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## A Review of the Frogs Of the Hyla bistincta Group

 $\mathbf{BY}$ 

#### WILLIAM E. DUELLMAN

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## INTRODUCTION

In the mountainous regions of Middle America there are several groups of hylid frogs that inhabit mountain streams. Some of these groups, such as *Plectrohyla* and *Ptychohyla*, have been elevated to generic rank, whereas others are retained in the large and complex genus *Hyla*. In the mountains of México five species of hylids that seem to compose a phyletic unit are herein referred to as the *Hyla bistincta* group. Since 1955 I have been accumulating specimens of, and data on, this group with the result that all specimens known to me, including the types of all named taxa, have been studied. Detailed observations have been made on the ecology and life histories of three of the species; the other two species are known to me only from preserved specimens.

#### Acknowledgments

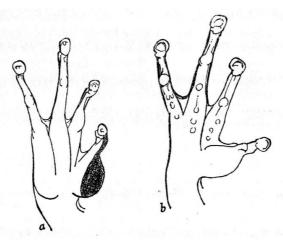
For permission to examine specimens in their care I am indebted to Charles M. Bogert, American Museum of Natural History (AMNH); Doris M. Cochran, United States National Museum (USNM); Jean Guibé, Museum National d'Histoire Naturelle, Paris (MNHN); Robert F. Inger, Chicago Natural History Museum (CNHM); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ). (Abbreviations of institutions given above in parentheses are used throughout; the Museum of Natural History, University of Kansas is abbreviated KU.)

For their willing assistance in the field I am grateful to Ann S. Duellman, Dale L. Hoyt, and John Wellman. Permits for collecting in México were generously issued by the late Ing. Luis Macías Arellano, Departamento de la Fauna Silvestre, Dirección General de Caza. The drawings in figures 1 and 3 were executed by Gail Selfridge. This research has been supported by the National Science Foundation (NSF G-9827).

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## THE HYLA BISTINCTA GROUP

The five species comprising the *Hyla bistincta* group are moderate-sized hylids having rather blunt heads and robust bodies. The fingers are long and have little webbing (Fig. 1). The skin of the dorsum is thick and glandular, but not tuberculate. An anal sheath is present. The skull is rather broad, flat, and solidly roofed. The ethmoid is broad, curved downward laterally, and solidly sutured to the frontoparietal. The nasals are broad, sutured for their entire width with the ethmoid, and broadly in contact medially. The premaxillaries are in contact medially; each has a long, flat nasal process. The quadratojugal is absent, and the maxillary tapers to a point posteriorly. There is no squamosal-maxillary connection. The maxillary and premaxillary teeth are rather long, bifid, and moderately spatulate. Some teeth on the premaxillary and anterior part of the maxillary are hooked. The vomerine teeth are spatulate and bifid. A broad, flat, ossified prepollex is present but does not project as a spine. The known tadpoles have ventral mouths, ½ tooth-rows, two or more rows of labial papillae, and long tails with low fins.



As thus defined the *Hyla bistincta* group can be distinguished from all other groups of Middle American frogs by the combination of absence of the quadratojugal, non-projecting prepollex, long fingers with little webbing, and stream-inhabiting tadpoles having ½ tooth rows and two or more rows of labial papillae.

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Possibly Hyla arborescandens and Hyla hazelae belong in this group. Because these species are somewhat different from the included species and because their tadpoles are as yet unknown, I have refrained from including these two species in the Hyla bistincta group. Taylor (1948:261) assigned Hyla proboscidea (= H. dalquesti) and (1949:272) Hyla cyclomaculata to this group, but because these two species have a quadratojugal and notably different tadpoles, they are excluded from the group.

Frogs of the genus Plectrohyla closely resemble species in the Hyla bistincta group but differ principally in having a projecting prepollex. In the highlands of Costa Rica a group of species, of which Hyla moesta is best known, resembles species in the Hyla bistincta group. At present insufficient information is available on the Costa Rican species to determine their affinities.

## **Analysis of Characters**

The characters used in the systematic study of the frogs in this group are those usually employed in anuran systematics. Of the various measurements and proportions, the snout-vent length and the relative size of the tympanum to the eye apparently are of more taxonomic importance than the others (Table 1). In all of the species the tympanum is at least partially covered by a heavy, dermal supratympanic fold, and in some specimens of H. pachyderma the tympanum is completely obscured. In two species (H. bistincta and H. charadricola) the snout is square, whereas in the other species it is round.

The fingers are long and slender in H. crassa, pachyderma, and robertsorum and somewhat shorter with more webbing in H. bistincta and charactricola. Breeding males of Hyla pachyderma have moderately large nuptial spines; the other species have small spines, except H. charadricola in which spines apparently are absent. A well-defined thoracic fold is present in H. pachyderma, and a weak fold is present in H. robertsorum; the other species lack folds. In all species there is an anal sheath; this sheath is longest in H. bistincta, in which the anal opening is directed ventrally at the level of the lower edge of the thighs.

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TABLE 1.—COMPARISON OF CERTAIN MEASUREMENTS AND PROPORTIONS IN THE SPECIES OF THE HYLA BISTINCTA GROUP. (DATA FROM ADULT MALES; MEANS ARE GIVEN IN PARENTHESES BELOW THE RANGES.)

	Species	N Spout-wont longth		<u>Tibia length</u>	<b>Head width</b>	<b>Tympanum</b>
	SPECIES	N Snout-vent length	nout-vent length	Snout-vent lengtl	n Eye	
	H. bistincta	38	43.0-53.8	0.47-0.52	0.32-0.37	0.35-0.48
		30	(46.3)	(0.49)	(0.34)	(0.42)
	H. charadricola10	10	35.3-44.4	0.50-0.54	0.31-0.33	0.30-0.37
		110	(40.4)	(0.52)	(0.32)	(0.34)
F	H. robertsorum	26	39.9-47.9	0.48-0.51	0.30-0.36	0.36-0.47
	n. robertsorum	20	(43.1)	(0.49)	(0.32)	(0.41)
	H. pachyderma	1	39.9	0.53	0.32	
	H. crassa	1	53.7	0.50	0.33	0.28

Frogs in this group are rather drab in appearance. The dorsal color varies from dull green to various shades of brown. The most distinct aspect of the coloration is the different color patterns on the flanks and posterior surfaces of the thighs. The flanks in all species are marked with spots or reticulations.

