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Systematics of the frogs allocated to *Sarcohyla bistincta* sensu lato (Cope, 1877), with description of a new species from Western Mexico

JONATHAN A. CAMPBELL^{1,7}, EDMUND D. BRODIE, JR.², ITZUE W. CAVIEDES-SOLIS³,
ADRIÁN NIETO-MONTES DE OCA⁴, VÍCTOR H. LUJA⁵, OSCAR FLORES-VILLELA⁴,
URI OMAR GARCÍA-VÁZQUEZ⁶, GOUTAM CHANDRA SARKER¹, ELIJAH WOSTL¹ & ERIC N. SMITH¹

¹Department of Biology, The University of Texas at Arlington, Arlington, TX 76019, USA.

E-mail: gsarker@uta.edu; ewostl@uta.edu; e.smith@uta.edu; campbell@uta.edu

²Department of Biology, Utah State University, Logan, UT 84322, USA. E-mail: e.brodie@usu.edu

³Department of Biology and Burke Museum of Natural History and Culture, University of Washington, Box 351800, Seattle, WA 98195, USA. E-mail: itzuecs@uw.edu

⁴Departamento de Biología Evolutiva and Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Cd. Universitaria, Coyoacán, Cd. De México, C. P. 04510, México D.F., México.

E-mail: anietomontesdeoca@me.com; sapofv@gmail.com

⁵Universidad Autónoma de Nayarit, Unidad Académica de Turismo, Cordinación de Investigación y Posgrado, Ciudad de la Cultura s/n, 63000 Tepic, Nayarit, México. E-mail: lujastro@yahoo.com

⁶Facultad de Estudios Superiores Zaragoza, UNAM, Batalla 5 de Mayo s/n, Ejercito de Oriente, Iztapalapa, Cd. De México, C.P. 09230, México D.F., México. E-mail: urigaracia@gmail.com

⁷Corresponding author

Abstract

A new species of hylid frog is described from the southwestern edge of the Mexican Plateau from the states of Morelos and Mexico through Michoacán and Jalisco, reaching the Sierra Madre Occidental in Sinaloa and western Durango. The new species is part of the widespread Mexican hylid *Sarcohyla bistincta* (*sensu amplo*) complex, comprised of *S. bistincta*, *S. pentheter*, *S. calthula*, and *S. ephemera*. One subspecies of *S. bistincta* (*labeculata*) was proposed for an isolated population in Oaxaca. We restrict the group's nominal species, *S. bistincta* (*sensu stricto*), to the Sierra Madre Oriental of Mexico and southward into the Sierra Madre del Sur of Guerrero and Oaxaca. Examination of type material places *S. calthula* and *S. ephemera* in the synonymy of *S. labeculata* (new combination). The species allied to *S. bistincta*, namely, *S. bistincta*, *S. labeculata*, *S. pentheter*, and the new species described herein, are diagnosed and described following recent suggested taxonomic changes and new available material.

Resumen

Se describe una nueva especie de rana arborícola hylida del borde suroeste del Altiplano Mexicano de los estados de Morelos y Estado de México, hacia el oeste por Michoacán y Jalisco, Nayarit, Durango, y Sinaloa alcanzando la Sierra Madre Occidental en Sinaloa y el oeste de Durango. La nueva especie es parte de la rana hylida *Sarcohyla bistincta* (*sensu amplo*), comprendido de *S. bistincta*, *S. pentheter*, *S. calthula*, and *S. ephemera*. Una subespecie de *S. bistincta* (*labecula*) fue propuesta para una población aislada en Oaxaca. Restringimos la especie nominal del grupo *S. bistincta* (*sensu stricto*) a la region desde la Sierra Madre Oriental y hasta la Sierra Madre del Sur de Guerrero y Oaxaca. El examen de material tipo colocan a *S. calthula* y *S. ephemera* en la sinonimia de *S. labeculata* (nueva combinación). Las especies relacionadas a *S. bistincta*, específicamente, *S. bistincta*, *S. labeculata*, *S. pentheter*, y la nueva especie descrita en este trabajo, se diagnostican y describen de acuerdo a la nueva taxonomía propuesta y al examen de nuevo material disponible.

Key words: Amphibia, Anura, New species, *Sarcohyla bistincta*, *Sarcohyla hapsa* sp. nov., *Sarcohyla labeculata*, *Sarcohyla pentheter*, Taxonomy

Introduction

The genus *Plectrohyla* was recently considered to be composed of two large groups: the *P. guatemalensis* group containing 18 species found east of the Isthmus of Tehuantepec and the *P. bistincta* group containing 24 described species restricted west of the Isthmus of Tehuantepec. In his review of the *Hyla bistincta* group, Duellman (1964) included only five species. Subsequently, several species were discovered or added and the *H. bistincta* group was transferred to the genus *Plectrohyla* (Faivovich *et al.* 2005). More recently, all frogs placed in *Plectrohyla* occurring west of the Isthmus of Tehuantepec were placed in a new genus, *Sarcohyla* by Duellman *et al.* (2016).

The doctoral dissertation of Caviedes-Solis (2012), later formally published as Caviedes-Solis and Nieto-Montes de Oca (2018), evaluated the phylogenetic relationships among the frogs of the genus *Sarcohyla*, using a multilocus dataset consisting of the mitochondrial genes ND2 and 12S, and the nuclear genes Rag-1, Rhodopsin, and POM-C. This work estimated the phylogenetic relationships of *Sarcohyla*, with a representation of 18 species. Caviedes-Solis and Nieto-Montes de Oca (2018) used a concatenated gene and a species-tree approach, using Bayes factor species delimitation to evaluate populations sampled. In every case, Caviedes-Solis & Nieto-Montes de Oca (2018) obtained a monophyletic *Sarcohyla bistincta* complex, sister to a clade consisting of *S. chryses* and *S. mykter*. These two species were also suggested to be close relatives of the *Sarcohyla bistincta* complex by Kaplan *et al.* (2016).

Sarcohyla bistincta (*sensu lato*) is widespread across the Mexican highlands, occurring in the Sierra Madre Oriental, the Sierra Madre Occidental, the Trans-Mexican Volcanic Range, and the Sierra Madre del Sur. It ranges from Durango and Nayarit southward to Jalisco and Michoacán and across the southern portion of the Mexican Plateau to west-central Veracruz, southward into Oaxaca and Guerrero, and inhabits many physiographic and vegetational zones. Few other Mexican highland species of anurans are known to have such an extensive range over such varied terrain.

Several populations closely allied to *Sarcohyla bistincta* have been described. *Hyla* [*Sarcohyla*] *calthula* (Ustach *et al.* 2000) and *Hyla* [*Sarcohyla*] *ephemera* (Meik *et al.* 2005) were described from cloud forests of northern Oaxaca in the Sierra Mixe, and *Hyla* [*Sarcohyla*] *pentheter* (Adler 1965) from the southern slopes of the Sierra Madre del Sur of Oaxaca. Shannon (1951) described *Hyla* [*Sarcohyla*] *bistincta labeculata* from near the village of San Lucas Camotlán in northern Oaxaca, also located in the Sierra Mixe. He did not indicate what comparative material he used, but it is probable that examination of multiple species in the *S. bistincta* complex misled him in concluding his material was conspecific with *S. bistincta*.

The *S. bistincta* group as here defined contains four species: *S. bistincta*, *S. labeculata*, *S. pentheter*, and one species herein described. This definition is in agreement with Caviedes-Solis and Nieto-Montes de Oca (2018). Morphological features common to these frogs include: a moderately large size; robust bodies; short snout; blunt heads; tympanic fold moderately to well developed; no axillary membrane; short to moderately long fingers with vestigial webbing; thick, glandular skin, especially on throat, chest, and ventral surfaces of brachium and antibrachium; absence of quadratojugal; tarsal fold extending almost length of tarsus, variably as raised ridge or series of tubercles; nuptial excrescences present in breeding males, and presence of vocal slits variable. Tadpoles with ventral mouths, 2/3 tooth rows, and long muscular tails with low fins. Variation within the group in flank markings and tarsal fold was noted by Taylor and Smith (1945); these characters are often subtle, and sometimes the condition of the tarsal fold can be misleading due to preservation artifacts. Members of this genus are all stream-breeders, usually found along streams or high-flow rivers, although individuals may stray far from water during the non-breeding season.

We describe the population of *S. bistincta* from the Sierra Madre Occidental. As suggested by Caviedes-Solis and Nieto-Montes de Oca (2018) we also investigate the taxonomic status of *Hyla* [*Sarcohyla*] *bistincta labeculata*, with respect to *S. calthula* and *S. ephemera*. Caviedes-Solis and Nieto-Montes de Oca (2018) recovered *S. pentheter* sister to *S. calthula*/*S. ephemera* and a possible new species from Puerto del Gallo, forming a monophyletic group with other Sierra Madre del Sur of Guerrero populations. The work by Caviedes-Solis and Nieto-Montes de Oca (2018) is not without serious weakness, as they are missing 66% of the gene sampling within *S. bistincta* (*sensu amplo*) (see their Supplementary Table 1), resulting also in the recognition of an additional species within the *S. bistincta* group. Recognition of the population of frogs from Puerto del Gallo as a new species will have to await further clarification of relationships, and we treat it herein as *S. bistincta* (*sensu stricto*).

Material and methods

For ease of comparison and consistency, in our descriptions we have followed the format of Duellman (1970, 2001) and Campbell and Duellman (2000). We use standard terminology, abbreviations and measurements as defined by Duellman (1970). Measurements were made using digital calipers held under a dissecting microscope and rounded to 0.1 mm. Sex was determined by the presence of secondary sexual characters such as nuptial excrescences. The webbing formula is that of Savage and Heyer (1967) as modified by Myers and Duellman (1982) and Savage and Heyer (1997). Standard abbreviations for anatomical structures follow Meik *et al.* (2005). Cephalic index was calculated as HW/HL. Color was taken from field notes when available and color images catalogued in the UT-Arlington collection. We provide abbreviated synonymies. Specimens examined in this study (see Appendix) are housed in the herpetological collections of the American Museum of Natural History (AMNH), the Academy of Natural Sciences, Philadelphia (ANSP), the California Academy of Sciences (CAS), the Field Museum of Natural History (FMNH), the Los Angeles County Museum of Natural History (LACM), the University of Kansas Natural History Museum (KU),—Museo de Zoología Facultad de Ciencias (MZFC–UNAM), the University of California Museum of Vertebrate Zoology (MVZ), the University of Michigan Museum of Zoology (UMMZ), the National Museum of Natural History (USNM), and the University of Texas at Arlington (UTA). We examined the types of *Hyla bistincta* Cope (1878), *Hyla bistincta labeculata* Shannon (1951), *Hyla calthula* Ustach *et al.* (2000), and *Hyla ephemera* Meik *et al.* (2005).

