

Historically, direct-developing frogs of the genus *Eleutherodacylus* (Family: Eleutherodactylidae) have been some of the most perplexing and taxonomically challenging amphibians in the New World to investigate. In the following paper, the authors studied these frogs in western Mexico, and conducted a series of morphological, molecular, and vocalization analyses. Their results revealed the existence of six new species. Pictured here is an individual from Ixtlahuacán, Colima, in its natural habitat, one of the species being described.

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Six new species of *Eleutherodactylus* (Anura: Eleutherodactylidae: subgenus *Syrrhophus*) from Mexico, with a discussion of their systematic relationships and the validity of related species

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Abstract: We present an analysis of morphological, molecular, and advertisement call data from sampled populations of *Eleutherodactylus* (subgenus *Syrrhophus*) from western Mexico and describe six new species. We use morphological comparisons and molecular data from all continental species of the subgenus *Syrrhophus* to define coherent species groups, and provide a key for the species groups in this subgenus. Additionally, based on morphological and molecular data, we synonymize two taxa formerly described in different genera. Finally, we discuss the conservation status of the subgenus *Syrrhophus*.

Key Words: Amphibians, call analysis, Colima, conservation, Jalisco, Mexico, Michoacán, taxonomy

Resumen: Presentamos un análisis de morfología, molecular y de cantos de poblaciones de *Eleutherodactylus* (subgénero *Syrrhophus*) del occidente de México. Basado en nuestros resultados describimos seis nuevas especies. Usamos comparaciones morfológicas y datos moleculares de todas las especies continentales del subgénero para definir grupos coherentes de especies, y proporcionamos una clave para los grupos de especies de este subgénero. Adicionalmente, basándonos en morfología y datos moleculares, sinonimizamos dos especies formalmente descritas en géneros distintos. Finalmente discutimos el estatus de conservación del subgénero *Syrrhophus*.

Palabras Claves: Análisis de cantos, anfibios, Colima, conservación, Jalisco, México, Michoacán, taxonomía

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INTRODUCTION

Frogs of the genus *Eleutherodactylus* Dumeril and Bibron (1841) are among the most diverse and taxonomically challenging groups of amphibians in the New World (Hedges et al., 2008). Their distribution extends from the southern United States to Central America, as well as in the West Indies (Hedges et al., 2008). The genus consists of five subgenera (Hedges et al., 2008), of which four are native only to the West Indies (*Eleutherodactylus*; *Euhyas* Fitzinger, 1843; *Pelorius* Hedges, 1989; and *Schwartzius* Hedges et al., 2008), as well the subgenus *Syrrhophus* Cope, 1878. *Syrrhophus* is native to Cuba and to continental North America, where it ranges from Texas to central Guatemala, and is most species-rich in Mexico (Hedges, 1989).

Whereas the systematics of the West Indian subgenera has been studied relatively well (Hedges et al., 2008), during the last half of the past century little attention has been given to the systematics of the subgenus *Syrrhophus*. Despite researchers suspecting that they were encountering undescribed taxa (J. Campbell, pers. comm.; W. Duellman, pers. comm.), no further studies of this group were undertaken. The last inclusive reviews of the subgenus were those of Dixon (1957a, b), who reviewed the members of the genus *Tomodactylus* Günther, 1900, which now is considered a synonym of *Syrrhophus* (Hedges et al., 2008), and that of Lynch (1970), who reviewed the species then assigned to the genus *Syrrhophus*.

Recent large-scale taxonomic works have redefined our understanding of New World direct-developing frogs, which includes the genus *Eleutherodactylus* and the subgenus *Syrrhophus* (Hedges, 1989; Frost et al., 2006; Heinicke et al., 2007; Hedges et al., 2008); however, after Lynch's (1970) review of the subgenus *Syrrhophus*, species level taxonomic studies have been lacking.

Hedges et al. (2008) assigned all species of the genera *Syrrhophus* and *Tomodactylus* to the genus *Eleutherodactylus*, subgenus *Syrrhophus*. Within the subgenus *Syrrhophus* they included two species series, the *Syrrhophus symingtoni* Species Series, containing two species from Cuba, and the *Syrrhophus longipes* Species Series, which includes all species native to the United States, Mexico, Belize, and Guatemala. These authors proposed that this latter species series contains six species groups, based loosely on morphological characters and taxonomy. While the macro-taxonomy of this group of frogs is outside the scope of this paper, our morphological analysis of all the known species in the *Syrrhophus longipes* Species Series, as well as preliminary molecular data of the group, provides an insight into the relationships of these frogs.

Since 2003, a renewed interest in this group led us to sample all of the currently recognized species of *Syrrhophus* in the United States, Mexico, and Guatemala. This work resulted in the descriptions of two new species of *Eleutherodactylus* from western Mexico by Reyes-Velasco et al. (2015), which increased the number of recognized species of the subgenus *Syrrhophus* at that time to 26 in continental North America, plus two more species from Cuba (Frost, 2017; accessed 15 March 2017). The present work is a continuation of our efforts to study the diversity of *Syrrhophus*.

Here we detail the discovery and description of six new species of *Syrrhophus* from the states of Jalisco, Colima, and Michoacán. We provide results from both morphological and molecular analyses of all the known continental species of the subgenus *Syrrhophus*, and use these results to arrange the species of the subgenus into coherent species groups. Finally, we synonymize two little-understood taxa that formerly were placed in different genera.

MATERIALS AND METHODS

Taxonomic Sampling

Between 2003 and 2007, we conducted numerous trips in an effort to collect specimens of all the known species of the subgenus *Syrrhophus* in Mexico, the United States, and Central America. We focused on the west coast of Mexico, in the states from Jalisco to Guerrero, where this subgenus apparently is the most diverse (Dixon, 1957a; Reyes-Velasco, 2015). We examined the type material for two species, as well as the representative material for the species described herein. We collected and examined the topotypic material for 17 species (Table 1). For five other species we were unable to obtain material from their respective type localities, but we examined specimens from other localities (Table 1). We examined material of every recognized species in the subgenus *Syrrhophus*, except for *E. verruculatus* (Peters, 1870), which has not been collected since its original description, and whose validity has been questioned by various authors (Firschein, 1954; Lynch, 1970). We visited the type locality of *E. verruculatus* on two occasions, but did not find any *Syrrhophus* that were not readily referrable to *E. cystignathoides*.

We photographed all the frogs we collected in life, including their lateral, dorsal, and ventral profiles, and for each individual obtained images showing the colors of the flanks and flash colors on the groin and thigh. We euthanized the frogs and obtained tissue samples from the thigh muscle, and preserved them in 96% ethanol (see Beaupre et al., 2004). We fixed the specimens in 10% formalin and stored them in 70% ethanol, and deposited the materials in the Museo de Zoología, Facultad de Ciencias (MZFC), Universidad Nacional Autónoma de Mexico (UNAM) in Mexico City, Mexico (see Appendix 1).

We measured additional specimens of the subgenus *Syrrhophus* housed in the Museo de Zoología, Facultad de Ciencias (MZFC) of Universidad Nacional Autónoma de México (UNAM) and in the Amphibian and Reptile Diversity Research Center (ARDRC) of the University of Texas at Arlington (UTA). We also examined photographs of specimens in the University of Kansas Natural History Collection (KU), and at the University of Michigan Museum of Zoology (UMMZ). We did not remeasure type specimens of previously described taxa (except for *E. grunwaldi* and *E. wixarika*), so we used the measurements provided in their respective original descriptions. We provide specimen numbers for all material examined in Appendix 1. Many specimens in both collections were not catalogued at the time of our study, so we listed them with their original field numbers and included a legend indicating which field numbers will be catalogued in each museum.

Morphological Measurements

The characters and terminology we use herein follow those of Lynch and Duellman (1997) and Savage (2002), with some variation noted below. We took the following measurements for each specimen (abbreviations listed in parenthesis): snout–vent length (SVL); head length (HL); head width (HW); eyelid width (EW); interorbital distance (IOD); internarial distance (IND); eye–naris distance (END); diameter of eye (ED); width of tympanum (TW); height of tympanum (TH); eye–tympanum distance (ETD); upper arm length (UpL); forearm length (FoL); hand length (HaL); length of 1st finger (F1L); width of pad on 1st finger (F1PW); width of 1st finger (F1W); length of 2nd finger (F2L); width of pad on 2nd finger (F2PW); width of 2nd finger (F2W); length of 3rd finger (F3L); width of pad on 3rd finger (F3PW); width of 3rd finger (F3W); length of 4th finger (F4L); width of pad on 4th finger (F4PW); width of 4th finger (F4W); inner palmar tubercle length (IPTL); middle palmar tubercle length (MPTL); outer palmar tubercle length (OPTL); femur length (FeL); tibia length (TL); tarsal length (TaL), foot length (FL), total foot length (TotFL); length of 2nd toe (T2L); width of pad on 2nd toe (T2PW); width of 2nd toe (T2W); length of 3rd toe (T3L); width of pad on 3rd toe (T3PW); width of 3rd toe (T3W); length of 4th toe (T4L); width of pad on 4th toe (T4PW); width of 4th toe (T4W); length of 5th toe (T5L); width of pad on 5th toe (T5PW); width of 5th toe (T5W); inner metatarsal tubercle length (IMTL); and outer metatarsal tubercle length (OMTL). We measured hand length (HA) from the tip of the longest finger to the base of the palm, and foot length (FL) from the tip of the longest toe to the base of the tarsus. The outer palmar tubercle refers to a small tubercle on the outer surface of the palm, but is not one of the larger supernumerary tubercles. While these tubercles usually are present in *Syrrhophus*, they generally are absent in some species and their presence is variable in others. We found that the presence and condition of the palmar tubercles only was of limited taxonomic use when working with these frogs. We included measurements, descriptions and drawings of the palmar tubercles for sake of continuity with previous works on this group (Lynch, 1970).

Molecular Analysis

DNA extraction and PCR amplification.—We extracted DNA from the tissue samples by using the standard potassium acetate protocol. We measured DNA concentration using a high sensitivity kit in a Qubit fluorometer (Life Technologies) for each of the samples. We sequenced a fraction of the 16s rRNA mitochondrial gene (n = 135) by using the primers LX12SN1a (forward) and LX16S1Ra (reverse) of Zhang et al. (2013) or with the modified primers 16Sar and 16Sbr of Bossuyt and Milinkovitch (2000). We performed polymerase chain reactions (PCR) to amplify the DNA fragments, and performed the PCR reactions in total volumes of 25 µl with the use of regular Taq (Invitrogen). We used the following PCR conditions: initial denaturation step at 96°C for 2 min, 35 cycles of denaturing at 95°C for 15 sec, annealing at 58°C for one min, and extension at 72°C for two min, and a final extension at 72°C for 10 min. We shipped unpurified PCR products for sequencing to BGI Tech Solutions (Hong Kong).

Sequence alignment and phylogenetic analysis.—We manually trimmed the 5' and 3' ends of all sequences using the program Genious to remove regions with poor quality base calls. We then aligned all sequences in Muscle (Edgar, 2004), with a final alignment of 581 base pairs. We deposited all the new sequences in GenBank, and included the accession numbers in Appendix 2.

We selected the best-fit models of nucleotide substitution for the 16s gene using the Bayesian Information Criterion (BIC) implemented in PartitionFinder v1.1.1 (Lanfear et al., 2012). We then performed Bayesian inference of phylogeny (BI) in MrBayes v3.2.2 (Ronquist and Huelsenbeck, 2003), implemented on the CIPRES Science gateway server (Miller et al., 2010). Our Bayesian analysis consisted of four runs; each ran for 10^7 generations with four chains (one cold and three heated), sampling every 1,000 generations. We confirmed that independent runs had converged based on overlap in likelihood and parameter estimates among runs, as well as effective sample size (ESS) and Potential Scale Reduction Factor value estimates (PSRF), which we evaluated in Tracer v1.6 (Drummond and Rambaut, 2007). PSRF indicated that individual runs had converged by 10^5 generations, and thus we discarded the first 25% of the runs as burn-in.

We annotated posterior probability values on the resulting topology using the program TreeAnnotator v1.8.3 (Rambaut et al., 2014). Additionally, we constructed phylogenetic networks using the NeighborNet algorithm implemented in SplitsTree 4 (Huson and Bryant, 2006) to visualize conflicting phylogenetic signal or ambiguities in the molecular data.

Reproductive Advertisement Call Analysis

We recorded vocalizations of individuals of all the new species described herein, as well as of all other members of the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group (as defined below). We recorded the frogs while they were actively calling in the field, using the WavePad free recording software (NCH Software 2015) on an Apple iPhone 5S. We recorded the calls at distances ranging from 50 cm to 150 cm, although when possible we tried to be within 100 cm of the frog.

We transfered the calls to a personal computer, and isolated the individual calls from other calls and background noise using Adobe Audition CC. We then analyzed the calls using the Raven Pro software, version 1.5, 64-bit version (Bioacoustic Research Program, 2012). The Raven Pro settings were as follows: window size = 256 samples; window type = Hanning; overlap = 50%; DFT size = 256 samples; and grid spacing = 188 Hz. We obtained sound figures using the Seewave version 1.6.4 package (Sueur et al., 2008) of the R platform, version 3.3.2, 64-bit version (R Core Team, 2016). The Seewave settings were as follows: window name (Fourier transform window) = Hanning; window length = 256 samples; and overlap = 80%.

Species Descriptions

In order to simplify the identification of the new species, in the species descriptions we include comparisons of all the related species. Recently it has become a common practice for the curators of online databases to "copy and paste" the information from digital species descriptions directly onto their online databases (e.g., Frost, 2017). Furthermore, these databases have become a primary resource for herpetological researchers, especially for those active in the field in countries where libraries with herpetological publications are rare or non-existent (CIG, pers. observ.) For the sake of consistency and completeness, we compare each new species being described to others being described in this paper. In an effort to avoid confusion as to the point where each species formally is being

described, we use the new species names followed by "sp. nov." until the point in the paper where a holotype is designated. Furthermore, for the sake of clarity we also use the epithet "sp. nov." in the tables, figures, maps, appendices, and the molecular tree.

Table 1. List of the species of *Eleutherodactylus* (subgenus *Syrrhophus*) in the United States, Mexico, and Central America specifying whether the type specimen was examined, as well as the nature (topotypic or non-topotypic) of the other material examined.

Subgenus *Syrrhophus*	**Type Examined**	**Topopic Material Examined**	**From Localities other than Type**
***E. longipes* Species Group**			
E. campi	_	–	X
E. cystignathoides	_	X	X
E. dennisi	–	X	X
E. guttilatus	–	X	X
E. leprus	–	–	X
E. longipes	–	–	X
E. marnocki	–	–	X
E. verrucipes	–	–	X
E. verruculatus	–	–	–
***E. nitidus* Species Group**			
E. albolabris	–	X	X
E. dilatus	–	X	X
E. maurus	–	X	X
E. nitidus	–	X	X
E. orarius	–	X	X
E. pipilans	–	X	X
E. rubrimaculatus	–	X	X
E. syristes	–	X	X
***E. modestus* Species Group**			
E. angustidigitorum	–	X	X
E. colimotl sp. nov.	X	X	X
E. erendirae sp. nov.	X	X	X
E. floresvillelai sp. nov.	X	X	–
E. grandis	–	–	X
E. grunwaldi	X	X	X
E. interorbitalis	–	X	X
E. jaliscoensis sp. nov.	X	X	X
E. manantlanensis sp. nov.	X	X	–
E. modestus	–	X	X

E. nietoi sp. nov.	X	X	X
E. pallidus	–	X	X
E. rufescens	–	X	X
E. saxatilis	–	X	X
E. teretistes	–	–	X
E. wixarika	X	–	–

RESULTS

Based on the morphological comparisons and molecular analyses, we identify six new species of the genus *Eleutherodactylus*, subgenus *Syrrhophus* from western Mexico, which we describe below.

New Species Descriptions

Eleutherodactylus colimotl sp. nov.

Figs. 1, 2, 3, 7A, 45B

***Holotype*:** (Figs. 1, 2). MZFC 29282 (CIG-00468). Adult male, collected by Christoph I. Grünwald, Jason M. Jones, Alexander I. Hermosillo-López, André João Grünwald, and Ámbar Lanomy Grünwald on 28 June 2015 at 3.5 km N of the junction of Highway 54 and the road to Ixtlahuacán, on the Hwy 54 frontage road, Municipio de Tecomán (19.052126°, -103.786360°; datum WGS 84; elev. 337 masl), Colima, Mexico (Fig. 8B).

***Paratypes*:** (Fig. 3). Ten specimens. MZFC 33115–33120 (CIG-00462–467), six adult male topotypes, collected on the same date as the holotype; MZFC 33036 (CIG-00340), one adult male collected by Christoph Grünwald, Hector Franz-Chávez, and Nadia Pérez-Rivera on 6 June 2015 at 0.6 km W of the bridge across the Río Aquila, near the entrance of Aquila, Municipio de Aquila (18.583654°, -103.518408°; datum WGS 84; elev. 107 masl), Michoacán, Mexico; MZFC 33329–333230 (CIG-00960–961), two adult males collected by Christoph I. Grünwald, Angelica Márquez-López, Jason M. Jones, Karen I. Morales-Flores, André João Grünwald, Ámbar Lanomy Grünwald, and Janelle Morales-Flores on 1 July 2016 at Grutas de San Gabriel, Municipio de Tecomán (18.906949°, -103.734853°; datum WGS 84; elev. 516 masl), Colima, Mexico; and MZFC 33299 (CIG-00901), one adult male collected by Christoph I. Grünwald, Angelica Márquez-López, Jason M. Jones, Karen I. Morales-Flores, André João Grünwald, Ámbar Lanomy Grünwald, and Janelle Morales-Flores on 3 July 2016 at Grutas de Tampumachay, near Los Ortices, Municipio de Colima (19.077620°, -103.726309°; datum WGS 84; elev. 248 masl), Colima, Mexico.

***Diagnosis*:** A member of the genus *Eleutherodactylu*s, subgenus *Syrrhophus*, as defined by Hedges et al. (2008). In the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Series and the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group, as defined in this paper (see discussion below). A small frog, adult males measure 22.9–28.4 mm SVL; vocal slits present in males; digital tips greatly expanded, 2.3–3.1 times width of narrowest part of finger on 3rd and 4th fingers; fingers relatively short, with 3rd finger length 12–17% of SVL (see Fig. 7A); compact lumbar gland above inguinal region absent; epidermis not translucent and abdominal vein not clearly visible on venter of live specimens; limbs moderate; TL/SVL ratio 0.43–0.48, FeL/SVL ratio 0.41–0.49 and TotFL/SVL ratio 0.61–0.69; snout relatively short, END/ SVL ratio 0.10–0.12; tympanum small, indistinct, and round; and TW/ED ratio 0.20–0.29; dorsal, lateral, and ventral skin smooth; dorsal coloration tan or pale brown, with darker brown reticulations forming indistinct dark brown saddle on upper back; interorbital bar present, the same color as the pale ground coloration; indistinct transverse bands present on legs; upper arms pale ground coloration and unbanded; venter immaculate white with a dark brown throat in males; bright inguinal flash colors absent; and mating call of adult males a short, high-pitched chirp (see below; Fig. 26).

***Comparisons*:** *Eleutherodactylus colimotl* can be distinguished from all species in the *Eleutherodactylus* (*Syrrhophus*) *longipes* Species Series (as defined herein, see below) by the presence of a small and indistinct tympanum with no visible tympanic annulus and a diameter less than 30% of the eye diameter; by a non-translucent abdominal epidermis, and thus a visible abdominal vein on the venter is not evident in life; and by the presence of a 3rd (outer) palmar tubercle that is smaller than 40% of the 2nd (middle) palmar tubercle.

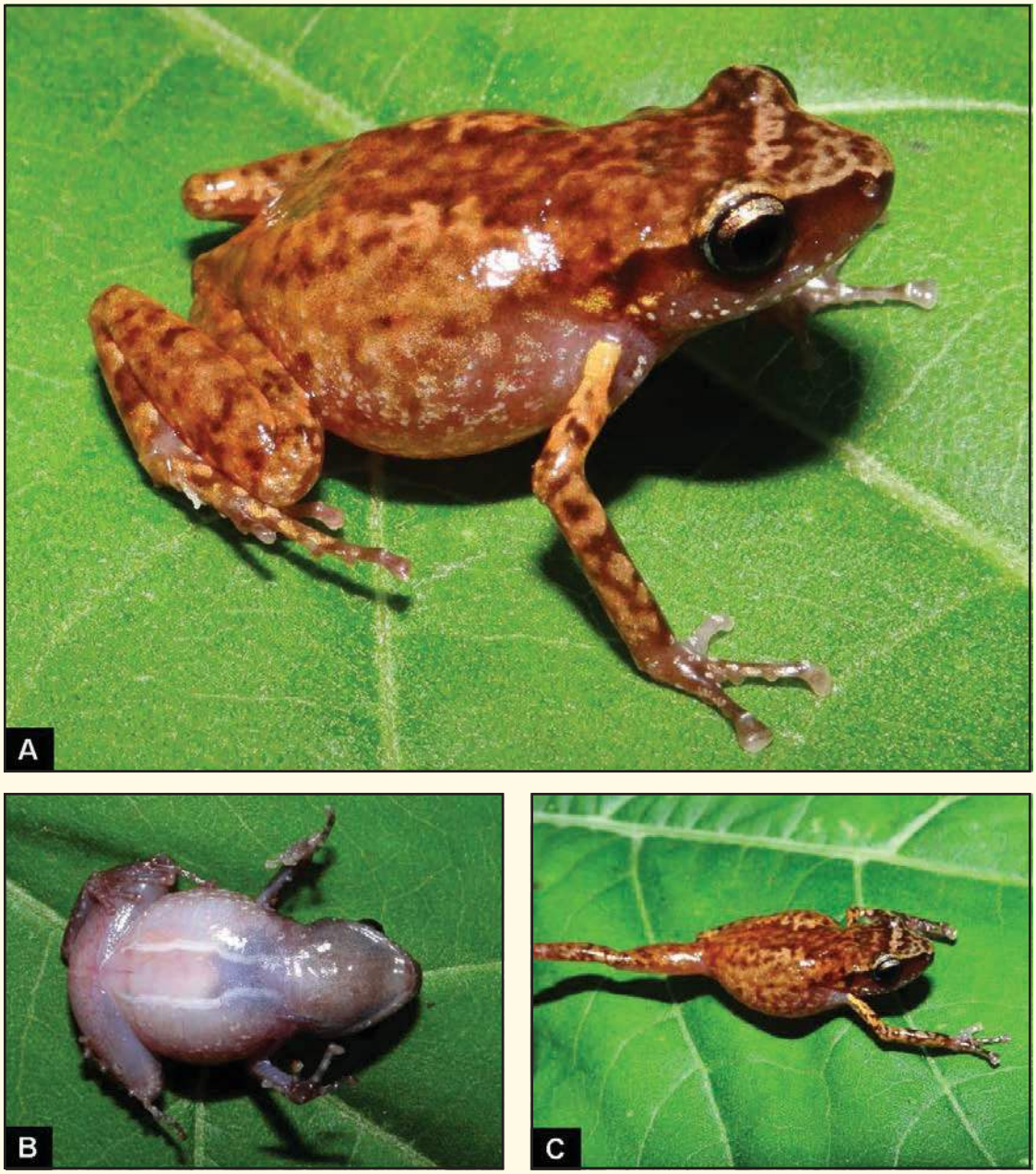


Fig. 1. Holotype of *Eleutherodactylus colimotl* sp. nov. in life, MZFC 29282 (CIG-00468). (A) Full body view; (B) ventral view; and (C) lateral view. © Christoph I. Grünwald

Eleutherodactylus colimotl can be distinguished from most species in the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Group (as defined herein, see below) by lacking a compact, protruding lumbar gland above the inguinal region. This species can be distinguished from the remaining two species in the species group, *E. pipilans* and *E. rubrimaculatus*, by its significantly more expanded digital tips on the 3rd and 4th fingers and by the presence of an interorbital bar.

Within its own species group, *E. colimotl* can be distinguished from *E. angustidigitorum* and *E. grandis* by its expanded finger pads, as opposed to fingertips that are as narrow, or narrower, than the narrowest part of the digit, and by lacking prominent lumbar glands above the inguinal region. It can be distinguished from *E. modestus*, *E. pallidus*, *E. teretistes*, and *E. wixarika* by a combination of digital tips that are expanded at least 2.3 times the

narrowest part of the finger on the 3rd and 4th fingers and a pale-colored interorbital bar, versus digital tips on the 3rd and 4th fingers that are expanded twice or less the narrowest part of the digit and the absence of a pale-colored interorbital bar. It also can be distinguished from all other species in its species group, except for *E. rufescens* (as defined herein) and potentially *E. teretistes*, by its relatively short fingers, typically 13–15% of the SVL and less than 17%. *Eleutherodactylus colimotl* can be distinguished from *E. rufescens* (including *E. nivicolimae*, see below), *E. erendirae* sp. nov. (see below), *E. floresvillelai* sp. nov. (see below), and *E. jaliscoensis* sp. nov. (see below), which share a similar pale-colored interorbital bar and a similar dorsal coloration, by lacking flash coloration on the anterior and posterior portions of the thigh and in the groin, by the presence of smooth dorsal skin, and by its significantly more expanded digital tips on the 3rd and 4th fingers (2.3–3.1 times in *E. colimotl*, compared to less than 2.3 times in the other species). *Eleutherodactylus colimotl* differs from the larger saxicolous species of the *E. modestus* Species Group (as defined herein) as follows: from *E. interorbitalis* by the presence of a 3rd (outer) palmar tubercle, a distinct dorsal coloration lacking dark-colored reticulations, and by more expanded fingertips, which are expanded more than 2.1 times the narrowest part of the finger (as opposed to 1.7–1.9 times in *E. interorbitalis*); from *E. saxatilis* by lacking compact lumbar glands and by the presence of a pale-colored interorbital bar; from *E. grunwaldi* by lacking distinct dark-colored dorsal reticulations, the presence of a smaller tympanum (less than 30% TW/ED ratio in *E. colimotl* vs. 38–50% in *E. grunwaldi*), and a shorter SVL in adults (max 26.5 mm in *E. colimotl*, 28.0–32.0 mm in *E. grunwaldi*). The species most similar to *E. colimotl* are *E. manantlanensis* sp. nov. (see below) and *E. nietoi* sp. nov. (see below). *Eleutherodactylus colimotl* can be distinguished from *E. manantlanensis* sp. nov. by its visible tympanum, which is absent in the latter species, by the lack of flash colors in the inguinal region of *E. colimotl*, and by presence of tubercles around the rictus. *Eleutherodactylus colimotl* can be distinguished from *E. nietoi* sp. nov. by its smooth dorsal skin, as opposed to slightly pustulate, and the absence of bright flash colors. The simplest and most definitive way to distinguish *E. colimotl* from *E. manantlanensis* sp. nov. and *E. nietoi* sp. nov., as well as the superficially similar *E. erendirae* sp. nov., *E. jaliscoensis* sp. nov., and *E. teretistes* is by its mating call, which consists of a short single chirp, as opposed to the trills of varying lengths in these similar species.

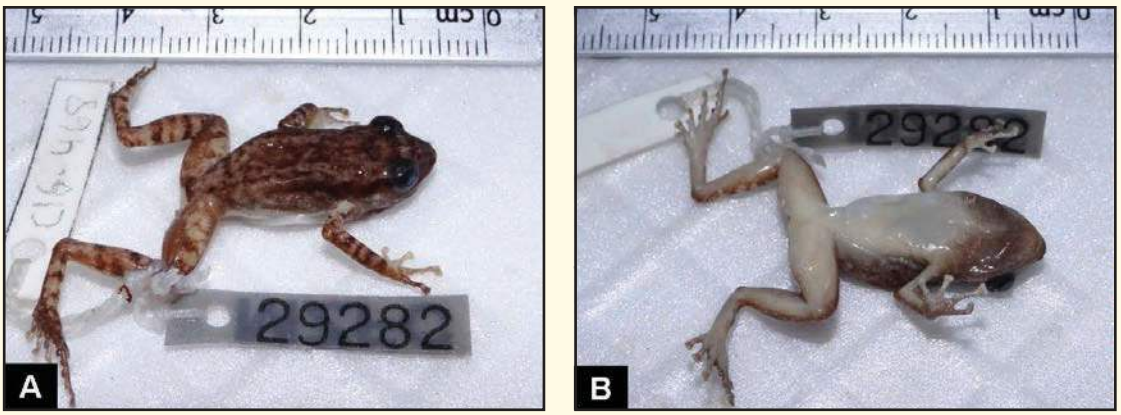


Fig. 2. Holotype of *Eleutherodactylus colimotl* sp. nov. in preservative, MZFC 29282 (CIG-00468). (A) Dorsal view; and (B) ventral view. © Christoph I. Grünwald

***Description of Holotype*:** A relatively small frog (24.5 mm SVL); male; head slightly longer (8.4 mm) than wide (7.3 mm), head slightly wider than body; snout subovoid from dorsal view and rounded from lateral view; tympanum indistinct, rounded with no supratympanic fold present; tympanum small, circular, greatest width of tympanum 0.7 mm; greatest diameter of eye 2.8 mm; tympanum width to eye diameter ratio 0.24; eyelid width 2.1 mm, approximately 40% of IOD; 1st finger shorter than 2nd finger; finger lengths from shortest to longest 1-2-4-3, with 1 and 2 subequal; digital pads on fingers 2, 3, and 4 widely expanded, 1.8 times the narrowest point of digit on 2nd finger and 2.5 times narrowest with moderate point of digit on fingers 3 and 4; expanded finger pads slightly rounded; 3 palmar tubercles; inner palmar tubercle about 66% as large as middle palmar tubercle, outer palmar tubercle about

40% size of middle palmar tubercle; toe lengths from shortest to longest 1-5-2-3-4, lengths of TL2 and TL5 similar to one another; outer metatarsal conical with round base, approximately 70% of inner metatarsal tubercle; inner metatarsal tubercle spherical with oval base, large, approximately 1.0 mm in length; IND 2.1 mm, IOD 4.8 mm, END 2.7 mm, ETD 0.8 mm, UpL 5.9 mm, FoL 6.6 mm, HaL 5.6 mm, F1L 1.8 mm, F1PW 0.9 mm, F1W 0.7 mm, F2L 2.0 mm, F2PW 0.9 mm, F2W 0.5 mm, F3L 3.5 mm, F3PW 1.3 mm, F3W 0.5 mm, F4L 2.7 mm, F4PW 1.4 mm, F4W 0.6 mm, IPTL 0.6 mm, MPTL 1.1 mm, OPTL 0.4 mm, FeL 10.8 mm, TL 10.7 mm, TaL 6.5 mm, FL 9.9 mm, T2L 3.3 mm, T2PW 0.9 mm, T2W 0.6 mm, T3L 5.2 mm, T3PW 1.0 mm, T3W 0.5 mm, T4L 7.0 mm, T4PW 1.0 mm, T4W 0.5 mm, T5L 3.0 mm, T5PW 0.6 mm, T5W 0.4 mm, IMTL 1.0 mm, OMTL 0.6 mm, FeL/SVL 44%, TL/SVL 48%, Ha/SVL 23%, TotFL/SVL 67%, HL/SVL 34%, and HW/SVL 30%; dorsal skin smooth, lateral skin slightly shagreened, ventral skin smooth to slightly areolate; skin smooth in life; vocal slits present; in life, dorsal coloration of holotype reddish-tan, with denser darker brown mottling along middorsal area; head cream with dark brown mottling, with distinct cream interorbital bar; flanks tan, with indistinct darker brown mottling and small white spots; hind legs reddish-tan, with irregular brown transverse bars; upper arms yellow with disperse brown mottling, and lower arms reddish-tan with dark brown reticulations, similar to those on back, flanks, and hind legs; lateral portions of head dark brown, with darker brown stripe extending from tip of snout through middle of eye and tympanum, terminating just behind rictus; dark brown stripe paler brown below, outlined in darker brown above, and bordered by pale cream stripe on snout; small white spots present on labial region; bright flash colors absent on groin and thighs; and ventral coloration white with pale gray on throat and upper chest (see Fig. 1 for photographs of holotype in life); dorsal coloration in preservative pale brown, with darker brown indistinct reticulations; interorbital bar pale gray; legs pale cream with darker brown transverse bands; groin and posterior surfaces of thighs brown; and venter white, with pale brown on throat (Fig. 2).

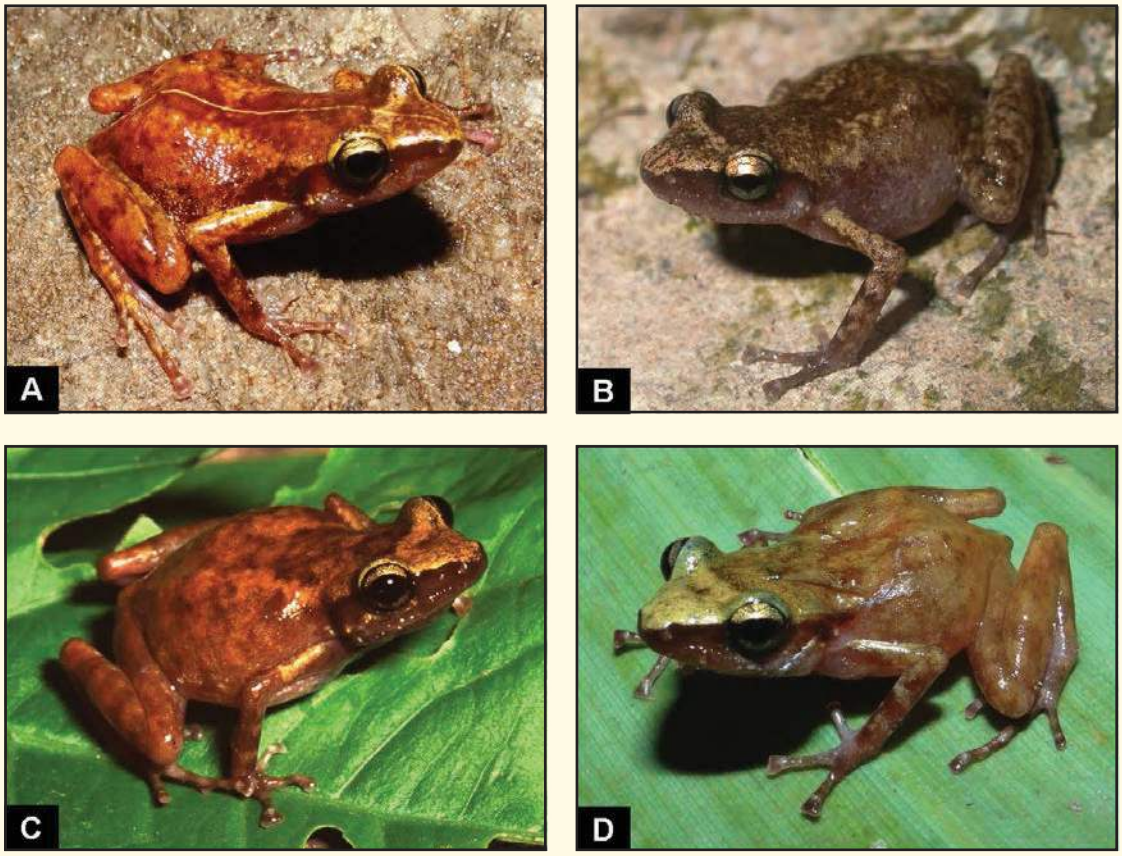


Fig. 3. Variation in *Eleutherodactylus colimotl* sp. nov. (A) Male from Grutas de San Gabriel, Municipio de Tecoman, Colima, MZFC 33329 (CIG-00960); (B) female from the vicinity of Ixtlahuacán, Municipio de Ixtlahuacán, Colima, MZFC 33120 (CIG-00467); (C) male from the vicinity of La Placita, Municipio de Aquila, Michoacán, JAC 24000; and (D) male from Aquila, Municipio de Aquila, Michoacán, MZFC 33036 (CIG-00340). © Christoph I. Grünwald (A, B, D) and Jonathan A. Campbell (C)

***Variation*:** The 10 paratypes show little variation in the morphological characters (Table 2). The SVL ranges from 22.9 mm to 28.4 mm; the expanded finger pads on both the 3rd and 4th fingers range from 2.3 to 3.1 times the narrowest part of the digit; the dorsal ground coloration ranges across different shades of tan, red, or brown; different amounts of dark-colored mottling are present on the dorsal surfaces; and the venter is white, but with varying amounts of gray on throat and chest. We show the morphological variation in Table 2.

Table 2. Morphological measurements of external morphological characters of *Eleutherodactylus colimotl* sp. nov. Type specimen in dark yellow. SVL = snout–vent length; HL = head length; HW = head width; TW = tympanum width; EW = eye width; ElW = eyelid width; IOD = interorbital distance; IND = internarial distance; END = eye–naris distance; ETD = eye–tympanum distance; UpL = upper arm length; FoL = forearm length; HaL = hand length; F3PW/F3W = 3rd finger pad width (widest measurement) to 3rd finger width (narrowest measurement) ratio; F4PW/F4W = 4th finger pad width (widest measurement) to 4th finger width (narrowest measurement) ratio; FeL = femur length; TL = tibia length; TotFL = total foot length (tarsal tubercle to tip of 4th toe); IPT = inner palmar tubercle length; MPT = middle palmar tubercle length; OPT = outer palmar tubercle length; IMTL = inner metatarsal tubercle length; and OMTL = outer metatarsal tubercle length.

Measurements	MZFC 33036	MZFC 33115	MZFC-33116	MZFC 33117	MZFC 33118	MZFC 33119	MZFC 33120	MZFC 29282	MZFC 33299	MZFC 33329	MZFC 33330
SVL	25.61	24.62	23.38	24.83	22.92	23.91	26.49	24.46	25.07	25.3	24.93
HL	9.03	8.63	8.53	8.18	7.94	8.05	8.66	8.25	8.79	7.9	7.74
HW	8.35	7.11	7.93	7.38	7.03	7.29	7.63	7.19	7.26	7.2	7.11
TW	0.69	0.58	0.75	0.54	0.59	0.64	0.6	0.67	0.76	0.95	0.9
EW	2.82	2.43	2.56	2.42	2.35	2.23	2.97	2.81	3.09	3.1	3.41
ElW	2	1.74	1.94	1.8	1.72	1.78	1.86	2.15	1.9	1.64	1.74
IOD	5.28	4.49	5.5	4.97	4.78	4.76	4.97	4.84	4.74	4.83	4.87
IND	2.25	2.14	2.51	2.16	2.2	2.27	2.41	2.07	2.48	2.35	2.25
END	2.8	2.47	2.74	2.5	2.5	2.78	2.6	2.69	2.8	2.73	2.66
ETD	0.71	0.78	0.89	0.71	0.75	0.93	0.91	0.79	0.84	0.9	0.87
UpL	5.27	4.43	6.15	5.7	5.6	4.8	5.97	5.16	5.23	5.78	5.79
FoL	6.98	6.46	8.71	7.23	6.13	5.64	6.64	6.21	6.43	6.79	6.77
HaL	5.86	5.53	5.26	5.6	5.15	5.38	6	5.6	5.78	5.5	5.41
F3PW/F3W	2.25	2.06	2.76	2.51	2.31	2.44	2.33	2.57	2.71	2.73	2.98
F4PW/F4W	2.7	2.29	3.07	2.64	2.19	2.6	2.82	2.48	2.91	2.61	3.0
FeL	10.59	10.27	11.78	11.9	11.33	10.98	11.67	10.75	10.27	10.85	10.4
TL	11.82	10.9	11.87	11.71	10.73	10.49	11.36	11.74	11.13	11.68	11.09
TotFL	16.64	16	15.21	16.1	15	15.54	17.2	16.4	16.25	17.42	15.22
IPT	0.56	0.56	0.44	0.62	0.45	0.54	1.16	0.55	0.54	0.61	0.63
MPT	0.84	0.74	0.89	0.95	0.95	0.99	0.65	0.83	0.93	0.97	0.92
OPT	0.34	0.32	0.36	0.38	0.38	0.4	0.3	0.4	0.33	0.41	0.37
IMTL	0.97	0.88	1.2	0.96	0.63	0.89	1.09	1.04	0.82	0.92	0.91
OMTL	0.49	0.4	0.66	0.44	0.44	0.48	0.65	0.62	0.48	0.61	0.55

***Distribution and Ecology*:** *Eleutherodactylus colimotl* is known from two different areas, the type locality and its immediate vicinity in the state of Colima, and from Municipio de Aquila in western Michoacán. In both areas this species is known to inhabit elevations from 100 to 400 m; both are karstic foothills in tropical deciduous forest. This species perhaps is more widespread throughout the limestone hills of eastern Colima and coastal Michoacán (see Fig. 8A) than presently understood. In both areas it also occurs in sympatry with *E. orarius*. Generally, *E. colimotl* seems to prefer steep rocky hillsides, rock cuts, and canyons, whereas *E. orarius* appears to be more of a habitat generalist and is more common in flatter, open environs or disturbed habitat. In Michoacán, specimens of both species were collected within 20 m of one another on the same hillside. All specimens of this species have been collected in June and July, while calling from rocks, low-growing vegetation, and high up on tree trunks. One was collected from a tree trunk 3 m above the ground on a steep slope.

***Etymology*:** Named after Hueytlatoani Colímotl, the last ruler of the Kingdom of Colliman, who was nicknamed Rey Coliman by Hernán Cortés. The Kingdom of Colliman was located around the population centers of Colima and Tecomán, and the type locality of this frog lies between these two cities.

***Referred Specimens*:** We examined detailed photographs of two specimens of *Syrrhophus* from the Municipio de Aquila, Michoacán (JAC 24000–01), housed at the Amphibian and Reptile Diversity Research Center, University of Texas at Arlington, which clearly are referable to *E. colimotl*.

Eleutherodactylus erendirae sp. nov.

Figs. 4, 5, 6, 7B, 45C

***Holotype*:** (Figs. 4, 5). MZFC 29274 (CIG-00319). Adult male, collected by Christoph I. Grünwald, Hector Franz-Chávez, and Nadia Pérez-Rivera on 4 June 2015 at Aparícuaro, Municipio de Tancítaro (19.33798°, -102.26986°; datum WGS 84; elev. 2,045 masl), Michoacán, Mexico (Fig. 8C).

***Paratypes*:** (Fig. 6). Sixteen specimens. MZFC 33019–33024 (CIG-00320–325), six adult males collected at the same locality and on the same date as the holotype; MZFC 33000–33009 (CIG-00300–309), 10 adult males, collected by Christoph I. Grünwald, Hector Franz-Chávez, and Nadia Pérez-Rivera on 2 June 2015 at El Montoso (27 air km SSE of Mazamitla), Municipio de Quitupan (19.684258°, -102.927096°; datum WGS 84; elev. 2,005 masl), Jalisco, Mexico.