Hyla bistincta differs from other members of the group in having vocal slits and a distensible vocal sac. Only this species has been reported to call (Shannon, 1951:473). Insofar as is known, the other species are mute. Examination of skeletal preparations of H. bistincta, charadricola, and robertsorum and X-rays of the other species shows no notable specific differences in the osteology. Since the tadpoles of only H. bistincta (Duellman, 1961:47) and H. robertsorum (Rabb and Mosimann, 1955) are known, larval characters are of limited use in intra-group systematics.

#### Key to the Species of the Hyla bistincta Group

1. Snout, in dorsal profile, short and bluntly rounded; canthus rounded, sometimes indistinct, vocal slits absent

Snout, in dorsal profile, longer, squared; canthus distinct, vocal slits present or absent

2 4

2. Feet webbed to base of discs; dorsum dull olive green; flanks having cream-colored spots H. *crassa*, p. 486

3. Tarsal fold strong; thoracic fold heavy; webbing on feet extending to middle of penultimate phalanx of fourth toe; distinct white stripe above anus; cluster of largo spines on thumb in breeding males, *H. pachyderma*, p. 485

Tarsal fold weak and short; thoracic fold absent or barely indicated; webbing of feet extending to base of penultimate phalanx of fourth toe; no distinct white stripe above anus; nuptial tuberosities in breeding males consisting of small spines *H. robertsorum*, p. 481

4. Tarsal fold strong; anal flap elongate; anus opening at lower edge of femur; dorsum tan or brown; flanks mottled with cream and brown; venter immaculate creamy white; no anal stripe; vocal slits present, *H. bistincta*, p. 475

Tarsal fold faint and short; anal flap not elongate; anus opening at middle of femur; dorsum olive-green with black reticulations; flanks greenish gray with brown or black spots; a row of white flecks above and below anus, vocal slits absent *H. charadricola*, p. 478

## ACCOUNTS OF THE SPECIES

In the following accounts complete synonymies are given for each species. In each account one specimen is described in detail; after this description the variation is discussed. In the list of specimens examined, localities are arranged alphabetically within the states, which also are given in alphabetical order. Localities given in italics are not shown on the accompanying maps (Figs. 2 and 4) due to crowding of symbols.

#### Hyla bistincta Cope

Hyla bistincta Cope, Proc. Amer. Philos. Soc, 17:87, August, 1877 [Holotype.—USNM 32261 from "most probably Veracruz," México; Francis Sumichrast collector]. Brocchi, Étude des batraciens de l'Amérique Centrale, p. 43, 1881. Boulenger, Catalogue Batrachia Salientia, 2nd Ed., p. 401, February 1, 1882. Sumichrast, La Naturaleza, 6:81, 1882. Cope, Bull. U. S. Natl. Mus., 32:14, 1887; Bull. U. S. Natl. Mus., 34:351, 1889. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, pp. 265-6, June, 1901. Díaz de León, Indice de los batracios que se encuentran en la República Mexicana, p. 17, June, 1904. Nieden, Das Tierreich, Amphibia, Anura I, p. 247, June, 1923. Kellogg, Bull. U. S. Natl. Mus., 160:163-164, March 31, 1932. Taylor, Proc. Biol. Soc. Washington, 50:50-53, April 21, 1937; Univ. Kansas Sci. Bull., 26:389, November 27, 1940. Taylor and Smith, Proc. U. S. Natl. Mus., 194:87, June 7, 1948. Taylor, Univ. Kansas Publ. Mus. Nat. Hist., 1:261, August 16, 1948; Copeia, no. 4:272-273, December 15, 1949. Smith and Taylor, Univ. Kansas Sci. Bull., 33:346, March 20, 1950 [Type locality restricted to Acultzingo, Veracruz, México]. Rabb and Mosimann, Occas. Papers Mus. Zool. Univ. Michigan, 563:6-9, March 29, 1955. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15:47-49, December 20, 1961.

Hyla bistincta labeculata Shannon, Proc. U. S. Natl. Mus., 101:470-473, figs. 92a, 93d, May 17, 1951 [Holotype.—USNM 123689 from San Lucas Camotlán, Oaxaca, México; Walter S. Miller collector]. Smith and Williams, Herpetologica, 19:23, April 11, 1963.

*Hyla bistincta bistincta*, Shannon, Proc. U. S. Natl. Mus., 101:472, May 17, 1951. Shannon and Werler, Herpetologica, 11:85, July 15, 1955. Smith and Williams, Herpetologica, 19:23, April 11, 1963.

*Diagnosis.*—Maximum snout-vent length in males 54 mm.; snout in dorsal profile truncate; tarsal fold strong; inner metatarsal tubercle large, high, and elongate; outer metatarsal tubercle absent; webbing on foot extending to middle of antepenultimate phalanx of fourth toe; nuptial spines on thumb small; thoracic fold absent; anal opening at level of lower edge of femur; dorsum brown or tan; belly cream-color; flanks creamy yellow with brown reticulations or spots; anal stripe absent; vocal slits present.

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Description.—The following description is based on KU 68078 from Uruapan, Michoacán, México. Adult male having a snout-vent length of 43.2 mm.; tibia length, 22.1 mm., 51.1 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 20.8 mm.; greatest width of head, 15.4 mm., 35.6 per cent of snout-vent length; head length, 13.9 mm., 32.1 per cent of snout-vent length; diameter of eye, 5.1 mm.; diameter of tympanum, 2.4 mm., 47.1 per cent of diameter of eye. Snout in lateral profile bluntly rounded, in dorsal profile truncate; canthus pronounced, rounded, not angular; loreal region slightly concave; lips thick, round, not flaring; nostrils slightly protuberant; internarial distance, 3.4 mm.; interorbital distance, 4.5 mm., somewhat broader than width of eyelid, 3.5 mm. A heavy dermal fold from posterior corner of eye above tympanum and curved downward to insertion of forearm; tympanum round, its diameter slightly more than its distance from eye. Forearm not robust; row of small pustules on ventral surface of forearm; fold on wrist; prepollex moderately enlarged, covered with small, horny, nuptial spines continuous on edge of digit; row of spines on inner surface of second finger; subarticular tubercles large, round, none bifid; supernumerary tubercles rather large, round; palmar tubercles rather small, flat, elliptical; fingers long, moderately slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large, that on third finger slightly larger than tympanum; rudimentary web between first and second and between second and third fingers; web between third and fourth fingers extending about one-fourth length of fourth finger. Heels overlap by about one-third length of shank when hind limbs adpressed; tibiotarsal articulation extends to anterior edge of eye; tarsal fold strong, extending to heel; inner metatarsal tubercle large, high, and elongate; outer metatarsal tubercle absent; subarticular tubercles moderately large, round; supernumerary tubercles small, in single rows on proximal segments of digits; toes moderately short; length of toes from shortest to longest, 1-2-3-5-4, third and fifth toes about equal in length; toes about two-thirds webbed; web extending to middle of antepenultimate phalanx of fourth toe, to discs of first, second, and fifth toes, and to base of penultimate phalanx of third toe; discs rather small, about two-thirds size of those on fingers. Anal opening at level of lower edge of thighs; anal sheath elongate, deeply creased medially; transverse dermal fold above anus. Skin of dorsal surfaces of head, body, and limbs faintly areolate; skin of chin, belly, and ventral surfaces of thighs granular, that of ventral surfaces of limbs, except thighs, areolate; thoracic fold absent. Tongue nearly round, slightly longer than wide, shallowly notched behind and barely free posteriorly. Vomerine teeth 4-4, situated on

