Image of a campsite along the headwaters of the Río Warunta in the department of Gracias a Dios, Honduras, which the campers named Warunta Tingni Kiamp. Solitary individuals of the hylid treefrog (genus *Smilisca*) discussed in the following contribution occasionally were encountered at night in the environs of this watercourse, which becomes a major river in its lower courses. The photo was taken on 12 February 2006.

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Morphological and systematic comments on the Caribbean lowland population of *Smilisca baudinii* (Anura: Hylidae: Hylinae) in northeastern Honduras, with the resurrection of *Hyla manisorum* Taylor

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Abstract: I present an external morphological study of the northeastern Honduran lowland broadleaf rainforest (La Mosquitia; Caribbean versant) population of the arboreal hylid frog *Smilisca baudinii*. I compare a series of specimens from northeastern Honduras to those from other areas of the country, as well as to various populations of *S. baudinii* from Mexico to Costa Rica (both Caribbean and Pacific versants). The northeastern Honduran frogs differ from all other populations of *S. baudinii* I examined, except for the eastern Nicaragua and Costa Rican populations, by consistently reaching a larger adult size, the presence of more webbing on the hind limbs, and a longer, narrower, flatter, and barely raised inner metatarsal tubercle. The northeastern Honduran population of *S. baudinii* shows notable similarities to *Hyla manisorum*, currently considered a synonym of *S. baudinii*. Edward H. Taylor described *H. manisorum* in 1954 based on a single adult female from the Caribbean lowlands of eastern Costa Rica. The data I present strongly suggest that *H. manisorum* should be resurrected from the synonymy of *S. baudinii* for the Caribbean lowland population extending from northeastern Honduras to eastern Costa Rica, and also that *S. baudinii* represents a complex of species that requires further study. I hope my conclusions will lead someone to undertake a combined molecular and morphological analysis to test the results presented in this study.

Key Words: External morphology, Mexico and Central America, Honduran Mosquitia

Resumen: Presento un estudio de la morfología externa de la población del bosque lluvioso del noreste de Honduras (La Mosquitia; vertiente del Caribe) de la rana hílida arboricola *Smilisca baudinii*. Comparo una serie de los especímenes del noreste de Honduras con especímenes provenientes de otras poblaciones del país además de otras poblaciones de *S. baudinii* desde México hasta Costa Rica (ambas vertientes del Caribe y del Pacífico). Las ranas hondureñas del noreste difieren de todas las otras poblaciones de *S. baudinii* que examiné, excepto las poblaciones del este de Nicaragua y Costa Rica, por la combinación de alcanzar un tamaño adulto consistentemente grande, tener mayor extensión en sus membranas de las extremidades posteriores, y por tener un tubérculo metatarsiano interno que es más largo, más estrecho, más plano y que es apenas moderadamente elevado. La población de *S. baudinii* del noreste de Honduras muestra notables similitudes con *Hyla manisorum*, actualmente considerada un sinónimo de *S. baudinii*. Edward H. Taylor describió *H. manisorum* en 1954 basado en una sola hembra adulta de las tierras bajas caribeñas del este de Costa Rica. Los datos que presento sugieren fuertemente que el *H. manisorum* debe de ser resucitada de la sinonimia de *S. baudinii* para la población de las tierras bajas del Caribe que se extiende desde el noreste de Honduras hasta el este de Costa Rica, y también que *S. baudinii* representa

un complejo de especies que requiere estudio adicional. Espero que mis conclusiones incentiven a alguien a realizar una combinación de análisis moleculares y morfológicos para poner a prueba los resultados presentados en este estudio.

Palabras Claves: México y Centroamérica, morfología externa, Mosquitia Hondureña

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INTRODUCTION

In September of 1992, I made my first trip into the majestic broadleaf lowland rainforest (Evergreen Broadleaf Forest *sensu* McCranie et al., 2006: map 1) that historically extended from the Mosquitia region of northeastern Honduras southward along the eastern Caribbean lowlands to Costa Rica. That forest was unlike any "lowland rainforest" I was familiar with in areas to the west in Honduras. The broadleaf lowland rainforest in the Mosquitia region of Honduras shows considerable differences from other lowland humid forests in the country (see McCranie, 2017b), and in McCranie (2007), I wrote about some of my impressions and adventures in this region. During the 1992 trip I was surprised by the number of herpetofaunal species I was finding (see McCranie, 1993) that were not known to occur west of the Mosquitia (for summaries of the reptiles, see McCranie, 2011, *In Press*; McCranie and Köhler, 2015; for summaries of the amphibians, see McCranie and Castañeda, 2007; McCranie et al., 2006). Another lasting impression was the larger size and greater leaping abilities of the individuals of *Smilisca baudinii* (A. M. C. Duméril and Bibron, 1841: 564) I encountered. Indeed, the three largest Honduran *S. baudinii* I previously measured (see McCranie and Wilson, 2002) all came from this region. Subsequent fieldwork in the Mosquitia and the consistently large size of the *S. baudinii* I came across led me to question if a different evolutionary species might be involved. I also realized, however, that a substantial amount of work would be necessary to conduct a thorough evaluation of such a wide-ranging species.