TABLE 1. Selected characteristics for samples of the *Sarcohyala bistincta* group. All measurements in mm.

Character	<i>Sarcohyala bistincta</i>	<i>Sarcohyala labeculata</i>	<i>Sarcohyala pentheter</i>	<i>Sarcohyala hapsa</i>
Maximum size SVL	56.6	59.2	51.1	49.5
Males				
Females	59.5	61.3	57.8	56.1
Distance tympanum separated from eye	~ diameter of tympanum	> diameter of tympanum	< diameter of tympanum	~diameter of tympanum
Supratympanic dermal fold	Heavy	Heavy	Heavy	Moderate
Relative finger disc size	Moderate	Large	Large	Medium
Foot webbing	I1–III1–2III1–2IV2–1V	I1–2III1–2III1–2IV2–1V	I2–2II2–3III2–3IV3–2V	I1–2III1–2III1–2IV2–1V
Vocal slits	Present/absent	Absent	Absent	Absent
Flank pattern	Cream or yellowish with irregular dark markings and large pale blotches	Usually with continuous dark marking, sometimes broken into bold dark spots	Often with continuous dark marking, sometimes interrupted in groin area; thin pale line separating flank from dorsal color	White to yellowish with pattern of irregular blackish vermiculations, spots, or fine to coarse reticulations
Posterior surface of thigh	Coarse dark reticulations usually with large spots	Mostly dark, sometimes with spots	Uniformly dark	Cream to yellow with irregular dark markings
Iris color	Deep reddish bronze	Gold to pale copper	Deep bronze	Copper to pale Bronze

Maps were prepared using the specimen information provided in the text and records obtained through VertNet (<http://vertnet.org>; accessed 22 February 2016). The program AUDACITY 2.1.2 (Audacity Team 2016) was used to trim the recording of the vocalization to its working length and to filter out background noise. Oscillograms and spectrograms were produced in RAVEN LITE 1.0 (Charif *et al.* 2006). Time between notes, time between pulses, fundamental frequency, and dominant frequency were calculated using SOUND RULER 0.9.6.0 (Gridi-Papp 2007). Terminology follows Duellman (1970).

Results

Evaluation of material representing *S. bistincta* (*sensu amplo*) over its entire range indicates that it is a composite of at least four species. We herein describe one of these as new and provide a redefinition for the nominal species and two closely related, previously described species. Our redescrptions of *S. bistincta* and *S. labeculata* are based on examination of holotypes and other applicable museum material available. We did not re-examine the type of the distinctive *S. pentheter* but had benefit of the excellent description provided by Adler (1965) and near topotypic material. This group of four frogs is referred to as the *Sarcohylla bistincta* group, which is contained within the genus *Sarcohylla* as defined by Duellman *et al.* (2016). Comparisons of selected features for this group are provided in Table 1.

Sarcohylla bistincta (Cope 1878)

Standard English/Spanish name: Cope's Streamside Treefrog/Rana Trepadora Ribereña de Cope
Figs. 1A and F, 2A–B

Hyla bistincta Cope 1877[1878]: 87. Holotype:USNM 32261, according to Kellogg (1932: 163, erroneously given as USNM 32361) and Cochran (1961: 51). Type-locality “Vera Cruz most probably,” Mexico; restricted to Veracruz: Acultzingo: Lake San Bernardino, Mexico, by Smith and Taylor (1950: 346).

Plectrohyla bistincta—Faivovich *et al.* 2005: 105.

Sarcohylla bistincta—Duellman *et al.* 2016: 18.

Diagnosis. Adult size in males to 56.6 mm, in females to 59.5 mm; eye–tympanum distance slightly smaller than tympanum diameter; finger disc size moderate; foot webbing **I1–III1–2III1–2IV2–1V**; vocal slits variably present or absent in breeding males; nuptial excrescences on prepollex and along medial edge second finger; flank pattern cream or yellowish with irregular dark markings and large pale blotches; thigh pattern of coarse dark reticulations with usually large spots.

Description. Adult size in males to 56.6 mm, in females to 59.5 mm; head wider than long; top of head slightly convex; snout broadly rounded in dorsal profile, in lateral profile rounded; snout short, nostrils about two-thirds distance from eyes to tip of snout; canthus rounded; loreal region slightly concave; lips thick, not flared; heavy dermal fold extending posteriorly from eye, across upper edge of tympanum, then downward to above insertion of forelimb, obscuring upper edge of tympanum; eye–tympanum distance slightly less than tympanum diameter; forelimbs robust, especially in males; few pale ulnar tubercles, sometimes highly inconspicuous; transverse dermal fold on wrist; fingers moderately long and slender; discs moderately large, disc on third finger about equal in size to tympanum; subarticular tubercles large and round, none bifid; supernumerary tubercles small, round, arranged in single row on proximal segments of each digit; outer palmar tubercle low and rounded, sometimes bifid, inconspicuous; elongate tubercle on prepollex; prepollex enlarged; adult breeding males with dark nuptial excrescences consisting of minute spinules, mainly on prepollex, but also on inner edge of second finger; webbing on hand vestigial; hind limbs long and robust; heels of adpressed limbs barely overlapping by less than one-tenth of shank length; tibiotarsal articulation barely reaching, or not, eye; transverse dermal fold on heel; tarsal fold strong, extending full length of tarsus, usually raised into distinct sharp ridge and sometimes low flap; inner metatarsal tubercle large, elliptical, with raised (free) median edge; outer metatarsal tubercle small, round, and low; toes moderately long and slender; toe discs nearly as large as on fingers; subarticular tubercles large, round, and subconical; supernumerary tubercles large, low, arranged in single row on proximal segments of each digit; toe webbing **I1–2III1–2III1–2IV2–1V**; cloacal opening directed ventrally at level of middle of thighs in males and females; cloacal tube long, curved downward; skin on ventral surfaces of body and thighs granular, especially glandular on throat, chest, ventral surface of upper arm, and medial surface of forearm; skin smooth on dorsum; tongue broadly cordiform, shallowly notched behind, free posteriorly for about one-fourth of length; prevomerine teeth situated on small transverse processes between small, ovoid choanae, almost in contact with each other, males with 5–6 teeth on each process, females with 5–8; vocal slits absent; dorsum on head, body, and limbs yellowish brown to dark brown; flanks yellow to pale brownish tan with pattern of coarse dark brown to black anastomosing lines; posterior surface of thighs blackish with bold yellow spots, some equal in size or larger than finger discs; anterior surface of thighs also with yellow spotting; ventral surfaces pale yellow, usually uniformly colored but sometimes with sparse dark vermiform mottling, especially on throat and chest; iris deep reddish bronze.



FIGURE 1. Species in the *Sarcophyla bistincta* group. (A) *S. bistincta*, UTA A-13148, female, 38.1 km E Teotitlán on road to Huautla de Jiménez, Oaxaca; (B) *S. labeculata*, breeding pair, UTA A-5883 (male and UTA A-5881 (female), near Totontepec, Sierra Mixe, Oaxaca; (C) *S. pentheter*, UTA A-62065, female, carretera entre Santa Catarina Juquila and Puerto Escondido, Oaxaca; (D) *S. hapsa*, MZFC 28167, female, Rancho La Noria, 9 km W Tepic, Nayarit; (E) *S. hapsa*, female, 42 km S (by road) of highway connecting Valle de Juárez with Quitupan, on highway to Santa Maria del Oro, Sierra del Tigre, Jalapa, image by C. Grünwald; (F) *S. cf. bistincta*, UTA A-61989, female paratype, Sierra Madre del Sur, Carretera La Laguna, Guerrero.

Juveniles of some populations in Oaxaca and Guerrero, and perhaps most populations, possess a dorsum with a considerable amount of green. UTA A-61990 from Guerrero, small female (43.6 mm SVL) with small eggs in ovaries, apparently nearing first reproductive cycle, with distinctive bright green on dorsal surfaces of head, body and exposed surfaces of limbs; blackish brown stripe extending from snout, curving upwards across loreal region, through eye and across top of tympanum and over insertion of forelimb, anastomosing on flanks, surrounding or partially surrounding large cream spots and blotches; black markings on head and anterior part of flanks distinctly edged in bright gold, also present on upper forearm and on hands and feet; throat and chest cream, belly pale yellow, grading posteriorly to reddish on lower belly and undersurface of thighs; iris gold.



A. *Sarcophyla bistincta* OAX UTA A-17133



E. *Sarcophyla hapsa* MICH UMMZ 119194



B. *Sarcophyla bistincta* GRO KU 140421



F. *Sarcophyla hapsa* MICH MZFC 12306



C. *Sarcophyla labeculata* OAX UTA A-5881



G. *Sarcophyla hapsa* JAL MZFC 25669



D. *Sarcophyla* cf. *bistincta* GRO UTA A-61989



H. *Sarcophyla pentheter* OAX UTA A-62065

FIGURE 2. Flank (upper) and posterior surface of thigh (lower) patterns in the *Sarcophyla bistincta* group. (A) *S. bistincta*, UTA A-17133, El Tejocote, Oaxaca, 2375 m. (B) *S. bistincta*, KU 140421, 4.5 km (by road) E El Limón (= 6 km SW Chilapa), 1525 m, Guerrero. (C) *S. labeculata*, UTA A-5881, Totontepec, Sierra Mixe, Oaxaca, 1829 m. (D) *S. cf. bistincta*, UTA A-61989, Sierra Madre del Sur, Carretera La Laguna (17.52701N, 99.93703W), 1875 m. (E) *S. hapsa*, UMMZ 119194, 12.5 km ENE Dos Aguas, Michoacán. (F) *S. hapsa*, MZFC 12306, Michoacán, 2 km NE Las Aguitas. (G) *S. hapsa*, MZFC 25669, Nayarit, Sierra de Quila, Arroyo El Ahogado. (H) *S. pentheter*, UTA A-62065, Carretera Santa Catarina Juquila–Puerto Escondido, 1494 m.

