Zootaxa 3914 (3): 301–317
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3914.3.4
http://zoobank.org/urn:lsid:zoobank.org:pub:C83CDA14-8528-4E15-B5A5-ECE88621196B

Two new species of *Eleutherodactylus* (subgenus *Syrrhophus*) from western Mexico

JACOBO REYES-VELASCO[1,2,6], IVAN AHUMADA-CARRILLO[3],
TIMOTHY R. BURKHARDT[4] & THOMAS J. DEVITT[5]

[1]*Department of Biology, University of Texas at Arlington, 501 S. Nedderman Drive 337 Life Science. Arlington, TX 76010-0498*
[2]*Entorno Biotico A.C., Simon Bolivar #145, San Pablo. Colima, Colima, Mexico. 28000.*
[3]*Centro Universitario de Ciencias Biológicas y Agropecuarias, Carretera a Nogales Km. 15.5. Las Agujas, Nextipac, Zapopan, Jalisco, Mexico*
[4]*10150 West Rudasill Rd.Tucson, AZ 85743, USA*
[5]*Department of Integrative Biology, The University of Texas at Austin, Austin, TX 78712, USA*
[6]*Corresponding author. E-mail: jacoborv@uta.edu*

Abstract

We describe two new species of *Eleutherodactylus*, subgenus *Syrrhophus*, from two separate mountain ranges in western Mexico. *Eleutherodactylus grunwaldi* **sp. nov.** inhabits the Sierra de Manantlán in Colima and Jalisco from 1300 to 2200 m, whereas *E. wixarika* **sp. nov.** is known from a single locality in the Sierra Huichola of northern Jalisco at 2400 m, but is probably more widespread. *Eleutherodactylus grunwaldi* is readily distinguishable from most members of mainland *Syrrhophus* by a combination of its large size, broad, truncate digital pads more than three times the narrowest part of the digit, and a black and green marbled color pattern. This species is saxicolous, inhabiting limestone outcrops, and has been found in caves during the dry season. *Eleutherodactylus wixarika* is a moderate sized species, most similar to *E. teretistes, E. pallidus* and *E. modestus.* It is distinguished from all other members of the subgenus by the combination a tuberculate, reddish dorsum, lack of compact lumbar glands, and expanded digital pads less than twice the width of the narrowest part of the digit. This species inhabits areas with secondary vegetation in pine forest. Males of both species call at night during the rainy season. The advertisement call of both species consists of a short, narrow band, pure-tone note organized into a discrete train at a rate of about six times per minute. Spectral and temporal acoustic properties differ between species. The subgenus *Syrrhophus* of the genus *Eleutherodactylus* is one of the most poorly studied groups of frogs in Mexico but probably one of the most diverse.

Key words: Amphibia, Anura, Eleutherodactylidae, taxonomy, Terrarana, *Tomodactylus*, Jalisco, Colima, Sierra Manantlán, Sierra Huichol

Resumen

Describimos dos nuevas especies de *Eleutherodactylus*, subgenero *Syrrhophus* de dos sistemas montañosos diferentes en el occidente de México. *Eleutherodactylus grunwaldi* **sp. nov.** habita la Sierra de Manantlán en Colima y Jalisco, entre los 1300 y 2200 m, mientras que *E. wixarika* **sp. nov.** se conoce de una sola localidad a 2400 m en la Sierra Huichola en el norte de Jalisco, pero probablemente su distribución sea más amplia. *Eleutherodactylus grunwaldi* se distingue de los demás miembros del subgenero por su gran tamaño, almohadillas digitales muy expandidas y una coloración de manchas verdes y negras. Esta especie parece ser estrictamente saxícola, habitando rocas kársticas y también se ha recolectado en cuevas durante la temporada seca. *Eleutherodactylus wixarika* es una especie de tamaño mediano, más similar a *E. teretistes*, *E. pallidus* y *E. modestus.* Se distingue de todos los miembros del subgenero *Syrrhophus* por su piel áspera y una coloración dorsal rojiza, así como por no presentar glándulas lumbares y por tener almohadillas digitales que son menos de dos veces el ancho de la parte más angosta del dedo. Esta especie habita zonas de vegetación secundaria en bosque de pino. Los machos de ambas especies cantan durante la noche en la temporada de lluvias. El canto de ambas especies consiste en una nota corta de banda estrecha, organizada en pulsos discretos a un ritmo de seis veces por minuto. Las propie-

Accepted by J. Padial: 11 Dec. 2014; published: 28 Jan. 2015

dades acústicas temporales y espectrales difieren entre estas especies. El subgenero *Syrrhophus* del genero *Eleutherodactylus* es uno de los grupos de ranas menos estudiados de México pero probablemente uno de los más diversos.

Palabras clave: Amphibia, Anura, Eleutherodactylidae, taxonomía, Terrarana, *Tomodactylus,* Jalisco, Colima, Sierra Manantlán, Sierra Huichol

Introduction

Frogs of the genus *Eleutherodactylus* are among the most diverse groups of amphibians in the New World (Hedges *et al.*, 2008). They inhabit a vast array of environments and range from the southern United States to Central America and the West Indies. Until recently, *Eleutherodactylus* was the most species rich genus of vertebrates, but it was split into several genera, with *Eleutherodactylus sensu stricto* further divided into five subgenera (Hedges *et al.*, 2008). Four of these subgenera are restricted to the Caribbean islands, while the subgenus *Syrrhophus* ranges from Texas to Guatemala and Belize, with two species in western Cuba. The 26 species of this subgenus had previously been allocated to two genera, *Syrrhophus* and *Tomodactylus* (Smith & Taylor, 1948). Myers (1962) synonymized these genera under *Eleutherodactylus.* Subsequent workers ignored Myers' (1962) change, including Hedges (1989), who proposed that species previously placed in the genera *Syrrhophus* and *Tomodactylus* be placed in the subgenus *Syrrhophus* Cope 1978 based on osteological characters (Joglar, 1989; Lynch, 1971). Within *Syrrhophus*, Hedges (1989) recognized two groups as species series, the *E. longipes* species series (corresponding to species of the former genus *Syrrhophus*) and the *E. nitidus* species series (corresponding to species of the former genus *Tomodactylus*). Frost *et al.* (2006) resurrected *Syrrhophus* to include members of *Eleutherodactylus* previously allocated to *Syrrhophus* and *Tomodactylus,* but Heinicke *et al.* (2007) and Hedges *et al.* (2008) considered *Syrrhophus* a subgenus of *Eleutherodactylus* following Hedges (1989), and added two member of the genus *Euhyas* from Cuba (*E. zeus* & *E. symingtoni*).

Hedges *et al.* (2008) recognized two higher-level clades as species series within *Syrrhophus*, the *Eleutherodactylus longipes* series, which includes all species in the USA, Mexico and Central America, and the *E. symingtoni* series, which includes only the two Cuban species, *E. zeus* and *E. symingtoni.* The *E. longipes* series was defined by Hedges *et al.* (2008) as having a robust to moderate body shape and small to moderate snout-vent length (SVL), by the absence of a dentigerous process in the vomers and by the lack of compact lumbar glands. However, all members of the former genus *Tomodactylus* (sensu Dixon, 1957) have conspicuous lumbar glands. Since the revisions of *Tomodactylus* by Dixon (1957) and *Syrrhophus* by Duellman (1958) and Lynch (1970), no inclusive studies on this group have been undertaken; in Mexico this may be attributed to their small size, their inconspicuous nature, and the difficulty of locating them in the field, despite their relative abundance.

Since 1970 no additional species of *Syrrhophus* have been described but recent fieldwork in the states of Colima and Jalisco in western Mexico resulted in the discovery of two unnamed species of *Syrrhophus*, which we describe herein.

Material and methods

We performed multiple collecting trips in western Mexico between 2005 and 2012. Surveys focused mainly on four areas: Sierra de Manantlán and Sierra Perote in the states of Colima and Michoacán; Sierra del Tigre between Jalisco and Michoacán; Sierra Huichola in Jalisco, and the coastal lowlands of the state of Michoacán. Here we report on the frogs from the Sierra Huichola and Sierra Manantlán. We also collected and examined topotypic specimens of *Eleutherodactylus modestus*, *E. nivicolimae, E. saxatilis* and *E. pallidus.* All frogs captured were photographed alive and euthanized with 10% ethanol or with topical benzocaine. Specimens were later fixed in 10% formalin and preserved in 70% ethanol. All material collected has been deposited at the Museo de Zoología, Facultad de Ciencias (MZFC) of the Universidad Nacional Autónoma de Mexico (UNAM) in Mexico City. We did not measure type specimens, so we have used the measurements provided in the original descriptions of *E. dennisi* (Lynch, 1970), *E. nivicolimae* (Dixon & Webb, 1966), *E. pallidus* (=*E. modestus pallidus*; Duellman, 1958), *E. saxatilis* (Webb, 1962) and *E. teretistes* (Duellman, 1958). We measured additional specimens of the subgenus *Syrrhophus* for 15 other Mexican species in the Amphibian and Reptile Diversity Research Center (ARDRC) of the

University of Texas at Arlington (UTA), and at the Museo de Zoología, Facultad de Ciencias (MZFC) of UNAM. Locality information and museum codes for specimens measured are given in Appendix 1.

Morphological measurements. Characters and terminology used here follow Lynch and Duellman (1997) and Savage (2002). We took the following measurements from each specimen: snout-vent length (SVL), head width (HW), head length (HL), snout length (SL), tympanum height (TH), tympanum width (TW), eye width (EW), internarinal distance (IND), eye-to-naris distance (END), interorbital distance (IOD), forearm length (FoL), femur length (FeL), tibia length (TL), foot length (FL), finger 2 length (F2L), finger 2 pad width (F2PW), finger 3 length (F3L), finger 3 pad width (F3PW), finger 4 length (F4L), finger 4 pad width (F4PW), toe 2 length (T2L), toe 2 pad width (T2PW), toe 3 length (T3L), toe 3 pad width (T3PW), toe 4 length (T4L), toe 4 pad width (T4PW), toe 5 length (T5L) and toe 5 pad width (T5PW).