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rounded vomerine ridges between rather small ovoid inner nares; vocal slits present, situated along posterior edge of each ramus.

Color (in alcohol) pale brown on dorsal surfaces of head, body, and limbs; flanks and anterior surfaces of thighs creamy white with dark brown reticulations; posterior surfaces of thighs tan with creamy white spots; belly cream-color; anal stripe absent.

Color (in life) pale tan on dorsal surfaces; flanks and anterior surfaces of thighs pale creamy yellow with purplish brown reticulations; posterior surfaces of thighs tan with yellow spots; ventral surfaces yellow; iris pale copper-color.

*Variation.*—There is little variation in structure. The total number of vomerine teeth varies from 6 to 14. In some individuals the supratympanic fold covers the upper part of the tympanum, but at least the lower part of the tympanum is always visible. The extent of the webbing between the toes varies from three-fourths to two-thirds complete. Usually the web extends to some point on the antepenultimate phalanx of the fourth toe, but in some specimens the web extends to the base of the penultimate phalanx.

In the large series of specimens from Uruapan, Michoacán, the coloration of the flanks and anterior surfaces of the thighs varies from nearly uniform creamy yellow with only fine dark reticulations to bold reticulations enclosing yellow spots. Some specimens from Oaxaca and Veracruz have slightly different markings on the flanks; in these the dark pigment is in the form of irregular spots or dashes, instead of reticulations.

There is considerable variation in color in the living frogs. The dorsum varies from greenish tan and pale yellowish tan to reddish brown, and some individuals are dark chocolate brown.

Remarks.—Shannon (1951:470) named Hyla bistincta labeculata on the basis of a single male from San Lucas Camotlán, Oaxaca; he diagnosed the subspecies as differing from Hyla bistincta bistincta by having "the gray reticulation of the sides entirely broken up into elongate black blotches; tarsal fold moderately elevated." The condition of the tarsal fold is characteristic of the species. The dispersion of dark pigment on the flanks is variable. The type of Hyla bistincta labeculata (USNM 123689) is extreme in the development of dark dashes on the flanks, but this condition is approached in several specimes from Oaxaca and Veracruz. For example, in some specimens from Cumbres de Acultzingo, Veracruz, the mottling on the flanks is bold; in others the flanks are reticulated. The specimen from San Vicente, Oaxaca, has black dashes on the flanks (Smith and Williams, 1963:23), whereas a specimen from Cerro San Felipe, Oaxaca, has no pattern on the flanks. In general, specimens from western México have reticulate mottling on the flanks as compared with the marbling on the flanks in specimens from eastern México. On the basis of available data, the recognition of subspecies in Hyla bistincta is unwarranted.

The tadpoles of this species described by Duellman (1961:47) are like those of Hyla robertsorum in having  $\frac{2}{3}$  tooth-rows, peglike serrations on the beaks, and long, rounded tails. At Uruapan tadpoles were found in a rocky stream on April 24, 1956, and metamorphosing young were found there on August 2, 1956. A completely metamorphosed juvenile has a snout-vent length of 24.8 mm.

*Hyla bistincta* is found only along streams, where individuals can be seen clinging to vines and other vegetation closely over-hanging fast-moving parts of the stream.

Distribution.—Hyla bistincta occurs at elevations from 1400 to 2600 meters in the mountains of the Sierra Madre Occidental in western Jalisco southward through the Cordillera Volcánica in Michoacán, México, and Morelos, the Sierra de Coalcomán in Michoacán, and the Sierra Madre del Sur in Guerrero and Oaxaca, and thence northward in the Sierra Madre Oriental to central Veracruz (Fig. 2).

Specimens examined.—Guerrero: Omiltemi, UIMNH 38023-5. Jalisco: 25 km. SE Autlán, UMMZ 102076. Mexico: 19 km. W Villa Victoria, UIMNH 28162, USNM 114513. Morelos: Cuernavaca, USNM 121523; 3 km. N Cuernavaca, UIMNH 28168-70. Michoacan: Cerro San Andrés, UMMZ 102075; Dos Aguas, UMMZ 119193; 12.5 km. ENE Dos Aguas, UMMZ 119194; Los Conejos, UMMZ 94238-40; Uruapan, KU 68077-8, 69093 (skeleton), UIMNH 20457, 28167, UMMZ 85452-3, 112838, 112839 (16), 115231 (tadpoles), 115232, 115233 (12), 121515, S-1699 (skeleton), S-1826 (skeleton), USNM 114514-5, 114517-24. Oaxaca: Cerro San Felipe, UIMNH 28163; Pluma Hidalgo, AMNH 13447; San Lucas Camotlán, USNM 123689; San Vincente, UIMNH 51346 (Smith and Williams, 1963:23). Veracruz: no specific locality, USNM 32261; Cumbres de Acultzingo, CNHM 105482-3, UIMNH 28164-6, 49133-4, USNM 114525.

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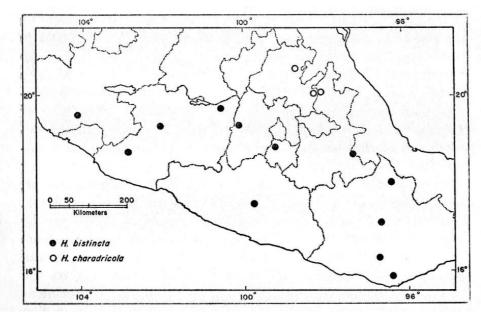


Fig. 2. Map showing locality records for *Hyla bistincta* and *Hyla charadricola*.]