Distribution and habitat (Fig. 3). *Sarcohyala bistincta* occurs on both sides of the Continental Divide in Puebla, Veracruz, Oaxaca, and Guerrero in pine-oak forest at 1219–2900 m and is narrowly separated from *S. labeculata*. It occurs along the Sierra Madre del Sur of Guerrero, almost the length of the state. Duellman (1970, 2001) reported this species from as far north as Hidalgo and this report was cited by Ramírez-Bautista *et al.* (2010) and Lemos-Espinal and Smith (2015), but apparently, no further material has been collected in this state or between the Hidalgo locality and the nearest locality to the south in Veracruz. This species is encountered along rapidly flowing streams and rivers, where it often sits on large streamside boulders or on vegetation or exposed tree roots. It has also been found in undisturbed pine-oak forest far from flowing water.

Comments. Cope (1877) did not provide provenance for the specimen he designated as holotype of *Hyla bistincta*, but surmised that it came from the state of Veracruz similar to much of the other material provided to him by Sumichrast. Cope described the holotype as being a male in breeding condition, with a thick dermal fold obscuring the dorsal edge of a small tympanum, robust forelimbs with nuptial excrescences on thumb, a SVL of .045 “lines” (as reported by Cope 1877), sides marbled with dark-plumbeous and yellow, and the posterior surface of femur pale brown with only a few yellow specks along the superior border. Examination of the type of *Hyla bistincta* (USNM 32261) reveals it is a male with dark nuptial excrescences and the following measurements: 41.7 mm SVL, 13.9 mm HW, 13.6 mm HL, 21.1 mm tibia, 1.8 mm tympanum diameter, and 1.8 mm eye–tympanum distance. It appears not to have vocal slits, although slits are present on both sides of the tongue that appear to have been made by previous examiners probing too enthusiastically for slits. The specimen is greatly faded and a pattern of dark spotting on the flanks is barely discernible. Duellman (1970: plate 62, no.2) provided a color illustration of *Sarcohyala bistincta* (*sensu stricto*).

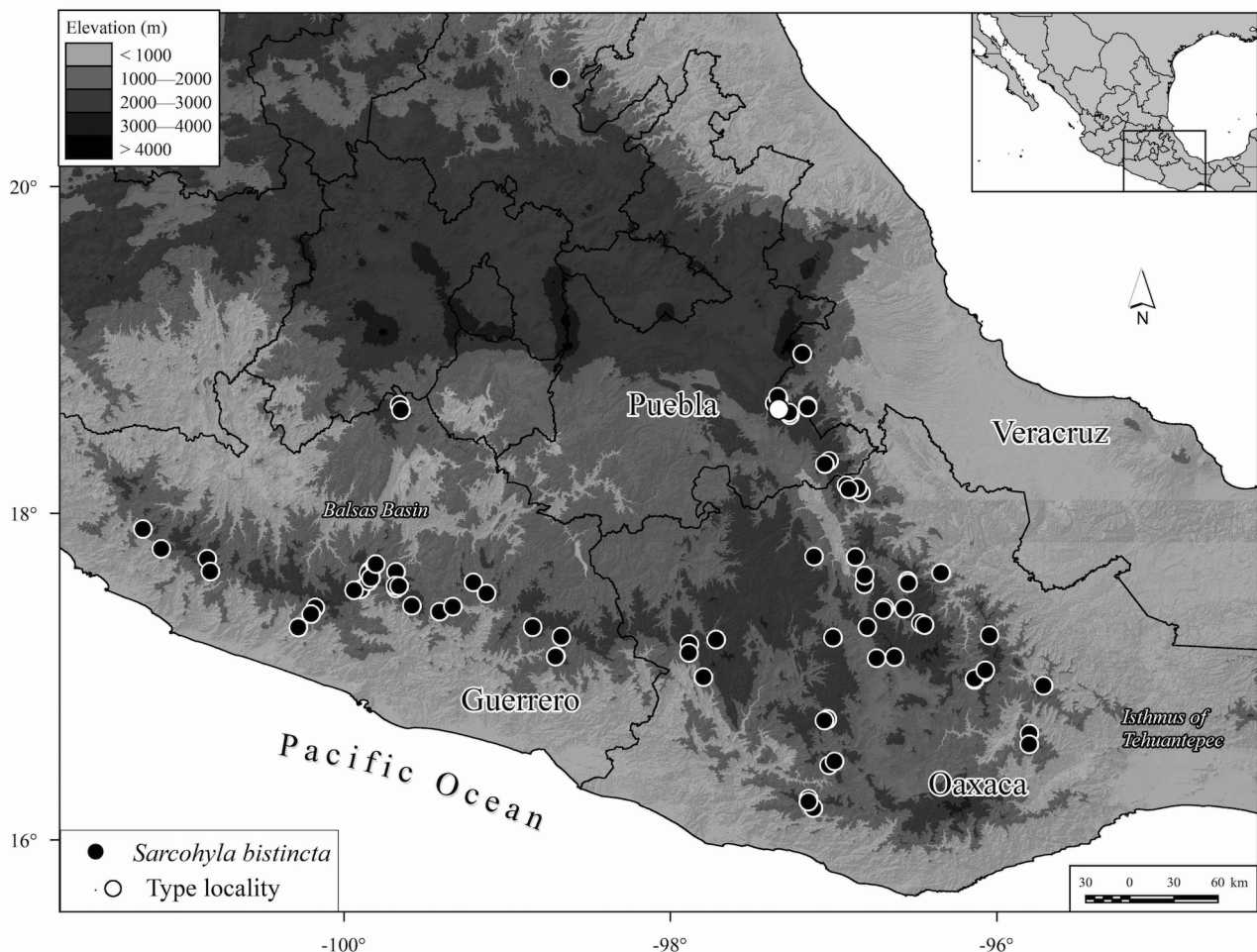


FIGURE 3. Distribution of *Sarcohyala bistincta* in central and southern Mexico.

The pattern is highly variable in this species. A dark bar is usually present from the edge of the upper lip on the snout, curving upwards through the nostril and loreal region to the anterior edge of the eye. This dark streak continues from the posterior edge of the eye, across the top of the tympanum (sometimes including the tympanum), to above the insertion of the forelimb. The flanks are cream or yellowish with a pattern between axilla and groin of irregular black markings, sometime coalescing into an almost continuous streak, or an anastomosing pattern of heavy dark markings enclosing or partially enclosing large pale blotches. The posterior surface of the thigh possesses dark reticulation with yellowish spots exhibiting considerable individual variation in size.

***Sarcohyala labeculata* (Shannon 1951)**

Standard English/Spanish name: Mixe Streamside Treefrog/Rana Trepadora Ribereña Mixe

Figs. 1B, 2C

Hyla bistincta labeculata Shannon 1951: 470. Holotype: USNM 123689, by original designation. Type-locality: “San Lucas Camotlán, Oaxaca”, Mexico.

Hyla calthula Ustach *et al.* 2000: 239. Holotype: UTA A-5885. Type-locality: “Mexico: Oaxaca: Sierra Mixes, Totontepec.

Plectrohyla calthula—Faivovich *et al.* 2005: 105.

Hyla ephemera Meik *et al.* 2005: 20. Holotype: MZFC 17049. Type-locality: ...between Santa María Guienagati and Lachidola, 1100 m (16.759° N, 95.461 W), north slope of Cerro Las Flores, Oaxaca, Mexico.

Sarcohyala calthula—Duellman *et al.* 2016: 18.

Sarcohyala ephemera—Duellman *et al.* 2016: 18.

Diagnosis. Adult size in males to 59.2 mm, in females to 61.3 mm; eye–tympanum distance larger than tympanum diameter; finger disc size relatively large; foot webbing **I1–2III1–2III1–2IV2–1V**; vocal slits absent; nuptial excrescences on prepollex and along medial edge of first, second and, often a few, on third finger; flank pattern usually with continuous dark marking, sometimes broken into bold spots; thigh pattern mostly dark, sometimes with a few pale dots.

Description. Large, robust, reaching adult size of 56.1 mm in males, 61.3 in females; top of head flat, internarial region concave; snout short, bluntly rounded in dorsal profile, in lateral profile truncate; nostrils about 60% distance from eyes to tip of snout; canthus rounded; loreal region slightly concave; lips not flared; heavy dermal fold extending posteriorly from eye, across upper edge of tympanum, then downward to above insertion of fore limb, obscuring upper edge of tympanum; tympanic annulus approximately 35% eye diameter; tympanum diameter 60% eye–tympanum distance; forelimbs robust, especially in males; few small, low, pale ulnar tubercles, usually highly inconspicuous; transverse wrist dermal fold present, often inconspicuous; fingers long, slender, narrow lateral fringe; discs moderately large, disc on finger III about as wide as tympanum; subarticular tubercles large and round, about one-half diameter of terminal disc on same finger, none bifid; supernumerary tubercles small, low, arranged in 1–2 irregular rows on proximal segments of each digit; outer palmar tubercle large, bifid, diffuse; prepollex enlarged, especially in males; adult breeding males with dark nuptial excrescences consisting of minute spinules on dorsal and medial surface of prepollex and also on inner edge of thumb and fingers II and III; webbing vestigial on hand; ulnar tubercles inconspicuous; hind limbs long and robust; heels of adpressed limbs overlap by about one-fifth of length of shank; tibiotarsal articulation extending to eye; indistinct shallow transverse dermal fold on heel; tarsal fold moderately distinct, extending full length of tarsus, raised into low, rounded ridge; inner metatarsal tubercle large, ovoid, with raised (free) median edge; outer metatarsal tubercle barely evident, low, diffuse; toes moderately long, slender, with broad lateral fringe; toe discs nearly as large as on fingers; subarticular tubercles large, round, and subconical; supernumerary tubercles very small, inconspicuous, slightly darkened, arranged in single row on proximal segments of each digit; toe webbing **I1–2II2–2III1–2IV2–1V**; cloacal opening directed ventrally at level of middle of thighs in males and females; cloacal tube long, curved downward; skin on venter granular, smooth on dorsum and ventral surfaces of limbs; tongue round to broadly cordiform, shallowly notched behind, barely free posteriorly; dentigerous processes transverse, situated at midlevel of choanae, narrowly separated, each bearing 5–9 teeth in males, 8–11 in females; round choanae, widely separated; vocal slits absent.

In males dorsum of head, body, limbs and lateral surface of head yellowish tan; often 10–16 small distinct black markings on posterior of dorsum; black stripe from snout through loreal region and eye following supratympanic fold to insertion of forelimb, thence onto flank to the groin; dark flank marking usually continuous, but sometimes interrupted posteriorly or with elongate, horizontal blotches; axillary and inguinal regions below

black stripe pale lemon-yellow to bright yellow; anterior and posterior surfaces of thigh uniformly dark, but sometimes with a few inconspicuous, small pale dots; medioventral surfaces of forelimb, shank, and foot uniformly dark; often a dark suborbital spot, triangle, or bar; ventral surfaces mostly cream, often with coarse dark vermiculations on throat and chest; iris gold, pale copper, or bronze with black reticulations.