Advertisement call analysis. Advertisement vocalizations were recorded from *E. grunwaldi* and *E. wixarika* during July 2011. Calls were recorded between 22:00–00:00 hours using a Zoom H2 recorder (*E. grunwaldi*) or a Sony DSC-HX1 camera (*E. wixarika*) at a sampling rate of 44.1 kHz, held 30–45 cm from the calling frog. Because recordings of focal males contained vocalizations from nearby males and background noise, we first filtered recordings using the free sound editing software Audacity 2.0.3 (Audacity Team 2014). Five consecutive calls were retained from one individual each of *E. grunwaldi* and *E. wixarika* for analysis. These focal individuals were subsequently designated as the holotype for each species. Although temporal acoustic properties (and to a lesser extent, spectral properties) vary in a predictable fashion with temperature (Gerhardt & Huber, 2002), we were unable to determine these correlations using regression because of sample size limitations. While calls were not recorded at the same ambient temperature, the basic call structure is unlikely to be affected by temperature differences. Edited recordings are available upon request from the first author.

Temporal and spectral characteristics of the selected vocalizations were analyzed using the Seewave 1.7.6 package (Sueur *et al.* 2008) implemented in R v3.1.1 (R Core Team, 2012). We measured four traditional call characters known to be important in communication, including fundamental frequency, dominant frequency, call duration, and call rate (Cocroft & Ryan 1995). We also measured three additional characters that may or may not be relevant in communication but which are additional descriptors of calls, including call rise time (Cocroft & Ryan, 1995), Rényi spectral entropy (Han *et al.*, 2011), and spectral flatness (Sueur *et al.* 2008). Rényi entropy has been used in the analysis of anuran communication to describe the noise content of a signal, and thus its complexity (Han *et al.*, 2011). Similarly, spectral flatness is another measure of signal "pureness" which varies from 0 (pure tone) to 1 (noisy tone). See Sueur *et al.* (2014) for the spectral flatness formula.

We estimated dominant frequency in Seewave via a fast Fourier transform, and fundamental frequency via a short-term cepstral transform (Hanning window length = 512 samples, 95% overlap between successive windows). 2D spectrograms were obtained using a sliding window analysis of short-term Fourier transform calculations. Temporal properties were measured using the function *timer*, with a 10% amplitude threshold for signal detection for call duration and call rate, and a 99% threshold for call rise time. The frequency spectrum of the entire signal (i.e., the relative amplitude of the frequency content) was obtained using the function *spec*. Rényi spectral entropy (alpha=3) and spectral flatness were measured using the functions *sh* and *sfm*, respectively, based on analysis of data obtained using the *spec* function.

Results

Eleutherodactylus grunwaldi, new species

Holotype. MZFC 27472. Adult male, collected by Jacobo Reyes-Velasco and Alexander Hermosillo-Lopez on July 17, 2011, 3.5 km ESE of El Sauz, on road to El Terrero, Municipality of Minatitlán (19.43161 N, -103.97871 W, 1,329 m; datum = WGS84), Colima, Mexico (Fig. 1).

Paratypes. MZFC 27467–27471, five adult males, collected along the side of a dirt road between El Sauz and El Terrero, Municipality of Minatitlán, Colima, Mexico, collected by Chris I. Grünwald, on July 14, 2008; MZFC 27473–27475, two adult males and a young adult, dirt road between El Sauz and El Terrero, collected on the same day as the holotype by Jacobo Reyes-Velasco and Alexander Hermosillo-Lopez; MZFC 27483, adult male, 6.7 km SW of El Terrero, on road to El Sauz, collected by Jacobo Reyes-Velasco and Gabriela Zamora-Silva on July 15, 2012 (Fig. 2).

FIGURE 1. Holotype of *Eleutherodactylus grunwaldi* **sp. nov.** in life. MZFC 27472, UNAM. Field number JRV 139.

FIGURE 2. Paratypes of *Eleutherodactylus grunwaldi,* **sp. nov.** A) MZFC 27474, UNAM. B) MZFC 27473, UNAM.

Diagnosis. *Eleutherodactylus grunwaldi* is a member of the *E. longipes* species series of the subgenus *Syrrhophus* as defined by Hedges *et al.* (2008). It is one of the largest members of the species series, with adult males measuring 28.4–32.4 mm SVL. Vocal slits are present in males; digital discs are greatly expanded, usually three times the width of narrowest part of digit on fingers three and four (Fig. 3A); shape of digital discs is similar to the condition seen in *E. longipes* in Lynch (1970; Fig. 1F), which were described as triangular; first finger shorter than second finger; snout angular in dorsal view (as defined by Savage, 2002 p. 171), and acuminate in

profile; the head slightly longer than wide; tympanum width 40% –50% of eye width, never more than 50%; body robust but thinner than head; no compact lumbar glands; dorsal coloration consisting of greenish or yellowish irregular blotches, spots, or reticulations on dark background; no mid-dorsal stripe or light interorbital bar are present; dorsal and ventral skin smooth; ventral coloration white; no dark or pale interorbital bar or bars on thighs; tympanum medium to small, diameter of tympanum maximum 50% of diameter of eye; iris copper-green.

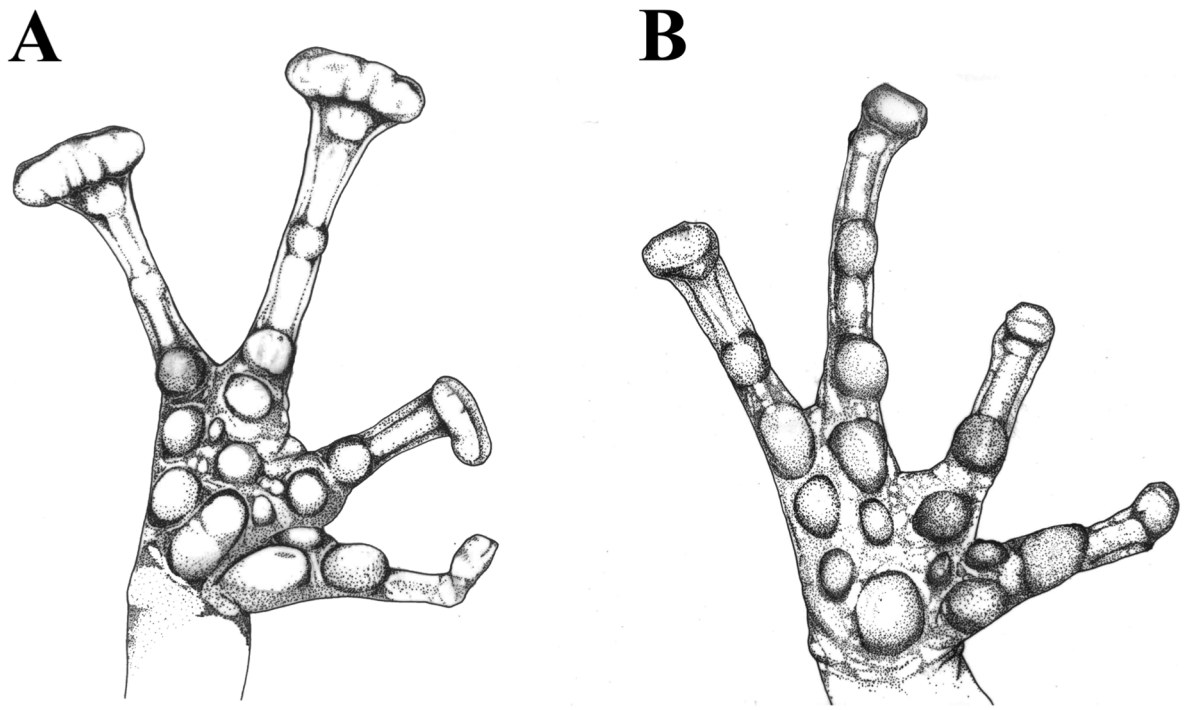

FIGURE 3. Underside of the right hands of the holotypes of (A) *Eleutherodactylus grunwaldi* **sp. nov.**, MZFC 27472, and (B) *E. wixarika* **sp. nov.**, MZFC 27477. Hands are not drawn to scale.

Eleutherodactylus grunwaldi differs from the other members of the subgenus, with the exception of *E. dennisi, E. longipes* and *E. saxatilis* by the presence of digital discs on the hands which are three times the width of the narrowest part of the digit (Fig 3A). It can readily be distinguished from *E. saxatilis* by the absence of compact lumbar glands, as well as broader digital discs on the fingers, usually double the narrowest width of the third and fourth digits in *E. saxatilis* and from two and a half times to three times the width of the narrowest part of the third and fourth digits in *E. grunwaldi*. This species can be distinguished from *E. dennisi* and *E. longipes* by having a smaller tympanum to eye ratio, always 50% or less, as opposed to 50–65% in male *E. dennisi* and 60–90% in male *E. longipes*; *E. dennisi* also has a conspicuous light interorbital bar, which *E. grunwaldi* lacks. While *E. longipes* has a light ground color with darker blotches and/or spots, and a dark brown interorbital bar or triangle, *E. grunwaldi* shows a dark ground color with yellowish marbling or reticulations and no interorbital marks. The new species is distinguished from most other members of *Syrrhophus*, except for *E. saxatilis* and some members of the *E. marnockii* species group of Hedges *et al.* (2008) by its dorsal coloration.

