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A new species of *Charadrahyla* (Anura: Hylidae) from the cloud forest of western Oaxaca, Mexico

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Abstract

A new species of treefrog from the genus *Charadrahyla* is described from the cloud forest of western Sierra Madre del Sur of Oaxaca, Mexico. *Charadrahyla sakbah* **sp. nov.**, is distinguished from the rest of the species in the genus by the large body size (81.15–85.75 mm and 67.91–73.21 mm in adult females and males respectively), axillary membrane, adult males with hypertrophied webbings between toes I and II, nuptial excrescences, one enlarged conical tubercle on either side of vent, vocal slits absent, and sexual dimorphism in the snout shape in dorsal profile (rounded and acuminate in females and males respectively). The hypertrophied webbings are a unique character among other hylids of Middle America, and are only present in *C. trux*, *C. tecuani* and the species described herein. These three species inhabit the cloud forest of the Sierra Madre del Sur, and are probably closely related. However, more detailed phylogenetic analyses are needed to define the internal relationships of the genus. The cloud forest in the Sierra Madre del Sur continues to be known for a high number of endemic species. However, the cloud forest faces several threats due to its limited distribution that make it a priority ecosystem for conservation.

Key words: cloud forest, highlands, hylids, Sierra Madre del Sur

Resumen

Se describe una nueva especie de rana arborícola del género *Charadrahyla* del bosque nublado de la Sierra Madre del Sur del oeste de Oaxaca, México. *Charadrahyla sakbah* **sp. nov.**, se distingue del resto de las especies del género por su talla corporal grande (81.15–85.75 mm y 67.91–73.21 mm en hembras y machos adultos respectivamente), membrana axilar, machos adultos con membrana hipertrofiada entre los dedos I y II, presencia de excrecencias nupciales, un tubérculo cónico agrandado a cada lado de la cloaca, ausencia de hendiduras bucales y dimorfismo sexual en la forma de la nariz en vista dorsal (redonda y acuminada en hembras y machos respectivamente). La membrana hipertrofiada es una característica única entre otros hylidos de Mesoamérica y solo está presente en *C. trux*, *C. tecuani* y la especie descrita aquí. Estas tres especies habitan en el bosque nublado de la Sierra Madre del Sur, y probablemente estén estrechamente emparentadas. Sin

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embargo, son necesarios trabajos filogenéticos subsecuentes para definir con precisión las relaciones internas del género. El bosque de niebla de la Sierra Madre del Sur destaca por el alto número de especies endémicas. Sin embargo, enfrenta diversas amenazas debido principalmente a su limitada distribución, que lo convierte en un ecosistema prioritario para la conservación.

Palabras clave: bosque mesófilo, tierras altas, hylidos, Sierra Madre del Sur

Introduction

The Mexican herpetofauna is distinguished by a high number of endemic species (61.1%; Johnson *et al.* 2017), with 67% amphibian species endemic (Parra-Olea *et al*. 2014). The Sierra Madre del Sur (SMS) stands out as the second physiographic region with the highest number of the total endemic amphibian species (77 species, 28.83%; Johnson *et al.* 2017). The SMS is located in South Central Mexico at an altitude above 1000 m from southern Michoacán to Guerrero and Oaxaca, including portions of Puebla (Morrone 2014). The type of vegetation corresponds to pine, oak and cloud forest, with the latter composed of abrupt transitions throughout the SMS (Rovito 2017). The SMS is characterized by abrupt changes in elevation in short distances, generating different microclimates throughout its distribution, which has been associated with the diversification of amphibians (Duellman 2001; Campbell *et al*. 2009; Rovito *et al*. 2013).

The treefrogs of the genus *Charadrahyla* Faivovich, Haddad, Garcia, Frost, Campbell & Wheeler 2005 are restricted to Mexico and predominantly inhabit cloud forest in the Atlantic and Pacific versants. This genus is diagnosed by molecular divergences between species without morphological synapomorphies and is composed of nine species (Faivovich *et al*. 2005; Faivovich *et al*. 2018). Five species are found in the Pacific versant. In Guerrero, *C. tecuani* (Campbell, Blancas-Hernandez & Smith 2009) and *C. trux* (Adler & Dennis 1972) are both restricted to their type localities and surrounding areas (Santos-Barrera & Canseco Márquez 2004a; Duellman 2001; Grünwald *et al*. 2016). In the SMS of Oaxaca, *C. altipotens* (Duellman 1968) occurs in the vicinities of San Gabriel Mixtepec, Santa Maria Jalatengo, and San Agustin Loxicha (Duellman 2001; Santos-Barrera & Canseco-Márquez 2004b; Barrio-Amoros et al. 2016; DeSantis et al. 2016). *Charadrahyla juanitae* and *C. pinorum* show a disjunct distribution, with localities recorded in both Guerrero and Oaxaca (Duellman 2001; Santos-Barrera & Canseco-Márquez 2004c; Santos-Barrera & Canseco-Márquez 2004d) (Fig. 1).

During a recent survey in the SMS focused on obtaining ecological and natural history data of the herpetofauna, we discovered specimens of an undescribed species belonging to the genus *Charadrahyla*. This treefrog was recorded in one stream in the cloud forest of the Mixteca region in the SMS in Oaxaca, close to the Guerrero border. The presence of hypertrophied (defined as enlargement of the web; Adler & Dennis 1972) webbings between toes I and II in adult males (as in *C. trux*: Adler & Dennis 1972 and *C. tecuani*: Campbell *et al*. 2009), similarities in the color pattern, ossified quadratojugals in contact with the maxillaries and other morphological characters strongly suggests that this new form belongs to the genus *Charadrahyla*. In addition, the combined presence of axillary membranes, hypertrophied webbings, large body size and nuptial excrescences, among other morphological traits, differentiate the new species from its congeners.

Material and methods

Field surveys and collection of specimens were carried out in January 2018 in a stream surrounded by cloud forest in San Isidro Paz y Progreso, in Oaxaca. The specimens were collected during night sampling. We followed Adler & Dennis (1972) and Duellman (2001) to define all measurements and terminology. Digital calipers were used to take all morphological measurements to the nearest 0.01 mm (Mitutoyo CD-15DC; Mitutoyo Corp., Tokyo, Japan). Sex of specimens was determined by presence or absence of nuptial excrescences. We follow the webbing formulae of Myers & Duellman (1982) as modified by Savage & Heyer (1997). Format of the description follows Adler & Dennis (1972), Campbell *et al.* (2009), and the comparisions with other species follow Orrico *et al.* (2018). Our proxy of body size was snout–vent length and is abbreviated SVL throughout. We determined the presence of quadratojugals in contact with the maxillaries by radiographs (Adler & Dennis 1972). We define the nuptial excrescences based on Luna, McDiarmid & Faivovich (2018) with the use of the images of nuptial pad in

life. Description of coloration was taken from field notes and photographs of live specimens. The type series was deposited in the Coleccion Nacional de Anfibios y Reptiles (CNAR) of the Instituto de Biologia, Universidad Nacional Autonoma de Mexico. Comparative material is given in Appendix 1.