***Diagnosis*:** A member of the genus *Eleutherodactylus*, subgenus *Syrrhophus*, as defined by Hedges et al. (2008). In the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Series and the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group, as defined in this paper (see discussion below). A small frog, adult males measure 17.5–22.9 mm SVL; vocal slits present in males; digital tips expanded, but only 1.1–1.5 times width of narrowest part of finger on 3rd and 4th fingers; finger lengths moderate, 14–20% of SVL (See Fig. 7B); compact lumbar gland in inguinal region absent; epidermis not translucent and abdominal vein not visible on venter of live specimens; limbs short, TL/SVL ratio 0.31–0.46, FeL/SVL ratio 0.36–0.44, and TotFL/SVL ratio 0.61–0.88; snout short, END/SVL ratio 0.09–0.11; tympanum small, indistinct, and round; TW/EW ratio 0.26–0.31; dorsal skin slightly to moderately pustulate, although at least one specimen from type locality with relatively smooth skin, and skin becomes smoother after preservation; dorsal coloration variable, and can be gray, brown, red, or tan; pale-colored interorbital bar present, dark-colored transverse bands present on legs and arms, and venter pale-colored with variable amount of melanophores that can form spots or indistinct reticulations; mating call of adult males a short trill, best described as a "reep," unlike the chirp ("peep") or the drawn out multinote trill of other species of subgenus *Syrrhophus* (see below, Fig. 27).

***Comparisons*:** *Eleutherodactylus erendirae* can be distinguished from all species in the *Eleutherodactylus* (*Syrrhophus*) *longipes* Species Series (as defined herein, see below) by the presence of a small and indistinct tympanum with no tympanic annulus visible and with a diameter less than 31% of the eye diameter; by a non-translucent abdominal epidermis, and thus a visible abdominal vein on the venter is not evident in life; and by the presence of a 3rd (outer) palmar that is smaller than 50% of the middle palmar tubercle.

Eleutherodactylus erendirae can be distinguished from most species in the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Group by a combination of the expanded finger pads on the 3rd and 4th fingers and also lacking a compact, protruding lumbar gland in the inguinal region. It can be distinguished from the remaining two species, *E. pipilans* and *E. rubrimaculatus*, by its pustulate skin and a pale-colored interorbital bar.

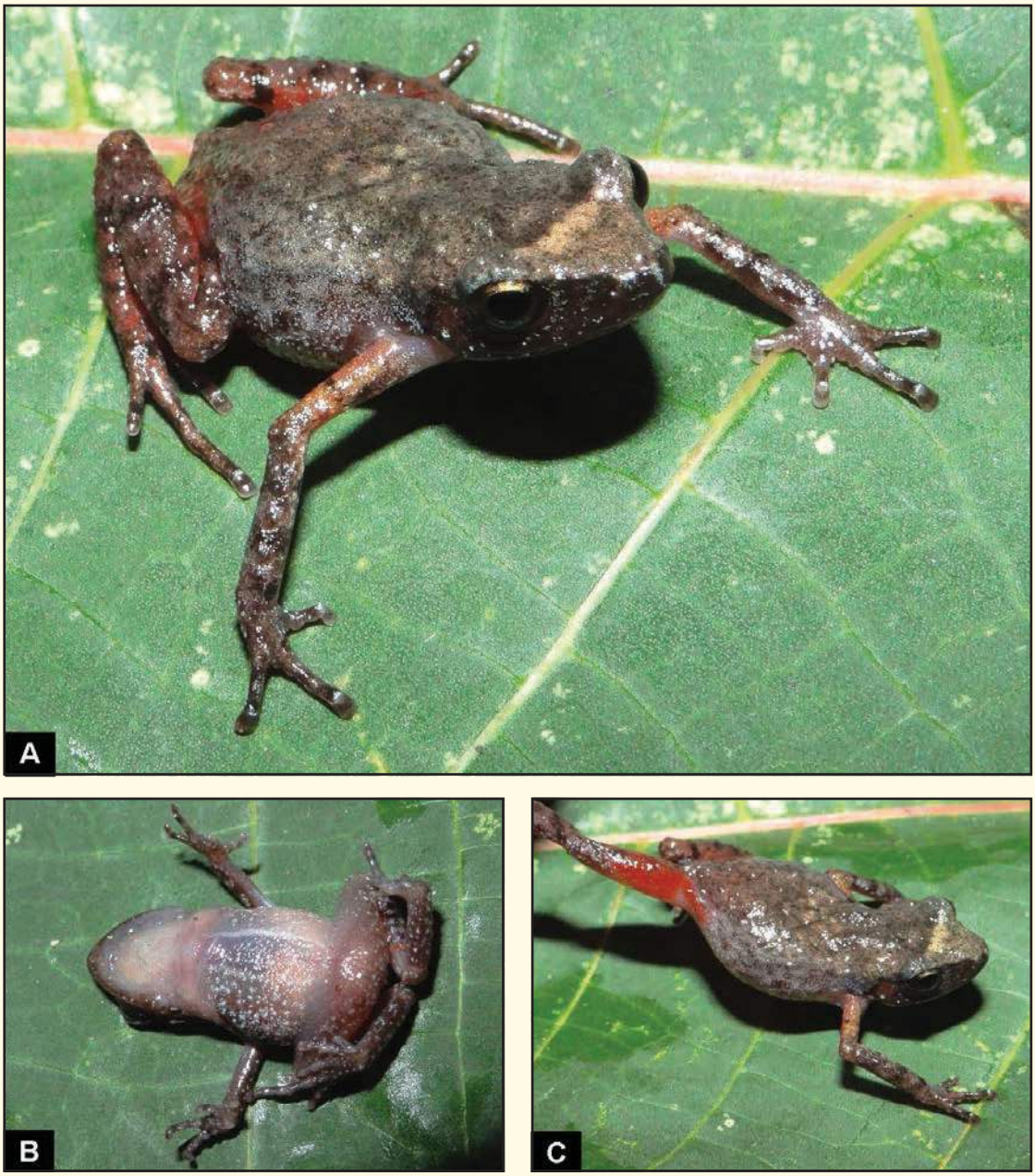


Fig. 4. Holotype of *Eleutherodactylus erendirae* sp. nov. in life, MZFC 29274 (CIG-00319). (A) Full body view; (B) ventral view; and (C) lateral view.

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Within its own species group, *E. erendirae* can be distinguished from *E. angustidigitorum*, *E. grandis*, and *E. saxatilis* by the lack of compact lumbar glands above the inguinal region and its small size. *Eleutherodactylus erendirae* can be distinguished from *E. grunwaldi*, *E. modestus*, *E. pallidus*, *E. saxatilis*, *E. teretistes*, and *E. wixarika* by the flash colors on the anterior and posterior parts of the thigh, as well as in the inguinal region, and by the pale-colored interobital bar. *Eleutherodactylus interorbitalis* lacks flash colors and the color of its interobital bar is darker than the ground coloration. *Eleutherodactylus erendirae* can be distinguished from *E. colimotl*, *E. grunwaldi*, *E. jaliscoensis* sp. nov., *E. manantlanensis* sp. nov., *E. nietoi* sp. nov., and *E. rufescens* (as defined herein), by its

expanded finger pads on the 3rd and 4th fingers, which are wider than the narrowest part of the digit but less than 1.5 times as wide as its narrowest part. The species that *E. erendirae* can be confused with most readily are *E. floresvillelai* sp. nov. and *E. rufescens*, both which occur sympatrically or nearby in the states of Michoacán and Jalisco. *Eleutherodactylus erendirae* can be distinguished from *E. rufescens* by its pustulate dorsal skin, the presence of finger pads on the 3rd and 4th fingers that are 1.1–1.5 times the width of the narrowest part of the digit, and a variable dorsal pattern; also a pale-colored middorsal stripe is absent. In *E. rufescen*s the dorsal skin is smooth, the finger pads on the 3rd and 4th fingers are 1.5–2.2 times the width of the narrowest part of the digit, and the dorsal pattern is variable, and individuals with a pale-colored but conspicuous middorsal stripe are recorded from all known populations. In the Sierra del Tigre, Jalisco, where *E. erendirae* and *E. rufescens* occur in sympatry, *E. erendirae* tends to be smaller than *E. rufescens*. This difference, however, is not a diagnostic trait. *Eleutherodactylus erendirae* can be distinguished from the superficially similar *E. floresvillelai* sp. nov. by the lack of flash colors on the groin and thighs of the latter species, as well as a smaller and less distinctive tympanum, and less pustular skin. Furthermore, *E. erendirae* can be distinguished from both *E. rufescens* and *E. floresvillelai* by its distinct mating call; *E. erendirae* produces a strong trill that sounds like a "reep," whereas both *E. rufescens* (see below, Fig. 34) and *E. floresvillelai* produce a short, high-pitched chirp that sounds like a peep (see below, Fig. 28A).

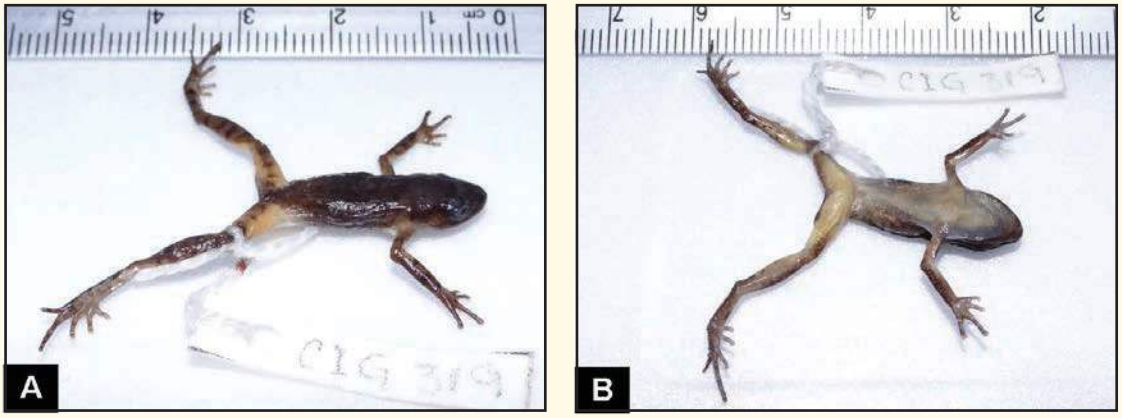


Fig. 5. Holotype of *Eleutherodactylus erendirae* sp. nov. in preservative, MZFC 29274 (CIG-00319).(A) Dorsal view; and (B) ventral view. © Christoph I. Grünwald

***Description of Holotype*:** A small frog (21.1 mm SVL); male; head slightly longer (6.8 mm) than wide (6.2 mm), head slightly wider than body; snout subovoid from dorsal view and rounded from lateral view; tympanum indistinct, rounded with no supratympanic fold present; tympanum small, circular, greatest width of tympanum 0.6 mm; greatest diameter of eye 2.2 mm; ratio of tympanum width to eye diameter ratio 0.27; eyelid width 1.5 mm, approximately one-third of IOD; 1st finger shorter than 2nd finger; finger lengths from shortest to longest 1-2-4-3, with 1 and 2 subequal; digital pads on fingers 2, 3, and 4 slightly expanded, 1.2 times the narrowest point of digit on 2nd finger and 1.4 times narrowest point of digit on fingers 3 and 4; expanded finger pads slightly rounded; 3 palmar tubercles; inner palmar tubercle about 70% as large as middle palmar tubercle; outer palmar tubercle about one-half size of middle palmar tubercle; toe lengths from shortest to longest 1-2-5-3-4; outer metatarsal conical with round base, small, approximately 50% size of inner metatarsal tubercle; inner metatarsal tubercle of spherical shape with oval base, large, approximately 0.7 mm in length; IND 2.1 mm, IOD 4.0 mm, END 2.0 mm, ETD 0.8 mm, UpL 4.9 mm, FoL 5.6 mm, HaL 4.6 mm, F1L 1.8 mm, F1PW 0.5 mm, F1W 0.4 mm, F2L 2.4 mm, F2PW 0.5 mm, F2W 0.4 mm, F3L 4.0 mm, F3PW 0.6 mm, F3W 0.5 mm, F4L 2.7 mm, F4PW 0.6 mm, F4W 0.4 mm, IPTL 0.5 mm, MPTL 0.8 mm, OPTL 0.4 mm, FeL 8.0 mm, TL 8.7 mm, TaL 5.0, FL 7.9 mm, T2L 3.2 mm, T2PW 0.5 mm, T2W 0.4 mm, T3L 4.5 mm, T3PW 0.5 mm, T3W 0.4 mm, T4L 7.2 mm, T4PW 0.5 mm, T4W 0.4 mm, T5L 3.6 mm, T5PW 0.4 mm,

T5W 0.4 mm, IMTL 0.8 m, OMTL 0.4 mm, FeL/SVL 38%, TL/SVL 41%, Ha/SVL 22%, TotFL/SVL 61%, HL/SVL 32%, and HW/SVL 29%; dorsal skin smooth to slightly pustulate, lateral skin slightly shagreened, and ventral skin smooth to slightly areolate; skin pustular in life; vocal slits present; in life, dorsal coloration of holotype pale brown, with darker brown and olive mottling; lateral portions of head covered with dark brown, with small white specks on labial and loreal regions, and interobital bar pale cream; legs and arms ochre with dark brown transverse bars; upper arms pale orange and lack banding, and vivid orange flash colors present on groin and posterior surfaces of thighs; ventral coloration pale gray with white spots and black melanophores that form dark-colored reticulations along lateral portions (see Fig. 4 for photographs of holotype in life); dorsal coloration in preservative dark brown, with paler brown areas along lower portion of back; cream interorbilar bar indistinct; legs pale brown with darker brown transverse bands; groin and posterior surfaces of thighs pale yellow; and ventral surfaces pale cream with small melanophores, which form indistinct reticulations on outer surfaces of venter (see Fig. 5)

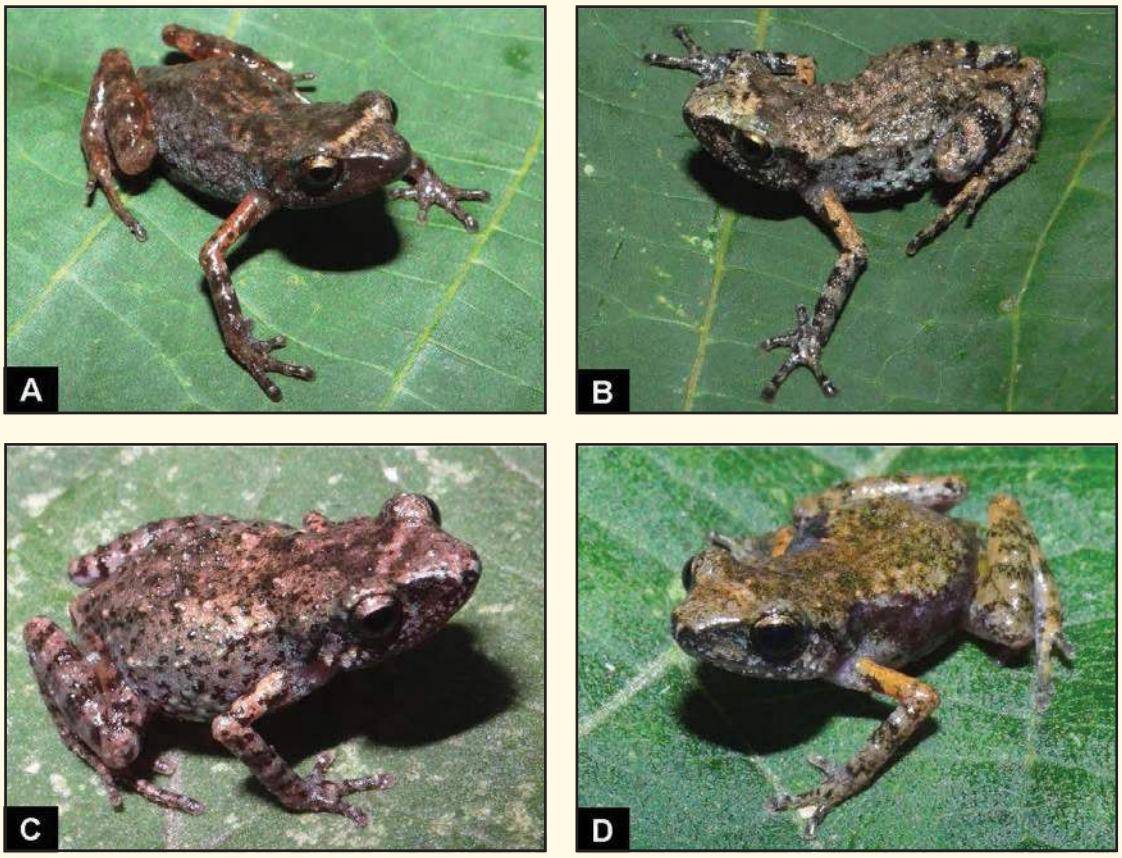


Fig. 6. Variation in *Eleutherodactylus erendirae* sp. nov. (A) Male from Aparicuaro, Municipio de Tancítaro, Michoacán, MZFC 33020 (CIG-00321); (B) male from Aparicuaro, Municipio de Tancítaro, Michoacán, MZFC 33022 (CIG-00323); (C) male from the vicinity of El Montoso, Municipio de Quitupan, Jalisco, MZFC 33009 (CIG-00309); and (D) male from the vicinity of El Montoso, Municipio de Quitupan, Jalisco, MZFC 33007 (CIG-00307). © Christoph I. Grünwald

***Variation*:** The 16 paratypes show little variation in the morphological characters (Table 3). The SVL ranges from 17.5 to 21.2 mm; the expanded finger pads on the 3rd and 4th fingers range from 1.1 to 1.5 times the narrowest part of the digit; the dorsal skin texture ranges from almost smooth (one specimen) to conspicuously pustulate; the dorsal ground coloration ranges across different shades of gray, brown, and olive-green; the flash colors on the groin, thighs, and upper arms range from yellow through orange to red; the venter typically is gray, with white and black markings, although the markings range from sparse to an almost complete reticulation. We present the morphological variation in Table 3.

Table 3. Morphological measurements of external morphological characters of *Eleutherodactylus erendirae* sp. nov. Type specimen in dark yellow. SVL = snout–vent length; HL = head length; HW = head width; TW = tympanum width; EW = eye width; ElW = eyelid width; IOD = interorbital distance; IND = internarial distance; END = eye–naris distance; ETD = eye–tympanum distance; UpL = upper arm length; FoL = forearm length; HaL = hand length; F3PW/F3W = 3rd finger pad width (widest measurement) to 3rd finger width (narrowest measurement) ratio; F4PW/F4W = 4th finger pad width (widest measurement) to 4th finger width (narrowest measurement) ratio; FeL = femur length; TL = tibia length; TotFL = total foot length (tarsal tubercle to tip of 4th toe); IPT = inner palmar tubercle length; MPT = middle palmar tubercle length; OPT = outer palmar tubercle length; IMTL = inner metatarsal tubercle length; and OMTL = outer metatarsal tubercle length.

Measure-ments	MZFC 33001	MZFC 33002	MZFC 33003	MZFC 33004	MZFC 33005	MZFC 33006	MZFC 33007	MZFC 33008	MZFC 33009	MZFC 29274	MZFC 33019	MZFC 33020	MZFC 33021	MZFC 33022	MZFC 33023	MZFC 33024
SVL	19.55	18.64	17.51	19.13	17.96	17.40	18.95	18.24	17.96	21.14	19.73	20.29	19.88	19.18	19.76	21.20
HL	6.03	6.24	5.85	6.10	6.20	5.82	6.11	6.09	5.98	6.95	6.90	6.82	6.80	6.72	6.87	7.32
HW	5.58	5.82	5.15	5.57	5.92	5.21	5.58	5.42	5.61	6.20	6.11	5.98	5.82	6.66	5.98	6.21
TW	0.57	0.58	0.56	0.62	0.55	0.59	0.61	0.59	0.59	0.60	0.60	0.61	0.59	0.77	0.59	0.62
EW	1.98	2.08	1.78	1.98	2.26	1.92	2.10	2.04	2.12	2.23	2.13	2.25	2.22	1.88	2.24	2.39
ElW	1.34	1.40	1.24	1.34	1.42	1.25	1.34	1.30	1.35	1.49	1.47	1.44	1.40	1.60	1.44	1.49
IOD	3.61	3.77	3.47	3.83	3.15	3.70	3.82	3.61	3.61	4.03	4.01	4.00	3.92	4.38	4.17	4.37
IND	1.77	1.91	1.73	1.78	1.82	1.83	1.82	1.87	1.83	2.11	2.07	2.06	2.02	1.86	2.08	2.09
END	1.81	1.82	1.71	1.81	1.90	1.85	1.85	1.79	1.81	2.02	2.03	1.98	1.95	1.41	1.93	2.00
ETD	0.68	0.64	0.63	0.68	0.30	0.67	0.68	0.68	0.67	0.80	0.77	0.77	0.77	0.78	0.75	0.80
UpL	4.42	4.44	4.40	4.58	2.81	4.11	4.66	4.11	4.14	4.94	4.85	5.00	4.80	3.62	4.65	4.80
FoL	5.01	4.93	4.81	4.90	4.61	4.83	5.00	4.96	4.97	5.57	5.58	5.60	5.73	5.15	5.65	5.77
HaL	4.30	4.10	3.85	4.21	3.95	3.83	4.17	4.01	3.95	4.60	4.34	4.46	4.37	4.22	4.35	4.66
F3PW/F3W	1.46	1.36	1.17	1.32	1.50	1.50	1.26	1.32	1.56	1.40	1.44	1.29	1.57	1.12	1.52	1.50
F4PW/F4W	1.56	1.41	1.25	1.33	1.33	1.77	1.28	1.50	1.54	1.45	1.44	1.33	1.58	1.02	1.50	1.53
FeL	7.36	6.67	6.65	7.13	5.84	6.83	6.91	6.81	6.73	8.53	8.38	7.96	8.40	7.40	7.84	9.23
TL	7.26	7.30	7.19	7.29	5.61	7.16	7.34	7.20	7.56	8.73	8.59	8.12	8.80	8.21	8.89	9.54
TotFL	15.10	12.70	11.00	11.60	12.00	12.10	11.20	13.40	14.30	12.90	16.60	16.10	17.50	15.20	14.80	16.80
IPT	0.47	0.41	0.38	0.45	0.37	0.42	0.45	0.48	0.48	0.50	0.52	0.48	0.48	0.24	0.45	0.56
MPT	0.69	0.60	0.53	0.58	0.50	0.52	0.53	0.63	0.56	0.70	0.72	0.74	0.68	0.76	0.65	0.77
OPT	0.30	0.30	0.23	0.20	0.25	0.23	0.22	0.30	0.25	0.35	0.35	0.34	0.30	0.34	0.32	0.35
IMTL	0.63	0.61	0.58	0.68	0.54	0.65	0.67	0.65	0.62	0.75	0.78	0.71	0.74	0.77	0.76	0.80
OMTL	0.43	0.40	0.37	0.44	0.29	0.37	0.40	0.37	0.36	0.42	0.40	0.48	0.45	0.28	0.32	0.39

***Distribution and Ecology*:** *Eleutherodactylus erendirae* is known from two different localities, the type locality in west-central Michoacán, and the Sierra del Tigre in east-central Jalisco; both localities are in the Trans-Volcanic Belt (Eje Neovolcánico) of central Mexico (see Fig. 8A). This species is known to inhabit elevations from 1,800 to 2,300 m, and both localities are steep mountainsides in humid pine-oak forest and humid oak woodland. At the type locality, this species is sympatric with *E. nitidus*. Here, *E. erendirae* apparently occupies wooded areas with abundant undergrowth, whereas *E. nitidus* typically is encountered in open areas, including cleared forest and agricultural fields. At the second locality in Jalisco, *E. erendirae* is sympatric with both *E. nitidus* and *E. rufescens*. Whereas *E. nitidus* appears to be more tolerant of open areas and mesquite savanna, *E. erendirae* and *E. rufescens* inhabit the same cleared woodland habitat. *Eleutherodactylus rufescens* also occurs at higher elevations in pine forest, however, where we have not observed *E. erendirae*. *Eleutherodactylus angustidigitorum* occurs nearby, and also might occur sympatrically. All of the specimens of *E. erendirae* were observed after the onset of the rainy season during the months of June, July, and August; typically, mating activity ceases in August. Most of the *E. erendirae* we encountered are adult males, which we collected at night while they were calling from grass, bushes, and small trees.

***Etymology*:** This species is named after Princess Eréndira, a legendary warrior princess of the P'urhépecha (*Tarasco* in Spanish) people of west-central Mexico. As legend has it, Eréndira led a defensive war against the Spanish after their conquest of the Aztecs and subsequently push west. From a base on a mountaintop, she is said to have killed a Spanish horseman and stolen his horse, teaching herself to ride and using it to train her people to ride into battle. Her fate remains a mystery, but her legend lives on. *Eleutherodactylus erendirae* appears to be endemic to the heartland of the P'urhépecha people, and thus we name it after their legendary princess.

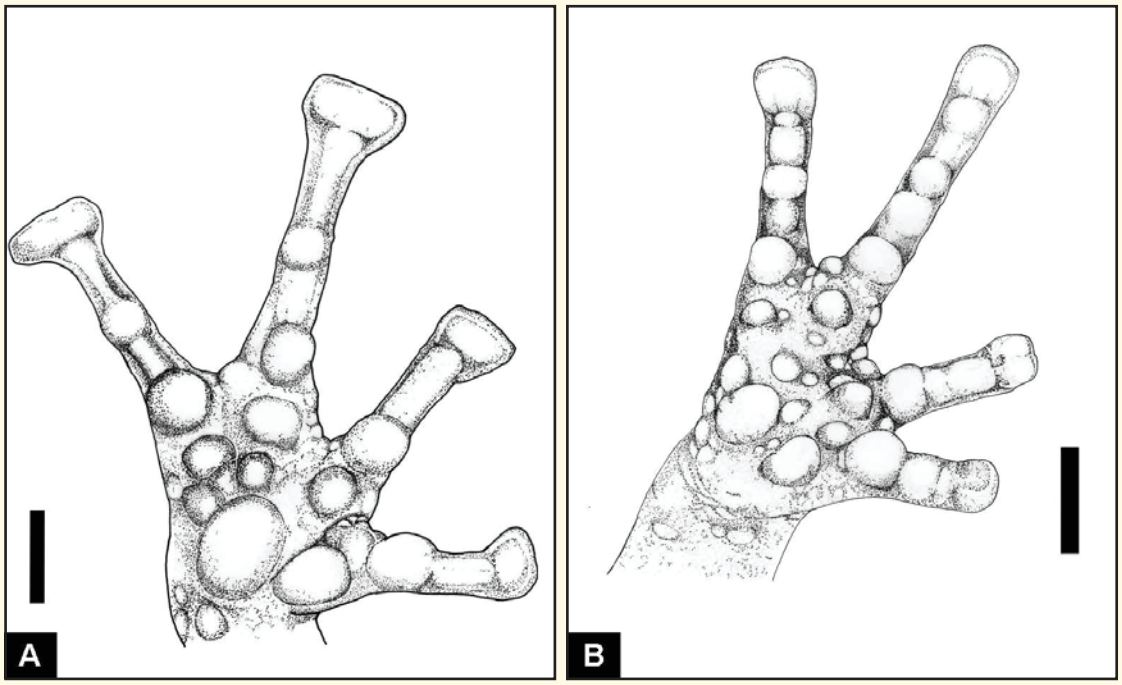


Fig. 7. Hand drawings of *Eleutherodactylus*. (A) *Eleutherodactylus colimotl* sp. nov.; and (B) *Eleutherodactylus erendirae* sp. nov. Vertical bars = 1 mm. Drawings by Iván T. Ahumada-Carrillo.

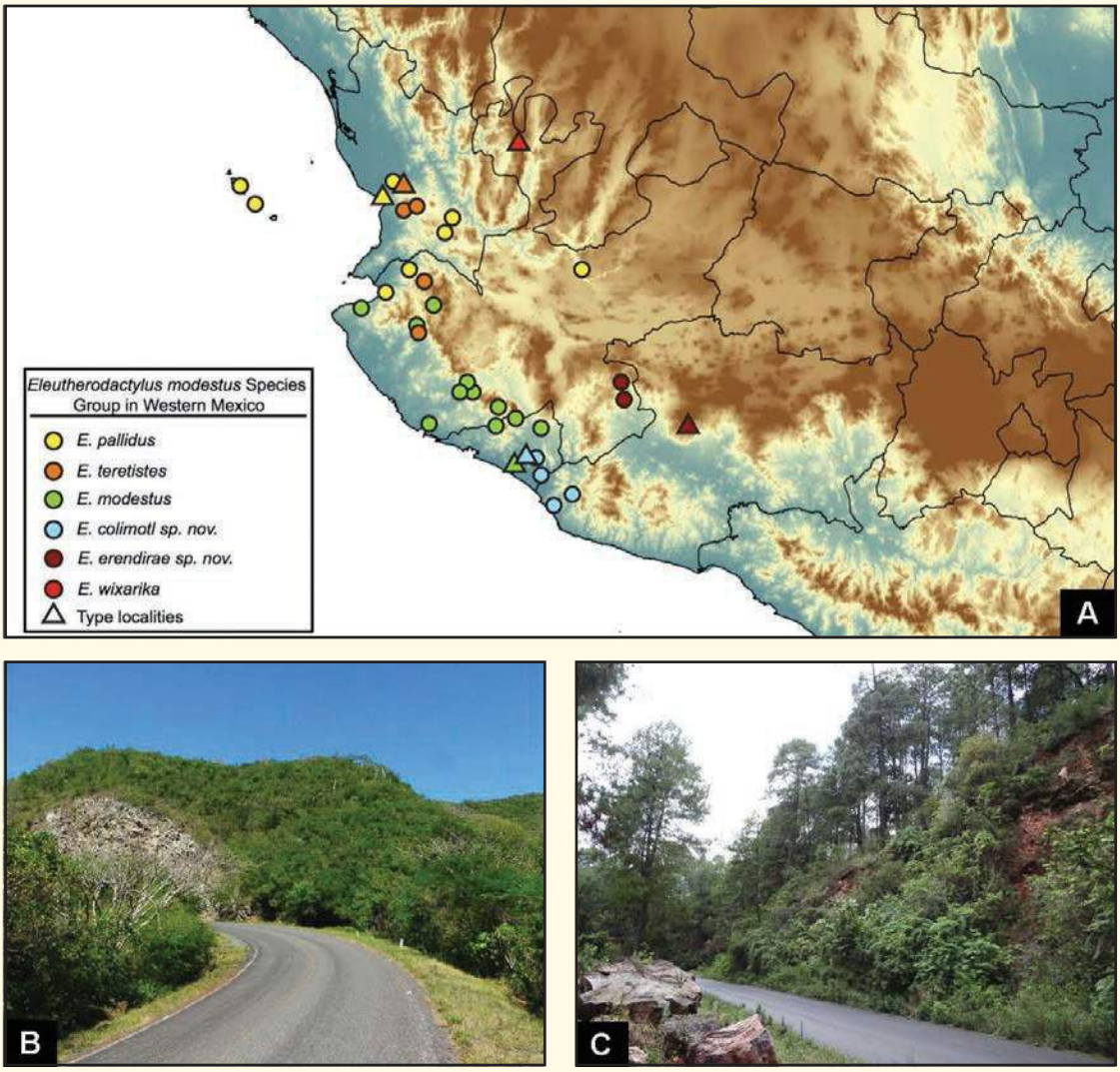


Fig. 8. (A) Map showing the distribution of some members of the *Eleutherodactylus modestus* Species Group from western Mexico, including *Eleutherodactylus colimotl* sp. nov. and *Eleutherodactylus erendirae* sp. nov. (B) photo of the type locality of *Eleutherodactylus colimotl* sp. nov., near La Salada, Municipio de Tecomán, Colima; and (C) photo of the type locality of *Eleutherodactylus erendirae* sp. nov., near Aparícuaro, Municipio de Tancítaro, Michoacán. Map by Jacobo Reyes-Velasco. © Christoph I. Grünwald

Eleutherodactylus floresvillelai sp. nov.

Figs. 9, 10, 11, 15A, 45D

***Holotype*:** (Figs. 9, 10). MZFC 33060 (CIG-00368). Adult male, collected by Christoph I. Grünwald, Hector Franz-Chávez, and Nadia Pérez-Rivera on 12 June 2015 at the junction of Mexico Hwy. 15 and the Tzitzio Rd. (Highway 49), approximately 25 km E of the outskirts of Morelia, Municipio de Charo (19.650774°, -100.943879°; datum WGS 84; elev. 2,225 masl), Michoacán, Mexico (Fig. 16B).

***Paratypes*:** (Fig. 11). Eleven specimens. MZFC 33053–33059 and MZFC 33061–33064 (CIG-00361–367 and CIG-00369–372), adult males collected at the same locality and on the same date as the holotype.

***Diagnosis*:** A member of the genus *Eleutherodacytlus*, subgenus *Syrrhophus*, as defined by Hedges et al. (2008). In the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Series and the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group, as defined in this paper. A small frog, adult males measure 16.1–21.4 mm SVL; vocal slits present

in males; digital tips slightly expanded, 1.4–1.9 times width of the narrowest part of finger on 3rd finger, and 1.5–1.9 times width of narrowest part of finger on 4th finger, although usually more than 1.6 times narrowest part of finger on both 3rd and 4th fingers; fingers relatively short, with 3rd finger length ranging from 17–19% of SVL (see Fig. 15A); compact lumbar gland above inguinal region absent; epidermis not translucent, and abdominal vein not visible on venter of live specimens; limbs short, TL/SVL ratio 0.44–0.50, FeL/SVL ratio 0.40–0.49, and TotFL/SVL ratio 0.7–0.8; snout short, END/SVL ratio 0.10–0.11; tympanum small, indistinct, and round; TW/EW ratio 0.26–0.30; dorsal skin pustulate, and color of pustules yellow or pale orange; dorsal coloration brown, with dark brown or gray inverted "V" saddle blotch on shoulders; pale-colored middorsal stripe present or not; pale-colored interorbital bar present; upper arms pale and unmarked, same color or paler than interorbital bar; dark brown transvers bars present on forearms, thighs, and legs; ventral coloration gray with white reticulations; no bright flash colors present in inguinal region or thighs and legs; and mating call of adult males a single chirp (see below; Fig. 28A).



Fig. 9. Holotype of *Eleutherodactylus floresvillelai* sp. nov. in life, MZFC 33060 (CIG-00368). (A) Full body view; ventral view; and (C) lateral view. © Christoph I. Grünwald

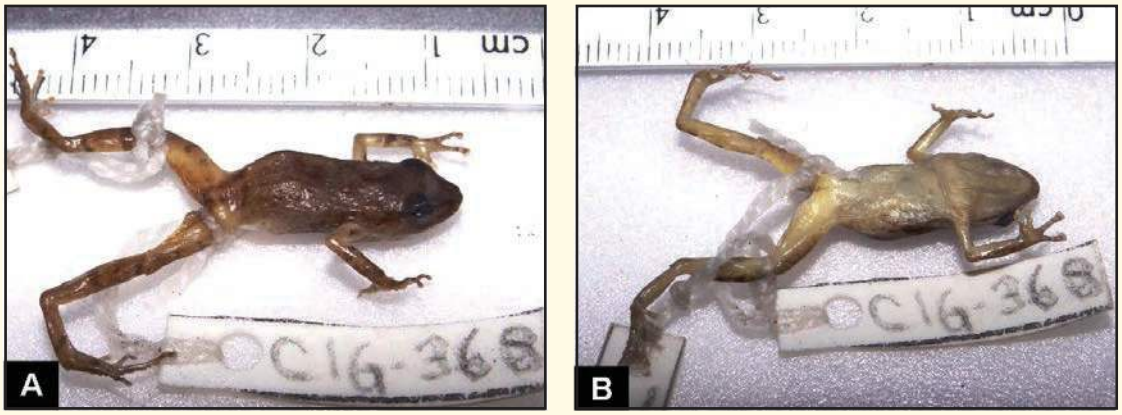


Fig. 10. Holotype of *Eleutherodactylus floresvillelai* sp. nov. in preservative, MZFC 33060 (CIG-00368). (A) Dorsal view; and (B) ventral view. © Christoph I. Grünwald

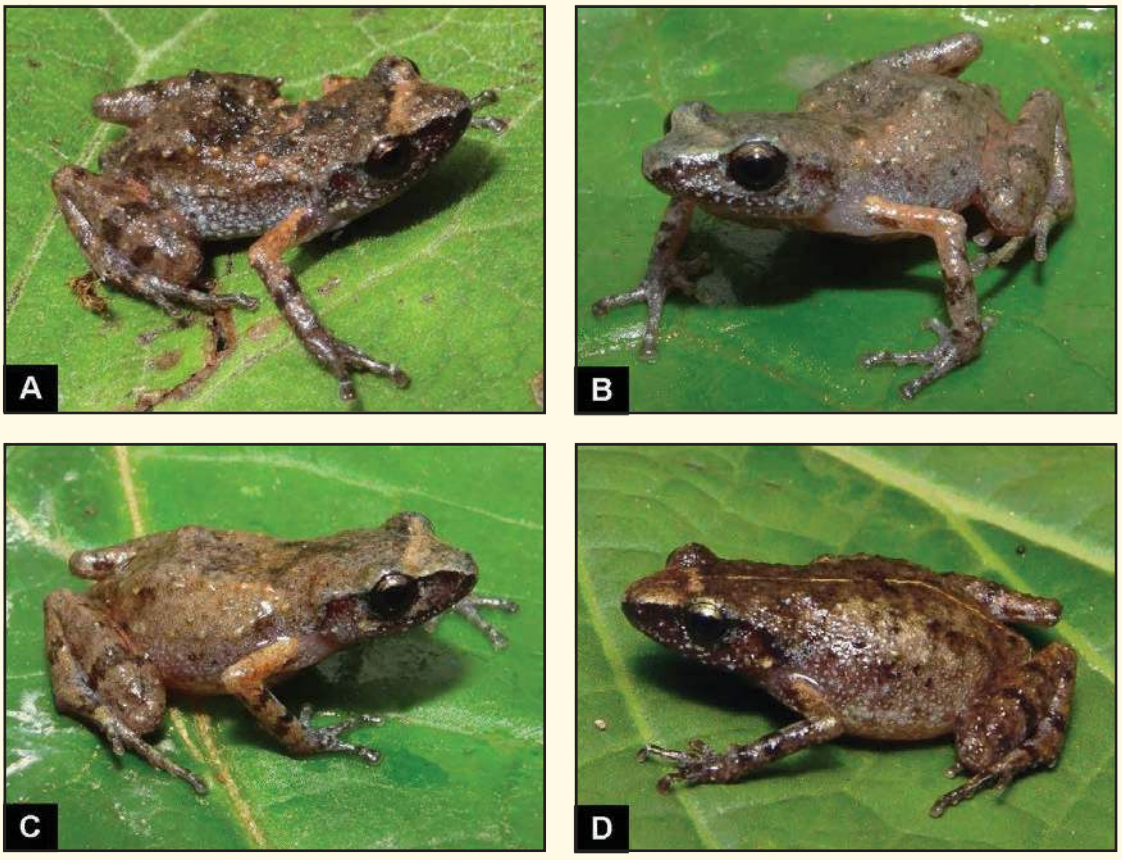


Fig. 11. Variation in *Eleutherodactylus floresvilleli* sp. nov. (A) Male from 25 km E of Morelia, Municipio de Charo, Michoacán, MZFC 33058 (CIG-00366); (B) male from 25 km E of Morelia, Municipio de Charo, Michoacán, MZFC 33053 (CIG-00361); (C) male from 25 km E of Morelia, Municipio de Charo, Michoacán, MZFC 33061 (CIG-00369); and (D) male from Los Cantiles, Municipio de Charo, Michoacán (no museum number). © Christoph I. Grünwald

***Comparisons*:** *Eleutherodactylus floresvillelai* can be distinguished from all species in the *Eleutherodactylus* (*Syrrophus*) *longipes* Species Series (as defined herein, see below) by the presence of a small and indistinct tympanum with no visible tympanic annulus and with a diameter less than 30% of the diameter of the eye; by a non-translucent abdominal epidermis, and thus a visible abdominal vein on the venter is not evident in life; and by the presence of a 3rd (outer) palmar that is smaller than 50% of the middle palmar tubercle.

Eleutherodactylus floresvillelai can be distinguished from most species in the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Group by a combination of the expanded finger pads on the 3rd and 4th fingers, and by lacking a compact, protruding lumbar gland in the inguinal region. It can be distinguished from the remaining two species, *E. pipilans* and *E. rubrimaculatus*, by its pustulate skin and pale-colored interorbital bar.

Within its own species group, *E. floresvillelai* can be distinguished from *E. angustidigitorum*, *E. grandis*, and *E. saxatilis* by the lack of compact lumbar glands above the inguinal region and its small size. *Eleutherodactylus floresvillelai* can be distinguished from *E. grunwaldi*, *E. modestus*, *E. pallidus*, *E. saxatilis*, *E. teretistes*, and *E. wixarika* by the presence of a pale-colored interobital bar, and from both *E. manantlanensi*s sp. nov. and *E. colimotl* by its lesser expanded finger pads (less than twice the width of the narrowest part of the digit, as opposed to more than twice in the other species), and further from *E. manantlanensis* sp. nov. by the presence of an indistinct but visible tympanum. Additionally, it also differs from *E. colimotl* by the presence of pustulate rather than smooth skin. *Eleutherodactylus interorbitalis* differs from *E. floresvillelai* by the presence of smooth skin and its interorbital bar is darker than the ground coloration.

Superficially, *E. floresvillelai* is similar to *E. jaliscoensis* sp. nov. (see below) but differs by its smaller size, paler ventral coloration, and the lack of flash colors in the inguinal area. *Eleutherodactylus floresvillelai* differs *E. nietoi* sp. nov. (see below) by its lesser expanded finger pads (less than 1.9 times the narrowest part of the digit, as opposed to more than 2.1 times the narrowest part of the finger), as well as by lacking flash colors. The two species have distinctive mating calls, as *E. floresvillelai* emits a single chirp and *E. nietoi* emits a short, multi-note trill. The species that *E. floresvillelai* can be most confused with are *E. erendirae* and *E. rufescens*; both occur in Michoacán, but have not been found near the range of *E. floresvillelai*.