Smilisca baudinii currently is considered to occur on both the Atlantic (Caribbean) and Pacific versants from southern Texas, United States, and southern Sonora, Mexico, southward to southern Costa Rica (Duellman, 1970, 2001; McCranie and Wilson, 2002; McCranie and Castañeda, 2007; Fouquette and Dubois, 2014), which is an unusually large geographical distribution for a Western Hemisphere treefrog. Another obstacle for conducting such a study is that six names are considered to be junior synonyms of *S. baudinii* (see Duellman and Trueb, 1966; Duellman, 1970; Fouquette and Dubois, 2014). The imprecise type locality of "Mexique" and the brief diagnostic characters provided in the description of the type specimen of *S. baudinii* (A. M. C. Duméril and Bibron, 1841: 564–565) further contribute to these problems. Of the "diagnostic" characters used in the type description, only the snout–vent length (SVL) can be used to distinguish some populations. Also, no images of the holotype of *S. baudinii* apparently have been published that might assist in assigning that population to a currently known population with locality data. The type locality restrictions of *S. baudinii* to "Mexico, Veracruz, Córdoba" by Smith and Taylor (1950: 347) and to "Mexico; restr. to Mexico City" by Schmidt (1953: 69) are invalid, and thus are not helpful. On a positive note, Guibé (1950) listed the holotype of *S. baudinii* (MNHN 4798) as an adult male with an SVL of 58 mm. Kellogg (1932) provided a brief redescription of that holotype, but indicated the SVL as 54.8 mm; he also noted (p. 160) "a large inner … metatarsal tubercle." I discuss both of these characters below.

In July of 2015, while in lowland broadleaf rainforest in the Mosquitia region of Honduras, I was photographing an adult female *S. baudinii* (Fig. 1) when the frog leaped from an elevated perch (nearly 2 m above the ground) and landed on the ground at a distance > 5 m from that perch. I had never seen any *S. baudinii*, or for that matter any other hylid, make such an extended leap, even though I have encountered numerous populations of *Smilisca* in the field, in addition to populations of all the other hylid groups known to occur in Honduras. This event left me convinced that the population of *S. baudinii* in this region should be examined further and compared with other populations of this taxon. That leaping event also was the final emphasis for me to undertake this study.

The purpose of this contribution, therefore, is to provide information on the external morphology of the population of *S. baudinii* from the Honduran Mosquitia, and to compare these results to those available for other populations of this species from other parts of the country. Additionally, I compared these results with those available in the literature for various populations of *S. baudinii* ranging from Mexico to Costa Rica, and also examined a select group of specimens from this region. I hope this work will spur curiosity among co-workers who might be interested in using molecular techniques, along with equally important external morphological data, to study the phylogenetics of populations of this species. Such a study should be rewarding for all biologists interested in the hylid frogs of the Western Hemisphere.

MATERIALS AND METHODS

I gathered detailed external morphological data from 20 adult specimens (10 males, 10 females) *Smilisca baudinii* from lowland broadleaf rainforest in the Honduran Mosquitia, and included several characters I did not investigate previously and were published in McCranie and Wilson (2002; see McCranie, *In Press* for a discussion on citing authorship in sections of that work, the collection of data [as it applies to this study], and other details). I also reexamined some Honduran specimens from outside the lowland broadleaf rainforest of the Mosquitia, and examined specimens from select populations from other countries ranging from Mexico to Costa Rica (see Appendix 1). I then compared the new data to those for 46 adults of *S. baudinii* (30 males, 16 females) from Honduran localities outside the Mosquitia, which appeared in McCranie and Wilson (2002), and also reexamined some of those specimens for this study (see Appendix 1). I made all measurements to the nearest 0.1 mm with dial calipers, with the aid of a dissecting microscope.

The abbreviations herein are as follows: DW = third finger disc width; EL = eye length; EW = width of upper eyelid; FL = foot length (distance from proximal edge of IMT to tip of longest toe); HL = head length; HLL = combined hind limb length (thigh length, SHL, and ankle to tip of longest toe distance; includes both legs combined into a single value); HW = head width; IMTH = inner metatarsal tubercle height; IMTL = inner metatarsal tubercle length; IMTW = inner metatarsal tubercle width; IOD = interorbital distance at midlength of upper eyelid; SHL = shank length; SL = snout length in distance from anterior edge of orbit to tip of snout; SVL = snout–vent length; and TPL = tympanum length. The literature sources for published data are Duellman and Trueb (1966), Hardy and McDiarmid (1969), Duellman (1970), and McCranie and Wilson (2002). The color names and numeric codes for color in life descriptions are those suggested by Smithe (1975–1981) and Köhler (2012). The museum acronyms follow those suggested by Sabaj (2016). The methods for the modal webbing formulae of the hind limbs are those suggested by Savage and Heyer (1997).

RESULTS

I reexamined the external morphology of 63 of the 106 known specimens of *Smilisca baudinii* from the lowlands of the Mosquitia of northeastern Honduras; in contrast, only two old and relatively poorly preserved specimens from this region were available to William E. Duellman for his pioneering studies. Most of the specimens from the Mosquitia were collected in lowland broadleaf rainforest at an elevation below 200 m (but specimens from one locality in this region are known to occur at elevations up to 540 m), but eight also came from open pine savanna. I used the Holdridge (1967) classification of Lowland Moist Forest (LMF), as discussed in McCranie (2011), which includes such variations as broadleaf closed canopy rainforest and open pine savanna where these *Smilisca* occur in northeastern Honduras. I found no external morphological differences when comparing specimens from either forest type, other than three of the eight from open pine savanna (USNM 573030, 573038, 580134) show a tendency for slightly less webbing than typically seen in specimens from lowland broadleaf rainforest.