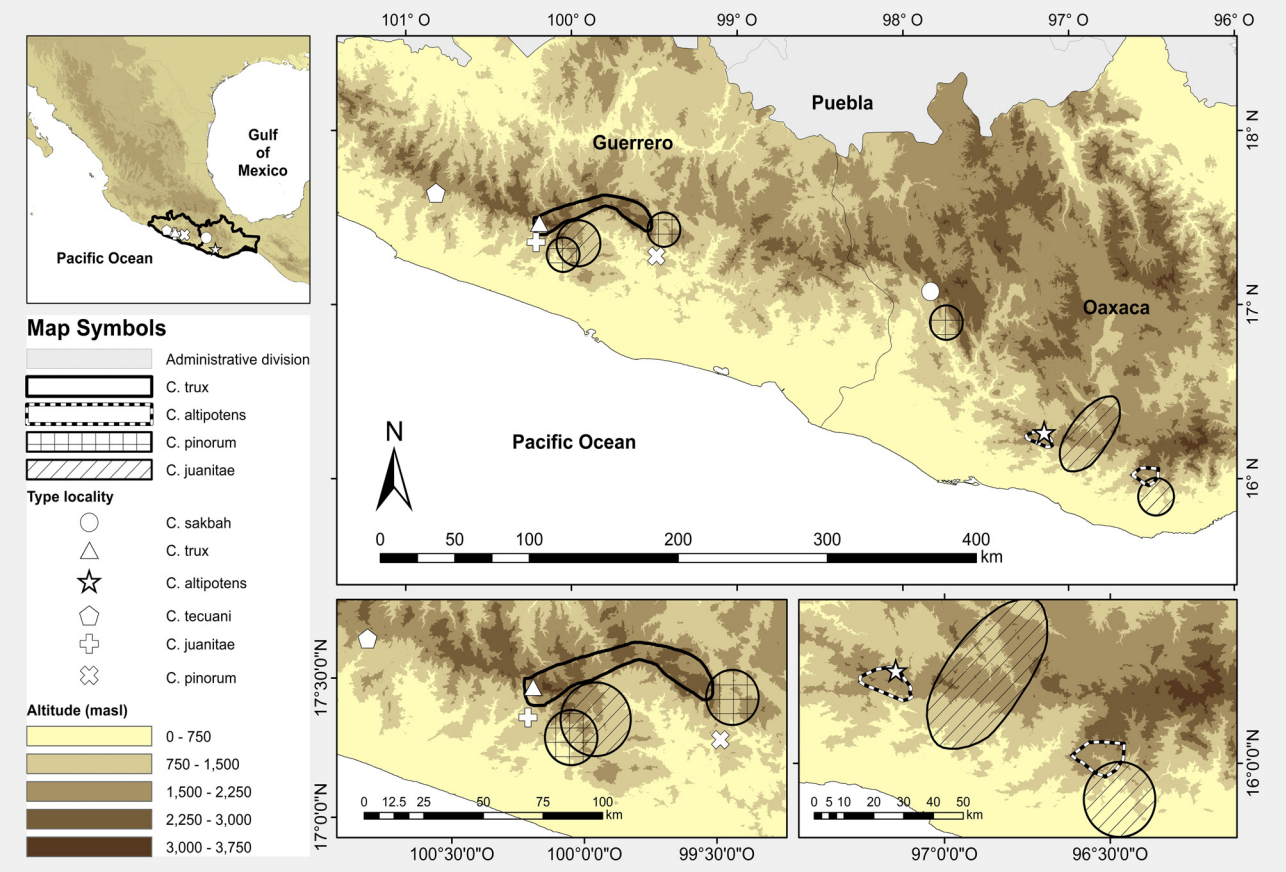

FIGURE 1. Map of southern Mexico showing the type locality of *Charadrahyla sakbah*, and the other species of *Charadrahyla* in the Pacific versant of Guerrero and Oaxaca. The distribution polygons were estimated based on literature records cited in the main text. The borders in the states are the administrative divisions.

Description of new species

***Charadrahyla sakbah* sp. nov.**
Jiménez-Arcos, Calzada-Arciniega, Alfaro-Juantorena, Blair & Parra-Olea
Mixteca Cloud-forest Treefrog, Rana arborícola de la Mixteca

Holotype. (Fig. 2A in life; Fig. 4A, B in preservative). IBH 30989. Adult male. Río Chite ku'e (Río de las Mil Cascadas), San Isidro Paz y Progreso, Santa Maria Yucuhiti, Oaxaca, Mexico. 1390 mts. 17.074902° N, 97.834758° W, 26 January 2018. Collected by Víctor H. Jiménez Arcos and Liz A. Alfaro Juantorena.

Paratypes. IBH 30990 (Fig. 2B), IBH 30991. Adult males. IBH 30992, IBH 30993, IBH 30994. Adult females (Fig 2 C, D, E). All bearing identical locality data as the holotype. 26 January 2018. Collected by Víctor H. Jiménez-Arcos and Rafael Alejandro Calzada Arciniega.

Diagnosis. A large member of the genus *Charadrahyla* with females showing larger SVL (mean 84.04 mm; range 81.15–85.75 mm) than males (70.07 mm; 67.91–73.21 mm). *Charadrahyla sakbah* differs for all other species of the genus by the presence of the following character combination: (1) axillary membrane present in male and female adults (Fig. 3A, B), (2) hypertrophied webbings between toes I and II in adult males (Fig. 3C, D), (3) one conical tubercle on either side of the vent in females and males (Fig. 2F), (4) nuptial excrescences in adult males (Fig. 3E), (5) vocal slits absent, and (6) females with snout dorsal profile rounded and males acuminate.