#### Hyla charadricola new species

*Holotype.*—University of Kansas Museum of Natural History No. 58414 from the Río Totolapa, 14.4 kilometers by road west of Huachinango, Puebla, México, 2280 meters; obtained by John Wellman on June 8, 1960.

Paratypes.—KU 58415-58423, same data as holotype, and UIMNH 50966, obtained at the type locality by William E. Duellman on February 11, 1961.

Diagnosis.—Maximum snout-vent length in males, 45 mm.; snout in dorsal profile truncate; tarsal fold short and weak; inner metatarsal tubercle moderately large, elliptical, and flat; outer metatarsal tubercle minute, round, and indistinct; webbing extending to base of terminal phalanx of fourth toe; nuptial spines on thumb absent; thoracic fold absent; anal opening at level of middle of thigh; dorsum olive-green with black reticulations; venter cream color with brown flecks on chin; flanks pale grayish green with brown spots; anal stripe absent; row of white flecks above and a row below anus; vocal slits absent.

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Description of Holotype.—Adult male having a snout-vent lenth of 44.4 mm.; tibia length, 22.2 mm., 50 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 20.4 mm.; greatest width of head, 14.0 mm., 31.5 per cent of snout-vent length; head length, 13.6 mm., 30.6 per cent of snout-vent length; diameter of eye, 5.0 mm.; diameter of tympanum, 1.6 mm., 32.0 per cent of diameter of eye. Snout in lateral profile bluntly rounded, in dorsal profile truncate (Fig. 3); canthus pronounced, rounded, not angular; loreal region slightly concave; lips thick, rounded, not flaring; nostrils slightly protuberant; internarial distance, 3.7 mm.; interorbital distance, 4.1 mm., somewhat broader than width of eyelid, 3.3 mm. A heavy dermal fold from posterior corner of eye above tympanum and then to insertion of forearm; tympanum round, its diameter three-fourths its distance from eye. Forearm rather slender; a short axillary membrane; no fold on wrist; no nuptial excrescence or spines on enlarged prepollex; subarticular tubercles moderately small, round; none bifid; few supernumerary tubercles on proximal segments of digits; large, flat palmar tubercle present; fingers long and slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large, that on third finger about equal to diameter of tympanum; rudimentary web between first and second fingers; web between third and fourth fingers extending to about one-fifth length of fourth finger (Fig. 1). Heels overlap by about one-third length of tibia when hind limbs adpressed; tibiotarsal articulation extends to middle of eye; tarsal fold weak, extending from moderately large, flat, elliptical inner metatarsal tubercle to middle of tarsus; outer metatarsal tubercle minute, round, indistinct; subarticular tubercles round; single row of small, round supernumerary tubercles on proximal segments of each digit; toes moderately short and slender; length of toes from shortest to longest, 1-2-3-5-4, third and fifth about equal in length; toes about three-fourths webbed; web extending to base of terminal phalanx of fourth toe; discs small, about two-thirds size of those on fingers. Anal opening directed posteroventrally at middle of thighs; two transverse dermal folds above anus; short, thin anal sheath present; many small tubercles lateral and ventral to anal opening. Skin of dorsum, chin, and ventral surfaces of limbs smooth; belly moderately granular; posterior surfaces of thighs heavily granular; no thoracic fold. Tongue nearly round, shallowly notched behind, free posteriorly for about one-fourth its length; vomerine teeth, 3-4, long, situated on posteroventral edges of narrow transverse vomerine ridges between moderately large, round inner nares; no vocal slits.

Color (in alcohol) purplish brown on dorsal surfaces of head, body, and limbs; fine darker reticulations on dorsum; flanks pale tan with dark brown spots; posterior surfaces of thighs tan; chin creamy white with brown spots; belly dusty white; undersides of thighs and shanks yellow; webbing grayish brown; undersides of first two fingers dusty white, of third and fourth fingers and of feet brown; anal stripe absent; small white flecks above and below anal opening.

Color (in life) dark green on dorsal surfaces of head, body, and limbs; darker green reticulations on back; flanks dusty white with dark olive-gray mottling; dark olive-gray stripe from nostril through eye and then to insertion of forelimb; upper lips pale green; inguinal region, anterior and posterior surfaces of thighs dark yellowish orange; ventral surfaces of tarsi and shanks, and webbing of feet dusty yellow; belly white; iris silvery gold.

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Fig. 3. Holotype of *Hyla charadricola* (KU 58414).  $\times$  1.5.

*Variation.*—Adult males have snout-vent lengths from 35.3 to 44.4 mm., and adult females from 43.4 to 50.9 mm. No notable variation in structure is displayed in the type series. In some individuals the dark reticulation on the dorsum is faint. Juveniles in life had dorsal colorations varying from rich brown with darker reticulations to pale green or gray with dark green reticulations. Some adults when collected were pale green with faint or no dorsal reticulations; later these individuals darkened. In all specimens the anal stripe is absent, and the flanks are heavily spotted.

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Comparisons.—Hyla charadricola differs from all other members of the Hyla bistincta group in the following combination of characters: truncate snout, green dorsum, and absence of a thoracic fold. From other hylids that occur in the same area, Hyla charadricola differs from Hyla miotympanum and H. arborescandens, both of which are green dorsally, by having a truncate snout and longer fingers with less webbing. Hyla eximia, though green, has brown dorsal spots, shorter fingers, and a round snout. Hyla robertsorum differs in having a round snout and brown dorsum, and Hyla taeniopus is much larger, has transverse bands on the limbs, and has extensive webbing between fingers.

Remarks.—At the type locality, a shallow rocky stream in pine forest, *Hyla charadricola* was found beneath rocks at the edge of fast moving sections of the stream and beneath rocks in shallow riffles in the stream. Most of the frogs were in water. At night they were found sitting on rocks in the stream. *Hyla miotympanum*, which is abundant at the type locality, lives in bushes and beneath rocks along the stream but usually is not found in the riffles inhabited by *Hyla charadricola*. At Lago de Tejocotal *Hyla charadricola* was found beneath rocks near the shore of the lake and by a stream in the pine forest. Individuals were found on low vegetation overhanging a small stream in pine-oak forest four kilometers southwest of Tianguistengo.

Five recently metamorphosed young (KU 58424-9) found at the type locality on June 8, 1960, have snout-vent lengths of 22.4 to 24.0 (average 23.2) mm. The young are colored like the adults, except that in life the dorsum is a brighter green and the flanks are more yellow than tan and have less dark spotting than in adults.

