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A novel species of piping frog *Eleutherodactylus* (Anura, Eleutherodactylidae) from southern Mexico

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Abstract

We describe a new species of *Eleutherodactylus* (subgenus *Syrrhophus*) from Guerrero, Mexico, based on morphological and molecular data, as well as advertisement call analysis. *Eleutherodactylus franzi* **sp. nov.** has unique features including widely expanded fingertips, indistinct, but visible lumbo-inguinal glands, an immaculate white venter and dark reticulations on a cream dorsal background colouration. The new species belongs to the *Eleutherodactylus nitidus* species group. *Eleutherodactylus franzi* **sp. nov.** is micro-endemic, restricted to a small range in karstic hillsides on the southern extreme of the Mexican Transverse Ranges. We discuss conservation needs of this species, which we provisionally classify as Critically Endangered.

Resumen

Describimos una especie nueva de *Eleutherodactylus* (subgénero *Syrrhophus*) de Guerrero, México basado en datos morfológicos y moleculares, así como análisis de llamadas de apareamiento. *Eleutherodactylus franzi* **sp. nov.** tiene características únicas, incluyendo puntas de los dedos ampliamente expandidas, glándulas lumbo-inguinales indistintas pero visibles, un vientre blanco inmaculado y una coloración dorsal de reticulaciones oscuras sobre un fondo crema. La especie nueva pertenece al grupo de especies de *Eleutherodactylus nitidus*. *Eleutherodactylu. franzi* **sp. nov.** es micro-endémica, restringida a un pequeño rango en laderas kársticas en el extremo sur del Eje Neovolcánico. Presentamos mapas de distribución y gráficos de llamadas de apareamiento de los machos de la nueva especie y sus parientes más cercanos, así como recomendaciones de conservación.

Kurzfassung

Wir beschreiben eine neue Art von *Eleutherodactylus* (Untergattung *Syrrhophus*) aus Südmexiko, auf der Grundlage morphologischer und molekularer Daten sowie einer Analyse des Anzeigerufs. *Eleutherodactylus franzi* **sp. nov.** ist einzigartig in der Gattung durch eine Kombination von Merkmalen, darunter weit verbreiterte Fingerspitzen, undeutliche, aber sichtbare lumbo-inguinale Drüsen, ein makellos weißer Bauch und eine einzigartige Rückenfärbung aus dunklen Netzen auf einem cremefarbenen Hintergrund.. Die neue Art gehört zur *Eleutherodactylus nitidus* Artengruppe. *Eleutherodactylus franzi* **sp. nov.** ist mikroendemisch und auf ein kleines Verbreitungsgebiet in Karsthängen am südlichen Ende der Mexikanischen Querketten beschränkt. Wir präsentieren eine Verbreitungskarte der neuen Art, analysieren ihren Anzeigeruf und geben Empfehlungen für ihren Schutz.

Key Words

amphibians, Anura, conservation, Guerrero, Mexican Transverse Ranges, taxonomy

Palabras clave

anfibios, Anura, conservación, Eje Neovólcanico, Guerrero, taxonomía

Schlüsselwörter

Amphibien, Anura, Eje Neovólcanico, Guerrero, Naturschutz, Taxonomie

Introduction

Frogs of the genus *Eleutherodactylus* Duméril & Bibron, 1841 from continental North America are amongst the least understood and most taxonomically challenging groups of New World anurans (Hedges et al. 2008). The subgenus *Syrrhophus* Cope, 1878, in particular, has received little attention until recently. Recent studies that sampled all of the currently recognised species of *Syrrhophus* from continental North America led to the description of twelve new species. Reyes et al. (2015) identified two distinctive species of *Eleutherodactylus* from western Mexico using morphological and molecular data. Grünwald et al. (2018) analysed the morphological and molecular data of all known species within the subgenus *Syrrhophus* and assigned the continental North American species to three species groups contained in two species series: the *Eleutherodactylus longipes* species series (including the *E. longipes* species group) and the *E. nitidus* species series (including the *E. nitidus* and *E. modestus* species groups). They described six new species and synonymised one, while also providing data on advertisement calls for species in the *E. modestus* species group.

Recent studies have expanded the diversity within the *E. nitidus* species group. Palacios-Aguilar and Santos-Bibiano (2020) described a new species of *Eleutherodactylus* from the foothills of Guerrero, while Grünwald et al. (2021) reviewed the group and described two new species from the Sierra Madre del Sur of Guerrero. In addition, Hernández-Austria et al. (2022) presented a more detailed phylogeny of the *E. longipes* species group and described one new species of *Eleutherodactylus* and re-elevated one species from synonymy. Finally, Devitt et al. (2023) published a further review of the *E. modestus* and *E. nitidus* species groups, in which they named one of the species closely related to *E. petersi* and described a new species from the Eje Neovólcanico. These rearrangements resulted in the recognition of 43 named species as valid within the subgenus *Syrrhophus*.

The present study provides evidence, based on molecular, morphological and mating call data, for the occurrence of an additional undescribed species of *Syrrhophus* in the State of Guerrero, in southern Mexico. Our molecular phylogenetic analysis indicates that the species belongs to the *Eleutherodactylus nitidus* species group and is most closely related to *E. humboldti*. We analyse the male advertisement call of the new species, compare it to closely-related species and discuss its limited distribution. Finally, we make conservation recommendations.

Materials and methods

Taxonomic sampling

We examined specimens of all currently recognised species of the subgenus *Syrrhophus* (Frost, 2020) and measured specimens of all species, except for the enigmatic *E. verruculatus* (Peters, 1870), whose existence has been questioned by several authors (Firschein 1954; Lynch 1970; Grünwald et al. 2018, 2021).

We photographed all specimens used in this study alive, including dorsal, lateral and ventral profiles, as well as photographs of each showing colours of flanks and flash colours on the groin and thigh. We then euthanised the frogs with 10% ethanol or with topical benzocaine and took tissue samples from the thigh muscle or liver upon death and preserved them in 96% ethanol. We preserved specimens in 10% formalin and transferred them to 70% ethanol for storage. We measured additional specimens of the subgenus *Syrrhophus* in the Museo de Zoología, Facultad de Ciencias (MZFC) of the 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 did not measure type specimens of some previously-described taxa so we used the measurements of the type specimens provided in their original descriptions and

published literature. Measurements of *Eleutherodactylus dilatus* (Davis & Dixon, 1955), *E. maurus* (Davis & Dixon, 1955) (= *E. fuscus*), *E. albolabris* (Taylor, 1943) are given in their original descriptions and in Dixon (1957a, 1957b). Measurements for *E. nitidus* (Peters, 1870) and *E. petersi* (Duellman, 1954) were taken from Dixon (1957a, b), while measurements for *E. orarius* (Duellman, 1958) and *E. syristes* (Hoyt, 1965) were taken from their original descriptions. In the case of *Eleutherodactylus pipilans* (Taylor, 1940), *E. nebulosus* (Taylor, 1943) and *E. rubrimaculatus* (Taylor & Smith, 1945), we used the measurements provided in their original descriptions and from Lynch (1970). Measurements of *E. erythrochomus* Palacios-Aguilar & Santos-Bibiano, 2020), *E. maculabialis* Grünwald, Reyes-Velasco, Franz-Chávez, Morales-Flores, Ahumada-Carrillo, Rodriguez & Jones, 2021 and *E. sentinelus* Grünwald, Reyes-Velasco, Franz-Chávez, Morales-Flores, Ahumada-Carrillo, Rodriguez & Jones, 2021 were taken from the descriptions. Measurements of each one of the above species were also taken from specimens collected during this study from or near the type locality.

The material collected was deposited at the Instituto de Investigaciones sobre los Recursos Naturales (INIRENA), which is now officially known as Colección Herpetológica de la Universidad Michoacana (CHUM) of the Universidad Michoacana de San Nicolás de Hidalgo in Morelia, Michoacán, Mexico; at the Museo de Zoología, Facultad de Ciencias (MZFC) of the Universidad Nacional Autónoma de México (UNAM) in Mexico City; and at the University of Texas at Arlington, Texas (UTA). While we formally catalogued the specimens we collected, several specimens examined from both the MZFC and UTA collections have not been catalogued, in which case we list the original field numbers and the respective museum in which they were deposited. Furthermore, several of the sequences generated were submitted to GenBank using the original field numbers and not final museum catalogue numbers. Original field number abbreviations are as follows: CIG (Christoph I. Grünwald) to be catalogued at MZFC; ENS (Eric N. Smith) to be catalogued at UTA; JAC (Jonathan A. Campbell) to be catalogued at UTA; JRV (Jacobo Reyes-Velasco) to be catalogued at UTA; RHA (Raquel Hernández-Austria) and GP (Gabriela Parra-Olea) both to be catalogued at the Colección Nacional de Anfibios y Reptiles, Instituto de Biología (CNAR) at the Universidad Nacional Autónoma de México (UNAM) in Mexico City. Specimen numbers for all materials examined are provided in Appendix 1.

Morphological measurements

The characters and terminology we use herein follow those of Lynch and Duellman (1997), Savage (2002) and Grünwald et al. (2018, 2021). We took the following measurements for each specimen (abbreviations listed in parentheses): 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); palm length (PaL), total 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.

Measurements were made with Truper (Mexico) brand digital calipers and rounded to the nearest 0.1 mm. The sex of adult specimens was determined by presence of vocal slits.

Molecular analysis

DNA extraction and PCR amplification

A detailed description of the DNA extraction and PCR amplification protocols can be found in Grünwald et al. (2018). In brief, we extracted DNA from tissue samples by using a standard potassium acetate protocol and sequenced a fraction of the 16s rRNA mitochondrial gene 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 then shipped ExoSap purified PCR products to Eurofins Genomics (Lexington, KY, USA) for sequencing.