This species has been collected in sympatry with *Eleutherodactylus nivicolimae* and *E. modestus*, and at slightly higher elevation than *E. nitidus*. *Eleutherodactylus grunwaldi* differs from *E. nivicolimae* in size, with males over 28 mm in *E. grunwaldi* and under 23.5 mm in *E. nivicolimae*, as well as by having a dark gray ground color with yellow or yellowish-green spots and reticulations, whereas *E. nivicolimae* has a grayish, reddish or yellowish ground color without spots (Fig. 4A). *Eleutherodactylus nivicolimae* occasionally has a pale middorsal stripe, which is not present in *E. grunwaldi*. *Eleutherodactylus modestus* is smaller, with males never reaching over 22 mm, and has a shorter, narrower head with a rounded snout (as defined by Savage, 2002). *Eleutherodactylus modestus* further differs from *E. grunwaldi* by having a reddish or orange ground color, which is covered in darker gray or black spots, dashes or reticulations (Fig. 4B–C), very distinct from the greenish or yellowish spots present in *E. grunwaldi*. The new species can be distinguished from *E. nitidus* by size (males >28 mm in SVL vs. <27 mm in SVL in *E. nitidus*); they also differ by the very expanded toe pads of *E. grunwaldi*, reaching more than twice the

width of the narrowest part of the digit in the new species, but only to less than one and a half the width of the narrowest part of the digits in *E. nitidus*, and by the presence of compact lumbar glands in the latter species (Fig. 4D).

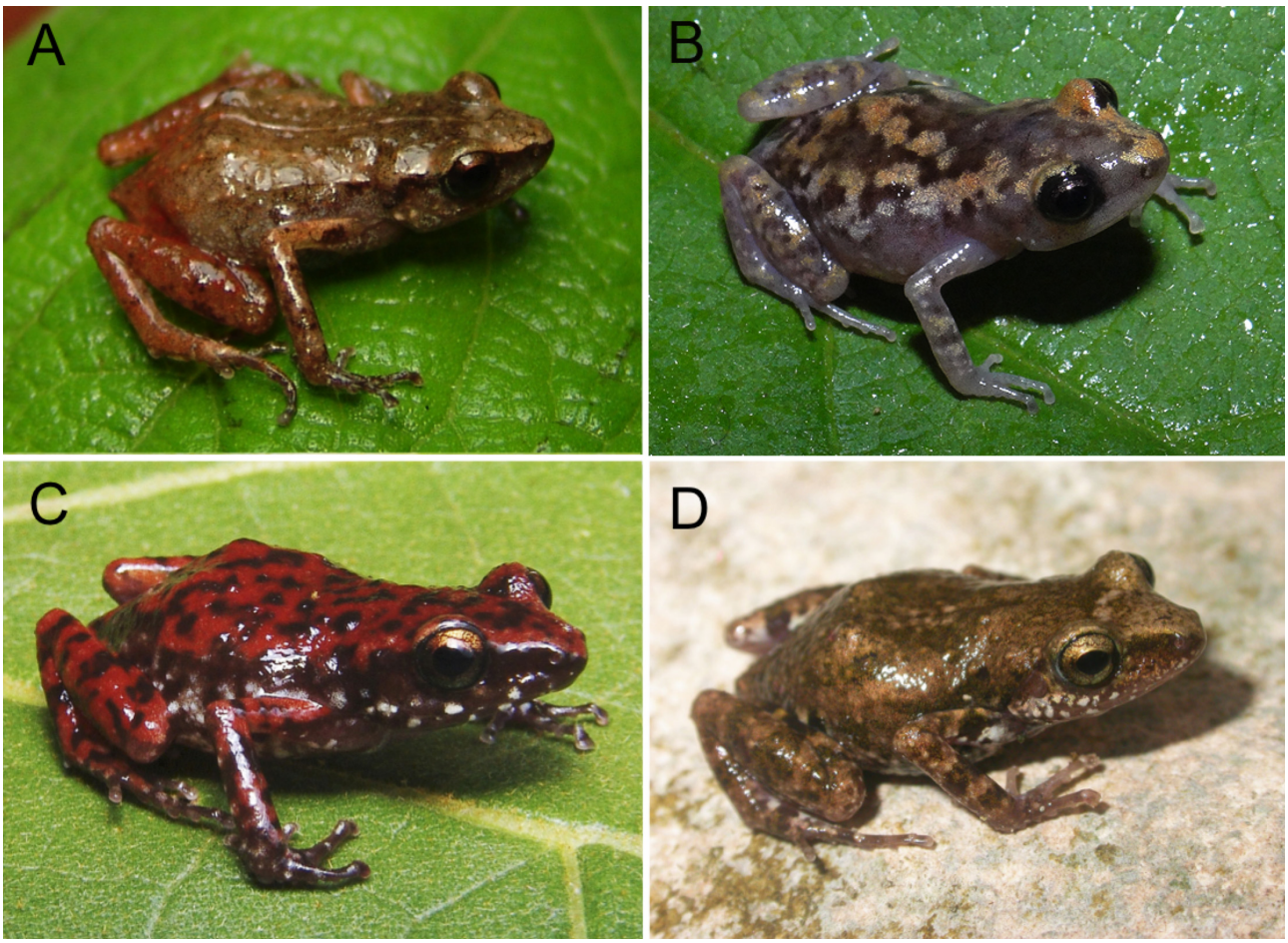

FIGURE 4. Species of *Eleutherodactylus,* subgenus *Syrrhophus* from western México. A) *E. nivicolimae,* Volcán de Colima, Jalisco. B) *E. modestus,* adult male, Ixtlahuacán, Colima. C) *E. modestus,* subadult. Minatitlán, Colima D) *E. nitidus orarius*, Ixtlahuacán, Colima.

Description of the holotype. Male of moderate size (29.7 mm SVL); head as wide as long, 10.7 mm. in length and width, wider than body; snout truncate, angular, non-rounded from a dorsal view, acuminate from a lateral profile; lip slightly flared; tympanum rounded, upper edge indistinct, no supratympanic fold, greatest tympanum diameter 1.7 mm; greatest eye diameter 3.6 mm; tympanum-to-eye ratio 0.5; eyelid 2 mm wide, about half as wide as interorbital distance; first finger shorter than second; finger lengths from shortest to longest 1-2-4-3; digital pads on fingers three and four greatly expanded, approximately three times the narrowest point of the digit; three palmar tubercles, inner palmar tubercle just over a third as large as middle tubercle, outer palmar tubercle about a fifth as large as middle palmar tubercle; toe lengths from shortest to longest 1-2-5-3-4. Both dorsal and ventral skin texture smooth. FL 13.8 mm, TL 15.3 mm, FeL 13.5 mm, FoL 8.3 mm, IND 2.8 mm, IOD 4 mm, END 3.6 mm. FeL to SVL 45%, TL to SVL 52%, FL to SVL 46%, HL to SVL 36%, HW to SVL 36%. Dorsal, lateral and ventral skin texture smooth. Vocal slits present. See Figure 1 for a photograph of the holotype in life. Figures 5A–B show the holotype in preservative.

Coloration in life pale gray on the lateral surfaces, with almost no pattern, while dorsal surfaces dark gray to blackish, with network of greenish-yellow botches forming reticulations on the back, head, neck, forelimbs and hind limbs; venter white; hands and feet pale gray without markings, though some faint markings present on hands; uninterrupted gray line running from snout through nares and lower half of eye, continuing past tympanum and axilla where it grades into lateral gray coloration. Coloration in preservative dark, ground coloration of varying shades of brown, with pale blotches sometimes forming uniformly pale grayish tan reticulations; ventral coloration is white.

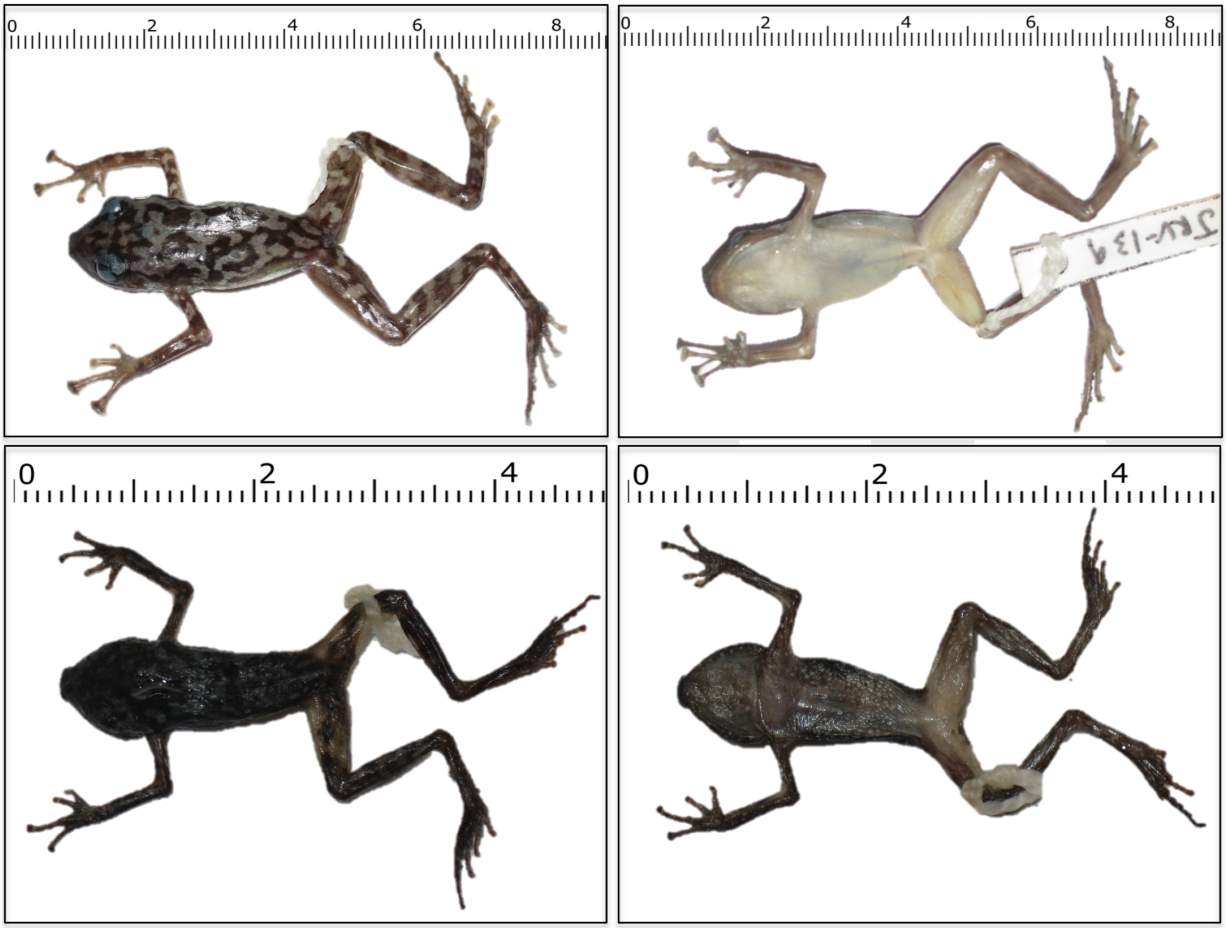

FIGURE 5. Holotypes in preservative. A) Dorsal photo of *Eleutherodactylus grunwaldi* **sp. nov.**, MZFC 27472, (B) Ventral photo of *Eleutherodactylus grunwaldi* **sp. nov.**, MZFC 27472, (C) Dorsal photo of *Eleutherodactylus wixarika* **sp. nov.**, MZFC 27477, (D) Ventral photo of *Eleutherodactylus wixarika* **sp. nov.**, MZFC 27477.