Distribution.—Hyla charadricola inhabits streams in pine and pine-oak forests at elevations of 2000 to 2300 meters in northern Puebla and eastern Hidalgo (Fig. 2).

Specimens examined.—Hidalgo: Lago de Tejocotal, 11 km. E Acaxochitlán, KU 58438, UMMZ 104032, 118165; 4 km. SW Tianguistengo, KU 53811-2. Puebla: *11.7 km. W Huachinango*, UMMZ 121567 (5); Río Totolapa, 14.4 km. W Huachinango, KU 53813-5, 55624, 58414-37, 59813 (skeleton), 59886 (skeleton), MCZ 34964-5, UIMNH 50966, UMMZ 118166 (5), S-2242 (skeleton).

#### **Hyla robertsorum** Taylor

Hyla robertsorum Taylor, Univ. Kansas Sci. Bull., 26:393-396, figs. 5-6, November 27, 1940 [Holotype.—CNHM 100124 (formerly EHT-HMS 16264) from El Chico Parque Nacional, Hidalgo, México; Mr. and Mrs. Radclyffe Roberts and Edward H. Taylor collectors]; Univ. Kansas Sci. Bull., 28:310, November 15, 1942. Taylor and Smith, Proc. U. S. Natl. Mus., 95:589, June 30, 1945. Smith and Taylor, Bull. U. S. Natl. Mus., 194:87, June 17, 1948; Univ. Kansas Sci. Bull., 33:333, March 20, 1950. Rabb and Mosimann, Occas. Papers Mus. Zool.

Univ. Michigan, 563:1-9, March 29, 1955. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15:48, December 20, 1961.

*Diagnosis.*—Maximum snout-vent length in males, 48 mm.; snout in dorsal profile rounded; tarsal fold short and weak; inner metatarsal tubercle moderate in size and elliptical; outer metatarsal tubercle small, round, and indistinct; webbing extending to base of penultimate phalanx of fourth toe; nuptial spines on thumb small; weak thoracic fold present; anal opening above level of middle of thighs; dorsum dark brown with dark reticulations; venter brown with cream-colored flecks; flanks brown with creamy white spots; anal stripe absent; small white spots in anal region; vocal slits absent.

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Description.—The following description is based on KU 57651 from El Chico Parque Nacional, Hidalgo. Adult male having a snout-vent length of 45.1 mm.; tibia length, 22.1 mm., 49.0 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 21.5 mm.; greatest width of head, 13.7 mm., 30.4 per cent of snout-vent length; head length, 12.6 mm., 27.9 per cent of snout-vent length; diameter of eye, 4.0 mm.; diameter of tympanum, 1.8 mm., 45 per cent of diameter of eye. Snout short, in lateral profile blunt, in dorsal profile round; canthus rounded; loreal region slightly concave; lips thick, round, and not flaring; nostrils slightly protuberant; internarial distance, 3.6 mm.; interorbital distance, 4.0 mm., slightly broader than width of eyelid, 3.5 mm. A moderately heavy dermal fold from posterior corner of eye above tympanum and curving downward towards insertion of forearm; tympanum nearly round, covered by dermal fold above, its diameter slightly less than its distance from eye. Forearm moderately robust: distinct fold on wrist; prepollex much enlarged with patch of small nuptial spines continuous on side of digit; similar line of nuptial spines on inner edge of second finger; subarticular tubercles round, moderate in size, none bifid; supernumerary tubercles small and present only proximally; fingers long and slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large, that on third finger about size of tympanum; no web between first and second fingers; rudimentary web between other fingers. Legs robust; heels over-lap by about one-fourth length of shank when hind limbs adpressed; tibiotarsal articulation extending to posterior corner of eye; tarsal fold weak, extending to about middle of tarsus; inner metatarsal tubercle moderately large, flat, and elliptical; outer metatarsal tubercle small, round, and indistinct; subarticular tubercles round; supernumerary tubercles small, in single row on proximal segments of each digit; toes moderately long and slender; length of toes from shortest to longest, 1-2-5-3-4, the fifth nearly as long as third; toes nearly fully webbed; web extending to base of penultimate phalanx of fourth toe and to discs on other toes; discs small, about two-thirds size of those on fingers. Anal opening above middle of thighs; anal sheath short, deeply creased medially; heavy transverse dermal fold above anus; no large anal tubercles. Skin of all dorsal surfaces, chin, and ventral surfaces of limbs, except proximal parts of thighs, smooth; belly and proximal parts of thighs areolate; thoracic fold present, weak. Tongue elliptical, slightly longer than wide, not notched behind, and free posteriorly for about one-fourth of its length; vomerine teeth 3-3, situated on small, widely separated, transverse ridges between rather small elliptical inner nares; no vocal slits.

Color (in alcohol) dark brown with irregular darker reticulations on dorsal surfaces of head, body, and limbs; flanks brown with small creamy white spots; posterior surfaces of thighs dark brown; chin creamy tan; belly grayish brown with cream-colored flecks; ventral surfaces of limbs pale brown; webbing on feet gray; small white spots in anal region.

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Color (in life) chocolate brown with darker brown reticulations and irregular blotches above; flanks brown with yellow spots; belly gray to grayish brown with faint cream-colored spots; iris a deep bronze color.

Variation.—In males the total number of vomerine teeth varies from 4 to 7. In many specimens the vomerine ridges are larger and more closely approximated medially than in the specimen described above. Females attain snout-vent lengths of 51 mm., have as many as 9 vomerine teeth, and have a proportionately larger tympanum than males. Some of the largest specimens of both sexes have indistinct cream-colored pustules scattered on the ventral surface of the forearm. Some individuals have nearly uniform grayish brown ventral surfaces; in others the chin, as well as the abdomen, is brown with cream-colored spots. The dorsal surfaces of some specimens are nearly uniform dark brown with no reticulations. In others the dorsum is paler brown with distinct darker mottling; in some of these there is little mottling laterally, so that there is the effect of an irregular, pale brown, dorsolateral stripe.

Tadpoles.—The tadpoles of this species were described by Rabb and Mosimann (1955). Tadpoles obtained from streams at 3.3 kilometers north and at 8.5 kilometers southeast of Zacualtipán, Hidalgo, are like those described by Rabb and Mosimann in having ½ tooth rows, peglike serrations on the beaks, and long rounded tails. The largest tadpole (KU 60078) has small hind legs, a body length of 22 mm., and a total length of 61 mm.