Eleutherodactylus erendirae differs from *E. floresvillelai* by the presence of bright flash colors on the groin and hind legs and by its more pustulate skin. *Eleutherodactylus erendirae* produces a noltably different mating call, which consists of a short, multi-note trill as opposed to a single chirp. Morphologically, *E. rufescens* is similar to *E. floresvillelai* and both species have a similar mating call, but molecularly and geographically they are distant from one another. *Eleutherodactylus rufescens* differs from *E. floresvillelai* in that bright flash coloration most often is present in the inguinal region, and by its generally red coloration. The tympanum also is more visible and slightly larger in *E. rufescens*, but this character is of little use in the field.

***Description of Holotype*:** A small frog (20.1 mm SVL); male; head longer (6.6 mm) than wide (5.8 mm), head same width as body; snout subovoid from dorsal view and rounded from lateral view; tympanum small, indistinct but visible, circular with greatest width of tympanum 0.6 mm; greatest diameter of eye 2.3 mm; ratio of tympanum width to eye diameter ratio 0.27; eyelid width 1.5 mm, 33% of IOD; 1st finger shorter than 2nd finger; finger lengths from shortest to longest 1-2-4-3; digital pads on fingers moderately expanded, 1.3 times width of narrowest point of digit on 2nd finger, 1.8 times width of narrowest point of digit on 3rd finger and 1.9 times width of narrowest point of digit on 4th finger; expanded finger pads truncate; 3 palmar tubercles, outer palmar tubercle small; inner palmar tubercle 75% as large as middle palmar tubercle, outer palmar tubercle 43% size of middle palmar tubercle; toe lengths from shortest to longest 1-2-5-3-4, TL2 and TL5 similar in length; outer metatarsal tubercle conical with round base, approximately 55% size of inner metatarsal tubercle; inner metatarsal tubercle spherical in shape with oval base, moderate, 0.8 mm in length; IND 2.0 mm, IOD 4.1 mm, END 2.1 mm, ETD 0.8 mm, UpL 5.2 mm, FoL 5.4 mm, HaL 5.7 mm, F1L 2.0 mm, F1PW 0.6 mm, F1W 0.4 mm, F2L 2.5 mm, F2PW 0.5 mm, F2W 0.4 mm, F3L 3.7 mm, F3PW 0.8 mm, F3W 0.4 mm, F4L 2.9 mm, F4PW 0.8 mm, F4W 0.4 mm, IPTL 0.5 mm, MPTL 0.7 mm, OPTL 0.4 mm, FeL 8.5 mm, TL9.0 mm, TaL 5.4 mm, FL 9.2 mm, T2L 3.0 mm, T2PW 0.5 mm, T2W 0.4 mm, T3L 4.4 mm, T3PW 0.6 mm, T3W 0.4 mm, T4L 7.0 mm, T4PW 0.6 mm , T4W 0.4 mm, T5L 4.0 mm, T5PW 0.4 mm, T5W 0.3 mm, IMTL 0.8 mm, OMTL 0.4 mm, FeL/SVL 42%, TL/SVL 45%, Ha/SVL 24%, TotFL/SVL 74%, HL/SVL 33%, and HW/SVL 29%; dorsal skin smooth with tubercles, lateral skin shagreened, ventral skin smooth; skin smooth with tubercles in life; vocal slits present; in life, dorsal coloration of holotype tan, with indistinct darker

brown blotches on back and pale yellow tubercles; head same color as dorsum, with unmarked interorbital region forming indistinct tan interorbital bar; interorbital bar bordered posteriorly by gray stripe, and thereafter by grayish-tan region slightly darker than dorsum; flanks tan with white and dark brown flecking hind legs and forearms tan with dark brown crossbands; upper arms pale tan and unmarked, slightly paler than dorsum; lateral portions of head tan, with thin darker brown stripe extending from tip of snout posteriorly through eyes, upper portion of the tympanum, and to axillas. Labial region dark brown with white spotting; bright flash colors absent on groin and thighs, although posterior surface of thighs showed slightly more orange tint than on remainder of body; ventral coloration pink with white mottling on chest and lower flanks (see Fig. 9 for photographs of holotype in life); dorsal coloration in preservative solid pale brown; distinct pale gray interorbital bar present on head; dorsal tubercles pale gray; hind legs and forearms pale brown with dark brown crossbands; upper arms and anterior and posterior surfaces of thighs pale yellowish-cream; and venter uniform yellowish-cream (see Fig. 10).

***Variation*:** The type series shows little variation (Table 4). The SVL ranges from 16.1 to 21.4 mm; the expanded fingertips range from 1.4 to 1.9 times the narrowest part of the finger on the 3rd and 4th fingers; and the finger pad shapes are both slightly rounded and slightly truncate. We present the morphological variation in Table 4.

Table 4. Morphological measurements of external morphological characters of *Eleutherodactylus floresvillelai* sp. nov. Type specimen in dark yellow. SVL = snout–vent length; HL = head length; HW = head width; TW = tympanum width; EW = eye width; ElW = eyelid width; IOD = interorbital distance; IND = internarial distance; END = eye–naris distance; ETD = eye–tympanum distance; UpL = upper arm length; FoL = forearm length; HaL = hand length; F3PW/F3W = 3rd finger pad width (widest measurement) to 3rd finger width (narrowest measurement) ratio; F4PW/F4W = 4th finger pad width (widest measurement) to 4th finger width (narrowest measurement) ratio; FeL = femur length; TL = tibia length; TotFL = total foot length (tarsal tubercle to tip of 4th toe); IPT = inner palmar tubercle length; MPT = middle palmar tubercle length; OPT = outer palmar tubercle length; IMTL = inner metatarsal tubercle length; and OMTL = outer metatarsal tubercle length.

Measurements	MZFC 33053	MZFC 33054	MZFC 33055	MZFC 33056	MZFC 33057	MZFC 33058	MZFC 33059	MZFC 33060	MZFC 33061	MZFC 33062	MZFC 33063	MZFC 33064
SVL	21.43	19.48	19.63	18.99	17.96	16.05	20.39	20.09	19.72	19.25	18.98	19.51
HL	6.91	6.43	6.61	6.95	6.24	5.82	6.80	6.62	6.15	6.50	6.41	6.56
HW	6.02	5.81	6.02	6.17	5.50	5.24	5.78	5.79	5.57	5.79	5.60	5.64
TW	0.63	0.62	0.64	0.59	0.57	0.55	0.66	0.61	0.59	0.60	0.58	0.63
EW	2.31	2.15	2.14	2.26	2.16	1.96	2.36	2.28	2.29	2.24	2.17	2.23
ElW	1.57	1.51	1.57	1.60	1.43	1.36	1.50	1.51	1.45	1.51	1.46	1.47
IOD	4.25	4.03	4.07	4.27	3.85	3.61	4.33	4.06	3.91	4.03	3.83	4.07
IND	2.03	1.97	1.97	2.07	1.90	1.75	2.16	2.00	1.96	1.98	1.91	2.02
END	2.11	2.08	2.09	2.00	1.97	1.83	2.13	2.06	2.05	2.00	1.96	2.06
ETD	0.80	0.81	0.80	0.76	0.76	0.76	0.80	0.82	0.77	0.77	0.76	0.77
UpL	4.60	4.74	4.86	4.73	4.92	3.79	4.69	5.23	4.74	5.04	4.56	4.84
FoL	5.35	5.47	5.42	5.11	5.03	4.75	5.56	5.41	5.47	5.40	5.30	5.72
HaL	6.06	5.51	5.56	5.37	5.08	4.54	5.77	5.69	5.58	5.45	5.37	5.52
F3PW/F3W	1.90	1.72	1.59	1.76	1.64	1.41	1.54	1.77	1.76	1.48	1.63	1.58
F4PW/F4W	1.86	1.49	1.56	1.88	1.50	1.70	1.54	1.90	1.88	1.55	1.64	1.51
FeL	8.60	8.19	8.43	9.10	8.33	7.82	8.62	8.52	8.87	8.70	9.00	8.80
TL	9.50	9.10	9.07	9.20	8.56	8.02	9.22	8.96	8.93	9.01	9.51	9.23
TotFL	18.95	19.30	19.30	18.57	16.80	15.80	18.65	14.60	19.75	19.52	18.85	18.50

IPT	0.45	0.46	0.47	0.45	0.50	0.43	0.55	0.53	0.55	0.50	0.55	0.51
MPT	0.73	0.80	0.72	0.70	0.61	0.57	0.77	0.71	0.73	0.67	0.78	0.75
OPT	0.35	0.40	0.30	0.35	0.30	0.28	0.35	0.35	0.35	0.30	0.30	0.30
IMTL	0.77	0.69	0.84	0.83	0.71	0.66	0.79	0.78	0.79	0.79	0.86	0.74
OMTL	0.47	0.45	0.47	0.49	0.37	0.38	0.45	0.43	0.50	0.45	0.46	0.45

***Distribution and Ecology*:** *Eleutherodactylus floresvillelai* is known to occur at elevations ranging from 2,100 to 2,400 m along the windward slopes of the Sierra de Mil Cumbres, within the Transverse ranges of east-central Michoacán, and is known only from the immediate vicinity of the type locality (see Fig. 16A). This species appears to be a habitat generalist, and has been collected in herbacious vegetation, oak woodland, and pine-oak forest. This frog occurs in sympatry with *E. angustidigitorum* and *E. nitidus*.

***Etymology*:** This species is named after Dr. Oscar Flores-Villela, a renowned Mexican herpetologist who has had a profound impact on Mexican herpetology, and authored the 1993 publication *Herpetofauna Mexicana* (Flores-Villela, 1993), which was the first complete modern list of the Mexican herpetofauna that included general distributional information for each species.

***Referred Specimens*:** UMMZ-119156. Adult of unknown sex collected by J. Wellman on 26 June 1958 at Los Cantiles, "21 mi E of Morelia," Michoacán, Mexico. "Los Cantiles" lies approximately 2.6 km E of the type locality of *E. floresvillelai* (19.659862°, -100.921520°; datum WGS 84; elev. 2,225 masl); Duellman (1961) discussed three specimens from near "Los Cantiles, Michoacán" that he identified as "*Tomodactylus fuscus*" (= *E. maurus*). We examined photographs of one of these specimens (Duellman, 1961: Plate 3, Fig. 2), and it is referable to *E. floresvillelai*.

Eleutherodactylus jaliscoensis sp. nov.

Figs. 12, 13, 14, 15B, 46B

***Holotype*:** (Figs. 12, 13). MZFC 33275 (CIG-00862). Adult male, collected by Omar Chávez-Orozco, Hector Franz-Chávez, Christoph I. Grünwald, André João Grünwald, Ámbar Lanomy Grünwald, and Mateo Chávez-Pérez on 25 June 2016 on the dirt portion of the old highway between Mascota and San Sebastian del Oeste, 20.8 airline km NNW of Mascota, Sierra Mascota, Municipio de Mascota (20.69802°, -104.86718°, datum WGS 84; elev. 2,037 masl), Jalisco, Mexico (Fig. 16C).

***Paratypes*:** (Fig. 14). Fourteen specimens. MZFC 33131–33140 (CIG-00480–489) 10 adult males collected by Hector Franz-Chávez, Christoph I. Grünwald, Karen I. Morales Flores, Ámbar Lanomy Grünwald, and André João Grünwald on 10 July 2015 at Peña del Cuervo, near Cumbre de Guadalupe, Sierra Cacoma, Municipio de Talpa de Allende (20.21916°, -104.73579°; datum WGS 84; elev. 2,150 masl), Jalisco, Mexico; MZFC 33141 (CIG-00490) an adult male collected by Hector Franz-Chávez, Christoph I. Grünwald, Karen I. Morales Flores, Ámbar Lanomy Grünwald, and André João Grünwald on 10 July 2015 at Bosque de Maple, below Cumbre de Guadalupe, Sierra Cacoma, Municipio de Talpa de Allende (20.20854°, -104.74780°, datum WGS 84; elev. 1,940 masl), Jalisco, Mexico; MZFC 33274 and 33276 (CIG-00861 and CIG-00863) two adult males collected at the same locality and on the same date as the holotype; MZFC 33280 (CIG-00876) adult male collected by Christoph I. Grünwald, Hector Franz-Chávez, Ámbar Lanomy Grünwald, and André João Grünwald on 26 June 2016, near the river crossing on the Cumbre de Guadalupe–Malpaso Road, Sierra Cacoma, Municipio de Talpa de Allende (20.235737°, -104.711389°; datum WGS 84; elev. 1,700 masl), Jalisco, Mexico.

***Diagnosis*:** A member of the genus *Eleutherodactylus*, subgenus *Syrrhophus*, as defined by Hedges et al. (2008). In the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Series and the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group, as defined in this paper (see discussion below). A small frog, adult males measure 20.8–26.2 mm SVL; vocal slits present in males; digital tips expanded, rounded in shape and 1.4–2.1 times width of narrowest part of 3rd finger and 1.7–2.3 times width of narrowest part of 4th finger; fingers relatively short, with 3rd finger length 12–17% of SVL (see Fig. 15B); compact lumbar gland above inguinal region absent; epidermis not translucent and

abdominal vein not clearly visible on venter of live specimens; limbs moderate, TL/SVL ratio 0.43–0.48, FeL/SVL ratio 0.40–0.50, and TotFL/SVL ratio 0.69–0.73; snout short, END/SVL ratio 0.09–0.11; tympanum small, visible but indistinct, round; TW/ED ratio 0.22–0.36; dorsal skin not smooth, moderately to heavily pustulate; dorsal coloration tan, red, or pale to dark brown, with darker brown reticulations on dorusm; no pale-colored saddle blotches; middorsal stripe absent; interorbital bar present between orbits, usually as pale or paler than palest colors on dorsum; upper arms same pale color as interorbital bar, but with one or two dark-colored transverse bars; dark-colored irregular transverse bars present on forearms, thighs, and legs; ventral coloration gray to dark gray with white spots or reticulations; bright red, yellow, or orange flash coloration present on inguinal region and anterior and posterior portions of thighs, and occasionally on the legs, axillar region, upper arms, and flanks. The mating call of adult males is a short trill (see below; Fig. 28B).

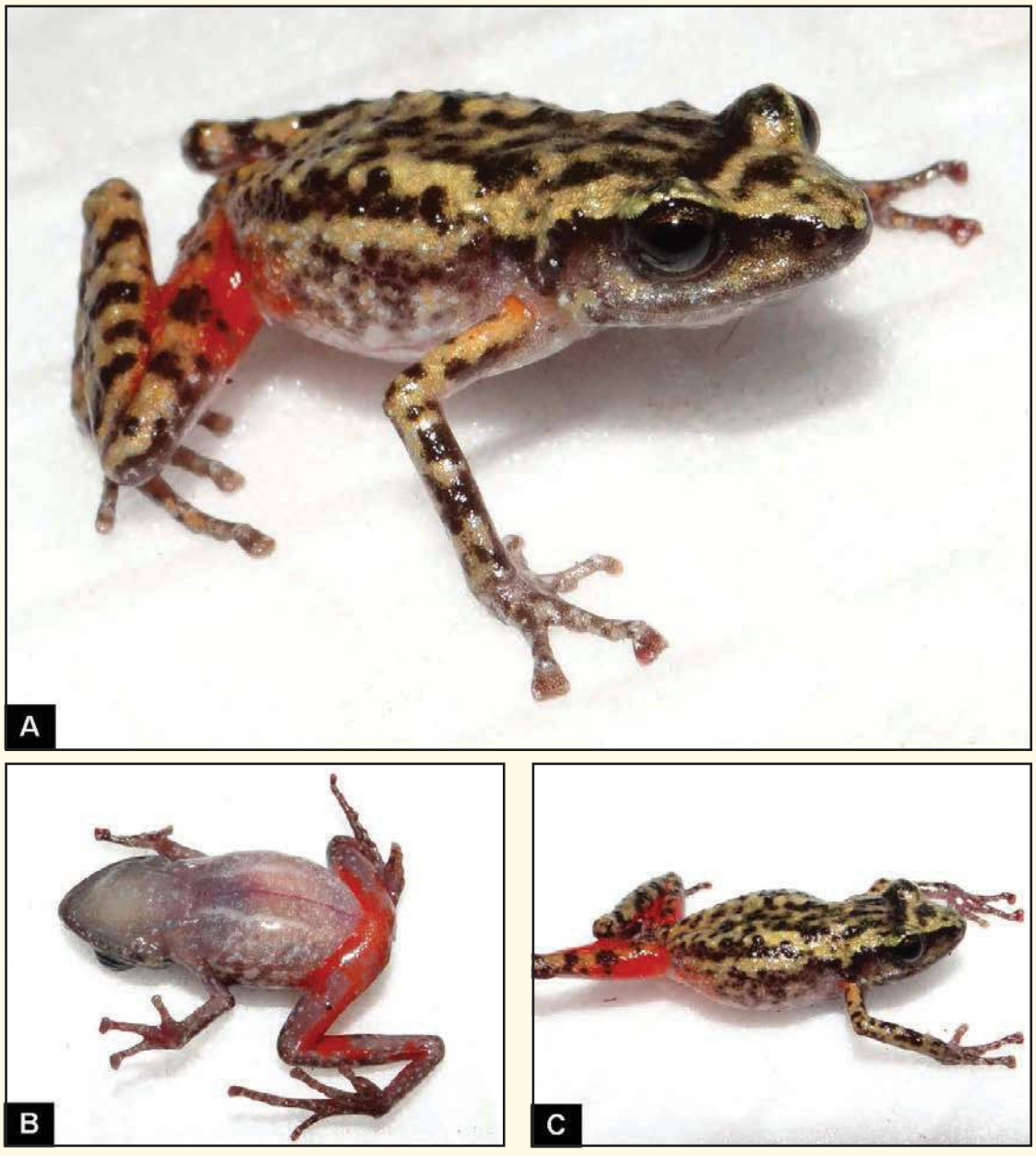


Fig. 12. Holotype of *Eleutherodactylus jaliscoensis* sp. nov. in life, MZFC 33275 (CIG-00862). (A) Full body view; (B) ventral view; and (C) lateral view. © Christoph I. Grünwald

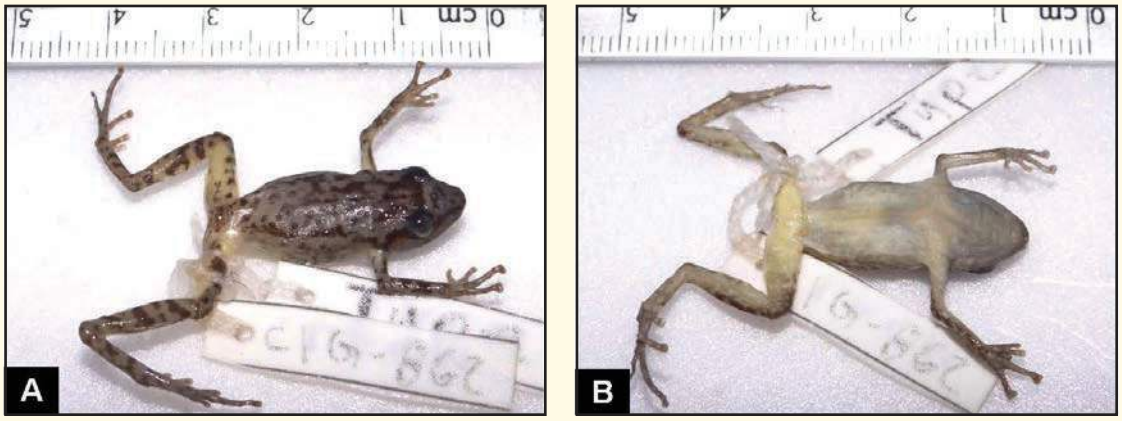


Fig. 13. Holotype of *Eleutherodactylus jaliscoensis* sp. nov. in preservative, MZFC 33275 (CIG-00862). (A) Dorsal view; and (B) ventral view. © Christoph I. Grünwald

***Comparisons*:** *Eleutherodactylus jaliscoensis* can be distinguished from all species in the *Eleutherodactylus* (*Syrrhophus*) *longipes* Species Series (as defined herein, see below) by the presence of a small, indistinct tympanum with no visible tympanic annulus and with a diameter less than 31% of the eye diameter; by a non-translucent abdominal epidermis, and thus a visible abdominal vein on the venter is not evident in life, and by the presence of an outer palmar tubercle that mesures 41–45% of the middle palmar tubercle.

Eleutherodactylus jaliscoensis can be distinguished from most species of the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Group (as defined herein, see below) by a combination of the expanded finger pads on the 3rd and 4th fingers and lacking a compact, protruding lumbar gland in the inguinal region. It can be distinguished from the remaining two species, *Eleutherodactylus pipilans* and *Eleutherodactylus rubrimaculatus*, by its pustulate skin and pale-colored interorbital bar.

Within the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group (as defined herein, see below), E. *jaliscoensis* can be distinguished from *E. angustidigitorum*, *E. grandis*, and *E. saxatilis* by the lack of protruding, compact lumbar glands above the inguinal region. It can be distinguished from *E. grunwaldi*, *E. modestu*s, *E. teretistes*, and *E. pallidus* by its pustulate skin and presence of an interorbital bar. The skin of *E. interorbitalis* also is smooth, and its interorbital bar is darker than the pale-colored dorsum. *Eleutherodactylus colimotl* differs from *E. jaliscoensis* by its smooth skin and an immaculate white ventral coloration. *Eleutherodactylus wixarika* can be distinguished from *E. jaliscoensis* by the absence of bright flash coloration in the inguinal region and thighs and the lack of a pale-colored interorbital bar. Superficially, both *E. erendira*e and *E. floresvillelai* are similar to *E. jaliscoensis*, but the former is a smaller frog with less expanded fingertips, not more than 1.6 times the narrowest part of the digit, and the latter lacks the bright flash coloration in the inguinal region and has a distinctive mating call of a single note chirp, as opposed to a multi-note trill. The skin of *E. rufescens* is smoother, and this species also emits a distinctive mating call that consists of a single note chirp, as opposed to a multi-note trill. *Eleutherodactylus manantlanensis* sp. nov. (see below) and *E. nietoi* sp. nov. (see below) are the most similar morphologically to *E. jaliscoensis* and also have similar mating calls that consist of a multi-note trill, which can be confused with that of *E. jaliscoensis*. Both species differ from *E. jaliscoensis* by the presence of more expanded finger pads on the 3rd and 4th digits (1.8–3.4 times the narrowest part of the digit, compared to 1.6–2.3 in *E. jaliscoensis*), and by their pale-colored saddle blotches on the shoulders, which are paler than the pale-colored dorsum; these blotches are absent in *E. jaliscoensis*. Further, the nearby *E. manantlanensis* sp. nov. (see below) can be distinguished by its larger size (25.2–28.9 mm), lack of a distinct, visible tympanum, smooth skin, and a pale-colored venter. *Eleutherodactylus nietoi* sp. nov. (see below) usually lacks the bright flash coloration in the inguinal zone, which is present in *E. jaliscoensis*, and might display a pale-colored middorsal stripe, which is absent in *E. jaliscoensis*. Furthermore, it also lacks the dark gray or black reticulated venter that is common in *E. jaliscoensis*.

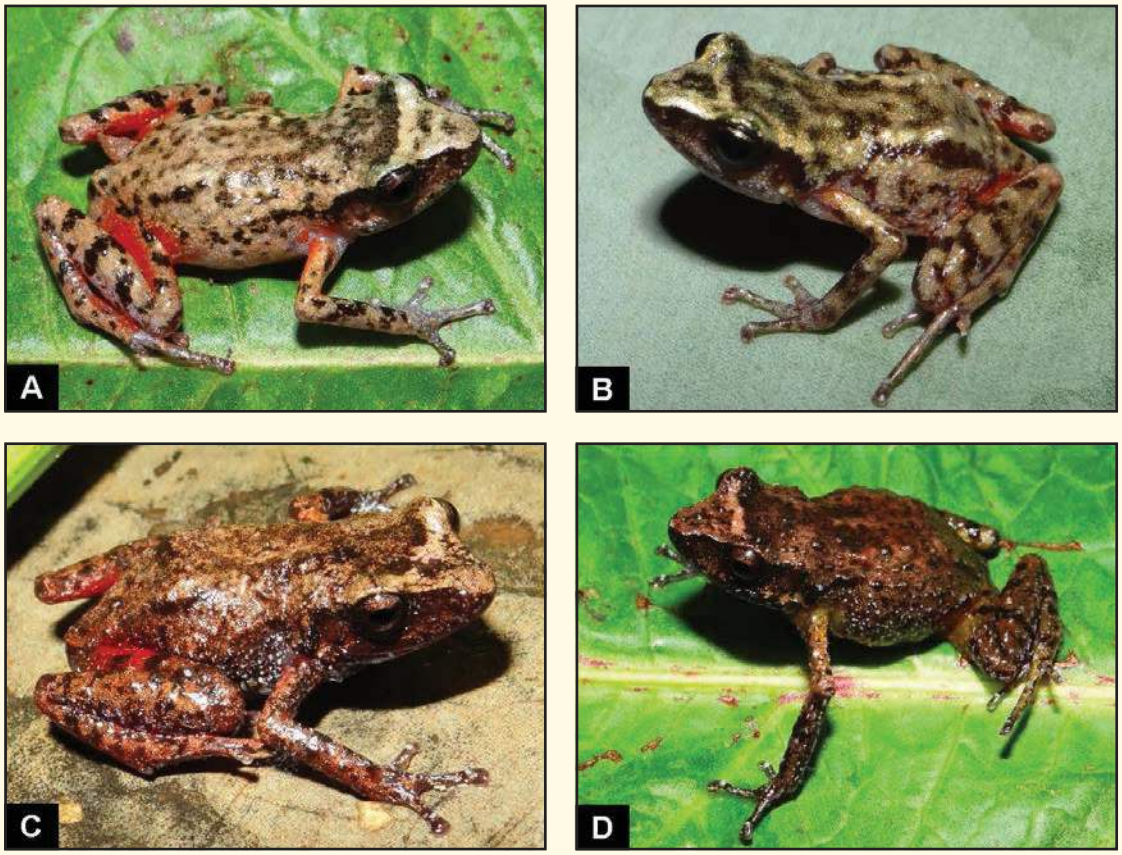


Fig. 14. Variation in *Eleutherodactylus jaliscoensis* sp. nov. (A) Male from Cumbre de Guadalupe, Talpa de Allende, Jalisco, MZFC 33139 (CIG-00488); (B) male from the type locality, Municipio de Mascota, Jalisco, MZFC 33276 (CIG-00863); (C) male from Cumbre de Guadalupe, Municipio de Talpa de Allende, Jalisco, Michoacán, MZFC 33141 (CIG-00490); and (D) male from Cumbre de Guadalupe, Municipio de Talpa de Allende, Jalisco, Michoacán, MZFC 33132 (CIG-00481). © Christoph I. Grünwald

***Description of the Holotype*:** A small frog (24.0 mm SVL), male, head slightly longer (7.7 mm) than wide (7.1 mm), same width as body; snout subovoid from dorsal view and rounded from lateral view; tympanum indistinct, but visible, rounded in shape with no supratympanic fold present; tympanum small, circular, greatest width of tympanum 0.7 mm; greatest diameter of eye 2.7 mm; ratio of tympanum width to eye diameter ratio 0.26; eyelid width 1.5 mm, 33% of IOD; 1st finger shorter than 2nd finger; finger lengths from shortest to longest 1-2-4-3, with 1 and 2 subequal; digital pads on fingers 2, 3, and 4 expanded, 1.3 times the narrowest point of digit on 2nd finger, 2.0 times the narrowest point of digit on 3rd finger, and 2.1 times the narrowest point of digit on 4th finger; expanded finger pads emarginate, truncate; 3 palmar tubercles; inner palmar tubercle about 70% as large as middle palmar tubercle, outer palmar tubercle 43% size of middle palmar tubercle; toe lengths from shortest to longest 1-2-5-3-4, with toes 2 and 5 subequal; outer metatarsal tubercle conical with round base, moderately sized, 70% size of inner metatarsal tubercle; inner metatarsal tubercle spherical shape with oval base, large, 1.0 mm in length; IND 2.5 mm, IOD 4.5 mm, END 2.4 mm, ETD 0.9 mm, UpL 5.2 mm, FoL 6.6 mm, HaL 5.7 mm, F1L 2.0 mm, F1PW 0.6 mm, F1W 0.5 mm, F2L 2.2 mm, F2PW 0.7 mm, F2W 0.5 mm, F3L 3.5 mm, F3PW 1.0 mm, F3W 0.5 mm, F4L 3.1 mm, F4PW 1.0 mm, F4W 0.5 mm, IPTL 0.7 mm, MPTL 1.0 mm, OPTL 0.4 mm, FeL 9.7 mm, TL 10.3 mm, TaL 6.6 mm, FL 10.5 mm, T2L 3.0 mm, T2PW 0.8 mm, T2W 0.5 mm, T3L 4.6 mm, T3PW 0.8 mm, T3W 0.5 mm, T4L 7.9 mm, T4PW 0.9 mm, T4W 0.6 mm, T5L 3.7 mm, T5PW 0.6 mm, T5W 0.4 mm, IMTL 1.0 mm, OMTL 0.7 mm, FeL/SVL 41%, TL/SVL 43%, HA/SVL 23%, TotFL/SVL 71%, HL/SVL 32%, and HW/SVL 30%; dorsal skin smooth with sparse tubercles, lateral skin shagreened with sparse tubercles; ventral skin smooth (skin slightly tuberculate in life); vocal

slits present; in life, dorsal coloration of holotype pale tan, with dark brown reticulations throughout; head same color as pale tan interorbital bar, posteriorly bordered by continuous dark brown nuchal blotch; dorsal surface of snout pale tan, same as paler parts of body; flanks also same pale tan color as dorsum, but with dark brown and white spots; hind legs pale tan with irregular dark brown crossbands; upper arms unmarked and same pale tan ground color as dorsum; lower arms pale tan with dark brown crossband; dark brown stripe extends laterally from snout through middle of eye, above tympanum, and to above axilla; small pale tan area, same color as dorsal coloration, below dark-colored stripe; lips darker in color with small white spots; tympanum gray, distinct from surrounding coloration; blood-red flash coloration present on groin and inguinal region, and on ventral surfaces of thighs, legs, and feet; traces of flash coloration also present on dorsal surfaces of thighs and posterior portions of flanks; venter pale gray, with white blotches on abdomen and white spots on ventral surfaces of thighs and legs; iris copper above, dark brown below (see Fig. 12 for photographs of holotype in life); dorsal coloration in preservative cream with dark brown reticulations; interorbital bar cream; legs cream with dark brown crossbars; groin and posterior surfaces of thighs pale yellow; and venter pale gray, with slightly darker shade of gray on ventral surface of head (See Fig. 13).

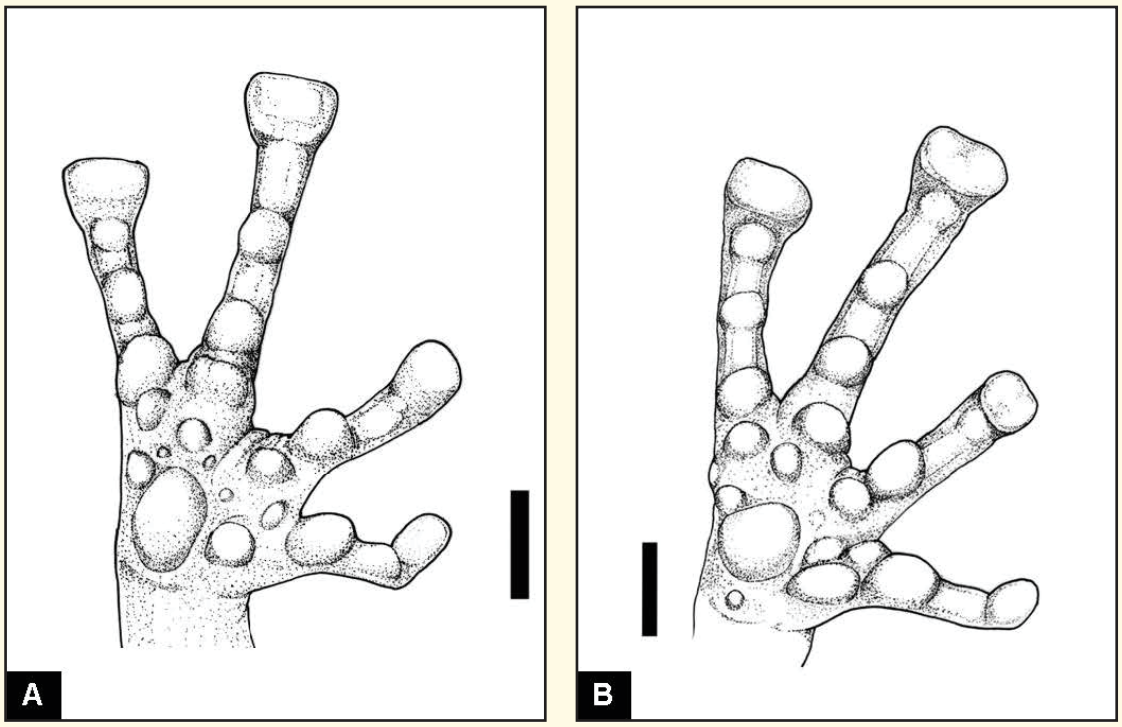


Fig. 15. Hand drawings of *Eleutherodactylus*. (A) *Eleutherodactylus floresvillelai* sp. nov.; and (B) *Eleutherodactylus jaliscoensis* sp. nov. Vertical bars = 1 mm. Drawings by Iván T. Ahumada-Carrillo.

***Variation*:** The 14 paratypes show little variation in morphological characters, but significant variation in coloration (Table 5). The SVL ranges from 20.8 to 26.2 mm; the expanded finger pads on the 3rd finger range from 1.6 to 2.1 times the narrowest part of the digit, and on 4th finger from 1.7 to 2.4 times the narrowest part of the digit; the skin condition varies from slightly pustulate to heavily pustulate; the dorsal coloration can be pale (tan, pale brown, or grayish-green) with dark brown blotches, or it can be dark brown with darker brown blotches (the darker individuals exhibit pale brown or orange interorbital bars and upper arms, and typically a darker gray to nearly black ventral coloration); the venter of two specimens is pale-colored (one white, one pale gray), but in all other specimens the venter is gray to dark gray with whites spots and flecks; and the bright flash colors that are characteristic on the inguinal region vary from yellow, orange, and fiery orange to bright red. We present the morphological variation in Table 5.

Table 5. Morphological measurements of external morphological characters of *Eleutherodactylus jaliscoensis* sp. nov. Type specimen in dark yellow. SVL = snout–vent length; HL = head length; HW = head width; TW = tympanum width; EW = eye width; ElW = eyelid width; IOD = interorbital distance; IND = internarial distance; END = eye–naris distance; ETD = eye–tympanum distance; UpL = upper arm length; FoL = forearm length; HaL = hand length; F3PW/F3W = 3rd finger pad width (widest measurement) to 3rd finger width (narrowest measurement) ratio; F4PW/F4W = 4th finger pad width (widest measurement) to 4th finger width (narrowest measurement) ratio; FeL = femur length; TL = tibia length; TotFL = total foot length (tarsal tubercle to tip of fourth toe); IPT = inner palmar tubercle length; MPT = middle palmar tubercle length; OPT = outer palmar tubercle length; IMTL = inner metatarsal tubercle length; and OMTL = outer metatarsal tubercle length.

Measure-ments	MZFC 33131	MZFC 33132	MZFC 33133	MZFC 33134	MZFC 33135	MZFC 33136	MZFC 33137	MZFC 33138	MZFC 33139	MZFC 33140	MZFC 33141	MZFC 33274	MZFC 33275	MZFC 33276	MZFC 33280
SVL	23.73	22.04	24.33	23.45	24.94	24.44	23.13	26.18	21.21	21.38	25.02	21.65	23.97	23.87	20.80
HL	8.17	7.05	8.29	8.01	8.76	8.71	7.78	9.08	7.17	7.61	8.91	7.42	7.72	7.66	7.32
HW	7.33	6.94	7.74	7.30	7.67	7.41	6.73	7.70	6.67	6.65	8.08	6.70	7.14	7.08	6.20
TW	0.67	0.50	0.69	0.77	0.81	0.84	0.63	0.67	0.63	0.68	0.69	0.66	0.69	0.69	0.66
EW	2.25	2.29	2.49	2.17	2.30	2.36	2.21	2.51	2.16	2.24	2.48	2.47	2.70	2.70	2.40
ElW	1.60	1.51	1.69	1.59	1.67	1.62	1.47	1.68	1.45	1.45	1.76	1.35	1.46	1.50	1.50
IOD	4.74	4.11	5.00	4.87	5.03	4.79	4.55	4.89	4.64	4.33	5.48	4.37	4.47	4.47	4.45
IND	2.59	2.14	2.32	2.56	2.41	2.41	2.50	2.62	2.18	2.26	2.72	2.35	2.45	2.45	2.22
END	2.28	2.06	2.43	2.19	2.53	2.30	2.30	2.58	2.15	2.15	2.40	2.20	2.35	2.35	2.28
ETD	0.73	0.67	0.73	1.01	1.00	1.02	0.99	1.02	1.05	0.82	0.99	0.85	0.88	0.90	0.84
UpL	4.57	3.54	4.44	4.45	4.45	4.30	5.10	5.35	5.07	5.77	5.03	5.02	5.24	5.20	4.85
FoL	6.51	6.41	6.74	6.70	6.78	6.78	6.01	7.25	5.53	6.41	6.33	6.31	6.60	6.55	5.70
HaL	5.79	5.38	5.94	5.72	6.09	5.96	5.64	6.39	5.18	5.22	6.10	5.40	5.65	5.66	5.20
F3PW/F3W	1.48	1.56	2.11	1.43	1.55	1.60	1.67	1.62	1.70	1.54	1.80	1.72	1.96	1.85	1.65
F4PW/F4W	1.84	2.10	2.27	1.78	1.90	1.98	1.96	1.74	2.11	1.79	1.76	1.87	2.12	1.96	1.93
FeL	10.43	9.68	11.37	11.54	11.00	10.85	10.07	11.27	9.16	9.76	11.42	8.60	9.77	9.77	8.85
TL	10.97	10.33	11.46	11.19	11.84	11.31	10.30	12.07	9.96	10.11	11.51	9.40	10.30	10.24	9.27
TotFL	16.85	15.65	17.27	16.65	17.71	17.35	16.42	18.59	15.06	15.18	17.76	15.70	17.11	17.05	14.35
IPT	0.55	0.79	0.62	0.57	0.53	0.40	0.64	0.77	0.58	0.54	0.78	0.56	0.67	0.67	0.60
MPT	0.85	0.65	0.88	0.77	0.85	0.75	0.82	1.08	0.77	0.97	1.00	0.92	0.95	0.96	0.85
OPT	0.34	0.26	0.35	0.31	0.34	0.30	0.33	0.43	0.31	0.39	0.40	0.38	0.41	0.41	0.38
IMTL	0.80	0.72	0.89	0.89	0.91	0.91	0.78	0.99	0.80	0.93	0.96	0.94	0.97	0.97	0.88
OMTL	0.57	0.61	0.61	0.47	0.61	0.67	0.50	0.63	0.57	0.57	0.73	0.59	0.67	0.65	0.48

***Distribution and Ecology*:** *Eleutherodactylus jaliscoensis* occurs at elevations ranging from 1,700 to 2,300 m in the higher portions of the Sierra Mascota, Sierra Cuale, and Sierra Cacoma in the municipalities of Mascota and Talpa de Allende, Jalisco (see Fig. 16A). This frog has been collected alongside or in close proximity to *E. pallidus*, *E. nitidus*, and *E. teretistes*. Of these, the last species is the most similar, and has been found living sympatrically with *E. jaliscoensis*. *Eleutherodactylus teretistes*, however, tends to occur at lower elevations, and appears to be closely associated with oak trees (*Quercus*). *Eleutherodactylus jaliscoensis* is more cold tolerant and apparently is more of a habitat generalist, as it has been collected among oaks, pine trees, and herbacious growth.

***Etymology*:** This species is named after the state of Jalisco, a mega-diverse state in western Mexico from where this species appears to be endemic.

***Referred Specimens*:** We examined detailed photographic material of *Syrrhophus* housed at the Amphibian and Reptile Diversity Research Center, University of Texas at Arlington, of which various specimens are referable to *E. jaliscoensis*. Most importantly, JAC-30723, and JAC-30725–30728 clearly are representatives of this species, and were collected around the summit of Cerro Tetilla in the Sierra Cuale of western Jalisco. Furthermore, we examined a specimen housed at the Colección Nacional de Anfibios y Reptiles, Instituto de Biología, Universidad Nacional Autónoma de México (CNAR-5926) that originated from the Cerro Tetilla area of Sierra Cuale. We refer all these specimens to *E. jaliscoensis.*

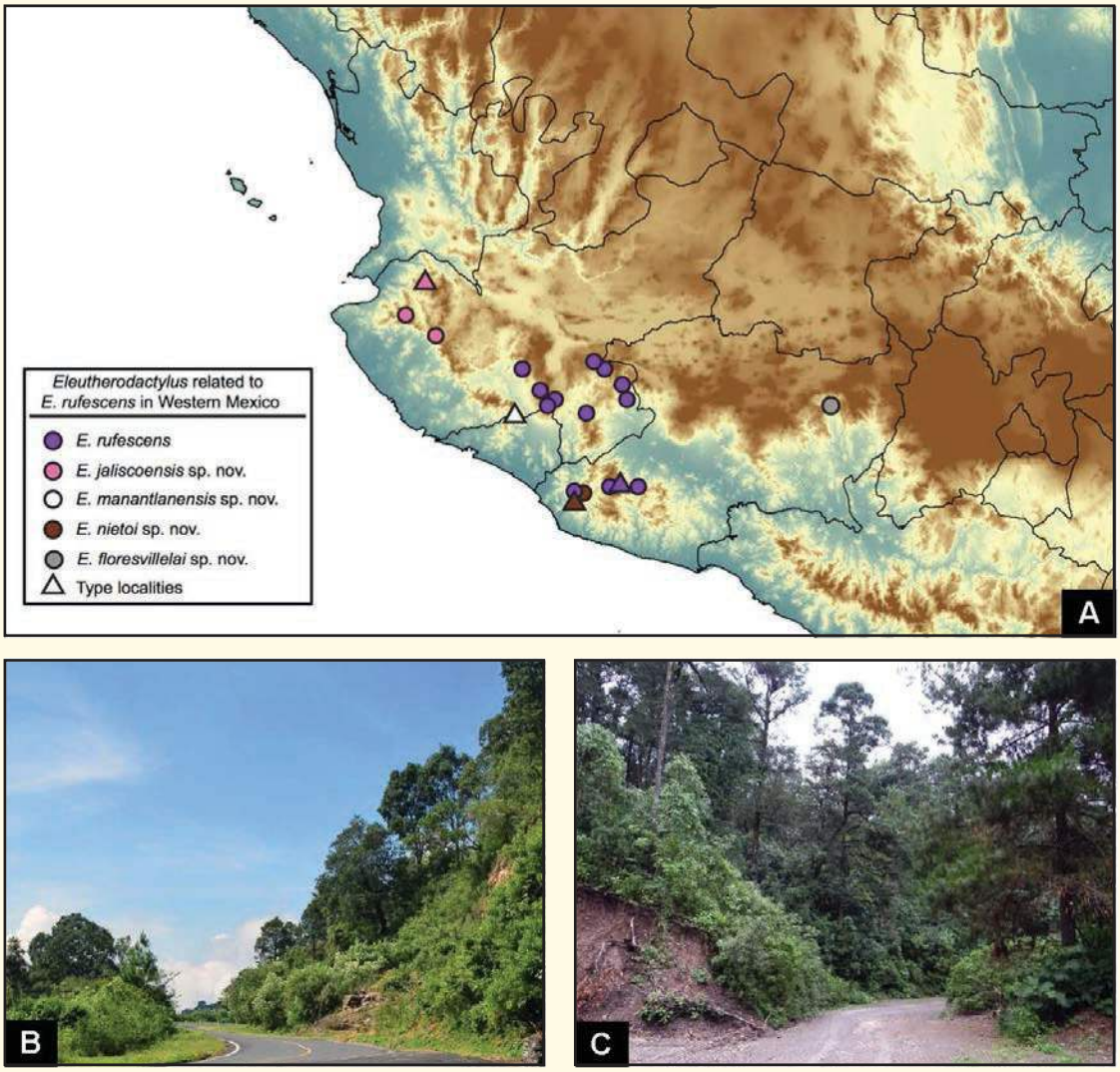


Fig. 16. (A) Map showing the distribution of some members of the *Eleutherodactylus modestus* Species Group from western Mexico, including *Eleutherodactylus floresvillelai* sp. nov., *Eleutherodactylus jaliscoensis* sp. nov., *Eleutherodactylus nietoi* sp. nov., and *Eleutherodactylus manantlanensis*; (B) photo of the type locality of *Eleutherodactylus floresvillelai* sp. nov., near Los Cantiles, Municipio de Charo, Michoacán; and (C) photo of the type locality of *Eleutherodactylus jaliscoensis* sp. nov., in the Sierra de Mascota, Municipio de Mascota, Jalisco. Map by Jacobo Reyes-Velasco. © Juan M. Gonzalez-Villa (B) and Christoph I. Grünwald (C)

Eleutherodactylus manantlanensis sp. nov.