Variation. Mensural variation is presented in Table 1. This species shows remarkably little color variation when compared to some other species in the subgenus (e.g., *E. modestus*). The color pattern consists of greenish yellow or yellowish blotches, spots or reticulations on a black ground color. The amount and intensity of the pale blotches varies such that some specimens appear to be dark frogs with pale colored blotches, while others have more intense reticulation.

TABLE 1. Intraspecific morphological variation in *Eleutherodactylus grunwaldi* and *E. wixarika.* This table shows only a subset of all measurements taken, which showed to be the most useful for distinguishing between members of *Syrrhophus.* SVL = snout-vent length, TH = tympanum height, TW = tympanum width,), F3L = finger 3 length, F3PW = finger 3 pad width. Asterisk marks the type specimens.

Species	Catalogue #	SVL	HW	HL	SL
E. grunwaldi	MZFC 27467	29.8	11.1	10.2	9.6
E. grunwaldi	MZFC 27468	28.8	10.9	10.4	9.6
E. grunwaldi	MZFC 27470	28.1	10.6	9.8	9.5
E. grunwaldi	MZFC 27472*	29.7	10.8	10.7	10.2
E. grunwaldi	MZFC 27473	32.0	11.0	11.1	10.1
E. grunwaldi	MZFC 27474	32.4	11.4	10.7	10.3
E. grunwaldi	MZFC 27475	21.6	7.8	7.6	7.6
E. wixarika	MZFC 27477*	21.9	7.7	7.3	6.4
E. wixarika	MZFC 27478	21.2	7.8	7.2	6.7
E. wixarika	MZFC 27479	24.5	8.9	8.2	7.6

TABLE 1. (Continued)

Species	TH	TW	EWD	Hand Length	Foot Length	F3L	F3PW
E. grunwaldi	1.9	1.4	3.9	7.4	13.9	4.2	1.6
E. grunwaldi	1.7	1.3	4.0	7.2	12.3	4.2	1.6
E. grunwaldi	2.8	1.5	3.6	7.3	13.4	3.9	1.4
E. grunwaldi	1.9	1.7	3.6	8.2	13.8	5.1	2.3
E. grunwaldi	2.0	1.7	3.7	8.5	13.6	4.9	2.3
E. grunwaldi	2.0	1.7	3.3	8.3	14.5	4.9	2.1
E. grunwaldi	1.2	1.0	2.6	5.6	9.9	3.3	1.4
E. wixarika	1.1	1.0	2.4	5.6	8.5	2.9	0.8
E. wixarika	1.1	0.8	2.6	5.2	7.9	2.8	0.8
E. wixarika	1.2	1.0	2.7	5.7	8.8	3.3	0.9

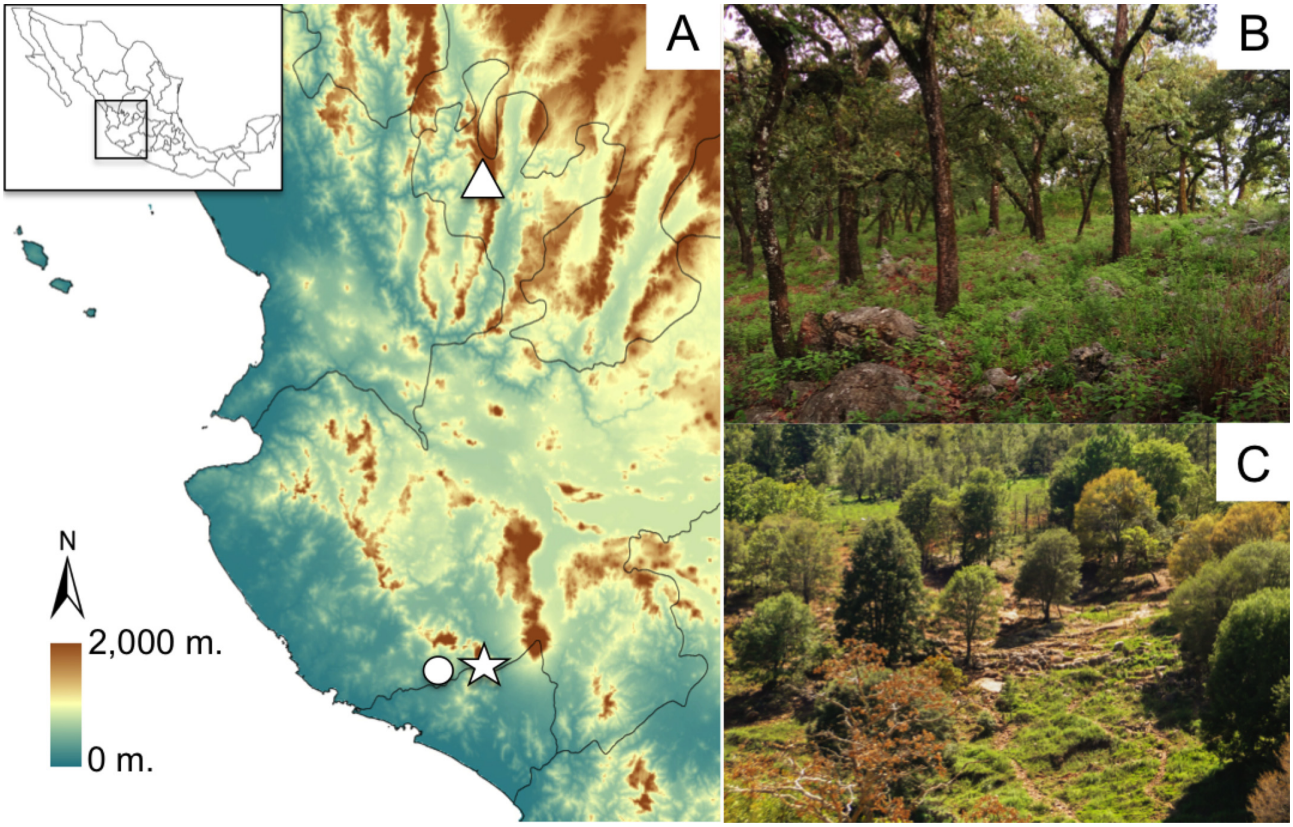

FIGURE 6. A) Map showing the type localities of *Eleutherodactylus grunwaldi* **sp. nov.** (white star) and *E. wixarika* **sp. nov.** (white triangle) in western Mexico. White circle represents an additional locality of *E. grunwaldi* in the state of Jalisco. B) Type locality of *E. grunwaldi*, 3.5 km ESE of El Sauz, on road to El Terrero, Municipality of Minatitlán, Colima. C) Type locality of *E. wixarika*, Bajio de los Amoles, Municipality of Mezquitic, Jalisco.

Distribution and ecology. This species is known from the Sierra de Manantlán in the municipalities of Minatitlán, Colima, and Tolimán, Jalisco (Fig. 6A). It is probably distributed throughout the Sierra de Manantlán, and may range north into some of the other coastal sierras of Jalisco (Sierra de Cacoma, Sierra de Talpa). This species has been collected between 1300–2200 m in the Sierra de Manantlán Biosphere Reserve and at lower elevations (~800m) in the Grutas de Toxín in Jalisco. It inhabits tropical deciduous forest, Madrean pine-oak woodland and the ecotone between tropical deciduous forest and pine-oak woodland. Like *E. saxatilis*, this species appears to be strictly saxicolous and found almost exclusively on limestone outcrops. All specimens have been found on limestone, either in outcrops, sink holes or caves. A single specimen was found while calling from a tree, however the ground consisted of soil mixed with broken limestone. Frogs were collected during the months of

June, July and August, which correspond to the beginning of the rainy season and when breeding appears to take place. One specimen was collected in the dry season (February) from inside a cave, and many other individuals were seen active on the walls of the cave. A photograph of the type locality is shown in Figure 6B.

Etymology. The species epithet is a patronym for German-Mexican naturalist Christoph I. Grünwald, who collected the original specimen (now lost) on July 18th, 2005. This original specimen came from near 2200 m at 4.8 km E of El Terrero, Municipality of Minatitlán, Colima.

Eleutherodactylus wixarika, new species

Holotype. MZFZ 27477. Adult male collected by Ivan Ahumada-Carrillo on July 6, 2011, at Bajío de los Amoles, Municipality of Mezquitic, Jalisco, Mexico (22.059429, -103.933983, 2,467 m; datum = WGS84; Figs. 7, 5C–D).

Paratypes. MZFC 27478-27479, adult males, collected on the same day and place as the holotype by Ivan Ahumada-Carrillo (Fig. 8).

FIGURE 7. Holotype of *Eleutherodactylus wixarika*, **sp. nov.** in life, MZFC 27477. Field number JRV 159.