The measurements and proportions for 10 adult males (USNM 514472, 514478, 514481–82, 534159, 534161–64, 559247) and 10 adult females (USNM 514468, 514471, 514473, 534166, 559250, 559255–56, 565374, 573811–12) from the Mosquitia region of Honduras I examined for this study are as follows: SVL 60.2–67.0 ($\bar{x}$ =

63.7 ± 2.1) mm in males, 62.9–79.6 ($\bar{x}$ = 68.4 ± 6.3) mm in females; SHL/SVL 47.6–51.9% in males, 50.1–56.0% in females; FL/SVL 38.7–46.9% in males, 43.5–48.9% in females; IMTL/IMTW 1.7–3.4% in both sexes combined (*n* = 23; includes those listed above plus USNM 514469, 559246, 573813); IMTL/IMTH 1.7–3.5% (both sexes combined, *n* = 23); HLL/SVL 314.5–353.2% in males, 336.5–378.3% in females; HL/SVL 30.6–35.0% in males, 31.3–35.6% in females; HW/SVL 31.5–35.7% in males, 33.1–38.1% in females; EW/IOD 80.3–110.6% in males, 66.7–106.9% in females; TPL/EL 66.2–83.1% in males, 64.0–94.0% in females; IOD/EL 68.2–115.4% in males, 65.2–131.3% in females; DW/TPL 33.3–71.1% in males, 40.0–71.9% in females; SL/HL 37.5–43.5% in males, 25.9–42.9% in females; EN/EL 71.1–102.9% in males, 71.3–107.5% in females. The modal hind limb webbing formula for specimens from the Mosquitia population is I 0–1 II 0–1 1/2 III 0–1 IV 3/4–0 V. Late in this project, once specimens had been returned to their museum (USNM), in my images I noticed several specimens in which the body shape of individuals from the Honduran Mosquitia appeared to be elongated, with the distance between the forelimb insertion point and the tip of the snout greater than that of specimens from other areas (compare Figs. 1 and 2 with Fig. 3). Future workers conducting morphological studies on *S. baudinii* might consider taking these measurements, because aside from this study, the work of William E. Duellman, and my previous work, such data rarely have been collected.

The color in life of an adult female (USNM 514473; Fig. 2) was as follows: dorsal surfaces Lime Green (159) with a pale brown interorbital bar, blotches on back, and crossbars on limbs; postorbital stripe dark brown; upper labial region Lime Green with pale brown vertical bars; flank mottled with white and pale brown; posterior surface of thigh pale brown with yellow flecking; ventral surfaces yellowish white with brown flecking on chin, throat, chest, and thigh; and iris pale brown with darker brown reticulations. The color in life of another adult female (USNM 514471; see plate 15A *In* McCranie and Wilson, 2002) was as follows: dorsal surfaces Clay Color (26) with a Raw Umber (23) interorbital bar, blotches on back, and crossbars on limbs; postorbital stripe Raw Umber; upper labium dirty white with Raw Umber vertical bars; flank mottled with Clay Color and dirty white; posterior surface of thigh pale Clay Color with yellow flecking; ventral surfaces yellowish white with dark brown flecking, and with small spots throughout. The color in life of a subadult female (USNM 534158) was as follows: dorsal surface of body Grayish-Olive (43) with a Brownish Olive (29) central marking; dorsal surface of head copper with Brownish Olive interorbital bar; dorsal surfaces of limbs pale brown with brown crossbars; flank pale yellow with brown mottling; posterior surface of thigh brown with scattered pale yellow spots; and ventral surface of body cream with scattered brown punctations on chest.

The holotype of *S. baudinii* (from Mexico) was noted to be an adult male with an SVL of either 55 mm (Kellogg, 1932) or 58 mm (Guibé, 1950). If that holotype indeed happens to be an adult male, as stated, either measurement would be somewhat smaller than that of the smallest of the 10 male specimens from the Honduran Mosquitia I measured for this study. Also, Kellogg (1932) indicated a large inner metatarsal tubercle [= raised, globular] for the holotype, which seems to associate that specimen with the populations on the Pacific versant, but not from the Mosquitia (i.e., with a low, relatively long, flat, inner metatarsal tubercle).

The color in preservative of the specimens of *S. baudinii* from the Honduran Mosquitia is as follows: a single color phase was evident in most of the 63 specimens examined for this study, which resembles that of the living adult female shown in Fig. 1 (compare with typical preserved specimen of that color phase in Fig. 4). The dorsal surfaces of the few specimens that were green with brown mottling in life are brown with darker brown mottling in preservative.