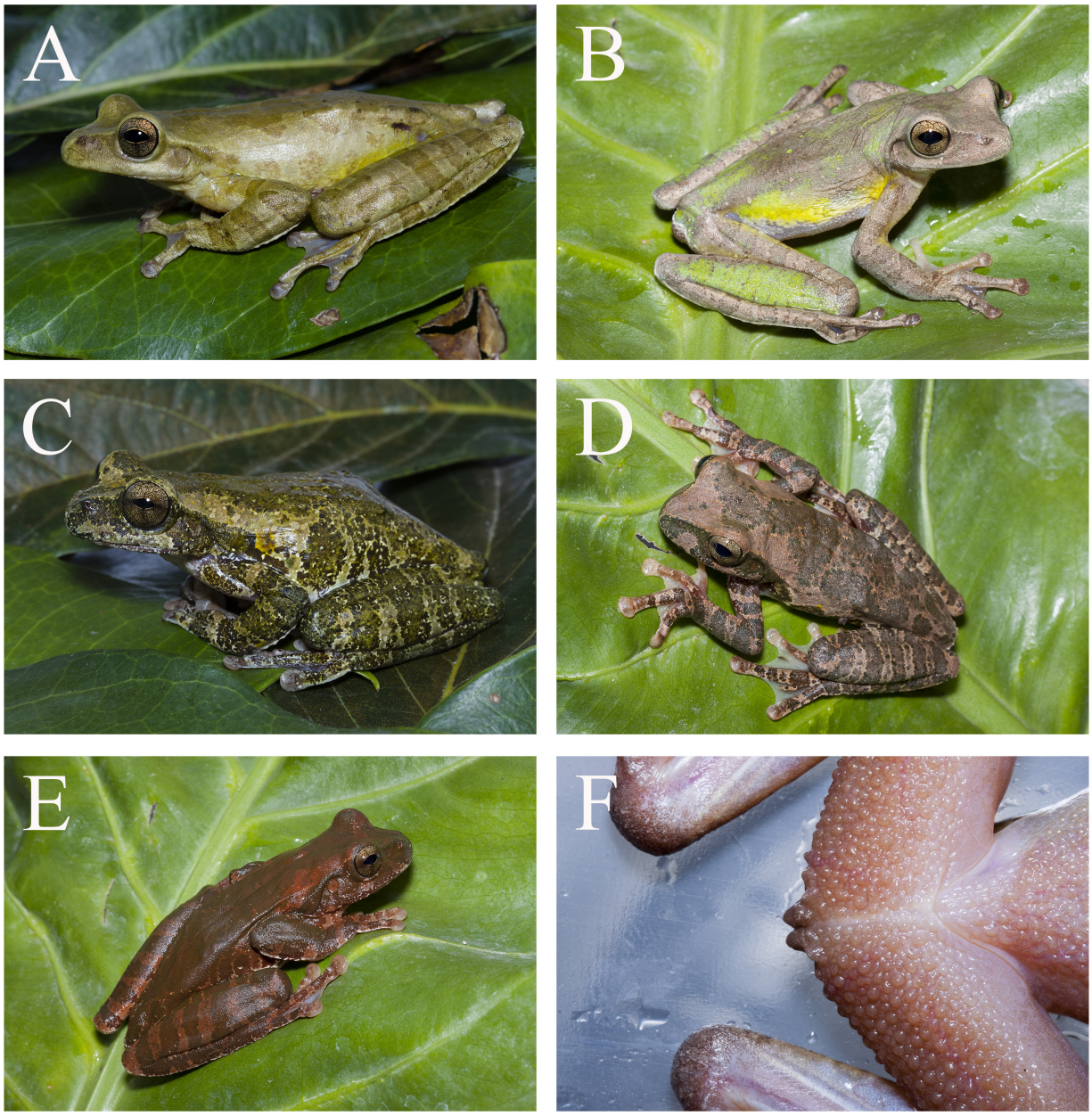

FIGURE 2. Specimens in life of *C haradrahyla sakbah*. (A) male holotype (IBH 30989). (B) male paratype (IBH 30990). (C) Female paratype (IBH 30992). (D) Female paratype (IBH 30993). (E) Female paratype (IBH 30994). (F) Enlarged vent tubercles in ventral view of *C. sakbah* of male holotype (IBH 30989) in life.

Comparison with other species. Character states of *Charadrahyla sakbah* in parentheses. Specimens of *C. taeniopus* (Günther 1901), *C. chaneque* (Duellman 1961), *C. nephila* (Mendelson & Campbell 1999) and *C. esperancensis* (Canseco-Márquez, Ramírez-González & González-Bernal 2017) lack axillary membrane (present), lack conical tubercles in both sides of the vent (present) and have normal webbings between toes I and II in adult males (hypertrophied). Moreover, these species are distributed in the Atlantic versant. *Charadrahyla taeniopus* has been recorded in localities in the states of Hidalgo, Veracruz, and Puebla (Duellman 2001). *Charadrahyla chaneque* is restricted to the east of the Isthmus of Tehuantepec in Oaxaca and Chiapas (Duellman 2001). *Charadrahyla nephila* is recorded in the Sierra de Juarez and Sierra Mixe (Mendelson & Campbell 1999), whereas *C. esperancensis* is restricted to Sierra de Juarez (Canseco-Márquez *et al.* 2017), both mountain systems located at northern Oaxaca.

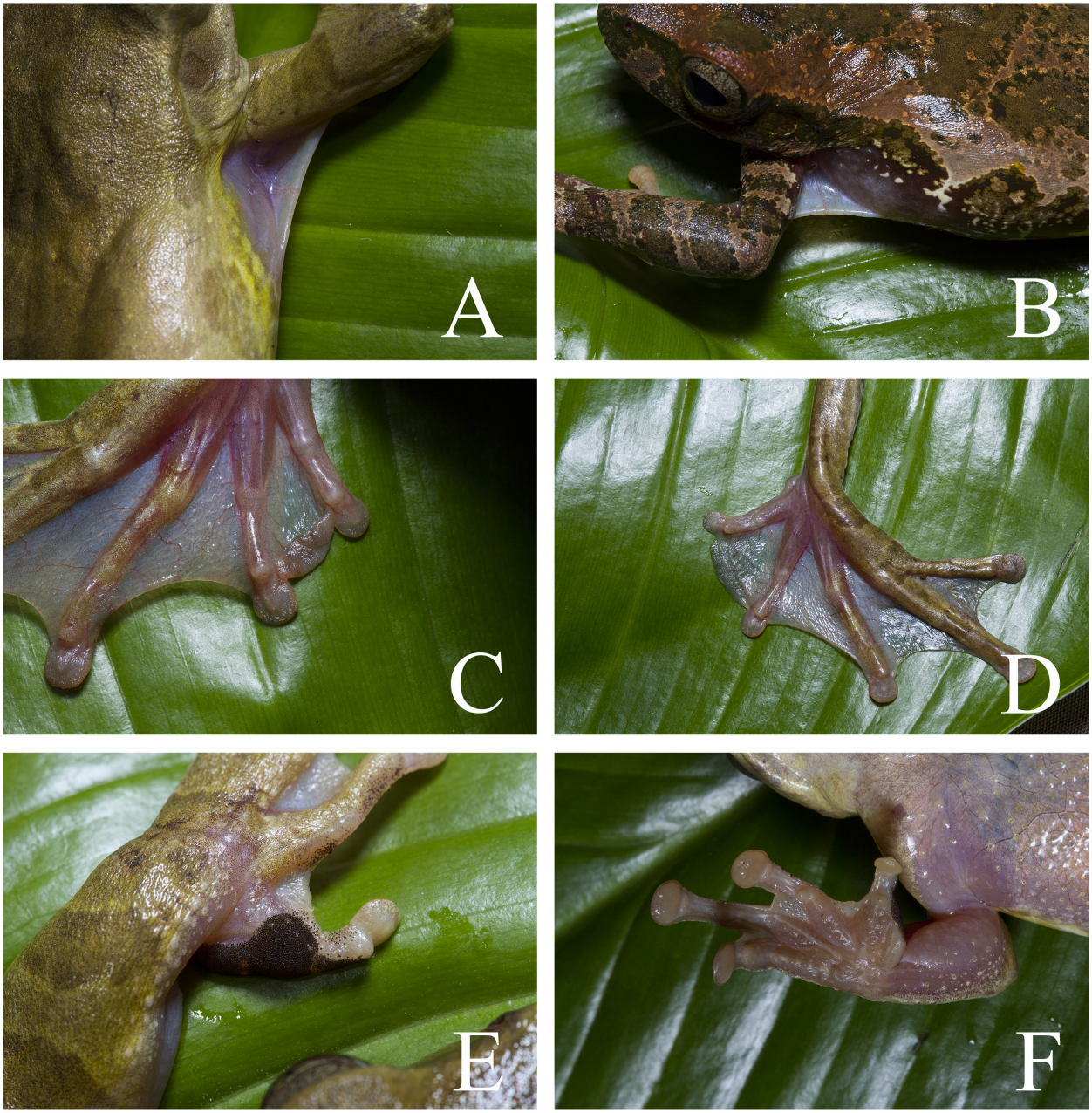

FIGURE 3. Morphological characters of *Charadrahyla sakbah*. (A) Axillary membrane of male holotype (IBH 30989). (B) Axillary membrane of female paratype (IBH 30992). (C) Retracted and (D) extended hypertrophied webbing in male holotype (IBH 30989). (E) Nuptial excrescences in dorsal view and (F) view of the palm of the hand without nuptial excrescences in Finger I in male holotype (IBH 30989).

The only adult female recorded in the literature of *C. pinorum* has a SVL of 34.6 mm and adult males range from 28.5 to 33.1 mm (81.15–85.75 and 67.91–73.21 mm females and males respectively), webbings between toes I and II normal (hypertrophied), vocal slits present (absent), male snout shape in dorsal profile rounded (acuminate), and tympanum not evident (visible). The adult females of *C. juanitae* have a SVL range from 37.6 to 39.8 and adult males from 27.7 to 35.8 mm (81.15–85.75 and 67.91–73.21 mm females and males respectively), webbings between toes I and II normal (hypertrophied), nuptial excrescences underdeveloped (present in finger I and isolated patches in finger II), vocal slits present (absent), male snout shape in dorsal profile rounded (acuminate), and tympanum not evident (visible). Specimens of *C. altipotens* present normal webbings between

toes I and II (hypertrophied), absent nuptial excrescences (present), yellow belly coloration in males (white to pale brown), and adult male dorsal coloration without blotches (darker blotches). Specimens of *C. trux* lack axillary membrane (present), conical tubercles on either side of vent absent (two conical tubercles present), vocal slits present (absent), and quadratojugals not articulating with the maxillaries (articulated) in five of nine specimens (see Adler & Dennis 1972). *Charadrahyla tecuani* adult males have SVL range from 52.5 to 57.8 mm (67.91–73.21 mm adult male), axillary membrane absent (present), vocal slits present (absent), and yellow belly coloration in males (white to pale brown). Table 1 summarizes the comparison of the main diagnostic characters among *Charadrahyla* species.