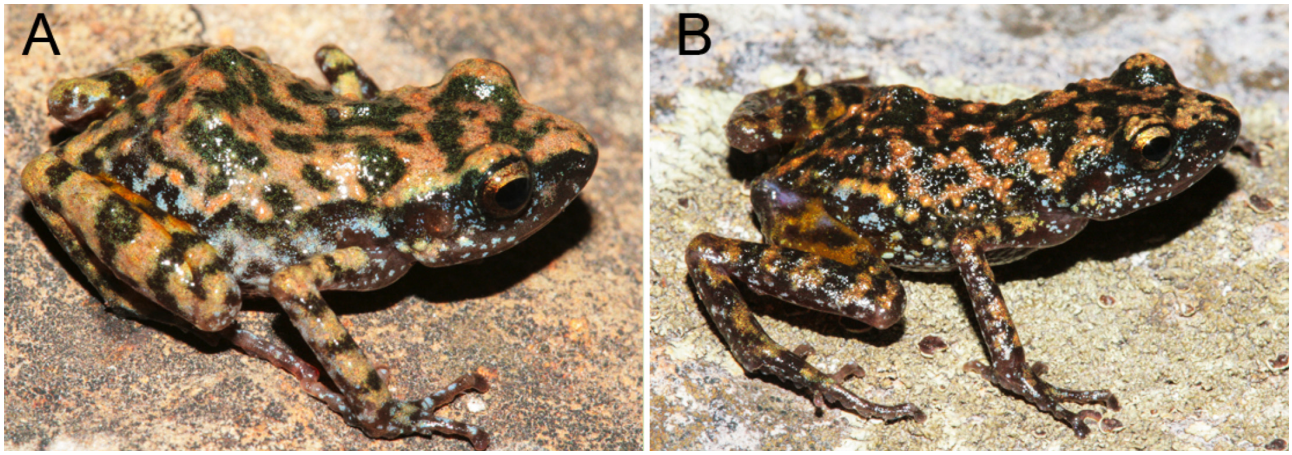

FIGURE 8. Paratypes of *Eleutherodactylus wixarika,* **sp. nov.** in life. A) MZFC 27478, Field number JRV 160. B) MZFC 227478, Field number, JRV 161.

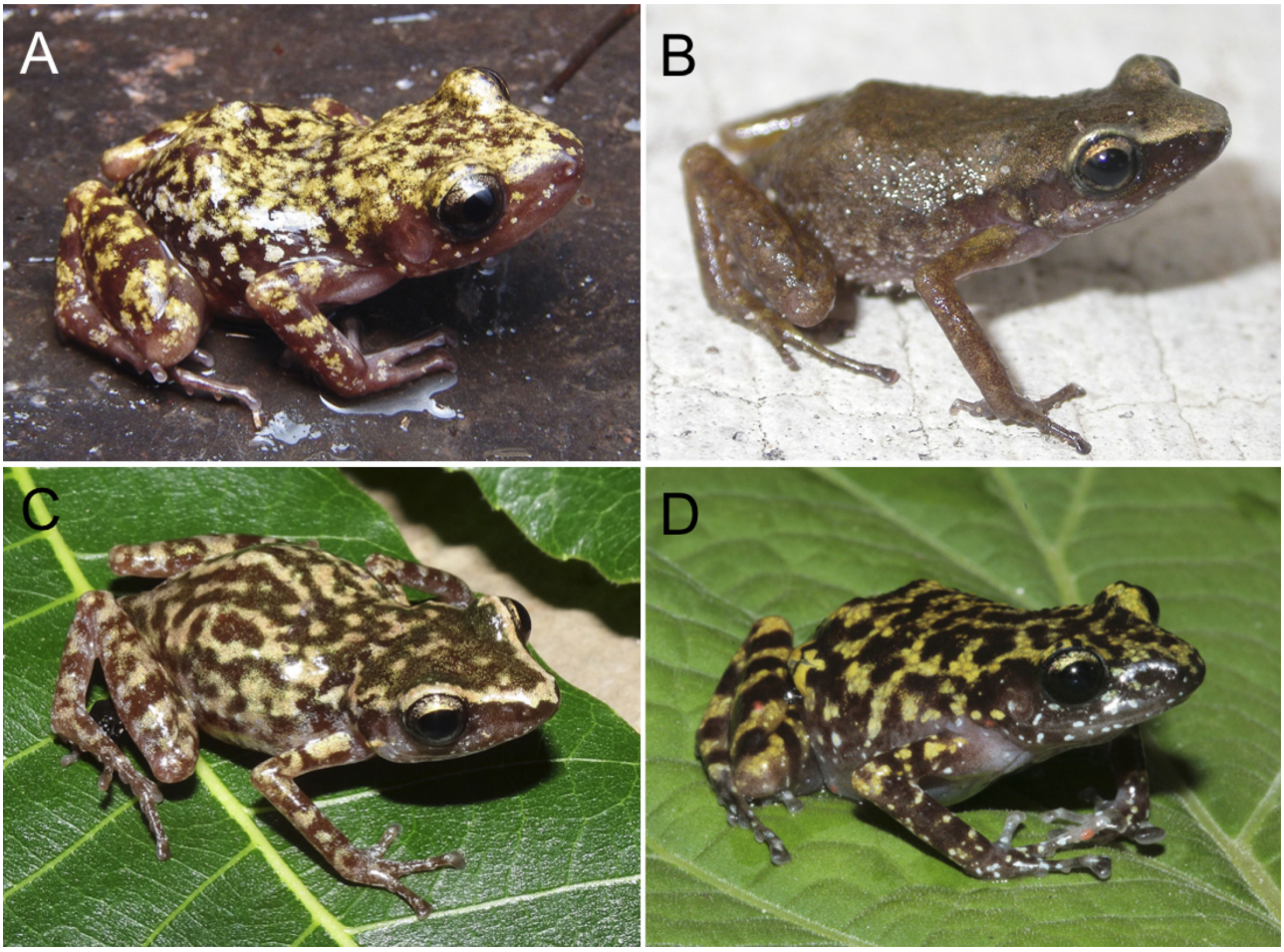

FIGURE 9. Species of *Eleutherodactylus,* subgenus *Syrrhophus* from northwestern México. A) *E. guttilatus,* subadult from El Rodeo, Durango. B) *E. pallidus,* San Blas, Nayarit. C) *E. teretistes,* Mascota, Jalisco. D) *E. saxatilis*, Revolcaderos, Durango.

Diagnosis. *Eleutherodactylus wixarika* (Huichol pronunciation: /wiˈraɾika/) is a member of the *E. longipes* species series of the subgenus *Syrrhophus* as defined by Hedges *et al.* (2008). It is a medium sized frog compared to other members of the species series, with adult males measuring 21.2–24.5 mm in SVL; snout truncate and angular, not rounded from above (as defined by Savage, 2002 p. 171), but rounded in profile; head slightly wider than long, forming a flattened snout; tympanum visible, rounded, and small, with a diameter of tympanum/diameter of eye ratio of 0.3–0.4; vocal slits absent in males; digital tips expanded conspicuously, but less than twice

the width of narrowest part of digit on fingers three and four; digital discs slightly rounded to slightly truncate at tips (Fig. 3B); body about as wide as head; dorsal coloration consisting of reddish orange or red ground color with white or pale gray on lateral portions and upper lip, totally covered in dark military green, brown to almost black blotches, which range from spots to reticulations; tuberculate dorsum; ventral coloration generally gray with some white spots and a bit of darker mottling; ventral skin areolate; no dark or pale interorbital bar present; no bars on thighs; iris orange.

This new species is distinguished from other members of the *E. longipes* species series by the following combination of characters: (1) absence of compact lumbar glands; (2) digital pads of third and fourth finger expanded, but less than twice width of narrowest part of finger; (3) medium size, adult males 21–25 mm; (4) tympanum visible; (5) red, reddish or rusty orange ground color covered by dark green, dark gray, or black reticulations and spots.

While *Eleutherodactylus wixarika* has not been collected in sympatry with any other species of the subgenus *Syrrhophus*, we believe that further collecting will find *E. guttilatus*, *E. pallidus*, *E. teretistes* and *E. saxatilis* either in near proximity or in sympatry with this species. *Eleutherodactylus pallidus* and *E. teretistes* are known from the lowlands and barrancas of Nayarit and west-central Jalisco, and there are faunal corridors entering deep into the southern portions of the Sierra Madre Occidental to the Sierra Huichola (e.g. Cox *et al.*, 2012). *Eleutherodactylus guttilatus* is known from central Durango, and *E. saxatilis* occurs in southwestern Durango, and both may follow the eastern and western flanks respectively of the Sierra Madre to the Sierra Huichola. *Eleutherodactylus wixarika* may be distinguished from *E. guttilatus* by its smaller size, tuberculate dorsum, smaller and more concealed tympanum, and reddish ground color with dark green or gray reticulations (Fig. 9A). It can be distinguished from *E. pallidus* primarily by size and color pattern, as *E. pallidus* is a smaller frog, rarely over 20 mm; the color pattern of *E. pallidus* consists of plain brown ground color, as opposed to reddish in the new species; and *E. pallidus* lacks all traces of dark markings and reticulations on the dorsum. Also, in *E. pallidus* the tympanum is concealed, whereas in *E. wixarika* it is discernable (Fig. 9B). *Eleutherodactylus saxatilis* can be distinguished from *E. wixarika* by the following characteristics: larger body size, which is usually over 26 mm and up to 31 mm; outer digits more widely expanded, usually twice or more the width of the narrowest part of the finger on the third and fourth fingers; venter immaculate white as opposed to *E. wixarika*, which has a gray venter with both darker and lighter markings; presence of a distinguishable lumbar gland in *E. saxatilis* (Fig. 9D). *Eleutherodactylus teretistes* has smooth dorsal skin, while *E. wixarika* has a tuberculate dorsum; *E. teretistes* has a light brown or tan ground color vermiculated with dark brown, as opposed to *E. wixarika* which has a red or reddish orange ground color, and dark green or gray reticulations which may be broken up into spots. Furthermore, *E. teretistes* has a diagnostic light colored line, starting on the snout, following the outline of the head above the nostrils, above the eyes, onto the shoulders and then fading towards the back. This light line is present on all specimens of *E. teretistes* that were observed in the field, including individuals from Sinaloa, Nayarit and Jalisco. This line is not present on any of the three specimens of *E. wixarika*. This new species can be distinguished from *E. modestus* by its larger size (males 21–25 mm SVL, vs < 20 mm in *E. modestus*); also *E. modestus* has a uniform white or cream ventral coloration, whereas in *E. wixarika* it is darker gray with white spots and darker mottling.

