supraocular. Boulenger (1893) saw no difference between *E. albifrons* and *E. phenops* and synonymized them, while recognizing *E. goudotii* as a valid species. Smith (1939) recognized that *E. phenops* was distinct from *E. albifrons*, with which it previously had been confused. Klauber (1939) separated *E. tenella* from *E. albifrons* based on the contact between the anterior supralabial and supraocular. Orejas-Miranda (1967: 439) considered *E. albifrons* distinct from *E. tenella* by “presencia de supraoculares de tamaño medio, mayores en tamaño que la escama prefrontal. Poseer dos supralabiales, la primera no estableciendo contacto con la supraocular.” Peters et al. (1970: 166) separated *E. goudotii* from *E. albifrons* by pale and dark middorsal stripes of equal width vs. dark middorsal stripes bordered by narrow or indistinct pale lines, respectively. Worth (1967) pointed out that two species of *Epictia* occurred on Trinidad, the rarer form (*E. goudotii*) with a pink spot at each end whereas the more common form (*E. albifrons*) with only white on the head. Not surprisingly, Adalsteinsson et al. (2009) found a sister group relationship between *E. albifrons* and the *E. goudotii* complex. Thomas (1965), Hoogmoed and Gruber (1983), and Franco and Pinto (2009) pointed out rare variability in the supralabial-supraocular contact.

Currently, there are three competing opinions as to the proper nomenclatural action regarding *E. albifrons* and *E. tenella*. Researchers in the “*albifrons* school of thought” (Smith and List, 1958; Orejas-Miranda, 1967; Hoogmoed and Gruber, 1983; Pérez-Santos and Moreno, 1988; Kornacker, 1999; McDiarmid et al., 1999; Aviles-Pires et al., 2010) believe in nomenclatural stability, and since *albifrons* is the oldest available name and is entrenched in the literature dating back to 1824, that Article 23.1 of the Code (ICZN, 1999) applies. Since the type is lost and the name cannot be unambiguously associated with a single known species, however, a neotype must be designated for *E. albifrons* in accordance to Article 75.1 of the Code (ICZN, 1999). Ideally, this could be achieved with a selection of a topotype from Belém, Pará, Brazil. Unfortunately, although Orejas-Miranda (1967) mentioned that such topotypic material was available, he did not designate a neotype or suggest possible candidates; possibly, he was aware of the BYU material. Vanzolini (1970: 13) considered *E. tenella* to be a synonym of *E. albifrons*, reiterating that the problem could “only be settled by collecting around Belém, the type locality” of *E. albifrons*. To further complicate matters, Cunha and Nascimento (1978, 1993) did not record a single specimen of *E. albifrons* from the Pará region, and neither did the following authors describing snakes from the Manaus region: Yuki and Santos (1996), Martins and Oliveira (1998), Fraga et al. (2013), and Moreira-Rodrigues et al. (2016). Cunha and Nascimento (1993) and Ávila-Pires et al. (2010) proposed that the type locality might be in error, and that *E. albifrons* might have originated from the Guayanian side of the Amazon.

Members of the “*tenella* school of thought” (Wilson and Hahn, 1973; Hahn, 1980; Pérez-Santos and Moreno, 1990; Franco and Pinto, 2009; Starace, 2013; Koch et al., 2014) are in favor of considering *Stenostoma albifrons* Wagler a *nomen dubium* because the original description is inadequate for determining the characters needed to separate this species from other currently known *Epictia*. They believe that the next oldest name, *E. tenella* (Klauber, 1939), should be recognized as the name of this Brazilian taxon.

The “*albifrons-tenella* school of thought” considers that both species are valid and should be recognized (Peters et al., 1970; Adalsteinsson et al., 2009; Wallach et al., 2014). In order for both *E. albifrons* and *E. tenella* to be considered valid, an *albifrons* neotype must be designated or a species similar to but distinct from *E. tenella* must be discovered near the original type locality of Belém (or, if Wagler’s type locality was in error, as some researchers think, the correct locality from which Wagler’s specimen originated). Hoogmoed and Gruber (1983) concluded that *E. tenella* was identical to *E. albifrons*, and regarded *E. tenella* as a junior synonym. The distinguishing characters of the two taxa were cited as being (1) large bulging eyes not covered by skin; (2) large pentagonal ocular scales covered with pits; (3) a quadrangular yellow spot on tip of the snout; (4) a yellow-tipped tail; and (5) a dorsal pattern of wide blackish brown longitudinal stripes separated by narrow, pale, zigzag lines. To this could be added (6) the elongated subquadrangular supraoculars mentioned by Wagler (1824) and shared with *E. tenella*.

The designation of a neotype is necessary to finally settle the uncertainty in Neotropical leptotyphlopoid nomenclature and taxonomy. The name *Epictia albifrons* (and its various combinations of *Stenostoma albifrons*, *Typhlops albifrons*, *Glauconia albifrons*, and *Leptotyphlops albifrons*) has been attributed erroneously to a variety of species from Mexico, Central America, South America, and the Antilles for more than 170 years (McDiarmid et



al., 1999). Boulenger (1893: 63) recorded the distribution of *E. albifrons* as “Tropical America, from Tehuantepec and the Lesser Antilles to Peru and Argentina” and Werner (1917) summarized the distribution as Antilles, Mexico, Venezuela, Trinidad, Guyana, Brazil, Peru, Bolivia, Paraguay, Uruguay, and Argentina. *Epictia albifrons* might be restricted, at most, to Amazonian South America (Colombia, Venezuela, Trinidad, Guyana, Suriname, French Guiana, northern Brazil, eastern Peru, and eastern Bolivia), as first elucidated by Peters et al. (1970), but likely occurs in a much smaller geographic region. Recent studies have shown that the distributions of scolecophidians, in general, are not extensive (Broadley and Wallach, 2007a, b, 2009; this paper).

The original description of *E. albifrons* by Wagler cited several key characters (supraocular shape, large eye, zigzag stripes, and yellow spots on the head and tail), all of which pertain to a number of species in the genus *Epictia*. The only subsequent examination of the holotype of *Stenostoma albifrons* was by Jan (1859), who borrowed Wagler’s snake collection for study. Jan (1861 and 1864) provided an amplified description of *S. albifrons*, and in 1861 Jan and Sordelli included a figure in their snake atlas (1860–1866, livr. 2, pl. 5–6, fig. 1); however, instead of using Wagler’s Brazilian type from Munich’s ZSM for the illustration, they used a Peruvian specimen from Lima in Milan’s MSNM. Lima is located on the arid Pacific coast of western Peru more than 3,000 km away, and separated by the Andes from the type locality of *S. albifrons* in the wet tropical rainforest of the Atlantic coast.

In light of the restricted distributions of most scolecophidians, it can be assumed, with confidence, that Jan and Sordelli’s figure does not depict the type of *S. albifrons*, but represents a different species of the genus *Epictia*. Jan and Sordelli’s lateral head figure reveals contact between the supraocular and anterior supralabial, a diagnostic feature of the *E. tessellata* species group. Jan (1861: 187) reported *S. albifrons* to have “*Il primo labiale è molto alto e termina quasi all’altezza dell’occhio, il quale giace nell’angolo dell’oculare formato dal primo labiale e dalla prima squama della serie cefalica laterale*” and Jan (1864: 34) wrote the “*première labiale élevée jusqu’au niveau de l’oeil, qui est placé dans l’angle formé par la première labiale et la première écaille surcéphalique latérale.*” In neither of these descriptions did Jan state that the supralabial and supraocular were in contact (as in the Jan and Sordelli figure), nor that he was describing Wagler’s type specimen. Jan (1861) cited Duméril & Bibron’s (1844) description of *Stenostoma albifrons* in his synonymy. Duméril & Bibron included *Typhlops undecimstriatus* Cuvier (1829), *Typhlops undecimstriatus* Griffith and Pidgeon (1831), and *Typhlops undecimstriatus* Gray (1831), all of which are *nomina nuda*, as synonyms of *S. albifrons*. Jan (1863 and 1864) thus considered *Typhlops undecimstriatus* Schlegel (1839 *In* 1837–1844), which was based on d’Orbigny’s *Stenostoma* “*albifrons*” (1847: 9, pl. 6, figs. 1–6) from Bolivia and had supranasal-ocular contact, also to be a synonym of *S. albifrons*. Jan’s concept of *S. albifrons*, therefore, included specimens with both supraocular-supralabial contact and supranasal-ocular contact. This fact contributed to the erroneous belief that the presence or absence of supraocular-supralabial contact was variable in *E. albifrons* and unreliable as a systematic character (Boulenger, 1893; Thomas, 1965; Franco and Pinto, 2009).

According to W. Hellmich *In* Smith and List (1958) and Hoogmoed and Gruber (1983), the holotype of *S. albifrons* was destroyed on 11 April 1945 by the bombing of Planegg, Germany, during World War II. Hahn (1980), Hoogmoed and Gruber (1983), and Franzen and Glaw (2007) confirmed the loss of the type specimen.

Mumaw et al. (2015: 288–291, figs. 346–349), in a non-peer-reviewed book on the snakes of Venezuela, made an inappropriate and ill-advised change by designating MCZ R-2885 as the neotype of *Stenostoma albifrons*. Although originating from the state of Pará (without specific locality), this specimen was collected by the Thayer Expedition between 10 August 1865 and 26 March 1866, and now is in a state of poor preservation, broken in two pieces, partly decomposed with the epidermis sloughed off, and nearly completely faded from light (Fig. 14AC–AI). The exact body length, middorsal scale count, body proportions, original color pattern of body and head, and head shield configurations cannot be determined precisely due to the poor condition of the specimen.

I contest the neotype designation of MCZ R-2885 for *E. albifrons* because this action was made in opposition to Article 75.3.3 of the Code (ICZN, 1999: 84), whereby in order for a neotype selection to be valid it must contain “data and description sufficient to ensure recognition of the specimen designated.” Since a topotypic series of *E. albifrons* is available from Belém, the designation of Mumaw et al. (2015) also violates Article 75.3.6 (ICZN, 1999: 85) because it does not come “as nearly as practicable from the original type locality.” By being published in a book instead of a peer-reviewed journal, where objections to this designation might have occurred, it also ignores Recommendation 75B (ICZN, 1999: 85), which states that “an author should be satisfied that the proposed designation does not arouse serious objection from other specialists in the group in question.” Additionally,

Recommendation 75A (ICZN, 1999: 85) cites reasons that would preclude specimens from neotype designation, such as “data inadequate to meet taxonomic requirements” and “poor condition of the specimens,” both of which apply to this situation.

In addition to the above objections, the neotype designation of Mumaw et al. (2015) is detrimental to the taxonomy of the Leptotyphlopidae, because all of the discernible characters of MCZ R-2885 indicate that it is identical to *E. tenella*. The taxon *E. tenella* is represented by a well-preserved and documented series of eight type specimens (holotype: AMNH 14269; paratypes: AMNH 14270; CM S-4888–90, CM S-4893; MCZ R-48774; and SDSNH 32761) with precise localities. If the Mumaw et al. (2015) neotype designation is recognized, *E. tenella* thereby would become a junior synonym of *E. albifrons*, which would be represented by a damaged specimen with incomplete morphological data and inexact locality data (MCZ R-2885). Thus, even if the neotype designation of Mumaw et al. (2015) were valid under the Rules, the action would result in more taxonomic confusion than presently exists and would represent a regression in our knowledge of the systematics of the Neotropical Leptotyphlopidae.