Description of holotype. Head wider than the body; body shape slender towards the cloaca (Fig. 4A, B), SVL 73.21 mm, tibia length 39.98, foot length 33.61, head length 22.35, head width 21.66, diameter of tympanum 2.85, diameter of eye 6.85, interorbital distance 7.22, eye–tympanum distance 3.31. head slightly longer than wide; lateral profile rounded with snout sloping downward posterior to the nostril; snout shape in dorsal profile acuminate; canthus rostralis distinct and angular; loreal region concave; slightly protuberant nostril oval, which are directed posterolaterally; internarial region concave; vocal slits absent. Top of the head flat; interorbital region 33.33% of head width; eye diameter 31.63% of head width. Supratympanic fold distinct, thick, extending posteroventrally from posterior margin of orbit until anterior insertion of forearm; tympanum distinct, round; tympanic annulus distinguishable, obscured by supratympanic fold dorsally; width of tympanum 44.82% diameter of eye; width of tympanum 92.75% eye–tympanum distance.

Axillary membranes present extending slightly beyond the first third of the forearm (more visible in life); thoracic fold absent; dermal fold on wrist present. Fingers long and slender, with slight lateral fringes, bearing large rounded terminal discs, less developed on the Finger I; relative finger lengths: I < II < IV < III; discs on Fingers II, III, IV of similar size (Fig. 4B), slightly wider than the tympanum; disc on Finger I smaller, width 62.54% width of tympanum. Subarticular tubercles large, diameter about two-third width of terminal disc on same finger, rounded, none bifid; supernumerary tubercules smaller than subarticular tubercules, rounded and distinguishable.

Hand webbing formula: **I 2-2½ II 1¼-2 III 2-1 IV** (Fig. 4C). Tarsal fold absent; tibia length 54.61% SVL; foot length 45.91% SVL. Inner metatarsal tubercle distinct, large, ovoid, 2.1 times larger than subarticular tubercules; outer metatarsal small but distinct; subarticular tubercules distinct, elongated, elevated, diameter about one-half width of terminal disc on the same toe; supernumerary tubercles small, circular, arranged in row along axis of proximal portions of phalanges. Nuptial excrescences present, dark-colored with cone-shaped papillae (see Luna *et al.* 2018) (Fig. 3E) Toes long and slender, bearing rounded: I < II < V < III < IV; terminal discs smaller than discs on fingers. Foot webbing formula: **I ¼-½ II 1-2 III 1-2½ IV 2-1 V** (Fig. 4D). Webbings between toes I and II hypertrophied; in life the edge of the web rolled up dorsally forming a flap (Fig. 3C), which can be extended (Fig. 3D); was extended for preservation; larger and with irregular edges than the other webbings (Fig. 4D). Cloacal opening directed posteroventrally at mid-level of thighs; conical tubercle on either side of vent, partially covered by distinctive vent sheath. Skin on dorsal surfaces smooth; skin on ventral surfaces distinctly granular; skin on flanks between forelimbs and hind limbs smooth.

Tongue cordiform, and slightly free in the back and less anteriorly. Vocal slits absent. Vomerine odontoids 6–5 on each side, left-right respectively, situated on transverse dentigerous process at anterior level of choanae, separated medially by a length slightly smaller than odontoid process; choanae subtriangular, widely separated. The quadratojugals ossified and in contact with the maxillaries (determined by radiographs; Adler & Dennis 1972)

Color. In life, dorsum of body and head, including lateral surfaces of head, are dark yellowish with golden tones (Fig. 2A). A brown stripe begins almost near the nostrils, continues to the middle of the eye and surrounding it below, continuing through supratympanic fold. Dorsum with irregular dark brown blotch, extending up to two-thirds of the back; the last third with brown spots. Dorsal surfaces of forearm dark yellowish, with distinct brown transverse bars, four in forearms; thighs yellow through the internal area towards the body up to the middle zone; the middle zone of the thighs, towards the tibia, greenish with transverse bars dark brown; discs on fingers III and IV darker that fingers. Flanks of the body yellow with three brown spots on each side. Venter of throat pale cream. Chest pale cream with smooth skin. Belly white in the middle; granular skin towards the area of the hindlimbs which are pale pink to yellowish; palpebral membrane clear on three-quarters and gray in the last quarter.

In preservative, dorsum of body and head, including lateral surfaces of head, are pale gray. A dark gray mask in the lateral surfaces of head that begins almost at the tip of the snout and continues until anterior insertion of forearm. Dorsum with irregular dark gray blotch, extending up to two-thirds of the back; the last third of the back

with smaller spots. Dorsal surfaces of limbs pale gray with distinct dark gray transverse bars, four on forearm, three and five (left and right) on thigh, and six on tibia (both sides); discs of fingers III and IV darker than fingers, fingers and disc I and II whitish; flanks whitish with three irregular dark gray spots in each side (Fig. 4A, B). Venter of throat whitish. Chest white with smooth skin. Belly light brown, granular. Undersurface of thighs white, granular area light brown; palpebral membrane clear on first three-quarters and gray in the last quarter.