Remarks.—Taylor (1940:393) found frogs of this species in plants along small spring-fed rivulets in an open meadow at El Chico Parque Nacional. Also, he noted that active frogs dove into the streams and took refuge in the mud on the bottom. Rabb and Mosimann (1955:1) found this species along banks of tiny streams in open meadows and noted that the frogs sought refuge in the water. At El Chico Parque Nacional on June 8, 1960, I found *Hyla robertsorum* under rocks along small rivulets by day; at night, when the temperature was 14° C., frogs were sitting on rocks and in junipers overhanging a small stream. At the same locality on June 23 and 24, 1962, frogs of this species were found on rainy nights, when the temperature varied from 10 to 12° C. At this time the frogs were sitting on the grassy banks of rivulets in the meadow. During the day *Hyla robertsorum* was found on the earthen banks of the rivulets in places where dense growths of grass overhung the streams. On December 23, 1959, one specimen of *Hyla robertsorum* was found beneath a rock in a small stream in pine forest at 3.3 kilometers north of Zacualtipán.

Rabb and Mosimann (1955:1) obtained tadpoles of *Hyla robertsorum* from quiet pools of a stream at El Chico Parque Nacional. I found tadpoles in pools in rocky streams in pine forest at 3.3 kilometers north and at 8.5 kilometers southeast of Zacualtipán. Four completely metamorphosed juveniles obtained on June 8, 1960, at El Chico Parque Nacional have snout-vent lengths of 30.6 to 32.0 mm. Gravid females were found at the same locality on June 8, 1960, and June 23, 1962.

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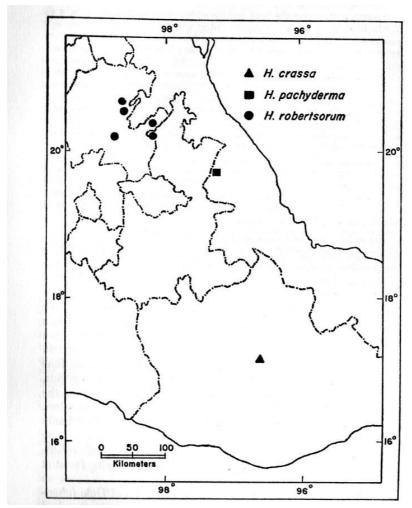


Fig. 4. Map showing locality records for *Hyla crassa, Hyla pachyderma*, and *Hyla robertsorum*.

Distribution.—Hyla robertsorum inhabits streams in the pine and fir forests in the higher parts (2250 to 3050 [Pg 485] meters) of the Sierra Madre Oriental in extreme northern Puebla and eastern Hidalgo (Fig. 4).

Specimens examined.—HIDALGO: 16 km. W Agua Blanca, UMMZ 106432 (6); El Chico Parque Nacional, CNHM 75786, 100124, KU 57650-71, 59824-5 (skeletons), 59914-5 (skeletons), 71269-95, 71757 (skeleton), UIMNH 10349-64, 27022-35, 39434-49, UMMZ 92462, 106401 (5), 106443 (tadpoles), USNM 114762-85, 134268; 3.3 km. N Zacualtipán, KU 53810, 60078 (tadpoles); 8.5 km. SE Zacualtipán, KU 60079 (tadpoles). Puebla: Honey, UMMZ 95245.

## **Hyla pachyderma** Taylor

Hyla pachyderma Taylor, Univ. Kansas Sci. Bull., 28:308-310, pl. 27, figs. 1-4, November 12, 1942 [Holotype.—USNM 115029 from Pan de Olla, Veracruz, south of Tezuitlán, Puebla, México; Hobart M. Smith collector]. Taylor and Smith, Proc. U. S. Natl. Mus., 95:588, June 30, 1945. Smith and Taylor, Bull. U. S. Natl. Mus., 194:86, June 17, 1948; Univ. Kansas Sci. Bull, 33:350, March 20, 1950. Rabb and Mosimann, Occ. Papers Mus. Zool. Univ. Michigan, 563:7-8, March 29, 1955.

Diagnosis.—Maximum snout-vent length in males 40 mm.; snout in dorsal profile round; tarsal fold strong; inner metatarsal tubercle round and moderate in size; outer metatarsal tubercle small and indistinct; webbing on foot extending to middle of penultimate phalanx of fourth toe; nuptial spines on thumb large; thoracic fold present; anal opening at level of middle of thighs; dorsum dull grayish brown with scattered indistinct dark flecks; venter cream-color mottled with brown on throat and chest; flanks grayish brown with cream-colored reticulations; anal stripe distinct, creamy white, sometimes extending outward on thighs; white spots or line below anus; vocal slits absent.

Description.—The following description is based on USNM 115028 from Pan de Olla, Veracruz. Adult male having a snout-vent length of 39.9 mm.; tibia length, 21.0 mm., 52.6 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 20.5 mm.; greatest width of head, 12.8 mm., 32.1 per cent of snout-vent length; head length, 12.3 mm., 30.8 per cent of snout-vent length. Snout short, in lateral profile bluntly rounded, in dorsal profile rounded; canthus rounded; loreal region slightly concave; lips thick, round, and not flaring; nostrils slightly protuberant; internarial distance, 2.7 mm.; interorbital distance, 3.7 mm., somewhat broader than eyelid, 2.9 mm. A heavy dermal fold from posterior corner of eye above tympanic region and then to insertion of forearm; tympanum completely concealed. Forearm moderately robust; distinct fold on wrist; prepollex enlarged bearing cluster of moderate-sized, horny, nuptial spines continuous on edge of digit; row of spines present on second finger; subarticular tubercles round, small proximally and slightly larger distally; supernumerary tubercles small and indistinct; three palmar tubercles, median and outer partly fused; fingers long, moderately slender; discs moderately large; length of fingers from shortest to longest, 1-2-4-3; second and fourth fingers subequal in length; webbing between fingers rudimentary. Heels overlap by about one-fourth length of shank when hind limbs adpressed; tibiotarsal articulation extends to anterior edge of eye; tarsal fold thick, low, extending nearly to heel; inner metatarsal tubercle moderately large and round; outer metatarsal tubercle small and indistinct; subarticular tubercles small and round; supernumerary tubercles small, present on proximal segments of digits; toes moderately long

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and slender; length of toes from shortest to longest, 1-2-3-5-4; third and fifth toes subequal in length; toes about three-fourths webbed; web extending to middle of penultimate phalanx of fourth toe; discs rather small, about two-thirds size of those on fingers. Anal opening directed posteroventrally at level of middle of thighs; anal flap slightly elongate; thick, transverse dermal fold above anus. Skin of dorsum and ventral surfaces of limbs, except thighs, smooth; skin of chin, belly, and ventral surfaces of thighs granular; thoracic fold present. Tongue nearly round, slightly notched behind, and barely free posteriorly; vomerine teeth 3-3, situated on posteroventral edges of small, transverse vomerine ridges between rather large triangular inner nares; no vocal slits.