The topotypic material described above meets the requirements for neotype designation if two assumptions are accepted. The first assumption is that the supraocular-supralabial contact in *E. albifrons* either is not present (Orejas-Miranda, 1967) or unknown. The second assumption is that the only purported illustration of *E. albifrons*, found in Jan and Sordelli (1861 *In* 1860–1866: livr. 2, pls. 5–6, fig. 1), depicts a specimen from Lima, Peru, that represents a different species of the *E. tessellata* species group. Both assumptions appear to be true based on the available literature. With acceptance of the BYU neotype, examination of museum material now would be able to define the actual distribution of *E. albifrons*, *E. tenella*, and the other species with which *E. albifrons* has been confused for so many years.

The latest revision of snakes from eastern Pará, Brazil (Cunha and Nascimento, 1978) listed two species of Anomalepididae, *Liotyphlops ternetzii* (Boulenger, 1896) and *Typhlophis squamosus* (Schlegel, 1839), one species of Typhlopidae, *Typhlops reticulatus* (Linnaeus, 1758), and two species of Leptotyphlopidae, *Siagonodon septemstriatus* (Schneider, 1801) and *Trilepida macrolepis* (Peters, 1857). With the confirmation of *E. albifrons* as part of the fauna of Pará, Brazil, seven scolecophidians are known from the state, each representing a different genus, with the exception of two species in *Epictia* (Table 8): two species of Anomalepididae (*Liotyphlops ternetzii* and *Typhlophis squamosus*), one species of Typhlopidae (*Typhlops reticulatus*), and four species of Leptotyphlopidae (*Epictia albifrons*, *E. tenella*, *Siagonodon septemstriatus*, and *Trilepida macrolepis*).

**Table 8.** Morphometric data on the Scolecophidia of the state of Pará, Brazil. CS = cloacal shield shape; MSR = midbody scale rows; TSR = midtail scale rows; and SL = supralabials. See Table 5 for other character abbreviations.

Character	<i>Liotyphlops ternetzii</i>	<i>Typhlophis squamosus</i>	<i>Typhlops reticulatus</i>	<i>Epictia albifrons</i>	<i>Epictia tenella</i>	<i>Siagonodon septemstriatus</i>	<i>Tricheilostoma macrolepis</i>
MSR	22–28	22	20	14	14	14	14
TMD	463–515	341–390	207–299	206–218	205–242	213–247	211–255
SC	10–19	9–14	7–15	11–15	13–20	8–12	14–26
SL	4	4	4	2	2	2	3
LOA	88–413	130–300	38–522	63–168	71–215	129–300	126–378
L/W	47–52	40–61	18–34	35–49	37–60	30–54	32–68
RTL	1.7–4.0	1.7–2.4	1.6–4.3	4.4–6.2	5.1–7.7	2.1–5.0	6.0–11.8
TSR	—	—	—	10	10	12	10
RTW	1.4–1.8	1.1–1.5	0.9–1.1	2.1–3.6	2.5–5.0	1.2–1.3	2.8–6.7
RRW	0.42	0.25	0.26–0.48	0.25–0.37	0.26–0.34	0.42–0.57	0.25–0.40
CS	multiple	multiple	multiple	semilunate	subtriangular	semilunate	subtriangular

### Key to the of Scolecophidia in the state of Pará, Brazil

- 1a. Midbody scale rows 14; supralabials 2–3 (*Leptotyphlopidae*) . . . . . 2  
 1b. Midbody scale rows 20–28; supralabials 4 . . . . . 5  
 2a. Supralabials 3; dorsum unicolor . . . . . *T. macrolepis*  
 2b. Supralabials 2; dorsum striped . . . . . 3  
 3a. Midtail scale rows 12–14; tail length/width ratio < 1.5 . . . . . *S. septemstriatus*  
 3b. Midtail scale rows 10; tail length/width ratio > 2.0 . . . . . 4  
 4a. Supraocular contacts 1<sup>st</sup> supralabial; rostral apex rounded; nasal suture  
 horizontal . . . . . *E. tenella*  
 4b. Supraocular not in contact with 1<sup>st</sup> supralabial; rostral apex truncated; nasal  
 suture inclined 45° . . . . . *E. albifrons*  
 5a. Midbody scale rows 20; middorsals < 300; length/width ratio < 35; TL/TW <  
 1.1 (*Typhlopidae*) . . . . . *T. reticulatus*  
 5b. Midbody scale rows 22–28; middorsals > 340; length/width ratio > 40; TL/  
 TW > 1.1 (*Anomalepididae*) . . . . . 6  
 6a. Middorsals > 450; body and head uniform brown; enlarged head shields  
 present; RW/HW > 0.33 . . . . . *L. ternetzii*  
 6b. Middorsals < 400; black body with pale head; lacking enlarged head shields;  
 RW/HW < 0.33 . . . . . *T. squamosus*

#### *Epictia tenella* (Klauber, 1939)

Figs. 14A–AJ, 16AC–AF

*Stenostoma albifrons*—Jan 1861: 187–188 (part), 1863: 15 (part), 1864: 34 (part); Jan and Sordelli, 1861 *In* 1860–1866 (livr. 2): 2, pls. 5–6, fig. 1 (part); De Verteuil, 1858: 445; Cope, 1862: 350, 1875: 128 (part), 1887: 63 (part); Garman, 1887: 278; Hoogmoed and Gruber, 1983: 339; Kretzschmar, 2006: 45, 47; Hoser, 2012: 34 (part).

*Typhlops reticulatus*—Müller, 1878: 588; Hoogmoed, 1977: 114.

*Glauconia albifrons*—Boettger, 1891: 347, 1892: 103, 1898: 6 (part); Boulenger, 1893: 63 (part), 1896: 591, 1898: 129; Mole and Urich, 1894a: 82, 1894b: 517; Mole, 1895: 211, 1924a: 142–143, 1924b: 235; Wirsing, 1895: xxxiii; Koslowsky, 1898a: 26 (part); Werner, 1899: 483, 1910: 210, 1917: 203 (part); Lidth de Jeude, 1904: 84; Ditmars, 1907: 322, 1910: xvii, 196, 217, pl. 42 (upper); Procter, 1923: 1061; Roux, 1926: 291; Essex, 1927: 910, 920, figs. 48–49; Briceño-Rossi, 1934: 1, 132; McDowell and Bogert, 1954: 73; Boos, 1975: 22; Emsley, 1977: 234; Hoogmoed, 1977: 114; Kretzschmar, 2006: 46.

*Leptotyphlops albifrons*—Perraca, 1904: 7; Stejneger, 1905: 335, 338; Dunn, 1923: 186, 1934: 111; Amaral, 1930a: 76 (part), 1948: 6; Ditmars, 1933: xviii, 137, pl. 27 (upper); Briceño-Rossi, 1934: 1132; Parker, 1935: 528, 1938: 443, 449; Gorham and Ivy, 1938: 180; Angel and Rochon-Duvigneaud, 1942a: 166, 1942b: 257–258; Rochon-Duvigneaud, 1943: 446–447, 449–450, fig. 294F; Beebe, 1946: 12–13, 1952: 175; Marcuzzi, 1950: 3; Schmidt and Inger, 1951: 456; Wehekind, 1955: 9; Lynn, 1957: 53; Underwood, 1962: 97, 164, figs. x, xv; Thomas, 1965: 9; List, 1966: 5, 44; Boos and Quesnel, 1968: 15, col. photo; Grassé, 1970: 416, 426, fig. 311F; Orejas-Miranda *In* Peters et al., 1970 and 1986: 167 (part); Vanzolini, 1970: 14, 1981: xviii, 1986a and 1986b: 10; Mertens, 1972: 12; Amaral, 1977 and 1978: 28, figs. 1–3; Emsley, 1977: 234; Hardy, 1982: 80; Hoogmoed and Gruber, 1983: 319, 339–340; Tanner, 1985: 626; Lamar, 1987: 54, 71, 107, 122; Pérez-Santos and Moreno, 1988: 417, map 27; Pregill et al., 1988: 9; Lancini and Kornacker, 1989: 103; Fugler and Riva, 1990: 24; Mittermeier et al., 1990: 29; Donnelly and Myers, 1991: 51; Bertonatti, 1994: 169; Fugler et al., 1995: 42; Williams, 1992: 75; Rodrigues and Puerto, 1994: 393; Carrillo de Espinoza and Icochea, 1995: 19; Murphy, 1995: 62, 1996: 209, 212, 1997: 203–204, fig. F, map 107; Sánchez et al., 1995: 317; Silva and Sites, 1995: 894 (part); Hedges, 1996: 111, 115;



Rodrigues, 1996: 520; Lamar, 1997: 75; La Marca, 1997: 142; Gorzula and Señaris, 1998: 187, 230 (part); Heckman, 1998: 302; Wallach, 1998a: 461 (part), 550, 1998b: 184; Crother, 1999: 320, 2002: 538; Kornacker, 1999: 46, 220 (part); McDiarmid et al., 1999: 19–20 (part); Galán, 2000: 15; Lehr, 2000: 186, 2002: 100, 196; Péfaur, 2000: 66; Suárez et al., 2000: 71–72, fig. 1; Colli et al., 2002: 241; Giraud and Scrocchi, 2002: 3; Lehr and Lara, 2002: 356, 359; Markezich, 2002: 72; Reynolds et al., 2002: 11; Murphy, 2004: 146; Schlüter et al., 2004: 150, 160; Señaris, 2004: 351; Ávila-Pires, 2005: 38 (part); Carvalho et al., 2005: 50; McDiarmid and Donnelly, 2005: 498, 515, 523, 533; Rivas-Fuenmayor and Barrio-Amorós, 2005: 208; Carvalho, 2006: 26; Galán and Herrera, 2006: 53; Kretzschmar, 2006: 43, 46–47, 50; Navarrete et al., 2006: 43, 2009: 55; Passos et al., 2006: 347; Young, 2006: 6; Börschig, 2007: 167, 229–230 (part); Cavalcanti, 2007: 265; Embert, 2007: 32; Freitas and Santos-Silva, 2007: 157 (col. photo); Purtschert, 2007: 4; Silva-Rodrigues, 2007: 81; Adalsteinsson, 2008: 3–6, 13, 18, 26, 29, 37, 41, 46, figs. 3.2, 3.5; Barrio-Amorós and Brewer-Carias, 2008: 60; Carvalho-Cordeiro, 2008: 41, 104; Cundall and Irish, 2008: 374, 597; McDowell, 2008: 562; Varin, 2008: 122; Silveira-Bérnils, 2008: 9; Winer, 2008: 1007; Adalsteinsson et al., 2009: 7, fig. 3A; Delhay, 2009: 180 (part); Lira-da-Silva, 2009: 75; Señaris et al., 2009: 109; Acosta-Galvis et al., 2010: 601; Ávila-Pires et al., 2010: 70, 97, 111, fig. 64; Nogueira et al., 2010: 369; Hailey and Cazabon-Mannette, 2011: 189; Kawashita-Ribeiro et al., 2011: 159; Rodriguez et al., 2011: 14; Rovida, 2011: 58; Pyron et al., 2013: 24; Fearnside, 2014: 684.