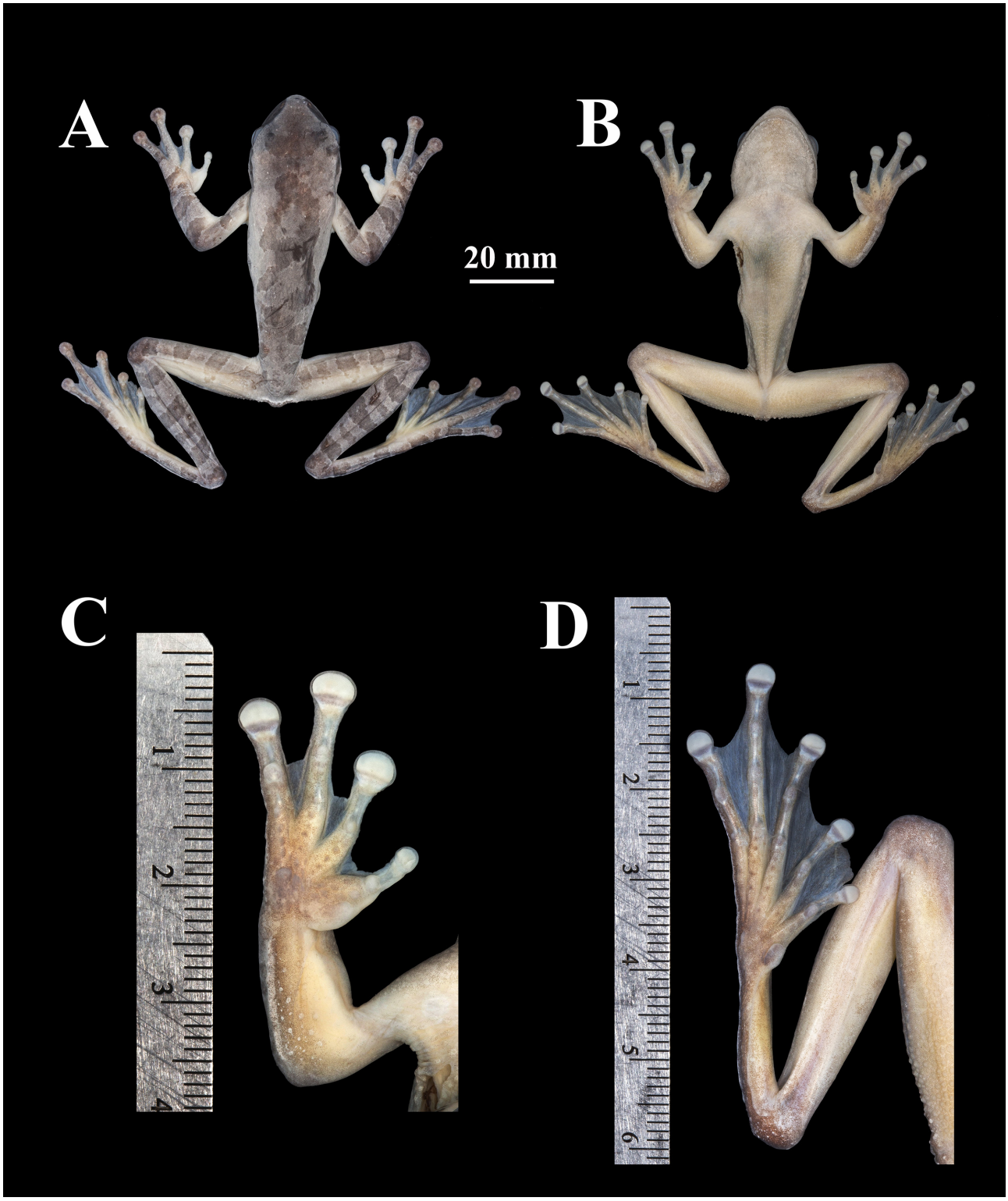

FIGURE 4. Dorsal (A) and ventral view (B) of the preserved holotype of *Charadrahyla sakbah*. (C) Ventral aspect of hand and (D) foot of male holotype (IBH 30989).

TABLE 1. Comparison of ten morphological characters used in the diagnosis of species in the genus *Charadrahyla*. Data were taken from Adler and Dennis (1972), Duellman (1970, 2001), Mendelson & Campbell (1999), Campbell *et al.* (2009), Canseco-Márquez *et al*. (2017) and specimens examined.

	C. sakbah	***C. taeniopus***	***C. pinorum***	***C. chaneque***	***C. altipotens***	***C. trux***	***C. juanitae***	***C. nephila***	***C. tecuani***	***C. esperancensis***
1. Maximum adult SVL (mm)	85.75 ♀ 73.21 ♂	70.0 ♀ 65.9 ♂	34.6 ♀ 33.1 ♂	79.3 ♀ 60.7 ♂	78.8 ♀ 80.6 ♂	– ♀ 81.0 ♂	39.8 ♀ 35.8 ♂	80.7 ♀ 70.9 ♂	– ♀ 57.8 ♂	– ♀ 48.9 ♂
2. Axillary membranes	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Absent	Absent
3. Webbing foot males	Hypertrophied	Normal	Normal	Normal	Normal	Hypertrophied	Normal	Normal	Hypertrophied	Normal
4. Conical tubercles in vent	Present	Absent	Present	Absent	Absent	Absent	Present[1]	Absent	Present	Absent
5. Nuptial excrescences	Present	Present	Absent	Present	Absent	Present	Present	Present	Present	Present
6. Vocal slits	Absent	Present	Present	Absent	Absent	Present	Present	Present	Present	Absent
7. Quadratojugal in contact with maxillary	Yes	Yes	–	Yes	Yes	Variable[2]	–	Yes	Yes	–
8. Male snout shape in dorsal view	Acuminate	Acuminate	Rounded	Rounded	Acuminate	Rounded	Rounded	Rounded	Acuminate	Pointed
9. Testes size	Enlarged	Enlarged	–	Normal	Enlarged	Enlarged	–	Normal	Enlarged	–
10. Belly coloration	White-pale brown	Brownish-black	Creamy white	Creamy brown	Yellow	Creamy brown	Creamy white	Purplish tan	Yellow	White

[1]Duellman (2001) describes slightly larger pigmented tubercles present immediately around the cloacal opening.
[2]According to Adler & Dennis (1972), four of nine individuals is articulated in one or both sides with the maxillaries.

Variation. All the males show a lateral profile rounded with snout sloping downward posterior to the nostril and snout dorsal profile acuminate; in contrast females are bluntly rounded, in both lateral and dorsal profiles. The axillary membrane is more noticeable in life (Fig. 3A, B) and in the females, possibly due to their larger body size. The three males (holotype and two paratypes) show hypertrophied webbing. The nuptial excrescences are almost indistinguishable in the males, perhaps by the preservation process, but brown to black in life (Fig. 3E). In the three males of the type series the nuptial excrescences correspond to dark-colored nuptial pads with cone-shaped papillae. The testes of two males (paratypes: IBH 30990-91) were ovoid, white and not visibly granular (mean 8.48 mm; range 8.12–8.62 mm; 12.49; 12.32–12.66% of SVL). The females and males show a conical tubercle on either side of vent like the holotype (Fig. 2F). In four specimens examined (IBH 30989, IBH 30991, IBH 30992 and IBH 30993) the quadratojugals are present, ossified and in contact with the maxilla. The variation in the proportions for females and males are given in Table 2.

TABLE 2. Mean and range in parenthesis of morphological proportions recorded in *Charadrahyla sakbah* type series. HW: head width and SVL: snout-vent length.

Morphological proportions	Females	Males
Interorbital / HW	30.15 (29.04–32.35)	33.68 (33.22–34.48)
Diameter of eye / HW	33.19 (30.19–37.26)	32.18 (31.63–32.91)
Diameter of tympanum/Diameter of eye	34.16 (31.47–36.33)	40.21 (35.54–44.82)
Diameter of tympanum/Distance eye-tympanum	60.92 (60.34–61.71)	75.62 (67.54–86.11)
Width of Disc Finger I/Diameter of tympanum	88.51 (81.12–98.94)	66.10 (64.50–67.37)
Tibia length/SVL	52.19 (51.56–53.23)	53.76 (52.74–54.61)
Foot length/SVL	43.42 (41.92–44.95)	46.17 (45.82–46.77)

Considerable color variations are present mainly in females. One female paratype (IBH 30992) shows a dorsal ground color yellow to greenish, with large irregular dark green blotches on the dorsum (Fig. 2C). A second female paratype (IBH 30993) shows a dark cream to brownish dorsal ground color. Irregular blotches are also present, with greenish-brown tonalities (Fig. 2D). The last female in the type series (IBH 30994) exhibits a dorsal ground color brownish-orange, and blotches with a chocolate color (Fig. 2E). The three females show transverse bars in the limbs of a similar color to the dorsal blotches of each (Fig. 2 C, D and E). A similar pattern was observed in one female not collected—the dorsal ground color was green with blotches and transverse bars a darker green (Fig. 5A). All the females observed show lateral pattern of enlarged spots dark brown to black, like the female shown in Fig. 5A. The throats in all female paratypes show irregular blotches dark brown to black. For males, the blotches are less conspicuous. One male (IBH 30990) shows a similar dorsal ground color in life as the holotype, but differs in that coloration is gray, blotches and transverse bars in limbs are darker gray, tibias and lower part of the back green with more intense yellow in the flanks (Fig. 2B). The other paratype male (IBH 30991; not showed) presented a coloration almost identical to holotype. The three males show throats white in life and cream to light brown in preservative.

Etymology. The specific epithet is taken from the Mixteco language word “sa’bah” which mean “frog”. This is recognition to the San Isidro Paz y Progreso community for their conservation efforts towards their natural and cultural resources.