In discussing the Honduran populations of *S. baudinii* in McCranie and Wilson (2002: 332; also see Methods) I wrote, "The largest Honduran male (USNM 534164) has a SVL of 67.6 mm, whereas the two largest Honduran females (USNM 514471, 514473) have SVL's of 79.6 and 79.8 mm, respectively." As noted above, all three specimens are from lowland broadleaf rainforest in the Honduran Mosquitia, and this study verifies the large size of this population. Duellman and Trueb (1966) noted a maximum SVL of 76 mm in males and 90 mm in females for this species; the largest male came from southern Sinaloa, Mexico, and the female likely came from the same location. Duellman and Trueb (1966) also indicated the SVL of 10 males from southern Sinaloa as 62.3–75.9 mm (68.6), which is a larger size than the males from the Honduran Mosquitia, but their inner metatarsal tubercle (IMT) is elevated and globular-shaped and their toe webbing is less extensive (see Table 1) than in specimens from the Honduran Mosquitia (also see toe webbing and IMT drawings in Duellman and Trueb [1966] and Duellman [1970]; KU 87177, 81782, both from Guerrero, Mexico; the Duellman [1970] drawing reprinted in Duellman [2001]; and compare these drawings with Figs. 5–9). Other drawings or photographs that show the reduced webbing of specimens from the Pacific versant of Mexico and Central America appear in Köhler (2011; although locality of specimen not provided); Köhler et al. (2005); and Rorabaugh and Lemos-Espinal (2016). In addition, Hardy and McDiarmid (1969: 94–95) noted the SVL for 27 males from Sinaloa as 52–72 (62.5) mm and eight females as 45–78 (58.0) mm. Those values are similar to the ones presented here for specimens from the Honduran Mosquitia. Nevertheless, the consistently larger size of adults combined with their increased hind limb webbing, and their longer, narrower, and flatter inner metatarsal tubercle will distinguish the Mosquitia (northeastern Honduras to eastern Costa Rica) population (compare IMT in Figs. 7–9) from all other populations of *S. baudinii* range-wide. Those data, therefore, strongly suggest that the northeastern Honduran Mosquitia population is distinct from all other populations of *S. baudinii* I examined for this project, except for two specimens from coastal southeastern Nicaragua. Additionally, when I placed 10 adults from the Honduran Mosquitia in a tray with 10 of the larger adults from other populations, I immediately distinguished the ones from the Honduran Mosquitia based on their color and pattern.

Table 1. Characters used to define the population of *Smilisca baudinii* in the Honduran Mosquitia from other populations examined. The abbreviations are as follows: CR (= Costa Rica); H (= Honduras); IMTH, IMTL, IMTW (= inner metatarsal tubercle height, length, width, respectively; all of these values represent percentages); Mex (= Mexico); PV (= Pacific versant); and SVL (= snout–vent length, in mm). Known variations in webbing formulae are in parentheses. Only SVL is separated by sex.

Population	SVL	IMTL/IMTW	IMTL/IMTH	Hind Limb Webbing
La Mosquitia, H				
Males (10)	60.2–67.6 ($\bar{x}$ = 63.7 ± 2.1)	1.7–3.4 (23)	1.7–3.5	I 0–1 II 0–1 1/2 III 0–1 IV 3/4–0 V
Females (10)	62.9–79.8 ($\bar{x}$ = 68.4 ± 6.3)			
Petén, Guatemala				
Males (6)	49.0–60.8 ($\bar{x}$ = 55.2 ± 1.8)	1.3–1.9 (9)	1.2–1.6	I 1–2 II 0–2 1/3 III 1–2 IV 2–(0–1/3) V
Females (3)	55.2–58.4 ($\bar{x}$ = 57.1 ± 1.7)			
Yojoa, H				
Males (10)	46.5–54.6 ($\bar{x}$ = 50.7 ± 2.7)	1.4–2.1 (10)	1.0–1.7	I 1/3–2 II 0–2^+ III 1^+–2 IV 2–0 V
Females (10)	48.0–65.6 ($\bar{x}$ = 57.7 ± 5.3)			
Islas Bahía, H				
Males (10)	51.0–60.4 ($\bar{x}$ = 55.8 ± 3.0)	1.2–2.0 (3)	1.0–1.5	I 1–2 II 1/2–2^+ III 1^+–1 3/4 IV 1 1/2–1/3 V
Females (3)	70.6–74.1 ($\bar{x}$ = 72.8 ± 1.9)			
PV, Mex to CR				
Males (23)	52.1–65.4 ($\bar{x}$ = 57.1 ± 3.7)	1.1–2.0 (28)	1.0–1.8	I 1/3–2 II (1–1 1/2)–2^+ III 1/2–(2 1/3–2^+) IV 2–(1/3–1/2) V
Females (14)	47.4–72.2 ($\bar{x}$ = 59.3 ± 7.0)			

In summary, based on external morphology, the population of *S. baudinii* from the Honduran Mosquitia apparently is not conspecific with at least the subhumid Pacific versant populations found from Sonora, Mexico, to Costa Rica, and other populations in Honduras (see Table 1). Thus, two of the names Duellman and Trueb (1966) placed in the synonymy of *S. baudinii* need to be considered for this study.

Brocchi (1877) described *Hyla pansosana* with a type locality of Panzos, Alta Verapaz, Guatemala. Unfortunately, the Brocchi description is poor and does not distinguish that nominal form from any species of *Smilisca*. The same holds true for the Brocchi (1882) redescription of that holotype, and the drawings he presented are inadequate and cannot be used to distinguish even the genus, using the current classification of hylid frogs. Duellman (1968) indicated that the holotype of *H. pansosana* is a subadult male, and Guibé (1950) noted its SVL as 48 mm (MNHN 6313). Given the poor descriptions provided by Brocchi, no further comments can be made on the holotype of the nominal form *H. pansosana* Brocchi.

I examined a small series of *S. baudinii* from El Petén, Guatemala (six males, 71334, 71794–96, 11469–70; and three females, USNM 25137, 114471–72), and reexamined 10 specimens from the Lago de Yojoa region in Honduras (USNM 243063–64, 243066–67, 243070, 243079, 243082, 243085, 243089, 243187), which are located both north and south, respectively, of the Panzos type locality for *H. pansosana.* After comparing the external morphology of the Petén and Yojoa specimens to each other, and then both to the ones from the Honduran Mosquitia, I concluded that those two populations (Petén and Yojoa) are more similar to each other than either is to the Honduran Mosquitia population. I show the most outstanding characters that define the Mosquitia population in Table 1, and compare them to those of the Petén and Yojoa populations, specimens from the Pacific versant, and those from the Islas de la Bahía, Honduras. Based on my data, the two populations north and south of the *H. pansosana* type locality eliminate the nominal form *H. pansosana* from consideration as being conspecific with the population in the Honduran Mosquitia.