*Leptotyphlops tenella* Klauber, 1939: 59–61, fig. 1A, B, 1945: 149; Bailey and Carvalho, 1946: 5–7, fig. 4; Barbour and Loveridge, 1946: 143; Beebe, 1952: 175; Underwood, 1953: 175 (lower photo); Pope, 1955: fig. 65; Wehekind, 1955: 9; Roze, 1955: 180, 1957: 180–181, 1966: 45–46, fig. 5, map. 5, 1970: 70; Thomas, 1965: 6, 9; McCoy and Richmond, 1966: 261; Orejas-Miranda, 1967: 435–437, fig. 2; Orejas-Miranda *In* Peters et al., 1970 and 1986: 172; Vanzolini, 1970: 13; Aitken et al., 1973: 19; Boos, 1975: 22, 2001: 39–41, figs. 2, 3; Schwartz and Thomas, 1975: 189; Thomas, 1975: 250–252, fig. 1; Emsley, 1977: 233–234, 266, fig. 3; Hoogmoed, 1977: 100, 114–118, figs. 9A–C, 10, 1979: 274, 1983: 236, 251; Maclean et al., 1977: 37, 47; Moonen et al., 1979: 84–85, col. pl.; Schwartz, 1978: 45; Lancini, 1979: 171–172, 1986: 171–172; Gasc and Rodrigues, 1980: 567; Hahn, 1980: 27; Abuys, 1982: 74–75, fig. 2, map 3 figs., 2003, 75–76, col. fig.; Freiberg, 1982: 118; Hardy, 1982: 80; Miyata, 1982: 19; Hoogmoed and Gruber, 1983: 319, 339–340; Branch, 1986: 293–294; Vanzolini, 1986a and 1986b: 10; Chippaux, 1987: 25, figs. 9E, 10C; Chippaux et al., 1988: 9, 20 (col. photo); Pregill et al., 1988: 9; Schwartz and Henderson, 1988: 223–224, 1991: 621–622, map; Duellman, 1990: 504; Cunha and Nascimento, 1993: 11; Welch, 1994: 37; Murphy, 1995: 62, 1996: 212, 1997: 203–204, fig. F, pl. 165; Sánchez et al., 1995: 316; Hedges, 1996: 111; Powell et al., 1996: 89; Gorzula and Señaris, 1998: 187 (part); Starace, 1998: 81–82, col. fig. and map; Censky and Kaiser, 1999: 186, 215; Crother, 1999: 320; McDiarmid et al., 1999: 19–20; Fitzgerald et al., 2002: 77; Giraud and Scrocchi, 2002: 3; Claessen, 2002: 57; M. Lee et al., 2007: 387; Suárez de Oliveira, 2007: 265; Dewynter et al., 2008: 13; Dias-Lima, 2008: 44; Silveira-Bérnils, 2008: 9; Daltry, 2011: 25, 28.

*Leptotyphlops albifrons* ssp.—Roze, 1957: 181.

*Leptotyphlops albifrons albifrons*—Roze, 1952: 156–157, 1970: 68; Peters, 1960a: 526–527 (part).

*Leptotyphlops albifrons tenella*—Roze, 1952: 155; Hahn, 1980: 27; McDiarmid et al., 1999: 20; Claessen, 2002: 57.

*Leptotyphlops* sp.—Mertens, 1972: 12; Hardy, 1975: 80.

*Leptotyphlops goudotii goudotii*—Boos, 1975: 22; Maclean et al., 1977: 43–44, 46.

*Leptotyphlops goudotii*—Emsley, 1977: 2, 34; McDiarmid et al., 1999: 30–31; Boos, 2001: 41.

*Leptotyphlops tenellus*—Schmidt, 1977: 169–170, figs. 2, 3; Hahn, 1980: 27; Orejas-Miranda and Zug, 1974: 172, fig. 2; Zimmerman and Rodrigues, 1990: 444, 448; Almendáriz, 1991: 155; Pérez-Santos and Moreno, 1991: 430–431, fig. 110; Péfaur, 1992: 12; Frank and Ramus, 1995: 251; Martins and Oliveira, 1998: 88; Wallach, 1998b: 184; Mattison, 1999: 146; McDiarmid et al., 1999: 20; Péfaur, 2000: 66; Claessen, 2001: 223, 229, 2002: 57–58 (col. photo); Wrobel, 2004: 288; Tipton, 2005: 27; Watkins-Colwell et al., 2006: 353; Carvalho et al., 2007: 43–44; Purtschert, 2007: 18–19; Adalsteinsson, 2008: 6; Cisneros-Heredia, 2008: 178, 179; Dewynter et al., 2008: 13; Silveira-Bérnils, 2008: 9; Acosta-Galvis et al., 2010: 601; Barros-Amorós et al., 2011: 25; Mendes-Pinto et al., 2011: 245; Toledo and Morais, 2013: 522; EOL, 2015: 792044.

*Leptotyphlops* sp.—Quesnel, 1977: 2; Boos, 1978: 1.

*Leptotyphlops macrolepis*—Bernarde and Abe, 2006: 105, 110.

*Epictia tenella*—Adalsteinsson et al., 2009: 10, 16–17, figs. 2B, 3A; Arredondo and Zaher, 2010: 189, 191, 194–195, 197, figs. 1C–D, 2B, 3; Pinto, 2010: 249–250; Barros-Amorós et al., 2011: 25, 37, 40, pl. 9B (col. photo); Hailey and Cazabon-Mannette, 2011: 189; Meireles dos Santos et al., 2011: 457, 459; Pinto and Curcio, 2011: 61; Bernarde, 2012: 66, fig. 109 (col. photo), 2014, 29, fig. 42 (col. photo); Bernarde et al., 2012a: 25, fig. 27 (col. photo), 2012b: 157, fig. 2A (col. photo); Çinar, 2012: 122; Rivas-Fuenmayor et al., 2012: 27; Valencia, 2012: 8; Fraga et al., 2013: 94–95, col. figs. A–E; Pantoja-Leite, 2013: 200; Starace, 2013: 134–135, fig. 73; Costa and Silveira-Bérnils, 2014: 83; Rutherford, 2014: 9, 20; Wallach

et al., 2014: 279; Fraga et al., 2013: 41, 48, 62, 70, 94, 95 (five col. photos), 242–243, 274–275; Mumaw et al., 2015: 423, 428–433, pl. 5, fig. 6A–D; McCranie and Hedges, 2016: 20–21.

*Epictia albifrons*—Adalsteinsson et al., 2009: 31, 46, figs. 6A, 12; Arredondo and Zaher, 2010: 189; Hoser, 2012: 34, 63 (part); Manuel et al., 2011: 76; Reynolds and MacCulloch, 2012: 213; Rivas-Fuenmayor et al., 2012: 27; Cole et al., 2013: 516, pl. 36A–B; MacCulloch and Reynolds, 2013: 1381; Koch et al., 2014: 228; Mumaw et al., 2015: 288–291, 326, 423, 428–431, 433, figs. 346–351, map 59; Pinto et al., 2015: 1,729; McCranie and Hedges, 2016: 8, fig. 2.

*Epictia tenela* (sic)—Silveira-Bérnils and Costa, 2012: 12.

*Epictia (Leptotyphlops) tenella*—Nielsen et al., 2013: 144.

*Epictia albifrons* (sic)—Mumaw et al., 2015: 432.

*Epictia fallax*—Mumaw et al., 2015: 294–295, 326, 423, 428–433, figs. 339–342, 369–372, 376, map 59.

*E. albifrons/E. tenella*—McCranie and Hedges, 2016: 4.

**Holotype:** AMNH 14269, a 177 mm (LOA) specimen collected by C. William Beebe between 10 and 23 June 1919, from “Kartabo, British Guiana” [= Kartabo, New York Zoological Society Tropical Research Laboratory at junction of Cuyuni and Mazaruni rivers, Bartica District, Cuyuni-Mazaruni, Guyana, 06°23'N, 58°42'W, elev. 50 m asl].

**Paratypes** (7): GUYANA: CUYUNI-MAZARUNI: Kartabo, collected by C. William Beebe in June of 1919, AMNH 14270; TRINIDAD: TUNAPUNA/PIARICO: Saint George: Mount Saint Benedict, collected by M. Graham Netting on 8 September 1927, CM S-4888; collected by M. Graham Netting on 10 September 1927, CM S-4889; collected by M. Graham Netting on 16 September 1927, CM S-4890, CM S-4892, MCZ R-48774 (exchange of CM S-4891 to MCZ on 8 May 1945), SDSNH 32761 (exchange of CM S-4890 to SDNHM on 31 August 1939); and El Dorado, collected by M. Graham Netting on 19 September 1927, CM S-4893.

**Etymology:** The specific epithet of this snake is derived from the Latin *tenellus*, meaning quite delicate, apparently in reference to the small size and gracile proportions of the snake.

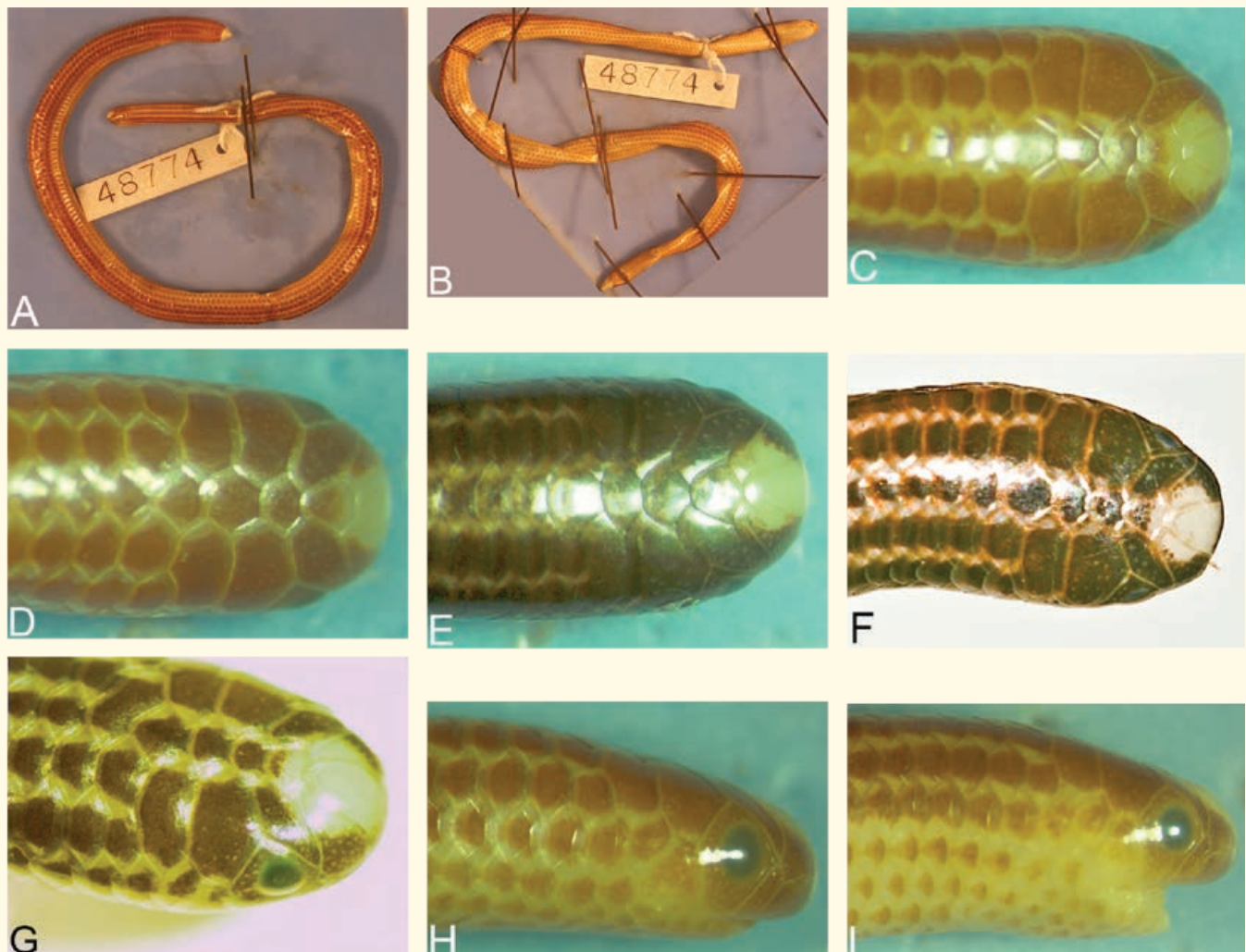
**Diagnosis:** (1) scale row formula = 14-14-14; (2) midtail scale rows = 10; (3) total length 71–215 ( $\bar{x}$  = 147.3) mm; (4) total midodorsals = 215–233 ( $\bar{x}$  = 224.5); (5) subcaudals = 13–20 ( $\bar{x}$  = 17.2); (6) relative body proportion = 37–60 ( $\bar{x}$  = 48.5); (7) relative tail length = 5.1%–7.8% ( $\bar{x}$  = 6.4%); (8) relative tail width = 2.8–4.1 ( $\bar{x}$  = 3.5); (9) relative rostral width = 0.26–0.34 ( $\bar{x}$  = 0.29); (10) relative eye size = 0.36–0.46 ( $\bar{x}$  = 0.41); (10) rostral subtriangular with a truncated apex, extending to pre- or mid-eye level; (11) supralabials 2, tall anterior supralabial in contact with supraocular at mid-eye level; (12) frontal pentagonal, 1½ times broader than deep; (13) supraoculars large and quadrangular with oblique borders, twice as broad as deep; (14) widest anteriormost vertebral scale 5<sup>th</sup>; (15) parietals deeper than occipitals, oriented transversely; (16) infralabials 4; (17) cloacal shield subtriangular in shape; (18) head brown, with a large yellow spot covering rostral and adjacent scales (supranasals and frontal); (19) dorsum with 7 dark brown stripes of contiguous ovals bordered by 8 moderate zigzag yellow stripes (= 7 dark stripes); (20) venter pale brown, each scale narrowly outlined in yellow; (21) midbody stripe formula (7 + 0) and middorsal pattern (3); (22) tail with a pale terminal spot covering 0–2 ( $\bar{x}$  = 1.1) dorsocaudals and 1–3 ( $\bar{x}$  = 1.8) subcaudals (ventral/dorsal ratio 1.6); and (23) apical spine a thorn-like compressed cone.