Distribution and natural history. *Charadrahyla sakbah* is only known from one locality in San Isidro Paz y Progreso, on the river Chite ku'e at 1390 m in elevation. This river is surrounded by cloud forest, presents several rocky outcrops, with steep slopes that generate numerous waterfalls. In some points the river flow extends to more than 10 m wide (Fig 5B,C). The mean temperature in the area is 20°C and the rainfall annually is 1893.3 mm (SMN 2018). The first specimen was found at night (00.10 hrs CST) on a rock wall about 1.8 m high and less than a 1 m from a waterfall. The air temperature at the time of discovery was 16.9°C with a relative humidity of 70%. Of the 12 observed individuals, 10 were found on a rocky-wall similar to the first specimen, one inside of a pool by the riverside, and one more in vegetation 2 m high from the substrate. The mean air temperature, considering all encounters, was 16.4°C (15.3-17.6) with 75% (70-80%) relative humidity. We recorded two other sympatric frogs, *Ptychohyla leonhardschultzei* (categorized as endangered by IUCN; Santos-Barrera *et al.* 2006) and *Lithobates*

sierramadrensis, as well as the salamander *Isthmura maxima* (categorized as endangered by IUCN; IUCN SSC Amphibian Specialist Group 2016).

During collecting, females and males made low intensity "beeps", similar to the warning sounds of other treefrogs (e.g. *Agalychnis dacnicolor*; Duellman 2001). We observed that the color and tonality varied substantially within the same individual, perhaps due to the temperature or stress of the collection. Moreover, *C. sakbah* shows a marked sexual dimorphism in body size, snout shape, coloration, and hypertrophied webbings. For the other two species with hypertrophied webbings (*C. trux* and *C. tecuani*) the adult females are unknown. Therefore, *Charadrahyla sakbah* is the first species of the genus where the dimorphism in this trait is confirmed.

Considering the limited knowledge about reproductive biology in frogs of the genus *Charadrahyla*, we made a dissection of one of the female paratypes (IBH 30992) in order to determine the oocyte number and pigmentation. The oocytes number estimated was 750 in both parts of the oviduct. The pigmentation was yellow and we observed different developmental stages, but no mature oocyte. We found the size of the testes in *C. sakbah* (ranging 12.32–12.66% of SVL) to be smaller than reported in *C. taeniopus* (without measurements but see Fig. 5 in Duellman 1965), *C altipotens* (average of five males 20.65% of SVL; Duellman 1968), *C. trux* (average of two males 20.49% of SVL; Adler & Dennis 1972;) and *C tecuani* (23.2–24.1% of SVL; Campbell *et al*. 2009).

Discussion

The *Hyla taeniopus* group (later *Charadrahyla* genus; Faivovich *et al*. 2005) was originally defined by Duellman (1965) on specimens of *C. taeniopus* and *C. chaneque*. With the subsequent description of more species integrating the group, Duellman (1970; 2001) defined this group as large treefrogs (comparatively with other hylid genera), usually having distinct bands on the limbs, blotched dorsal pattern (except in adult males of *C. altipotens*), palpebral membranes clear, tarsal fold, and quadratojugals articulating with the maxillary. The tadpoles have two or three upper rows of teeth, three or four lower rows of teeth, lips bordered by papillae, body depressed, and tail large relative to body (Duellman 1965; 1970; 2001). The inclusion of *C. pinorum* and *C. juanitae* (Faivovich *et al*. 2018) increases the range of body size, adds two more species with axillary membranes, conical tubercles on vent, and tympanum not visible (visible in the other eight species including *C. sakbah*). However, the state of quadratojugals is unknown in these two species. While tarsal fold, palpebral membranes clear and quadratojugals articulating with the maxillary are potentially present in all *Charadrahyla* species they are also recorded in other hylid genera (e.g. *Smilisca*, *Triprion*; Duellman 2001). Perhaps the tadpoles could show some shared, derived characters among the *Charadrahyla* species. However, tadpole morphologies are unknown for *C. chaneque*, *C. tecuani*, *C. esperancensis* and the species described herein. The sampling of *Charadrahyla* species remains incomplete, and only molecular data are available for three (*C. taeniopus*, *C. nephila*, and *C. juanitae*; Faivovich *et al*. 2018) of the ten species (considering *C. sakbah*). In addition to this limited sampling, the complexity of the character states makes it difficult to understand the evolutionary relationships in the *Charadrahyla* genus. Detailed taxonomic studies (including tadpoles), greater sampling effort of the remaining species, and other tests (e.g. development patches) are necessary to propose possible synapomorphies that define the genus.

Considering the limitation of detailed taxonomic work, we can only propose a tentative internal relationship. *Charadrahyla sakbah* and *C. trux* are overall morphologically more similar to each other than with the other eight species (Table 1). It is likely these two species could be close relatives on the basis of shared characters like large body size in males (adult females are unknown for *C. trux*), hypertrophied webbings, nuptial excrescences, quadratojugals in contact with the maxillaries (although variable in *C. trux*), snout dorsal profile acuminate, and similarities in coloration pattern. Campbell *et al*. (2009) reported that *C. trux* lacks quadratojugals in contact with maxillaries, but Adler & Dennis (1972) describe that four of nine individuals present quadratojugals in contact with maxillaries on one or both sides of head. The other species that shares more similarities with *C. sakbah* is *C. tecuani*, particularly coloration pattern, the two conical tubercles on vent and the hypertrophied webbing. Specifically, the hypertrophied webbings are a unique character to these three species among the all other Middle American hylids (Duellman 2001). It is likely that the three hypertrophied webbings species form a well-defined group within the *Charadrahyla* genus. However the precise divergences among these three and the other seven species in the genus remain to be tested.

FIGURE 5. (A) A female (not collected) of *C. sakbah* in the riverside. (B) Panoramic view of the Chite ku'e river. (C) Typical pool and waterfall where *C. sakbah* individuals are usually found.

If these relationships are confirmed in subsequent phylogenetic analyses, perhaps vicariant events could be associated with the diversification of hypertrophied webbing species. The western portion of SMS in Guerrero is delimited in the south by the dry forest of the Pacific lowlands, west and north by the Balsas Basin and to the east by the low dry-xeric pass between north Chilpancingo and Tierra Colorada (Adler 1996; Campbell *et al*. 2009). The Chilpancingo-Tierra Colorada pass isolates the western portion of the SMS of Guerrero from the eastern part of SMS highlands of Guerrero and Oaxaca. The Guerrero SMS portion houses 12 endemic species of salamanders in three genera, as well as other endemic frogs, lizards and snakes species (Palacios-Aguilar & Flores Villela 2018), and *C. trux* and *C. tecuani* are also located in this area. It is likely that *C. sakbah*, to be distributed east of the Chilpancingo-Tierra Colorada pass, could has evolved in isolation of its close relatives, *C. trux* and *C. tecuani*, distributed in the western portion of the SMS in Guerrero. However, additional studies incorporating molecular data are needed to explicitly test alternative divergence hypotheses.

The highest species richness of the genus *Charadrahyla* occurs in the cloud forests of SMS of Guerrero and Oaxaca with six of the ten species present. The high species richness could be a product of the complex topography and geological history of the SMS (Morrone 2017). Overall, the large number of mountains throughout the SMS results in abrupt changes in climatic conditions among the several low-altitude valleys and higher-altitude peaks (Adler 1996; Koleff & Soberon 2008). The climatic variation can shape the evolution of different physiological tolerances especially in ectotherms, and possibly favoring local adaptation processes (Janzen 1967). The mountains and valleys can also act as effective barriers to dispersal, favoring isolation and diversification. Similar evolutionary processes have been suggested for other hylid genera (Duellman 2001; *Sarcohyla bistincta* group *sensu lato*: Caviedes Solis & Nieto-Montes de Oca 2017; Campbell *et al.* 2018), salamanders (Adler 1996; Rovito *et al.* 2013; Rovito 2017), as well as other animal groups (reptiles: Campbell & Frost 1993; Nieto-Montes de Oca *et al*. 2016; birds: Bertelli *et al*. 2017). This makes the SMS an important conservation area, housing a high number of endemic species and possibly new lineages. In particular, the cloud forest of the SMS in Guerrero and western Oaxaca is one of the least explored biotas in Mexico, due to the scarcity of roads as well as several social conflicts that have limited scientific research.