Description of the holotype. Relatively small size (21.9 mm SVL); head slightly wider than long, 7.3 mm in length, 7.7 in width, about as wide as body; snout truncate, angular, non-rounded from a dorsal view but rounded from a lateral profile; tympanum distinct and rounded, no distinct supratympanic fold, greatest diameter of tympanum 1 mm; greatest diameter of eye 2.4 mm, tympanum-to-eye ratio 0.4; eyelid 1.9 mm wide, approximately three fifths of the IOD; first finger same length as second finger; finger lengths from shortest to longest 1-2-4-3, with 1 and 2 equal; digital pads on fingers three and four moderately expanded, approximately 1.8 times the narrowest point of the digit; three palmar tubercles; inner palmar tubercle about 70% as large as middle palmar tubercle, outer palmar tubercle about half as large as the middle palmar tubercle; toe lengths from shortest to longest 1-2-5-3-4. FL 8.5 mm, TL 10.1 mm, FeL 9.1 mm, FoL 6.6 mm, IND 2.2 mm, IOD 2.9 mm, END 2.3 mm. FeL to SVL 42%, TL to SVL 46%, FL to SVL 39%, HL to SVL 33%, HD to SVL 35%. Dorsal skin tuberculate; lateral skin and ventral skin areolate. Vocal slits absent in males. See Figure 7 for a photograph of the holotype in life. Coloration in preservative is a light ground color of tan to orange, with dark gray almost black reticulations covering the entire dorsal surface of the head, back and arms. Thighs orange-yellow with some dark gray blotches. Ventral coloration is cream and gray with some darker and paler spots.

Variation. The three known specimens of this species vary little in morphology and color pattern. One

specimen is larger than the type, measuring 24.5 mm. The dorsal ground color is always reddish with darker reticulations, the intensity and width of which varies from individual to individual, making one individual seem darker. Measurements for the holotype and paratypes are given in Table 1.

Distribution and ecology. This species has been collected in the Sierra Huichol in the municipality of Mezquitic, Jalisco (Fig. 6A). It likely occurs continuously at high elevations throughout this mountain range and possibly also in other nearby mountain ranges in Jalisco, Zacatecas, Nayarit and Durango. It has been collected between 2400–2500 m at the type locality in pine forest (Fig. 6C). All specimens were collected in July, which is the beginning of the rainy season in western Mexico and likely the breeding season for these frogs.

Etymology. *Eleutherodactylus wixarika* is a patronym honoring the Wixárika people, better known by their Spanish name, Huicholes. Once widespread in the states of Nayarit, Jalisco, Zacatecas, Durango and San Luis Potosí, the Wixárika people still inhabit the area around the type-locality of this frog, and the Sierra Huichol mountain range remains one of the last outposts of their language and culture.

Advertisement calls. Like other members of the subgenus *Syrrhophus*, the advertisement call of these species consists of a short note best described as a "chirp" or "peep". These notes are relatively narrow band (<500 Hz), nearly pure-tone bursts of acoustic energy organized into a discrete train repeated about 6 times per minute (Table 1, Fig. 10). The fundamental frequency contains nearly the same amount of energy as the dominant frequency in both species (not shown). Compared to *E. wixarika*, the call of the larger species *E. grunwaldi* is much shorter (70 vs. 130 ms), ascends to its dominant frequency more rapidly, and has a lower dominant (and thus fundamental) frequency (2100 vs. 2700 Hz). The calls of both species show substructure within a call, but the pulses of acoustic energy are irregular in timing and duration. The signals of both species show very slight frequency modulation from beginning to end. Although *Syrrhophus* may produce an irregular introductory trill prior to a call bout (Fouquette 1960), our recordings do not contain any trills.

TABLE 2. Call measurement summary (mean of five consecutive calls ± SD) for one individual each of *Eleutherodactylus grunwaldi* and *E. wixarika*. Call descriptors follow Cocroft & Ryan (1995) except for Rényi spectral entropy (Han *et al.* 2011) and spectral flatness (Sueur *et al.* 2014).

	E. grunwaldi	*E. wixa**rika***
Dominant frequency (kHz)	2.13 ± 0.02	2.75 ± 0.04
Call length (ms)	70 ± 10	130 ± 40
Call rate (/m)	6.13 ± 1.35	6.43 ± 2.74
Call rise time (ms)	20 ± 10	90 ± 30
Rényi spectral entropy	5.46 ± 0.52	5.74 ± 0.36
Spectral flatness measure	0	0

Discussion

Advertisement calls. Spectral and temporal acoustic properties of male advertisement calls differ between the two new species described here. Few descriptions (and even fewer recordings) of *Syrrhophus* advertisement calls have been published. Fouquette (1960) described the calls of *Eleutherodactylus marnockii*, *E. pipilans*, and *E. nitidus*. Dixon (1957) reported reciprocal calling by female *E. angustidigitorum*, a behavior that has been reported in at least two other eleutherodactylids (Schlaepfer & Figeroa-Sandí, 1998; Stewart & Rand, 1991). It is not known whether female *E. grunwaldi* or *E. wixarika* call.

The small size of *Syrrhophus* imposes constraints for acoustic communication (Gerhardt & Huber, 2002), namely the limited communication range of high-frequency calls. Like many other eleutherodactlyids, *Syrrhophus* increase their broadcast range by calling from elevated perches. Males of some species call from rock crevices (Fouquette 1960), which may serve to amplify the signal by acting as a secondary resonator (Penna & Solís, 1996).

Evolutionary relationships and biogeography. Twenty-four species of *Syrrhophus* occur in mainland Central and North America, all of them included in the *Eleutherodactylus (Syrrhophus) longipes* species series as defined by Hedges *et al.* (2008). This species series is further split into six species groups, which were first defined by Lynch (1970) and revised by Hedges (1989) and Hedges *et al.* (2008).

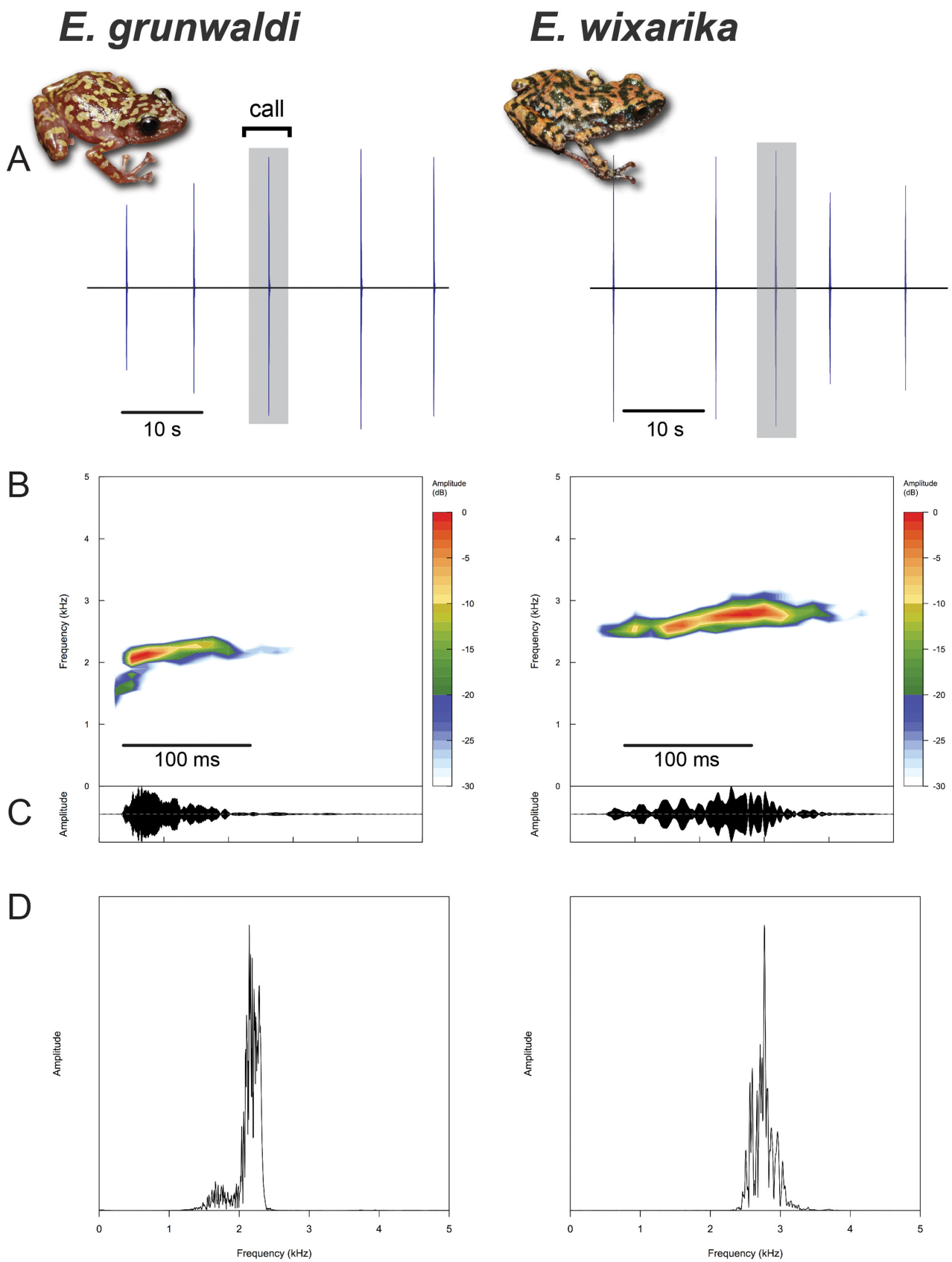

FIGURE 10. Advertisement calls of *Eleutherodactylus grunwaldi* and *E. wixarika* showing A) oscillograms (relative amplitude vs. time) of five calls; (B) spectrograms (energy in each frequency vs. time) and oscillograms (C) of a single call; and D) power spectra. Note the spectral and temporal property differences between species.