Distribution and habitat (Fig. 4). The Sierra Mixe in the north-central Oaxacan highlands where it is known from along small streams and seeps in cloud forest and secondary growth near the village of Totontepec at 1780–1896 m, and also west of the village of Zacatepec (17.190° N 95.987° W) at an elevation of 1360 m. An isolated population occurs on Cerro Las Flores, an uplift somewhat isolated from the rest of the Sierra Mixe and about 90 km southeast of Totontepec, where it has been taken in cloud forest at 1100–1220 m.

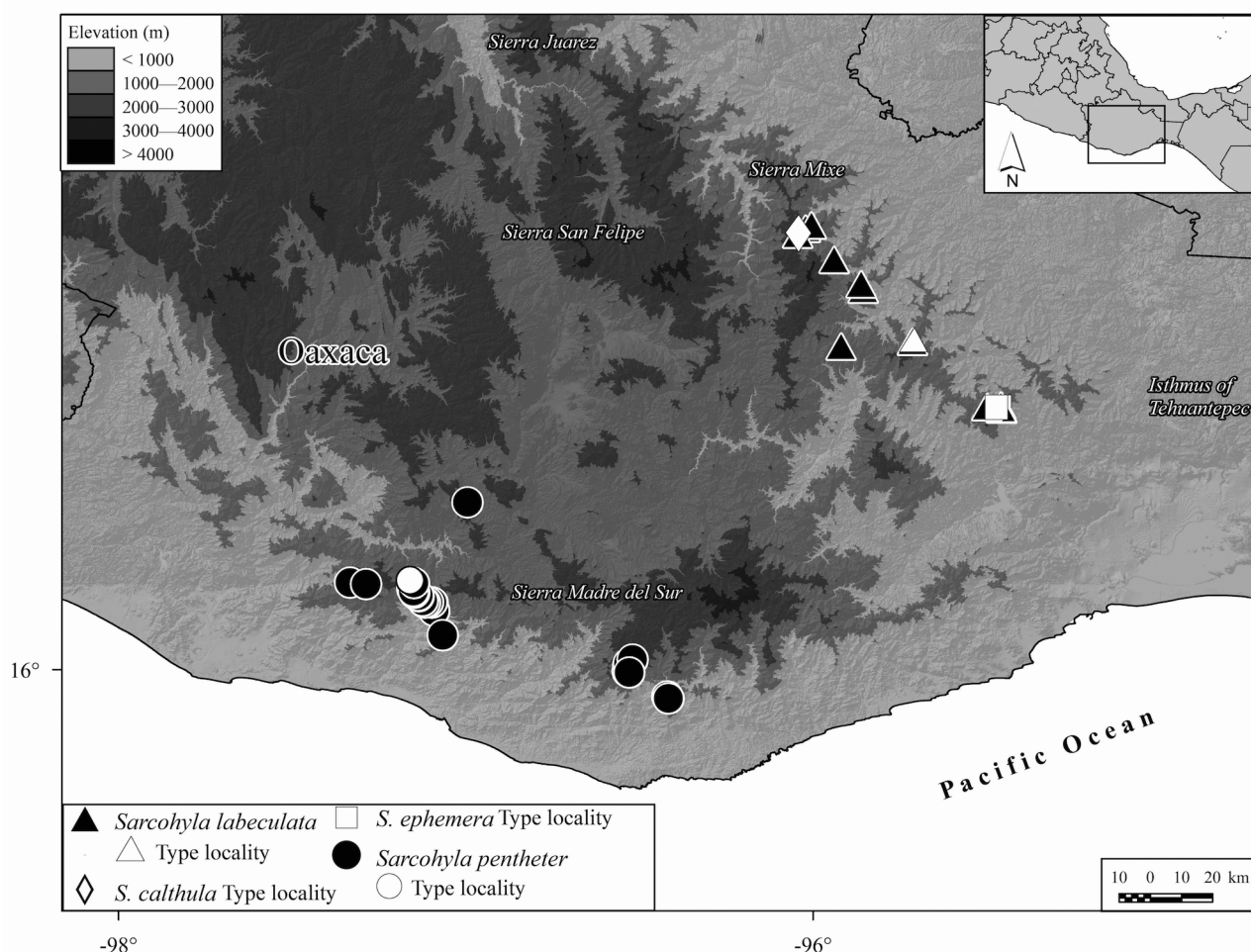


FIGURE 4. Distribution of *Sarcophyla labeculata* and *S. pentheter* in Oaxaca, Mexico.

Comments. Re-examination of the holotype of *Hyla bistrincta labeculata* Shannon (1951), an adult male, reveals its measurements are: 54.0 mm SVL, 20.5 mm HW, 17.8 mm HL, 29.4 mm tibia, 2.8 mm tympanum diameter, and 2.8 mm eye–tympanum distance. The flanks are cream with horizontally elongate spots and streaks, the posterior surface of the thigh is dark with large yellowish spots and there are no vocal slits. A metamorph (USNM 123690) collected at the type-locality (San Lucas Comotlán) is 22.3 mm in SVL and has a tail 19.5 mm long. Although faded from preservative, large spots are still evident on the flanks, limbs, and tail.

Based on multilocus molecular analyses of mitochondrial and nuclear genes (Caviedes-Solis & Nieto-Montes de Oca 2018), *Hyla ephemera* and *H. calthula* represent the same species. The only known adult of *H. ephemera*, a male, possesses a distinct phenotype—it is larger (59.2 mm), and has a relatively shorter snout and tibia, a relatively wider head, and larger tympanum than type males of *H. calthula* (see Table 2). The holotype of *Sarcophyla labeculata* is almost indistinguishable in coloration from that of *H. ephemera* [= *S. labeculata*], and its type locality lies geographically between those of *H. calthula* and *H. ephemera*. Table 2 compares the known male types of these species; all holotypes are males. The holotype of *S. labeculata* differs from male *H. calthula* only in

foot length, being slightly shorter, and tympanum diameter, being slightly larger, but smaller than that of *H. ephemera*. With these new measurements, comparisons, and available molecular evidence, we justify recognizing *H. calthula* and *H. ephemera* as junior synonyms of *S. labeculata*.

TABLE 2. Selected characteristics comparing male type material of *Sarcohyla labeculata* (*Hyla bistincta labeculata* Shannon 1951) and proposed synonyms, *Hyla calthula* Ustach, Mendelson, McDiarmid, and Campbell (2000) and *H. ephemera* Meik, Canseco-Márquez, Smith, and Campbell (2005). All measurements in mm; means followed by SD, over ranges in parentheses (for *H. calthula*). Measurements for USNM 123689 taken by us (those of Shannon 1951 follow in parentheses); all other measurements from original descriptions. Dimensions in bold represent those outside of the range presented for *H. calthula* (largest sampled population).

	Holotype <i>Hyla bistincta labeculata</i>	Holotype <i>Hyla calthula</i>	All type material <i>Hyla calthula</i>	Holotype <i>Hyla ephemera</i>
Specimens	USNM 123689	UTA A-5885	UTA A; N = 18	MZFC 17049
SVL	54.0 (53)	53.7	52.3 ± 1.9 (49.5–56.1)	59.2
HW	20.5 (20)	19.6	19.8 ± 1.0 (18.1–21.9)	23.4
HL	17.8 (20)	17.2	17.2 ± 0.8 (15.7–18.5)	18.8
Tibia	29.4 (28.5)	28.5	28.0 ± 1.4 (26.4–31.8)	28.7
Foot	20.9	25.2	24.9 ± 1.4 (21.6–27.4)	25.9
Eye	6.2	5.1	5.6 ± 0.4 (4.9–6.3)	5.9
Tympanum	2.8 (3.0)	1.8	2.0 ± 0.1 (1.7–2.2)	3.0
Tibia/SVL	0.54	0.53	0.51–0.60	0.48
Foot/SVL	0.39	0.47	0.45–0.50	0.44
Tympanum/Eye	0.45	0.35	0.32–0.44	0.51
Flanks	Cream with horizontal and elongate spots and streaks	Black/dark lateral stripe, with cream/yellow color towards venter	Black/dark lateral stripe, interrupted or not, and with cream/yellow color border or spots towards venter, axilla, and/or groin	Cream with black stripe on left side and elongate spots and streak on right side
Posterior surface of thigh	Dark with large yellow/cream spots	Dark	Dark, sometimes with large yellow/cream spots on lower area	Cream with diffuse black markings
Vocal slits	Absent	Absent	Absent	Absent

Sarcohyla pentheter (Adler 1965)

Standard English/Spanish name: Miahuatlán Streamside Treefrog/Rana Trepadora Ribereña de Miahuatlán
Figs. 1C, 2H

Hyla pentheter Adler 1965: 5. Holotype: UMMZ 125381. Type-locality: “about 37 km N of San Gabriel Mixtepec [about 100 km airline SSW of Oaxaca de Juárez], Oaxaca, 1700 m.”

Plectrohyla pentheter—Faivovich *et al.* 2005: 105.

Sarcohyla pentheter—Duellman *et al.* 2016: 18.

Diagnosis. Adult size in males to 51.1 mm, in females to 57.8 mm; eye–tympanum distance smaller than tympanum diameter; finger disc size relatively large; foot webbing **I2–2II2–3III2–3IV3–2V**; vocal slits absent; nuptial excrescences on prepollex and on inner edge of thumb and second finger; flank pattern often of irregular black stripe; thigh pattern uniformly dark.