Conservation status. The cloud forest represents around 0.26% of the earth's surface, and only 2.5% of the tropical forests around the word (Sánchez-Ramos & Dirzo 2014; Ochoa-Ochoa *et al.* 2017). Due to the small area covered, and their fragmented distribution, the cloud forest is the terrestrial ecosystem in greater risk, making it a priority for conservation (Ochoa-Ochoa *et al.* 2017). In Mexico, less than 1% of the territory is occupied by primary vegetation of cloud forest, and approximately 50% of the original surface has been lost (CONABIO 2010). The SMS in Guerrero and Oaxaca is known for having the greatest coverage of this type of vegetation (Ochoa-Ochoa *et al.* 2017). Nevertheless, its distribution is highly fragmented, and the climatic conditions differ from the rest of the Mexican cloud forest (lower atmospheric humidity; Mejía-Domínguez *et al.* 2004). This suggests that the communities in the SMS cloud forest represent unique entities of animals and plants (Ochoa-Ochoa *et al.* 2017).

Charadrahyla sakbah is known from a river in the cloud forest of Oaxaca, very close to the Guerrero border. The area is subject to conservation strategies by the municipality (Santa María Yucuhiti) and local (San Isidro Paz y Progreso) authorities. However, the legal instruments (e.g., Natural Protected Areas) of federal or state governments have not been formally established. In the region, the change of land use associated with agricultural (e.g. coffee plantations), livestock activities, and upstream contamination where *C. sakbah* was recorded, suggest that this species may be threatened. Fortunately, the conservation actions of the community of San Isidro Paz y Progreso, which must be supported legally, provide an opportunity for the prevalence of the species.

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References

Adler, K. (1996) The salamanders of Guerrero, Mexico, with descriptions of five new species of *Pseudoeurycea* (Caudata: Plethodontidae). *Occasional Papers of The Museum of Natural History, University of Kansas*, 177, 1–28.

Adler, K. & Dennis, D.M. (1972) New tree frogs of the genus *Hyla* from the cloud forests of western Guerrero, Mexico. *Occasional Papers of The Museum of Natural History, University of Kansas*, 7, 1–19.

Barrio-Amorós, C.L., García-Vázquez, U.O., Domínguez-Laso, M. & Nieto-Montes de Oca, A. (2016) *Charadrahyla altipotens* (Anura: Hylidae), a Critically Endangered treefrog rediscovered in Oaxaca, Mexico. *Mesoamerican Herpetology*, 3, 787−790.

Bertelli, S., Szumik, C., Goloboff, P.A., Giannini, N.P., Navarro-Sigüenza, A.G., Townsend Peterson, A. & Cracraft, J. (2017) Mexican land birds reveal complexity in fine-scale patterns of endemism. *Journal of Biogeography*, 44, 1836−1846. https://doi.org/10.1111/jbi.12987

Campbell, J.A. & Frost, D.R. (1993) Anguid lizards of the genus *Abronia*: revisionary notes, descriptions of four new species, a phylogenetic analysis, and key. *Bulletin of the American Museum of Natural History*, 216, 1−121.

Campbell, J.A., Blancas-Hernández, J.C. & Smith, E.N. (2009) A New Species of Stream-breeding Treefrog of the Genus *Charadrahyla* (Hylidae) from the Sierra Madre del Sur of Guerrero, Mexico. *Copeia*, 2009 (2), 287–295. https://doi.org/10.1643/CH-08-143

Campbell, J.A., Brodie Jr., E.D., Caviedes-Solis, I.W., Nieto-Montes de Oca, A. Luja, V.H., Flores-Villela, O., García-Vázquez, U.O., Chandra, G.S., Wostl, E. & Smith, E.N. (2018) Systematics of the frogs allocated to *Sarcohyla bistincta* sensu lato (Cope, 1877), with description of a new species from Western Mexico. *Zootaxa*, 4422 (3), 366–384. https://doi.org/10.11646/zootaxa.4422.3.3

Canseco-Márquez, L., Ramírez-González, C.G. & González-Bernal, E. (2017) Discovery of another new species of *Charadrahyla* (Anura, Hylidae) from the cloud forest of northern Oaxaca, México. *Zootaxa*, 4329 (1), 64–72. https://doi.org/10.11646/zootaxa.4329.1.2

Caviedes Solis, I.W. & Nieto-Montes de Oca, A. (2017) A multilocus phylogeny of the genus *Sarcohyla* (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

CONABIO (2010) *El Bosque Mesófilo de Montaña en México: Amenazas y Oportunidades para su Conservacion y Manejo Sostenible*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México D.F., 197 pp.

DeSantis, D.L., Mata-Silva, V., García-Padilla, E., Rocha, A., David, L.W. & Ramírez-Bautista, A. (2016) Additional comments on the geographic distribution and conservation status of the recently rediscovered Voiceless Treefrog, *Charadrahyla altipotens* (Duellman 1968) from Oaxaca, Mexico. *Mesoamerican Herpetology*, 3 (4), 1073–1076.

Duellman, W.E. (1961) Description of a New Species of Tree Frog from México Studies of American Hylid Frogs VI. *Herpetologica*, 17, 1–5.

Duellman, W.E. (1965) Frogs of the *Hyla* taeniopus Group. *Copeia*, 2, 159–168. https://doi.org/10.2307/1440718

Duellman, W.E. (1968) Descriptions of New Hylids Frogs from Mexico and Central America. *University of Kansas Publications, Museum of Natural History*, 17 (13), 559–578. https://doi.org/10.5962/bhl.part.7138

Duellman, W.E. (1970) Hylid frogs of Middle America. *Museum of Natural History, University of Kansas, Monographs*, 1, 1–752.

Duellman, W.E. (2001) *The Hylid Frogs of Middle America*, Society for the Study of Amphibians and Reptiles, Ithaca, New York, 1170 pp.

Faivovich, J., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., 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 of the American Museum of Natural History*, 294 (1), 1–240. https://doi.org/10.1206/0003-0090(2005)294[0001:SROTFF]2.0.CO;2

Faivovich, J., Pereyra, M.O., Luna, M.C., Hertz, A., Blotto, B.L., Vásquez-Almazán, C.R., McCranie, J.R., Sánchez, D.A., Baêta, D., Araujo-Vieira, K., Köhler, G., Kubicki, B., Campbell, J.A., Frost, D.R., Wheeler, W.C. & Haddad, C.F.B. (2018) On the Monophyly and Relationships of Several Genera of Hylini (Anura: Hylidae: Hylinae), with Comments on Recent Taxonomic Changes in Hylids. *South American Journal of Herpetology*, 13, 1–32. https://doi.org/10.2994/SAJH-D-17-00115.1

Grünwald, C.I., Franz-Chávez, H. & García-Vázquez, U.O. (2016) Rediscovery of the Critically Endangered treefrog *Charadrahyla trux* in the Sierra Madre del Sur of Guerrero, Mexico. *Mesoamerican Herpetology Herpetology*, 3 (3), 790–793.

Günther, C.L.G.A. (1901) Reptilia and Batrachia. *In*: Godman, F. & Salvin, O. (Ed.), *Biologia Centrali-Americana, London*, Zoology, 1901, pp. 1–326.