Sequence alignment and phylogenetic analysis

We included additional sequences of multiple members of the subgenus *Syrrhophus* obtained from GenBank to infer the phylogenetic relationships of the new individuals

sequenced in this study. We have included all sequences used in this study with their accession numbers in GenBank in Appendix 2. As our main interest is to understand the evolutionary relationships of the new species to members of the *Eleutherodactylus nitidus* species group, we included all of the species currently recognised in that group. We also included two members each of the *E. longipes* and the *E. modestus* species groups in our analysis.

We removed regions with poor-quality base calls by manually trimming the 5' and 3' ends of all sequences using the programme Geneious v.6.1.6 (Biomatters Ltd., Auckland, NZ). We then aligned all sequences in Muscle (Edgar 2004), with a final alignment of 560 base pairs. Our final alignment included 83 samples, of which 13 are new.

We performed Bayesian Inference of phylogeny (BI) in MrBayes v.3.2.2 (Ronquist et al. 2012), implemented on the CIPRES Science Gateway server (Miller et al. 2010). First, we selected the best-fit models of nucleotide substitution for the 16s rRNA mitochondrial gene using the Bayesian Information Criterion (BIC) implemented in PartitionFinder v.1.1.1 (Lanfear et al. 2012). Our Bayesian analysis consisted of four runs of 10 million generations each, with four chains (one cold and three heated), sampling every 1,000 generations. We used Tracer v.1.6 (Drummond and Rambaut 2012) to confirm convergence of the independent runs, based on overlap in likelihood and parameter estimates amongst runs, as well as effective sample size (ESS) and Potential Scale Reduction Factor value estimates (PSRF). PSRF indicated that individual runs had converged by 100,000 generations, so we discarded the first 25% of the runs as burn-in. Finally, we annotated posterior probability values on the resulting topology using the programme TreeAnnotator v.1.8.3 (Rambaut et al. 2014) and collapsed all nodes with less than 0.50 posterior support. Additionally, we obtained genetic distances for the members of the group with the use of Mega X (Kumar et al. 2018).

Bioacoustic analysis

We recorded vocalisations of several individuals of the new species described here, as well as all other members of the *Eleutherodactylus* (*Syrrhophus*) *nitidus* species group (sensu Grünwald et al. (2018, 2021)). We recorded the frogs while they were actively calling in the field, using the WavePad free recording software (NCH Software 2015) on various Apple iPhones. We recorded the calls at distances ranging from 50–150 cm, although when possible, we tried to be within 100 cm of the frog. Ambient temperatures were not taken at the time of recording, but we did record the time of day the recordings were made. The calls were recorded at a sampling rate of 44.1 kHz and an amplitude resolution of 16 bits.

We isolated the individual calls from other calls and background noise using Adobe Audition CC, using default settings in the application. We then analysed the calls using the software Raven Pro 1.5 (The Cornell Lab of Ornithology 2014). Spectrograms were constructed using a Blackman-type window with a size of 5 ms, 80% overlap and DFT of 512 samples. Temporal parameters were measured from the oscillogram in ms. Spectrogram and oscillogram graphics were generated using Seewave v.1.6 (Sueur et al. 2008) in RStudio v.1.1.423 (RStudio Team 2016). Values in the call descriptions are given as mean ± standard deviation. 2D spectrograms were visualised using a sliding window analysis of short-term Fourier transform calculations.

Results

Molecular phylogenetic results

Our phylogenetic results (Fig. 1) are mostly in concordance with other molecular phylogenies of the subgenus *Syrrhophus* (Grünwald et al. 2018, 2021; Hernandez-Austria et al. 2022; Devitt et al. 2023). The novel species is nested within the *Eleutherodactylus nitidus* species group as defined by Grünwald et al. (2018, 2021). Our analysis recovered all members of the *E. nitidus* species group as sister to the *E. modestus* species group, with strong support (posterior support (pp) = 1). Within the *E. nitidus* species group, there was a trichotomy with one strongly-supported clade (pp = 1) comprised of *E. dilatus*, *E. sentinelus*, *E. maculabialis*, *E. syristes*, *E. maurus*, *E. humboldti*, the novel species described here, *E. nitidus*, *E. petersi*, *E. orarius*, *E. jamesdixoni* and *E. albolabris*. The relationship of the remaining members of the *E. nitidus* species group including *E. pipilans*, *E. erythrochomus*, *E. rubrimaculatus* and *E. nebulosus* to one another and to the larger supported clade were not well resolved, except that *E. rubrimaculatus* and *E. nebulosus* are closely related to each other. The new species was recovered as a sister species to the sympatric *E. humboldti*, although with low support (pp = 0.61).

Systematic account

Eleutherodactylus franzi sp. nov.

https://zoobank.org/18CE837E-C4B3-4468-BA37-AFB9213A9509

Figs 2–4, 5A

Franz's Piping Frog / Rana gaitera de Franz

Type material. ***Holotype*.** INIRENA 2900 (CIG 01725). Adult male (Fig. 2), El Cucharillo, Municipio de Ixcateopan de Cuauhtémoc (18.5331, -99.7335, 2,315 m a.s.l.; datum = WGS84), Guerrero, Mexico, collected on 27 June 2020 by Héctor Franz-Chávez, Christoph I. Grünwald, André J. Grünwald and Kimberly Montelongo-Chávez.

***Paratypes* (n = 14; Fig. 3).** INIRENA 2901–10 (CIG 01716–24, 01726), 10 adult males, collected at same locality and on same date as holotype; INIRENA 2895–97 (CIG 01727–29), 3 adult males, 3 km E of Ixcateopan de Cuauhtémoc, Municipio de Ixcateopan de Cuauhtémoc

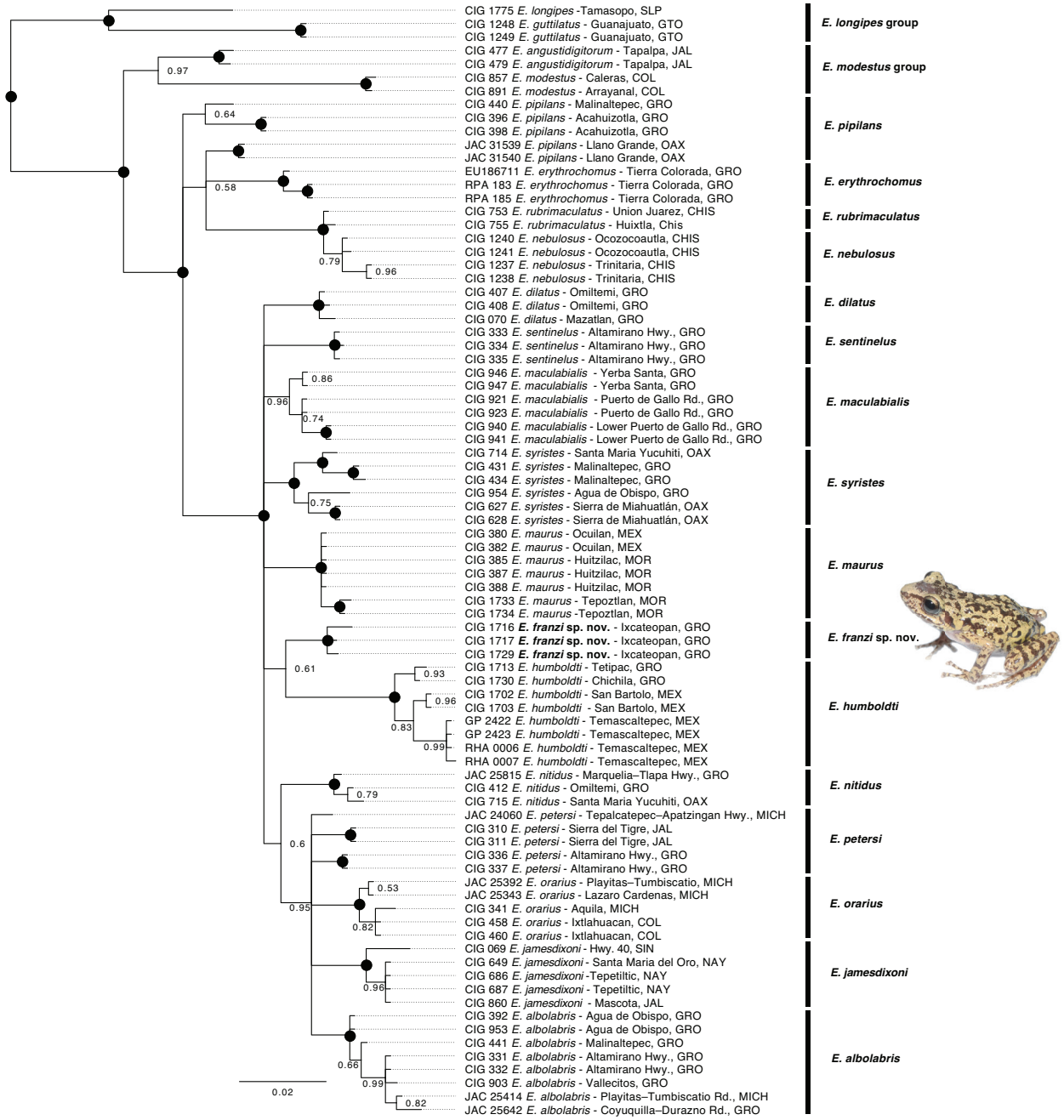

Figure 1. Bayesian phylogenetic inference of members of the *Eleutherodactylus* subgenus *Syrrhophus*, with a focus on the *E. nitidus* species group, based on the mitochondrial locus 16S rRNA. Black circles represent nodes with a posterior support of 1. All nodes with support of less than 0.5 are collapsed.

(18.5076, -99.7329, 2,060 m a.s.l.; datum = WGS84), Guerrero collected on 27 June 2020 by Héctor Franz-Chávez, Christoph I. Grünwald, André J. Grünwald and Kimberly Montelongo-Chávez; INIRENA 2898 (CIG 01731), 1 adult male, between El Cucharillo and Chichila, Municipio de Taxco de Alarcón, (18.5335, -99.7117, 2,260 m a.s.l.; datum = WGS84), Guerrero, Mexico, collected on 27 June 2020 by Héctor Franz-Chávez, Christoph I. Grünwald, André J. Grünwald and Kimberly Montelongo-Chávez.