Figs. 17, 18, 19, 23A, 46B

***Holotype*:** (Figs. 17, 18). MZFC 33295 (CIG-00895). Adult male, collected by Christoph I. Grünwald, Alexander I. Hermosillo-López, Karen I. Morales-Flores, André João Grünwald, Ámbar Lanomy Grünwald, and Janelle Morales-Flores on 2 July 2016 at 13 km NE of Colima–Minatitlán highway on the road to El Terrero, Municipio de Minatitlán (19.43502°, -103.95984°, datum WGS 84; elev. 2,127 masl), Colima, Mexico (Fig. 24B).

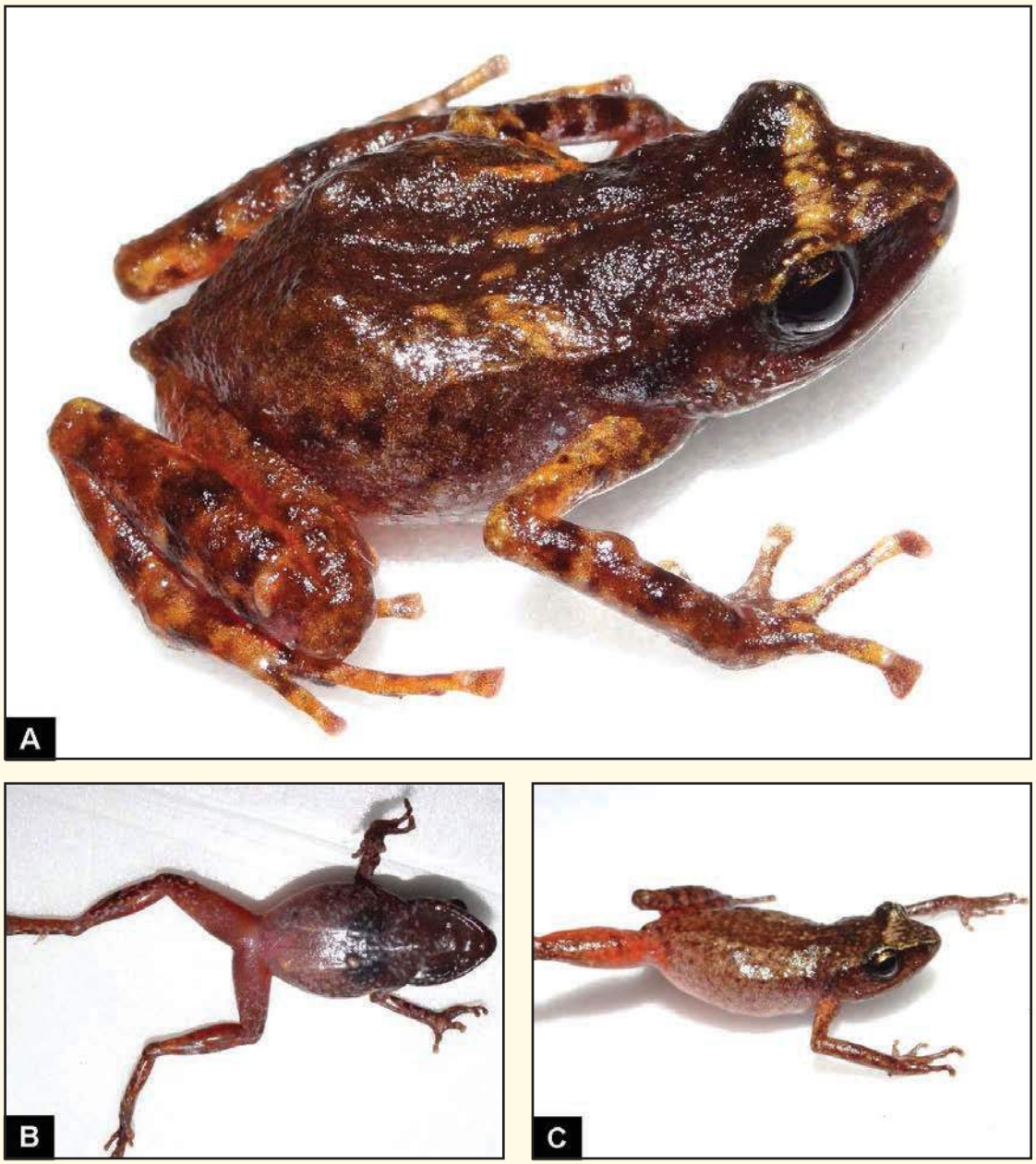


Fig. 17. Holotype of *Eleutherodactylus manantlanensis* sp. nov. in life, MZFC 33295 (CIG-00895). (A) Full body view; (B) ventral view; and (C) lateral view. © Christoph I. Grünwald

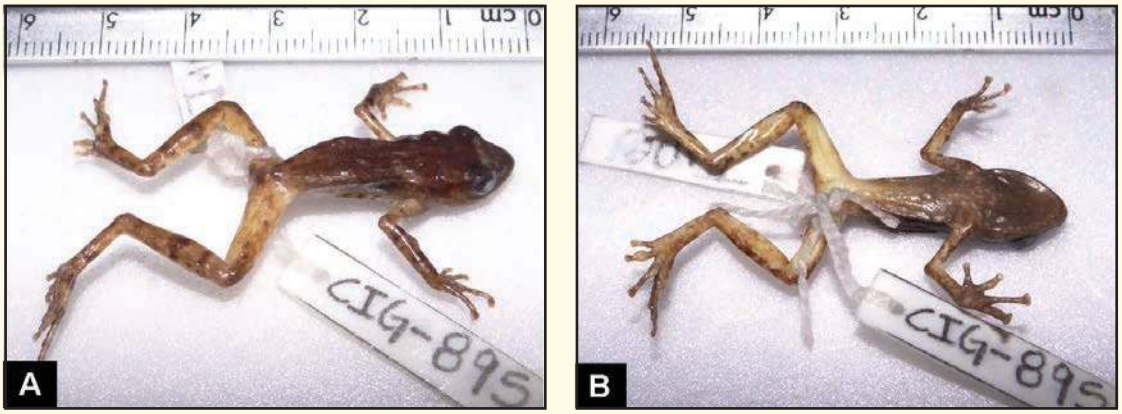


Fig. 18. Holotype of *Eleutherodactylus manantlanensis* sp. nov. in preservative, MZFC 33295 (CIG-00895). (A) Dorsal view; and (B) ventral view. © Christoph I. Grünwald

***Paratypes*:** (Fig. 19). Thirteen specimens. MZFC 33372–33377 (CIG-00530–535), six adult males collected by Hector Franz-Chávez, Christoph I. Grünwald, and André João Grünwald on 21 June 2014 at the same locality as the holotype; MZFC 33379–33381 (CIG-00646–648), three adult males collected by Iván T. Ahumada-Carrillo and Ginny N. Weatherman on 22 June 2014 at the same locality as the holotype; and MZFC 33292–33294 and 33296 (CIG-00892–894 and CIG-00896), four adult males collected at the same locality and on the same date as the holotype.

***Diagnosis*:** A member of the genus *Eleutherodactylus*, subgenus *Syrrhophus*, as defined by Hedges et al. (2008). In the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Series and the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group, as defined in this paper (see discussion below). A moderately-sized frog; adult males measure 25.1–28.9 mm SVL; vocal slits present in males; digital tips widely expanded, 1.9–2.8 times width of narrowest part of finger on 3rd and 4th fingers; fingers relatively short, 3rd finger 14–17% of SVL (see Fig. 23A); compact lumbar gland above inguinal region absent; epidermis not translucent and abdominal vein not visible on venter of live specimens; limbs moderate in size; TL/SVL ratio 0.40–0.49, Fe/SVL ratio 0.36–0.48, TotFL/SVL ratio 0.62–0.7; snout relatively short, END/SVL ratio 0.09–0.11; tympanum small, round, not visible in live individuals, difficult to see in properly preserved specimens; TW/ED approximately 28–30%; dorsal skin varies from smooth to pustulate; lateral and ventral skin smooth; dorsal coloration variable, pale to dark brown, tan, or yellow; pale-colored "saddle blotches" present on shoulders; pale-colored interorbital bar present; dark-colored transverse bars present on tibia, tarsus, and forearms; upper arms pale-colored and usually unmarked; venter gray with white spots or white flecking; bright flash colors sometimes present on inguinal region, hind legs, and flanks; and mating call of adult males a long trill (see below; Fig. 29A).

***Comparisons*:** *Eleutherodactylus manantlanensis* can be distinguished from all species in the *Eleutherodactylus* (*Syrrhophus*) *longipes* Species Series (as defined herein, see below) by the presence of a small, indistinct tympanum with no tympanic annulus visible and with a diameter less than 31% of the eye diameter; by its non-translucent abdominal epidermis, and thus a visible abdominal vein on the venter is not evident in life; and by the presence of a 3rd (outer) palmar tubercle that is smaller than 45% of the middle palmar tubercle.

Eleutherodactylus manantlanensis can be distinguished from most species in the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Group (as defined herein, see below) by a combination of the expanded finger pads on the 3rd and 4th fingers and the absence of a compact, protruding lumbar gland in the inguinal region. It can be distinguished from the remaining two species, *E. pipilans* and *E. rubrimaculatus*, by its more expanded finger pads, pustulate skin, and pale-colored interorbital bar.

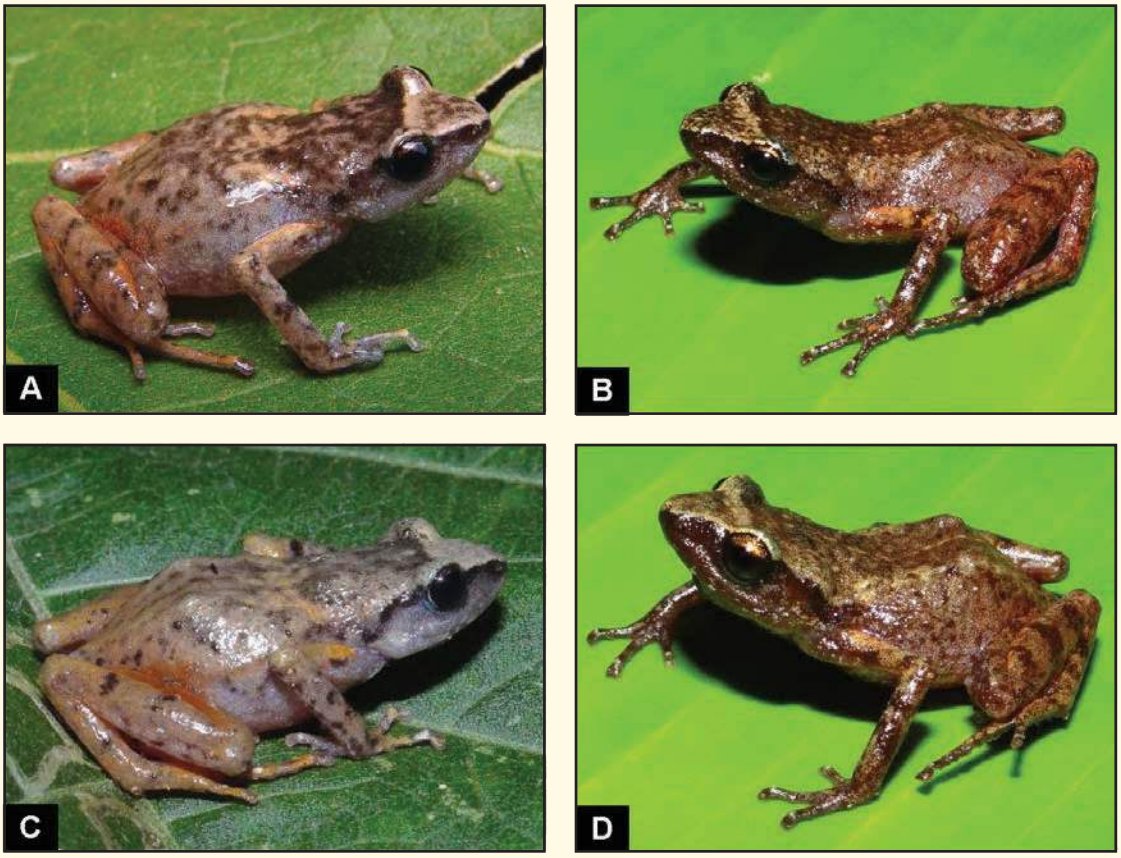


Fig. 19. Variation in *Eleutherodactylus manantlanensis* sp. nov. (A) Male from near El Terrero, Municipio de Minatitlán, Colima (no museum number); (B) male from near El Terrero, Municipio de Minatitlán, Colima, MZFC 33292 (CIG-00893); (C) male from near El Terrero, Municipio de Minatitlán, Colima, (no museum number); and (D) male from near El Terrero, Municipio de Minatitlán, Colima, MZFC 33292 (CIG-00892). © Christoph I. Grünwald

Within the *Eleutherodactylus* (*Syrrhophus*) *modestus S*pecies Group (as defined herein, see below), *E. manantlanensis* can be distinguished from *E. angustidigitorum*, *E. grandis*, and *E. saxatilis* by the lack of protruding compact lumbar glands above the inguinal region. It can be distinguished from *E. grunwaldi*, *E. modestus*, *E. teretistes*, and *E. pallidus* by its pustulate skin and interorbital bar. The skin of *E. interorbitalis* also is smooth, and its interorbital bar is darker than its pale-colored dorsum. *Eleutherodactylus wixarika* can be distinguished from *E. manantlanensis* by the lack of bright flash coloration in the inguinal region and on the thighs, and the absence of a pale-colored interorbital bar. Superficially, *E. rufescens* and *E. floresvillelai* are similar to *E. manantlanensis*, but both are much smaller frogs (under 24.0 mm, whereas *E. manantlanensis* measures over 25.0 mm) and their mating call consists of a single peep, as opposed to a long trill. *Eleutherodactylus erendirae* also is a much smaller frog (under 23.0 mm), but with a similar trill. Further, *E. erendirae* can be distinguished from *E. manantlanensis* by its significantly less expanded fingertips, which are expanded less than 1.6 times the narrowest part of the digit on both fingers 3 and 4 in *E. erendirae*, whereas they are expanded more than 1.6 times (usually more than 2.5 times) the width of the narrowest part of the digit on both fingers 3 and 4. *Eleutherodactylus manantlanensis* is a variable frog that apparently is most closely related to *E. colimotl*, *E. jaliscoensis*, and *E. nietoi* sp. nov. (see below). To complicate matters more, *E. manantlanensis* is confined to one locality that lies relatively close to the ranges of all three of its closest relatives, and geographically occurs in the middle of those ranges. *Eleutherodactylus manantlanensis* is unique among all of its congeners in that its tympanum is not evident in life. *Eleutherodactylus colimotl*

further differs from *E. manantlanensis* by its smooth skin and an immaculate white ventral coloration, as well as a distinct mating call that consists of a single, short chirp. The mating call of *E. jaliscoensis* is a similar trill to that of *E. manantlanensis*, but is a much shorter, concise trill. Further, it differs by its smaller size (20.8–26.2 mm in *E. jaliscoensis* vs. 25.2–28.9 mm in *E. manantlanensis*), a darker-colored venter, more prominent fiery red flash coloration on the groin and thighs, more pustulate skin and less expanded digits on the fingers (1.6–2.1 times the narrowest part of the digit on the 3rd finger of *E. jaliscoensis*, compared to 1.6–3.0 times the narrowest part of the digit on the 3rd finger of *E. manantlanensis*). *Eleutherodactylus nietoi* sp. nov. (see below) is even more variable than *E. manantlanensis*, and likely is the species most easily confused with *E. manantlanensis*. This species is a smaller frog (20.7–26.0 mm in *E. nietoi* sp. nov. vs. 25.2–28.9 mm in *E. manantlanensis*) that usually displays a more pustulate dorsum, shows a visible tympanum, generally lacks the characteristically pale-colored upper arms, tubercles are present on the rictus, and emits a multi-note trill that is slower and consists of fewer notes than the rapid multi-note trill of *E. mananltanensis*.

***Description of Holotype*:** A moderate-sized frog (27.4 mm SVL); male; head slightly longer (8.4 mm) than wide (7.5 mm), head wider than body; snout subovoid from dorsal view and acuminate from lateral view; tympanum indistinct, not visible in life and barely discernible in preservative; tympanum small, circular, greatest width of tympanum 0.9 mm; greatest diameter of eye 2.9 mm; tympanum width to eye diameter ratio 0.3; eyelid width 1.5 mm, 28% of the IOD; 1st finger shorter than 2nd finger; finger lengths from shortest to longest 1-2-4-3, with 1 and 2 subequal; digital pads on fingers 2, 3, and 4 expanded, 1.3 times the narrowest point of digit on 2nd finger, 2.0 times narrowest point of digit on 3rd finger, and 2.1 times narrowest point of digit on 4th finger; expanded finger pads slightly rounded; 3 palmar tuberrcles; inner palmar tubercle 57% as large as middle palmar tubercle, outer palmar tubercle 46% size of middle palmar tubercle; toe lengths from shortest to longest 1-2-5-3-4; outer metatarsal tubercle spherical with round base, of moderate size, approximately 60% size of inner metatarsal tubercle; inner metatarsal tubercle spherical with oval base, large, 1.2 mm in length; IND 2.6 mm, IOD 5.3 mm, END 2.8 mm, ETD 1.0 mm, UpL 0.9 mm, FoL 7.4 mm, HaL 6.7 mm, F1L 2.2 mm, F1PW 0.7 mm, F1W 0.5 mm, F2L 2.5 mm, F2PW 0.9 mm, F2W 0.6 mm, F3L 3.7 mm, F3PW 1.2 mm, F3W 0.6 mm, F4L 3.0 mm, F4PW 1.2 mm, F4W 0.6 mm, IPTL 0.7 mm, MPTL 1.2 mm, OPTL 0.6 mm, FeL 12.1 mm, TL 12.7 mm, TaL 6.7 mm, FL 11.2 mm, T2L 2.7 mm, T2PW 0.5 mm, T2W 0.5 mm, T3L 4.4 mm, T3PW 0.9 mm, T3W 0.5 mm, T4L 8.4 mm, T4PW 1.1 mm, T4W 0.6 mm, T5L 3.9 mm, T5PW 0.6 mm, T5W 0.5 mm, IMTL 1.2 mm, OMTL 0.7 mm, FeL/SVL 44%, TL/SVL 46%, Ha/SVL 25%, TotFL/SVL 66%, HL/SVL 30%, and HW/SVL 27%; dorsal skin slightly shagreened, lateral skin shagreened, and ventral skin smooth (in life, skin shagreened with no tubercles); vocal slits present; in life, dorsal coloration of holotype uniform dark brown, except for pale-colored saddle-band across dorsum, posterior to axilla; head also is dark brown, with small, pale orange spots on dorsal part of snout; pale orange interorbital bar present, paler than saddle band markings on shoulders; flanks same color as dorsum, but with pale orange and white speckling; hind legs reddish-tan, with irregular dark brown transverse bars; upper arms pale orange, largely unmarked except for sparse brown mottling; forearms brown with irregular dark-colored barring; lateral portions of head dark brown without distinct stripe markings; labial region also dark brown, but with white spotting; tympanum not visible, and tympanic region same color as surrounding areas; some orange flash coloration present on inguinal region, but absent on ventral portions of thighs, legs, and feet ventral coloration dark gray above abdomen, and pinkish-gray on abdomen, thighs, and legs; all ventral areas flecked with white; iris copper above, dark brown below (see Fig. 17 for photographs of holotype in life); dorsal coloration in preservative uniform dark brown, with slight trace of pale orange saddle-band on shoulders; interorbital bar pale gray; forearms and hind legs yellowish-tan with dark brown crossbands; upper arms yellowish-tan with no markings; venter gray-brown with white markings, darker along upper abdomen and throat and paler on hind legs and groin area (see Fig. 18).

Variation: The 13 paratypes show little morphological or color variation (Table 6). The SVL ranges from 25.1 to 28.9 mm; the expanded finger pads on the 3rd finger range from 1.7 to 2.5 times the narrowest part of the digit, and on 4th finger from 1.9 to 2.5 times the narrowest part of the digit; the tympanum sometimes is visible in preserved specimens, but not in live specimens, and we noticed that incorrectly preserved specimens dessicated and tend to have the tympanic annuli visible under the skin. Of the 13 paratypes, fiery orange flash coloration in life was present in six specimens, absent in four, and unknown in three.

Table 6. Morphological measurements of external morphological characters of *Eleutherodactylus manantlanensis* sp. nov. Type specimen in dark yellow. SVL = snout–vent length; HL = head length; HW = head width; TW = tympanum width; EW = eye width; ElW = eyelid width; IOD = interorbital distance; IND = internarial distance; END = eye–naris distance; ETD = eye–tympanum distance; UpL = upper arm length; FoL = forearm length; HaL = hand length; F3PW/F3W = 3rd finger pad width (widest measurement) to 3rd finger width (narrowest measurement) ratio; F4PW/F4W = 4th finger pad width (widest measurement) to 4th finger width (narrowest measurement) ratio; FeL = femur length; TL = tibia length; TotFL = total foot length (tarsal tubercle to tip of 4th toe); IPT = inner palmar tubercle length; MPT = middle palmar tubercle length; OPT = outer palmar tubercle length; IMTL = inner metatarsal tubercle length; and OMTL = outer metatarsal tubercle length.

Measurements	MZFC 33372	MZFC 33373	MZFC 33374	MZFC 33375	MZFC 33376	MZFC 33377	MZFC 33379	MZFC 33380	MZFC 33381	MZFC 33292	MZFC 33293	MZFC 33294	MZFC 33295	MZFC 33296
SVL	25.19	25.88	26.76	28.47	25.34	25.44	28.66	27.58	25.71	28.9	25.3	25.14	27.4	26.3
HL	8.75	8.6	9.1	9.26	8.27	8.3	9.56	9.3	8.24	8.9	7.96	7.9	8.4	8.48
HW	7.95	7.52	8.78	7.92	7.75	7.53	8.97	8.25	7.5	7.94	7.0	6.97	7.53	7.76
TW	0.68	0.7	0.6	0.71	0.72	0.7	0.8	0.73	0.66	–	–	–	0.86	–
EW	2.44	2.7	2.4	3.02	2.36	2.72	2.58	2.6	2.4	2.87	2.82	2.77	2.94	2.79
ElW	1.75	1.65	1.93	1.74	1.71	1.66	1.97	1.82	1.65	1.74	1.7	1.69	1.54	1.65
IOD	4.87	5.3	5.06	5.47	4.66	4.78	5.66	5.22	5.17	5.44	4.95	4.9	5.28	5.25
IND	2.39	2.32	2.43	2.47	2.37	2.21	2.68	2.43	2.39	2.55	2.26	2.26	2.58	2.55
END	2.5	2.38	2.55	3.17	2.71	2.41	2.79	2.88	2.63	2.77	2.48	2.45	2.76	2.68
ETD	1.01	1.0	1.1	1.0	0.98	0.98	0.95	0.86	0.86	–	–	–	1.0	–
UpL	5.79	5.32	5.5	6.63	5.2	6.59	6.45	6.21	5.79	6.45	6.05	6.03	5.63	6.2
FoL	7.3	7.49	7.7	8.54	7.25	7.91	8.43	8.04	7.75	7.51	6.95	7.0	7.4	7.14
HaL	6.15	6.31	6.53	6.95	6.18	6.21	6.99	6.73	6.27	6.7	6.3	6.0	6.71	6.82
F3PW/F3W	3.00	1.61	2.48	1.52	2.11	2.21	1.56	1.97	2.07	1.84	2.37	2.41	2.14	1.94
F4PW/F4W	2.80	1.96	2.71	2.17	1.93	1.91	1.98	2.15	2.19	2.02	2.40	2.42	2.18	2.09
FeL	11.89	11.15	11.57	12.59	12.04	12.45	13.12	12.44	11.65	10.3	11.67	11.35	12.06	10.35
TL	12.08	12.49	12.4	13.13	12.29	12.41	12.59	12.29	11.13	11.45	12.1	11.97	12.66	11.2
TotFL	16.98	17.44	18.04	19.19	17.08	17.15	19.32	18.59	17.33	18	17.74	17.38	18.22	18.43
IPT	0.6	0.62	0.54	0.72	0.58	0.57	0.75	0.68	0.63	0.6	0.74	0.71	0.68	0.62
MPT	0.73	0.78	0.82	0.99	0.83	0.99	1.2	1.15	1.05	1.12	1.18	1.08	1.2	1.08
OPT	0.33	0.35	0.37	0.45	0.37	0.45	0.54	0.52	0.47	0.45	0.43	0.42	0.55	0.42
IMTL	1.04	1.11	1.27	1.33	0.99	1.29	1.27	1.12	1.01	0.9	1.01	0.98	1.18	0.87
OMTL	0.68	0.67	0.72	0.63	0.57	0.6	0.82	0.75	0.66	0.65	0.67	0.64	0.72	0.63

***Distribution and Ecology*:** This species is known only from the immediate vicinity of its type locality and might be endemic to the higher portions of the limestone mountain known as Cerro Grande, which forms the eastern third of what collectively is referred to as the Sierra Manantlán (see Fig. 24A). The presence of chiggers (*Hannemannia* sp.), which are unique to saxicolous frogs, suggests that this species lives in the limestone formations present at the type locality. When calling, this frog seems to be closely associated with oak (*Quercus*). It was collected sympatrically only with *Eleutherodactylus grunwaldi*, which is significantly more saxicolous and readily distinguishable by both morphology and call.

***Etymology*:** *Eleutherodactylus manantlanensis* is named after the Sierra de Manantlán, to which it is likely endemic. The Sierra Manantlán is a Sierra Madre del Sur outlier mountain range that stretches across southwestern Jalisco and northern Colima, and has proven to be especially biodiverse.

***Referred Specimens*:** UTADC-1033. Adult of unknown sex collected by Jacobo Reyes-Velasco, Alexander I. Hermosillo-López, and Oscar Avila-López on 11 July 2004 at 2.3 km SW (by road) of El Terrero, Municipio de Minatitlán (19.44146°, -103.95836°, datum WGS 84; elev. 2,127 masl), Colima, Mexico. This specimen originally was identified as *Eleutherodactylus nivicolimae* (Reyes-Velasco et al., 2009). We examined photos of this specimen, and hereby refer it to *E. manantlanensis*.

Eleutherodactylus nietoi sp. nov.

Figs. 20, 21, 22, 23B, 46E

***Holotype*:** (Figs. 20, 21). MZFC 33336 (CIG-00974). Adult male, collected by Christoph I. Grünwald and Hector Franz-Chávez on 29 July 2016 at 18 km NNE of Aquila on the road to Coalcomán de Vázquez-Pallares, Municipio de Chinicuila (18.66666°, -103.42814°; datum WGS 84; elev. 1,130 masl), Michoacán, Mexico (Fig. 24C).

***Paratypes*:** (Fig. 22). Twelve specimens. MZFC 33042 and 33044 (CIG-00346 and CIG-00348), two adult males and MZFC 33043 (CIG-00347), one adult female collected by Christoph I. Grünwald, Hector Franz-Chávez, and Nadia Pérez-Rivera on 6 June 2015 at 3.3 km W of the western Villa Victoria turnoff on the Aquila–Coalcomán Road, Municipio de Chinicuila (18.698922°, -103.411503°; datum WGS 84; elev. 1,413 masl), Michoacán, Mexico; MZFC 33050–33052 (CIG-00355–357), three adult males collected by Christoph I. Grünwald, Hector Franz-Chávez, and Nadia Pérez-Rivera on 6 June 2015 at 3.3 km W of the western Villa Victoria turnoff on the Aquila–Coalcomán Road, Municipio de Chinicuila (18.702412°, -103.397384°; datum WGS 84; elev. 1,525 masl) Michoacán, Mexico; MZFC 33121 (CIG-00299), one adult male and 33045 (CIG-00349) one adult female collected by Christoph I. Grünwald, Hector Franz-Chávez, and Nadia Pérez-Rivera on 6 June 2015 at 1.2 km E of the eastern Villa Victoria turnoff on the Aquila–Coalcomán Road, Municipio de Chinicuila (18.702338°, -103.306424°; datum WGS 84; elev. 1,424 masl) Michoacán, Mexico; MZFC 33337 and 33344 (CIG-00975 and CIG-00994) two adult males, collected at the same locality and on the same date as the holotype; and MZFC 33342 (CIG-00983), one adult male and MZFC 33343 (CIG-00984), one adult female collected by Christoph I. Grünwald and Hector Franz-Chávez on 31 July 2016 in a cave at 1.7 km E of the eastern Villa Victoria turnoff on the Aquila–Coalcomán Road, Municipio de Chinicuila (18.70534°, -103.30393°, datum WGS 84; elev. 1,446 masl), Michoacán, Mexico.

***Diagnosis*:** A member of the genus *Eleutherodactylus*, subgenus *Syrrhophus*, as defined by Hedges et al. (2008). In the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Series and the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group, as defined in this paper (see discussion below). A moderate-sized frog, adult males measure 20.7–26.0 mm SVL; vocal slits present in males; digital tips widely expanded, 2.0–3.3 times width of narrowest part of finger on 3rd finger and 2.1–3.4 times width of narrowest part of finger on 4th finger; fingers relatively short, 3rd finger 12–17% of SVL (see Fig. 23B); compact lumbar gland above inguinal region absent; epidermis not translucent on venter, and abdominal vein not visible on venter of live specimens; limbs relatively short, TL/SVL ratio 0.32–0.50, FeL/SVL ratio 0.36–0.48, and TotFL/SVL ratio 0.60–0.71; snout short, END/SVL ratio 0.08–0.11; tympanum small, round, and indistinct, but visible; TW/EW ratio 0.16–0.31; dorsal skin slightly to moderately pustulate; ventral skin areolate; dorsal coloration variable, but usually brown, tan, yellow, or red, with pale-colored "saddle blotches" on shoulders; pale-colored middorsal stripe present or not; pale-colored interorbital bar present; upper arms pale, unmarked, same color as pale-colored shoulder "saddle"; indistinct dark-colored transverse bars on forearms, thighs, and legs; ventral coloration gray with distinct white blotches; flash coloration sometimes present on inguinal region and anterior portions of thighs, and when present flash coloration pale to fiery orange; and mating call of adult males a short trill (see below; Fig. 29B).

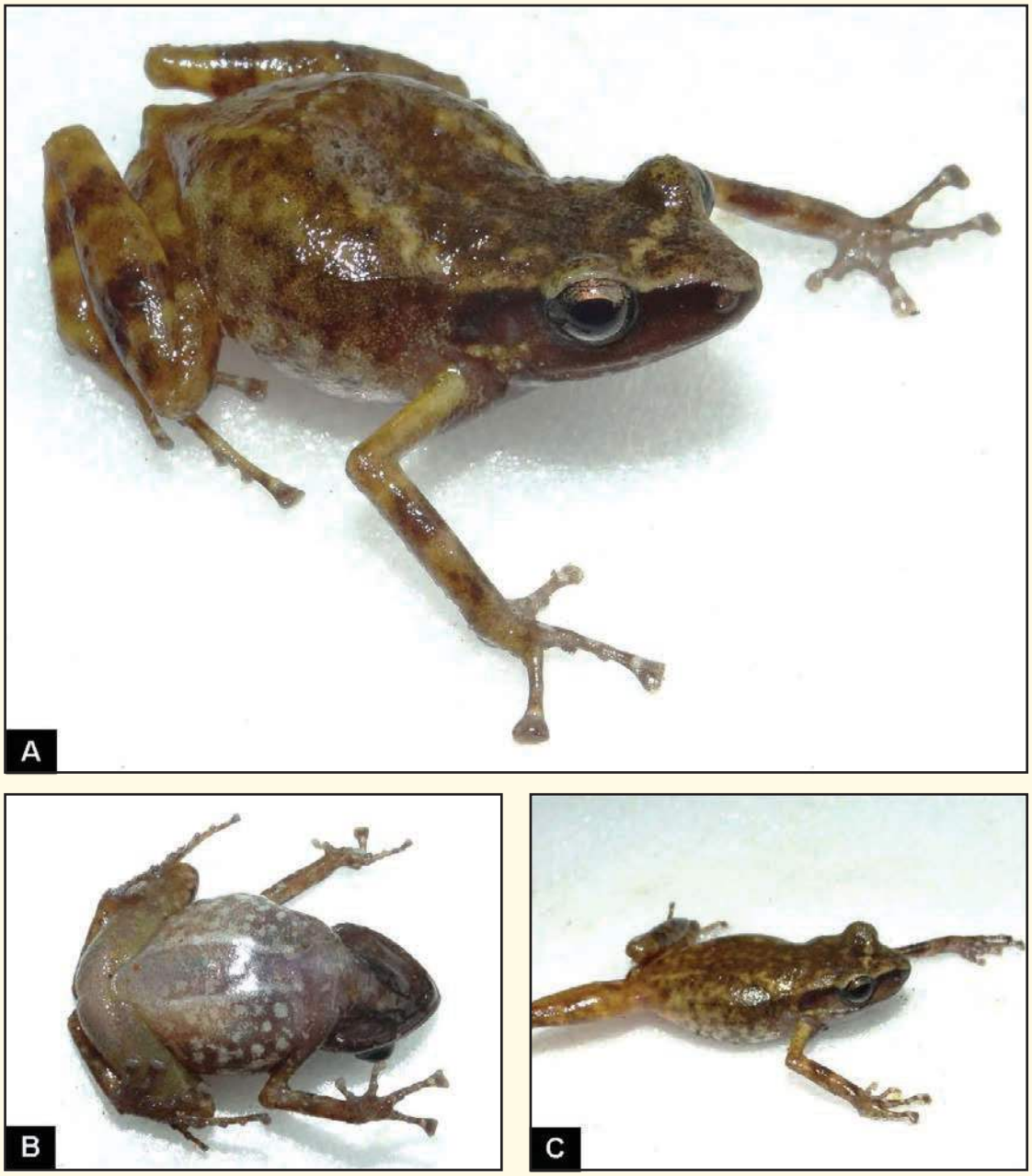


Fig. 20. Holotype of *Eleutherodactylus nietoi* sp. nov. in life, MZFC 33336 (CIG-00974). (A) Full body view; (B) ventral view; and (C) lateral view.

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***Comparisons*:** *Eleutherodactylus nietoi* can be distinguished from all species in the *Eleutherodactylus* (*Syrrhophus*) *longipes* Species Series (as defined herein, see below) by the presence of a small, indistinct tympanum with no tympanic annulus visible, and with a diameter less than 31% of the eye diameter; by a non-translucent abdominal epidermis, thus a visible abdominal vein on the venter is not evident in life; and by the presence of a 3rd (outer) palmar that is smaller than 46% of the middle palmar tubercle.

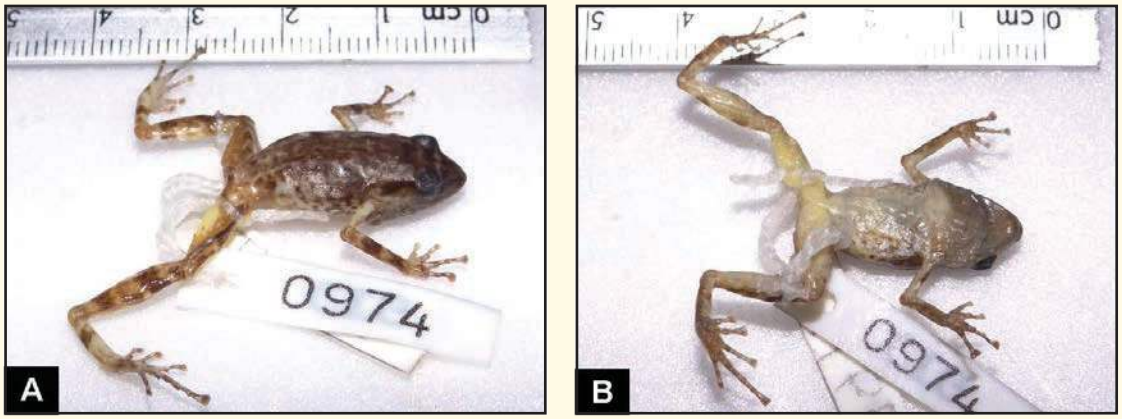


Fig. 21. Holotype of *Eleutherodactylus nietoi* sp. nov. in preservative, MZFC 33336 (CIG-00974). (A) Dorsal view; and (B) ventral view. © Christoph I. Grünwald

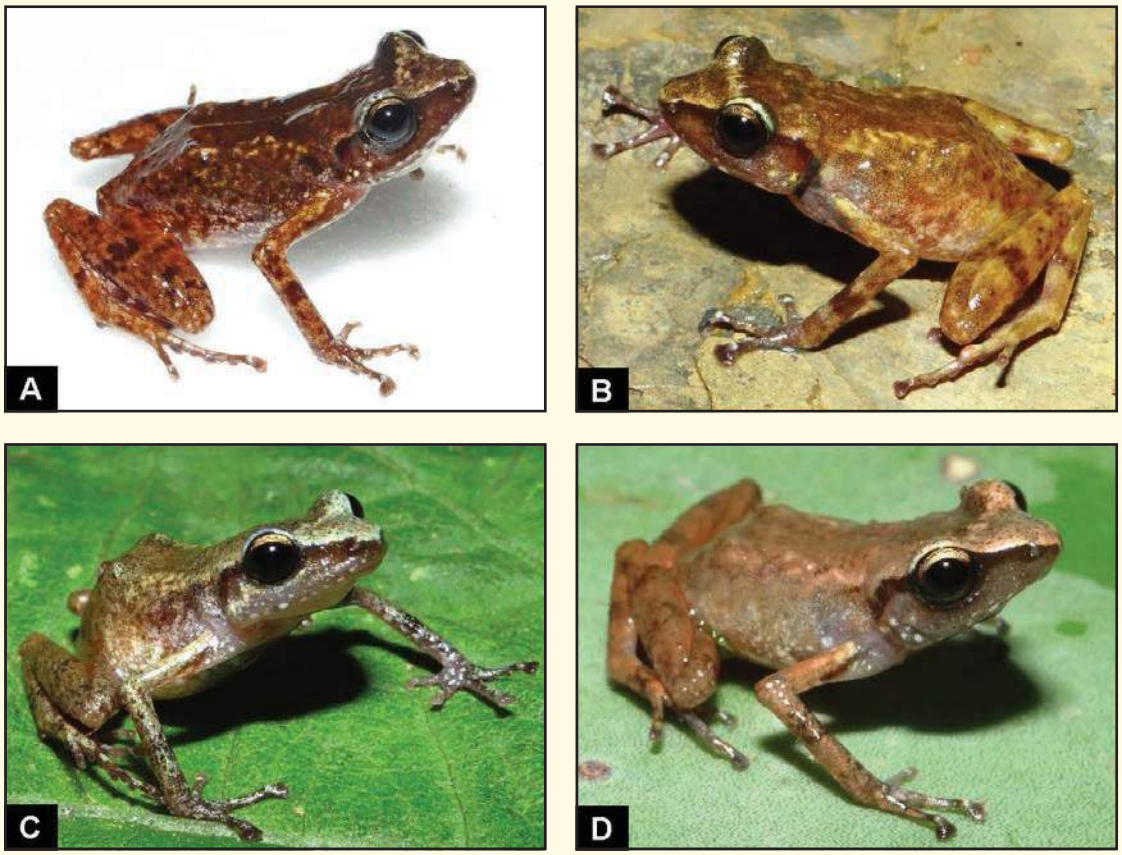


Fig. 22. Variation in *Eleutherodactylus nietoi* sp. nov. (A) Male from Municipio de Chinicuila, Michoacán, MZFC 33342 (CIG-00983); (B) female from Municipio de Chinicuila, Michoacán, MZFC 33343 (CIG-00984); (C) female from near Municipio de Chinicuila, Michoacán. MZFC 33052 (CIG-00357); and (D) male from the type locality, Municipio de Chinicuila, Michoacán, MZFC 33337 (CIG-00975). © Christoph I. Grünwald

Eleutherodactylus nietoi can be distinguished from most species of the *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Group (as defined herein, see below) by a combination of the expanded finger pads on the 3rd and 4th fingers and lacking a compact, protruding lumbar gland in the inguinal region. It can be distinguished from the remaining two species, *E. pipilans* and *E. rubrimaculatus*, by its more expanded finger pads, pustulate skin, and a pale-colored interorbital bar.