**Description:** Head wider than neck, smoothly rounded in dorsal profile, all head shields with large sensory pits (Fig. 14P); rostral short and sagittate or subtriangular with truncated apex, not or just reaching interocular level (Fig. 14C); frontal subhexagonal or subtriangular (Fig. 14D), slightly longer than wide; postfrontal semilunate, broader than long; broadest anteriormost vertebral scale 5<sup>th</sup>; interparietal and interoccipital larger than all other vertebrae, as broad as deep, subhexagonal in shape with rounded posterior contours; supraoculars large and elongated with unique shape in the form of attenuated hexagons, more than 3 times as wide as long, in contact with anterior supralabials; parietals distinctly deeper than occipitals, both shields transverse in orientation (Fig. 14C); lateral head profile rounded; nasal entirely divided, suture forming a deep V-shaped angle along anterior supralabial and infranasal, nostril oval and positioned closer to rostral than supralabial; infranasal 2–2½ times as tall as long, narrowing toward lip; supralabials 2, anterior supralabial tall with nearly parallel sides, three times as high as wide, extending to the level of the pupil and contacting the attenuated supraocular to exclude ocular from supranasal contact (Fig. 14I–K), its labial border equal to that of infranasal; ocular large, twice as high as long, nearly pentagonal in shape with triangular anterior and posterior borders, in contact with 4 other shields (Fig. 14J); eye moderate in size, lacking distinct iris, slightly oval or elliptical in vertical plane, with a small eye/ocular ratio (ED/OH = 0.36–0.46,

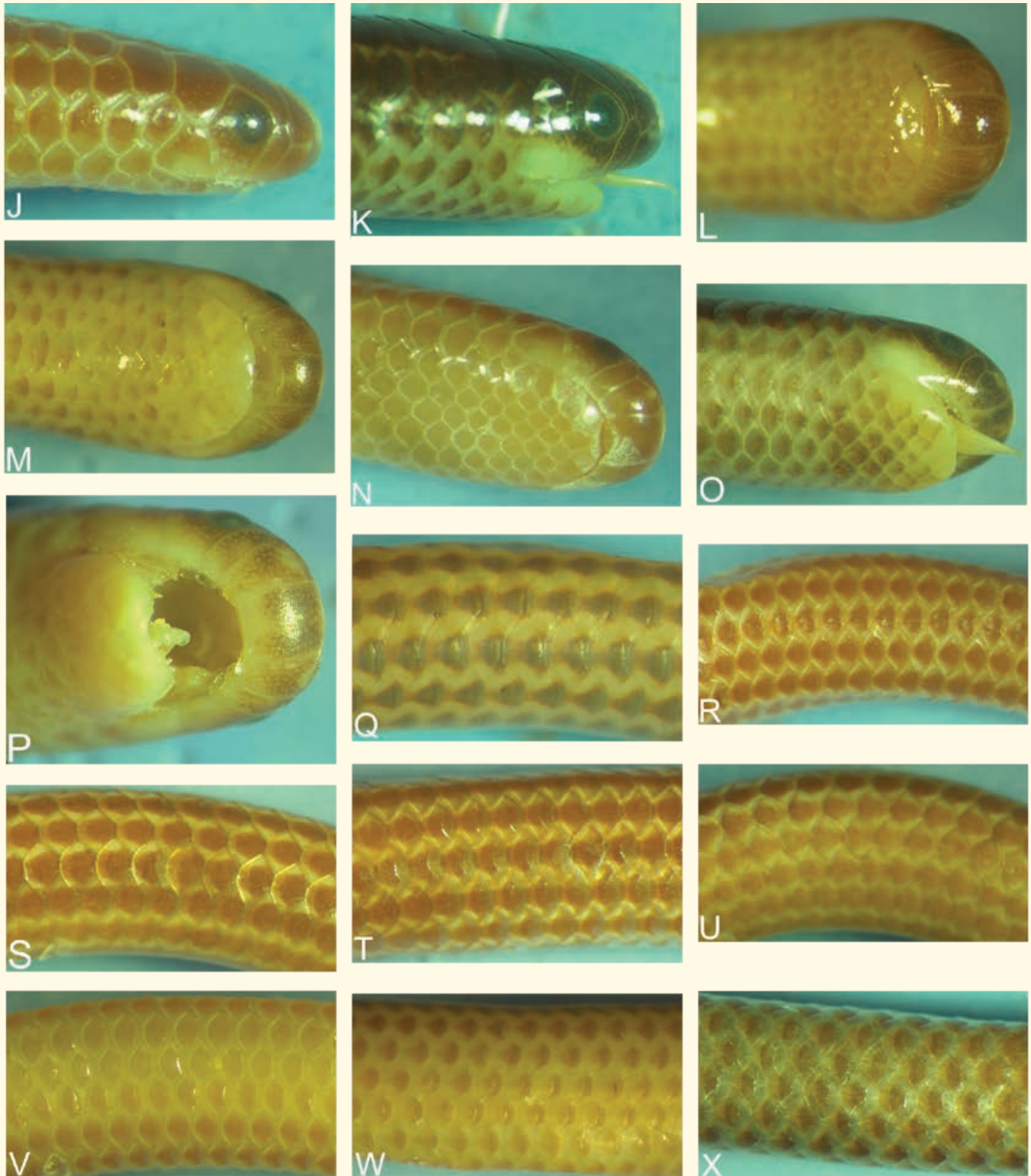
$\bar{x} = 0.41$ ), completely beneath ocular shield, protuberant and visible in dorsal view; posterior supralabial as long as high with rounded apex, shorter than anterior supralabial; ventral rostral lacking a preoral groove; mental butterfly-shaped, infralabials 4, the last shield elongated and twice the size of other three; costal scales rounded and imbricate, in 14 rows throughout; cloacal shield subtriangular; apical spine in form of a vertically compressed cone with stout termination (Fig. 14AB–AC).

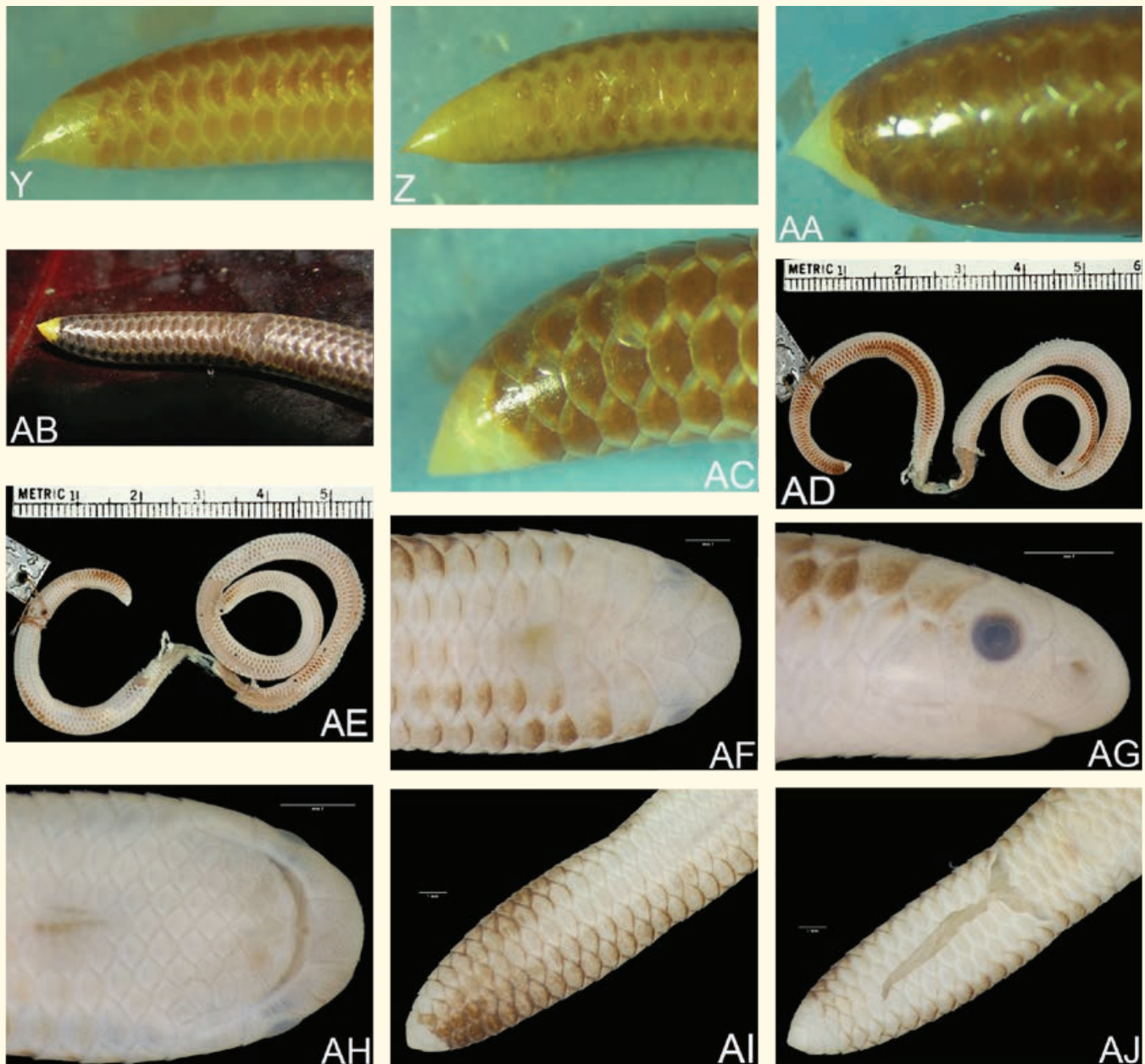
Overall coloration in life vividly bicolored in yellow and dark brown, with a large yellow spot on the dorsum of head and a small yellow tail spot (Fig. 16AB–AF). Midbody color pattern in preserved specimens consists of 7 brown to dark brown dorsal stripes (formed by strings of connected oval-shaped spots) separated by moderate to broad, yellow, zigzag stripes (Fig. 14Q–R), and 7 ventral rows of pale brown scales with moderate to broad yellow borders (Fig. 14V–W; midbody stripe formula 7 + 0). Head brown with a large yellow spot on snout that covers rostral and usually edges of frontal and supranasals (Fig. 14F, G; occasionally also the supraoculars); a pair of pale paravertebral stripes extends to occipitals and parietals; lateral head brown with a weak yellow bar on part of the lower edge of posterior supralabial and ocular; lower lip yellow (Fig. 14M, O). Cloacal shield either entirely pale or heavily infused with brown vermiculations; cloacal region pale yellow. Tail normally brown with pale stripes but may be unicolored brown; small yellow tail spot symmetrically disposed with a mean dorsocaudal spot of 1.1 scales (range = 0–2), a mean subcaudal spot of 1.8 scales (range = 1–3), and a ventral/dorsal ratio of 1.6 (Fig. 14AA–AC).