Diagnosis. Based on our phylogenetic analysis, this is 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*) *nitidus* species group as defined by Grünwald et al. (2018), based on the condition of the tympanic annuli, ventral epidermis and visceral peritoneum. A small frog, but relatively large *Syrrhophus*, adult males measure 25.6–29.5 mm SVL; vocal slits are present in males, readily visible under partially translucent ventral epidermis; digital tips are widely expanded, 1.8–2.6 times the width of the narrowest part of the finger on the third and fourth fingers; fingers moderately long, finger lengths are I-II-IV-III with third finger

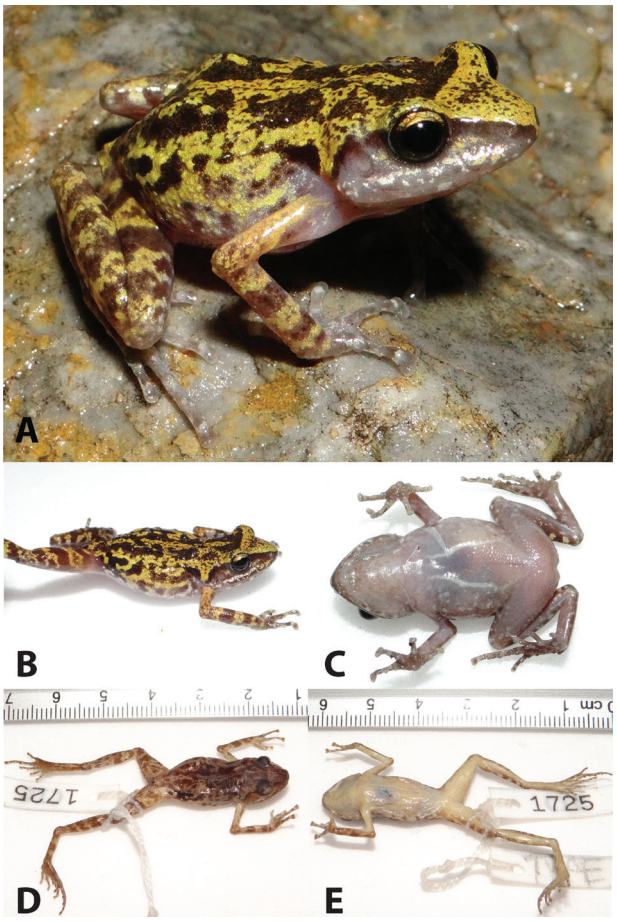

Figure 2. Holotype of *Eleutherodactylus franzi*, sp. nov., INIRENA 2900 (CIG 01725), El Cucharillo, Municipio de Ixcateopan de Cuauhtémoc, Guerrero, Mexico in life (**A–C**) and in preservative (**D, E**).

length ranging from 15–18% of SVL; compact lumbo-inguinal gland above the inguinal region present, raised, indistinct, but visible in live specimen; ventral epidermis is partially translucent and visceral peritoneum is clear, not white, thus abdominal vein is not clearly visible against a white background on the venter of live specimens and viscera is partially visible through translucent dark grey ventral epidermis; limbs moderate, TL/SVL ratio is 0.40–0.50, FeL/SVL ratio is 0.31–0.38 and TotFL/ SVL ratio is 0.50–0.60; snout relatively short, END/ SVL ratio is 0.08–0.11; tympanum small, indistinct and round, tympanic annuli not visible in live specimen; TW/ED ratio is 0.40–0.60. The dorsal and lateral skin is slightly shagreened, whereas the ventral skin is smooth. Dorsal colouration cream or tan, with darker brown reticulations on dorsal and lateral portions of head and back; loreal and region dark brown, from snout to behind tympanum, with some pale spots and speckling present on labial region same colour as pale dorsal colouration; pale interorbital bar variable, may be present or absent, when present same colour as pale dorsal colouration of head and body; distinct irregular-edged dark brown transverse bands present on legs; upper arms same colouration and pattern as forearms; no pale mid-dorsal stripe; upper flanks same colour as dorsum, lower flanks whitish with some grey marbling; venter pale lavender with some sparse white spotting and pale grey on throat. No inguinal flash colours present on thighs and groin. The mating call of adult males is a short low-pitched pipe (see below; Fig. 4).

Comparisons. *Eleutherodactylus franzi* can be distinguished from all species in the *Eleutherodactylus* (*Syrrhophus*) *longipes* species series by: possessing a small, indistinct tympanum with no tympanic annulus visible and with a diameter less than 50% of the diameter of the eye; by possessing a ventral epidermis which is semi-translucent and combined with a visceral peritoneum which is not white, an abdominal vein on the venter is not clearly evident against a white background in life; by possessing indistinct, but visible raised lumbo-inguinal gland above the inguinal region.

Eleutherodactylus franzi can be distinguished from most species of the *Eleutherodactylus* (*Syrrhophus*) *modestus* species group by the combination of possessing a compact, protruding lumbo-inguinal gland above the inguinal region, digital tips which are expanded more than 1.8 times the width of the narrowest part the finger on the third and fourth fingers and the lack of a distinct interorbital bar a colour distinct from the dorsal ground colouration. It can further be distinguished from the superficially similar *E. grunwaldi* by its smaller body size, 25.6–29.5 mm (vs. 28.4–32.4 mm), less expanded fingertips, 1.8–2.5 times the width of the narrowest part of the finger on fingers three and four (vs. 2.8–3.2) and the presence of a visible raised lumbo-inguinal gland. From the superficially very similar *E. saxatilis*, it can be distinguished by snout shape, eye size and head colouration. These two frogs, although not closely related, are very similar in appearance, but come from two widely-separated mountain ranges in central Mexico and are genetically distinct. *Eleutherodactylus franzi* has an angular canthus rostralis, with a shorter snout that is distinctly truncated from a lateral profile. It has a larger eye, with a larger ETD and, generally, there is a pale interorbital region that lacks dark markings. In *E. saxatilis*, the canthus rostralis is noticeably rounded and the snout is acuminate from a lateral profile. The eyes are smaller and located closer to the tympanum and there is no noticeable lack of dark dorsal markings in the interorbital area.

Within its own species group, *E. franzi* can be distinguished from most species by possessing a compact inguinal gland that is indistinct, but visible in live specimens. This character may or may not be visible in preserved specimens depending on how they were preserved. This species differs from *E. pipilans*, *E. erythrochomus* and *E. nebulosus*, which lack visible compact lumbo-inguinal glands altogether. All other known species in the *E. (Syrrhophus) nitidus* species group have readily visible compact lumbo-inguinal glands above the inguinal region, except *E. maculabialis*, which has similarly visible, but indistinct lumbo-inguinal glands. *Eleutherodactylus franzi* can be