Eleutherodactylus grunwaldi shares similarities with several members of the subgenus, including the species of the *E. longipes* and *E. marnockii* species groups as defined by Lynch (1970), as well as *E. saxatilis* and *E. interorbitalis*. Similarities include general coloration, size and the presence of greatly expanded digital discs (Figs. 1–4). Lynch (1970) considered *E. longipes* and *E. dennisi* to be closely related and Farr *et al.* (2013) commented that they might be conspecific. *Eleutherodactylus longipes* is restricted to karst formations in the Sierra Madre Oriental, from Coahuila to Hidalgo (Lemos Espinal & Smith, 2007a, 2007b; Lynch, 1970), while *E. dennisi* is known from several caves in southern Tamaulipas and eastern San Luis Potosí (Lemos-Espinal & Dixon, 2013; Lynch, 1970). Both species resemble *E. grunwaldi* in general color pattern, large size and by having broad digital discs. The *marnockii* species group consists of *E. marnockii*, *E. guttilatus* and *E. verrucipes. Eleutherodactylus marnockii* is restricted to central Texas, eastern Chihuahua and northern Coahuila (Lynch 1970), while *E. guttilatus* it is restricted to the Chihuahuan Desert, the Mexican Plateau and the western versant of the Sierra Madre Oriental (Lynch, 1970). Finally, *E. verrucipes* is known from the Sierra Madre Oriental and associated ranges (Arenas-Monroy *et al.*, 2012; Farr, *et al.*, 2007). All three members of the *E. marnockii* species group are similar to *E. grunwaldi* in general dorsal coloration, body proportions and expanded digital discs, however they are smaller and their discs are not as broad as in *E. grunwaldi.*

While general morphology would suggest a close relationship of *E. grunwaldi* with the five species mentioned above, this seems unlikely from a biogeographical perspective. The entire range of the *E. longipes* and *E. marnockii* species groups falls east of the continental divide, in Atlantic or interior drainages, while *E. grunwaldi* is known only from one mountain range on the Pacific Coast. The only species resembling *E. grunwaldi* that inhabits the pacific versant of Mexico is *E. saxatilis.* This species was formerly assigned to the genus *Tomodactylus,* which was later synonymized with *Eleutherodactylus* by Myers (1962); all the former species of *Tomodactylus* are now included in the *E. nitidus* species group of the subgenus *Syrrhophus* (Hedges *et al.* 2008). *Eleutherodactylus saxatilis* is known only from the western flanks of the Sierra Madre Occidental in Durango and Sinaloa (Webb, 1962). Like several of the species mentioned above, *E. saxatilis* shares similarities in color pattern, digital pad shape and size to *E. grunwaldi.* However, in *E. saxatilis* the digital discs are not as broad and conspicuous lumbar glands are present.

Preliminary phylogenetic analysis of the 16S ribosomal RNA gene suggests that *E. grunwaldi* is not closely related to the members of the *E. longipes* and *E. marnockii* species groups of northeastern Mexico discussed above (Devitt, unpublished). It is important to note that these species that share similarities in coloration and morphology to *E. grunwaldi* also share a similar saxicolous existence, and thus these similarities are likely a result of adaptation to similar environments rather than recent, shared evolutionary history. Instead, *E. grunwaldi* appears to be most closely related to members of the *E. modestus* species group of Hedges *et al.* (2008) (Devitt, unpublished).

Eleutherodactylus wixarika shares several morphological similarities with other members of the subgenus, including *E. pallidus*, *E. modestus* and *E. teretistes*, which belong to the *E. modestus* species group of Lynch (1970) and Hedges *et al.* (2008). *Eleutherodactylus pallidus* is known from the Pacific lowlands, coastal sierras and inland barrancas of Nayarit and northwestern Jalisco (Lynch, 1970, Ponce-Campos *et al.*, 2003). This species is distinguishable from the *E. wixarika* by its smaller size and dorsal coloration lacking any dark markings. *Eleutherodactylus modestus* is known from the Pacific lowlands and nearby coastal mountain ranges of Jalisco and Colima (Lynch 1970). This species shares the red ground coloration of *E. wixarika,* however, *E. wixarika* is larger and has a dark gray ventral coloration, as opposed to light cream or white in *E. modestus*. *Eleutherodactylus teretistes* is known to occur along the Pacific versant of the Sierra Madre Occidental in southeastern Sinaloa and Nayarit, as well as in coastal mountain ranges of southwestern Nayarit and northwestern Jalisco (Lynch, 1970, Ahumada-Carrillo, *et al.*, 2014). *Eleutherodactylus teretistes* can be distinguished from *E. wixarika* primarily based on skin texture and color pattern (see above). *Eleutherodactylus pallidus* and *E. teretistes* occur in Nayarit and Jalisco at lower elevations, with *E. pallidus* known from 0–1225 m (Lynch 1970) and *E. teretistes* known from 300–1630 m (Lynch, 1970, Ahumada-Carrillo, 2014). The deep barrancas that intersect the southern Sierra Madre Occidental serve as corridors to many lowland species (Ahumada-Carrillo *et al.*, 2014; Cox *et al.*, 2012). In the case of *E. wixarika,* the Río Atengo, a tributary of the Río Grande de Santiago, might have allowed an ancestor of these three species to reach the higher elevations of the Sierra Huichola. Phylogenetic analysis of the 16S ribosomal gene shows that *Eleutherodactylus wixarika* is closely related to *E. teretistes* (Devitt, unpublished). Based on the data discussed above, we believe that *E. wixarika* might be closely related to *E. pallidus* and *E. teretistes*, and is probably a member of the *E. modestus* species group.

Several of the most important topographic features of Mexico converge in central-western Mexico; these include the Sierra Madre Occidental, the Trans-Mexican Volcanic Belt and the Pacific lowlands. The merging of these areas in the region has created a diverse assortment of unique habitats, and has made this region an important center of biodiversity, with many endemic species of vertebrates (e.g. Ceballos *et al.*, 1995; Ceballos & Garcia, 1995; Peterson & Navarro, 2000). Many herpetological collections exist from the states of west central Mexico (Colima, Jalisco, Michoacán and Nayarit), but despite this, the herpetofauna of many areas in these states is still poorly known. We believe that future fieldwork in that area will result in new species discoveries, especially in isolated mountain ranges like the Sierra Cacoma and Sierra de Pihuamo in Jalisco, or the Sierra de Coalcomán in Michoacán.

Frogs of the subgenus *Syrrhophus* are among the most diverse groups of anurans in Mexico, but because of the lack of attention that they have received, many species are still awaiting formal description (personal observation). Additional fieldwork in western Mexico and elsewhere will certainly result in the identification of new species of this group, and a careful revision of museum material along with molecular analyses will help us to better understand the species-level diversity and evolutionary history of the group.

Conservation. Iron ore mining is an important economic activity in the mountains surrounding the Manantlán Biosphere Reserve, which is inhabited by *E. grunwaldi*. Mining activities have had a negative impact in the ecosystems and communities around the area; for example, a new open pit mine has already destroyed one of the only localities for the rare Manantlán Long-tailed Rattlesnake (*Crotalus lannomi)* (Reyes-Velasco, personal observation; see also Reyes-Velasco *et al.* 2010 for a discussion on the biological importance of the region). The Sierra Huichol in northern Jalisco has some of the last remains of old growth forest in the Sierra Madre Occidental, which now contains less than 0.65% of its original extent (Lammertink, 1996). Logging and the conversion of forest into agricultural fields are some of the biggest threats to the biodiversity of the region. The Wixárika or Huichol people, for whom *E. wixarika* is named, have been greatly affected by new economic activities in the area, including new roads and mining projects, logging, agriculture and the expansion of drug cartels in recent years (authors personal observation; Boni, Garibay, & McCall, 2014; González-Elizondo *et al.*, 2012; Liffman, 2011; Tetreault & López, 2011). The culture and traditions of the Wixárika as well as the biodiversity of the area are increasingly threatened by human encroachment, and deserve protection if they are to persist in the long term.

Acknowledgments

We thank Christoph Grünwald and Jason Jones for their help in the field and generous donations of specimen to this project. We also thank Chris Rodriguez, Alexander Hermosillo, Gabriela Zamora-Silva and Ginny Weatherman for their help during fieldwork. We thank Jonathan A. Campbell, Eric N. Smith and Carl Franklin (UTA) for access to specimens under their care. We are also especially thankful to Jonathan A. Campbell for his assistance in reviewing this manuscript. Fieldwork was conducted under a collecting license issued to Oscar Flores by SEMARNAT (FAUT-0015).

References

Ahumada-Carrillo, I.T., River-Perez, N., Reyes-Velasco, J., Grünwald, C.I. & Jones, J.M. (2014) Notable Records of Amphibians and Reptiles from Colima, Nayarit, Jalisco, and Zacatecas, México. *Herpetological Review,* 45, 287–291.

Arenas-Monroy, J.C., Carbajal-Márquez, R.A., García-Balderas, C.M., Grunwald, C.I. & Jones, J.M. (2012) *ELEUTHERODACTYLUS VERRUCIPES* (Bigear Chirping Frog). Geographic Distribution. *Herpetological Review,* 43, 439.

Audacity Team (2014) Audacity®. Version 2.0.3. Audio editor and recorder. Available from: http://audacity.sourceforge.net/ (accessed 24 September 2014)

Boni, A., Garibay, C. & McCall, M.K. (2014) Sustainable mining, indigenous rights and conservation: conflict and discourse in Wirikuta/Catorce, San Luis Potosi, Mexico. *GeoJournal*, 1–22.