Bailey and Carvalho (1946) described the hemipenis of a Brazilian specimen, and Thomas (1975) that of a Peruvian specimen.









**Fig. 14.** Morphological variation in *Epictia tenella*. (A, B) dorsal and ventral views of paratype of *E. tenella* (MCZ R-48774); (C, D, E, F, G) dorsal head (ANSP 15985, MVZ 82446, MVZ 247608, USNM cat. no. unavailable, USNM cat. no. unavailable); (H, I, J, K) lateral head (ANSP 15985, FMNH 217237, MVZ 82446, MVZ 247608); (L, M, N, O, P) ventral head (ANSP 15985, FMNH 217237, MVZ 82446, MVZ 247608, FMNH 217238); (Q, R, S) dorsal midbody (MVZ 82447, MVZ 82446, FMNH 200292); (T) lateral midbody (FMNH 217237); (U, V, W, X) ventral midbody (FMNH 200292, MVZ 82446, MVZ 82447, MVZ 247608); (Y) lateral tail (MVZ 82446); (Z) ventral tail (MVZ 82447); (AA) lateral apical spine (FMNH 217237); (AB) ventral tail of live Guyana specimen; (AC) lateral apical spine (FMNH 200292); (AD) dorsal view of Mumaw et al. (2016) proposed neotype for *Epictia albifrons* (MCZ R-2885); (AE) ventral view of Mumaw et al. (2016) proposed neotype for *Epictia albifrons* (MCZ R-2885); (AF) dorsal head of Mumaw et al. (2016) proposed neotype for *Epictia albifrons* (MCZ R-2885); (AG) lateral head of Mumaw et al. (2016) proposed neotype for *Epictia albifrons* (MCZ R-2885); (AH) ventral head of Mumaw et al. (2016) proposed neotype for *Epictia albifrons* (MCZ R-2885); (AI) dorsal tail of Mumaw et al. (2016) proposed neotype for *Epictia albifrons* (MCZ R-2885); and (AJ) ventral tail of Mumaw et al. (2016) proposed neotype for *Epictia albifrons* (MCZ R-2885).

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**Distribution:** *Epictia tenella* is broadly distributed over cis-Andean South America, including Trinidad and Tobago (Trinidad, elev. NSL–600 m); eastern Colombia (Meta and Vichada, elev. 150 m); eastern Venezuela (Amazonas, Bolívar, Distrito Federal, Monagas, and Sucre, elev. 50–1,050 m); Guyana (Barima-Waini, Cuyuni-Mazaruni, Essequibo Islands-West Demerara, Mahica-Berbice, Potaro-Siparuni, Upper Demerara-Berbice, and Upper Takutu-Upper Essequibo, elev. NSL–350 m); Surinam (Brokopondo, Coronie, Marowijne, Nickerie, and Paramaribo, elev. NSL–825 m); French Guiana (Cayenne and Saint Laurent du Maroni, elev. 50–200 m); northern Brazil (Amapá, Amazonas, Mato Grosso, Pará, Rondônia, and Roraima, elev. NSL–225 m); northeastern Peru (Cajamarca, Cuzco, Huánuco, Loreto, and San Martín, elev. 150–1,750 m); and northern Bolivia (La Paz, elev. 1,400 m), overall elev. NSL–1,750 m (Map 14). An unconfirmed record from southern Ecuador (Azuay, elev. 2,700 m) requires verification.

**Ecology:** This species inhabits lowland evergreen and semi-evergreen seasonal forest (Murphy, 1997), and also occurs in lowland forest clearings (Nielsen et al., 2013).

**Remarks:** I examined MCZ R-2885 (Fig. 14AD–AJ) and it agrees in all available characters with those of *Epictia tenella*; thus, I have no reservations about identifying it as this species. This conclusion contradicts the assessment of Mumaw et al. (2016), who, as previously discussed, regarded MCZ R-2885 as the neotype of *E. albifrons*.

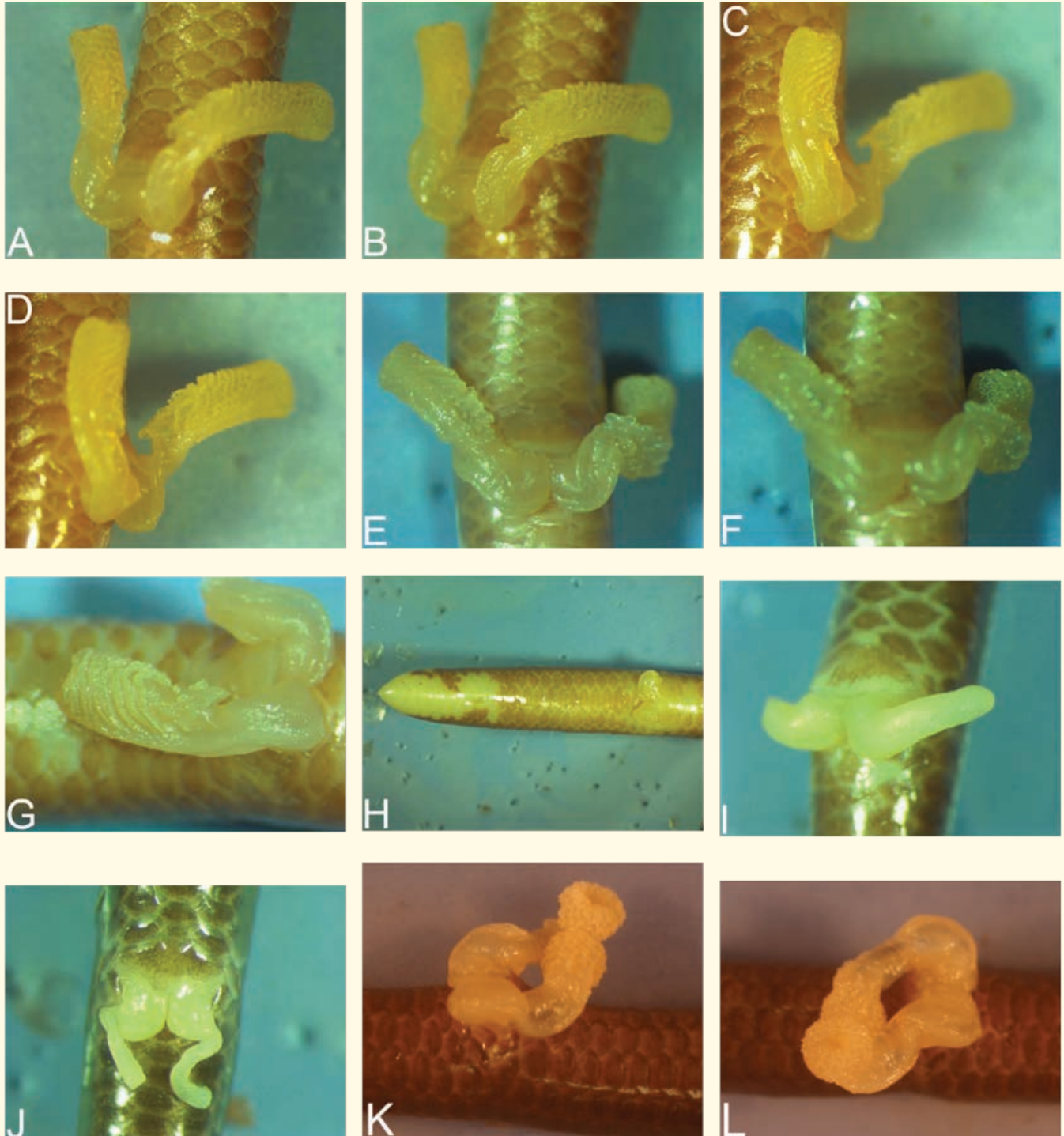
Hoogmoed (1977) presented the following data on 20 specimens from Surinam: TMD = 215–233 ( $\bar{x}$  = 223.5); SC = 16–20 ( $\bar{x}$  = 17.6); LOA = 71–215 mm; TL = 5–12 mm; MBD = 1.9–4.6 mm; L/W = 37–60 ( $\bar{x}$  = 49.5); and TL/LOA = 5.1–7.1 ( $\bar{x}$  = 6.4).

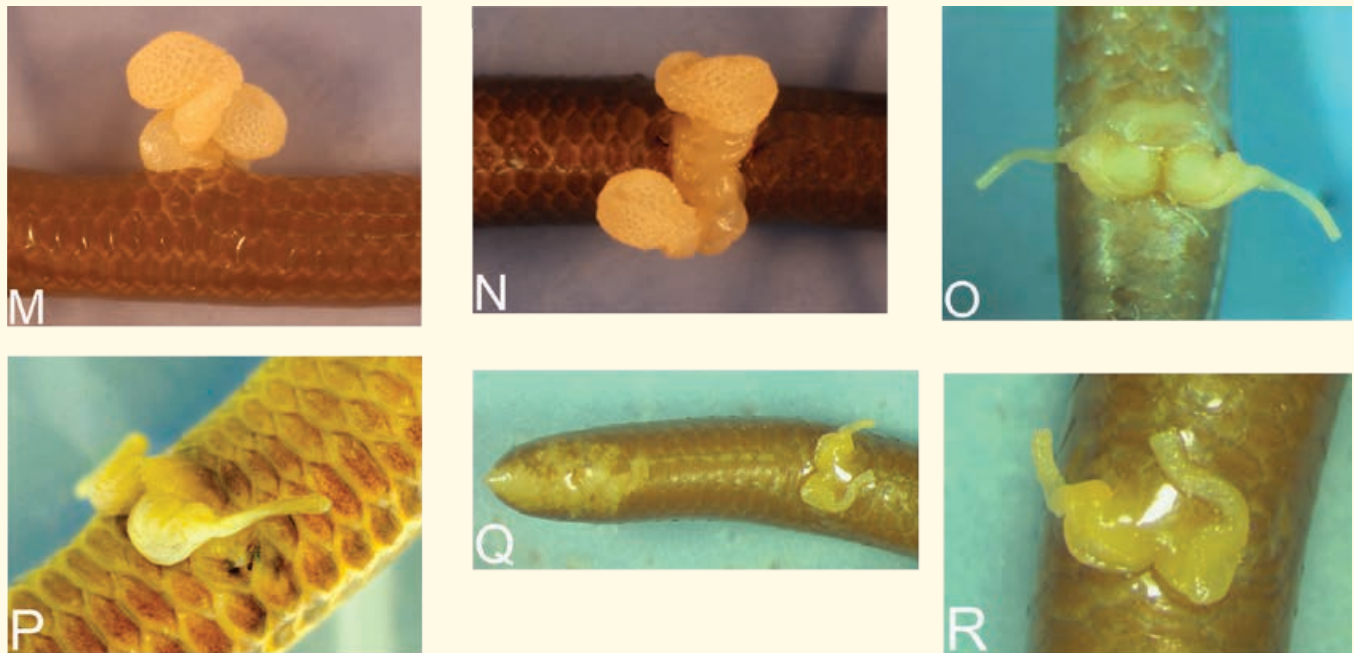


**Map 14.** Distribution of *Epictia tenella* in northern South America.



Pérez-Santos and Moreno (2008) included a specimen of *Leptotyphlops tenellus* (= *E. tenella*; USNM 232405, from Cuenca, Azuay) as a member of the Ecuadorian fauna. Cisneros-Heredia (2008) indicated, however, that the Ecuadorian specimen differs from *L. tenellus* (= *E. tenella*) and *L. albifrons* (= *E. albifrons*) by the presence of different morphological and scalation characters and apparently corresponds to an undescribed species, and thus did not recognize *L. tenellus* (= *E. tenella*) from Ecuador. If this specimen eventually were to be identified as *E. tenella*, it would increase the maximum elevation for the species from 1,750 to 2,700 m.