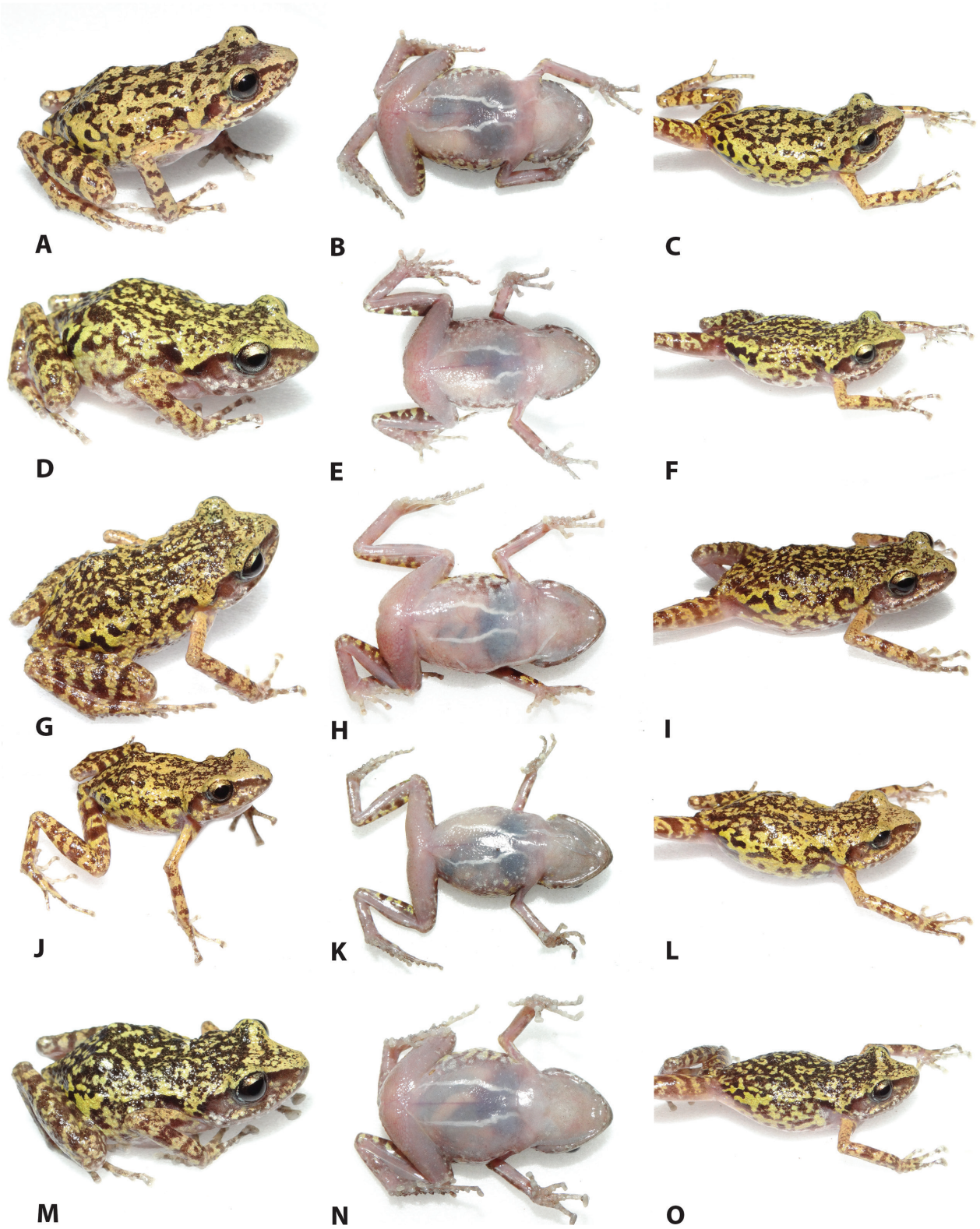

Figure 3. Some of the paratypes of *Eleutherodactylus franzi* sp. nov., in life. **A–C.** INIRENA 2902 (CIG 01717) El Cucharillo, Municipio de Ixcateopan de Cuauhtémoc, Guerrero, Mexico; **D–F.** INIRENA 2910 (CIG 01726) El Cucharillo, Municipio de Ixcateopan de Cuauhtémoc, Guerrero, Mexico; **G–I.** INIRENA 2895 (CIG 01727), 3 km E of Ixcateopan de Cuauhtémoc, Municipio de Ixcateopan de Cuauhtémoc, Guerrero, Mexico; **J–L.** INIRENA 2896 (CIG 01728), 3 km E of Ixcateopan de Cuauhtémoc, Municipio de Ixcateopan de Cuauhtémoc, Guerrero, Mexico; **M–O.** INIRENA 2898 (CIG 01731), between El Cucharillo and Chichila, Municipio de Taxco de Alarcón, Guerrero, Mexico.

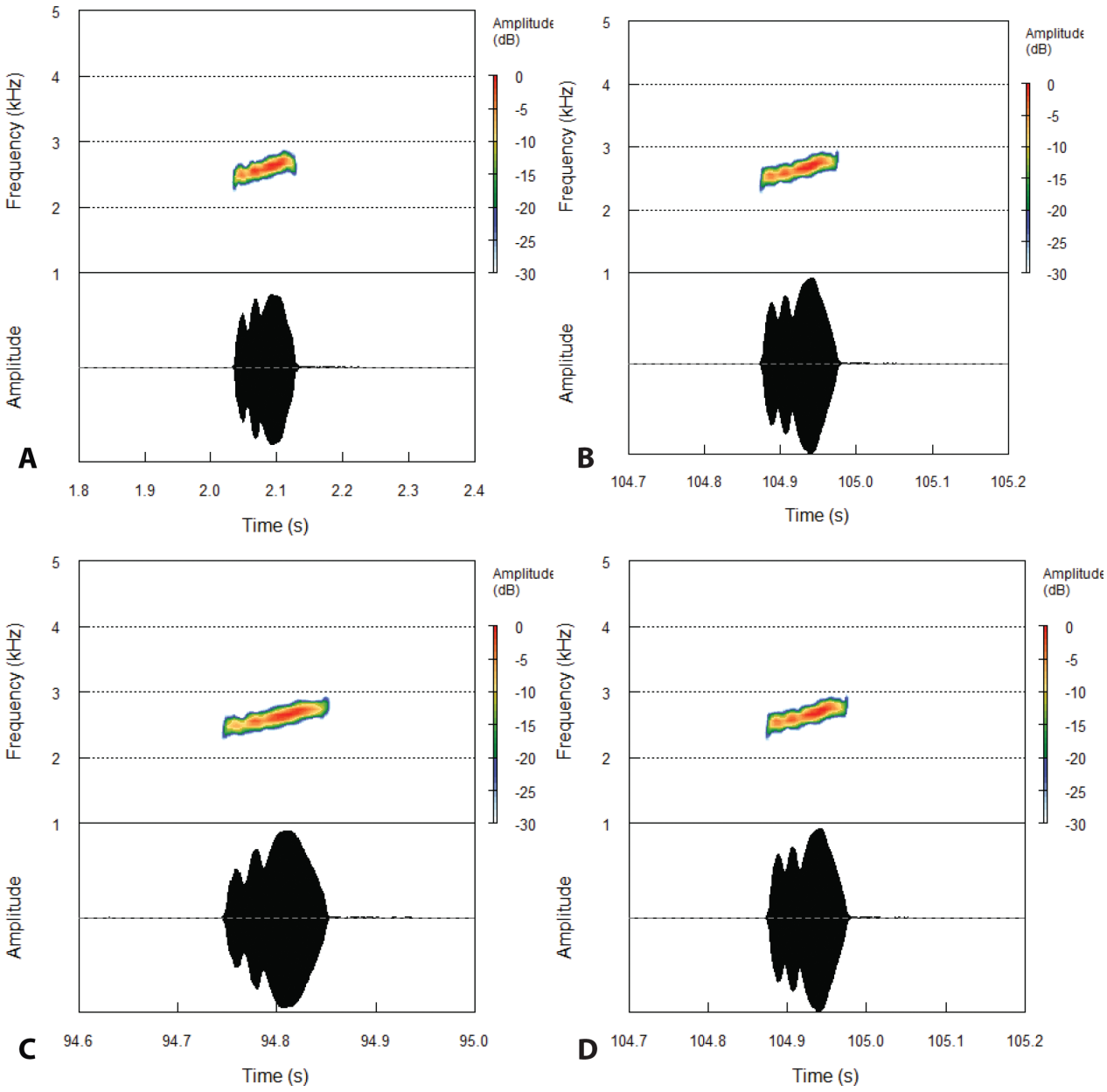

Figure 4. Spectrograms (top) and oscillograms (bottom) of the advertisement calls of *Eleutherodactylus franzi* sp. nov., recorded at El Cucharillo, Municipio de Ixcateopan de Cuauhtémoc, Guerrero, Mexico (**A, B**) and at 3 km E of Ixcateopan de Cuauhtémoc, Guerrero, Mexico (**C, D**).

further distinguished from *E. pipilans* and *E. nebulosus* by possessing digital tips which are expanded more than 1.8 times the width of the narrowest part of the finger and from *E. erythrochomus* by possessing digital tips which are more than 1.5 times, but less than 3.0 times, the width of the narrowest part of the finger. It is distinguished from *E. albolabris*, *E. nitidus*, *E. petersi*, *E. jamesdixoni* and *E. orarius* by the combination of larger size, smoother skin, longer limbs and tips of digits which are expanded more than 1.8 times the narrowest part of the finger on the third and fourth fingers. This species is distinguished from *E. dilatus*, *E. humboldti*, *E. maurus* and *E. sentinelus* by its larger size, smoother skin, pale dorsal colouration with dark reticulations and lack of a pale interorbital bar which is paler than the pale dorsal colouration. Furthermore, all these species, except *E. humboldti*, present multi-note whistles, while *E. franzi* has a call that consists of a single note, low-pitched pipe. *Eleutherodactylus franzi* may be distinguished from *E. maculabialis* and *E. syristes* by its larger size, more expanded fingertips, lack of inguinal flash colouration, as well as those species' unique advertisement call which consists of a trill rather than a short pipe. In Guerrero, two other species of saxicolous *Eleutherodactylus* (*E. pipilans* and *E. erythrochomus*) have similar colouration, similar smooth skin and widely expanded digital pads. Both are readily distinguishable from *E. franzi* by possessing an indistinct lumbo-inguinal gland which is barely visible in life and by a male advertisement call which is a peep instead of a pipe. Furthermore, *E. franzi* can be distinguished from *E. pipilans* by its more expanded digital tips on the third and fourth fingers, 1.8–2.5 times the width of the narrowest part of the finger

(vs. 1.3–1.9) and distinct lack of dark markings in the interorbital region (vs. no difference from rest of dorsum). It can further be distinguished from *E. erythrochomus* by the conspicuous dark pattern on a pale dorsal colouration, lesser expanded digital tips no more than 2.5 times the width of the narrowest part of the digit on the third and fourth fingers (vs. 2.3–3.8) and a less distinct tympanum. General characteristics for the *Eleutherodactylus nitidus* species group are given in Table 1.

Description of the holotype. Adult male, relatively large (26.2 mm SVL); head as wide (9.5 mm) as long (9.5 mm), head wider than body; snout rounded from a dorsal view and rounded to slightly truncate from a lateral profile; tympanum indistinct, rounded with no supra-tympanic fold present; tympanum small, oval, greatest width of tympanum 1.4 mm; greatest diameter of eye 2.8 mm; tympanum width to eye-diameter 0.51; eyelid width 1.6 mm, approximately 38% of the IOD; first finger shorter than second finger; finger lengths from shortest to longest I-II-IV-III; digital pads on fingers two, three and four expanded, 2.1 times the narrowest point of the digit on fingers three and four; expanded finger pads widely expanded, truncate, three palmar tubercles; inner palmar tubercle 70% of middle palmar tubercle and outer palmar tubercles about 60% as large as middle palmar tubercle, (Fig. 5A); toe lengths from shortest to longest I-V-II-III-IV, TL1 and TL5 very similar; outer metatarsal conical with a round base moderate, approximately 56% of inner metatarsal tubercle; inner metatarsal tubercle spherical shape with oval base, large, approximately 1.1 mm in length. Dorsal skin smooth, lateral skin slightly shagreened with some low tubercles; ventral skin smooth. Vocal slits present.