Taylor (1954) proposed the name *Hyla manisorum*, based on a single adult female (KU 34927; type locality, "Bataan [= Batán], Limón Province") for a Caribbean lowland broadleaf rainforest population from eastern Costa Rica. Duellman and Trueb (1966) placed that nominal form in the synonymy of *S. baudinii*, but did not provide any data to support their decision. The first character Taylor (1954: 630) used in his diagnosis of the *H. manisorum* holotype was "A large frog (female 76 mm)," which is similar to the Honduran Mosquitia lowland broadleaf rainforest frogs under study. Taylor (1954: 632) also mentioned that the *H. manisorum* holotype had "a rather small inner metatarsal tubercle" [= low and flat], which agrees with the specimens from the Honduran Mosquitia. Taylor (1954: 632) also wrote, "toes nearly four-fifths webbed," which also indicates increased webbing in that specimen, when compared to those from other populations (see Table 1). Those three characters ally the holotype of *H. manisorum* with the northeastern Honduran population. Taylor (1954) also provided a photograph of the preserved *H. manisorum* holotype, which shows that specimen to be similar in appearance, with its relatively elongated form, to those from the Honduran Mosquitia. I examined six specimens from lowland broadleaf rainforest on the Caribbean versant of southeastern Nicaragua, but only two were in good enough condition to gather reliable external morphological data (USNM 20701, an adult male; USNM 19766, an adult female). Historically, the forest in these regions of eastern Costa Rica and eastern Nicaragua continued northward to the Honduran Mosquitia, before the vegetation was destroyed or altered as a result of human activities. Although the female specimen is somewhat dehydrated, its measurements are similar to those of specimens from the Honduran Mosquitia (SVL = 69.0 mm, IMTL/IMTW = 1.6%, and IMTL/IMTH = 2.2%; Table 1). The measurements of the male also are similar (SVL = 56.9 mm, IMTL/IMTW = 2.3%, and IMTL/IMTH = 1.8%; Table 1). Additionally, these specimens show increased webbing on the hind limbs, similar to those from the Honduran Mosquitia. Photographs of the ventral surfaces and the increased webbing on the hind limbs (photographs not included) of the Costa Rican *Hyla manisorum* holotype (KU 34927) show that those characters are similar to specimens from the Honduran Mosquitia. More importantly, a recently obtained photograph of the IMT of KU 34927 (see Fig. 9) shows a long and flat IMT, like in all the specimens from the Honduran Mosquitia population. As a result of these similarities and the consistent differences when comparing the Honduran Mosquitia population to other populations of *S. baudinii*, I propose elevating *Hyla manisorum* Taylor from the synonymy of *Smilisca baudinii* and consider that nominal form to represent a distinct species, *Smilisca manisorum* (Taylor) new comb. Taylor (1954: 631–633, Fig. 11) provided a detailed description of the female holotype, and a good image of a dorsal view of that specimen in preservative. The detailed morphological data presented above for 20 adults from the Honduran Mosquitia also help define *S. manisorum*, as well as the color descriptions in life for three Honduran specimens given above. *Smilisca manisorum* is distinguished from all the remaining populations of *S. baudinii* by its consistently larger adult size, the long and flat inner metatarsal tubercle, and the increased hind limb webbing (also compare the *S. manisorum* data with those from several populations of *S. baudinii* in Table 1). I also present photographs of *S. manisorum* in this study (Figs. 1, 2, 4, 5, 7, 9), with the last mentioned demonstrating the shape of the inner metatarsal tubercle in the Costa Rican holotype (compare with Fig. 7). Also, a photograph of a young adult female *S. manisorum* from southeastern Nicaragua appears in Sunyer et al. (2009).

The geographical distribution of *S. manisorum* includes the eastern Caribbean lowland mesic forest, which historically extended from northeastern Honduras to eastern Costa Rica. Most known localities for this species lie below 200 m in elevation, but *S. manisorum* is known to reach an elevation of 540 m. Most of the known localities are in closed canopy lowland forest in areas that receive a large amount of rainfall, and usually undergo relatively short "dry seasons."

Fig. 1. An adult female *Smilisca manisorum* from Sadyk Kiamp, Departamento de Gracias a Dios, in the Mosquitia region of northeastern Honduras (released). SVL ca. > 80 mm. © James R. McCranie

Fig. 2. An adult female *Smilisca manisorum* (USNM 514473) from between the mouth of the Wampú and Yapuwás rivers, Departamento de Olancho, in the Mosquitia region of northeastern Honduras. SVL = 79.8 mm. © James R. McCranie

Fig. 3. An adult male *Smilisca baudinii* (USNM 514474) from near La Esperanza, Departamento de Intibucá, Honduras, showing the relatively short distance between the forelimb insertion and the tip of the snout. SVL = 52.4 mm. © James R. McCranie