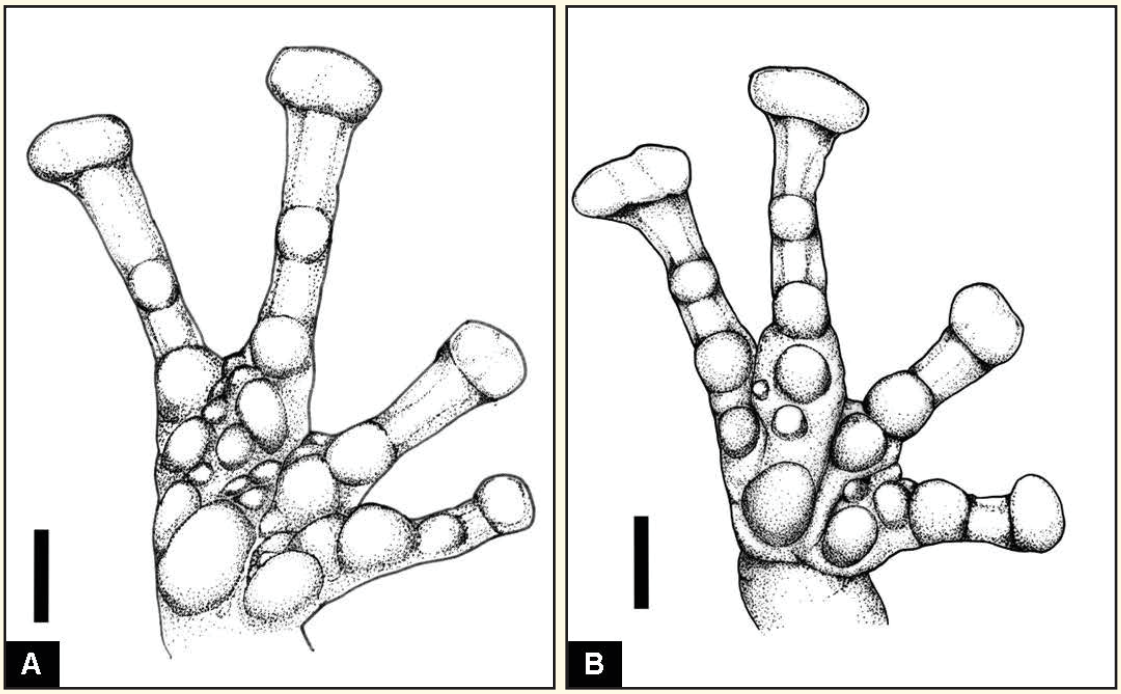


Fig. 23. Hand drawings of *Eleutherodactylus*. (A) *Eleutherodactylus manantlanensis* sp. nov.; and (B) *Eleutherodactylus nietoi* sp. nov. Vertical bars = 1 mm. Drawings by Iván T. Ahumada-Carrillo.

Within the *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group (as defined herein, see below), *E. nietoi* can be distinguished from *E. angustidigitorum*, *E. grandis*, and *E. saxatilis* by lacking protruding, compact lumbar glands above the inguinal region. It can be distinguished from *E. grunwaldi*, *E. modestus*, *E. teretistes*, and *E. pallidus* by its pustulate skin and the presence of an interorbital bar. The skin of *E. interorbitalis* also is smooth, and the interorbital bar is darker than its pale-colored dorsum. *Eleutherodactylus wixarika* can be distinguished from *E. nietoi* by the lack of bright flash coloration in the inguinal region and on the thighs, as well as a pale-colored interorbital bar. Superficially, *E. rufescens* and *E. floresvillelai* are similar to *E. nietoi*, but typically both are smaller frogs and their mating call consists of a single peep, as opposed to a long trill. *Eleutherodactylus erendirae* also is a smaller frog (under 23.0 mm), but its trill is similar. Further, *E. erendirae* can be distinguished from *E. nietoi* by its significantly less expanded fingertips, which are expanded less than 1.6 times the narrowest part of the digit on both fingers 3 and 4 in *E. erendirae*, but in *E. nietoi* are expanded more than 2 times (and usually more than 2.5 times) the width of the narrowest part of the digit on both fingers 3 and 4. *Eleutherodactylus nietoi* is a variable frog that seems to be most closely related to *E. colimotl*, *E. jaliscoensis*, and *E. manantlanensis*. *Eleutherodactylus colimotl* differs from *E. nietoi* by its smooth skin and an immaculate white ventral coloration, as well as by its distinct mating call, which consists of a single, short chirp. The mating call of *E. jaliscoensis* is similar, although it is a shorter and more concise trill than that of *E. nietoi*. *E. jaliscoensis* further differs by its a darker gray or black reticulated venter, more

prominent fiery red flash coloration, more pustulate skin, and less expanded digits on the fingers (1.6–2.1 times the narrowest part of the digit on the 3rd finger of *E. jaliscoensis*, compared to 2.0–3.3 times the narrowest part of the digit on the 3rd finger of *E. nietoi*). *Eleutherodactylus manantlanensis* is most similar to *E. nietoi*, and thus the most easily confused species. *Eleutherodactylus manantlanensis* is a larger frog (25.2–28.9 mm in *E. manantlanensis* vs. 20.7–26.0 mm in *E. nietoi*) in which the tympanum is not visible in life, its dorsum is less pustulate, pale-colored markings are absent in the upper arms, and its mating call consists of a faster multi-note trill than that of *E. nietoi* (See Fig. 29).

***Description of Holotype*:** A small frog (22.4 mm SVL); male; head slightly longer (7.4 mm) than wide (7.2 mm), head same width as body; snout subelliptical from dorsal view and rounded from lateral view; tympanum indistinct, but visible, rounded with no supra-tympanic fold present; tympanum small, circular, greatest width of tympanum 0.8 mm; greatest diameter of eye 2.7 mm; tympanum width to eye diameter ratio 0.3; eyelid width 1.5 mm, 28% of IOD; 1st finger similar to 2nd finger in length; finger lengths from shortest to longest 1-2-3-4, with 1 and 2 similar to one another; digital pads on fingers 2, 3, and 4 expanded, 2.1 times the narrowest point of digit on 2nd finger, 2.5 times width of narrowest point of digit on 3rd finger, and 2.7 times width of narrowest point of digit on 4th finger; expanded finger pads truncate; 3 palmar tubercles, outer palmar tubercle very small; inner palmar tubercle 62% as large as middle palmar tubercle, outer palmar tubercle 43% size of middle palmar tubercle, noticeably small; toe lengths from shortest to longest 1-2-5-3-4, TL2 and TL5 nearly equal; outer metatarsal tubercle spherical in shape with round base, large, approximately 42% size of inner metatarsal tubercle; inner metatarsal tubercle large, spherical with oval base, 1.1 mm; IND 2.0 mm, IOD 4.8 mm, END 2.5 mm, ETD 1.0 mm, UpL 5.9 mm, FoL 6.7 mm, HaL 5.5 mm, F1L 1.8 mm, F1PW 0.3 mm, F1FW 0.3 mm, F2L 2.0 mm, F2PW 0.8 mm, F2W 0.4 mm, F3L 3.2 mm, F3PW 1.1 mm, F3W 0.4 mm, F4L 2.5 mm, F4PW 1.1 mm, F4W 0.4 mm, IPTL 0.5 mm, MPTL 0.8 mm, OPTL 0.4 mm, FeL 10.4 mm, TL 11.1 mm, TaL 5.0 mm, FL 10.0 mm, T2L 2.8 mm, T2PW 0.8 mm, T2W 0.5 mm, T3L 4.0 mm, T3PW 0.9 mm, T3W 0.5 mm, T4L 6.6 mm, T4PW 0.9 mm, T4W 0.5 mm, T5L 2.7 mm, T5PW 0.5 mm, T5W 0.3 mm, IMTL 1.1 mm, OMTL 0.5 mm, FeL/SVL 46%, TL/SVL 50%, HA/SVL 25%, TotFL/SVL 67%, HL/SVL 33%, and HW/SVL 32%; dorsal skin smooth with sparse tubercles, lateral skin shagreened with sparse tubercles, and ventral skin smooth; skin much more tuberculate in life; vocal slits present; in life, dorsal coloration of holotype dark brown with indistinct yellow blotches; head same coloration as dorsum, with pale tan interorbital bar; lateral portions of head dark brown with no speckling; tan border separates dark-colored areas on side of head from dorsal coloration on top of head; flanks of body dark brown with some white reticulation; hind legs yellowish-brown with one dark brown transverse bar on tarsus, two dark brown transverse bars on tibia, and none on femur; front legs also yellowish-brown, with a dark brown transverse bar present on forearms and another on wrists; upper arms yellow, without dark-colored markings; tympanum dark brown, same color as surrounding coloration; bright flash colors absent on inguinal region, thigh, legs, and arms; ventral coloration gray with white blotches; throat and chin darker gray; iris copper, paler above than below (see Fig. 20 for photographs of holotype in life); coloration in preservative dark brown, with cream flecking on dorsum and cream reticulations on flanks; interorbital bar and upper arms cream and unmarked; one dark brown transverse bar present on forearms, wrists, and tarsus; two dark brown transverse bars present on tibia; femur yellowish-brown; and venter gray with white blotches, with slightly darker shade of gray with no blotching on throat and chin (see Fig. 21).

***Variation*:** The 13 paratypes show moderate amounts of variation in morphological characters and substantial variation in coloration (Table 7). The SVL ranges from 20.7 to 26.0 mm. The expanded finger pads on the 3rd finger range from 2 to 3.3 times the width of the narrowest part of the digit, and the expanded finger pads on the 4th finger range from 2.1 to 3.4 times the narrowest part of the digit. The dorsal skin varies from smooth ($n = 2$) to pustulate ($n = 4$), and varying degrees inbetween ($n = 7$). The size of the tympanum is variable, as the TW/ED ratio ranges from 16 to 31%. The characteristic "saddle blotches" on the shoulders and unmarked pale-colored upper arms usually are present, but were absent in at least two specimens. A pale-colored middorsal stripe usually was absent, but present in one specimen. The inguinal flash coloration also was variable, present in a few specimens but absent in most. The dorsal gound coloration is variable, as the paratypes range from pale tan and reddish-brown to dark brown. The ventral coloration varied from white with gray blotches to almost uniform gray with white spots. We present the morphological variation in Table 7.

Table 7. Morphological measurements of external morphological characters of *Eleutherodactylus nietoi* sp. nov. Type specimen in dark yellow. SVL = snout–vent length; HL = head length; HW = head width; TW = tympanum width; EW = eye width; ElW = eyelid width; IOD = interorbital distance; IND = internarial distance; END = eye–naris distance; ETD = eye–tympanum distance; UpL = upper arm length; FoL = forearm length; HaL = hand length; F3PW/F3W = 3rd finger pad width (widest measurement) to 3rd finger width (narrowest measurement) ratio; F4PW/F4W = 4th finger pad width (widest measurement) to 4th finger width (narrowest measurement) ratio; FeL = femur length; TL = tibia length; TotFL = total foot length (tarsal tubercle to tip of 4th toe); IPT = inner palmar tubercle length; MPT = middle palmar tubercle length; OPT = outer palmar tubercle length; IMTL = inner metatarsal tubercle length; and OMTL = outer metatarsal tubercle length.

Measurements	MZFC 33042	MZFC 33043	MZFC 33044	MZFC 33045	MZFC 33050	MZFC 33051	MZFC 33052	MZFC 33336	MZFC 33337	MZFC 33338	MZFC 33342	MZFC 33343	MZFC 33344
SVL	24.35	24.58	24.99	23.95	23.01	23.45	21.59	22.44	21.07	21.25	25.53	25.98	20.7
HL	8.24	8.17	8.42	8.13	8.22	8.48	7.03	7.4	6.65	6.7	8.21	8.4	7.07
HW	7.15	7.28	7.65	7.41	7.39	7.99	6.62	7.17	6.16	6.28	7.4	7.62	6.3
TW	0.59	0.61	0.57	0.52	0.78	0.55	0.4	0.75	0.72	0.72	0.8	0.8	0.73
EW	2.46	2.29	3.14	3.3	2.5	2.25	2.45	2.65	2.54	2.48	3.1	3.12	2.45
ElW	1.64	1.67	1.76	1.7	1.7	1.84	1.53	1.47	1.43	1.44	1.8	1.74	1.41
IOD	4.76	4.69	4.39	4.45	4.29	4.53	4.02	4.76	4.29	4.2	5.22	5.13	4.24
IND	2.08	2.07	2.31	2.27	1.99	2.28	1.86	1.99	1.95	1.93	2.46	2.4	1.98
END	2.35	2.39	2.07	2.13	2.01	2.43	2.05	2.46	2.26	2.22	2.78	2.7	2.27
ETD	0.74	0.84	1.0	0.73	0.62	0.88	0.7	0.98	0.96	0.97	0.96	0.97	0.85
UpL	5.23	5.21	4.95	5.1	4.44	5.41	4.26	5.92	5.0	4.58	6.72	6.82	5.32
FoL	6.75	7.17	5.09	7.38	6.17	7.04	6.02	6.73	5.83	5.33	7.32	7.65	5.77
HaL	6.21	6.27	6.4	6.1	5.3	5.4	5.0	5.5	4.85	4.4	6.64	6.6	4.66
F3PW/F3W	2.44	2.0	2.15	2.33	2.57	2.04	2.26	2.5	2.67	2.11	2.38	3.29	2.69
F4PW/F4W	2.24	2.69	2.4	2.88	2.48	2.09	2.32	2.74	2.7	2.13	2.75	3.4	2.74
FeL	9.8	11.89	10.94	11.6	8.39	9.07	9.1	10.38	8.7	9.22	12.3	12.32	8.57
TL	9.92	11.87	10.51	8.12	9.03	10.77	6.97	11.11	9.53	9.48	12.84	13.04	9.94
TotFL	16.31	16.47	16.74	16.05	15.42	15.71	14.47	16.00	13.50	12.90	18.10	18.40	13.50
IPT	0.68	0.65	0.71	0.66	1.23	0.62	0.48	0.54	0.52	0.44	0.67	0.61	0.52
MPT	0.94	0.9	1.04	0.98	0.57	1.04	0.63	0.87	0.74	0.81	1.0	1.03	0.8
OPT	0.4	0.4	0.46	0.43	0.25	0.46	0.28	0.5	0.33	0.34	0.45	0.47	0.17
IMTL	0.93	1.08	0.99	1.04	1.12	1.06	1.05	1.12	0.88	0.83	1.04	1.02	0.81
OMTL	0.61	0.57	0.67	0.66	0.53	0.53	0.4	0.47	0.4	0.55	0.68	0.53	0.47

***Distribution and Ecology*:** *Eleutherodactylus nietoi* occurs at moderate elevations on the windward slopes of the Sierra Coalcomán in western Michoacán (see Fig. 24A). This frog occurs at elevations ranging from 1,130 to 1,530 m. This species has been collected in tropical deciduous forest–oak woodland ecotone, pine-oak woodland (predominately oak), and humid pine-oak forest (predominately pine), and appears to prefer habitats with large leaf oak trees (*Quercus*). *Eleutherodactylus nietoi* has been found sympatrically with *E. nitidus*, *E. rufescens*, and in close proximity to *E. colimotl*.

***Etymology*:** This species is named after Adrian Nieto-Montes de Oca, a renowned Mexican herpetologist and co-curator of the herpetological collection at Museo de Zoólogia, Facultad de Ciencias at UNAM (MZFC).

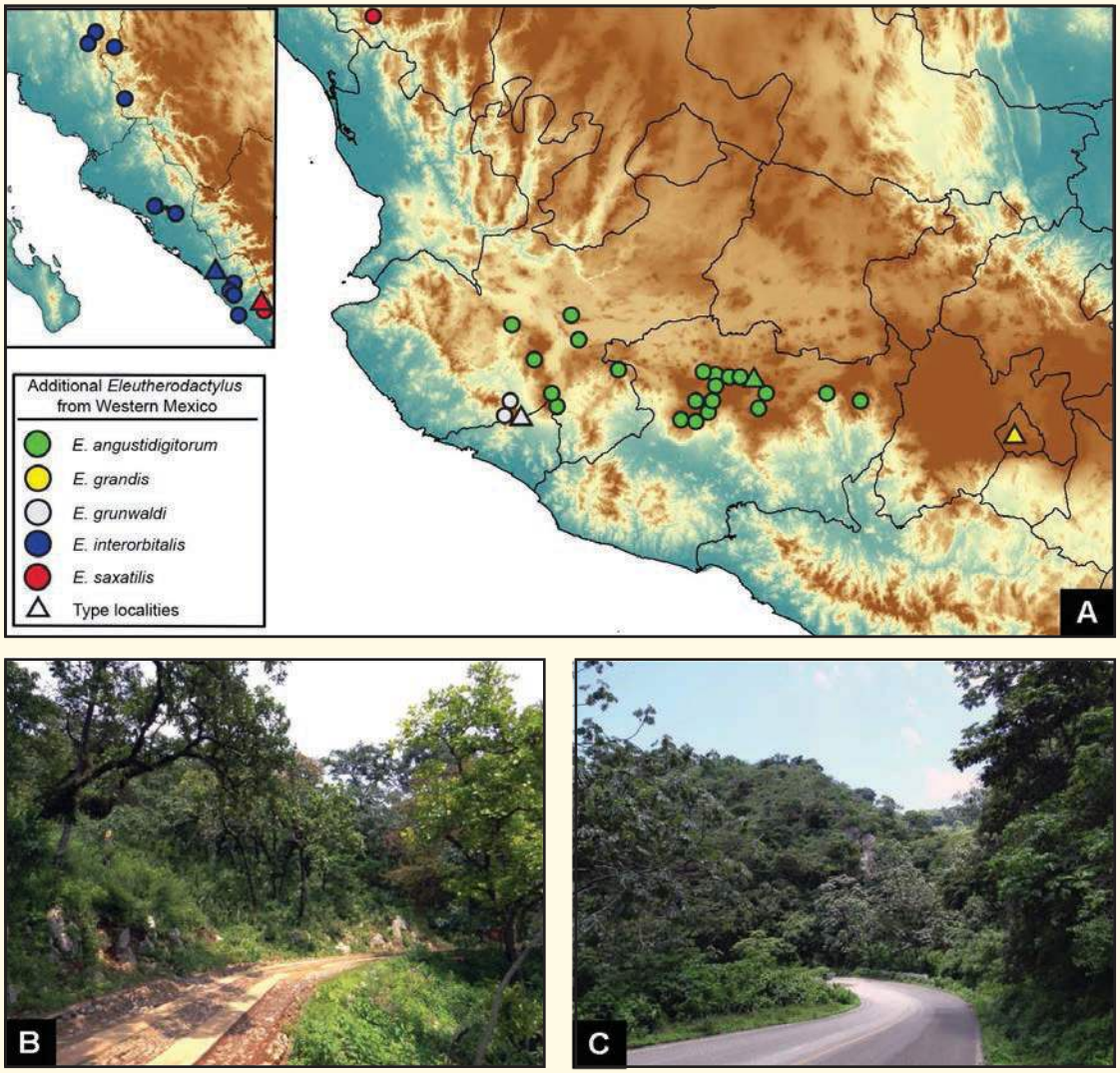


Fig. 24. (A) Map showing the distribution of some members of the *Eleutherodactylus modestus* Species Group from western Mexico; (B) photo of the type locality of *Eleutherodactylus manantlanensis* sp. nov., near El Terrero, Municipio de Minatitlán, Colima; and (C) photo of the type locality of *Eleutherodactylus nietoi* sp. nov., near Villa de Victoria turnoff, Municipio de Chinicuila, Michoacán. Map by Jacobo Reyes-Velasco. © Christoph I. Grünwald

Estimates of Evolutionary Relationships

Based on our phylogenetic analysis of the mitochondrial gene 16s, we recovered two main lineages in the subgenus *Syrrhophus*, of which one contains two distinct clades (Fig. 25). Following Hedges et al. 2008, we refer to these lineages as "species series" and define them below. We refer to the additional clades in one of the species series as "species groups," and focused our molecular work on the species group containing the new species described above.

The relationships between the main lineages were poorly supported; however, each species group received high posterior support (Fig. 25). The *Eleutherodactylus longipes* Species Series (as defined below) was sister to the *E. nitidus* Species Series, which consists of the *nitidus* and *modetus* species groups (as defined below). The relationships among many currently recognized species of each group also received strong support, with some exceptions.

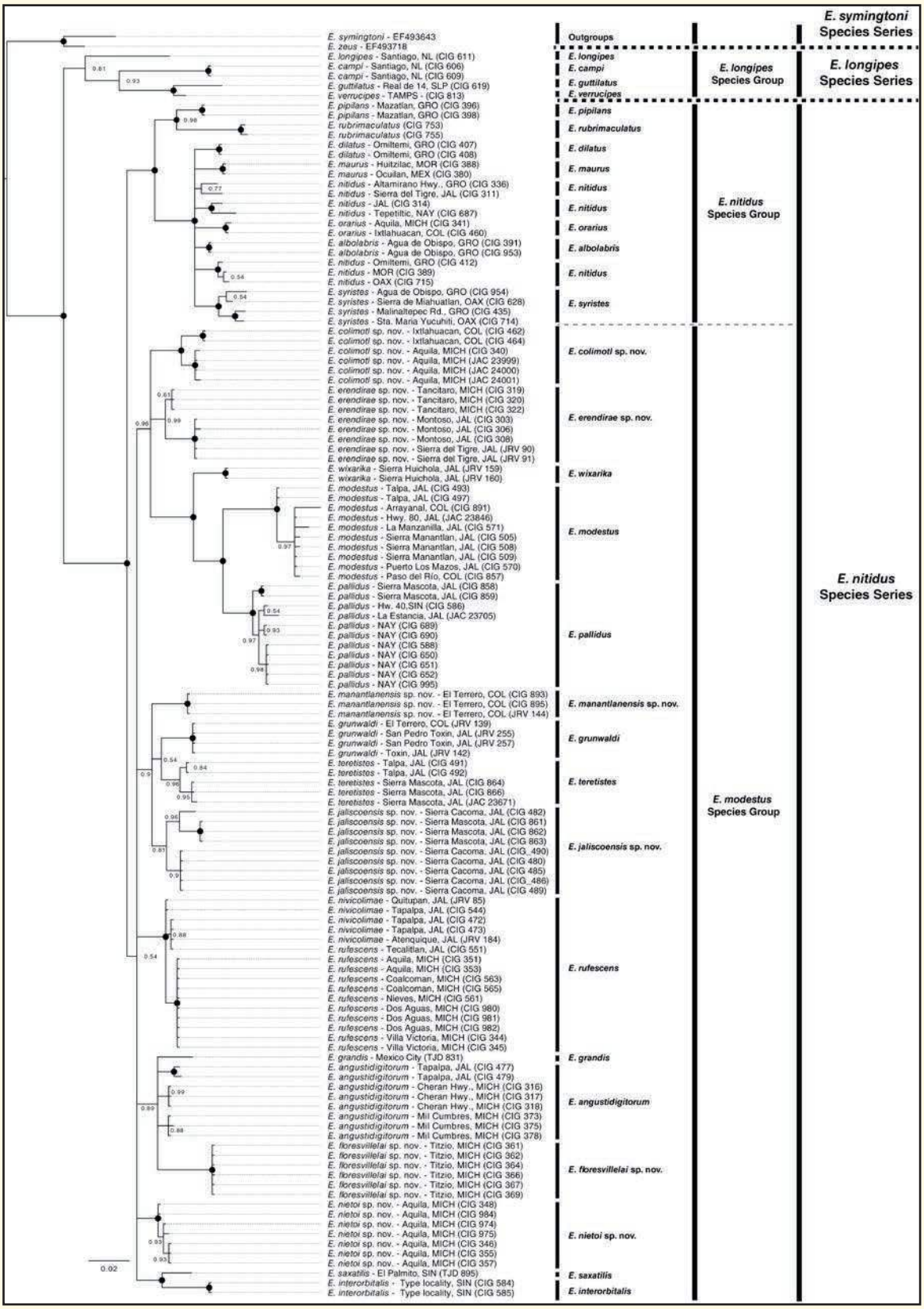


Fig. 25. Phylogenetic tree showing the relationships of *Eleutherodactylus* subgenus *Syrrhophus*, with a focus on the *E. nitidus* Species Series and specifically the *E. modestus* Species Group.

In the *Eleutherodactylus longipes* Species Series, *E. campi* was sister to *E. cystignathoides*, whereas *E. longipes* was the sister taxon to *E. guttilatus* + *E. verrucipes*. The *E. nitidus* Species Series contains two main clades that are sister to one another, and comprise the two species groups we describe below.

In the *Eleutherodactylus nitidus* Species Group, *E. pipilans* and *E. rubrimaculatus* were recovered as the sister taxa to all the other species. The remaining species were divided between two lineages, one composed of individuals of *E. maurus*, *E. dilatus*, and *E. syristes*, and the other includes all populations of *E. nitidus*, as well as *E. orarius* and *E. albolabris*.

In the *Eleutherodactylus modestus* Species Group, we recovered the species *E. interorbitalis* + *E. saxatilis* as the sister taxa to all other members of the group. The remaining species grouped into three lineages. One is composed of various populations of *E. rufescens*, including specimens previously asigned to "*E. nivicolimae*" (see Discussion). This species is the sister taxon to a lineage consisting of all the remaining species of the *E. modestus* Species Group, with low posterior support (Fig. 25).

Advertisement Call Analysis

We recorded 110 calling males of all 24 species of *Eleutherodactylus* from western Mexico. We found that the calls of the species analyzed fall into five different categories, and consist of a rapid whistle (Trill), a drawn out whistle (Whistle), a strong high-pitched chirp (Peep), a soft high-pitched chirp (Chirp), and a low-pitched chirp (Pipe). Of the species described herein, two (*E. colimotl* and *E. floresvillelai*) produce a strongly high-pitched chirp (Peep) and four (*E. erendirae*, *E. jaliscoensis*, *E. manantlanensis*, and *E. nietoi*) produce multi-note whistles (trills) of varying rates and notes.

***E. colimotl*:** The advertisement call of *E. colimotl* is a single high-pitched "chirp" best described as a "peep" (Fig. 26). Calls recorded at the type locality consist of a rapid chirp, with an average duration of 85 MS and a dominant frecuency ranging between 3,015 kHz and 3,400 kHz. At a second locality (Aquila, Michoacan), calls consisted of a slightly longer chirp, with an average duration of 125 MS and a dominant frecuency of 2910 kHz.

***E. erendirae*:** The advertisement call of *E. erendirae* is a rapid, multi-note "trill" best described as a "reep" (Fig. 27). Calls recored at the type locality consist of rapid seven note trills with an average duration of 107 MS, and a dominant frequency starting at 3,330 kHz and rising to 3,650 kHz. At a second locality (El Montoso, Jalisco), calls consisted of rapid elevn note trills with an average duration of 225 MS, and a dominant frecuency starting at 3,485 kHz and rising to 3,860 kHz.

***E. floresvillelai*:** The advertisement call of *E. floresvillelai* is a single high-pitched "chirp" best described as a "peep"(Fig. 28A). Calls recorded at the type locality consisted of one drawn out high-pitched chirp, with an average duration of 210 MS and a dominant frecuency ranging between 3,550 and 3,850 kHz.

***E. jaliscoensis*:** The advertisement call of *E. jaliscoensis* is a slow multi-note "trill" (Fig. 28B). Calls recorded at the type locality consisted of three note trills with an average duration of 166 MS, and a dominant frecuency of 2,625 kHz. At a second locality (Peña del Cuervo, Jalisco), calls consisted of four note trills with an average duration of 215 MS, and a dominant frecuency of 2,600 kHz.

***E. manantlanensis*:** The advertisement call of *E.manantlanensis* is a multi-note "trill" (Fig. 29A). Calls recorded at the type locality consisted of rapid nine note trills with an average duration of 220 MS and with a dominant frequency starting at 2,550 kHz and rising to 2,780 kHz.

***E. nietoi*:** The advertisement call of *E. nietoi* is a is a multi-note "trill" (Fig. 29B). Calls recorded at the type locality consisted of drawn out five note trills with an average duration of 257 MS, with a dominant frecuency starting at 3,470 kHz and rising to 3,750 kHz.

DISCUSSION

Ecological and Morpological Differences among the New Species of *Eleutherodactylus*

Eleutherodactylus erendirae and *E. floresvillelai* appear to fill a similar ecological niche to that of *E. modestus*, but at higher elevations. They share a similar high elevation habitat as *E. rufescens* (as defined below), another member

of the *E. modestus* Species Group. *Eleutherodactylus rufescens* is more of a habitat generalist than either *E. erendirae* or *E. floresvillelai*, and is more widespread in Jalisco and western Michoacán (see Fig. 16A). *Eleutherodactylus erendirae* and *E. floresvillelai* are restricted to very humid and semi-tropical highlands immediately bordering the Balsas-Tepalcatepec Depression. Although superficially similar, the three species are distinguished from one another by morphological characters and distinctive calls (see above).

Eleutherodactylus colimotl apparently is limited to karstic limestone habitat, whereas *E. modestus* is a habitat generalist. We collected *E. modestus* in areas of karstic limestone, but did not find this species exclusive to rocks. Interestingly, *E. modestus* has not been collected in sympatry with *E. colimotl.*

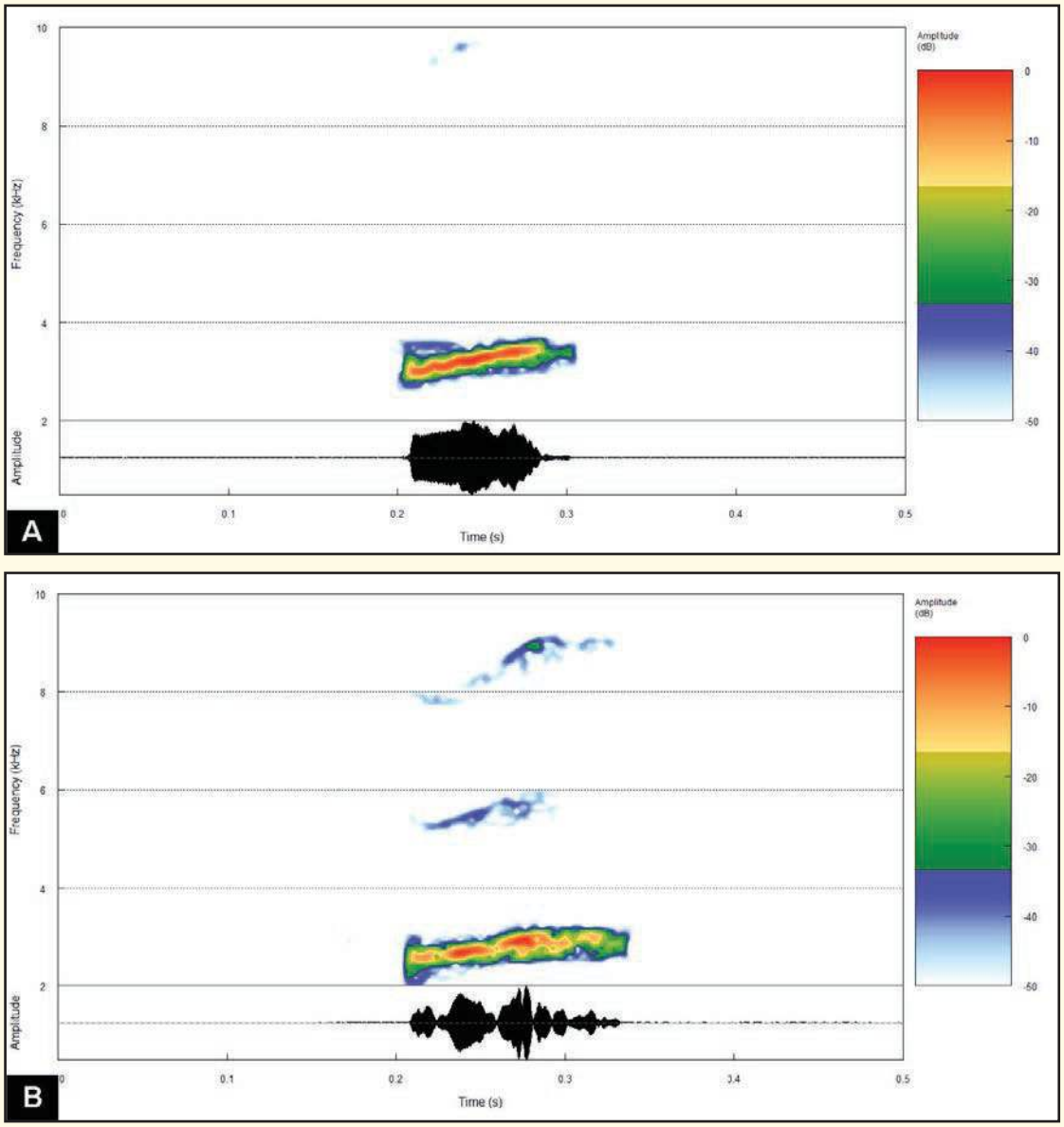


Fig. 26. (A) Sonogram of the call of a male *Eleutherodactylus colimotl* sp. nov. (Recording CIG-0046) from near the type locality at Ixtlahuacán Road Junction, Municipio de Ixtlahuacán, Colima; and (B) recording of a male *Eleutherodactylus colimotl* sp. nov. (Recording CIG-0087) from near Aquila, Municipio de Aquila, Michoacán. Graphics by Vinicius Guerra-Batista.

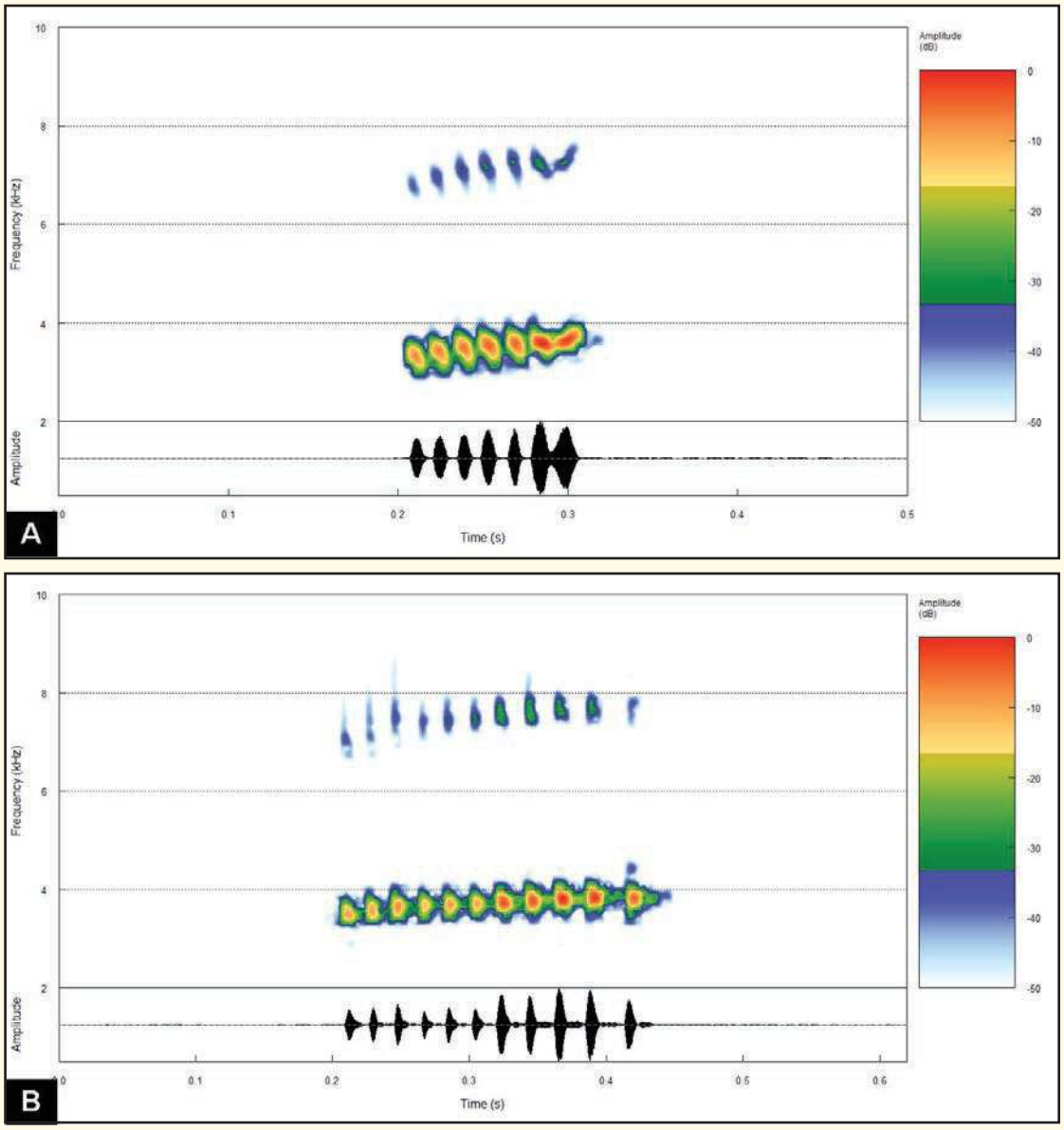


Fig. 27. (A) Sonogram of the call of a male *Eleutherodactylus erendirae* sp. nov. (Recording CIG-0015) from the type locality at Aparícuaro, Municipio de Tancítaro, Michoacán; and (B) recording of a male *Eleutherodactylus erendirae* sp. nov. (Recording CIG-0008) from El Montoso, Municipio de Quitupan, Jalisco. Graphics by Vinicius Guerra-Batista.

Based on our morphological data and call analyses, *E. jaliscoensis*, *E. manantlanensis*, and *E. nietoi* are similar to one another, as they occupy similar habitats in different mountain ranges of coastal Jalisco, Colima, and Michoacán (Fig. 16A). Collectively, they are similar to *E. teretistes*, but differ by the presence of an interorbital bar and more expanded fingertips. Among these three species, *E. manantlanensis* stands out by its larger size, and the presence of expanded fingertips and pale-colored saddle blotches on the shoulders, and the absence of a visible tympanum and flash colors. This species also is restricted to karstic oak woodlands in the Cerro Grande region of the Sierra Manantlán, where it has been collected only along a 3 km stretch of dirt road near the type locality (Fig. 16A).

Eleutherodactylus jaliscoensis differs from *E. manantlanensis* and *E. nietoi* based on its dark dorsal coloration and generally dark-colored venter, bright red, orange, or yellow flash colors, and granular dorsal skin. Unlike the other two species, this frog is not restricted to karstic regions. *Eleutherodactylus nietoi* is the most variable of the three species, and shares coloration and morphological characters with both of its most similar relatives. Nonetheless, this species most closely resembles *E. colimotl* in coloration, a species that occurs in close proximity, from which it can readily be distinguished by its advertisement call (see Figs. 26A, 29B).

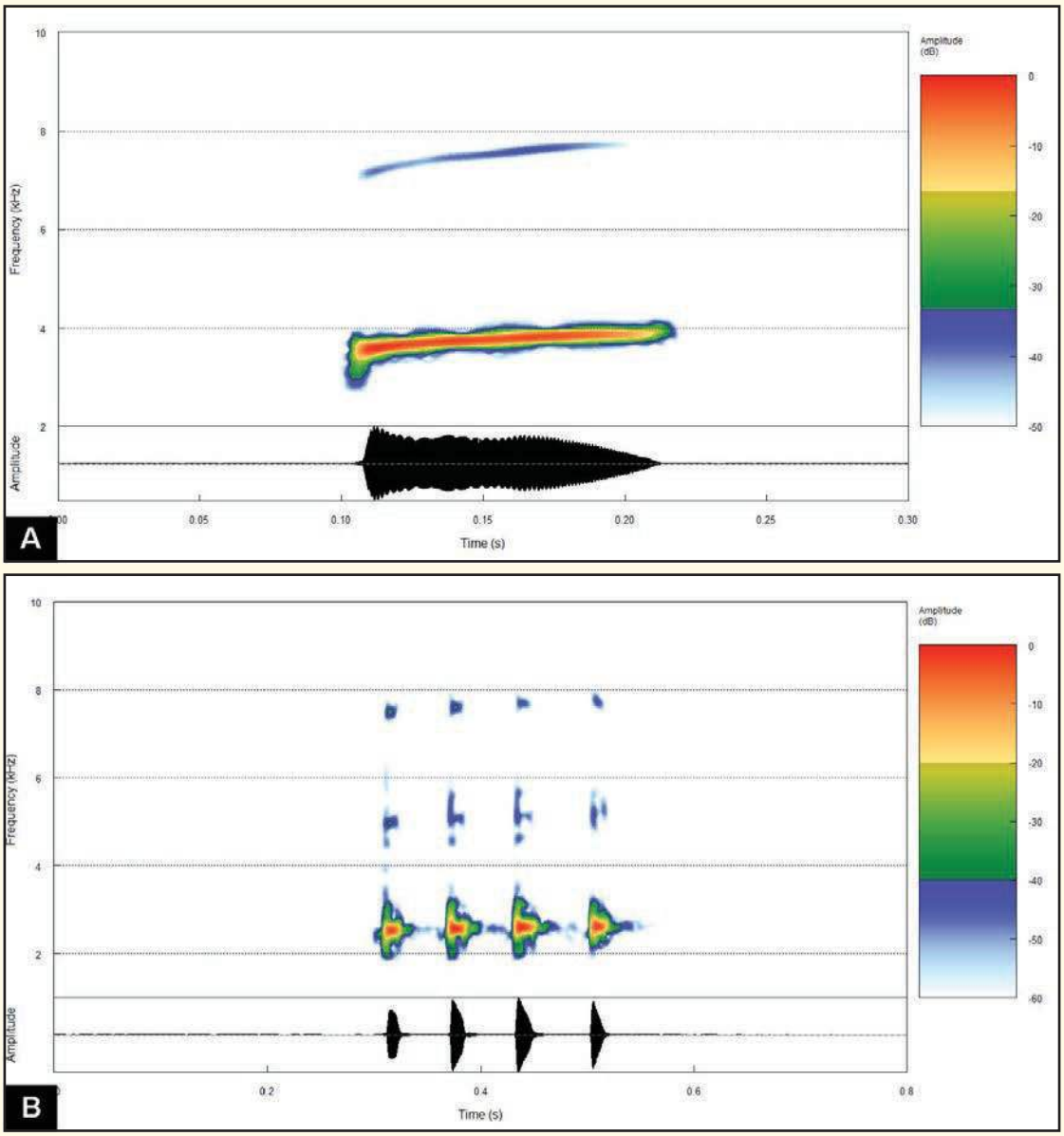


Fig. 28. (A) Sonogram of the call of a male *Eleutherodactylus floresvillelai* sp. nov. (Recording CIG-0022) from the type locality at the Tzitzio Junction, Municipio de Charo, Michoacán; and (B) recording of a male *Eleutherodactylus jaliscoensis* sp. nov. (Recording CIG-0027) from the type locality near Cumbre de Guadalupe, Municipio de Talpa de Allende, Jalisco. Graphics by Vinicius Guerra-Batista.