In life, the holotype had a yellowish-tan dorsal colouration on the back, with darker brown blotches on the back and flanks. Head yellowish-tan with some dark brown speckling, no pale interorbital bar; however, the interorbital region mostly lacks darker brown speckling giving it the resemblance of a pale interorbital bar. Labial region pale grey with some tan and some white speckling. Three and four white-tipped tubercles present at the rictal. A dark brown stripe present from the tip of the snout posteriorly through loreal region, eye and tympanum to right above rictal tubercles. Forearms, thighs, femur and tarsus tan with indistinct pale brown banding. The upper arms were unmarked, tan to slightly orange. No inguinal flash colouration was present on groin or thighs. Ventral colouration was lavender with some sparse white and on sides, ventral colouration on throat grey. Ventral skin was slightly translucent and visceral peritoneum clear, so no visible red abdominal vein and viscera were visible in life.

Colouration in preservative is pale tan on dorsum, with darker brown reticulations. Pale tan interorbital bar present. Dark canthal bar is dark brown. Unmarked upper arms are cream to white. Limbs cream with dark brown cross-banding. The dorsal surfaces of the legs are light

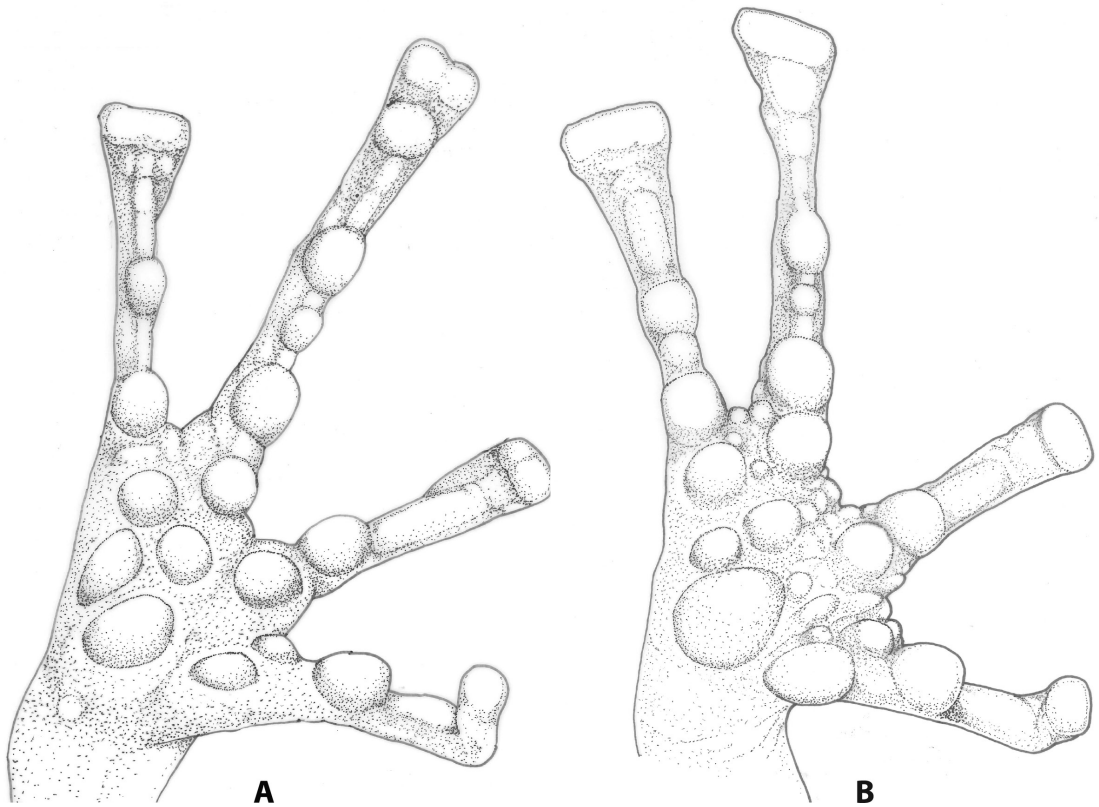

Figure 5. A. Ventral aspect of the hand of the holotype of *Eleutherodactylus franzi* sp. nov., INIRENA 2900 (CIG 01725) from El Cucharillo, Municipio de Ixcateopan de Cuauhtémoc, Guerrero, Mexico; **B.** Ventral aspect of the hand of a *Eleutherodactylus humboldti*, INIRENA 2911 (CIG 01703) from 9.4 km N of Valle de Bravo junction on Valle de Bravo – Toluca toll road, near San Bartolo, Municipio de Amanalco, Estado de México, Mexico.

Table 1. Key Comparative Characters of the *Eleutherodactylus nitidus* species group.

	E. albolabris	***E. dilatus***	***E. erythrochomus***	***E. franzi* sp. nov.**	***E. humboldti***	***E. jamesdixoni***	***E. maculabialis***	***E. maurus***	***E. nebulosus***	***E. nitidus***	***E. orarius***	***E. petersi***	***E. pipilans***	***E. rubrimaculatus***	***E. sentinelus***	***E. syristes***
Size	Medium	Medium	Large	Large	Medium	Medium	Small	Small	Medium	Medium	Medium	Medium	Large	Small	Medium	Small
SVL adult males (range) in mm	23.0–26.8	23.8–25.7	24.9–30.0	25.6–29.5	23.4–25.7	24.3–26.3	17.9–24.7	20.7–24.3	22.9–28.3	24.3–26.3	24.6–28.0	23.9–26.3	25.5–29.6	18.2–23.5	23.3–25.3	21.7–24.6
Condition of Interorbital Bar	Indistinct, Pale	Present, Pale	Absent	Absent	Usually Present, Pale	Indistinct, Pale	Present, Pale	Present, Pale	Absent	Indistinct, Pale	Indistinct, Pale	Indistinct, Pale	Absent	Absent	Present, Pale	Present, Pale
Pale Mid-dorsal Blotch	Sometime Present	Absent	Absent	Absent	Present	Present	Absent	Absent	Absent	Present	Sometimes Present	Present	Absent	Absent	Present	Absent
Colouration of Lip	White	Dark with pale flecking	As head	Grey, with flecking of dorsal colouration	Pale, with white flecking,	Mottled	Dark with pale spots	Dark with pale flecking	Dark with pale spots	Mottled	White, mottled with dark	Mottled	As head	Dark with white or pale spots	Dark with pale flecking	Dark, variedly spotted
Inguinal Flash Colouration	Orange	Yellow	Absent	Absent	Yellow or orange	Faint, yellow-orange	Varied, Yellow / Orange	Varied, usually Absent	Absent	Faint, yellow-orange	Faint, yellow-orange	Faint, yellow-orange	Absent	Absent	Yellow	Varied, Yellow / Orange
Ventral Colouration	White with black spots	Grey with white and black	Transparent	White or pinkish	Grey, with white and black	White with dark mottling	Grey with white and black	Grey with white and black	Transparent	White with dark mottling	White with dark mottling	White with dark mottling	Transparent	Pale grey with white spotting	Transparent with white and black	Transparent and White, with black spots
Dorsal Skin Texture	Smooth	Not Smooth	Smooth	Smooth	Not Smooth	Not Smooth	Smooth	Not Smooth	Smooth	Not Smooth	Not Smooth	Not Smooth	Smooth	Smooth	Smooth	Smooth
Ventral Skin Texture	Slightly Rugose	Rugose	Smooth	Smooth	Rugose	Slightly Rugose	Smooth	Rugose	Smooth	Slightly Rugose	Slightly Rugose	Slightly Rugose	Smooth	Smooth	Smooth	Smooth
Condition of Lumbo-Inguinal Gland	Very distinct	Very distinct	Indistinct	Distinct	Very distinct	Very distinct	Distinct	Very distinct	Indistinct	Very distinct	Very distinct	Very distinct	Indistinct	Indistinct	Very distinct	Distinct
3FPW/3FW	1.3–1.9	1.5–1.7	2.3–3.8	1.8–2.5	1.9–2.4	1.1–1.5	1.4–2.1	1.3–1.6	1.1–1.5	1.1–1.5	1.2–1.4	1.1–1.7	1.5–1.9	1.5–1.9	1.7–2.3	1.1–1.9
4FPW/4FW	1.3–1.9	1.5–1.8	2.3–3.5–	1.8–2.5	1.3–2.1	1.1–1.5	1.4–2.1	1.3–1.7	1.1–1.5	1.1–1.5	1.2–1.4	1.1–1.7	1.5–2.0	1.5–1.9	1.5–2.3	1.2–1.8
TW/ED	0.27–0.32	0.25–0.35	0.33–0.51	0.40–0.61	0.37–0.52	0.25–0.29	0.25–0.28	0.28–0.31	0.35–0.38	0.25–0.29	0.25–0.29	0.25–0.29	0.30–0.36	0.25–0.36	0.26–0.28	0.25–0.29
Call	Whistle	Peep	Peep	Pipe	Pipe	Whistle	Trill	Pipe	Peep	Whistle	Whistle	Whistle	Peep	Peep	Peep	Trill

brown and the groin and posterior surfaces of the thighs are brown. Ventral surfaces yellowish-cream, unmarked, slightly darker brownish pigmentation on throat and chin. Ventral surfaces of hands and feet brown, with dark brown spots. (Fig. 2D, E).

Measurements of the holotype (in millimetres). IND 2.2, IOD 4.2, END 2.5, ETD 0.9, UpL 6.4, FoL 7.5, PaL 2.3, HaL 6.7, F1L 2.3, F1PW 0.5, F1W 0.4, F2L 2.8, F2PW 0.8, F2W 0.4, F3L 4.7, F3PW 1.1, F3W 0.5, F4L 3.5, F4PW 1.1, F4W 0.5, IPTL 0.7, MPTL 1.0, OPTL 0.6, FeL 10.0, TL 11.0, TaL 7.1, TotFL 11.4, T1L 2.4, T1PW 0.62, T1W 0.5, T2L 3.6, T2PW 0.7, T2W 0.5, T3L 4.4, T3PW 0.7, T3W 0.5, T4L 6.0, T4PW 0.7, T4W 0.5, T5L 2.5, T5PW 0.6, T5W 0.4, IMTL 1.1, OMTL 0.6, FeL/SVL 38%, TL/SVL 42%, HaL/SVL 26%, TotFL/SVL 56%, HL/SVL 35%, HW/SVL 36%.