Description. Large, robust, males reaching adult size of 51.1 mm, females 57.8 mm; head slightly wider than long; top of head flat; snout short, bluntly rounded in dorsal profile, in lateral profile rounded; nostrils about 60% distance from eyes to tip of snout; canthus rounded; loreal region slightly concave; heavy dermal fold extending posteriorly from eye, across upper edge of tympanum, then downward to above insertion of forelimb, obscuring upper edge of tympanum; tympanic annulus 56–64% eye diameter; tympanum diameter greater than eye–tympanum distance; forelimbs robust, especially in males; transverse dermal fold on wrist; fingers long, slender, narrow lateral fringe; discs moderately large, disc on third finger about equal in size to tympanum; subarticular tubercles large and round, none bifid; supernumerary tubercles indistinct on proximal segments of each digit and palmar surface; outer palmar tubercle low and rounded, usually bifid or tripartite; prepollex enlarged; adult breeding males with dark nuptial excrescences consisting of minute spinules on prepollex and on inner edge of thumb and finger II (absent on finger III); webbing on hand vestigial; ulnar tubercles in longitudinal row of 5–6 pale yellow pustules; hind limbs long and robust; heels of adpressed limbs overlap by about one-tenth of length of shank; tibiotarsal articulation extending to about middle of eye; transverse dermal fold on heel; tarsal fold moderately strong on distal part of tarsus, extending full length of tarsus, usually forming a ridge distally and becoming series of tubercles closer to heel; inner metatarsal tubercle large, elliptical, with raised median edge; outer metatarsal tubercle absent; toes moderately long and slender; toe disc on fourth toe equal to about three-fourths tympanum diameter; subarticular tubercles large, round, and subconical; supernumerary tubercles indistinct, low, arranged on proximal segment of each digit and plantar surface; toe webbing $I2-2II2-3III2-3IV3-2V$; cloacal opening directed ventrally at level of middle of thighs in males and females; cloacal tube long, curved downward; skin on dorsum and undersurfaces of limbs smooth; skin on throat, chest, belly, and ventromedial surface of thighs granular; tongue broadly cordiform, shallowly notched behind, free posteriorly for about one-fourth of length; prevomerine teeth on small and high, transverse elevation between small, ovoid choanae, males with 7–11 teeth on each process, females with 15 per side; vocal slits absent.

Dorsum pale yellow-brown with slight greenish cast to dark brownish gray; band from lip to nostril posteriorly through eye to above tympanum continuing onto flank to groin, black anteriorly and fading to blackish brown on flanks; black flank markings bordered above by thin cream-white line; dorsum yellow-brown to pale tan; flank pattern sometimes interrupted in groin area; upper lip and edges of limbs with blackish brown band; anterior surface of thigh mostly pale with irregular dark streak above; posterior surface of thigh uniformly dark, without pale spots or reticulations; iris deep bronze to reddish brown.

Distribution and habitat (Fig. 4). The southern ridge system of the Sierra Madre del Sur in south-central Oaxaca known as the Sierra de Miahuatlán, where it occurs in moist pine-oak and cloud forest at about 1700 m. Frogs have also been found in secondary forest near small streams perched on mossy boulders in dense vegetation.

***Sarcohyla hapsa*, sp. nov.**

Standard English/Spanish name: Northern Streamside Treefrog/Rana Trepadora Ribereña Norteña (Figs. 1D–E, 2E–G, 5, 7)

Hyla bistincta—Duellman 1961: 1–148, in part.

Plectrohyla bistincta—Faivovich *et al.* 2005: 105, in part.

Sarcohyla bistincta—Duellman *et al.* 2016: 18, in part.

Holotype. UMMZ 244413, an adult male from Mexico: Michoacán, Parque Nacional Uruapan, 1676 m, collected 2 August 1956 by W. E. Duellman, A. S. Duellman, and R. E. Etheridge.

Paratypes (21). KU 68077–78, topotypic, collected by W. E. Duellman 15 July 1955; KU 148653, Michoacán, 14 mi from Rt. 15 on Valle de Bravo road, collected 27 May 1972; UMMZ 112838, topotypic, collected 23 June 1955 by L. D. Beatty and W. E. Duellman; UMMZ 244419–25 topotypic, collected 28 June 1955 by L. D. Beatty, W. E. Duellman, and F. G. Thompson; UMMZ 115232, topotypic, collected 23 April 1956 by W. E. Duellman; UMMZ 2444414–18, topotypic, collected 2 Aug 1956 by W. E. Duellman, A. S. Duellman, and R. E. Etheridge; UMMZ 244426–27, topotypic, collected 20 July 1960 by J. R. Winkelmann; UTA A-62257, Hwy 15 between Morelia and Ciudad Hidalgo, 19.61980 N, 100.77559 W, 2475 m, collected on 16 June 2008 by J. Streicher.

Diagnosis. Adult size in males to 49.5 mm, in females to 56.1 mm; eye–tympanum distance about equal to tympanum diameter; finger disc size moderate in size; foot webbing $I1-2III1-2III1-2IV2-1V$; vocal slits variably

present in breeding males; nuptial excrescences on prepollex and along medial edge of second finger; dorsum with pattern of spots, vermiculations, or reticulations; flank pattern of irregular blackish vermiculations, spots, or fine to coarse reticulations on cream to yellow background; thigh pattern cream to yellow with irregular dark markings.

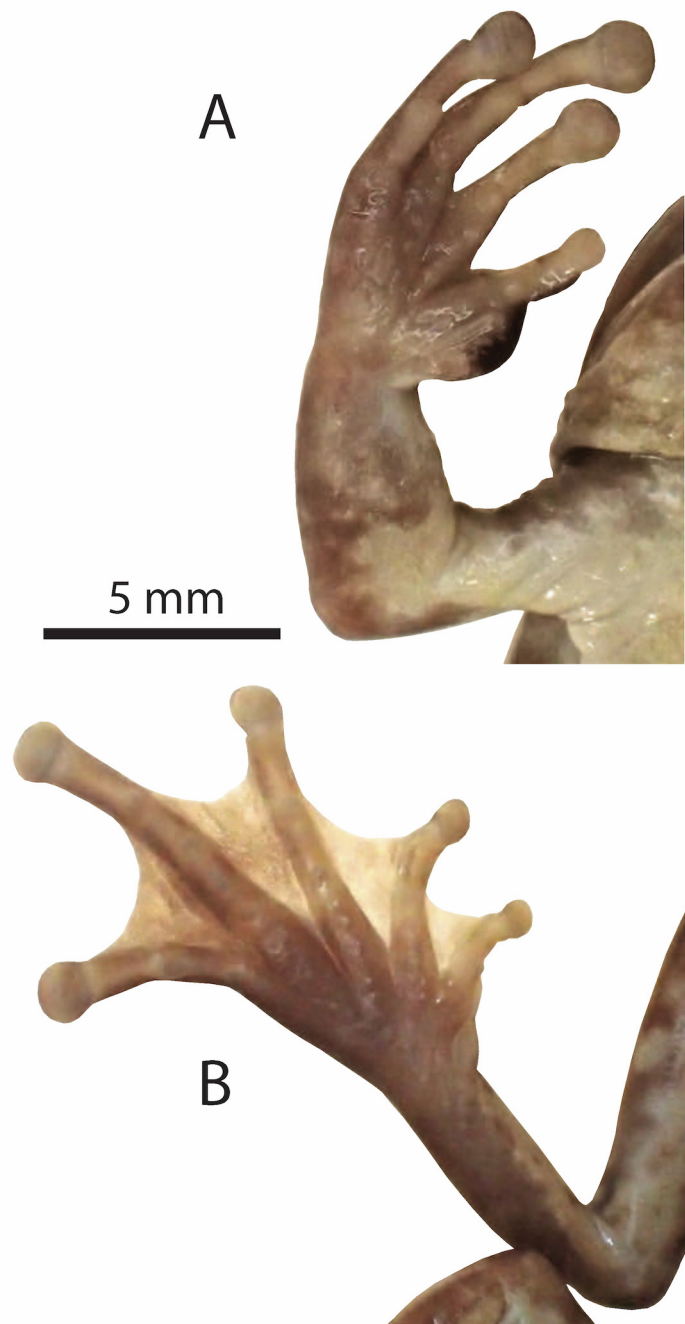


FIGURE 5. Ventral aspect of (A) hand and (B) foot of *Sarcohyla hapsa*, holotype UMMZ 244413.

Description of holotype. An adult male 44.9 mm SVL; head wider than long; cephalic index HW/HL 1.20 (14.8W/12.3L); HL/SVL 0.274; tympanum diameter 2.0 mm; tympanum diameter/eye diameter 0.455; tibia length 21.7 mm; tibia length/SVL 0.483; top of head slightly convex; snout round in dorsal profile, in lateral profile rounded; snout short, nostrils about two-thirds distance from eyes to tip of snout; canthus rounded; loreal region concave; lips thick not flared; relatively light dermal fold extending posteriorly from eye across upper edge of tympanum then downward to above insertion of fore limb, obscuring upper edge of tympanum; tympanic annulus separated from eye by distance about equal to diameter of tympanum; forelimbs robust; few small inconspicuous

ulnar tubercles present along ventral surface of forearm; transverse dermal fold on wrist; fingers moderately short and stout; discs moderately large, disc on third finger larger in diameter than tympanum; subarticular tubercles large and round, none bifid; supernumerary tubercles small and round, arranged in single row on proximal segments of each digit; outer palmar tubercle low and round, usually bifid or tripartite; elongate tubercle on prepollex; prepollex enlarged; adult breeding males with dark nuptial excrescences consisting of minute spinules; mainly on prepollex, but also on inner edge of length of second finger; webbing on hand vestigial; hind limbs long and robust; heels of adpressed limbs overlap by about one-third of length of shank; tibiotarsal articulation barely reaching posterior edge of eye; transverse dermal fold on heel; tarsal fold low, usually extending almost full length of tarsus, often raised into series of tubercles at least though some of length; inner metatarsal tubercle large, elliptical, with raised (free) median edge; outer metatarsal tubercle usually absent, when present tiny and diffuse; toes moderately short and stout; toe discs nearly as large as on fingers; subarticular tubercles large, round, and subconical; supernumerary tubercles small, low, arranged in single row on proximal segments of each digit; toe webbing **I1–2III1–2III1–2IV2–1V**; cloacal opening variable, directed ventrally at level of middle of ventral surfaces of thighs; cloacal tube long, curved downward; skin on ventral surfaces of body and thighs granular, smooth on dorsum; tongue broadly cordiform, shallowly notched behind, free posteriorly for about one-fourth of length; prevomerine teeth situated on two small, transverse processes between small, ovoid choanae, dentigerous processes in contact or very narrowly separated from each other, males with 3–7 teeth on each process, females with 5–7; vocal slits present or absent; in preservative dorsum brown; flanks whitish or cream with pattern of medium heavy black reticulations enclosing pale spots usually larger than tympanum; posterior surface of thigh dark with pale yellow spots smaller than tympanum; anterior surface of thigh dark with yellow spots about equal to those on posterior of thigh; venter cream; iris color of holotype unknown, but assumed to be copper to pale bronze similar to topotypes.

Variation. In life dorsum gray, grayish brown, greenish brown, greenish tan, or reddish brown, usually with darker brown to black pattern consisting of reticulations or irregular spots and streaks on exposed surfaces, most conspicuous on head and trunk, less so or absent on limbs. Narrow black streak from edge of upper lip to anterior edge of eye present or absent; narrow black streak from posterior edge of eye across top of tympanum (not involving tympanum) to above insertion of forelimb.