In west-central Jalisco, *E. jaliscoensis* occurs sympatrically or in close proximity with at least four other species, *E. nitidus*, *E. pallidus*, *E. teretistes*, and *E. modestus*. All of these species (except *E. modestus*) have been collected along a short stretch of road in the Sierra Mascota of Jalisco. Areas with such high diversity for members of one genus are confusing to taxonomists and field herpetologists, and thus we include photographs of individuals of the five species collected in the same general area to serve as a reference for future studies (see Fig. 30).

The situation in southwestern Michoacán is even more complex, as both *E. colimotl* and *E. nietoi* occur on the Aquila–Coalcomán road, along with four other species, *E. orarius*, *E. nitidus*, *E. rufescens*, and *E. modestus*. We include photographs of all six species collected in this region for reference (see Fig. 31).

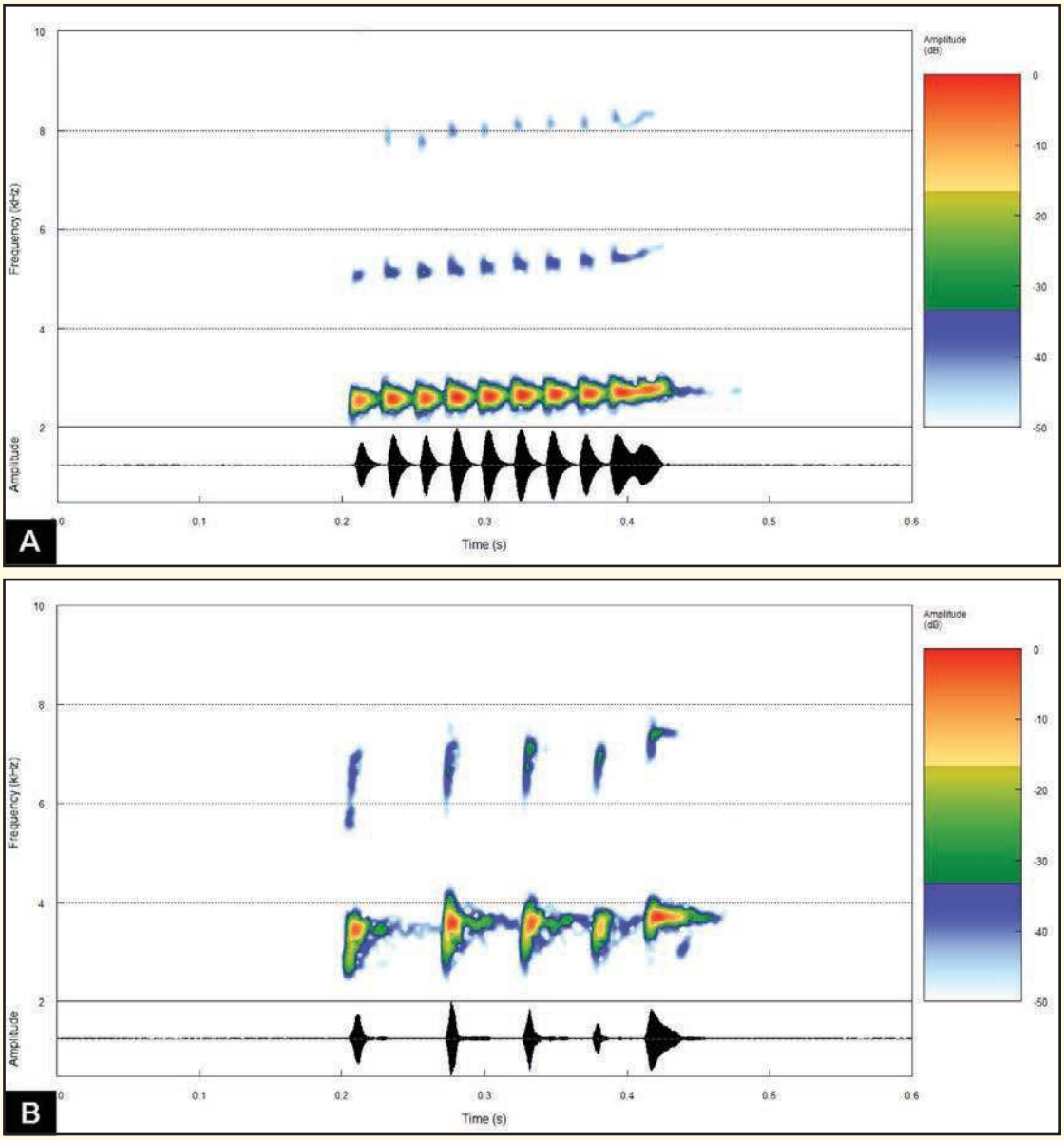


Fig. 29. (A) Sonogram of the call of a male *Eleutherodactylus manantlanensis* sp. nov. (Recording CIG-0056) from the type locality near El Terrero, Municipio de Minatitlán, Colima; and (B) recording of a male *Eleutherodactylus nietoi* sp. nov. (Recording CIG-0094) from the type locality on the Aquila–Coalcomán de Parres Road, Municipio de Chinicuila, Michoacán. Graphics by Vinicius Guerra-Batista.

In central Jalisco and central Michoacán, *E. erendirae* and *E. floresvillelai* have been collected in close proximity to *E. rufescens*, *E. angustidigitorum*, and *E. nitidus*. These species are more readily identified when compared to one another, and we include photographs of specimens collected from nearby areas for reference (see Fig. 32).

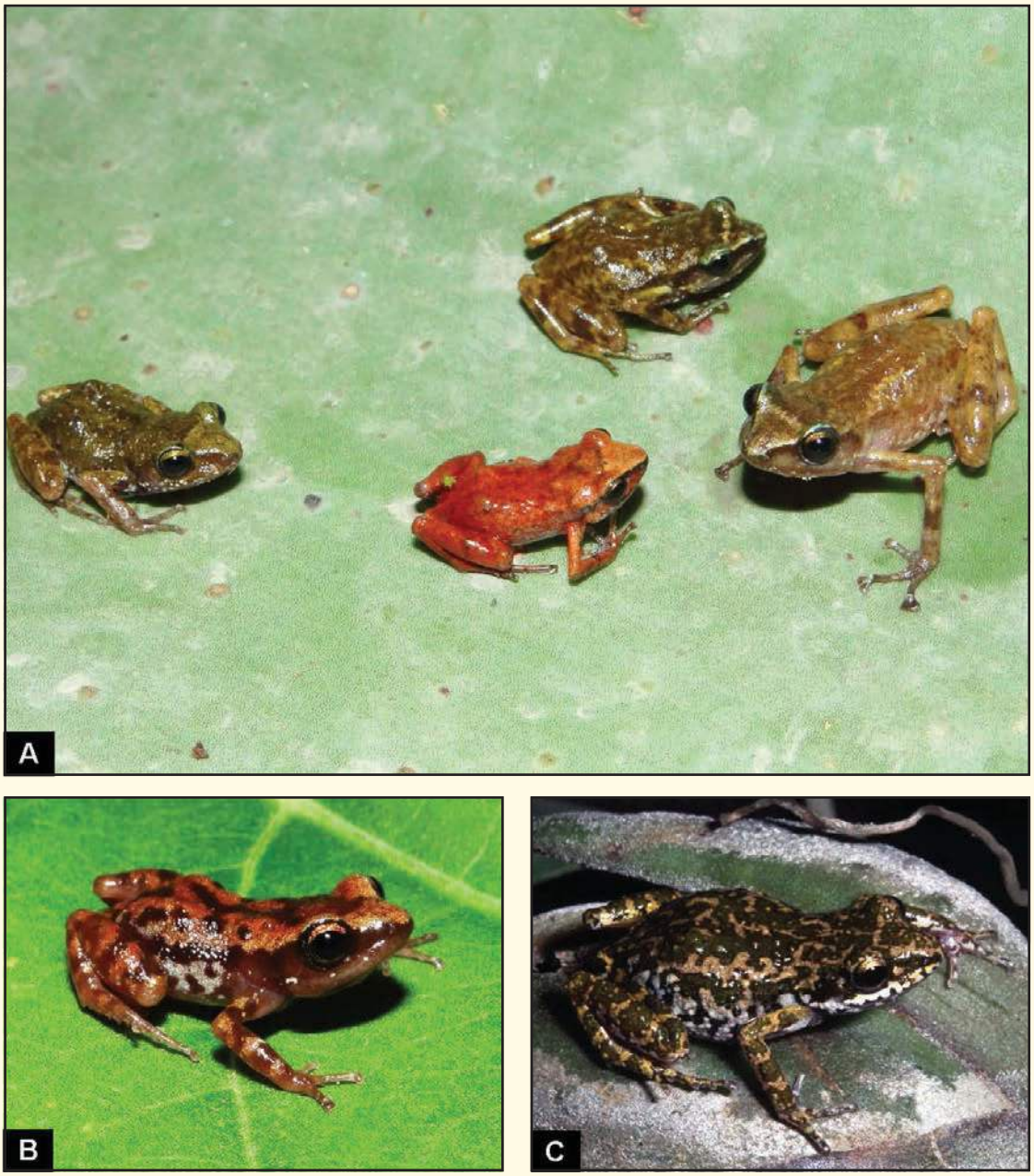


Fig. 30. Comparisons of species of *Eleutherodactylus* living sympatrically or in close proximity to one another in eastern Colima and southwestern Michoacán. (A) From left to right, *Eleutherodactylus orarius* (Aquila, Municipio de Aquila, Michoacán), *Eleutherodactylus rufescens* (type locality), *Eleutherodactylus nietoi* sp. nov. (type locality), *Eleutherodactylus colimotl* sp. nov. (Grutas de San Gabriel, Municipio de Tecoman, Colima); (B) *Eleutherodactylus modestus* (type locality); and (C) *Eleutherodactylus nitidus petersi* (Sierra Coalcomán, Michoacán). © Christoph I. Grünwald, (A, B) and Jonathan A. Campbell (C)

The Validity of *Eleutherodactylus nivicolimae* Dixon and Webb 1966

Duellman and Dixon (1959) described *Tomodactylus rufescens* from Dos Aguas, Sierra de Coalcomán, Michoacán, and assigned the species to this genus based on the supposed presence of lumbo-inguinal glands. Seven years later, Dixon and Webb (1966) described *Syrrhophus nivicolimae* from the Nevado de Colima, Jalisco, and assigned it to *Syrrhophus* based on its lack of lumbo-inguinal glands. Perhaps due to the generic placement of each taxon, the two species never were compared directly to one another. In 2004 one of us (CIG) collected topotypic specimens of each taxon, and noted them as indistinguishable. Since then, we collected both taxa from all known localities and found them to be indistinguishable from one another, both morphologically (Fig. 33) and genetically (Fig. 25). We collected specimens of *E. rufescens* at (or near) the type locality in 2004 (n = 3), 2005 (n = 2), 2015 (n = 2), and 2016 (n = 3). None of the specimens showed any sort of compact, raised lumbar gland in life (see Fig. 33). We also examined photos of the type specimen (UMMZ 118509) at the University of Michigan, Museum of Zoology. We did not expect to see the lumbar gland after nearly 60 years in preservative, as it can be difficult to distinguish even a short time after preservation. No lumbar glands are visible, and the type specimen looks similar to the animals we observed at the type locality, in which a lumbar gland was not evident. Whereas specimens of *E. rufescens* from near the type locality are larger than ones from the type locality of *E. nivicolimae*, specimens from another locality reported by Duellman and Dixon (1959), from 18 km E of Dos Aguas, Michoacán, are not larger than those from the type locality of *E. nivicolimae* (CIG, pers. observ.). Furthermore, molecular data comparing different populations from throughout the distribution of both species suggest that these populations are conspecific (Fig. 25). Finally, we analyzed the advertisement calls recorded near the type locality of *E. rufescens* (Fig. 34A) and compared them to the advertisement calls recorded near the type locality of *E. nivicolimae* (Fig. 34B). We found the calls similar, and consider any differences as intraspecific variartion. We hereby relegate *E. nivicolimae* as a junior synonym of *E. rufescens*. All of the "*E. nivicolimae*" records reported from Concepción de Buenos Aires, Jalisco (Ahumada-Carrillo et al., 2014), Sierra del Tigre, Jalisco (Reyes-Velasco et al., 2012), Tecalitlán, Jalisco (Ahumada-Carrillo et al., 2014), and Tapalpa, Jalisco (Grünwald et al., 2016) herby are referred to as *E. rufescens*. The population reported as "*E. nivicolimae*" from the Sierra Manantlán in Jalisco (Lynch, 1970) is referrable to *E. jaliscoensis*, whereas that from Cerro Grande in Colima (Reyes-Veleasco et al., 2009) is referrable to *E. manantlanensis* (see above). *Eleutherodactylus rufescens* shows relative low genetic diversity along a horseshoe-shaped distribution, from along the western edges of the Tepalcatepec Basin, ranging from the Sierra Coalcomán to to the Nevado the Colima, and through the Sierra del Tigre. We show the correct distribution of *E. rufescens* in Figure 16A.

The Validity of *Eleutherodactylus pallidus* Duellman, 1958 and *Eleutherodactylus teretistes* Duellman, 1958

Duellman (1958: 5–7) described *E. pallidus* as a subspecies of *E. modestus*, even though he found no intermediate specimens between the two species; his decision to treat them as subspecies was based on the "overlap in morphological characters and apparent adjacency of their ranges." In the same publication (Duellman, 1958) also described *E. teretistes* as a separate species, which he assumed to be closely related to *E. pipilans* and *E. interorbitalis*. Lynch (1970) found no overlap in the distinctive color patterns of *E. modestus* and *E. pallidus* and stressed that their distributions were allopatric, and elevated *E. pallidus* to species level; he was the first to note the similarity between *E. pallidus* and *E. teretistes*, and stated that (p. 41), "*S. teretistes* appears to be most closely related to *S. pallidus*. I consider it to be an upland derivative of *pallidus*." He also noted the lack of distinguishing morphological characters between the two species. Due to lack of evidence of interbreeding, however, he opted for retaining both taxa as separate species.

Since the publication of Lynch (1970), researchers working in western Mexico have confused the two species (J. Campbell, pers. comm., T. Devitt, pers. comm.). Their morphological similarity and the occasional appearance of specimens of *E. pallidus* with dark-colored reticulations (similar to those of *E. teretistes*) led us to question the validity of the two taxa (see Fig. 30A). During the course of this study, we collected *E. pallidus* at several localities in Jalisco, Nayarit, and Sinaloa, as well as *E. teretistes* in Jalisco. In Jalisco, we collected both species in close proximity to one another, on the road that connects the towns of Las Palmas and Mascota. In the field, the species readily are distinguished by their different advertisement calls (Fig. 35). *Eleutherodactylus pallidus* produces a short "peep," similar to *E. modestus* and *E. rufescens*, whereas *E. teretistes* produces a much longer "trill."

Furthermore, adult *E. teretistes* tend to be larger than *E. pallidus*, and their color pattern is bolder and shows more contrast (Fig. 40). We agree with Lynch (1970) that few morphological characters can distinguish individuals of these species from one another once they are preserved. We note, however, that even though the tympanum of both species is indistinct, that of *E. teretistes* is concealed and difficult to detect beneath the epidermis. Based on our findings, we confirm the validity of *E. modestus*, *E. pallidus*, and *E. teretistes* as distinct species, and provide photographs in life (Figs. 30, 40).

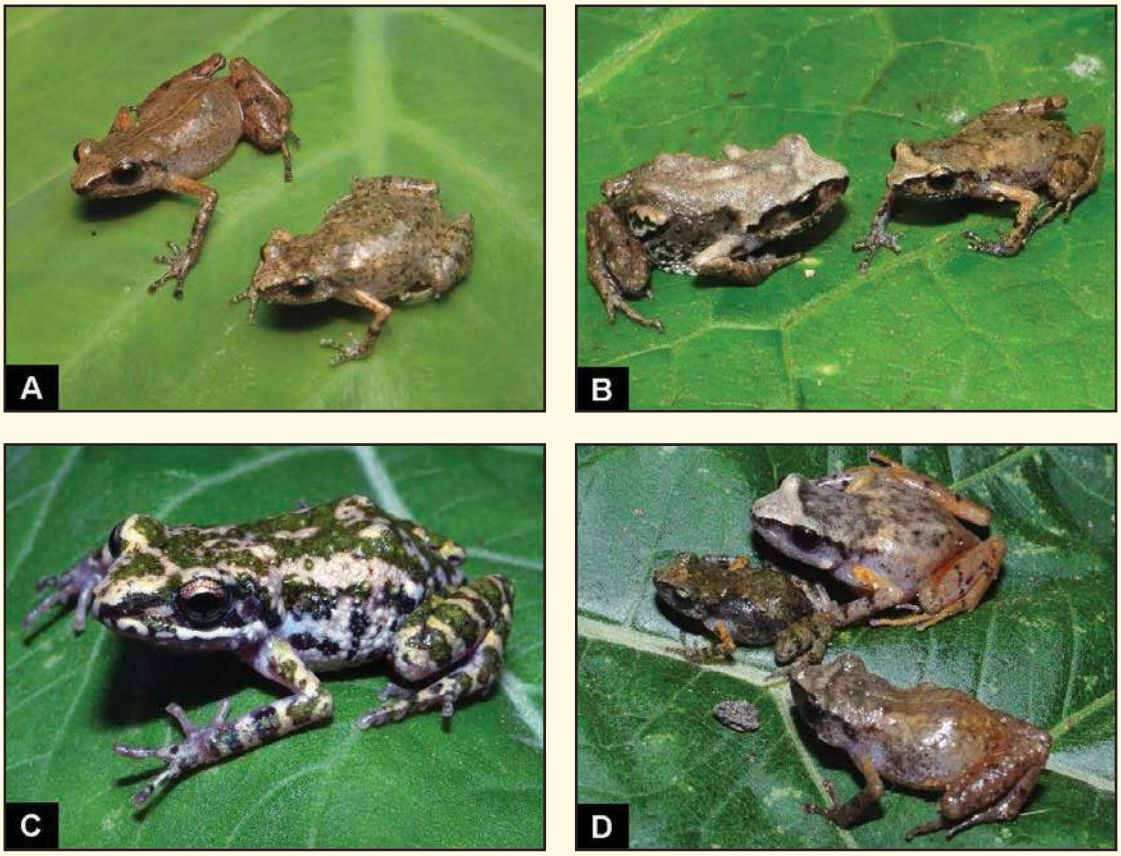


Fig. 31. Comparisons of species of *Eleutherodactylus* living sympatrically or in close proximity of each other in the highlands of Jalisco, Colima, and Michoacán. (A) From left to right, *Eleutherodactylus rufescens* and *Eleutherodactylus erendirae* sp. nov. (both from El Montoso, Municipio de Quitupan, Jalisco); from left to right, *Eleutherodactylus angustidigitorum* and *Eleutherodactylus floresvillelai* sp. nov. (both from the type locality of the latter); (C) *Eleutherodactylus nitidus petersi* (El Montoso, Municipio de Quitupan, Jalisco); and (D) from top to bottom, *Eleutherodactylus manantlanesis* sp. nov. (type locality), *Eleutherodactylus erendirae* sp. nov. and *Eleutherodactylus rufescens* (both from El Montoso, Municipio de Quitupan, Jalisco). © Christoph I. Grünwald

How to Distinguish Species of *Eleutherodactylus* (*Syrrhophus*) in Life and in Preservative

Frogs of the genus *Eleutherodactylus* (Subgenus *Syrrhophus*) notoriously have been difficult to identify, which has contributed to the confusion surrounding the taxonomy of this group (CIG, pers. observ., J. Campbell, pers. comm.). Different preservation methods can make specimens of the same taxon appear distinctive from one another, and poor preservation can make the different species appear indistinguishable. Fortunately, mating calls are distinctive among the species, and consistent within species, which allows for a positive identification based on their calls alone. A trained ear can identify all the species calling in a given locality.

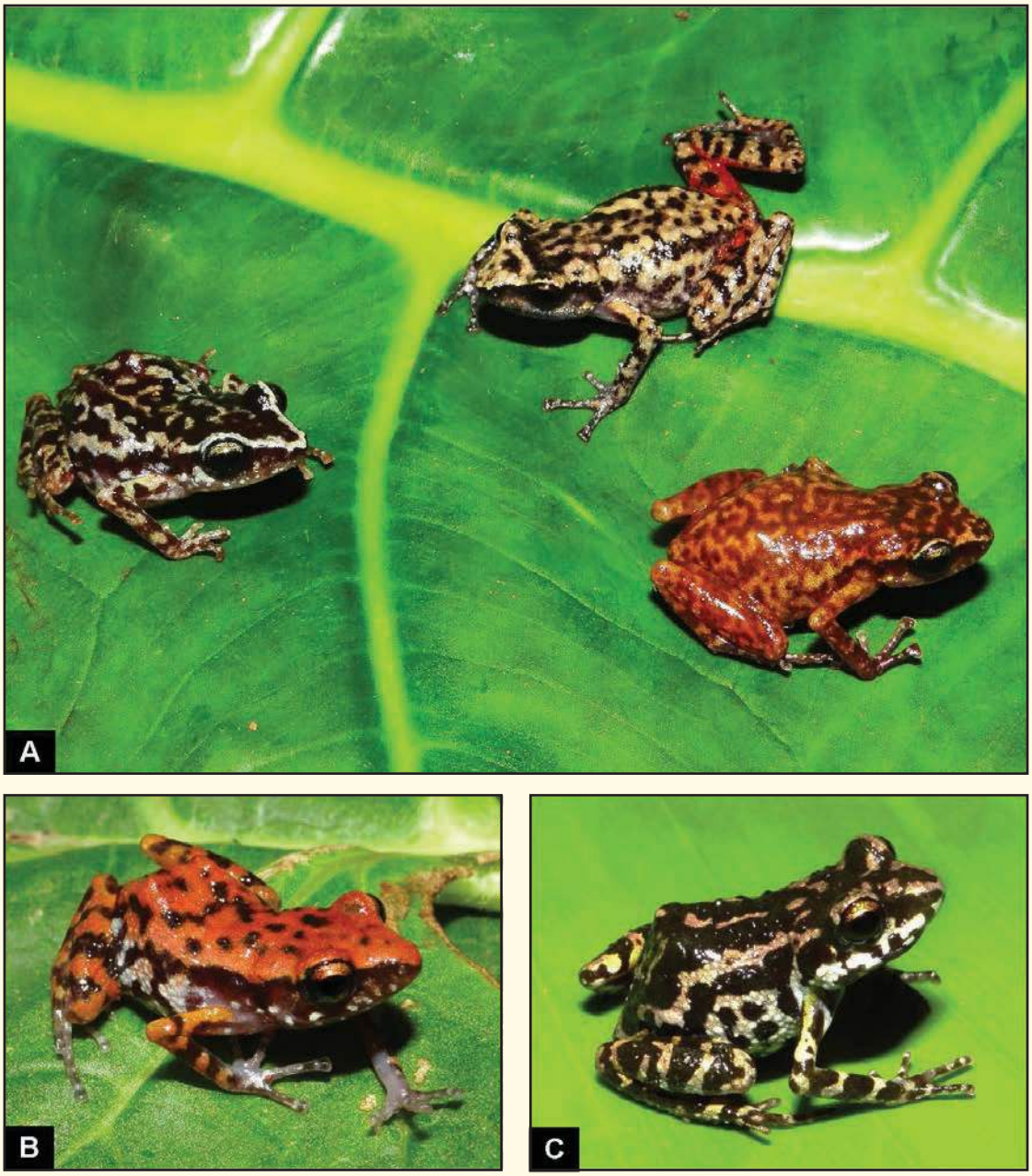


Fig. 32. Comparisons of species of *Eleutherodactylus* living sympatrically or in close proximity of each other in western Jalisco. (A) From left to right, *Eleutherodactylus teretistes*, *Eleutherodactylus jaliscoensis* sp. nov., *Eleutherodactylus pallidus* (all from the Sierra Mascota, Municipio de Mascota, Jalisco); (B). *Eleutherodactylus modestus* (from near La Cuesta, Municipio de Talpa de Allende, Jalisco); and (C) *Eleutherodactylus nitidus petersi* (from near Mascota, Municipio de Mascota, Jalisco). © Christoph I. Grünwald

Coloration in life also is one of the best ways to distinguish among the different species, but this character largely is lost soon after preservation. Thus, when possible, we urge researchers on this subgenus to make audio recordings, take photographs in life, and obtain tissues samples of specimens. At the very least, detailed photographs of the dorsal, ventral, flank, and groin coloration should be taken before preservation. In our experience, two separate species that occupy a similar habitat often will converge in morphology and coloration (see Figs. 30, 31, 32), but can be distinguished from one another by their call, and molecular analyses usually coincide with species boundaries as defined by their call analyses.

Certain morphological characters are useful in distinguishing among the species, but others are less so. Historically, the number and size of the palmar tubercles have been given substantial importance for distinguishing species in the subgenus *Syrrhophus*, and for determining relationships within the subgenus (see Fig. 36A). Unfortunately, this character is somewhat variable, and two or three palmar tubercles can be present in some species (e.g., *E. pipilans*, *E. interorbitalis*; CIG, pers. observ.), but in others the outer palmar tubercles can vary from well developed to greatly reduced (e.g., *E. dennisi*). We found the finger and toe lengths to be equally unreliable. The shape of the two metatarsal tubercles and their size relative to each other is a functional characteristic used to distinguish between species (see Fig. 36B). One of the most useful characters to distinguish among the species (especially on the west coast of Mexico) is whether the tips of the fingers are expanded, and their degree of expansion when compared to the width of the narrowest part of the digit. Another important character is the size and condition of the tympanum. The tympanum varies from very small (less than 25% ED) to as large as the eye. The condition of the typanum is an important taxonomic character when distinguishing between the eastern and western clades of the subgenus *Syrrhophus* (see Fig. 37). The presence of raised, compact lumbar glands has proven useful in distinguishing among some species of the western clade of *Syrrhophus*. Species either can show visible glands or not (see Fig. 38). Historically, this character was given a lot of weight in determining relationships among species, but our results show this to be inaccurate, as closely related species can differ from one another in that one contains lumbar glands, whereas the other does not (e.g., *E. saxatilis* vs. *E. interorbitalis*).

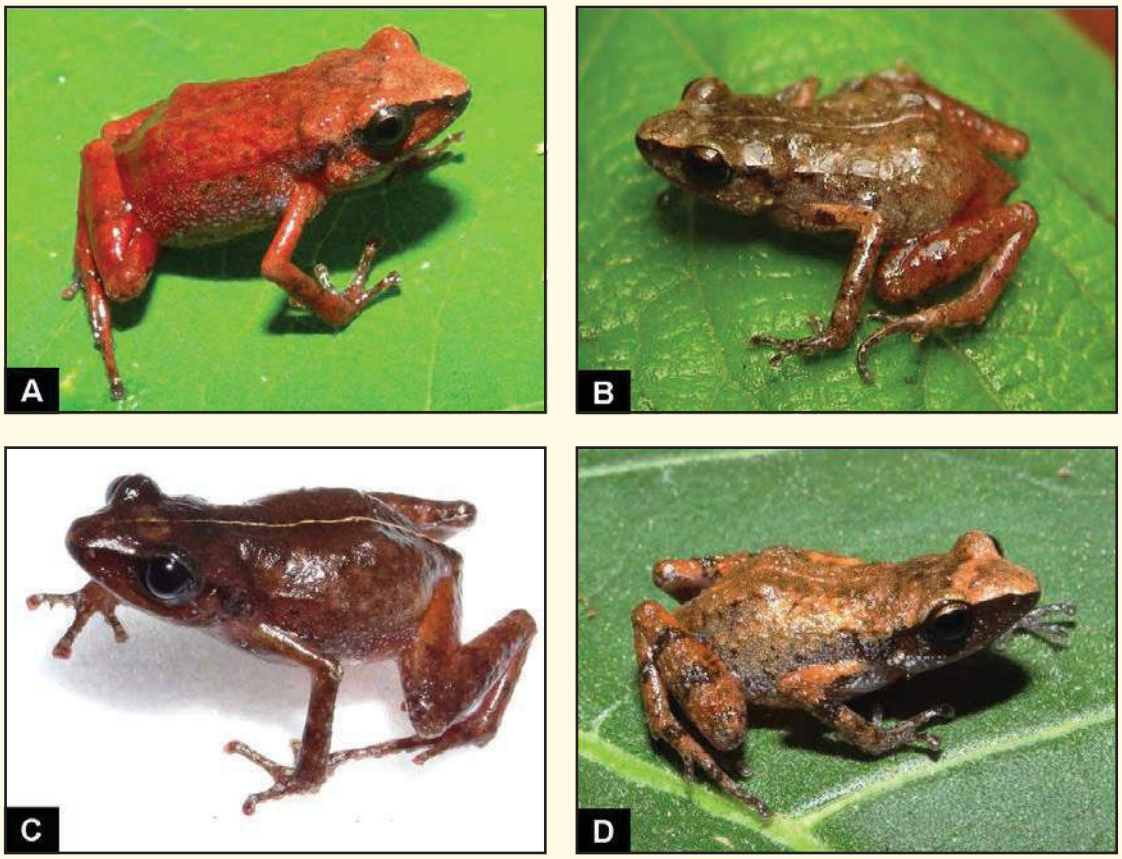


Fig. 33. Variation in *Eleutherodactylus rufescens*. (A) A nearly topotypic male of "*Tomodactylus rufescens*" from Rancho Las Torrecillas, vic. of Dos Aguas, Municipio de Coalcomán de Vázquez-Pallares, Michoacán, MZFC 33340 (CIG-0981); (B) a topotypic male of "*Syrrhophus nivicolimae*" from west of Atenquique, Municipio de Tuxpan, Jalisco. (no museum number); (C) male from near Mazamitla, Contla–Mazamitla highway, Municipio de Mazamitla, Jalisco, MZFC 33167 (CIG-0546); and (D) male from near Villa Victoria turnoff on the Aquila–Coalcomán de Vázquez Pallares highway, Municipio de Chinicuila, Michoacán, MZFC 33338 (CIG-0976).

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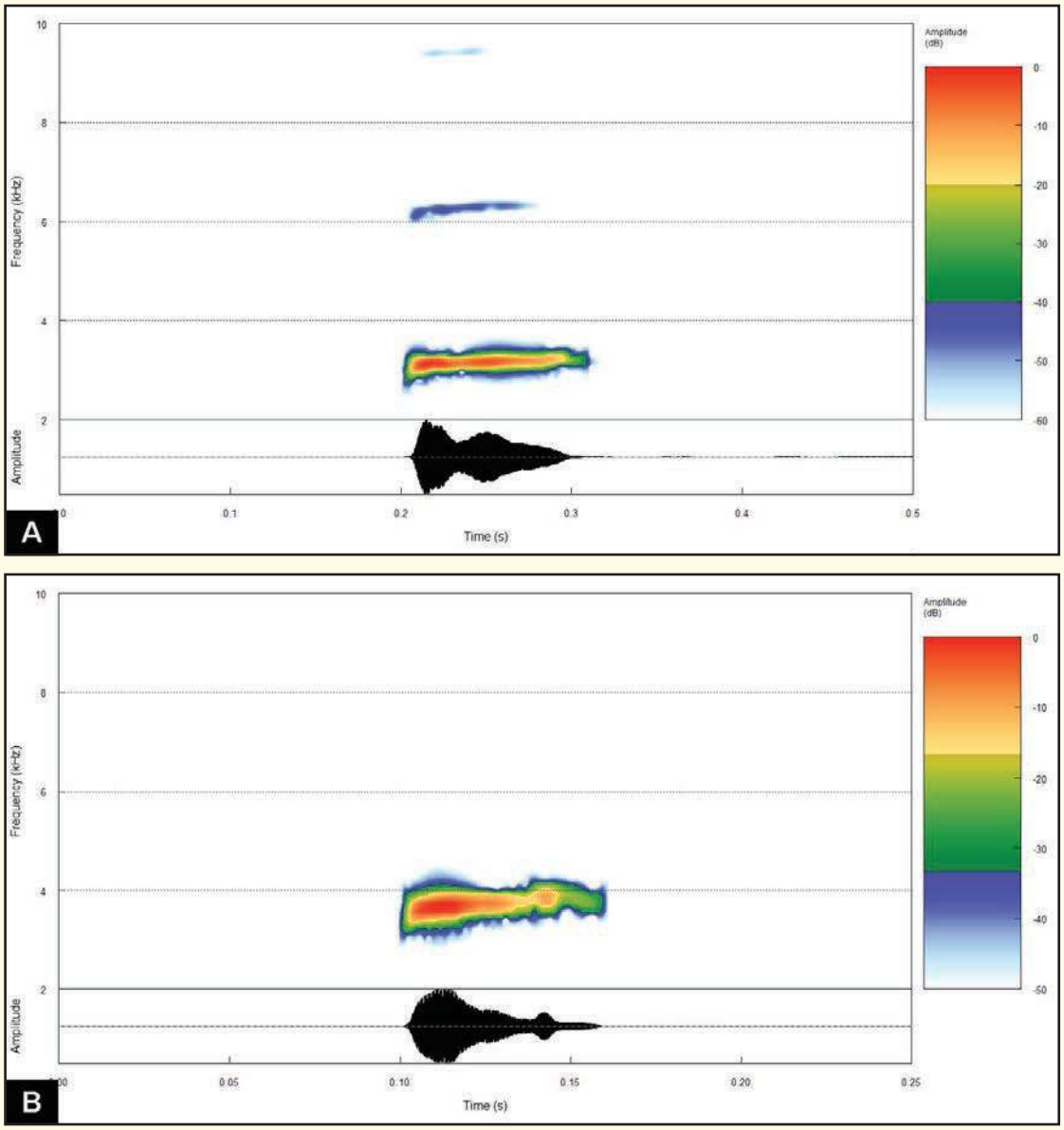


Fig. 34. A. Recording of a male *Eleutherodactylus rufescens* (Recording CIG-0101) from near the type locality at Dos Aguas, Municipio de Coalcomán de Vázquez Pallares, Michoacán; and (B) recording of a male *Eleutherodactylus rufescens* (Recording JRV-184) from El Floripondio, Municipio de Ciudad Venustiano Carranza, Jalisco near the type locality of "*Eleutherodactylus nivicolimae*." Graphics by Vinicius Guerra-Batista.

Differences in the coloration in life, which often can be subtle, can be a useful character in distinguishing among closely related species. For example, the presence or absence of an interorbital bar, and whether the bar is paler or darker than the ground coloration can be used to distinguish certain species (e.g., *E. jaliscoensis* vs. *E. teretistes* and *E. interorbitalis* vs. *E. manantlanensis*). Another important character is the presence of flash coloration on the inguinal region, as well as the anterior and posterior portions of the thighs, and sometimes on the legs, upper arms, and flanks. Likewise, the coloration of the upper arms and the amount of markings on them (or lack thereof) can be a helpful character in distinguishing among the species. Finally, certain aspects of the dorsal coloration (such as a pale loreal outline in *E. teretistes*) and ventral coloration (e.g., dark coloration on venter in *E. jaliscoensis*) can serve as identifying characters.

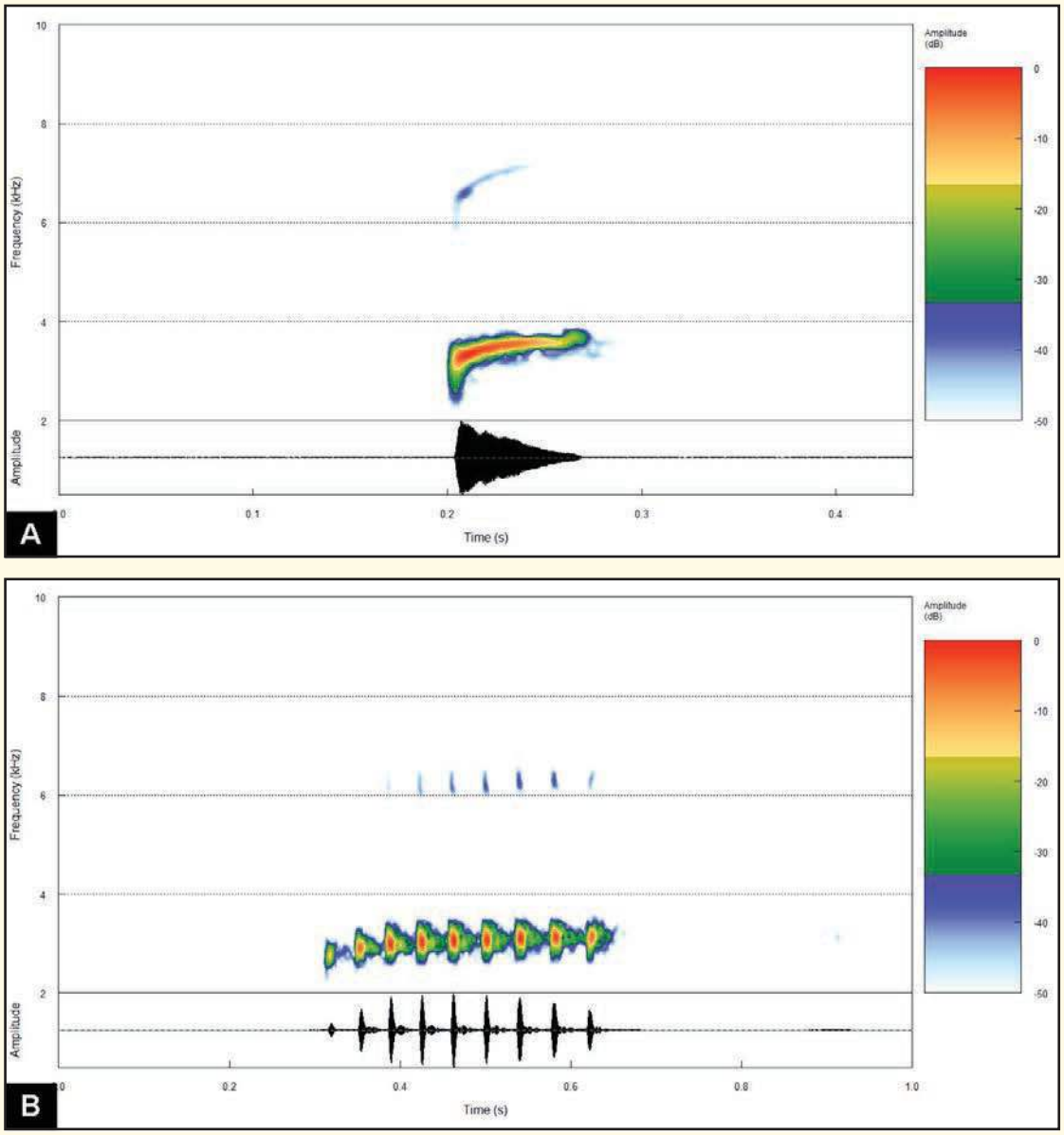


Fig. 35. (A) Recording of a male *Eleutherodactylus pallidus* (Recording CIG-0038) from the Sierra de Mascota, Jalisco; and (B) recording of a male *Eleutherodactylus teretistes* (Recording CIG-0042) from the Sierra de Mascota, Jalisco. Graphics by Vinicius Guerra-Batista.

One important character that can be used to determine the relationships within the subgenus *Syrrhophus* is the color of the visceral peritoneum and the associated visibility of the abdominal vein. *Syrrhophus* from the eastern clade display a white visceral peritoneum that does not reveal the viscera and allows the abdominal vein to be clearly seen against the white background. In the western clade of *Syrrhophus*, the visceral peritoneum is translucent and allows the viscera to be seen in live frogs, and obscures the visibility of the abdominal vein. In some western clade species the vein can be further obscured, or even covered completely by a colored empidermis (see Figs. 39, 40).

An analysis of molecular characters and advertisement calls ultimately might be the most reliable manner for distinguishing among the species. Certain preparations must be made beforehand, however, as calls only can be recorded in the field (these frogs rarely call in captivity) and tissues must be properly preserved.

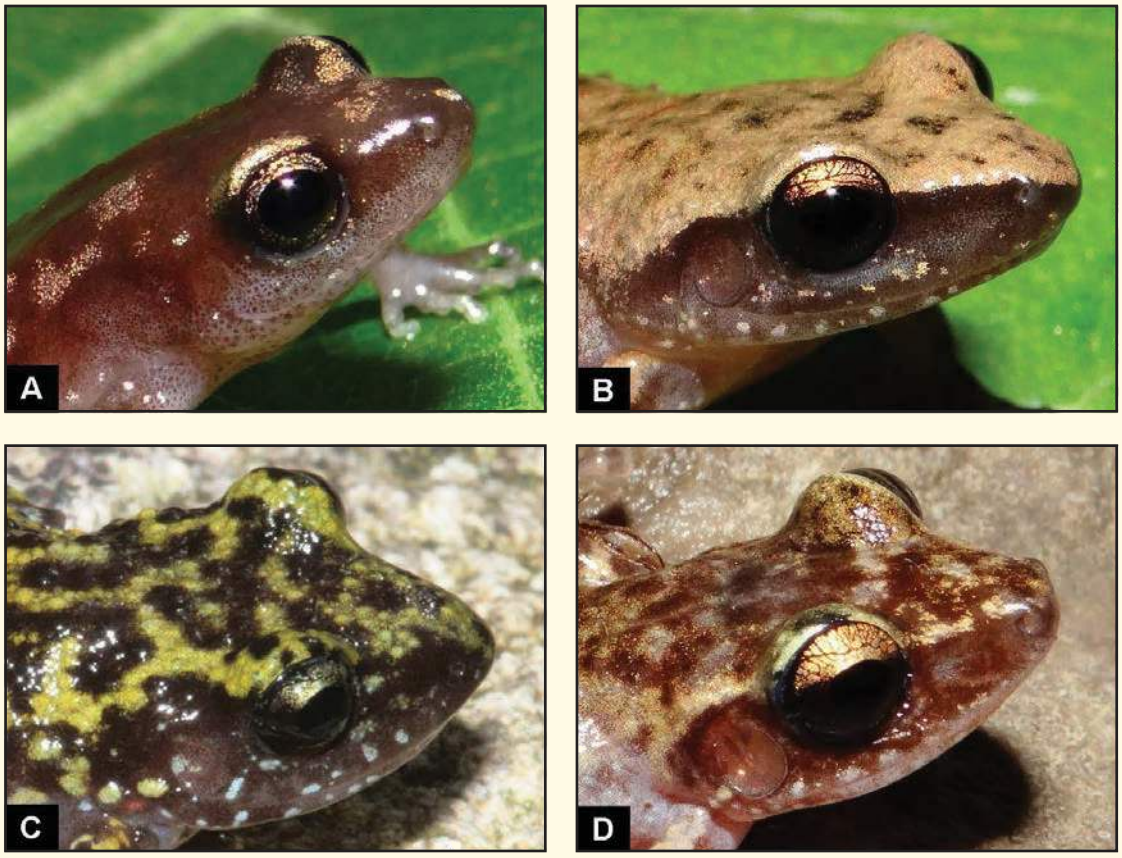


Fig. 36. (A) Close-up view of the head of *Eleutherodactylus modestus* showing an indistinct tympanum covered by skin; (B) close-up view of the head of *Eleutherodactylus cystignathoides* showing a distinct tympanum not covered by skin; (C) close-up view of the head of *Eleutherodactylus saxatilis* showing an indistinct tympanum covered by skin; and (D) close-up view of the head of *Eleutherodactylus dennisi* showing a distinct tympanum not covered by skin. © Christoph I. Grünwald (A, B, D) and Iván T. Ahumada-Carrillo (C)

A Redefinition of the Species Series and Species Groups among Species of *Eleutherodactylus* (Subgenus *Syrrhophus*)

The distinctiveness of Atlantic versant *Syrrhophus* (Eastern Clade) from Pacific versant *Syrrhophus* (Western Clade) long has been recognized. Smith and Taylor (1948) recognized two species groups within *Syrrhophus* (excluding *Tomodactylus*), one from the Atlantic/Sierra Madre Oriental and a second from the Pacific/Sierra Madre Occidental. They distinguished the two groups based on the number of palmar tubercles (three vs. two). Smith and Taylor (1948) treated *Tomodactylus* separately based on the presence of compact, prominent lumbar glands on species assigned to that genus.