**Fig. 15.** Hemipenes. (A, B, C, D) Everted hemipenes of Nicaraguan *Epictia ater* (KU 174119); (E, F) everted hemipenes of Nicaraguan *E. ater* (KU 174121); (G) everted hemipenes of Nicaraguan *E. ater* (KU 174135); (H) partially everted hemipenes of *E. bakewelli* (NLU40758); (I) everted hemipenes of Mexican (Cozumel) *E. magnamaculata* (LACM 127623); (J) everted hemipenes of Honduran (Roatán) *E. magnamaculata* (FMNH 282651); (K, L) everted hemipenes of Honduran *E. martinezi* (FMNH 283739); (M, N) everted hemipenes of Honduran *E. martinezi* (FMNH 283740); (O) everted hemipenes of Panamanian *E. pauldwyeri* (KU 125032); (P) everted hemipenes of Mexican (Veracruz) *E. resetari* (UMMZ 122826A); and (Q, R) everted hemipenes of Mexican (Querétaro) *E. wynni* (TCWC 45530).

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**Fig. 16.** Photographs of live individuals. *Epictia ater* from Guanacaste, Costa Rica (A, B, C, D), E; *E. ater* from Masaya, Nicaragua (F, G, H); *E. columbi* from San Salvador Island, Bahamas (I); *E. magnamaculata* from Cozumel, Mexico (J, K, L); *E. magnamaculata* from Isla de Guanaja, Honduras (M, N); *E. phenops* from Chiapas, Mexico (O); *E. phenops* from Oaxaca, Mexico (P, Q, R); *E. martinezi* paratype (FMNH 283737) from Ocotepeque, Honduras (S); *E. pauldwyeri* paratype (CHP H-5379) from Panama (T); *E. resetari* from Veracruz, Mexico (U, V, W); *E. schneideri* from Oaxaca, Mexico (X, Y); *E. vindumi* from Yucatán, Mexico (Z); *E. goudotii* from Bonaire, The Netherlands Antilles (AA, AB); *E. tenella* from Guyana (AC, AD, AE); and *E. tenella* from Trinidad, Trinidad and Tobago (AF).

© Alejandro Solórzano (A), Paul Freed (B, C, D, E), Laura Ruysseveldt (F, G, H), Ryann Rossi (I), Nate Nazdrowicz (J, K, L), Gunther Köhler (OM, N), Jim Conrad (O, Z), Andrea Stutz (P, Q, R), James R. McCranie (S), César A. Jaramillo (T), Maximilian Paradiz-Dominguez (U, V, W), Tim Burkhardt (X, Y), Jake Richter (AA, AB), William E. Magnusson (AC, AD, AE), and John C. Murphy (AF)

## CONCLUSIONS

Regrettably, Mumaw et al. (2015) designated a neotype for *Stenostoma albifrons* in a book when a topotypic series was available for proper neotype selection. The BYU series, collected in the 1950s, might have been what Orejas-Miranda (1967) was referring to when he mentioned that topotypes were available for *S. albifrons*. Since the epithet *albifrons* is the oldest leptotyphlopoid name in the New World, it has important consequences for taxonomy and nomenclature. Based upon the large topotypic series available from BYU and the criticisms based on Art. 75.3.3, Art. 75.3.6, and Recommendations 75A–B, I strongly urge the rejection of MCZ R-2885 as the neotype of *S. albifrons*, with the replacement of BYU 11490 as a more appropriate neotype.

Even though the 11 species of *Epictia* in the *E. phenops* group from Mesoamerica appear superficially similar in size, coloration, and scale counts, the results of this study reveal that a combination of (1) scale size, arrangement, and proportion, (2) color pattern, and (3) internal anatomy is sufficient to distinguish the different taxa. In terms of extremes of characters within the species studied herein, the following data stand out. The lowest middorsal scale counts (202–226,  $\bar{x}$  = 211.8) are found in *E. pauldwyeri*, and the highest middorsal counts are present in *E. bakewelli* (245–269,  $\bar{x}$  = 253.3), *E. columbi* (240–265,  $\bar{x}$  = 255.6), and *E. martinezi* (248–260,  $\bar{x}$  = 256.3). *Epictia phenops* (216–277) and *E. ater* (212–266) display exceptionally broad middorsal count ranges that nearly encompass those of all the other species, which is suggestive of cryptic species. The middorsal scale count range in the *E. phenops* group is as follows: *E. phenops* (61); *E. ater* (54); *E. magnamaculata* (43); *E. columbi* (25), *E. bakewelli* (24); *E. pauldwyeri* (24); *E. vindumi* (23); *E. schneideri* (22); *E. resetari* (20); *E. wynnii* (18); and *E. martinezi* (12). Among other characters, the highest subcaudal count is present in *E. columbi* (22–25,  $\bar{x}$  = 23.7) and the lowest in *E. pauldwyeri* (10–14,  $\bar{x}$  = 12.7); the broadest rostral (rostral width/head width) occurs in *E. pauldwyeri* (0.42–0.53,  $\bar{x}$  = 0.47) and the narrowest in *E. bakewelli* (0.31–0.37,  $\bar{x}$  = 0.34); and the largest eye (eye/ocular ratio) occurs in *E. martinezi* (0.47–0.54,  $\bar{x}$  = 0.50) and the smallest in *E. columbi* (0.35–0.41,  $\bar{x}$  = 0.38).

The largest (in length and midbody diameter) species is *E. magnamaculata* (length and diameter maxima of 220 mm and 4.5 mm) and the smallest is *E. pauldwyeri* (length and diameter maxima of 129 mm and 2.9 mm); the frontal is fused with the rostral in three species (*E. ater*, *E. bakewelli*, and *E. schneideri*); a preoral groove is present only in *E. columbi*, which also is the only species lacking both a dorsal and pale caudal spot; *E. martinezi* is the only species with a pale preocular spot on the infranasal; *E. wynnii* is the only species with 3 infralabials and a pale subcaudal spot 10 times as long as the dorsocaudal spot; *E. magnamaculata* and *E. pauldwyeri* are the only species with a pale dorsocaudal spot longer than the subcaudal spot; and *E. magnamaculata* is the only species with 11 dark stripes and an apical spine in the form of a broad compressed blade.

Most of the species studied herein are striped with a bicolored pattern of brown and yellow, but two species (*E. ater* and *E. columbi*) generally are unicolored brown to black, with at most a pale outlining of the costal scales. Photographs of living individuals of all of the species examined in this study (except *E. bakewelli*, *E. wynni*, and *E. albifrons*) are presented in Fig. 16. Four species were well represented with large samples of 83 (*E. phenops*), 54 (*E. magnamaculata*), 53 (*E. ater*), and 46 (*E. vindumi*); however, the sample sizes of five species (*E. bakewelli*, *E. columbi*, *E. martinezi*, *E. pauldwyeri*, and *E. resetari*) consisted of only 2 to 6 examined specimens, so the variation in their scale count ranges and character states can be expected to increase with collection and examination of additional material.

Smith and List (1958), Auth (1994), and Jaramillo et al. (2010) apparently did not examine the holotype of *Epictia* (as *Leptotyphlops*) *goudotii* in the Paris Museum. Because specimens from Panama were misidentified as *E. goudotii*, the species long has been recognized as occurring from Mexico to Venezuela, including the offshore islands (Orejas-Miranda *In* Peters et al., 1970; Hahn, 1980; Smith and Smith, 1993; McDiarmid et al., 1999; Tipton, 2005; Köhler, 2008; Wilson and Johnson, 2010), and McCranie and Hedges (2016) referred to all Mesoamerican *Epictia* as the “*E. goudotii* species complex.” *Epictia goudotii* is restricted to South America and only distantly related to the Mesoamerican species group, which should be known as the “*Epictia phenops* species group” (based on Cope’s name being the first species described from the region).

Three groups now are distinguishable among the 40 species of recognized *Epictia*, one from Mesoamerica and two from South America. The Mesoamerican assemblage (*Epictia phenops* species group) consists of 11 species (*E. ater*, *E. bakewelli*, *E. columbi*, *E. magnamaculata*, *E. martinezi*, *E. pauldwyeri*, *E. phenops*, *E. resetari*, *E. schneideri*, *E. vindumi*, and *E. wynni*). The western South American assemblage (*Epictia tessellata* species group; Orejas-Miranda, 1967) includes 10 species with supraocular-supralabial contact that only are known from Peru, except for *E. tenella* (*E. alfredschmidti*, *E. antoniogarciai*, *E. rubrolineata*, *E. rufidorsa*, *E. septemlineata*, *E. teaguei*, *E. tenella*, *E. tessellata*, *E. tricolor*, and *E. vanwallachi*). The eastern South American assemblage (*Epictia albifrons* species group) contains the remaining 19 species, all of which lack supraocular-supralabial contact (*E. albifrons*, *E. albipuncta*, *E. australia*, *E. borapeliotes*, *E. clinorostris*, *E. collaris*, *E. diaplocia*, *E. goudotii*, *E. hobartsmithi*, *E. melanoterma*, *E. melanura*, *E. munoai*, *E. peruviana*, *E. signata*, *E. striatula*, *E. subcrotilla*, *E. unicolor*, *E. vellardi*, and *E. weyrauchi*). The exact composition of each group only will be clarified with further molecular analyses.