Color (in alcohol) of dorsal surfaces of head, body, and limbs dull grayish brown with indistinct scattered darker flecks; flanks grayish brown with cream-colored reticulations; posterior surfaces of thighs tan; chin cream-color, mottled with brown; belly creamy yellow; anal stripe cream-color.

*Variation.*—In addition to the specimen described above three others are known. One is a juvenile having a snout-vent length of 29.5 mm., and two are females having snout-vent lengths of 46.9 and 41.6 mm. Variation in structure and coloration between the four specimens is slight. In the females the tympani are partly visible and are about one-third the diameter of the eye; the chest is mottled with brown; the anal stripe extends laterally in the form of a row of cream-colored dashes and spots onto the posterodorsal surfaces of the thighs.

Remarks.—On the basis of the four specimens available for study, *Hyla pachyderma* seems to be closely related to *Hyla crassa* and *Hyla robertsorum*. In the *Hyla bistincta* group, *Hyla pachyderma* is unique in having enlarged nuptial spines.

Taylor and Smith (1945:588) stated that the frogs were found on bushes and weeds beside a small, bounding stream near Pan de Olla. I have searched unsuccessfully for this species in the area around Pan de Olla and Tezuitlán.

Distribution.—This species is known only from a stream at an elevation of about 1600 meters on the Atlantic slopes of the Sierra Madre Oriental in central Veracruz (Fig. 4).

Specimens examined.—Veracruz: Pan de Olla, south of Tezuitlán, Puebla, USNM 115026-9.

#### Hyla crassa (Brocchi)

Cauphias crassus Brocchi, Bull. Soc. Philom. Paris, ser. 7, 1:130, 1877 [Holotype.—MNHN 6331 from "Mexico;" Adolphe Boucard collector].

Cauphias crassum Brocchi, Études des batraciens de l'Amérique Centrale, p. 64, pl. 12, fig. 4, 1882. Díaz de León, Indice de los batracios que se encuentran en la República Mexicana, p. 21, June, 1904. Kellogg, Bull. U. S. Nat. Mus., 160:118-120, March 31, 1932. Taylor, Univ. Kansas Sci. Bull., 26:392, November 15, 1940. Rabb and Mosimann, Occas. Papers Mus. Zool. Univ. Michigan, 563:7, March 29, 1955.

Hyla crassa, Boulenger, Catalogue Batrachia Salientia, 2nd. Ed., p. 396, February 1, 1882. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 281, September, 1901. Nieden, Das Tierreich, Amphibia, Anura 1, p. 248, June, 1923. Smith and Taylor, Bull. U. S. Natl. Mus., 194:86, June 17, 1948. Taylor, Amer. Mus. Novitates, 1437:20, December 7, 1949.

Hypsiboas crassus, Cope, Bull. U. S. Natl. Mus., 32:14, 1887.

Hyla robustofemora Taylor, Univ. Kansas Sci. Bull., 26:389-393, figs. 3-4, November 27, 1940 [Holotype.—UIMNH 25050 (formerly EHT-HMS 16314) from Cerro San Felipe, 15 kilometers northeast of Oaxaca, Oaxaca, México; Edward H. Taylor collector]; Univ. Kansas Sci. Bull., 28:310, November 15, 1942. Smith and Taylor, Bull. U. S. Natl. Mus., 194:86, June 17, 1948. Taylor, Amer. Mus. Novitates, 1437:20, December 7, 1949. Smith and Taylor, Univ. Kansas Sci. Bull., 33:339, March 20, 1950. Rabb and Mosimann, Occas. Papers Mus. Zool. Univ. Michigan, 563:7, March 29, 1955.

*Plectrohyla crassa*, Hartweg, Occas. Papers Mus. Zool. Univ. Michigan, 437:1, June 30, 1941. Stuart, Occas. Papers Mus. Zool. Univ. Michigan, 455:6, January 5, 1942.

Diagnosis.—Maximum snout-vent length in males 54 mm.; snout in dorsal profile round; tarsal fold strong; inner metatarsal tubercle small and elliptical; outer metatarsal tubercle small, flat, and indistinct; foot fully webbed; nuptial spines on thumb small; thoracic fold absent; anal opening at level of middle of femur; dorsum dull olive-green; belly creamy yellow; chin gray with yellow flecks; flanks dull olive-green with scattered cream-colored spots; and stripe faint, cream-color; vocal slits absent.

Description.—The following description is based on UIMNH 25050 from Cerro San Felipe, Oaxaca. Adult male having a snout-vent length of 53.7 mm.; tibia length, 26.9 mm., 50.1 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 25.4 mm.; greatest width of head, 17.6 mm., 32.8 per cent of snout-vent length; head length, 16.0 mm., 29.8 per cent of snout-vent length; diameter of eye, 5.4 mm.; diameter of tympanum, 1.5 mm., 27.8 per cent of diameter of eye. Snout short, in lateral profile bluntly rounded, in dorsal profile broadly round; canthus absent; loreal region nearly flat; lips thick and not flaring; nostrils barely protuberant; internarial distance, 3.8 mm.; interorbital distance, 4.7 mm., somewhat broader than width of eyelid, 3.8 mm. Heavy dermal fold from posterior corner of eye above tympanum and then to insertion of forearm; tympanum concealed above, its diameter about equal to its distance from eye. Forearm thick; distinct fold on wrist; prepollex enlarged bearing patch of small nuptial spines continuous on side of digit; similar patch on second finger; subarticular tubercles small and round, none bifid; few supernumerary tubercles on proximal segments of digits; large, flat palmar tubercle; fingers long and slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large; rudimentary web between second and third fingers and between third and fourth. Legs thick; heels overlap by about one-fourth length of shank when hindlimbs adpressed; tibiotarsal articulation extends to posterior corner of eye; tarsal fold thick, extending to heel; inner metatarsal tubercle small and elliptical; outer metatarsal tubercle small, flat, and indistinct; subarticular tubercles small and round; single row of supernumerary tubercles on proximal segments of each digit; toes moderately short and slender; length of toes from shortest to longest, 1-2-3-5-4; toes fully webbed; flap of skin on inner surface of first toe; discs about same size as those on fingers. Anal opening directed posteroventrally at middle of thighs; anal sheath moderately elongate; small tubercles below anal opening. Skin of dorsum rather smooth, somewhat granular on dorsal surfaces of limbs; skin of chin and

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belly moderately granular; that of posterior surfaces of thighs smooth; no thoracic fold. Tongue nearly round, shallowly notched posteriorly, and free for about one-fourth its length; vomerine teeth 5-5, situated on rounded ridges between small inner nares; no vocal slits.