Firschein (1954) followed this arrangement and provided a detailed discussion on the validity of several of the Eastern Clade species recognized at that time. Dixon (1957a; 1957b) reviewed all the species of the genus *Tomodactylus* recognized at the time, and considered it to be generically distinct from *Syrrhophus* based primarily on the presence and shape of the lumbar glands, the head narrower than the body, the limbs shorter proportionally to the body, and the texture of the skin on the venter. Dixon described several new taxa, including *T. dilatus* (= *E. dilatus*) Davis and Dixon, 1955, *T. fuscus* (= *E. maurus*) Davis and Dixon, 1955, *T. grandis* (= *E. grandis*) Dixon, 1957, *T. rufescens* (= *E. rufescens*) Duellman and Dixon, 1959, and *S. nivicolimae* (= *E. rufescens*) Dixon and Webb, 1966. Duellman (1958) later reviewed the Western Clade and described *S. modestus pallidus* (= *E. pallidus*) and *S. teretistes* (= *E. teretistes*). Duellman (1958: 13) also differentiated between the two clades by the number of palmar tubercles, although he noted that the Western Clade members also can have three palmar tubercles, but

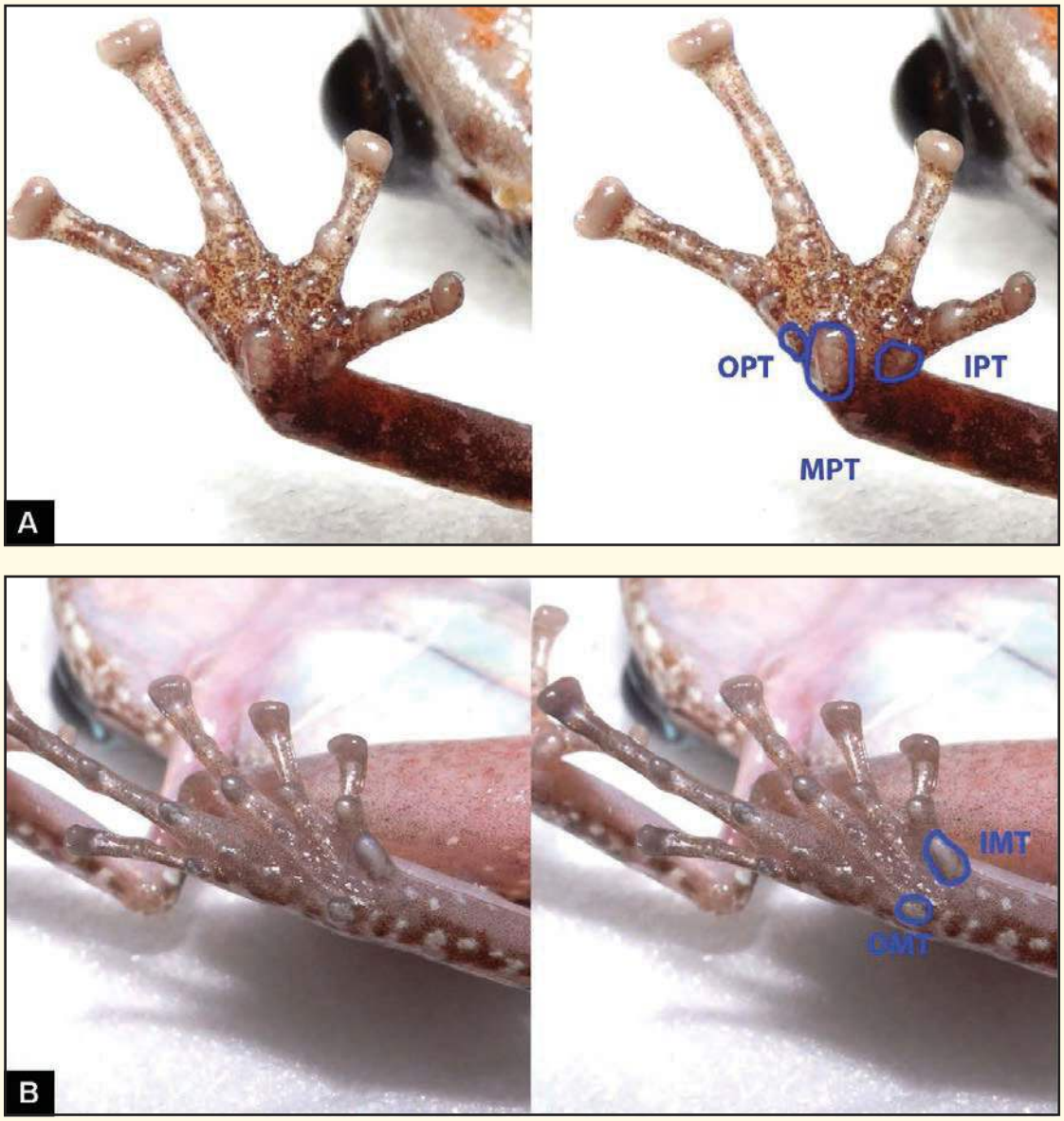


Fig. 37. (A) View of the underside of the hand of *Eleutherodactylus jaliscoensis* sp. nov., on the left without annotations and on the right showing outlines of the three palmar tubercles (Outer Palmar Tubercle, Middle Palmar Tubercle, and Inner Palmar Tubercle); and (B) view of the underside of the foot of *Eleutherodactylus longipes*, on the left without annotations and on the right showing outlines the two metatarsal tubercles (Outer Metatarsal Tubercle and Inner Metatarsal Tubercle). © Christoph. I. Grünwald

with the 3rd one "reduced or absent." Webb (1962) described *T. saxatilis* (= *E. saxatilis*) and Hoyt (1965) described *T. syristes* (= *E. syristes*), further adding to the known diversity of the frogs at that time assigned to *Tomodactylus*. Lynch (1968) redefined the genus *Syrrhophus* and removed numerous species erroneously associated with the genus. Lynch (1970) reviewed all species assigned to *Syrrhophus* at that time, and followed a similar arrangement of western and eastern "species complexes" as originally proposed by Smith and Taylor (1948: 48). Lynch (1970: 7) also distinguished the two clades by the condition of the palmar tubercles, defining the Eastern Clade as having three well-developed palmar tubercles and the Western Clade generally having two well-developed palmar tubercles and an outer palmar tubercle "that is indeed usually present and smaller than the first supernumerary tubercle." Lynch (1968, 1970, 1971) considered *Syrrhophus* and *Tomodactylus* to be two distinct, yet closely related genera.

Hedges (1989) proposed that all species previously placed in the genera *Syrrhophus* and *Tomodactylus* be placed in *Eleutherodactylus*, and considered *Syrrhophus* a subgenus based on osteological characters reviewed in detail in two previous studies (Joglar, 1989; Lynch, 1971). Within *Syrrhophus*, Hedges (1989) recognized two "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*). Lynch and Duellman (1997) followed Hedges (1989) in considering the former species of *Syrrhophus* and *Tomodactylus* as *Eleutherodactylus*, and placed them in the subgenus *Syrrhophus* with five species groups (*E. leprus* group, *E. longipes* group, *E. marnocki* group, *E. modestus* group, and *E. pipilans* group). Frost et al. (2006) resurrected the genus *Syrrhophus* and assigned to it the species formerly allocated to *Syrrhophus* and *Tomodactylus*; however, they did not recognize any species groups. Heinicke et al. (2007) and Hedges et al. (2008) did not follow Frost et al. (2006), and instead considered *Syrrhophus* a subgenus of *Eleutherodactylus,* following Hedges (1989), and to it added two members of the genus *Euhyas* from Cuba (*E. zeus* and *E. symingtoni*).

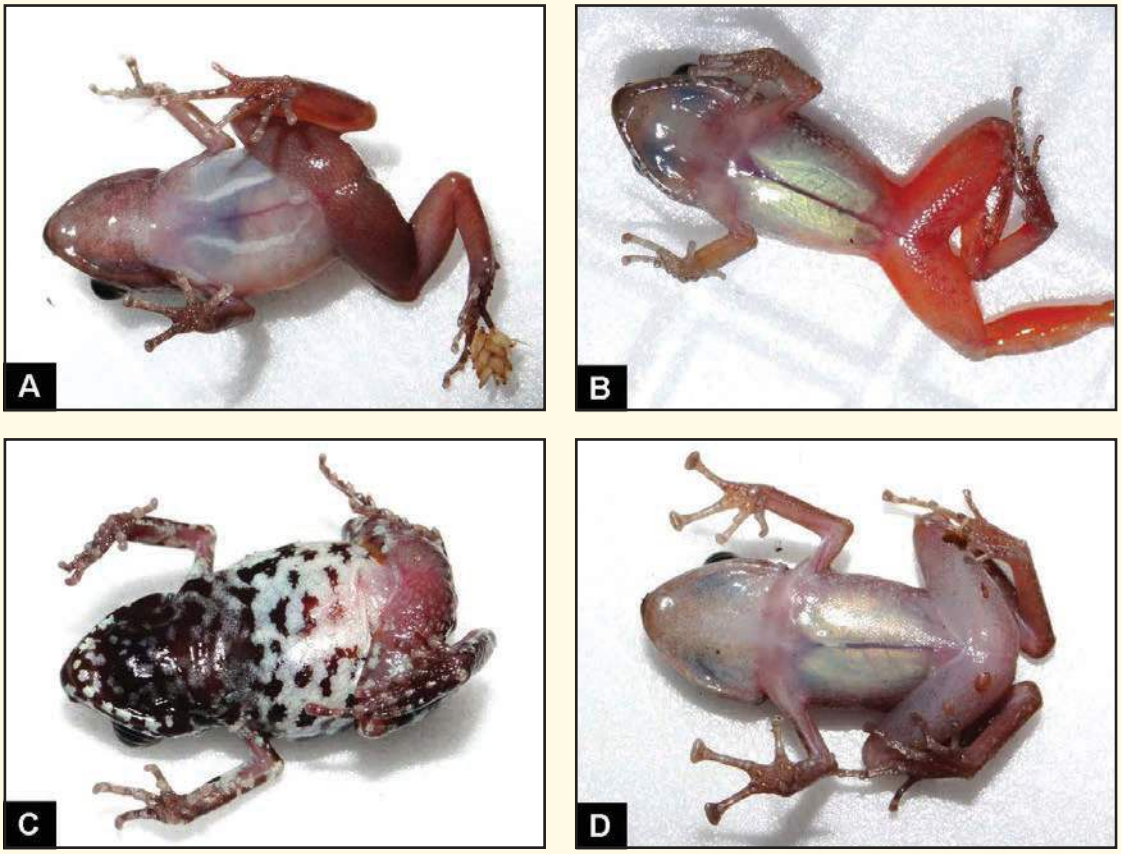


Fig. 38. (A) Ventral view of *Eleutherodactylus modestus* showing the abdominal vein against a clear visceral peritoneum, which allows the vein to be slightly visible against the background of viscera; (B) ventral view of *Eleutherodactylus cystignathoides* clearly showing the abdominal vein against a white visceral peritoneum; (C) ventral view of *Eleutherodactylus nitidus* showing a black and white epidermis that obscures the abdominal vein, and does not allow one to discern it or the viscera; and (D) ventral view of *Eleutherodactylus dennisi* showing the abdominal vein against a white visceral peritoneum. © Christoph I. Grünwald

We tentatively follow Hedges (1989), Lynch and Duellman (1997), Heinicke et al. (2007), Hedges et al. (2008), and Padial et al. (2014) in placing all the former species of *Syrrhophus* and *Tomodactylus* in the subgenus *Syrrhophus* of the genus *Eleutherodactylus*. Based on our extensive review of all recognized species of the subgenus *Syrrhophus*, however, we find that the currently recognized species series and their respective species groups are not diagnosable, and do not correctly portray the relationships of the taxa they contain.

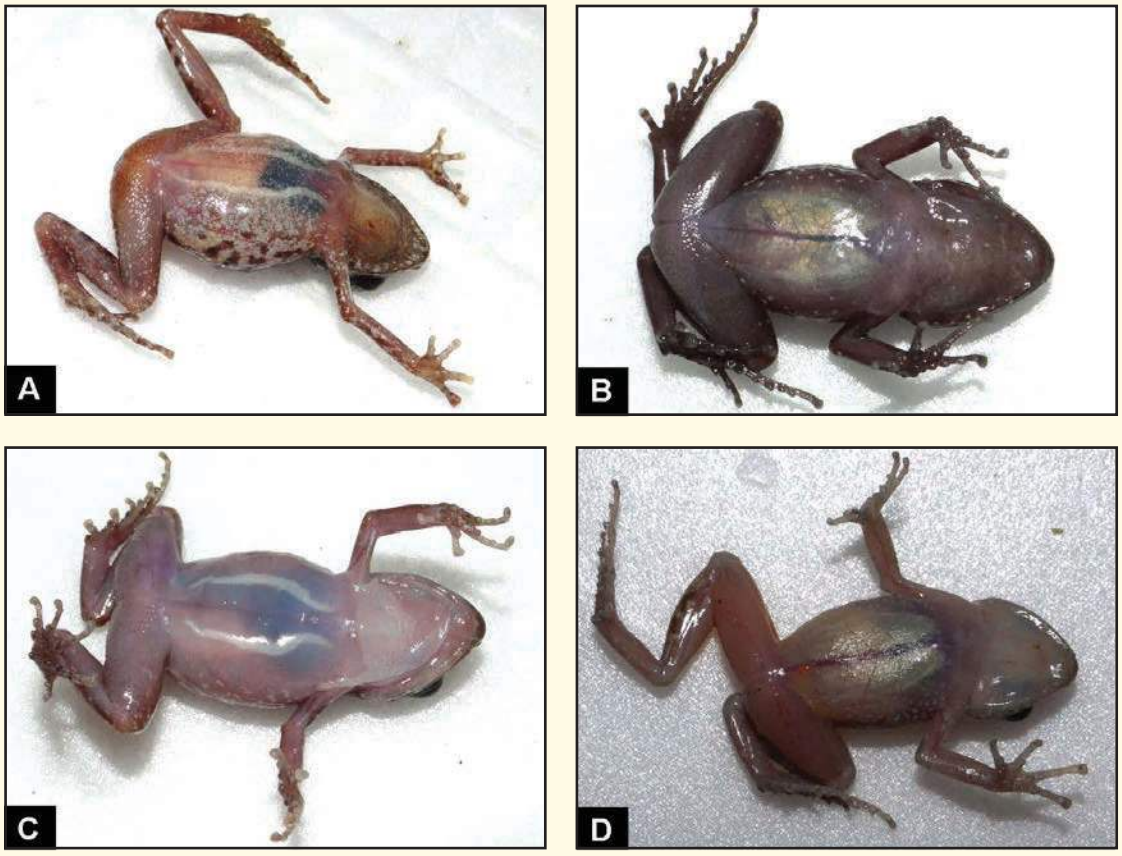


Fig. 39. (A) Ventral view of *Eleutherodactylus teretistes* showing the abdominal vein against a clear visceral peritoneum, which allows the vein to be slightly visible against a background of viscera; (B) ventral view of *Eleutherodactylus leprus* showing the abdominal vein against a white visceral peritoneum; (C) ventral view of *Eleutherodactylus pipilans* showing an opaque white epidermis that partially obscures the abdominal vein and viscera; and (D) ventral view of *Eleutherodactylus guttilatus* showing the abdominal vein against a white visceral peritoneum. © Christoph I. Grünwald

We propose two distinct species series for frogs of the subgenus *Syrrhophus* inhabiting the United States, Mexico, and Central America. Both are readily distinguishable when examining live animals in the field, and both are supported by molecular evidence (Fig. 25). The *Eleutherodactylus longipes* Species Series includes all the former *Syrrhophus* that were assigned to the Eastern Clade (*sensu* Smith and Taylor, 1948; Firschein, 1954; Lynch, 1970) and still are recognized as valid today. We define the *Eleutherodactylus longipes* Species Series below, and refrain from splitting the species series into species groups at this time. The *Eleutherodactylus nitidus* Species Series includes all the former *Syrrhophus* that were assigned to the Western Clade (*sensu* Smith and Taylor, 1948; Duellman, 1958; and Lynch, 1970) and still are considered valid today, as well as all the members of the former genus *Tomodactylus*. Within the *Eleutherodactylus nitidus* Species Series, we recognize two species groups based

primarily on molecular data (see Fig. 25). We define these species groups below, based on our molecular and morphological results. An ongoing PCA analysis of morphological characters and a molecular analysis of nuclear gene markers are necessary to further delineate the species groups within the subgenus *Syrrhophus*.

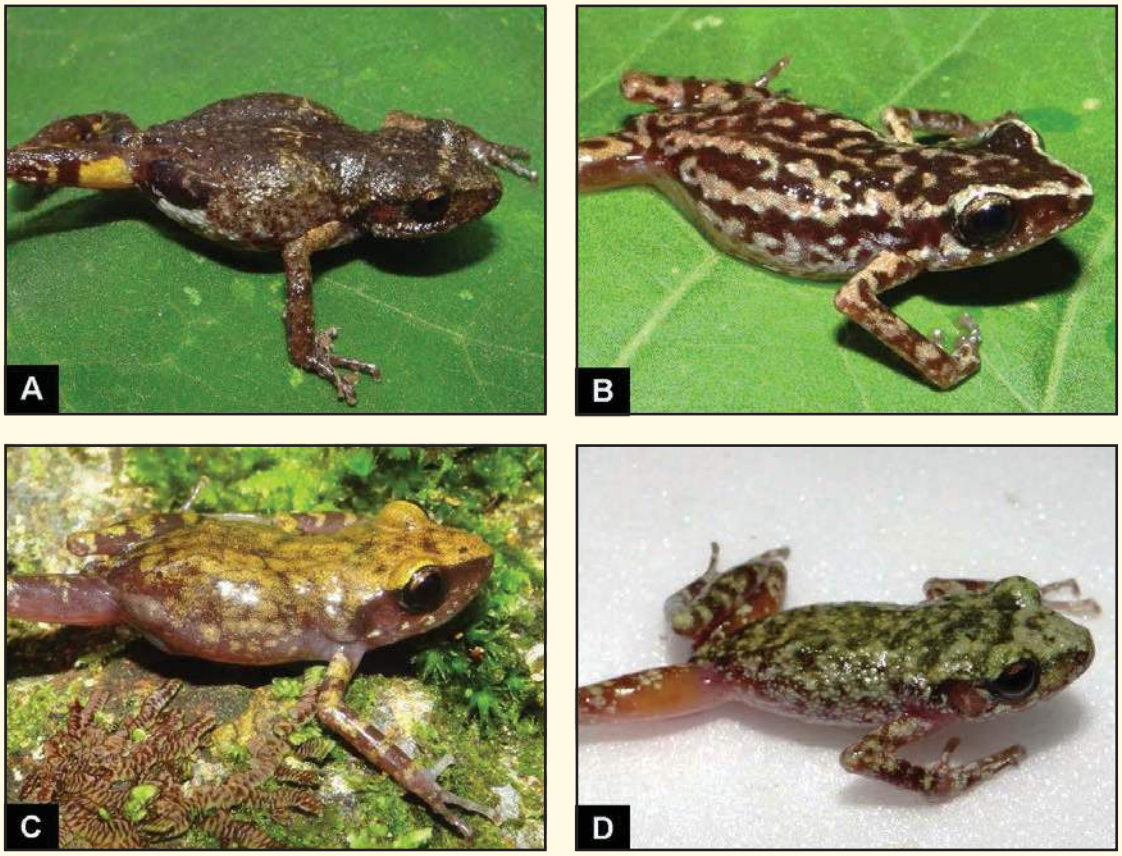


Fig. 40. (A) Lateral view of *Eleutherodactylus dilatus* showing the distinct compact lumbar gland; the lumbar glands are located high up on the dorsum and show contrasting colors, which draw attention to them; (B) lateral view of *Eleutherodactylus teretistes* showing no visible lumbar glands and no distinct coloration associated with them; (C) lateral view of *Eleutherodactylus pipilans* showing an indistinct, slightly raised, compact lumbar gland; the lumbar glands are located lower in the inguinal region and lack associated distinct coloration; and (D) lateral view of *Eleutherodactylus guttilatus* with no visible lumbar glands and lacking associated distinct coloration.

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The Eleutherodactylus (*Syrrhophus*) *longipes* Species Series

(Figs. 41, 42)

Definition. Small to moderately large frogs, SVL of adults from 16.0 mm (*E. campi*) to 39.6 mm (*E. longipes*); abdominal vein clearly visible under epidermis and above visceral peritoneum on ventral aspect of live specimens; visceral peritoneum white (Figs. 39B, 39D, 40B, 40D); tympanum relatively large, 50–90% width of eye; two tympanic annuli visible, not covered in skin, thus tympanum distinct in both living and preserved specimens (Figs. 37B, 37D); compact, protruding lumbar glands absent (Fig. 38D); tips of digits expanded, 3rd and 4th fingers expanded 1.2–3.2 times narrowest part of digit, digital tips of toes either not expanded, or when expanded maximum width

twice narrowest part of digit; three palmar tubercles present; and outer palmar tubercle usually as large as or larger than 1st suprernumery tubercle.

Content. Nine species: *Eleutherodactylus* (*Syrrhophus*) *campi*, *E. cystignathoides*, *E. dennisi*, *E. guttilatus*, *E. leprus*, *E. longipes*, *E. marnocki*, *E. verrucipes,* and *E. verruculatus* (Figs. 41, 42).

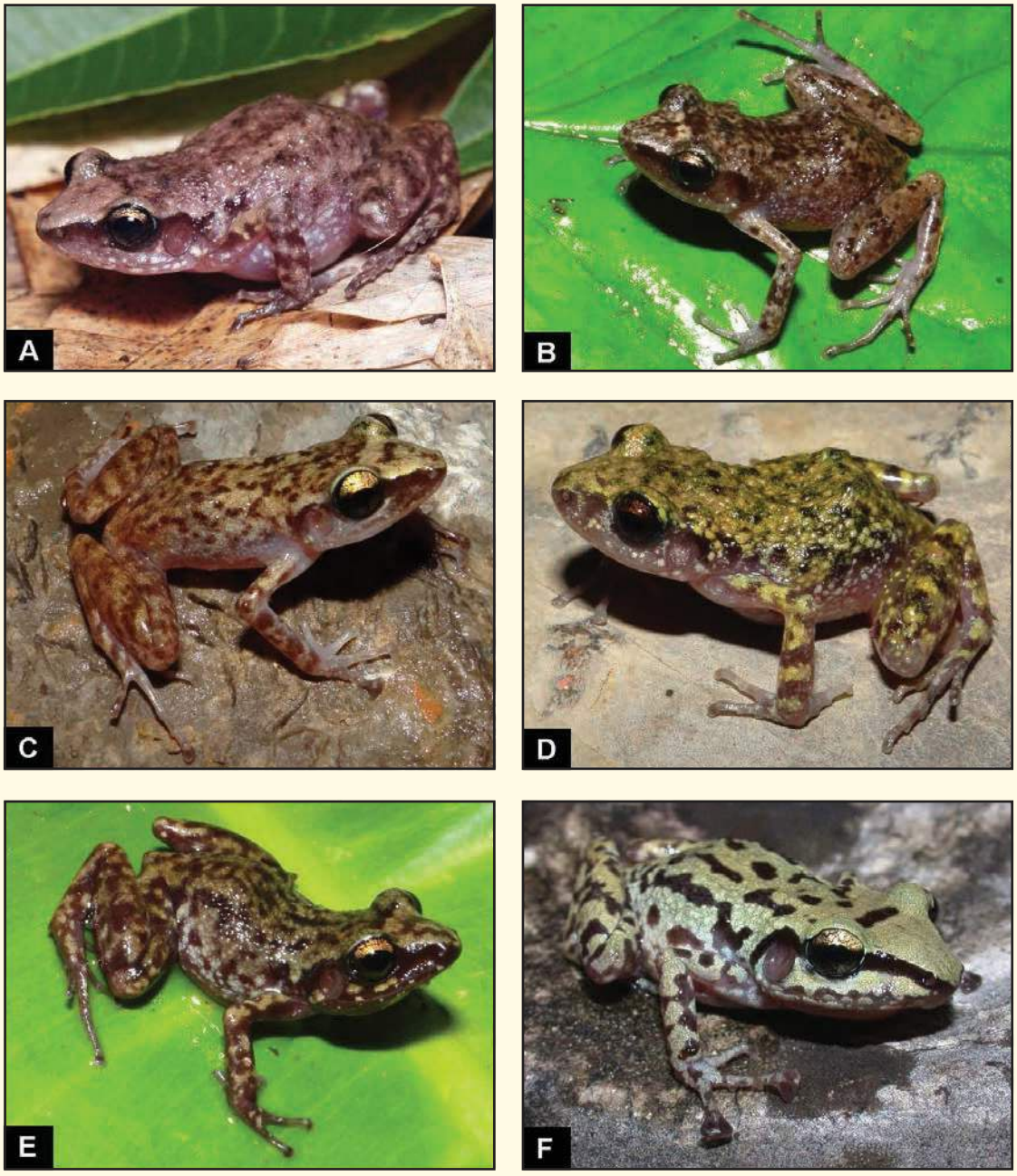


Fig. 41. Members of the *Eleutherodactylus longipes* Species Series. (A) *Eleutherodactylus campi*; (B) *Eleutherodactylus cystignathoides*; (C) *Eleutherodactylus dennisi* (D) *Eleutherodactylus guttilatus*; (E) *Eleutherodactylus leprus* and (F) *Eleutherodactylus longipes*.
© Gary Nafis (A) and Christoph I. Grünwald (B, C, D, E, F)

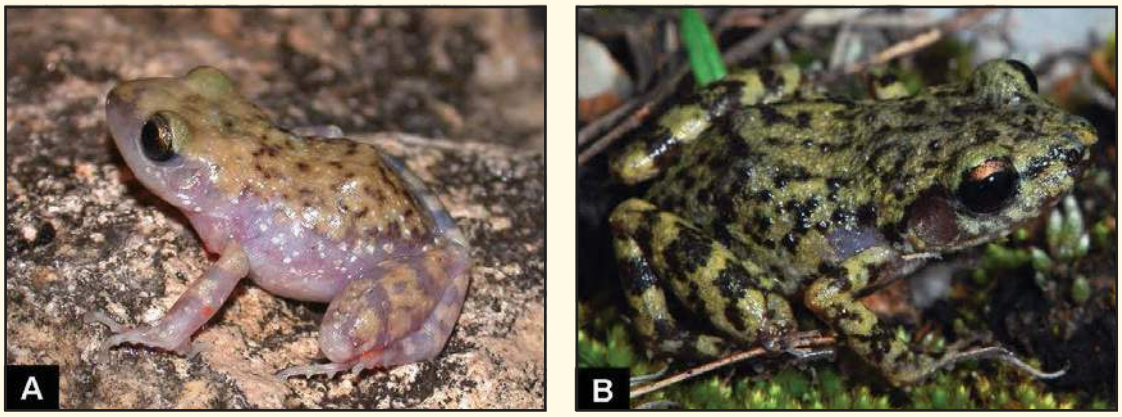


Fig. 42. Members of the *Eleutherodactylus longipes* Species Series. (A) *Eleutherodactylus marnocki*; and (B) *Eleutherodactylus verrucipes*. © Troy Hibbitts

Distribution. Distributed in the Chihuahuan Desert from western Texas, United States, and east-central Chihuahua, Mexico, south onto the Meseta Central of central Mexico, including eastern Jalisco, Guanajuato, Querétaro, and Hidalgo. Present on the Atlantic coastal plain from southern Texas, United States, to Belize and Guatemala. Distributed in the Sierra Madre Oriental from southeastern Coahuila to at least central Veracruz and northern Puebla. Apparently absent from the Sierra Madre Oriental of Oaxaca, although it occurs on the piedmont of the Sierra Madre Oriental. Absent from the highlands of Chiapas and the lowlands of the Yucatan Peninsula. Specimens assigned to this group (*Eleutherodactylus leprus*) from Pacific Chiapas and Guatemala likely are not in this species group, but more sampling is necessary in this area. Introduced populations occur in central Texas (Dixon, 2013), Louisiana (Boundy and Gregory, 2012), Alabama (McConnell et al., 2015), and central Arizona, in the United States (D. Ortíz, pers. comm.). The elevational range extends from sea level to approximately 2,500 m.

Remarks. We include *Eleutherodactylus campi* and *E. cystignathoides* as separate species. Whereas they were described as separate species, Lynch (1970) considered both as subspecies of *E. cystignathoides*, primarily based on intermediate specimens from Tamaulipas and San Luis Potosí. Our molecular data show that they are two closely related but distinct species (Fig. 25). A more detailed study is required to determine the status of the supposedly "intermediate" specimens and to define the ranges of both species in eastern Mexico. We consider *E. dennisi* a valid species, as there is no evidence to invalidate it at this point, despite Farr et al. (2013) suggesting it might be a junior synonym of *E. longipes*. We also include *Eleutherodactylus verruculatus*, despite Firschein (1954) and Lynch (1970) doubting its validity; more fieldwork around the supposed type locality of this species is necessary, as we have not been able to locate any *Syrrhophus* not identifiable as *E. cystignathoides* at the type locality.

Eleutherodactylus (*Syrrhophus*) *nitidus* Species Series

(Figs. 43–47)

Definition. Small to medium-sized frogs, SVL 16.1 (*E. floresvillelai*) to 32.4 (*E. grunwaldi*); abdominal vein not visible or barely discernible against visceral pertioneum on ventral aspect of live specimens, visceral peritoneum translucent (Figs. 39A, 39C, 40A, 40C); tympanum small to moderate, 15–50% width of eye; tympanic annuli covered in skin, two tympanic annuli not clearly visible, and thus tympanum indistinct (Figs. 37A, 37B); compact, protruding lumbar glands present or not (Figs. 38A, 38B, 38C); tips of digits narrower, equal to or wider than narrowest part of digit; two or three palmar tubercles present; outer palmar tubercle significantly smaller than middle palmar tubercle, also smaller than 1st supernumerary tubercle on 4th finger.

Content. 24 species: *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Group (see below) and *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group (see below) (Figs. 43–47).

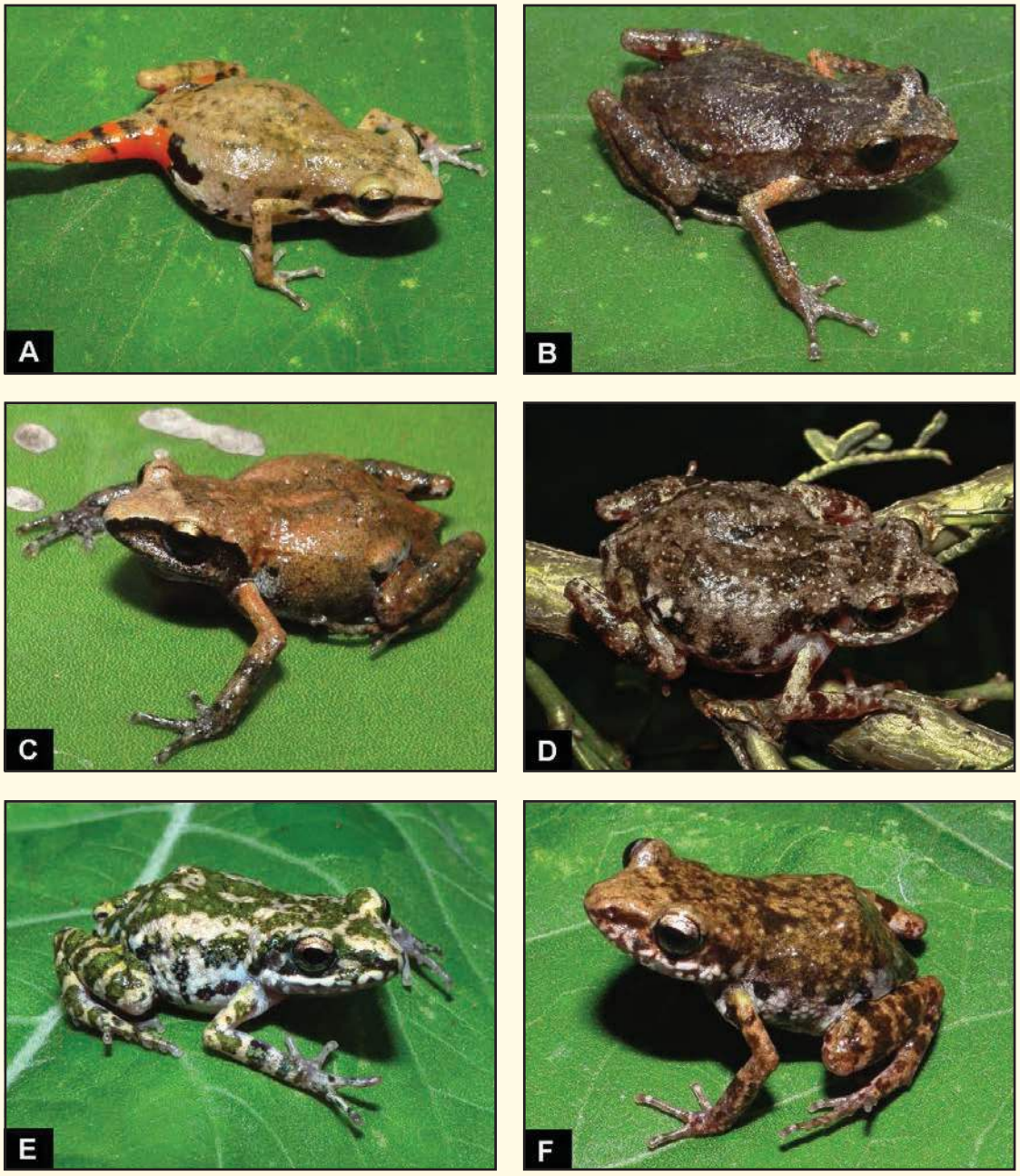


Fig. 43. Members of the *Eleutherodactylus nitidus* Species Group. (A) *Eleutherodactylus albolabris*; (B) *Eleutherodactylus dilatus* (C) *Eleutherodactylus maurus*; (D) *Eleutherodactylus nitidus nitidus*; (E) *Eleutherodactylus nitidus petersi*; and (F) *Eleutherodactylus orarius*.
© Christoph I. Grünwald (A, B, C, E, F) and Eric Centenero Alcala (D)

Distribution. Distributed in Mexico and Guatemala, predominately along the Pacific versant, from east-central Sonora and west-central Chihuahua south to central Guatemala. This group enters the Mexican highlands in the Sierra Madre Occidental, Meseta Central, Trans-Volcanic Belt, Sierra Madre del Sur, Sierra Madre del Sur de Chiapas, and Central Highlands of Chiapas. Additionally, members of this species series barely enter the drier slopes of the Sierra Madre Oriental in Tlaxcala, Puebla, Veracruz, and Oaxaca. Members of this species series occur almost entirely to the west of the continental divide, but enter the Atlantic drainages in Hidalgo, Puebla, Veracruz, and Oaxaca. The elevational range extends from sea level to approximately 2,600 m.

Eleutherodactylus (*Syrrhophus*) *nitidus* Species Group

(Figs. 43, 44)

Definition. Small to medium-sized frogs, SVL of adults from 18.2 mm (*E. rubrimaculatus*) to 29.4 mm (*E. pipilans*); abdominal vein not visible under colored epidermis or barely discernible under epidermis and above translucent visceral peritoneum, on ventral aspect of live specimens; tympanum small, 25–40% width of eye; tympanic annuli covered by skin, not clearly visible; tympanum indistinct but visible; compact, protruding lumbar glands present or not; tips of digits expanded, 3rd and 4th fingers expanded 1.1–1.9 times the narrowest part of digit; toes expanded 1.0–1.4 times narrowest part of digit; two or three palmar tubercles present, usually three; supernumerary tubercles on fingers and toes very long, conical and elevated, close together and thus giving the appearance of a saw blade (*Tomodactylus* means "saw finger").

Content. Eight species: *Eleutherodactylus* (*Syrrhophus*) *albolabris*, *E. dilatus*, *E. maurus*, *E. nitidus*, *E. orarius*, *E. pipilans*, *E. rubrimaculatus*, and *E. syristes* (Figs. 43, 44).

Distribution. Distributed in the highlands of western and central Mexico, from southern Sinaloa and Durango south across the Trans-volcanic Belt of central Mexico to Puebla, Tlaxcala, and western Veracruz. Present throughout the Sierra Madre del Sur and the highlands of Chiapas to central Guatemala, and also on the Pacific coast from southern Nayarit to Guatemala. This species group also occurs on the Meseta Central at least as far north as Zacatecas and Aguascalientes, and in the interior lowlands, including the Tepalcatepec Valley, the Balsas Basin, and the Atlantic drainages within the Tehuacán-Cuicatlán Valley and associated drier slopes of the Sierra Mazateca, Sierra Juárez, and Sierra Mixe. The elevational range extends from sea level to approximately 2,300 m.

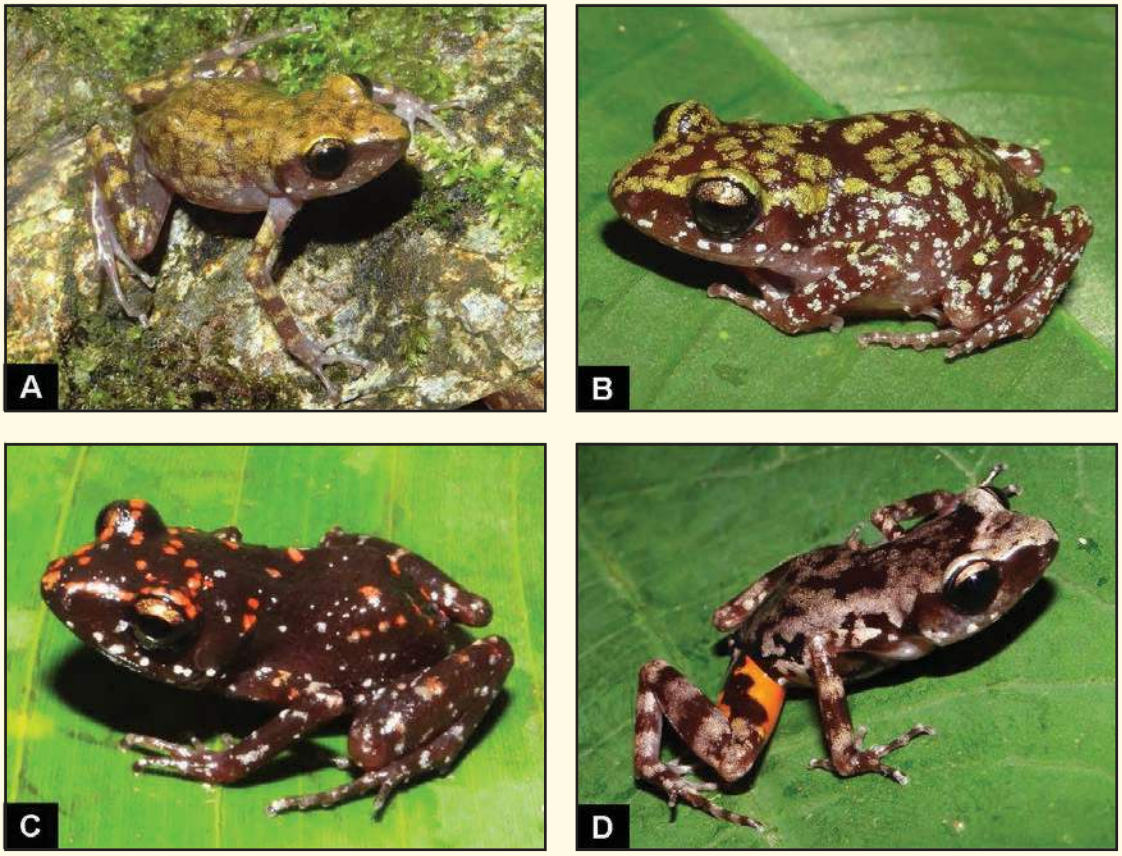


Fig. 44. Members of the *Eleutherodactylus nitidus* Species Group. (A) *Eleutherodactylus pipilans nebulosus*; (B) *Eleutherodactylus pipilans pipilans* (C) *Eleutherodactylus rubrimaculatus*; and (D) *Eleutherodactylus syristes*. © Christoph I. Grünwald

Remarks. Our results suggest that *Eleutherodactylus nitidus* is a species complex of several species in need of further review. Dixon (1957a) first described *E. orarius* as a subspecies of *E. nitidus*, but the same year Dixon (1957b) described this taxon a separate species. We follow the latter arrangement, because based on our molecular data not doing so would make *E. nitidus* paraphyletic with regard to *E. albolabris*. We do not recognize the remaining subspecies *E. nitidus nitidus* an *E. nitidus petersi* nor do we elevate them to species status at this time. Nonetheless, if *E. nitidus* results in being a species complex the name *E. petersi* would be available for the population occuring in southwestern Michoacán. We also do not recognize the subspecies of *E. pipilans*. We tentatively recognize *E. rubrimaculatus* as a species, although our molecular data suggest that this taxon might be conspecific with populations of *E. pipilans*. Based on our molecular results, we removed *E. angustidigitorum* and *E. grandis* from association with the *E.* (*Syrrhophus*) *nitidus* Species Group, as our molecular results clearly place these two species within the *E.* (*Syrrhophus*) *modestus* Species Group (as defined below).