Variation. SVL from 25.6–29.5 mm (27.15 ± 1.77). Expanded finger pads vary from 1.8–2.5 times the narrowest part of the digit on the third finger and from 1.8–2.6 times the narrowest part of the digit on the fourth finger, with average 2.0 ± 0.21 on the third finger and average 2.2 ± 0.21 on the fourth finger. Dorsal ground colouration cream or tan, but varied with some greenish, reddish or yellowish tinge, always with darker brown blotches or reticulations. The extent of the darker brown blotches or reticulation varied greatly. The condition of the interorbital area ranged from unmarked and same colour as ground colouration to heavily marked by dark speckling same colour as dark dorsal blotches or reticulation. Venter always lavender, but with varying amounts of white spots. Morphological variation of *E. franzi* is presented in Table 2.

Advertisement call. The advertisement call of the males of this species consists of a single, short, low-pitched pipe that lasts about 106 ms and has a dominant frequency of 2612.7 ± 40.6 Hz (Fig. 4A–D). The note has limited amplitude modulation and the highest energy is displayed at the end of the note. The call is similar to that of *E. pipilans* and *E. erythrochomus*. The call differs from the nearby *E. maurus* and the sympatric *E. humboldti*, which also have a pipe, by being shorter and lower pitched. We present call data for both *E. franzi* and the sympatric *E. humboldti* in Table 3. The advertisement call also differs from the sympatric or near sympatric *E. petersi* and *E. nitidus* as these two species have a call that consists of a multi-note whistle rather than a single-note pipe.

Distribution and ecology. *Eleutherodactylus franzi* appears to be endemic to the Sierra de Taxco Region of northern Guerrero (Fig. 6). This is an extension of the Mexican Transverse Volcanic Belt which extends south into the Balsas Basin. This frog occurs at high elevations between 2,000–2,400 m a.s.l. and has been collected in tropical deciduous forest, oak woodland and pine-oak forest, as well as mixtures of these assemblages. It is restricted to areas of karstic rock outcroppings and the associated sinkholes and caves systems. This species may also occur in nearby Estado de México, as habitat is continuous and the State line is near the type locality. Old reports of *E. pipilans* from that State may be referable to this species; however, we have made attempts to examine these specimens at MZFC and were not able to find the specimens (C. Grünwald, pers. obs.)

Etymology. This species is named after Héctor Franz-Chávez, Mexican herpetologist and avid field collector

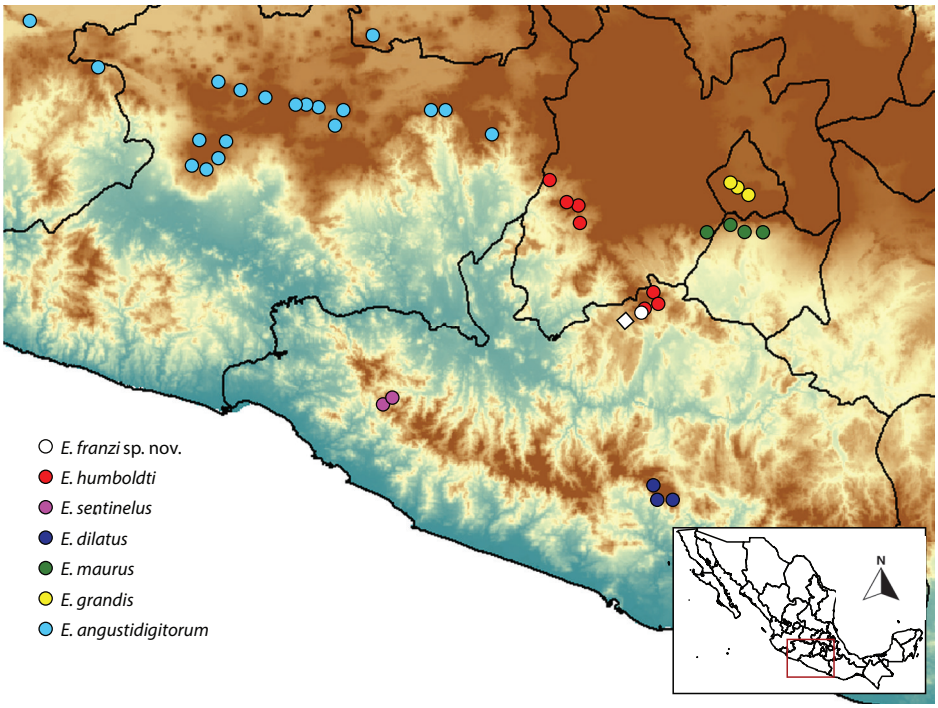

Figure 6. Map showing the type localities and distribution of *Eleutherodactylus* which are either closely related or superficially similar to the species described herein from southern Mexico. White diamond represents the type locality of *E. franzi* sp. nov. and white circle represents additional locality.

Table 2. *Eleutherodactylus franzi* sp. nov. Morphological Measurements (in millimetres).

	INIRENA 2901	INIRENA 2902	INIRENA 2903	INIRENA 2904	INIRENA 2905	INIRENA 2906	INIRENA 2907	INIRENA 2908	INIRENA 2909	INIRENA 2900	INIRENA 2910	INIRENA 2895	INIRENA 2896	INIRENA 2897	INIRENA 2898
SVL	27.72	25.58	27.72	26.86	26.4	26.04	28.62	26.68	25.55	26.24	27.97	28.7	27.12	29.51	26.56
HL	9.08	8.76	9.35	9.1	8.61	8.33	8.76	8.73	8.68	9.12	9.38	9.06	8.79	9.04	8.61
HW	9.78	9.03	9.81	9.78	9.82	9.07	9.4	9.41	9.42	9.5	9.99	9.68	9.67	9.66	9.61
TW	1.53	1.36	1.52	1.88	1.74	1.45	1.38	1.47	1.32	1.4	1.39	1.12	1.39	1.34	1.42
ED	3.74	2.62	2.79	3.08	2.9	2.63	2.74	2.78	2.81	2.76	2.77	2.78	2.38	2.8	2.94
EIW	1.13	1.39	1.52	1.68	1.19	1.45	1.49	1.67	1.69	1.59	1.35	1.78	1.51	1.62	1.9
IOD	5.1	5.02	5.19	5.09	5.04	4.32	5.06	5.09	5.05	4.24	4.4	5.09	5.14	5.08	5.37
IND	2.25	2.29	2.42	2.31	2.28	2.16	2.32	2.38	2.12	2.17	2.53	2.6	2.37	2.21	2.3
END	3.15	2.61	2.51	2.53	2.7	2.77	2.78	2.96	2.79	2.47	2.61	2.69	2.33	2.55	2.37
ETD	0.96	0.92	0.98	1	0.86	1.02	0.82	0.85	0.89	0.89	0.76	0.84	0.76	0.95	0.98
UpL	7.1	6.19	6.31	6.02	6.5	6	6.08	6.62	6.31	6.43	6.39	6.31	6.39	6.88	6.58
Fol	7.86	7.39	7.78	7.49	7.28	7.28	7.32	7.58	7.56	7.51	7.82	7.51	7.58	7.92	7.62
HaL	7.57	6.82	7.3	6.41	6.23	6.6	6.72	6.28	6.46	6.86	6.93	6.7	6.58	7.24	7.53
F3PW/F3W	1.78	1.85	1.94	2.33	2.23	1.77	1.97	2.13	2.08	2.09	1.75	2.43	1.87	2.12	2.53
F4PW/F4W	1.77	2.34	2.15	2.38	2.10	1.84	1.94	2.12	2.17	2.13	2.42	2.44	2.46	1.97	2.64
FeL	10	9.4	9.11	9.24	9.19	9.87	9.57	9	9.32	9.95	9.81	9.82	9.34	9.22	9.9
TL	12.78	11.79	11.88	11.82	11.46	11.5	11.42	12.41	12.69	11.05	11.81	11.47	11.21	12.39	11.34
TaL	7.41	7.47	7.36	7.51	7.31	7.18	7.93	6.84	7.92	7.14	7.42	7.59	7.42	7	7.83
FL	4.49	4.33	4.97	4.31	3.9	4.22	4.49	4.12	4.21	4.58	4.82	4.35	4.25	4.58	4.75
3TL	3.72	3.74	3.64	3.59	3.18	3.16	3.44	3.18	3.17	3.53	3.42	3.34	3.48	3.38	3.71
TotFL	11.9	11.37	11.08	11.41	11.15	10.82	12.44	11.16	11.44	11.42	11.47	11.31	11.42	11.96	12.46
IPT	0.68	0.89	0.86	0.88	0.86	0.64	0.92	0.91	0.86	0.68	0.62	0.94	0.8	0.8	0.78
MPT	1.09	1.19	1.1	1.12	1.16	1.18	1.17	1.06	1.14	1	1.06	1.02	1.08	1.18	1.26
OPT	0.52	0.56	0.58	0.54	0.62	0.58	0.76	0.66	0.68	0.58	0.52	0.6	0.71	0.76	0.64
IMTL	1.02	1.2	1.36	1.2	1.14	1.01	1.12	1.26	1.18	1.1	1.16	1.15	1.16	1.13	1.1
OMTL	0.72	0.77	0.6	0.78	0.74	0.92	0.75	0.68	0.74	0.62	0.78	0.65	0.91	0.81	0.98
TW/ED	0.41	0.52	0.54	0.61	0.60	0.55	0.50	0.53	0.47	0.51	0.50	0.40	0.58	0.48	0.48
F3PW	1.14	1.26	1.28	1.26	1.36	1.12	1.42	1.32	1.25	1.13	1.1	1.36	1.12	1.4	1.62
F3W	0.64	0.68	0.66	0.54	0.61	0.67	0.72	0.62	0.6	0.54	0.63	0.56	0.6	0.66	0.64
F4PW	1.1	1.36	1.33	1.31	1.3	1.14	1.4	1.44	1.41	1.13	1.26	1.34	1.23	1.38	1.48
F4W	0.62	0.58	0.62	0.55	0.62	0.62	0.72	0.68	0.65	0.53	0.52	0.55	0.5	0.7	0.56

Table 3. Advertisement call data of *Eleutherodactylus franzi* sp. nov. and the sympatric *Eleutherodactylus humboldti*.