### Key to the “*Epictia phenops* species group”

- |   |                         |
|---|-------------------------|
| 1a. Infralabials 3 . . . . .  | <i>E. wynni</i>         |
| 1b. Infralabials 4 . . . . .  | 2                       |
| 2a. Pale preocular spot . . . . .   | <i>E. martinezi</i>     |
| 2b. Lacking pale preocular spot . . . . .   | 3                       |
| 4a. Lacking discrete frontal . . . . .  | 4                       |
| 4b. Discrete frontal present . . . . .  | 6                       |
| 4a. Dark uniform dorsal color pattern . . . . .   | <i>E. ater</i>          |
| 4b. Dorsum vividly striped . . . . .  | 5                       |
| 5a. Pale paravertebral stripes border occipitals and parietals; 7 dark stripes . . . . .                | <i>E. bakewelli</i>     |
| 5b. Lacking paravertebral stripes on occipitals and parietals; 5 dark stripes . . . . .                 | <i>E. schneideri</i>    |
| 6a. Dorsum uniformly dark; preoral groove present . . . . .   | <i>E. columbi</i>       |
| 6b. Dorsum striped; lacking preoral groove . . . . .  | 7                       |
| 7a. Pale rostral spot extends beyond rostral; 11 dark stripes; apical spine a broad blade . . . . .     | <i>E. magnamaculata</i> |
| 7b. Pale rostral spot restricted to rostral; 5–9 dark stripes; apical spine not a broad blade . . . . . | 8                       |

- 8a. Pale caudal spots subequal (subcaudal/dorsocaudal spot ratio < 1.0) . . . . . *E. pauldwyeri*  
 8b. Pale caudal spot larger than dorsal spot (subcaudal/dorsocaudal spot ratio > 5.0) . . . . . 9  
 9a. Single broad midlateral dark stripe (2 rows wide) . . . . . *E. phenops*  
 9b. Pair of narrow midlateral dark stripes (1 row wide each). . . . . 10  
 10a. Midbody with narrow dark dorsal and broad dark lateral stripes (3D + 4L pattern) . . . . . *E. resetari*  
 10b. Midbody with 7–9 dark stripes of equal width (7–9 + 0 pattern). . . . . *E. vindumi*

**Key to the Mesoamerican *Epictia* plus *E. albifrons*, *E. goudotii*, and *E. tenella***

- 1a. Anterior supralabial in contact with supraocular; ocular shield pentagonal . . . . . *E. tenella*  
 1b. Anterior supralabial separated from supraocular by nasal-ocular contact; ocular shield hexagonal . . . . . 2  
 2a. Rostral fused with frontal . . . . . 3  
 2b. Rostral separate from frontal . . . . . 5  
 3a. Cloacal shield semilunate; pale subcaudal spot  $\leq 7$  scales ( $\bar{x} = 5$ ) . . . . . *E. schneideri* sp. nov.  
 3b. Cloacal shield subtriangular; pale subcaudal spot  $\geq 7$  scales ( $\bar{x} = 10$ ) . . . . . 4  
 4a. Pale rostral spot covers entire rostral; dorsum vividly striped . . . . . *E. bakewelli*  
 4b. Pale rostral spot indistinct or absent; dorsum lacking distinct stripes . . . . . *E. ater*  
 5a. Anterior supralabial not or barely reaching lower level of eye; pale subcaudal spot absent or less than 1 scale in length . . . . . *E. goudotii*  
 5b. Anterior supralabial reaching eye level; pale subcaudal spot greater than 1 scale in length . . . . . 6  
 6a. Subcaudals  $\geq 22$ ; dorsum uniform black, lacking pale rostral and tail spots; eye small; preoral groove present . . . . . *E. columbi*  
 6b. Subcaudals  $\leq 22$ ; dorsum striped in brown and yellow with pale rostral and caudal spots; eye large; preoral groove absent . . . . . 7  
 7a. Infralabials 3 . . . . . *E. wynni* sp. nov.  
 7b. Infralabials 4 . . . . . 8  
 8a. Pale spot on head enlarged, extending beyond rostral shield . . . . . *E. magnamaculata*  
 8b. Pale spot on head moderate, confined to rostral shield. . . . . 9  
 9a. Cloacal shield pyramidal with truncate apex; lacking distinct pale bar on posterior upper lip . . . . . *E. albifrons*  
 9b. Cloacal shield semilunate or subtriangular; posterior upper lip with distinct pale bar on lower border of labial and ocular . . . . . 10  
 10a. Rostral parallel; pale preocular spot present . . . . . *E. martinezi* sp. nov.  
 10b. Rostral sagittate or subtriangular; pale preocular spot absent . . . . . 11  
 11a. Total middorsals  $\leq 227$ ; pale dorsocaudal spot nearly equal in length to subcaudal spot . . . *E. pauldwyeri* sp. nov.  
 11b. Total middorsals  $\geq 227$ ; pale dorsocaudal spot averages 5 times longer than dorsocaudal spot . . . . . 12  
 12a. Three dark middorsal stripes with triangular spots and a lateral brown stripe 2 scales wide (3 + 1/1 + 0); eye oval, entirely beneath ocular shield . . . . . *E. phenops*  
 12b. Seven dark middorsal stripes with diamond spots, lacking broad midlateral stripe (3 + 2/2 + 0); eye round, partly beneath supranasal shield . . . . . 13



- 13a. Midbody stripe formula  $3 + 2/2 + 0$ ; rostral apex oval, extending to mid-eye level; supraocular and supranasal with parallel borders . . . . . *E. resetari* sp. nov.
- 13b. Midbody stripe formula  $7-9 + 0$ ; rostral apex truncated, extending posterior to eye level; supraocular and supranasal with oblique borders . . . . . *E. vindumi* sp. nov.

The biodiversity of scolecophidians worldwide is greatly underestimated (Rabowsky et al., 2004; Marin et al., 2013; Murphy, 2014; Nagy et al., 2015) and often unexpected (i.e., see Wynn et al., 2012), and, as this paper shows, Latin American *Epicitia* are no exception. The description of six new species from Mesoamerica more than doubles the previously recognized number. The collection of new material is needed, along with tissues for molecular data. Only with a combination of both morphological and molecular data can new taxa be identified. The molecular analyses of Adalsteinsson et al. (2009) and McCranie and Hedges (2016) pointed to the presence of undescribed species, and led me to search for distinguishing characters among these similar-looking and superficially identical snakes. Without the molecular data, this study never would have been contemplated or initiated.

**Acknowledgments.**—I sincerely acknowledge the following curators for sending loans to the FMNH for me to study, and allowed the internal examination of specimens: Ted Daeschler and Ned Gilmore (ANSP); Jack W. Sites, Jr., and Doug Brown (BYU); Robert C. Drewes, Jens V. Vindum and Lauren A. Scheinberg (CAS); Stephen P. Rogers (CM); Rafe Brown, Andrew Campbell, and Linda Trueb (KU); Neftali Camacho (LACM); Jimmy A. McGuire and Carol L. Spencer (MVZ); John L. Carr (NLU); Gunther Köhler (SMF); Toby Hibbitts (TCWC); Christy McCain, Mariko Kageyama, and Emily Braker (UCM); Eric A. Rickart and Shannen L. Robson (UMNH); Jonathan A. Campbell, Eric Smith, and Carl J. Franklin (UTA); and Eli Greenbaum and Carl S. Lieb (UTEP). The following researchers provided data on various *Epicitia*: Roberto Ibáñez (STRI); Albertina P. Lima (Brazil); James R. McCranie (Honduras); John C. Murphy (Trinidad); Beat Schätti (Oaxaca); and Addison H. Wynn (USNM). The following people provided photographs of critical specimens: *E. bakewelli*—Greg Schneider (UMMZ 80229); *E. goudotii*—Roberta R. Pinto (MNHN 1068 head) and Ivan Ineich (MNHN 1068 tail); *E. martinezi*—James R. McCranie (FMNH 283737); *E. pauldwyer*—Ned Gilmore (ANSP 25086), Rachel Grill (FMNH 130672), Mark F. O’Brien and Greg Schneider (UMMZ 167679), and Addison H. Wynn (USNM 63110–11); *E. resetari*—Rachel Grill (FMNH 178600) and Mark F. O’Brien (UMMZ 122826A); *E. schneideri*—Toby Hibbitts (TCWC 9450); *E. tenella*—Joe Martinez (MCZ 48774) and John C. Murphy (USNM unnumbered); *E. vindumi*—Rachel Grill (FMNH 153536); *E. wyntsi*—Toby Hibbitts (TCWC 32899); and *Stenosoma fallax*—Frank Tillack and Mark-Olivier Rödel (ZMB 9950). The following photographers kindly allowed permission to use their images of living specimens: Paul Freed, Laura Ruyseveldt, and Alejandro Solórzano (*E. ater*); Ryann Rossi (*E. columbi*); Jake Richter (*E. goudotii*); Gunther Köhler and Nate Nazdrowicz (*E. magnamaculata*); James R. McCranie (*E. martinezi*); César A. Jaramillo (*E. pauldwyeri*); Jim Conrad (*E. phenops* and *E. vindumi*); Andrea Stutz (*E. phenops*); Maximilian Paradiz (*E. resetari*); Tim Burkhardt (*E. schneideri*); and John Murphy and William E. Magnusson (*E. tenella*).

My hosts during the bulk of the work for this project were Alan Resetar and Kathleen Kelly (FMNH), for whom I am greatly indebted for support and aid over the years. I thank Jack Sites for the loan of the type series and permission to dissect a male and female and gather testis data on the other male specimens; Jim Hanken and Jose Rosado for access to the MCZ Herpetology Department; Joe Martinez for photographing *E. columbi*, *E. goudotii*, *E. martinezi*, and *E. tenella*, and the President and Fellows of Harvard College for permission to publish the photos; Mark O’Shea for instruction in plotting Google Earth localities; and Ann Powers for assisting with the final artwork. For assistance with obscure literature I thank Mary Sears and Ronnie Broadbent of the Mayr Library at the MCZ. Last but not least, I want to acknowledge the editor and two reviewers, Louis W. Porras, John C. Murphy and Larry D. Wilson, respectively, who meticulously labored through the entire manuscript and provided numerous helpful suggestions and important corrections that improved this paper, and Vicente Mata-Silva for translating the Abstract.

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**Appendix 1.** Material examined (specimens examined for visceral data in italics).

*Epictia albifrons*. **BRAZIL**: PARÁ: Belém: BYU 11487–898, *11489*, 11490 (neotype of *Stenostoma albifrons*), 11491, *11492*, 11493–94, 11497–502 (topotypes).

*Epictia albipuncta*. **ARGENTINA**: SALTA: Finca Camino a El Chorro: FML 1228; TUCUMÁN: San Miguel de Tucumán: FML 603, 921, 2334, 2584, 2617, FMNH 229949, MCZ R-126659. **BOLIVIA**: TARIJA: Villa Montes: MCZ R-163240. **PERU**: CALLAO: Bellavista: MCZ R-17394–95.

*Epictia alfredschmidti*. **PERU**: ANCASH: SMF 80066–67, LIMA: Lima, MCZ R-46193.

*Epictia ater*. **COSTA RICA**: GUANACASTE: Bagaces: KU 35608, Finca La Pacifica: KU 102491, 102496, 157800–01, LACM 114081–82, 154162; Finca Taboga: KU *102493*, 102494; 10 km N Guardia: KU *102495*; 7.7 km E Las Canas: MVZ 149889; 10 km W Las Canas: KU 144372; Liberia: LACM 154161; PUNTARENAS: Boca del Barranca: KU 125457–58. **EL SALVADOR**: San Salvador: FMNH 154796. **HONDURAS**: VALLE: Isla Zacate Blanco: KU 194335. **NICARAGUA**: CHINANDEGA: 1 km N Chinandega: KU 200596, Volcan Chongo: KU 194336; ESTELI: km 107 btw Sebaco and San Isidro: KU 174119–20, *174121*; GRANADA: Granada: KU 174122–23, Los Robles: KU 174124–34; MANAGUA: Lago de Xiloa: KU *174135*; Managua: LACM 74141, VW *308*, *510*, 1.7 km Sabana Grande: KU 42332–34; RIVAS: Finca Amayo: KU 101878.

*Epictia australis*. **ARGENTINA**: CATAMARCA: FML 1400.

*Epictia bakewelli*. **MEXICO**: COLIMA: FMNH 99676–79, Paso del Río: 100625 (paratype); 5.5 km E Armeria: NLU 40757–58.

*Epictia borapeliotes*. **BRAZIL**: ALAGOAS: MZUSP 8261.

*Epictia collaris*. **SURINAM**: BROKOPONDO: Brownsberg: MCZ R-149550 (paratype).