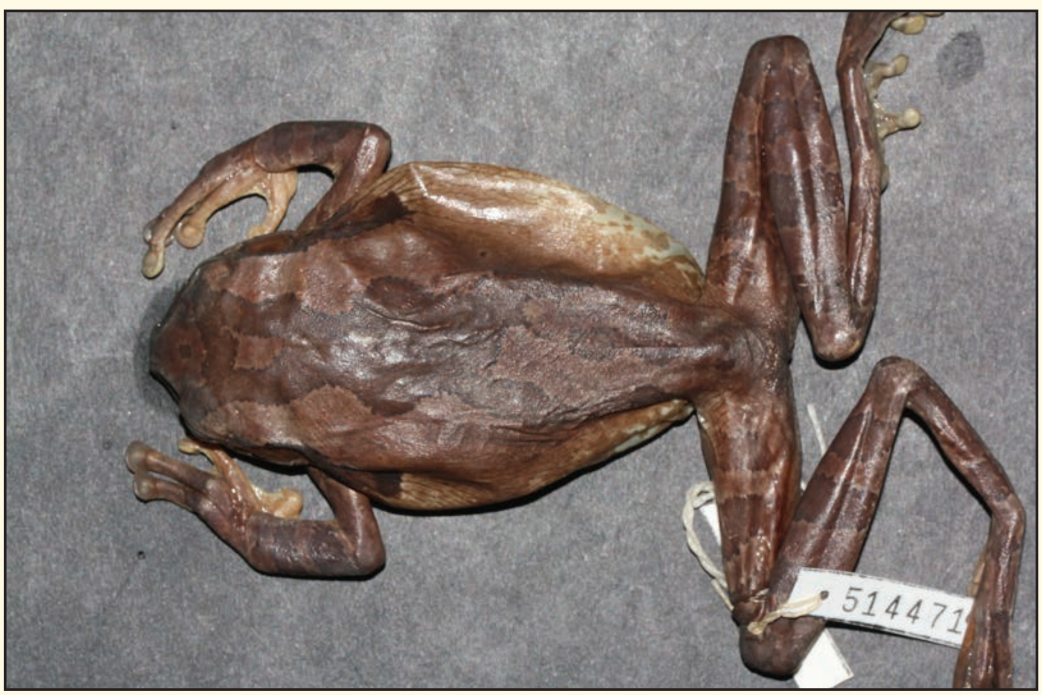

Fig. 4. An adult female *Smilisca manisorum* (USNM 514471; in preservative) showing the typical color pattern of individuals in the Mosquitia region of northeastern Honduras. Specimen from the confluence of Quebrada Waskista with Río Wampú, Departamento de Gracias a Dios, SVL = 79.6 mm. © James R. McCranie

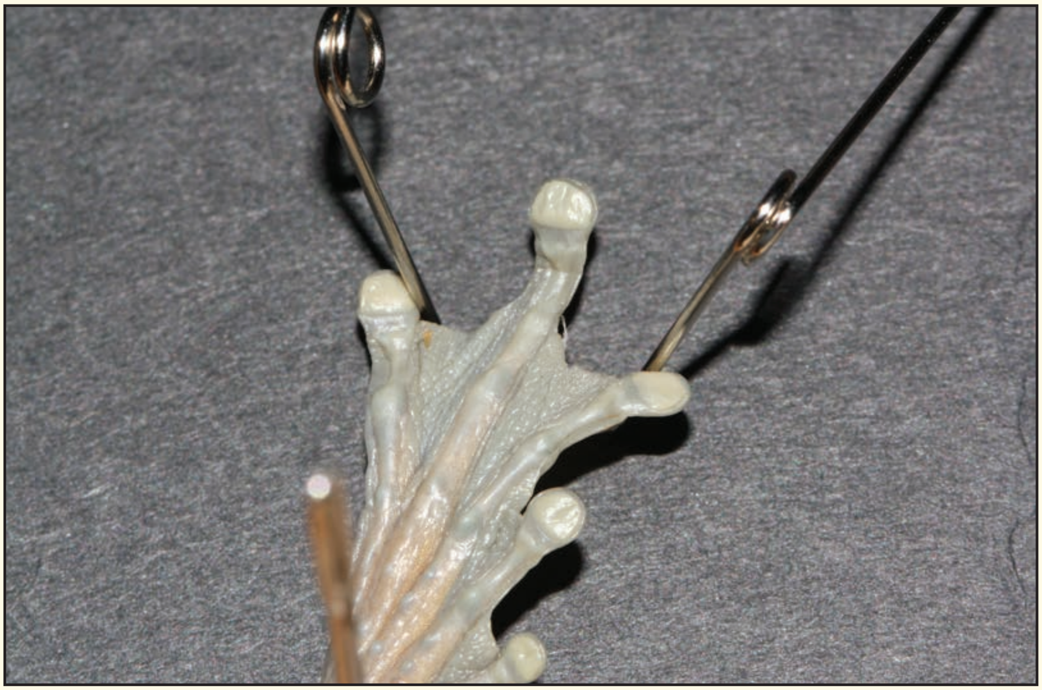

Fig. 5. Increased webbing on the hind foot of a Mosquitia specimen of *Smilisca manisorum* (USNM 559256; an adult female) from Awasbila, Departamento de Gracias a Dios. © James R. McCranie