	Eleutherodactylus franzi sp. nov.	*Eleutherodactylus humboldti*
Individuals	4	3
Call type	Pipe	Pipe
Dominant frequency (kHz)	2.61 ± 0.04	2.89 ± 0.23
Call length (ms)	106.0 ± 5.2	256.8 ± 12.8
Call rate (/m)	6.88 ± 0	2.16 ± 1.73
Call rise time (ms)	63.64 ± 4.06	90.82 ± 45.37
Pulse Rate	–	2.05 ± 0.62
Call Interval	13.03 ± 3.35	39.75 ± 14.77

who collected the type material and who helped collect an extensive sampling of the *Eleutherodactylus* specimens to be used in our succession of studies.

Discussion

In recent years, the subgenus *Syrrhophus* has received increasing attention from researchers. With the description of the new species here, the number of the taxa in the subgenus *Syrrhophus* increases to 44, with two in Cuba and 42 in mainland North America. Guerrero remains the most diverse State for the subgenus with 11 species occurring within its borders. The assignation of the novel species to the *E. nitidus* species group raises the number of species in that group to 16 (Grünwald et al. 2021; Devitt et al. 2023). This brings the west Mexican clades of the *E. modestus* species group (16 species) and the *E. nitidus* species group (16 species) to be equally diverse as currently understood. The east Mexican clade, the *E. longipes* group, currently is understood to contain nine species, although molecular results suggest that several undescribed species exist within this group as well (Hernández-Austria et al. 2022).

One of the most pressing questions regarding the taxonomy of these frogs is whether the subgenus *Syrrhophus* should be considered a genus. The genus *Eleutherodactylus* currently includes over 200 species distributed throughout North and Central America, including the Caribbean (Frost 2020). *Eleutherodactylus* was once the largest genus of vertebrates, but Heinicke, Duellman and Hedges (2007) split it into multiple genera. Currently, five subgenera are recognised in *Eleutherodactylus*: *Eleutherodactylus*, *Euhyas* Fitzinger, 1843, *Pelorius* Hedges, 1989, *Schwartzius* Hedges, Duellman & Heinicke, 2008 and *Syrrhophus*. Each of these subgenera is monophyletic and can be defined morphologically. For an in-depth review of *Eleutherodactylus*, see Hedges, Duellman and Heinicke (2008). The distinction between a genus and subgenus is arbitrary and a solid case can be made for *Syrrhophus* to be recognised as its own genus. *Syrrhophus* is a monophyletic group that diverged from its closest relatives, members of the subgenus *Euhyas*, over 20 million years ago (Heinicke et al. 2007). We suggest that a more detailed study of the macro-taxonomic relationships of these frogs should be performed and the current taxonomic status of the subgenera should be assessed in detail.

Conservation priorities

The species described herein has a very limited range, known only from near the type locality and restricted to one biogeographical formation as defined by Grünwald et al. (2015), namely the Central Mexican Transverse Range Pine-Oak Woodland (#44 on p. 409 in Grünwald et al. (2015).

Eleutherodactylus franzi is known from a karstic mountain range that has about 75 km^2 of habitat at elevations sufficiently high enough to support populations. It has not been collected anywhere else and may be restricted to the immediate vicinity of the type locality (Fig. 7). Other saxicolous specialised species of *Eleutherodactylus* have similarly only been collected near the type locality, including *E. erythrochomus*, *E. grunwaldi*, *E. manantlanensis*, *E. colimotl* and *E. saxatilis*. Due to its limited distribution and potential endemism near the type locality, we propose this species be provisionally classified as Critically Endangered B1ab(iii), based on the IUCN Red List Criteria that its occurrence is less than 100 km^2, it occurs in only one threat-defined location and there is ongoing decline in the extent and quality of its habitat due to small-scale cattle ranching, illegal logging and varied agricultural practices.

The frog subgenus *Syrrhophus* is the fastest-growing group of frogs in Mexico, in terms of the number of new taxa being described. Despite the recently augmented interest in the group, we believe that the current diversity may still be underestimated and might continue to increase in the coming years. Apart from collecting in regions currently under-sampled, like the mountains of Guerrero and Oaxaca, we suggest that it is important to re-examine specimens already housed in herpetological collections, as there are multiple errors in the identification of specimens of *Eleutherodactylus* and un-identified new taxa may be hiding in collections.

Additionally, we believe that it is of great importance that future molecular studies include additional markers,

Figure 7. Type locality of *Eleutherodactylus franzi* sp. nov., at El Cucharillo, Municipio de Ixcateopan de Cuauhtémoc, Guerrero, Mexico.

as this allows for a much better understanding of the relationships within this group of frogs. Finally, our data suggest that it is time to revise the status of the subgenus *Syrrhophus* and to determine if it should be elevated to generic level.

Competing interests

The authors have declared that no competing interests exist.

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Appendix 1

Specimens examined

Eleutherodactylus albolabris (*n* = 20): MEXICO: Guerrero: MZFC 33025–33030 (CIG 00327–00332), 33082–33085 (CIG 00390– 00393), MZFC 33108–33109 (CIG 00441–00442), MZFC 33230 (CIG 00668), MZFC 33300–33301 (CIG 00903–00904), MZFC 33323 (CIG 00953), MZFC 33325–33326 (CIG 00955–00956), JAC 25586, 25642.

Eleutherodactylus. angustidigitorum (*n* = 20): 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 (*n* = 13): MEXICO: Nuevo León: MZFC 33195–33198 (CIG 00606–00609); UNITED STATES: Texas: JHM 1390–1394.

Eleutherodactylus colimotl (*n* = 20): 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 (*n* = 6): MEXICO: Veracruz: MZFC 33351–33353 (CIG 01163–01165), MZFC 33354 (CIG 01170), JAC 30000–30001.

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

Eleutherodactylus dilatus (*n* = 19): 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 (*n* = 25): 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 erythrochomus (*n* = 2): MEXICO: Guerrero: INIRENA 2923–24 (CIG 01922–01923).

***Eleutherodactylus franzi* sp. nov.** (*n* = 15): MEXICO: Guerrero: INIRENA 2895–98, 2900–2910 (CIG 01716–01729, 01731).

Eleutherodactylus floresvillelai (*n* = 12): MEXICO: Michoacán: MZFC 33053–33064 (CIG 00361–00372).

Eleutherodactylus grandis (*n* = 1): MEXICO: Ciudad de Mexico: UTA 56845.

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

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

Eleutherodactylus humboldti (*n* = 17): MEXICO: Estado de México: INIRENA 2911–2916 (CIG 01703, 01702, 01704–01710); Guerrero: INIRENA 2899, 2920–2922 (, 01730, CIG 01713–01715); CIG 00962–00965.

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

Eleutherodactylus jaliscoensis (*n* = 15): MEXICO: Jalisco: MZFC 33131–33141 (CIG 00480–00490), MZFC 33274–33276 (CIG 00861–00863), MZFC 33280 (CIG 00876).

Eleutherodactylus jamesdixoni (*n* = 14): MEXICO: Jalisco: MZFC 33010–33014 (CIG 00310–00314), MZFC 33034–33035 (CIG 00336–00337), MZFC 33110 (CIG 00457), MZFC 33273 (CIG 00860), JAC 28612; Nayarit: MZFC 33211 (CIG 00649), MZFC 33240–33242 (CIG 00685–00687).

Eleutherodactylus leprus (*n* = 7): MEXICO: Veracruz: MZFC 33345–33350 (CIG 01139–01144), CIG 01270.

Eleutherodactylus longipes (*n* = 3): MEXICO: Nuevo León: MZFC 33199 (CIG 00611); Querétaro: UTA 59421–59422.

Eleutherodactylus maculabialis (*n* = 27): MEXICO: Guerrero: MZFC 33307–33319 (CIG 00916–00923, 00940–00941, 00945–00947), MZFC 33321 (CIG 00949), MZFC 33323 (CIG 00953), CIG 01484–01485, 01501, JAC 25643–25646.

Eleutherodactylus marnocki (*n* = 3): USA: Texas: JHM 1427–1429.

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

Eleutherodactylus maurus (*n* = 19): MEXICO: Estado de México: MZFC 33071–33076 (CIG 00379–00384), MZFC 33355 (CIG 01174); Morelos: MZFC 33077–33080 (CIG 00385–00388), INIRENA 2925–30 (CIG 01733–01737, 01742).

Eleutherodactylus modestus (*n* = 34): 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 nebulosus (*n* = 6): MEXICO: Chiapas: MZFC 33361–33366 (CIG 01236–01241).

Eleutherodactylus nietoi (*n* = 13): 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 (*n* = 31): MEXICO: Estado de México: JAC 27237; Guerrero: MZFC 33096–33097 (CIG 00411–00412), MZFC 33104–33105 (CIG 00437–00438), JAC 25815; Morelos: MZFC 33081 (CIG 00389); Oaxaca: MZFC 33357–33358 (CIG 01211–01212); Puebla: MZFC 33356 (CIG 01181), JAC 27256–27276.

Eleutherodactylus orarius (*n* = 13): MEXICO: Colima: MZFC 26890, MZFC 33262 (CIG 00849); Michoacán: MZFC 33037 (CIG 00341), MZFC 33335 (CIG 00973), JAC 24020, 25526, 25563–25564, 29107, 30500–30501, 30517, 30625.

Eleutherodactylus pallidus (*n* = 13): 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 petersi (*n* = 11): MEXICO: Guerrero: MZFC 33034–33035 (CIG 00336–00337); JAC 25219, 25265–25266, 25299; 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; Nayarit: MZFC 33211 (CIG 00649), MZFC 33240–33242 (CIG 00685–00687).