*Epictia columbi*. **BAHAMAS**: San Salvador Is.: CM 72262, R-MCZ 48773.

*Epictia diaplocia*. **PERU**: SAN MARTÍN: KU 212594.

*Epictia goudotii*. **COLOMBIA**: MAGDALENA: Magdalena Valley, MNHN 1068 (holotype of *Stenostoma goudotii*), nr. Río Frio: R-MCZ 33928; SANTA MARTA: Bahía Concha: MCZ R-152586. **NETHERLANDS ANTILLES**: Bonaire Is.: Bonaire: MCZ R-92795–97. **VENEZUELA**: BOLÍVAR: Guri: ZFMK 64415; DISTRITO FEDERAL: Puerto La Cruz: CM 7311, 7329, *7331–32*, Tarna: ZFMK 64423; SUCRE: Cumana: KU 116942.

*Epictia hobartsmithi*. **VENEZUELA**: BOLÍVAR: Guaiquinima Tepui: ZSM 107/1990.

*Epictia magnamaculata*. **COLOMBIA**: Isla Providencia: ANSP 25983–84, 25986–89, *25990*, *25994*, 25995–96, FMNH 87A, 87B, 87C; KU 269988–91. **HONDURAS**: ISLAS DE LA BAHÍA: Cayo Cochino Grande: KU 220132; Cisne Grande (Great Swan), CAS *39405*, 39406, MCZ R-*9624*, 192117–19; Isla Guanaja: CM 27618, 90324; KU *101446–47*; LACM 63428–29; Isla Roatán: FMNH 34593, 282651; KU *203163*, 203164–65; UTA 10717–18; Isla Utila: CM 29004, 90368–69. **MEXICO**: QUINTANA ROO: Isla Cozumel: CM *41316*, 41325a–b, LACM 127623, UCM *16012*.

*Epictia martinezi* sp. nov. **HONDURAS**: OCOTEPEQUE: bet. Río Lempa and Antigua: FMNH 283740 (holotype), FMNH 283738–39 (paratypes); Río Lempa near Antigua: FMNH 283735–37 (paratypes).

*Epictia melanoterma*. **ARGENTINA**: SALTA: Partido La Candelaria: FML 1421; TUCUMÁN: San Miguel de Tucumán: FML 699, 998, 2592; FMNH 229948; MCZ R-120055–57. **BOLIVIA**: CERCADO: Cochabamba: FMNH 161503.

*Epictia munoai*. **URUGUAY**: ARTIGAS: Arroyo de la Invernada: FMNH 216409; LAVALLEJA: Aguas Blancas: LSUMZ 27752; SAN JOSÉ: Sierra de Mahoma: FMNH 216398, 216402.

*Epictia pauldwyeri* sp. nov. **PANAMA**: CANAL ZONE: Ancon: KU 116897 (paratype);

Curundú: FMNH *130672* (holotype), KU *116896* (paratype); Gamboa: MVZ 78739 (paratype); PANAMÁ: Panama city: UMMZ 167679 (paratype); Tocúmen: KU *125032* (paratype); PANAMÁ OESTE: Bahía Serena: CHP H-5379 (paratype); Nueva Gorgona: KU 16898 (paratype); no specific locality: USNM 63110–11 (paratypes).

*Epictia* cf. *pauldwyeri*. **COLOMBIA**: CESAR: Loma Linda: MCZ R-141087.

*Epictia peruviana*. **PERU**: JUNÍN: Chanchamayo: FMNH 40626; UCAYALI: La Pampa de Sacramento: ZFMK 41475.

*Epictia phenops*. **EL SALVADOR**: CUSCATLAN: Tenancingo: KU 183843; LA LIBERTAD: Quezaltepeque: CAS 94257–58, *94797*; MORAZAN: Ciudad de San Francisco Gotera: KU 291287, Monte Cristo mine: MVZ 40398; SAN MIGUEL: 10 km NNE San Miguel: KU 183846; SAN SALVADOR: Ciudad Universitaria: KU 183844, Inst. Trop. Invest. Científica: KU 62094–95, El Refugio: KU 183847, Planes de Renderos: MVZ 40397, San Salvador: FMNH 154796, KU 183848–

50; SANTA ANA: 6 km S Metapan: KU 183845; SONSONATE: Acajutla: CAS-SUR 3527. **GUATEMALA:** BAJA VERAPAZ: Salama: KU 187254; ESCUINTLA: Escuintla: CAS 71913, 78688–89, 78690–91; Finca El Salto: MVZ 88461, 88465; IZABAL: El Estor: MVZ 160487; ZACAPA: Estanzuela: MCZ R-128841–42. **MEXICO:** CHIAPAS: San Ricardo: FMNH 105183; 7 km SW La Trinitaria: UTEP 8311–13; Ocozocoautla: CAS 163701, 163702, 163723, 163744–46; 1 km N Ocozocoautla: UTEP 5978–80; 6 km NW Tonala: KU 43559; Tuxtla Gutierrez: KU 43667, MCZ R-53909, 54330–33; OAXACA: Juchatengo: KU 87440; San José Lachiguirí: UCM 52581, Tehuantepec and vicinity: FMNH 111476, 111477, 111478–80, 111481, 111482–84, MCZ R-46471–72, 56409, 86313, LACM 105292, MVZ 61159, 80000, UCM 40088–90, 49381, 52648, UMNH 2549, 2588–90, 2799, UTEP 20218; 13 km W Oaxaca–Chiapas state line: LACM 8582; 6 km N Totolapan: LACM 58147; no specific locality: FMNH 99676–79, UCM 19029, 52646–47, 52664, 54156.

*Epicitia resetari* sp. nov. **MEXICO:** VERACRUZ: 15 km SE Alvarado: LACM 51798 (paratype); Cotaxtla Exp. Stn.: LACM 28170 (paratype); Finca Texquitipan: MVZ 128998 (paratype); Paso de Ovejas: FMNH 178600 (holotype); 20 km WNW Piedras Negras: KU 23252 (paratype); 34 km SE Veracruz: LACM 105291 (paratype).

*Epicitia rufidorsa*. **PERU:** CALLAO: Bellavista: MCZ R-17393, 17396–97; LA LIBERTAD: Chiclin: FMNH 34305; LIMA: Lima: USNM 49993.

*Epicitia schneideri* sp. nov. **MEXICO:** GUERRERO: Acahuizotla: TCWC 7502, 1.7 km W Acahuizotla: TCWC 7411, 1.7 km SW Colotlipa: TCWC 9450–51, 9452; Chilpancingo: MCZ R-43278; OAXACA: San José Lachiguirí: UCM 52850, 11.7 km S Putla: UTEP 5981.

*Epicitia signata*. **COLOMBIA:** CESAR: Loma Linda: UTA 3605, 3644, 3657.

*Epicitia striatula*. **ARGENTINA:** SALTA: Los Toldos: FML 1287a–b. **BOLIVIA:** NUESTRA SEÑORA DE LA PAZ: Chulumani: MCZ R-12361; La Paz: CBF 1449. **PERU:** CUZCO: Hacienda Cadena: FMNH 40210, 59169, 62125, 81509–10; PUNO: Santo Domingo: FMNH 40211.

*Epicitia subcrotilla*. **PERU:** APURÍMAC: Abancay: MHNSM 20643; LA LIBERTAD: Chiclin: MCZ R-48936, Trujillo: FMNH 229365; PIURA: Los Organos: MCZ R-160520.

*Epicitia teaguei*. **PERU:** no specific locality: JC 130006.

*Epicitia tenella*. **BRAZIL:** PARÁ: no specific locality, MCZ R-2885. **COLOMBIA:** CESAR: Loma Linda: UTA 3605, 3644, 3657. **ECUADOR:** AZUAY: Cuenca: USNM 232405. **GUYANA:** CUYUNI-MAZARUNI: Kartabo, USNM 304357. **PERU:** AMAZONAS: Tingo: MVZ 82446; CAJAMARCA: 29 km S and 13 km W Jaen: MVZ 82447. **SURINAM:** BROKOPONDO: Brownsberg Nature Park: MVZ 247608; SARAMACCA: nr. Dolopasi: MCZ R-154827. **TRINIDAD AND TOBAGO:** Trinidad: 11°37'N, 61°13'W: CAS 12510; 3 mi. S Arima-Blanchisseuse road: FMNH 215818; Arima-Blanchisseuse road, btw mi. 5–6: FMNH 217237–38; fishing pond: FMNH 69769; Manzanilla beach: MCZ R-160087; Port-of-Spain: FMNH 190745, 200292; San Rafael: FMNH 49914; Trintoc Well no. 32A: MCZ R-160088; no specific locality: FMNH 42721–22. **VENEZUELA:** DISTRITO FEDERAL: Puerto La Cruz: CM 7311, 7329, 7331–32; MONAGAS: Urocoa: CM 17397–98; no specific locality: ANSP 15985.

*Epicitia tessellata*. **PERU:** LIMA: La Molina: FMNH 36726, 134464; Lima: ZMB 26256.

*Epicitia tricolor*. **PERU:** ANCASH: KU 135177.

*Epicitia vanwallachi*. **PERU:** no specific locality: JC 12792.

*Epicitia vindumi* sp. nov. **MEXICO:** YUCATÁN: Chichén Itza: FMNH 20606, 20616–18, 36332, 36334–40, 36343–45, 40724–25 (paratypes), FMNH 153586 (holotype), MCZ R-7113, 22060–62, 28747 (paratypes); Dzibilchaltun: FMNH 153501, 153532–33, 153535, 153537–38, 153542, 153543–46, 153586–89, 153596 (paratypes); Kantunil: FMNH 36341–42 (paratypes); Merida: FMNH 40724–25, UCM 29978 (paratypes); Pisté: CM 45286, 46905, 47078–79, 49548–54 (paratypes); no specific locality: FMNH 36331, 36333 (paratypes).

*Epicitia wynni* sp. nov. **MEXICO:** QUERÉTARO: 3 km S Conca: UTEP 20217 (paratype); El Trapiche: TCWC 45525–26, 45528, 45530, 45532–35; Jalpan: TCWC 32899 (holotype); Hacienda Conca: TCWC 37722–23, 45539, 45542, 45544, 45547 (paratypes).

*Epicitia* sp. indet.: no specific locality: ANSP 11582.







**Van Wallach** is an ophiologist interested in the biodiversity, systematics, taxonomy, classification, nomenclature, comparative anatomy, and natural history of snakes. His four areas of specialization are the Scolecophidia, visceral anatomy, dicephalic snakes, and biodiversity. While an undergraduate at San Diego State University, he began his studies of snake viscera with Richard Etheridge as his mentor. After graduation, Van spent five years of fieldwork in pursuit of snakes in the Philippines (1977), Nicaragua (1978), and Zaire (1979–1981). Upon returning home, he continued his survey of snake viscera through museum collections (mainly at CAS, FMNH, and MCZ) and worked as a Curatorial Assistant in the San Diego Natural History Museum (1982–1984), Museum of Natural Sciences, Louisiana State University (1985–1989), and Museum of Comparative Zoology, Harvard University (1989–2011). His M.S. thesis from LSU focused on the internal anatomy of the African aparallactines and atractaspidids, and his Ph.D. from Northeastern University analyzed the visceral morphology of the Scolecophidia. Since 1980, Van has authored or co-authored 150 publications (including *The Lungs of Snakes* in 1998 and *Snakes of the World: A Catalogue of Living and Extinct Species* in 2014), examined the viscera of 6,000 specimens representing 1,900 species and 450 genera, and described two families, 12 genera, and 48 new species of snakes (mostly scolecophidians). Although seemingly entrenched with the scolecophidians, which few researchers are inclined to study, Van is interested in ophidian biodiversity, especially that of the colubroids.