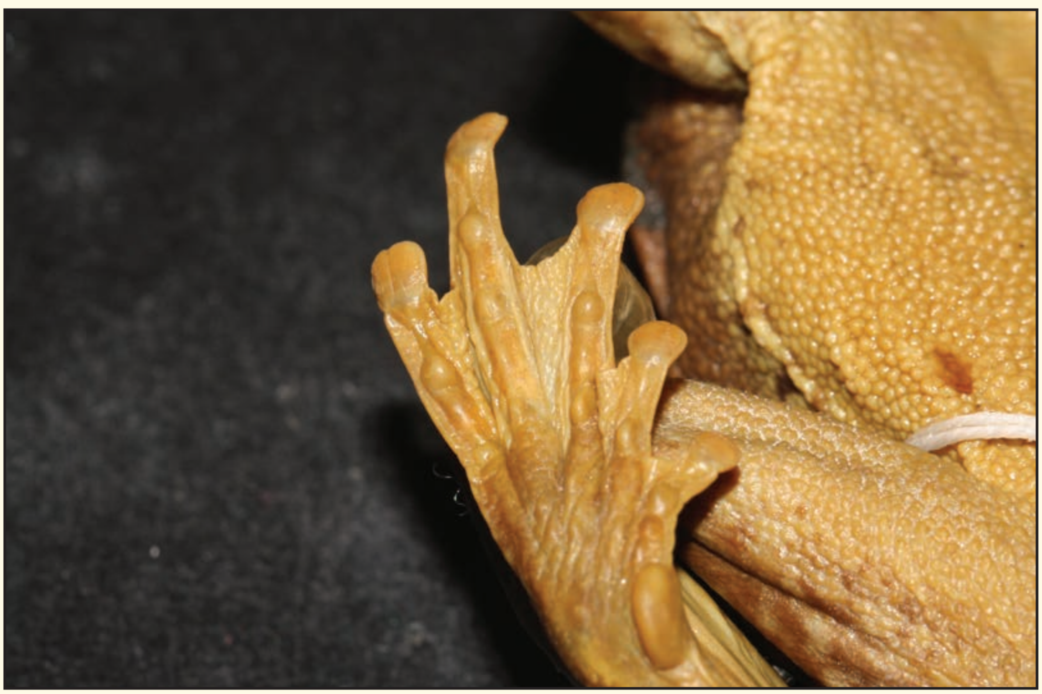

Fig. 6. Reduced webbing on the hind foot of a Pacific versant specimen of *Smilisca baudinii* from El Salvador (USNM 73284). IMTL = 3.3 mm. © James R. McCranie

Fig. 7. The long, flat, inner metatarsal tubercle of an adult female *Smilisca manisorum* (USNM 534166) from Quebrada Machín, Departamento de Colón, in the Mosquitia of northeastern Honduras. IMTL = 4.2 mm. © James R. McCranie

Fig. 8. The higher, raised, globular inner metatarsal tubercle of a Pacific versant specimen of *Smilisca baudinii* from El Salvador (USNM 73284). IMTL = 3.3 mm.

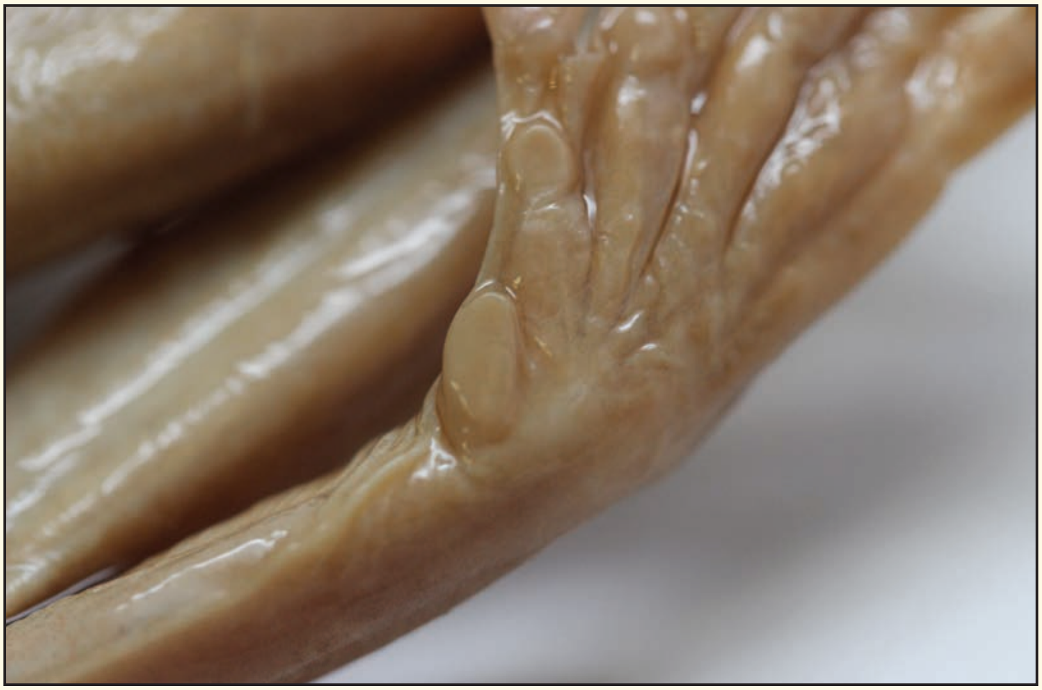

Fig. 9. The long, flat, inner metatarsal tubercle of the adult female holotype of *Smilisca manisorum* (KU 34927) from Batán, Providencia de Limón, Costa Rica. © Luke Welton