Flanks white to yellowish with pattern of dark lavender-brown to blackish vermiform markings or reticulations. Anterior and posterior surfaces of thighs cream to yellow with irregular dark markings. Ventral surfaces pale yellow to cream with irregular dark reticulations or vermiform markings. Iris copper to pale bronze. Vocal slits sometimes present (present in six of 26 males over 40 mm SVL), located along inner edge of rami of lower jaw; vocal sac single, median, subgular, barely distensible.

Distribution and habitat (Fig. 6). Southern Sierra Madre Occidental from Durango and southern Sinaloa (Duellman 1970), along the southern edge of the Mexican Plateau from Michoacán to Morelos, and the Sierra de Coalcomán in southern Michoacán. Occurring at 1280–2550 m most commonly in pine-oak forests, but also pine and pine-fir forests. Duellman (1961) reported that by day this frog hides in thick vegetation overhanging small montane streams. Members of the group have been found at night on stream-side vegetation (Duellman 1964) or by day in the axils of plants (Taylor and Smith 1945). Duellman (1970: plate 62, no.1) provided a color illustration of this species. Parra *et al.* (2003) found an individual in the state of México that was identified as *S. pentheter*; however, based on distribution and morphology, we assume this to be *S. hapsa*. López-Garduño and Rodríguez-Romero (2012) reported this species near Valle de Bravo, México, at 1895 m. Reyes-Velasco *et al.* (2012) reported this species south of La Estancia on the Mascota to Puerto Vallarta Hwy in pine forest at 1580 m. Luja and Grünwald (2015) reported this species from near Tepic. Their material was collected in an ecotone between cloud forest and pine-oak forest at 920–1546 m; at the lower elevation juveniles were collected on coffee plants along a stream.

Etymology. The specific name is derived from the Greek *hapsis*, meaning a mesh or network, in reference to the finely reticulated flank pattern of most individuals.

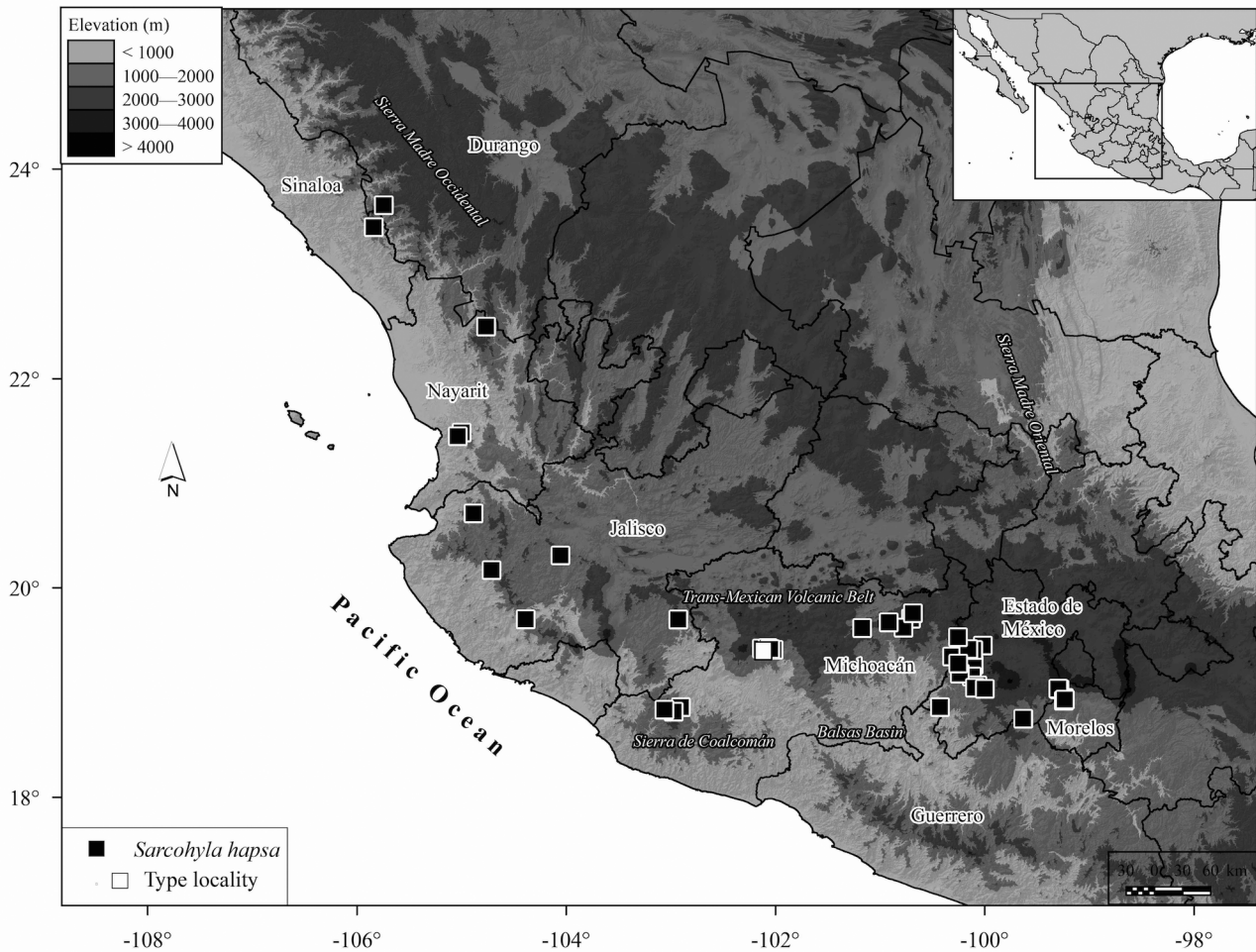


FIGURE 6. Distribution of *Sarcohyla hapsa sp. nova* in central Mexico showing the distribution of this species along the humid south fringe of the Central Plateau, flanked by the Trans-Mexican Volcanic Range and the northern Balsas River Valley, from the state of Nayarit to Morelos, and including the states of Michoacán and Mexico. Along the western part of the distribution this species is also restricted to the western slopes, along the Sierra Madre Occidental of Durango, Sinaloa, Nayarit and Jalisco, and the Sierra Madre del Sur of Jalisco, Colima and Michoacán.

Tadpoles. Tadpoles for several species of the *Sarcohyla bistincta* group have been reported. Duellman (1961) described a series of tadpoles from near Uruapan, Michoacán, which correspond to *Sarcohyla hapsa*. Features of these tadpoles include a total length of 61 mm for developmental stage 36 (Gosner 1961); moderately depressed body, as wide as deep; snout broad and rounded in dorsal profile; small nostrils directed anteriorly and located midway between eyes and tip of snout; small eyes, directed dorsolaterally; sinistral spiracle, opening on midline about two-thirds distance from snout to posterior edge of thighs; cloacal tube short and dextral; tail about twice as long as body, heavy musculature not extending to tip of tail, shallow fins; dorsal fin extending onto dorsum of body; tail rounded posteriorly; moderately large, ventral mouth; lips folded laterally; two rows small papillae completely bordering lips; row of larger papillae between upper lips and first upper row of teeth, similar row between lower lips and third row of teeth, these large papillae grading into small papillae in lateral fold; beaks moderately robust, bearing small peg-like serrations, slightly larger on lower beak; upper beak broad arch with short rounded lateral processes, lower beak broadly V-shaped; tooth rows 2/3, upper rows nearly equal in length, longer than lower subequal tooth rows; second upper tooth row interrupted medially, first lower tooth row variable, complete or interrupted.

Mating call (Fig. 7). The mating calls of members of the *S. bistincta* group have not been described, although some, if not all, of the species do call. Duellman (1964, 1970) reported that *Plectrohyla bistincta (sensu lato)* from Michoacán has vocal slits and he heard a low growling sound near Uruapan that possibly was attributable to *S. hapsa*. Shannon (1951) reported that the type of *Hyla bistincta labeculata* (= *Sarcohyla labeculata*) “was singing in

the river when collected. Other than some adult male *S. hapsa*, we have not observed vocal slits in other populations of frogs previously allocated to *S. bistincta*, although this does not preclude advertisement calls in breeding males. The call of an adult male from La Noria, Xalisco, Nayarit (21.483390° N, 104.999060° W), was recorded on 20 July 2013. The call is composed of poorly modulated notes given 0.67–0.83 seconds apart. Each note is 0.12–0.25 seconds in length and is composed of two–three distinct pulses with the number of pulses increasing over the length of the call. The time interval between pulses is 0.06–0.12 seconds and the pulse rate is 12.34–16.66 pulses/second. The second pulse of each note has a larger relative amplitude than the first or third. The fundamental and dominant frequencies of the vocalization are 559.83 Hz and 1119.72 Hz respectively. With the exception of the first note, the fundamental and dominant frequencies of the individual notes are the same as for the call. The first note is weaker with a fundamental frequency of 473.73 Hz and a dominant frequency of 947.46 Hz. There is a substructure to each pulse. Each show 3–4 distinct peaks in relative amplitude, the first of which are the strongest.

Sexual dimorphism. Sexual dimorphism in size appears to be consistent in all species of the *S. bistincta* group, with females attaining a large size than males. Several species (*S. bistincta*, *S. laberculata*, *S. hapsa*) and possibly all species of the group, exhibit sexual dichromatism. Adult males in *S. bistincta* are reddish brown and females are darker coffee brown. In *S. laberculata* males are yellowish tan and females are yellowish or grayish tan. *Sarcohyala hapsa* is a highly variable species, but adults of some populations are often reddish brown with males slightly paler than females. Generally, in all members of the group there is a tendency for more yellow on males, especially on the flanks, venter, and limbs, whereas females tend to be whitish or cream.