Eleutherodactylus. pipilans (*n* = 15): MEXICO: Guerrero: MZFC 33086–33088 (CIG 00396–00398), MZFC 33106–33107 (CIG 00439–00440), MZFC 33322 (CIG 00952), CIG 1465; Oaxaca: MZFC 33210 (CIG 00645), JAC 24283, 25809–25811.

Eleutherodactylus rubrimaculatus (*n* = 3): MEXICO: Chiapas: MZFC 33249–33251 (CIG 00753, 00755–00756),

Eleutherodactylus rufescens (*n* = 40): 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 (*n* = 4): MEXICO: Sinaloa: MZFC 26893, 26896, 26898–26899.

Eleutherodactylus sentinelus (*n* = 8): MEXICO: Guerrero: MZFC 33031–33033 (CIG 00333–00335), MZFC 33302– 33306 (CIG 00907–00913).

Eleutherodactylus syristes (*n* = 21): MEXICO: Guerrero: ANMO 2999; MZFC 33098–33103 (CIG 00431–00436), MZFC 33324 (CIG 00954), MZFC 33327–33328 (CIG 00957–00958) JAC 25701–25703; 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 (*n* = 5): MEXICO: Jalisco: MZFC 33142–33143 (CIG 00491–00492), MZFC 33277–33279 (CIG 00864–00866).

Eleutherodactylus verrucipes (*n* = 3): MEXICO: Tamaulipas: MZFC 33253–33254 (CIG 00813–00814); Querétaro: CIG 01273.

Eleutherodactylus wixarika (*n* = 3): MEXICO: Jalisco: MZFC 27477–27479.

Appendix 2

Table A1. Genetic accession numbers.

Field number	Organism	Museum number	Locality	GenBank number
CIG-00953	*E. albolabris*	MZFC-33323	Mexico: Guerrero	MG856956
JAC-25642	*E. albolabris*	UTA-61578	Mexico: Guerrero	MT872448
CIG-00392	*E. albolabris*	MZFC-33084	Mexico: Guerrero	MT872468
CIG-00441	*E. albolabris*	MZFC-33108	Mexico: Guerrero	MT872476
CIG-00331	*E. albolabris*	MZFC-33029	Mexico: Guerrero	MT872482
CIG-00332	*E. albolabris*	MZFC-33030	Mexico: Guerrero	MT872483
CIG-00477	*E. angustidigitorum*	–	Mexico: Jalisco	MG856963
CIG-00479	*E. angustidigitorum*	–	Mexico: Jalisco	MG856964
CIG-00407	*E. dilatus*	MZFC33091	Mexico: Guerrero	MG856973
CIG-00408	*E. dilatus*	MZFC33092	Mexico: Guerrero	MG856974
CIG-00070	*E. dilatus*	–	Mexico: Guerrero	**OP895113**
EU186711	*E. erythrochomus*	MZFC 16254	Mexico: Guerrero	EU186711
RPA-0183	*E. erythrochomus*	–	Mexico: Guerrero	MZ203201
RPA-0185	*E. erythrochomus*	–	Mexico: Guerrero	MZ203202
CIG-01716	*E. franzi sp. nov.*	INIRENA-2901	Mexico: Guerrero	**OP888987**
CIG-01717	*E. franzi sp. nov.*	INIRENA-2902	Mexico: Guerrero	**OP888988**
CIG-01729	*E. franzi sp. nov.*	INIRENA-2897	Mexico: Guerrero	**OP888989**
CIG-01248	*E. guttilatus*	–	Mexico: Guajuato	**OP895114**
CIG-01249	*E. guttilatus*	–	Mexico: Guajuato	**OP895115**
CIG-01702	*E. humboldti.*	INIRENA-2912	Mexico: Mexico	**OP888990**
CIG-01703	*E. humboldti.*	INIRENA-2913	Mexico: Mexico	**OP888991**
CIG-01713	*E. humboldti*	INIRENA-2920	Mexico: Guerrero	**OP888992**
CIG-01730	*E. humboldti*	INIRENA-2899	Mexico: Guerrero	**OP888993**
GP-2422	*E. humboldti*	–	Mexico: Mexico	**OP888994**
GP-2423	*E. humboldti*	–	Mexico: Mexico	**OP888995**
RHA-0006	*E. humboldti.*	–	Mexico: Mexico	**OP888996**
RHA-0007	*E. humboldti*	–	Mexico: Mexico	**OP888997**
CIG-00649	*E. jamesdixoni*	MZFC-33211	Mexico: Nayarit	MT872469
CIG-00687	*E. jamesdixoni*	–	Mexico: Nayarit	MG857035
CIG-00686	*E. jamesdixoni*	–	Mexico: Nayarit	**OP895111**
CIG-00860	*E. jamesdixoni*	–	Mexico: Jalisco	**OP895112**
CIG-00921	*E. maculabialis*	MZFC-33312	Mexico: Guerrero	MT872460
CIG-00923	*E. maculabialis*	MZFC-33314	Mexico: Guerrero	MT872461
CIG-00940	*E. maculabialis*	MZFC-33315	Mexico: Guerrero	MT872462
CIG-00941	*E. maculabialis*	MZFC-33316	Mexico: Guerrero	MT872463
CIG-00946	*E. maculabialis*	MZFC-33318	Mexico: Guerrero	MT872464
CIG-00947	*E. maculabialis*	MZFC-33319	Mexico: Guerrero	MT872465
CIG-00893	*E. manantlanensis*	MZFC-33293	Mexico: Colima	MG857007
CIG-00388	*E. maurus*	MZFC-33080	Mexico: Morelos	MG857010
CIG-00380	*E. maurus*	MZFC-33072	Mexico: Mexico	MG857011
CIG-00382	*E. maurus*	MZFC-33074	Mexico: Mexico	MT872478
CIG-00385	*E. maurus*	MZFC-33077	Mexico: Morelos	MT872479
CIG-0-387	*E. maurus*	MZFC-33079	Mexico: Morelos	MT872480

Field number	Organism	Museum number	Locality	GenBank number
CIG-01733	*E. maurus*	INIRENA-2925	Mexico: Morelos	**OP888998**
CIG-01734	*E. maurus*	INIRENA-2926	Mexico: Morelos	**OP888999**
CIG-00857	*E. modestus*	MZFC33270	Mexico: Colima	MG857021
CIG-00891	*E. modestus*	–	Mexico: Colima	MG857012
CIG-00753	*E. nebulosus*	MZFC-33249	Mexico: Chiapas	MG857056
CIG-00755	*E. nebulosus*	MZFC-33250	Mexico: Chiapas	MG857057
CIG-01237	*E. nebulosus*	MZFC-33362	Mexico: Chiapas	MT872429
CIG-01238	*E. nebulosus*	MZFC-33363	Mexico: Chiapas	MT872430
CIG-01240	*E. nebulosus*	MZFC-33365	Mexico: Chiapas	MT872431
CIG-01241	*E. nebulosus*	MZFC-33366	Mexico: Chiapas	MT872432
EU186712	*E. nitidus*	AMCC-118239	Mexico: Puebla	EU186712
CIG-00715	*E. nitidus*	MZFC-33248	Mexico: Oaxaca	MG857030
CIG-00412	*E. nitidus*	MZFC-33096	Mexico: Guerrero	MG857031
CIG-00336	*E. nitidus*	MZFC-33034	Mexico: Guerrero	MG857032
CIG-00311	*E. nitidus*	MZFC-33011	Mexico: Jalisco	MG857033
JAC-25815	*E. nitidus*	UTA-61584	Mexico: Guerrero	MT872459
CIG-00341	*E. orarius*	MZFC-33037	Mexico: Michoacán	MG857041
CIG-00460	*E. orarius*	MZFC-33113	Mexico: Colima	MG857042
JAC-24020	*E. orarius*	UTA-59508	Mexico: Michoacán	MT872434
JAC-25343	*E. orarius*	UTA-62402	Mexico: Michoacán	MT872442
JAC-25344	*E. orarius*	UTA-62403	Mexico: Michoacán	MT872443
CIG-00458	*E. orarius*	MZFC-33111	Mexico: Colima	MT872477
JAC-25392	*E. orarius*	–	Mexico: Michoacan	**OP895116**
CIG-00337	*E. petersi*	MZFC-33035	Mexico: Guerrero	MT872473
CIG-00310	*E. petersi*	MZFC-33010	Mexico: Jalisco	MT872487
CIG-00396	*E. pipilans*	MZFC-33086	Mexico: Guerrero	MG857054
CIG-00398	*E. pipilans*	MZFC-33088	Mexico: Guerrero	MG857055
CIG-00440	*E. pipilans*	MZFC-33107	Mexico: Guerrero	MT872475
JAC-31539	*E. pipilans*	–	Mexico: Oaxaca	**OP895117**
JAC-31540	*E. pipilans*	–	Mexico: Oaxaca	**OP895118**
CIG-00334	*E. sentinelus*	MZFC-33032	Mexico: Guerrero	MT872485
CIG-00335	*E. sentinelus*	MZFC-33033	Mexico: Guerrero	MT872486
CIG-00333	*E. sentinelus*	MZFC-33031	Mexico: Guerrero	MT872484
CIG-00954	*E. syristes*	MZFC-33324	Mexico: Guerrero	MG857070
CIG-00714	*E. syristes*	MZFC-33247	Mexico: Oaxaca	MG857072
CIG-00628	*E. syristes*	MZFC-33208	Mexico: Oaxaca	MG857073
CIG-00627	*E. syristes*	MZFC-33207	Mexico: Oaxaca	MT872467
CIG-00431	*E. syristes*	MZFC-33098	Mexico: Guerrero	MT872471
CIG-00434	*E. syristes*	MZFC-33101	Mexico: Guerrero	MT872472