Eleutherodactylus (*Syrrhophus*) *modestus* Species Group

(Figs. 45–47)

Definition. Small to medium-sized frogs, SVL of adults from 16.1 mm (*E. floresvillelai*) to 32.4 mm (*E. grunwaldi*); abdominal vein not visible or barely discernible under translucent or white epidermis on ventral aspect of live specimens; visceral peritoneoum translucent, with viscera visible; tympanum small, typically 15–35% width of eye, although in *E. interorbitalis*, *E. saxatilis*, and *E. grunwaldi* up to 50%; tympanic annuli covered by skin, not clearly visible; tympanum indistinct to invisible; compact, protruding lumbar glands present or not; tips of digits narrowed or expanded, when expanded tips of fingers expanded 1.1–3.5 times the narrowest part of the digit, toes expanded 0.8–1.8 times narrowest part of digit on 3rd toe; two or three palmar tubercles present, 3rd palmar tubercle either absent or significantly reduced in size; and when present, outer palmar tubercle significantly smaller than middle palmar tubercle, also smaller than 1st supernumerary tubercle on 4th finger.

Content. Sixteen species: *Eleutherodactylus* (*Syrrhophus*) *angustidigitorum*, *E. colimotl*, *E. erendirae*, *E. floresvillelai*, *E. grandis*, *E. grunwaldi*, *E. interorbitalis*, *E. jaliscoensis*, *E. manantlanensis*, *E. modestus*, *E. nietoi*, *E. pallidus*, *E. rufescens*, *E. saxatilis*, *E. teretistes*, and *E. wixarika* (Figs. 45–47).

Distribution. Limited to the lowlands and sierras of western Mexico, ranging from east-central Sonora and west-central Chihuahua south along the western and southern slopes of the Sierra Madre Occidental and into the coastal mountain ranges of Jalisco, Colima, and western Michoacán; also distributed along the Transverse Range from central Jalisco eastward to Ciudad de México. The elevation extends from sea level to approximately 2,600 m.

Remarks. The new species described herein are assigned to this species group based on our molecular and morphological analyses. Despite their prior association with species formerly assigned to *Tomodactylus*, we include *E. angustidigitorum*, *E. grandis*, and *E. saxatilis* in this species group. Based on our molecular results and on the size and shape of their supernumerary tubercles and visibility of the tympanum, we assign these species to the *Eleutherodactylus (Syrrhophus) modestus* Species Group (as defined herein).

Key to the *Eleutherodactylus* (*Syrrhophus*) Species Series and Species Groups

1a. Visceral peritoneum white, with abdominal vein obviously visible against a white background on venter of live individuals; tympanic annuli distinct, not covered by skin…… *Eleutherodactylus* (*Syrrhophus*) *longipes* Species Series.

1b. Visceral peritoneum translucent, with abdominal vein either obscured by epidermis or barely discernible against a background of viscera on venter of live individuals; tympanic annuli indistinct or invisible, covered by skin 2

2a. Digital tips on fingers 3 and 4 expanded, wider than narrowest part of finger. 3

2b. Digital tips on fingers 3 and four not expanded or narrower than narrowest part of finger 4

3a. Compact lumbar glands present but digital tips on fingers 3 and 4 expanded less than twice the narrowest part of finger; or compact lumbar glands absent but only two palmar tubercles present on hands . . . *Eleutherodactylus* (*Syrrhophus*) *nitidus* Species Group.

3b. Compact lumbar glands absent, or if compact lumbar glands present, digital tips on fingers 3 and 4 expanded twice or more the narrowest part of finger……*Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group (excluding *E. angustidigitorum* and *E. grandis*).

4. Compact lumbar glands present, digital tips narrower or as wide as narrowest part of the fingers . . . . . *Eleutherodactylus* (*Syrrhophus*) *modestus* Species Group (*E. angustidigitorum* and *E. grandis* only).



Fig. 45. Members of the *Eleutherodactylus modestus* Species Group. (A) *Eleutherodactylus angustidigitorum*; (B) *Eleutherodactylus colimotl* sp. nov.; (C) *Eleutherodactylus erendirae* sp. nov.; (D) *Eleutherodactylus floresvillelai* sp. nov.; (E) *Eleutherodactylus grandis*; and (F) *Eleutherodactylus grunwaldi*. © Christoph I. Grünwald (A, B, D, F), Jacobo Reyes-Velasco (C), and Jonathan A. Campbell (E)

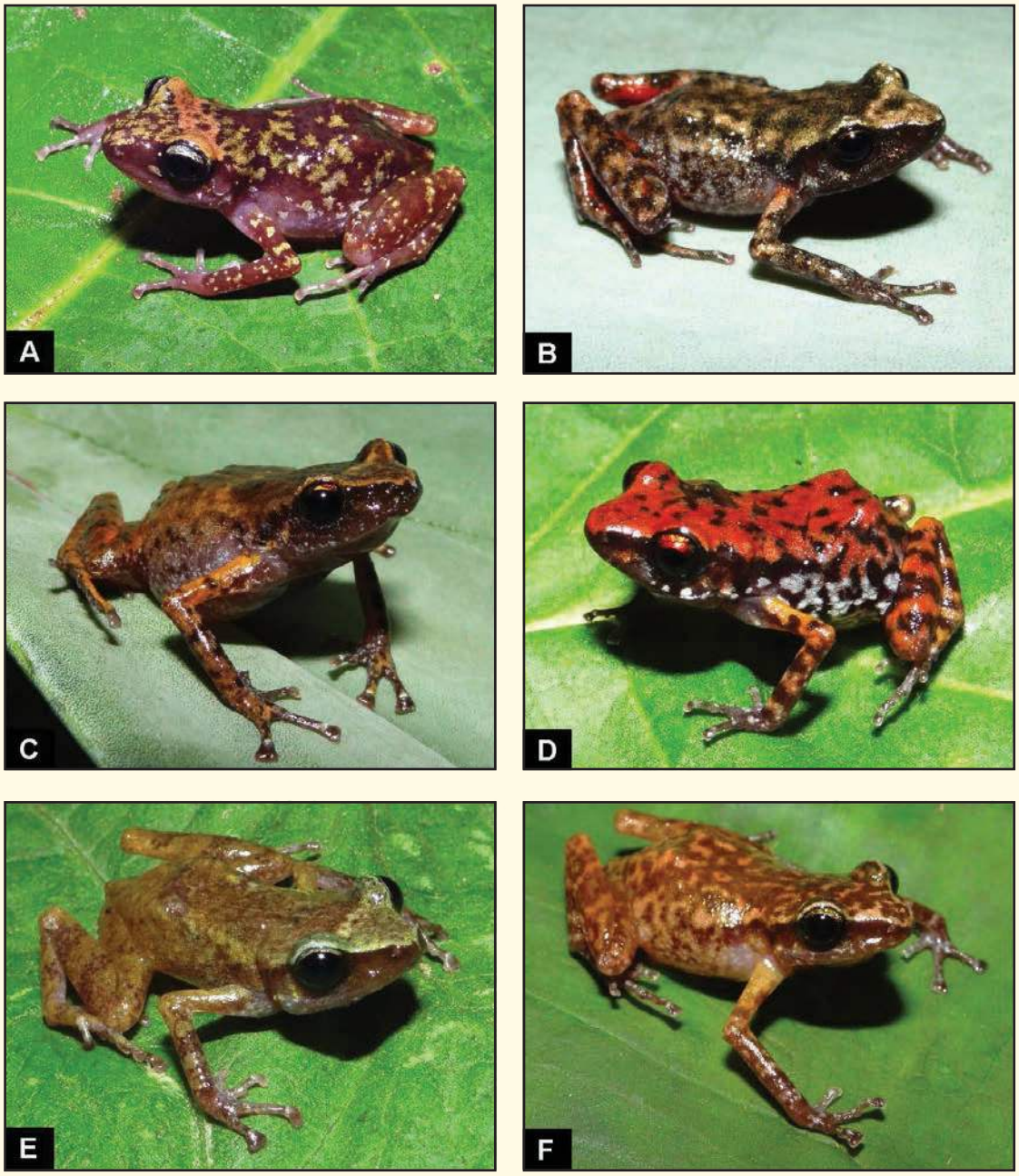


Fig. 46. Members of the *Eleutherodactylus modestus* Species Group. (A) *Eleutherodactylus interorbitalis*; (B) *Eleutherodactylus jaliscoensis* sp. nov.; (C) *Eleutherodactylus manantlanensis* sp. nov.; (D) *Eleutherodactylus modestus*; (E) *Eleutherodactylus nietoi* sp. nov.; and (F) *Eleutherodactylus pallidus*. © Christoph I. Grünwald

Environmental Vulnerability Scores for the *Eleutherodactylus modestus* Species Group and their Conservation Implications

The Environmental Vulnerability Score (EVS) was developed by Wilson and McCranie (1992) for use in the conservation of amphibians in Honduras. The EVS system later was applied to the amphibians and reptiles of Mexico by Wilson et al., (2013a, 2013b). This scheme was modified by Porras et al. (2013) for better application to animals outside of Honduras.

Grünwald et al. (2015) applied the EVS system as modified by Porras et al. (2013) and defined the Biogeographical Formations specific to reptiles and amphibians for Mexico. These more-inclusive biogeographical formations replaced the "forest formations" initially outlined by Wilson and McCranie (1992) in their application to Honduras. Herein, we apply the EVS system as outlined by Porras et al. (2013) and adapted by Grünwald et al. (2015) to the *Eleutherodactylus modestus* Species Group, as defined above.

E. angustidigitorum: 3 + 5 + 2 = 10

E. colimotl: 4 + 8 + 2 = 14

E. erendirae: 4 + 8 + 2 = 14

E. floresvillelai: 5 + 8 + 2 = 15

E. grandis: 5 + 8 + 2 = 15

E. grunwaldi: 5 + 8 + 2 = 15

E. interorbitalis: 4 + 8 + 2 = 14

E. jaliscoensis: 4 + 8 + 2 = 14

E. manantlanensis: 5 + 8 + 2 = 15

E. modestus: 4 + 7 + 2 = 13

E. nietoi: 5 + 8 + 2 = 15

E. pallidus: 3 + 5 + 2 = 10

E. rufescens: 3 + 5 + 2 = 10

E. saxatilis: 4 + 8 + 2 = 14

E. teretistes: 4 + 8 + 2 = 14

E. wixarika: 5 + 8 + 2 = 15

The results show *E. floresvillelai*, *E. grandis*, *E. grunwaldi*, *E. manantlanensis*, *E. nietoi*, and *E. wixarika* with the highest EVS scores in the group (15), because they are restricted to the immediate vicinity of their type localities within one biogeographical formation. *Eleutherodactylus colimotl*, *E. erendirae, E. jaliscoensis*, *E. interorbitalis*, *E. teretistes*, and *E. saxatilis* received the second highest EVS scores in the group (14), because they are limited to several localities within one biogeographical formation. Notably, *E. interorbitalis* has a significantly larger distribution than the other species, and likely should have been assessed a lower EVS score. The biogeographical formation to which it is limited, however, is one of the largest in Mexico, and all localities from which the species is known fall within it. *Eleutherodactylus angustidigitorum*, *E. modestus*, *E. pallidus*, and *E. rufescens* were given the lowest EVS scores for the group (10–13). They occur in at least two biogeographical formations, and their ranges are larger ranges and their elevational distribution is more extensive.

Reyes-Velasco et al. (2015) discussed some of the conservation concerns faced by *E. grunwaldi* and *E. wixarika* in their description of those species. Our EVS analysis agrees that these are among the most threatened species in the group. *Eleutherodactylus grunwaldi* is threatened by mining (both legal and illegal), which is rampant in the area. *Eleutherodactylus wixarika* is threatened by illegal logging. Of the species described herein, *E. erendirae* has been collected in areas highly modified by avocado farming. The monoculture avocado farms lack any species of *Eleutherodactylus*, and the species has been collected only in undisturbed or semi-disturbed areas between farms. Of the four species that received an EVS score of 14 in our analysis, this likely is the one with the most threatened habitat. The ranges of *E. manantlanensis* and *E. floresvillelai* appear to be extremely restricted, within the vicinity of their type localities. Fortunately, the habitat at both localities appears relatively undisturbed, and these species apparently are not under any immediate threat. *Eleutherodactylus nietoi* occurs in highly deforested areas in the Sierra Coalcomán, but appears to be abundant even after rampant deforestation.

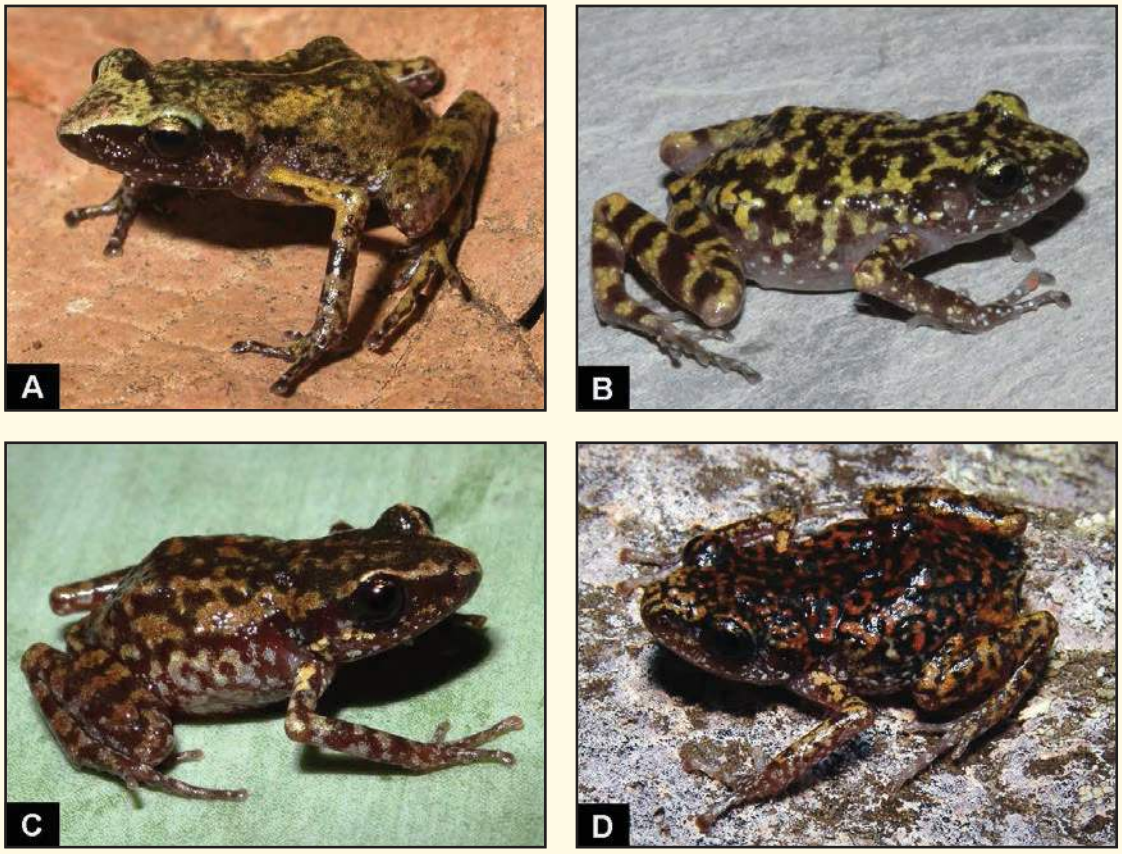


Fig. 47. Members of the *Eleutherodactylus modestus* Species Group. (A) *Eleutherodactylus rufescens*; (B) *Eleutherodactylus saxatilis*; (C) *Eleutherodactylus teretistes*; and (D) *Eleutherodactylus wixarika.* © Christoph I. Grünwald (A, C, D) and Iván T. Ahumada-Carrillo (B)

Defining Common Names based on Advertisement Call Analysis and New Proposed Common Names for the *Eleutherodactylus modestus* Species Group

As previously discussed, *Eleutherodactylus* (*Syrrhophus*) often are difficult to distinguish, but their advertisement calls are unique among the species. Since these frogs generally are located during the breeding season by following their advertisement calls, it is helpful to know what type of call each species emits. For this reason, we suggest that the common names attributed to these taxa should reflect the nature of their distinctive calls, as follows:

Eleutherodactylus angustidigitorum—Thin-fingered Piping Frog

Eleutherodactylus colimotl—Colima Peeping Frog

Eleutherodactylus erendirae—Erendira's Trilling Frog

Eleutherodactylus floresvillelai—Flores' Peeping Frog

Eleutherodactylus grandis—Great Piping Frog

Eleutherodactylus grunwaldi—Grünwald's Piping Frog

Eleutherodactylus interorbitalis—Sinaloa Piping Frog

Eleutherodactylus jaliscoensis—Jalisco Trilling Frog

Eleutherodactylus manantlanensis—Sierra Manantlán Trilling Frog

Eleutherodactylus modestus—Coastal Peeping Frog

Eleutherodactylus nietoi—Nieto's Trilling Frog

Eleutherodactylus pallidus—Pale Peeping Frog

Eleutherodactylus rufescens—Red Peeping Frog

Eleutherodactylus saxatilis—Sierra Madre Occidental Piping Frog

Eleutherodactylus teretistes—Duellman's Trilling Frog

Eleutherodactylus wixarika—Sierra Huichol Peeping Frog

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Appendix 1. List of specimens of *Syrrhophus* examined in this study. Museum Numbers: MZFC = Museo de Zoología de la Facultad de Ciencias, Universidad Autónoma de México (UNAM); and UTA = Amphibian and Reptile Diversity Research Center, University of Texas at Arlington. Field Numbers: CIG = Chris Grünwald, uncatalogued at MZFC; ENS = Eric Smith, uncatalogued at UTA; JAC = Jonathan A. Campbell, uncatalogued at UTA; JHM = John Malone, uncatalogued at UTA; JRV = Jacobo Reyes-Velasco, uncatalogued at MZFC; and TJD = Tom J. Devitt, uncatalogued at UTA.

Specimens Examined

409 Specimens:

Eleutherodactylus albolabris (16 specimens): MEXICO: Guerrero: MZFC 33082–33085 (CIG 00390–00393), MZFC 33108–33109 (CIG 00441–00442), MZFC 33230 (CIG 00668), MZFC 33323 (CIG 00953), MZFC 33325–33326 (CIG 00955–00956).

Eleutherodactylus. *angustidigitorum* (20 specimens): MEXICO: Jalisco: MZFC 33127–33130 (CIG 00476–00479), MZFC 33224–33225 (CIG 00662–00663), MZFC 33386–33388 (CIG 00991–00993), JAC 24912; Michoacán: MZFC 33015–33017 (CIG 00316–00318), MZFC 33065–33070 (CIG 00373–00378), JAC 26977.

Eleutherodactylus campi (13 specimens): MEXICO: Nuevo León: MZFC 33195–33198 (CIG 00606–00609); UNITED STATES: Texas: JHM 1390–1394.

Eleutherodactylus colimotl sp. nov. (20 specimens): MEXICO: Colima: MZFC 29282 (CIG 00468), MZFC 33115–33120 (CIG 00462–00467), MZFC 33237–33239 (CIG 00682–00684), MZFC 33299 (CIG 00901), MZFC 33329–3330 (CIG 00960–00961), JAC 30498–30499, 30631; Michoacán: MZFC 33036 (CIG 00340), JAC 23999–24001.

Eleutherodactylus cystignathoides (6 specimens): MEXICO: Veracruz: MZFC 33351–33353 (CIG 01163–01165), MZFC 33354 (CIG 01170), JAC 30000–30001.

Eleutherodactylus dennisi (13 specimens): MEXICO: Tamaulipas: MZFC 33255–33261 (CIG 00822–00828), UTA 59516–59521.

Eleutherodactylus dilatus (19 specimens): MEXICO: Guerrero: MZFC 33089–33094 (CIG 00405–00410), MZFC 33097 (CIG 00428), MZFC 33231 (CIG 00669), UTA 4017–4020, 4023–4024, 5269, 5276–5279.

Eleutherodactylus erendirae sp. nov. (25 specimens): MEXICO: Jalisco: MZFC 33000–33008 (CIG 00300–00309), MZFC 33226–33229 (CIG 00664–00667), MZFC 33232 (CIG 00673), MZFC 33234–33235 (CIG 00679–00681); Michoacán: MZFC 29274, 33019–33024 (CIG 00319–00325).

Eleutherodactylus floresvillelai sp. nov. (12 specimens): MEXICO: Michoacán: MZFC 33053–33064 (CIG 00361–00372).

Eleutherodactylus grandis (1 specimen): MEXICO: Ciudad de Mexico: UTA 56845.

Eleutherodactylus grunwaldi (12 specimens): MEXICO: Colima: MZFC 27467–27475, MZFC 27484, MZFC 33298 (CIG 00898); JRV 00230.

Eleutherodactylus guttilatus (10 specimens): MEXICO: Guanajuato: MZFC 33367–33369 (CIG 01248–01250); San Luis Potosí: MZFC 33200–33206 (CIG 00619–00625).

Eleutherodactylus interorbitalis (7 specimens): MEXICO: Sinaloa: MZFC 33186–33187 (CIG 00584–00585), MZFC 33190–33194 (CIG 00600–00604).

Eleutherodactylus jaliscoensis sp. nov. (15 specimens): MEXICO: Jalisco: MZFC 33131–33141 (CIG 00480–00490), MZFC 33274–33276 (CIG 00861–00863), MZFC 33280 (CIG 00876).

Eleutherodactylus leprus (6 specimens): MEXICO: Veracruz: MZFC 33345–33350 (CIG 01139–01144).

Eleutherodactylus longipes (3 specimens): MEXICO: Nuevo León: MZFC 33199 (CIG 00611); Querétaro: UTA 59421–59422;

Eleutherodactylus marnocki (3 specimens): UNITED STATES: Texas: JHM 1427–1429.

Eleutherodactylus manantlanensis sp. nov. (14 specimens): MEXICO: Colima: MZFC 33372–33377 (CIG 00530–00535), MZFC 33379–33381 (CIG 00646–00648), MZFC 33292–33296 (CIG 00892–00896).

Eleutherodactylus maurus (11 specimens): MEXICO: Estado de México: MZFC 33071–33076 (CIG 00379–00384), MZFC 33355 (CIG 01174); Morelos: MZFC 33077–33080 (CIG 00385–00388).

Eleutherodactylus modestus (34 specimens): MEXICO: Colima: MZFC 26888–26889, MZFC 33263–33270 (CIG 00850–00857), MZFC 33291 (CIG 00891), MZFC 33297 (CIG 00897); Jalisco: MZFC 33144-33149 (CIG 00493–00498), MZFC 33150–33154 (CIG 00505–00509), MZFC 33161 (CIG 00522), MZFC 33183–33185 (CIG 00570–00572), MZFC 33217–33223 (00655–00661).

Eleutherodactylus nietoi sp. nov. (13 specimens): MEXICO: Michoacán: MZFC 33121 (CIG 00299), MZFC 33042–33045 (CIG 00346–00349), MZFC 33050–33052 (CIG 00355–00357), MZFC 33336–33337 (CIG 00974–00975), MZFC 33342–33343 (CIG 00983–00984), MZFC 33344 (CIG 00994).

Eleutherodactylus nitidus (45 specimens): MEXICO: Estado de México: JAC 27237; Guerrero: MZFC 33034–33035 (CIG 00336–00337); MZFC 33096–33097 (CIG 00411–00412), MZFC 33104–33105 (CIG 00437–00438); Jalisco: MZFC 33010–33014 (CIG 00310–00314), MZFC 33034–33035 (CIG 00336–00337), MZFC 33110 (CIG 00457), MZFC 33273 (CIG 00860), JAC 28612; Michoacán: MZFC 33382–33385 (CIG 00675–00677), JAC 26947; Morelos: MZFC 33081 (CIG 00389); Nayarit: MZFC 33211 (CIG 00649), MZFC 33240–33242 (CIG 00685–00687); Oaxaca: MZFC 33357–33358 (CIG 01211–01212); Puebla: MZFC 33356 (CIG 01181), JAC 27256–27276.

Eleutherodactylus orarius (9 specimens): MEXICO: Colima: MZFC 26890, MZFC 33262 (CIG 00849); Michoacán: MZFC 33037 (CIG 00341), MZFC 33335 (CIG 00973), JAC 29107, 30500–30501, 30517, 30625.

Eleutherodactylus pallidus (13 specimens): MEXICO: Jalisco: MZFC 33271–33272 (CIG 00858–00859); Nayarit: MZFC 33189 (CIG 00588), MZFC 33212–33216 (CIG 00650–00654), MZFC 33243–33245 (CIG 00688–00690), MZFC 33018 (CIG 00995); Sinaloa: MZFC 33188 (CIG 00586).

Eleutherodactylus pipilans (13 specimens): MEXICO: Chiapas: MZFC 33361–33366 (CIG 01236–01241); Guerrero: MZFC 33086–33088 (CIG 00396–00398), MZFC 33106–33107 (CIG 00439–00440), MZFC 33322 (CIG 00952); Oaxaca: MZFC 33210 (CIG 00645).

Eleutherodactylus rubrimaculatus (3 specimens): MEXICO: Chiapas: MZFC 33249–33251 (CIG 00753, 00755–00756).

Eleutherodactylus rufescens (40 specimens): MEXICO: Jalisco: MZFC 33122–33126 (CIG 00471–00475), MZFC 33162–33164 (CIG 00527–00529), MZFC 33165–33174 (CIG 00544–00553), MZFC 33385 (CIG 00678); Michoacán: MZFC 33038–33041 (CIG 00342–00345), MZFC 33046–33049 (CIG 00350–00353), MZFC 33175–33182 (CIG 00559–00566), MZFC 33233 (CIG 00674), MZFC 33338 (CIG 00976), MZFC 33339–33341 (CIG 00980–00982).

Eleutherodactylus saxatilis (4 specimens): MEXICO: Sinaloa: MZFC 26893, 26896, 26898–26899.

Eleutherodactylus syristes (17 specimens): MEXICO: Guerrero: MZFC 33098–33103 (CIG 00431–00436), MZFC 33324 (CIG 00954), MZFC 33327–33328 (CIG 00957–00958); Oaxaca: MZFC 33207–33208 (CIG 00627–00628), MZFC 33209 (CIG 00644), 33378 (CIG00643), MZFC 33246–33247 (CIG 00713–00714), MZFC 33359–33360 (CIG 01232–01233).

Eleutherodactylus teretistes (5 specimens): MEXICO: Jalisco: MZFC 33142–33143 (CIG 00491–00492), MZFC 33277–33279 (CIG 00864–00866).

Eleutherodactylus verrucipes (2 specimens): MEXICO: 33253–33254 (CIG 00813–00814).

Eleutherodactylus wixarika (3 specimens): MEXICO: Jalisco: MZFC 27477–27479.

Appendix 2. GenBank Accession Numbers for the DNA sequences used in this study, listing sample number (original field number or museum number), locality to state level, species, and the accession number.

Sample	Locality	Species	GenBank Number
CIG-391	Mexico: Guerrero	*Eleutherodactylus albolabris*	MG856955
CIG-953	Mexico: Guerrero	*Eleutherodactylus albolabris*	MG856956
CIG-316	Mexico: Michoacán	*Eleutherodactylus angustidigitorum*	MG856957
CIG-317	Mexico: Michoacán	*Eleutherodactylus angustidigitorum*	MG856958
CIG-318	Mexico: Michoacán	*Eleutherodactylus angustidigitorum*	MG856959
CIG-373	Mexico: Michoacán	*Eleutherodactylus angustidigitorum*	MG856960
CIG-375	Mexico: Michoacán	*Eleutherodactylus angustidigitorum*	MG856961
CIG-378	Mexico: Michoacán	*Eleutherodactylus angustidigitorum*	MG856962
CIG-477	Mexico: Jalisco	*Eleutherodactylus angustidigitorum*	MG856963
CIG-479	Mexico: Jalisco	*Eleutherodactylus angustidigitorum*	MG856964
CIG-606	Mexico: Nuevo Leon	*Eleutherodactylus campi*	MG856965
CIG-609	Mexico: Nuevo Leon	*Eleutherodactylus campi*	MG856966
CIG-340	Mexico: Michoacán	*Eleutherodactylus colimotl* sp. nov.	MG856967
JAC-23999	Mexico: Michoacán	*Eleutherodactylus colimotl* sp. nov.	MG856968
JAC-24000	Mexico: Michoacán	*Eleutherodactylus colimotl* sp. nov.	MG856969
JAC-24001	Mexico: Michoacán	*Eleutherodactylus colimotl* sp. nov.	MG856970
CIG-462	Mexico: Colima	*Eleutherodactylus colimotl* sp. nov.	MG856971
CIG-464	Mexico: Colima	*Eleutherodactylus colimotl* sp. nov.	MG856972
CIG-407	Mexico: Guerrero	*Eleutherodactylus dilatus*	MG856973
CIG-408	Mexico: Guerrero	*Eleutherodactylus dilatus*	MG856974
CIG-303	Mexico: Jalisco	*Eleutherodactylus erendirae* sp. nov.	MG856975
CIG-306	Mexico: Jalisco	*Eleutherodactylus erendirae* sp. nov.	MG856976

CIG-308	Mexico: Jalisco	*Eleutherodactylus erendirae* sp. nov.	MG856977
JRV-090	Mexico: Jalisco	*Eleutherodactylus erendirae* sp. nov.	MG856978
JRV-091	Mexico: Jalisco	*Eleutherodactylus erendirae* sp. nov.	MG856979
CIG-319	Mexico: Michoacán	*Eleutherodactylus erendirae* sp. nov.	MG856980
CIG-320	Mexico: Michoacán	*Eleutherodactylus erendirae* sp. nov.	MG856981
CIG-322	Mexico: Michoacán	*Eleutherodactylus erendirae* sp. nov.	MG856982
CIG-361	Mexico: Michoacán	*Eleutherodactylus floresvillelai* sp. nov.	MG856983
CIG-362	Mexico: Michoacán	*Eleutherodactylus floresvillelai* sp. nov.	MG856984
CIG-364	Mexico: Michoacán	*Eleutherodactylus floresvillelai* sp. nov.	MG856985
CIG-366	Mexico: Michoacán	*Eleutherodactylus floresvillelai* sp. nov.	MG856986
CIG-367	Mexico: Michoacán	*Eleutherodactylus floresvillelai* sp. nov.	MG856987
CIG-369	Mexico: Michoacán	*Eleutherodactylus floresvillelai* sp. nov.	MG856988
TJD-831	Mexico: Ciudad de Mexico	*Eleutherodactylus grandis*	MG856989
JRV-139	Mexico: Colima	*Eleutherodactylus grunwaldi*	MG856990
JRV-255	Mexico: Jalisco	*Eleutherodactylus grunwaldi*	MG856991
JRV-257	Mexico: Jalisco	*Eleutherodactylus grunwaldi*	MG856992
JRV-142	Mexico: Jalisco	*Eleutherodactylus grunwaldi*	MG856993
CIG-619	Mexico: San Luis Potosí	*Eleutherodactylus guttilatus*	MG856994
CIG-584	Mexico: Sinaloa	*Eleutherodactylus interorbitalis*	MG856995
CIG-585	Mexico: Sinaloa	*Eleutherodactylus interorbitalis*	MG856996
CIG-490	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG856997
CIG-480	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG856998
CIG-485	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG856999
CIG-486	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG857000
CIG-489	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG857001
CIG-861	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG857002
CIG-862	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG857003
CIG-863	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG857004
CIG-482	Mexico: Jalisco	*Eleutherodactylus jaliscoensis* sp. nov.	MG857005
CIG-611	Mexico: Nuevo Leon	*Eleutherodactylus longipes*	MG857006
CIG-893	Mexico: Colima	*Eleutherodactylus manantlanensis* sp. nov.	MG857007
CIG-895	Mexico: Colima	*Eleutherodactylus manantlanensis* sp. nov.	MG857008
JRV-144	Mexico: Colima	*Eleutherodactylus manantlanensis* sp. nov.	MG857009
CIG-388	Mexico: Morelos	*Eleutherodactylus maurus*	MG857010
CIG-380	Mexico: Estado de Mexico	*Eleutherodactylus maurus*	MG857011
CIG-891	Mexico: Colima	*Eleutherodactylus modestus*	MG857012
JAC-23846	Mexico: Jalisco	*Eleutherodactylus modestus*	MG857013
CIG-571	Mexico: Jalisco	*Eleutherodactylus modestus*	MG857014
CIG-505	Mexico: Jalisco	*Eleutherodactylus modestus*	MG857015
CIG-508	Mexico: Jalisco	*Eleutherodactylus modestus*	MG857016
CIG-509	Mexico: Jalisco	*Eleutherodactylus modestus*	MG857017
CIG-570	Mexico: Jalisco	*Eleutherodactylus modestus*	MG857018
CIG-493	Mexico: Jalisco	*Eleutherodactylus modestus*	MG857019
CIG-497	Mexico: Jalisco	*Eleutherodactylus modestus*	MG857020
CIG-857	Mexico: Colima	*Eleutherodactylus modestus*	MG857021
CIG-346	Mexico: Michoacán	*Eleutherodactylus nietoi* sp. nov.	MG857022
CIG-348	Mexico: Michoacán	*Eleutherodactylus nietoi* sp. nov.	MG857023

CIG-355	Mexico: Michoacán	*Eleutherodactylus nietoi* sp. nov.	MG857024
CIG-357	Mexico: Michoacán	*Eleutherodactylus nietoi* sp. nov.	MG857025
CIG-974	Mexico: Michoacán	*Eleutherodactylus nietoi* sp. nov.	MG857026
CIG-975	Mexico: Michoacán	*Eleutherodactylus nietoi* sp. nov.	MG857027
CIG-984	Mexico: Michoacán	*Eleutherodactylus niet*oi sp. nov.	MG857028
CIG-389	Mexico: Morelos	*Eleutherodactylus nitidus*	MG857029
CIG-715	Mexico: Oaxaca	*Eleutherodactylus nitidus*	MG857030
CIG-412	Mexico: Guerrero	*Eleutherodactylus nitidus*	MG857031
CIG-336	Mexico: Guerrero	*Eleutherodactylus nitidus*	MG857032
CIG-311	Mexico: Jalisco	*Eleutherodactylus nitidus*	MG857033
CIG-314	Mexico: Jalisco	*Eleutherodactylus nitidus*	MG857034
CIG-687	Mexico: Nayarit	*Eleutherodactylus nitidus*	MG857035
JRV-085	Mexico: Jalisco	*Eleutherodactylus rufescens*	MG857036
CIG-472	Mexico: Jalisco	*Eleutherodactylus rufescens*	MG857037
CIG-473	Mexico: Jalisco	*Eleutherodactylus rufescens*	MG857038
CIG-544	Mexico: Jalisco	*Eleutherodactylus rufescens*	MG857039
JRV-184	Mexico: Jalisco	*Eleutherodactylus rufescens*	MG857040
CIG-341	Mexico: Michoacán	*Eleutherodactylus orarius*	MG857041
CIG-460	Mexico: Colima	*Eleutherodactylus orarius*	MG857042
CIG-586	Mexico: Sinaloa	*Eleutherodactylus pallidus*	MG857043
CIG-858	Mexico: Jalisco	*Eleutherodactylus pallidus*	MG857044
CIG-859	Mexico: Jalisco	*Eleutherodactylus pallidus*	MG857045
JAC-23705	Mexico: Jalisco	*Eleutherodactylus pallidus*	MG857046
CIG-588	Mexico: Nayarit	*Eleutherodactylus pallidus*	MG857047
CIG-650	Mexico: Nayarit	*Eleutherodactylus pallidus*	MG857048
CIG-651	Mexico: Nayarit	*Eleutherodactylus pallidus*	MG857049
CIG-652	Mexico: Nayarit	*Eleutherodactylus pallidus*	MG857050
CIG-689	Mexico: Nayarit	*Eleutherodactylus pallidus*	MG857051
CIG-690	Mexico: Nayarit	*Eleutherodactylus pallidus*	MG857052
CIG-995	Mexico: Nayarit	*Eleutherodactylus pallidus*	MG857053
CIG-396	Mexico: Guerrero	*Eleutherodactylus pipilans*	MG857054
CIG-398	Mexico: Guerrero	*Eleutherodactylus pipilans*	MG857055
CIG-753	Mexico: Chiapas	*Eleutherodactylus rubrimaculatus*	MG857056
CIG-755	Mexico: Chiapas	*Eleutherodactylus rubrimaculatus*	MG857057
CIG-351	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857058
CIG-353	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857059
CIG-563	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857060
CIG-565	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857061
CIG-561	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857062
CIG-551	Mexico: Jalisco	*Eleutherodactylus rufescens*	MG857063
CIG-980	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857064
CIG-981	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857065
CIG-982	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857066
CIG-344	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857067
CIG-345	Mexico: Michoacán	*Eleutherodactylus rufescens*	MG857068
TJD-895	Mexico: Sinaloa	*Eleutherodactylus saxatilis*	MG857069
CIG-954	Mexico: Guerrero	*Eleutherodactylus syristes*	MG857070

CIG-435	Mexico: Guerrero	*Eleutherodactylus syristes*	MG857071
CIG-714	Mexico: Oaxaca	*Eleutherodactylus syristes*	MG857072
CIG-628	Mexico: Oaxaca	*Eleutherodactylus syristes*	MG857073
CIG-491	Mexico: Jalisco	*Eleutherodactylus teretistes*	MG857074
CIG-492	Mexico: Jalisco	*Eleutherodactylus teretistes*	MG857075
CIG-864	Mexico: Jalisco	*Eleutherodactylus teretistes*	MG857076
CIG-866	Mexico: Jalisco	*Eleutherodactylus teretistes*	MG857077
JAC-23671	Mexico: Jalisco	*Eleutherodactylus teretistes*	MG857078
CIG-813	Mexico: Tamaulipas	*Eleutherodactylus verrucipes*	MG857079
JRV-159	Mexico: Jalisco	*Eleutherodactylus wixarika*	MG857080
JRV-160	Mexico: Jalisco	*Eleutherodactylus wixarika*	MG857081





Christoph I. Grünwald is a German-Mexican herpetologist who specializes in conservation through field research. He leads expeditions for the Herp.Mx Field Team, and to date his efforts have yielded the discovery of numerous herpetofaunal range extensions and state records, the descriptions of nine new species, and the rediscovery of several "presumably extinct" species. His specialty is rattlesnakes and pitvipers, and many important discoveries have involved this group. Recently, however, because of his interest in conservation he turned his attention to amphibians. In Mexico, many groups of amphibians remain poorly understood and are in need of scientific study, especially because certain taxa are threatened with extinction. Currently, he is leading research expeditions in southern Mexico aimed at documenting the existence of new species, especially in threatened environments, as well as collecting data for future conservation efforts. Chris is a co-founder of Biodiversa, A.C., an anti-extinction non-profit organization that is developing a system of micro-reserves aimed at conserving the most vulnerable high-endemism localities in Mexico.



Jacobo Reyes-Velasco originally is from Colima, Mexico. He received a Bachelor's degree in biology at the Universidad de Guadalajara (CUCBA), and later a Ph.D. at the University of Texas at Arlington. Presently, he is undergoing a postdoc at New York University Abu Dhabi, in the United Arab Emirates. Jacobo has authored numerous papers on the herpetofauna of western Mexico, and is the co-founder of Entorno Biótico A.C. and Herp.mx AC, two NGO's that focus on conservation initiatives and sustainable development in western Mexico.



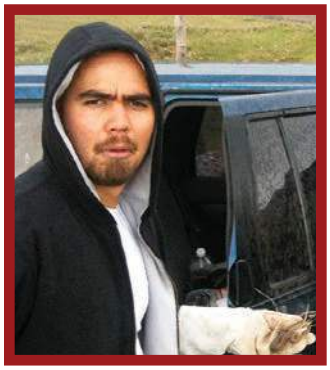
Hector Franz-Chávez was born in Guadalajara, Mexico, and presently is studying biology at the University of Guadalajara (CUCBA). He developed a curiosity for amphibians and reptiles during childhood, and today his primary interests include the biogeography, natural history, and ecology of the herpetofauna of Mexico. He also is an avid nature photographer. Hector has collaborated in various herpetological inventories in different parts of Jalisco, and is a co-author in the description of a new species of Horned Pitviper (genus *Ophryacus*) from the Sierra Madre Oriental. Currently he resides near La Paz, Baja California Sur, where he specializes in photographing and documenting the herpetofauna and marine life of the Baja California Peninsula.



Karen I. Morales-Flores is a native of Guadalajara, Mexico, but grew up in the United States where she developed an appreciation for nature, and specifically the desert reptiles in the state of Nevada. A student of biology at the University of Guadalajara (CUCBA), Karen (or "Kim") has participated in numerous field expeditions with the Herp.Mx field team. Her skills in the laboratory have encouraged her to take on ambitious projects, like measuring every external body part of 500 direct developing frogs. Kim's ambitions as a herpetologist are only matched by those as an explorer, and currently she is traveling the world in search of exciting research opportunities.



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



Jason M. Jones was born and raised in southern California, and studied biology and marketing at the University of California, Irvine. He currently resides in Colima, where he has spent the last 11 years studying and photographing the herpetofauna of Mexico. A specialist in rattlesnakes, he co-led the rediscovery of *Crotalus lannomi*, and also has collaborated in the recent descriptions of *C. campbelli*, *C. tlaloci*, and *Ophryacus smaragdinus*. Jason founded the *Herpetofauna Mexicana* group on Facebook, which currently contains about 6,000 members. He also developed the Herp Mx-Map Pack for Google Earth, which has been a valuable tool for biogeographers. As a co-founder of Biodiversa, A.C., he currently is working on developing a strategy for conserving limited range reptiles species, specifically those limited to isolated patches of cloud forest in the Sierra Madre del Sur.



Stephane Boissinot is head of the Biology program at New York University Abu Dhabi, United Arab Emirates. He previously, from 2003 to 2014, he was a professor at Queens College of the City University of New York. Stephane has authored numerous publications on a variety of topics, including the evolution of color vision, transposable elements, and more recently on the phylogeography of African frogs.