IUCN SSC Amphibian Specialist Group. 2016. *Isthmura maxima. The IUCN Red List of Threatened Species*, 2016, e.T61907A53989368.

Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, 101, 233–249. https://doi.org/10.1086/282487

Johnson, J.D. Larry, D.W., Mata-Silva, V., García-Padilla, E. & Desantis, D.L. (2017) The endemic herpetofauna of Mexico: organisms of global significance in severe peril. *Mesoamerican Herpetology*, 4 (3), 544–621.

Koleff, P. & Soberón, J. (2008) Patrones de diversidad espacial en grupos selectos de especies. *In Capital natural de México. Vol. I. Conocimiento actual de la biodiversidad*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D.F., pp. 323–364.

Luna, M.C., McDiarmid, R.W. & Faivovich, J. (2018) From erotic excrescences to pheromone shots: structure and diversity of nuptial pads in anurans. *Biological Journal of the Linnean Society*, 124, 403–446. https://doi.org/10.1093/biolinnean/bly048

Mejía-Domínguez, N., Meave, J. & Jiménez Ruiz, C.A. (2004) Análisis estructural de un bosque mesófilo de montaña en el extremo oriental de la Siera Madre del Sur (Oaxaca), México. *Boletín de la Sociedad Botánica de México*, 74, 13–29.

Mendelson, J.R. III & Campbell, J.A. (1999) The taxonomic status of populations referred to *Hyla chaneque* in southern Mexico, with the description of a new treefrog from Oaxaca. *Journal of Herpetology*, 33, 80−86. https://doi.org/10.2307/1565545

Morrone, J.J. (2014) Biogeographical regionalisation of the Neotropical region. *Zootaxa*, 3782 (1), 1–110. https://doi.org/10.11646/zootaxa.3782.1.1

Morrone, J.J. (2017) Biogeographic regionalization of the Sierra Madre del Sur province, Mexico. *Revista Mexicana de Biodiversidad*, 88, 710–714. https://doi.org/10.1016/j.rmb.2017.07.012

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, 1–32.

Nieto-Montes de Oca, A., Barley, A.J., Meza-Lázaro, R.N., García-Vázquez, U.O., Zamora-Abrego, J.G., Thomson, R.C. & Leaché, A.D. (2016) Phylogenomics and species delimitation in the knob-scaled lizards of the genus *Xenosaurus* (Squamata: Xenosauridae) using ddRADseq data reveal a substantial underestimation of diversity. *Molecular Phylogenetics and Evolution*, 106, 241–253. https://doi.org/10.1016/j.ympev.2016.09.001

Ochoa-Ochoa, L.M., Mejía-Domínguez, N.R. & Bezaury-Creel, J. (2017) Prioritization for Cloud Forest Conservation in Mexico. *Ecosistemas*, 26 (2), 27–37. https://doi.org/10.7818/ECOS.2017.26-2.04

Orrico, G.D.V., Dias, R.I. & Marciano-Junior, E. (2018) Another new species of *Phyllodytes* (Anura: Hylidae) from the Atlantic Forest of northeastern Brazil. *Zootaxa*, 4407 (1), 101–110. https://doi.org/10.11646/zootaxa.4407.1.6

Palacios-Aguilar, R. & Flores-VIllela, O. (2018) An updated checklist of the herpetofauna from Guerrero, Mexico. *Zootaxa*, 4422 (1), 1–24. https://doi.org/10.11646/zootaxa.4422.1.1

Parra-Olea, G., Flores-Villela, O. & Mendoza-Almeralla, C. (2014) Biodiversidad de Anfibios en México. *Revista Mexicana de Biodiversidad*, 85, 460–466. [S460–S466] https://doi.org/10.7550/rmb.32027

Rovito, S.M., Parra-Olea, G., Hanken, J., Bonett, R.M. & Wake, D.B. (2013) Adaptive radiation in miniature: The minute salamanders of the Mexican highlands (Amphibia: Plethodontidae: *Thorius*). *Biological Journal of the Linnean Society*, 109 (3), 622–643. https://doi.org/10.1111/bij.12083

Rovito, S.M. (2017) The Geography of Speciation in Neotropical Salamanders. *Herpetologica*, 73 (3), 229–241. https://doi.org/10.1655/HERPETOLOGICA-D-16-00077.1

Sánchez-Ramos, G. & Dirzo, R. (2014) El bosque mesófilo de montaña: un ecosistema prioritario amenazado. *In*: Gual-Díaz, M.& Rendón-Correa, A. (Ed.), *Bosques Mesófilos de Montaña de México. Diversidad, Ecología y Manejo*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Ciudad de Mexico, Mexico, pp. 109–140.

Santos-Barrera, G. & Canseco-Márquez, L. (2004a) *Charadrahyla trux*. *The IUCN Red List of Threatened Species*, 2004,

e.T55681A11338879.
Santos-Barrera, G. & Canseco-Márquez, L. (2004b) *Charadrahyla altipotens*. *The IUCN Red List of Threatened Species*, 2004, e.T55384A11288683.
Santos-Barrera, G. & Canseco-Márquez, L. (2004c) *Exerodonta juanitae*. *The IUCN Red List of Threatened Species*, 2004, e.T55523A1.
Santos-Barrera, G. & Canseco-Márquez, L. (2004d) *Exerodonta pinorum*. *The IUCN Red List of Threatened Species*, 2004, e.T55606A1.
Savage, J.M. & Heyer, R.W. (1997) Digital webbing formulae for Anurans: a refinement. *Herpetological Review*, 28 (3), 131.
SMN (2018) Información climatológica, database. Servicio Meteorológico Nacional, Mexico. Available from: http://smn.cna.gob.mx/es/component/content/article?id=42 (accessed 1 June 2018)
Snyder, D.H. (1972) *Hyla juanitae*, a New Treefrog from Southern México, and its Relationship to *H. pinorum*. *Journal of Herpetology*, 6 (1), 5–15.
https://doi.org/10.2307/1563087
Taylor, E.H. (1937) New species of hylid frogs from Mexico with comments on the rare *Hyla bistincta* Cope. *Proceedings of the Biological Society of Washington*, 50, 43–54.

APPENDIX I. Comparative specimens examined.

***Charadrahyla chaneque*: MEXICO: OAXACA:** Chalchijapa (MZFC 18911-12).**VERACRUZ:** Soteapan, cumbre de Santa Marta (IBH 18933).

***Charadrahyla esperancensis*: MEXICO: OAXACA:** holotype Los tres manantiales, La Esperanza (MZFC 28699); paratype dead on road near La Esperanza (MZFC 28693).

***Charadrahyla nephila*: MEXICO: OAXACA**: San Felipe Usila, Arroyo Tepetotutla, arboles pivotantes (IBH 24781, 24808); San Pedro Yolox, Puente San Isidro/San Pedro Yolox (IBH 24782, 30069); 4.2 km S Vista Hermosa on Hwy 175, ca 1.2 km S La Esperanza (MZFC 15974-75); stream crossing Hwy 175, 7.2 km S Vista Hermosa (MZFC 16796, 16822).

***Charadrahyla pinorum*: MEXICO: GUERRERO:** Chilpancingo de los Bravo, Santa Rita (UAGRO 190-193, 207)

***Charadrahyla trux*: MEXICO: GUERRERO:** holotype, 11.4 km (by road) southwest of Puerto del Gallo (KU 137551; reviewed in photographs); paratype: 10.4 km SW of Puerto del Gallo (KU 137550; reviewed in photographs).

***Megastomatohyla pellita*: MEXICO: OAXACA:** 25 km N San Gabriel Mixtepec, San Gabriel Mixtepec (IBH 27027).