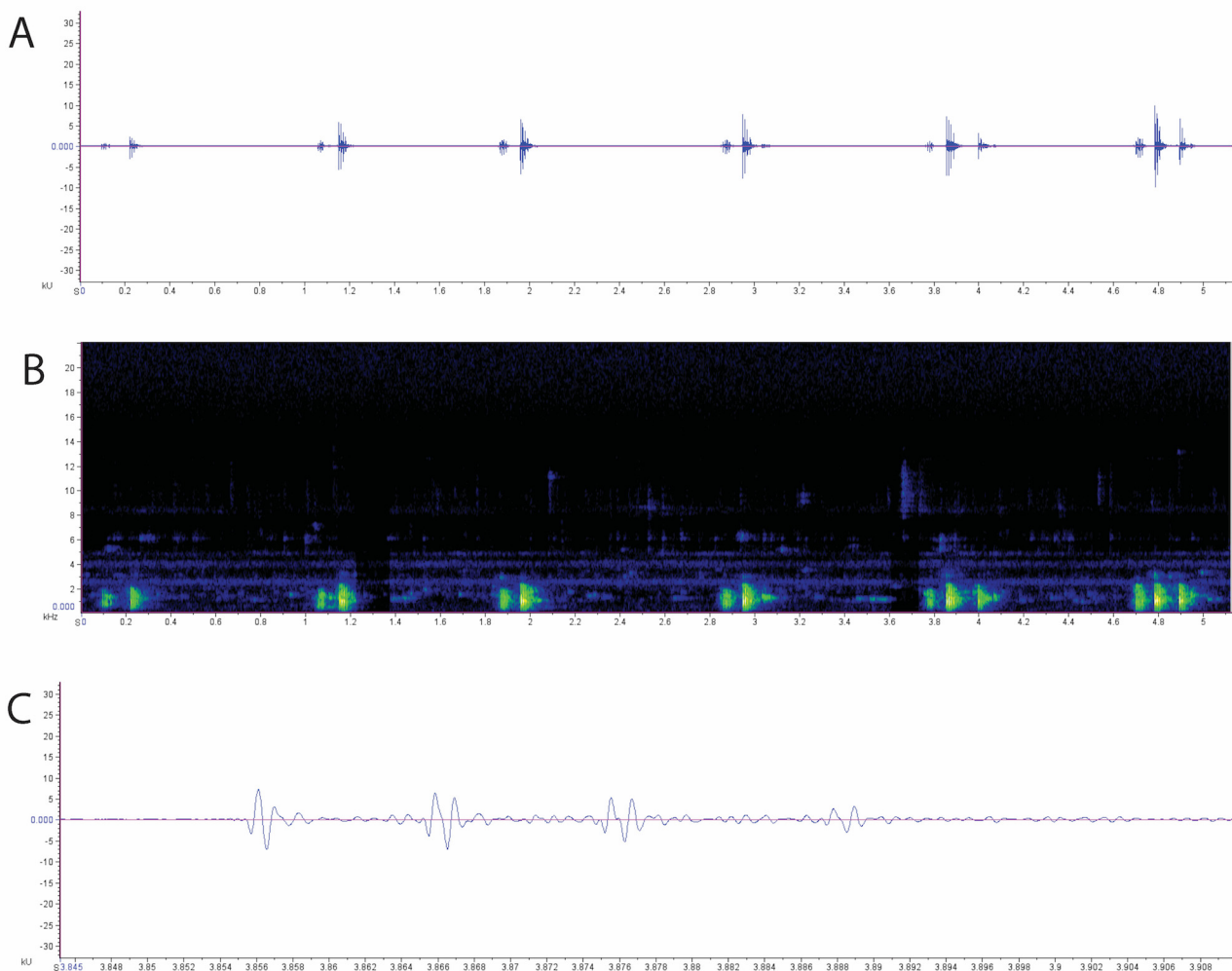


FIGURE 7. Aspects of the call of *Sarcohyala hapsa*. (A) Oscillogram of call. (B) Spectrogram of call. (C) Oscillogram of a single pulse within call.

Discussion

Previously *Sarcohylla bistincta* (sensu lato) was considered to range across the Mexican highlands including the Sierra Madre Occidental, Trans-Mexican Volcanic Range, Sierra Madre Oriental, central Oaxacan highlands, and Sierra Madre del Sur. This multi-species taxon occurs in cloudforest and pine-oak forests at elevations of 1200 to 2900 m. This is an exceptionally wide distribution rivaled by few other Mexican highland species of anuran. It is somewhat suspect that a single species of *Sarcohylla*, which contains about two dozen species, would have a distribution encompassing the geographic ranges of essentially the entire group, and range further north and about as far south as any congener. With the recognition of *S. hapsa*, a clearer biogeographic picture emerges that is not unlike that of several other species groups of vertebrates. *Sarcohylla hapsa* occurs in the Sierra Madre Occidental and Trans-Mexican Volcanic Range; *S. bistincta* inhabits the Sierra Madre Oriental, the Sierra Madre del Sur and many of the intervening highlands (Fig. 3); *S. labeculata* and *S. pentheter* are restricted to the Atlantic and Pacific versants of Oaxaca, respectively (Fig. 4).

Unfortunately, Caviedes-Solís and Nieto-Montes de Oca (2018)'s phylogenetic analysis of *Sarcohylla* and this study included different samples of *Sarcohylla*. Nonetheless, the geographic distribution of *S. hapsa* roughly corresponds to that of the “*S. bistincta* 1” clade in Caviedes-Solís and Nieto-Montes de Oca (2018)'s work, given that the samples of the clade came from the states of Nayarit, Jalisco, Michoacán, and Morelos. Also, in a phylogenetic analysis of mitochondrial and nuclear DNA sequences from a sample of *S. hapsa* examined in this study (UTA A-62257) and representatives of other *Sarcohylla* species, including *S. bistincta*, *S. labeculata*, and *S. pentheter* (unpublished data), *S. hapsa* was strongly supported as the sister taxon to a clade composed of *S. bistincta* + (*S. labeculata* + *S. pentheter*); that is, it showed the same relationships as Caviedes-Solís and Nieto-Montes de Oca (2018)'s “*S. bistincta* 1” clade. Furthermore, the sample of *S. hapsa* was collected only 16.1 km ESE from the locality of origin of one of the specimens (UOGV 1553) in Caviedes-Solís and Nieto-Montes de Oca (2018)'s “*S. bistincta* 1” clade. All of this strongly suggests that *S. hapsa* is the sister taxon to the clade (*S. bistincta* (*S. labeculata* + *S. pentheter*)).

Of biogeographic interest is the distribution of closely related species occurring in the Sierra Madre del Sur and on the southern slopes of the Trans-Mexican Volcanic Range from Morelos to Michoacán, with an apparent hiatus of 200+ kms from their distribution in Puebla. It is unlikely that the distribution of these trans-Balsas species can be explained by dispersal events across the arid, rainshadow valley of the Balsas, but it might be explained rather by vicariance, whereby several factors fragmented present day populations. Ancestral populations probably inhabited moderately high elevations drained by the upper tributaries of the Río Balsas along the Mexican Plateau in the north, the Sierra Madre Oriental to the east, and the Sierra Madre del Sur in the south. As the upper tributaries of the Río Balsas became more deeply entrenched, the high elevations of Pico de Orizaba and surrounding highlands took shape during the Pleistocene, causing rainshadow conditions to their west, a mesic corridor across southern Puebla was interrupted by an intervening *matorral xerófilo* [= xerophytic scrubland] (Rzedowski 1978), creating a hiatus in the broad arc of ranges of highland species.

We have examined individuals in the *S. bistincta* group from the steep slopes of the southern escarpment of the Sierra Madre del Sur of Guerrero that we are unable to place with certainty. These are referred to as *S. cf. bistincta*, although future investigations may well reveal their distinctiveness. Most of this material originated in the pine-oak highlands to the W of Chilpancingo at 1875–2685 m. Individuals have been observed sitting on rocks along streams and discovered by excavating dirt crevices along a road cut about half a mile from the nearest stream. Apparently, a large amount of variation is present in the Guerreran frogs, some of which are distinct from what we have seen in Oaxaca, whereas others are similar. *Sarcohylla cf. bistincta* occurs at localities close to where more typical *S. bistincta* have been found, but these entities have not been found in microsympatry. *Sarcohylla cf. bistincta* is characterized by adult males reaching 46.3 mm SVL, females to 50.6 mm; eye–tympanum distance < tympanum diameter; finger disc size relatively large; foot webbing I1–2III1 –2III1–2IV2–1V; vocal slits absent; flank pattern cream to yellowish tan with irregular blackish streaks or spots; thigh pattern dark brown punctuated with many small yellow spots; iris color gold to copper.

Geological events, subsequent landscape modifications, and climate changes during the Pleistocene have affected speciation and population structure of the species of the *Sarcohylla bistincta* group. It is a safe assumption that these factors have similarly influenced practically all organisms of the region, more so the ones with more extensive distributions. The geographic barriers to highland faunas provided by the extensive entrenchment of the

Río Balsas Basin and the discontinuity of habitats between the Guerreran and Oaxacan highlands has been emphasized by numerous authors (e.g., Campbell 1988; Myers and Campbell 1981). Nevertheless, a number of montane species occurring in upland pine-oak forests exhibit a biogeographic pattern extending through the Sierra Madre del Sur of Guerrero and Oaxaca and across the ranges of central Oaxaca into the southern portion of the Sierra Madre Oriental (e.g., *Exerodonta melanoma*, *Ptychohyala leonhardschultzei*, *Barisia imbricata*, *Crotalus intermedius*, *Ophryacus undulatus*, *Crotalus ravus*).

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References

- Adler, K. (1965) Three new frogs of the genus *Hyla* from the Sierra Madre del Sur of México. *Occasional Papers of the Museum of Zoology, University of Michigan*, 62, 1–18.
- Audacity Team (2016) Audacity® Free Audio Editor and Recorder. Version 2.1.2. Available from: <http://audacity.sourceforge.net> (accessed 28 March 2016)
- Campbell, J.A. (1988) The distribution, variation, natural history, and relationships of *Porthidium barbouri* (Viperidae). *Acta Zoologica Mexicana*, Nueva Serie, 26, 1–32.
- Campbell, J.A. & Duellman, W.E. (2000) New species of stream-breeding Hylid frogs from the northern versant of the highlands of Oaxaca, Mexico. *Scientific Papers, Natural History Museum, The University of Kansas*, 16, 1–28.
- Caviedes-Solis, I.W. (2012) *Molecular phylogeny of the Plectrohyla bistincta group (Anura: Hylidae)*. Master’s thesis. Universidad Nacional Autónoma de México, México, D.F., 50 pp. [please cite the total page number]
- Caviedes-Solis, I.W. & Nieto-Montes de Oca, A. 2018 (2018) A multilocus phylogeny of the genus *Sarcohyala* (Anura: Hylidae), and an investigation of species boundaries using statistical species delimitation. *Molecular Phylogenetics and Evolution*, 118, 184–193.
<https://doi.org/10.1016/j.ympev.2017.09.010>
- Charif, R.A., Ponirakis, D.W. & Krein, T.P. (2006) *Raven Lite 1.0 User’s Guide*. Cornell Laboratory of Ornithology, Ithaca, NY. Available from: <http://www.birds.cornell.edu/brp/RavenLite/RavenLite10UsersGuide.pdf> (accessed 8 May 2018)
- Cochran, D.M. (1961) Type specimens of reptiles and amphibians in the United States National Museum. *United States National Museum Bulletin*, 220, 1–291.
<https://doi.org/10.5962/bhl.part.26967>
- Cope, E.D. (1878 [dated 1877]) Tenth contribution to the herpetology of tropical America. *Proceedings of the American Philosophical Society*, 17, 85–98.
- Duellman, W.E. (1961) The amphibians and reptiles of Michoacán, México. *University of Kansas Publications of the Museum of Natural History*, 15, 1–148.
<https://doi.org/10.5962/bhl.part.7287>
- Duellman, W.E. (1964) A review of the frogs of the *Hyla bistincta* group. *University of Kansas Publications, Museum of Natural History*, 15, 469–491.
- Duellman, W.E. (1970) The hylid frogs of Middle America. *Monograph of the Museum of Natural History, University of Kansas*, 1, 1–753, 72 pls.
- Duellman, W.E. (2001) *The hylid frogs of Middle America. Vol. 1 & 2*. Society for the Study of Amphibians and Reptiles, Ithaca, NY, 603 pp. & 1159 pp., 92 pls.
- Faivovich, J., Haddad, C.F.B., García, P.C.A., Campbell, J.A. & Wheeler, W.C. (2005) Systematic review of the frog family