Color (in alcohol) dull olive-green on dorsal surfaces of head, body, and limbs; flanks dull olive-green with scattered cream-colored spots; posterior surfaces of thighs grayish brown with faint creamy mottling; chin gray with cream-colored spots; belly creamy yellow, suffused with gray posteriorly; undersides of feet and webbing gray; anal stripe faint, pale cream-color.

*Variation.*—The only other known specimen (MNHN 6331) is a female having a snout-vent length of 53.7 mm. and resembling the specimen described above in most details of morphology. In MNHN 6331 the tympanum is completely concealed, and the 8-7 vomerine teeth are arranged in two irregular rows. The female has more cream-colored mottling on the flanks and posterior surfaces of the thighs and more distinct mottling on the throat than the male described above.

Remarks.—The systematic status of Cauphias crassus Brocchi has been in doubt since the time of the original description. Brocchi (1877:130) stated: "Les dernieres phalanges sont obtuses, tronqués a leur extrémité antérieure." Brocchi placed the species in his genus Cauphias (type species, C. quatemalensis), which he considered to be related to Hylodes ( = Eleutherodactylus in the sense used by Brocchi); he thereby placed Cauphias in his Hylodidae ( = Leptodactylidae, in part). This idea of relationships was perpetuated by Barbour (1927:96), who reported on the second known specimen of *Cauphias guatemalensis* and stated: "When I dissected the sternum I was at once struck by its similarity to Noble's figures of transitional types between arciferal and firmisternal forms. The Cauphias sternum recalls some of his figures for Sminthillus and Eleutherodactylus. This genus is probably most closely related to the latter and has probably become highly modified to meet some peculiar environmental condition or on account of some specialized habits as yet unknown." Kellogg (1932:118) placed Cauphias in the Leptodactylidae and stated that the terminal phalanges are T-shaped. Hartweg (1941:1) considered Plectrohyla to be the correct generic name for Cauphias quaternalensis; he thereby relegated Cauphias to the synonomy of *Plectrohyla*. Hartweg (1941:9) further showed that the terminal phalanges of Plectrohyla guatemalensis were not T-shaped and that intercalary cartilages were present. Thus, he correctly concluded that Plectrohyla guatemalensis (and P. crassa by implication) was a member of the family Hylidae. Stuart (1942:6) followed Hartweg's allocations and further suggested that *Plectrohyla crassa* might be the same species as *Hyla robustofemora* Taylor. In his description of H. robustofemora Taylor (1940:392), who had not examined the type of Cauphias crassus, stated that were it not for the statements of Brocchi and Kellogg that C. crassus has Tshaped terminal phalanges, "I might suspect I had before me a specimen of Cauphias closely related to crassum."

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I have compared the type of *Cauphias crassus* with that of *Hyla robustofemora*. With the exception of the minor differences mentioned in the preceding section on variation, the specimens are alike, leaving little doubt that they represent the same species. The statements of Brocchi and Kellogg to the contrary, the type of *Cauphias crassus* possesses intercalary cartilages between the penultimate and terminal phalanges; the latter are not T-shaped, but as in the type of *Hyla robustofemora*, resemble those typical of *Hyla*. On the basis of the morphological characters, as pointed out for *Hyla robustofemora* by Taylor (1940:392), *Hyla crassa* is a member of the *Hyla bistincta* group.

Distribution.—This species is definitely known only from a small stream at an elevation of 2300 meters in the mountains of central Oaxaca (Fig. 4).

Specimens examined.—OAXACA: Cerro San Felipe, UIMNH 25050. "Mexico," MNHN 6331.

## RELATIONSHIPS

The evolutionary trend in the members of the *Hyla bistincta* group is towards aquatic habits. *Hyla bistincta*, the least specialized species in the group, has relatively short fingers, webbing between the fingers, a truncate, high snout, and relatively large subarticular and supernumerary tubercles. *Hyla charadricola* resembles *bistincta* in having relatively short fingers, a slight amount of webbing, and a truncate snout. Apparently these two species are more closely related to one another than either is to the other species in the group. *Hyla robertsorum*, *pachyderma*, and *crassa* are the most aquatic members of the group. These species are closely related, possibly conspecific. All have round, sloping snouts, robust forearms, long, unwebbed fingers, and large webbed feet. Both *H. pachyderma* and *H. crassa* seem to be advanced beyond *H. robertsorum*. If small nuptial spines, moderately webbed feet, and absence of a well-defined thoracic fold are considered to be less advanced than large nuptial spines and a strong thoracic fold, as in *H. pachyderma*, or fully webbed feet, as in *H. crassa*, then *H. robertsorum* must be considered to be less advanced than *H. pachyderma* or *H. crassa*.

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Members of the *Hyla bistincta* group inhabit mountain streams. The frogs can be found along these streams throughout the year. Since in most stream-breeding hylids there is no migration to breeding sites, the breeding call does not function to attract females to the breeding site. Apparently voices are lacking in all members of the *Hyla bistincta* group, except in *Hyla bistincta*. The presence of vocal slits and the ability to call further indicate that *Hyla bistincta* is the primitive member of this group.

Members of the *Hyla bistincta* group and the species of *Plectrohyla* closely resemble each other in osteology and body form of the adults and in structure of the tadpoles. This resemblance suggests a close relationship between the two groups. *Plectrohyla* apparently evolved from an

ancestral stock resembling the extant *Hyla bistincta*. Probably this stock gave rise independently to *Plectrohyla* and to the *Hyla robertsorum-pachyderma-crassa* complex. In the former the voice was retained, and a projecting prepollex spine developed, whereas in the latter the voice was lost, and the prepollex spine did not project. *Plectrohyla* lives in mountain streams in the Chiapan-Guatemalan highlands; the *Hyla robertsorum-pachyderma-crassa* complex inhabits similar environments in the Sierra Madre Oriental in México. *Hyla charadricola* also lives in the Sierra Madre Oriental, whereas *Hyla bistincta* is widespread in the mountains of México southeastward to the Isthmus of Tehuantepec.

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