Ceballos, G. & Garcia, A. (1995) Conserving neotropical biodiversity: the role of dry forests in western Mexico. *Conservation Biology*, 9, 1349–1353. http://dx.doi.org/10.1046/j.1523-1739.1995.09061349.x

Ceballos, G., Rodríguez, P. & Medellín, R.A. (1998) Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemicity, and endangerment. *Ecological Applications,* 8, 8–17.

http://dx.doi.org/10.1890/1051-0761(1998)008[0008:ACPIMM]2.0.CO;2
Cocroft, R.B. & Ryan, M.J. (1995) Patterns of advertisement call evolution in toads and chorus frogs. *Animal Behaviour,* 49, 283–303.
http://dx.doi.org/10.1006/anbe.1995.0043
Cope, E.D. (1878) A New Genus of Cystignathidae from Texas. *American Naturalist,* 12, 252–253.
Cox, C.L., Streicher, J.W., Sheehy III, C.M., Campbell, J.A. & Chippindale, P.T. (2012) Patterns of genetic differentiation among populations of Smilisca fodiens. *Herpetologica,* 68, 226–235.
Dixon, J.R. (1957) Geographic Variation and Distribution of the Genus Tomodactylus in Mexico. *Texas Journal of Science,* 9, 379–409.
Dixon, J.R. & Webb, R.G. (1966) A new *Syrrhophus* from Mexico (Amphibia: Leptodactylidae). *Contributions in Science, Los Angeles County Museum,* 102, 1–5.
Duellman, W.E. (1958) A review of the frogs of the genus *Syrrhophus* in western Mexico. *Occasional Papers of the Museum of Zoology, University of Michigan,* 594, 1–24.
Farr, W., Lavin Murcio, P.A. & Lazcano, D. (2007) New distributional records for amphibians and reptiles from the state of Tamaulipas, Mexico. *Herpetological Review,* 38, 226–233.
Farr, W.L., Lazcano, D. & Lavín-Murcio, P.A. (2013) New Distributional Records for Amphibians and Reptiles from the State of Tamaulipas, México III. *Herpetological Review,* 44, 631–645.
Fouquette, M. (1960) Call structure in frogs of the family Leptodactylidae. *Texas Journal of Science,* 12, 201–215.
Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F., De Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, 297, 1–291.
http://dx.doi.org/10.1206/0003-0090(2006)297[0001:TATOL]2.0.CO;2
Gerhardt, H.C. & Huber, F. (2002) *Acoustic communication in insects and anurans: common problems and diverse solutions*. University of Chicago Press, Chicago, 531 pp.
González-Elizondo, M., González-Elizondo, M., González, L.R., Enríquez, I.L., Rentería, F.R. & Flores, J.T. (2012) Ecosystems and diversity of the Sierra Madre Occidental. *USDA Forest Service Proceedings,* RMRS-P-67, 204–211.
Han, N.C., Muniandy, S.V. & Dayou, J. (2011) Acoustic classification of Australian anurans based on hybrid spectral-entropy approach. *Applied Acoustics,* 72, 639–645.
Hedges, S.B. (1989) Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. *Biogeography of the West Indies: past, present, and future*, 305–370.
Hedges, S.B., Duellman, W.E. & Heinicke, M.P. (2008) New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa,* 1737, 1–182.
Heinicke, M.P., Duellman, W.E. & Hedges, S.B. (2007) Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences,* 104, 10092–10097.
http://dx.doi.org/10.1073/pnas.0611051104
Joglar, R.L. (1989) Phylogenetic relationships of the West Indian frogs of the genus *Eleutherodactylus:* a morphological analysis. *In:* Wood, C.A. (Ed.), *Biogeography of the West Indies: past, present, and future*. Sandhill Crane Press, Gainesville, Florida, pp. 371–408.
Lemos Espinal, J.A. & Smith, H.M. (2007a) *Anfibios y reptiles del estado de Chihuahua, México*. UNAM, Mexico, 613 pp.
Lemos Espinal, J.A. & Smith, H.M. (2007b) *Anfibios y reptiles del estado de Coahuila, México.* UNAM, Mexico, 550 pp.
Lemos-Espinal, J.A. & Dixon, J.R. (2013) *Amphibians and Reptiles of San Luis Potosí*. Eagle Mountain Publishing, Eagle Mountain, Utah, 300 pp.
Liffman, P.M. (2011) *Huichol Territory and the Mexican Nation: Indigenous Ritual, Land Conflict, and Sovereignty Claims*. University of Arizona Press, Tucson, Arizona, 296 pp.
Lynch, J.D. (1970) A taxonomic revision of the leptodactylid frog genus *Syrrhophus* Cope. *University of Kansas Publications Museum of Natural History,* 20, 1–48.
Lynch, J.D. (1971) Evolutionary Relationships, Osteology, and Zoogeography of Leptodactyloid Frogs. *Miscellaneous Publications of the University of Kansas Museum of Natural History*, 53, 1–246.
Lynch, J.D. & Duellman, W.E. (1997) Frogs of the Genus *Eleutherodactylus* in Western Ecuador. *The University of Kansas Natural History Museum Special Publications*, 23, 1–252.
Myers, G.S. (1962) The American Leptodactylid Frog Genera *Eleutherodactylus*, Hylodes (= Elosia), and Caudiverbera (= Calyptocephalus). *Copeia*, 195–202.
http://dx.doi.org/10.2307/1439498
Penna, M. & Solís, R. (1996) Influence of burrow acoustics on sound reception by frogs *Eupsophus* (Leptodactylidae). *Animal Behaviour,* 51, 255–263.
http://dx.doi.org/10.1006/anbe.1996.0026
Peterson, A. & Navarro, A. (2000) Western Mexico: a significant center of avian endemism and challenge for conservation action. *Cotinga,* 14, 42–46.
Ponce-Campos, P., Huerta-Ortega, S.M., Heinze-Yothers, A. & Smith, H.M. (2003) Range extensions and variational notes on some amphibians and reptiles of Jalisco and Michoacan, Mexico. *Bulletin of the Maryland Herpetological Society,* 39, 1–7.

Reyes-Velasco, J., Grünwald, C.I., Jones, J.M. & Weatherman, G.N. (2010) Rediscovery of the rare Autlán long-tailed rattlesnake, *Crotalus lannomi*. *Herpetological Review,* 41, 19–25.

Savage, J.M. (2002) *The amphibians and reptiles of Costa Rica: a herpetofauna between two continents, between two seas*. University of Chicago Press, Chicago, 934 pp.

Schlaepfer, M.A. & Figeroa-Sandí, R. (1998) Female reciprocal calling in a Costa Rican leaf-litter frog, *Eleutherodactylus podiciferus*. *Copeia*, 1076–1080.

Smith, H.M. & Taylor, E.H. (1948) An Annotated Checklist and Key to the Amphibia of Mexico. *Bulletin of the United States National Museum,* 194, 1–118.
http://dx.doi.org/10.5479/si.03629236.194

Stewart, M.M. & Rand, A.S. (1991) Vocalizations and the defense of retreat sites by male and female frogs, *Eleutherodactylus coqui*. *Copeia*, 1013–1024.
http://dx.doi.org/10.2307/1446096

Sueur, J., Aubin, T. & Simonis, C. (2008) Equipment review: seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics,* 18, 213–226.
http://dx.doi.org/10.1080/09524622.2008.9753600

Sueur, J., Farina, A., Gasc, A., Pieretti, N. & Pavoine, S. (2014) Acoustic Indices for Biodiversity Assessment and Landscape Investigation. *Acta Acustica united with Acustica,* 100, 772–781.
http://dx.doi.org/10.3813/AAA.918757

Team, R.C. (2012) R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available: http://www.R-project.org (accessed 22 September 2014)

Tetreault, D.V. & López, C.F.L. (2011) Jalisco: pueblos indígenas y regiones de alto valor biológico. *Espiral,* 18, 165–199.

Webb, R.G. (1962) A new species of the frog (genus *Tomodactylus*) from western Mexico. *University of Kansas Publications of the Museum of Natural History,* 15, 175–181.

APPENDIX 1. Specimens examined.

Eleutherodactylus grunwaldi—Mexico: Colima: 3.5 km ESE of El Sauz, on road to El Terrero, Municipality of Minatitlán, 1,329 m (MZFC 27472); dirt road between El Sauz and El Terrero, Municipality of Minatitlán, 1,300–1,900 m (MZFC 27467–27471 & 27473–27475); 6.7 km SW of El Sauz, on road to El Terrero (MZFC 27484); Mexico: Jalisco: Grutas de Toxín, Municipality of Toliman, 770m (JRV-230).

Eleutherodactylus wixarika—Mexico: Jalisco: Bajío de los Amoles, Municipality of Mexquitic, 2,460 m. (MZFC 27477-27479).

Additional specimens examined at UTA:

Eleuterodactylus angustidigitorum: JAC 24912, JAC 26977. *E. cystignathoides*: JAC 30000–30001, JHM 1390–1394. *E. dennisi*: UTAA 59516–59521. E. dilatus: UTAA 4017–4020, 4023–4024, 5269, 5276–5279. E. grandis: UTAA 56845. *E. guttilatus*: JAC 29603, 29834, 29843. E. leprus: JAC 30833–30835, 30849. *E. longipes*: UTAA 59421–59422. *E. marnockii*: JHM 1427–1429. *E. modestus*: JAC 28295, 29117, 30498, 30499, 30518, 30519, 30631. *E. nitidus*: ENS 9557, JAC 26947. *E. nitidus nitidus*: JAC 27256-27276. *E. nitidus orarius*: JAC 29107, 30500, 30501, 30517, 30625. *E. nitidus petersi*: JAC 27237, 28612. *E. pipilans*: JAC 30813. *E.* sp: ENS 9931, JAC 27707, 30723, 30725–30728, 26663, 30840, 30841, TDH 1530–1531.

Additional specimens examined at MZFC:

Eleutherodactylus modestus: MZFC 26888–26889. *E. nivicolimae*: MZFC 26889, 26882–26887, 26905–26908. *E.* sp: MZFC 26893, 26896, 26898, 27476.