- Hylidae, with special reference to Hylinae: Phylogenetic analysis and taxonomic revision. *Bulletin American Museum Natural History*, 294, 1–240.
[https://doi.org/10.1206/0003-0090\(2005\)294\[0001:SR0TFF\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2005)294[0001:SR0TFF]2.0.CO;2)
- Duellman, W.E., Marion, A.B. & Hedges, S.B. (2016) Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae). *Zootaxa*, 4104 (1), 1–109.
<https://doi.org/10.11646/zootaxa.4104.1.1>
- Gridi-Papp, M. (ed.). (2007) SoundRuler: Acoustic Analysis for Research and Teaching. Available from: https://www.uaeh.edu.mx/investigacion/productos/6008/2010_lista_de_anfibios_y_reptiles_del_estado_de_hidalgo_mexico.pdf (accessed 29 March 2016)
- Gosner, K.L. (1961) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 3, 183–190.
- Kaplan, M., Heimes, P., Zarza, E. & McCormack, J.E. (2016) On the morphology of *Plectrohyla chryses* (Anura: Hylida; Hylini), with comments on some controversial characters, phylogenetic relationships, and diagnosis of this species. *Caldasia*, 38 (2), 257–273.
<https://doi.org/10.15446/caldasia.v38n2.60921>
- Kellogg, R. (1932) Mexican tailless amphibians in the United States National Museum. *United States National Museum Bulletin*, 160, 1–223.
<https://doi.org/10.5479/si.03629236.160.i>
- Lemos-Espinal, J.A. & Smith, G.R. (2015) Amphibians and reptiles of the state of Hidalgo, Mexico. *Check List*, 11 (1642), 1–11.
- López-Garduño, M.G. & Rodríguez-Romera, F. (2012) Geographic distribution: *Hyla bistincta* (Mexican Fringe-limbed Treefrog). *Herpetological Review*, 43, 299.
- Luja, V.H. & Grünwald, C.I. (2015) New distributional records of amphibians and reptiles from Nayarit. *Herpetological Review*, 46, 223–225.
- Meik, J.M., Canseco-Márquez, L., Smith, E.N. & Campbell, J.A. (2005) A new species of *Hyla* (Anura: Hylidae) from Cerro Las Flores, Oaxaca, Mexico. *Zootaxa*, 1046, 17–27.
- Myers, C.W. & Campbell, J.A. (1981) A new genus and species of colubrid snake from the Sierra Madre del Sur of Guerrero, Mexico. *American Museum Novitates*, 2708, 1–20.
- Myers, C.W. & Duellman, W.E. (1982) A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates*, 2752, 1–25.
- Parra-Olea, G., Casas-Andreu, G., Aguilar-Miguel, X. & Garcia-Paris, M. (2003) *Hyla pentheter*. Geographic distribution. *Herpetological Review*, 34, 162.
- Ramírez-Bautista, A., Hernández-Salinas, U., Mendoza-Quijano, F., Cruz-Elizalde, R., Stephenson, B.P., Vite-Silva, V.D. & Leyte-Manrique, A. (2010) *Lista anotada de los anfibios y reptiles del estado de Hidalgo, México*. CONABIO, México. Available from: https://www.uaeh.edu.mx/investigacion/productos/6008/2010_lista_de_anfibios_y_reptiles_del_estado_de_hidalgo_mexico.pdf (accessed 8 May 2018)
- Reyes-Velasco, J., Grünwald, C.I., Jones, J.M., Price, M.S. & Fisher, J.T. (2012) New distributional records for the herpetofauna of Mexico. *Herpetological Review*, 43, 451–453.
- Rzedowski, J. (1978) *Vegetación de México*. Editorial Limusa, México, 432 pp.
- Savage, J.M. & Heyer, R.W. (1967) Variation and distribution of the tree-frog genus *Phyllomedusa* in Costa Rica. *Beiträge zur Neotropical Fauna*, 5, 111–131.
<https://doi.org/10.1080/01650526709360400>
- Savage, J.M. & Heyer, R.W. (1997) Digital webbing formulae for anurans: a refinement. *Herpetological Review*, 28, 131.
- Shannon, F.A. (1951) Notes on a herpetological collection from Oaxaca and other localities in Mexico. *Proceedings of the United States National Museum*, 101, 465–484.
<https://doi.org/10.5479/si.00963801.101-3284.465>
- Smith, H.M. & Taylor, E.H. (1950) Type localities of Mexican reptiles and amphibians. *University of Kansas Science Bulletin*, 33, 313–380.
- Taylor, E.H. & Smith, H.M. (1945) Summary of the collections of amphibians made in México under the Walter Rathbone Bacon Traveling Scholarship. *Proceedings of the United States National Museum*, 95, 521–613.
<https://doi.org/10.5479/si.00963801.95-3185.521>
- Ustach, P.C., Mendelson III, J.R., McDiarmid, R.W. & Campbell, J.A. (2000) A new species of *Hyla* (Anura: Hylidae) from the Sierra Mixes, Oaxaca, Mexico, with comments on ontogenetic variation in tadpoles. *Herpetologica*, 56, 239–250.

APPENDIX. Specimens examined.

Museum acronyms follow Sabaj Pérez (2010).

***Sarcohyla bistincta*. MEXICO:** GUERRERO: Carrizal [= Corral] de Bravo (MVZ 110929); Corral de Bravo, 37.5 mi by rd (to Atoyac) SW Milpillas (LACM 92418); 4.5 km (by road) E El Limón (= 6 km SW Chilapa (KU 140420–23); between Puerto

Chico and Asoleadero (UMMZ 125376); 3.3 km N San Vicente (KU 87117); Sierra Madre del Sur, Bajos de Balsamar - La Sierrita, 1552 m (UTA A-61991-92); Sierra Madre del Sur, Carretera Escalerilla to La Laguna, approximately 15 km SW Corral del Bravo on road to Puerto del Gallo (17.52701N, 99.93703W), 1875 m (UTA A-61988-89). HIDALGO: Zacualtipan (ANSP 14744). OAXACA: Ayutla (ANSP 30335); 0.6 mi NE Ayutla, 6500 ft (AMNH 76422); Cuicatlán, Tutepetongo, 1619 m (UTA A-61912); El Tejocote (UTA A-17133); Huautla de Jiménez (AMNH A60413); Itlán de Juárez, Vivero Rancho Teja (LACM 64958-60); 16.5 mi S Sola de Vega, Hwy 131 (CAS 199832-35); 54.6 mi S Sola de Vega, Hwy 131 (CAS 199828); 38.1 km E Teotitlán on road to Huautla (UTA A-13148); 61 km E Teotitlán on road to Huautla, Puente de Hierro (UTA A-13149-50); 3.5 km WSW Tlaxiaco (UTA A-3652). VERACRUZ: mountain SW Acultzingo (USNM 114525); Cumbres de Acultzingo (FMNH 111070-72, 105482-83, USNM 114525); 4 km S Puerto del Aire (MVZ 114715); Xometla (LACM 119275).

***Sarcohyla hapsa*. MEXICO:** MÉXICO: Avándaro (UMMZ 239801); 8 mi W Villa Victoria (FMNH 111073-74); 19 km W Villa Victoria (USNM 114513). MICHOACÁN: W slope Cerro San Andrés, 11 mi WNW Ciudad Hidalgo (UMMZ 102075); Dos Aguas (UMMZ 119193); 12.5 km ENE Dos Aguas (UMMZ 119194); Los Conejos (UMMZ 94238-39); (KU 148653); Uruapan (KU 68077-78); UMMZ 94238-40, 112838-39, 115231-33, 121515, USNM 114514-24); Uruapan, probably near El Sabino (FMNH 111064). MORELOS: 2 mi N Cuernavaca (CAS 87826, FMNH 111065-69); 10 mi N Cuernavaca (FMNH 111075); 22.4 km from Route 15 on Valle de Bravo road. NAYARIT: Santa Teresa (USNM 46829); Municipality of Xalisco, Rancho La Noria, 9 km W Tepic, 1546 m (Luja and Grünwald, 2015); El Cuarenteño (*ibidem*); 25 km SE Autlán (UMMZ 102076). SINALOA: 1.6 km E Santa Lucía (KU 44567). See species description for other specimens examined, including type series.

***Sarcohyla labeculata*. MEXICO:** OAXACA: Cerro Las Flores, north slope, road between Santa Maria Guienagati and Lachidola, 1100 m (MZFC 17049 [previously UTA A-57683], holotype of *Hyla ephemera*); Sierra Mixe, Totontepec, headwaters of Río de la Lana, 1829 m (UTA A-5788, 5876-84, 5885-holotype *H. calthula*, 5886, 8508-09); Totontepec, 1896 m (UTA A-6929-32); Totontepec, 1798 m (UTA A-13369); E side Totontepec, 1780 m (UTA A-13370-71); San Lucas Comotlán (USNM 123689-holotype, 123690).

***Sarcohyla pentheter*. MEXICO:** OAXACA: 25.3 km N San Gabriel Mixtepec (UTA A-17165); Carretera Santa Catarina Juquila-Puerto Escondido, 1494 m (UTA A-62065).