DISCUSSION

Authors of several recent studies, one including only molecular data, two using only external morphological data, and one using both data types, have proposed that several wide-ranging species of anurans that also occur in Honduras actually represent complexes involving more than a single species (e.g., *Rhinella marina* [Acevedo et al., 2016; however, the large geographical distribution of that nominal form was poorly-defined and documented]; *Incilius valliceps* [Mulcahy and Mendelson, 2000]; *Plectrohyla guatemalensis* [McCranie, 2017a]; and *Trachycephalus venulosus* [Ron et al., 2016; but see above comment for Acevedo et al. [2016]). Fouquette and Dubois (2014) also included examples of United States and Canadian "species" that recently have been divided into two or more species. The morphological differences demonstrated between *Smilisca manisorum* and the various populations of *S. baudinii* in this study strongly suggest that several species are involved, and thus I regard this group of frogs as the "*Smilisca baudinii* complex." I expect that future phylogenetic analyses using both external morphology and molecular data from as many populations as possible, will confirm my assessment.

The findings discussed in this work are based solely on external morphology. Tissues of *S. manisorum* I collected are available from the northeastern Honduran Mosquitia population (one in the USNM collection) and others of the *S. baudinii* complex I collected are available from several localities in Honduras (two tissue samples are in the UTA collection, and three are in the FMNH collection). As far as I am aware, only one specimen (from Sonora, Mexico) of the *S. baudinii* complex has been used for molecular analyses (Faivovich et al., 2005; Duellman et al., 2016). The external morphological results presented herein strongly support that several other populations from throughout the extensive range of the *S. baudinii* complex likely represent separate evolutionary species. Examination of the El Petén, Guatemala, and the Lago de Yojoa, Honduras, populations suggest they are most similar to each other and can be distinguished from the Pacific versant populations of this complex by the presence of a less elevated inner metatarsal tubercle and slightly more hind limb webbing. The name *Hyla pansosana* Brocchi (type locality at Panzos, Guatemala) is available for the Petén and Yojoa populations should future work support the results of this study, which suggest they are distinct from populations of the *S. baudinii* complex on the Pacific versant.

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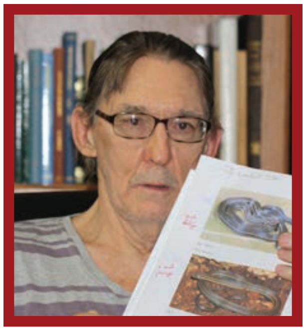
Appendix 1. Comparative specimens examined. Most of the Honduran specimens I examined for McCranie and Wilson (2002), with their locality data, and additional specimens are listed in McCranie (2006). Thus, only the specimens I reexamined and those from Honduras that subsequently were collected are listed below, along with their corresponding localities. An updated gazetteer listing all of the known Honduran collecting localities is included in the "Supplemental Data" of McCranie (*In Press*). The specimens examined for this project that are extralimital to Honduras are listed by country, and then by department, province, or state. All of the specimen numbers listed below are from the USNM collection.

Smilisca baudinii (56). **COSTA RICA (1):** ALAJUELA: 29991. **EL SALVADOR (2):** MORAZÁN: 73284; SAN SALVADOR: 140278. **GUATEMALA (12):** EL PETÉN: 25137, 71334, 71794–96, 114469–72; ESCUINTLA: 125239; SAN MARCOS: 128056–57. **HONDURAS (22):** CHOLUTECA: 514450–51; COPÁN: 514454, 514457; CORTÉS: 243063–64, 243066–67, 243070, 243079, 243082, 243085, 243089, 243187; EL PARAÍSO: 580136; INTIBUCÁ: 514474–75; ISLA DE LA BAHÍA: 514476, 563428 580142; VALLE: 580138–39. **MEXICO (17):** COLIMA: 58093; GUERRERO: 47909; NAYARIT: 51408; OAXACA: 10016, 30171–74, 30188, 47120–22, 70400, 114512; SINALOA: 14082, 47439–40. **NICARAGUA (2):** MANAGUA: 79989–90.

Smilisca manisorum (69). **HONDURAS (63):** COLÓN: 534159–66; GRACIAS A DIOS: 514468–72, 559241–43, 559246–57, 560963, 563429, 563978; Bachi Kiamp, 573811–12, 579674; Cacho Kiamp, 573813; Crique Kalka, 565373–74; Kakamuklaya, 573035–36; Puerto Lempira, 573029–30; Sisinbila, 580134; Warunta, 565374; Yahurabila, 573037–38; OLANCHO: 514473, 514477–83, 534158, 538596–98, 559240, 559244–45, 559253, 559255–56. **NICARAGUA (6):** ATLÁNTICO SUR: 19766, 20701; RÍO SAN JUAN: 19585–86, 19767–68.



James R. McCranie is a self-taught herpetologist with a passion for fieldwork, who specializes on the taxonomy and systematics of the Latin American herpetofauna. His main area of interest is Honduras, where he has been con- ducting fieldwork since 1976. During his career, McCranie has authored or co-authored five books (a sixth book is in press) and nearly 300 peer-reviewed scientific publications, including the descriptions of about 95 new taxa, mostly from Honduras. In 2015, he retired from fieldwork in Honduras because of the unavailability of scientific collecting permits. During his countless trips to Honduras, Randy witnessed a time when extensive forests dominated the landscape; sadly, as a result of deforestation and fragmentation, many of these habitats no longer remain. Because of the lack of governmental effort to curb these practices, he believes that the country has reached the point of no return regarding the conservation of many of its once magnificent natural habitats.