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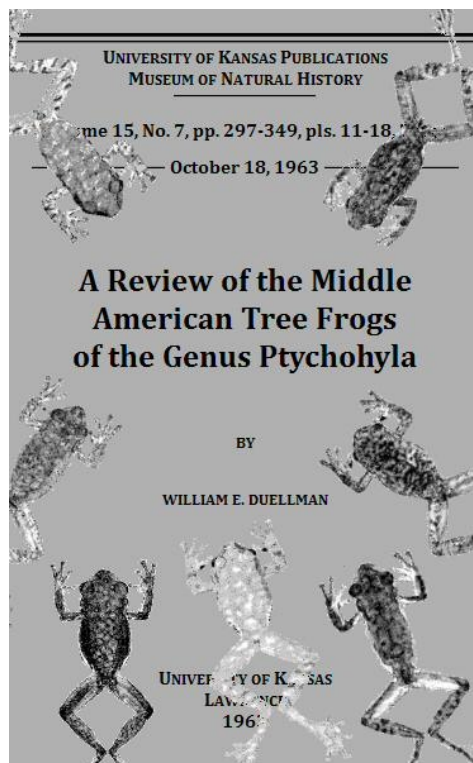
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*** START OF THE PROJECT GUTENBERG EBOOK A REVIEW OF THE MIDDLE AMERICAN TREE FROGS OF THE GENUS PTYCHOHYLA ***



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Volume 15, No. 7, pp. 297-349, pls. 11-18, 7 figs.

October 18, 1963

**A Review of the Middle American Tree
Frogs
of the Genus Ptychohyla**

BY

UNIVERSITY OF KANSAS
LAWRENCE
1963

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**A Review of the Middle American Tree Frogs
of the Genus *Ptychohyla***

[Pg 299]

BY

WILLIAM E. DUELLMAN

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INTRODUCTION

Probably no ecological group of hylid frogs (some *Hyla* plus *Plectrohyla* and *Ptychohyla*) in Middle America is so poorly known as those species that live in the cloud forests on steep mountain slopes and breed in cascading mountain streams. During the last half of the nineteenth century most of the species of hylids living in the lowlands of southern México and northern Central America were named and described. Despite the extensive collecting by Salvin and Godman, Nelson and Goldman, and the various expeditions of the *Mission Scientifique*, no members of the genus *Ptychohyla* were obtained until 1927, when in the mountains of El Salvador Ruben A. Stirton found a small tree frog that subsequently was described and named *Hyla euthysanota* by Kellogg (1928). Until recently frogs of this genus were known from few specimens and in the literature by nearly as many names.

Although I first collected *Ptychohyla* in 1956, it was not until 1960 that special efforts were made to obtain specimens of this genus. The summer of 1960 was spent in southern México and Guatemala, where every accessible stream in the cloud forests was searched for tree frogs, especially *Ptychohyla* and *Plectrohyla*. Similar, but less extensive, investigations were carried out in 1961 and 1962. The result of this field work is a rather large collection of *Ptychohyla* representing all of the known species, plus tape recordings of the breeding calls and tadpoles of all of the species.

Previously, I have discussed the nomenclature of one of the species (Duellman, 1960) and have described two new species (Duellman, 1961). In the latter paper I made reference to a future account (this one) that would deal with the systematics and biology of the entire genus. Although I have series of specimens, tadpoles, osteological preparations, and recordings of breeding calls, thereby having a wide array of data at my disposal, much still remains to be learned about these frogs, especially about various aspects of their life histories. Even the validity of the genus is open to question; this problem is discussed at length in the section beyond entitled "*Ptychohyla* as a Natural Assemblage."

Acknowledgments

I am indebted to the following persons for permitting me to examine specimens in their care: Miguel Alvarez del Toro, Museo Zoología de Tuxtla Gutierrez, México (MZTG); Charles M. Bogert and Richard G. Zweifel, American Museum of Natural History (AMNH); Doris M. Cochran, United States National Museum (USNM); Norman Hartweg and Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); Robert F. Inger, Chicago Natural History Museum (CNHM); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Heinz Wermuth, Zoologisches Museum Berlin (ZMB); and Ernest E. Williams, Museum of Comparative Zoology (MCZ). The abbreviations following names of institutions will be used throughout the text; the Museum of Natural History at the University of Kansas is abbreviated KU.

Throughout my work on these frogs I have profited from discussions with L. C. Stuart, who has made many valuable suggestions and with his characteristic generosity has placed at my disposal his extensive collections of tadpoles from Guatemala. For his aid I am indeed grateful. I am grateful to Thomas E. Moore for tapes of breeding calls of two species.

My own field work was made more enjoyable and profitable through the assistance of Dale L. Hoyt, Craig E. Nelson, Jerome B. Tulecke, and John Wellman, all of whom spent many hours in often unsuccessful attempts to collect specimens and record breeding calls of *Ptychohyla*. I am indebted to many residents of México, Guatemala, and El Salvador for permission to work on their land and for providing shelter, food, and guides. I am especially grateful to Mr. and Mrs. Horatio Kelly of "Colegio Linda Vista" at Pueblo Nuevo Solistahuacán, Chiapas, for a pleasant stay at their school; Jordi Juliá Z. of the Comisión del Papaloapan, Ciudad Alemán, Veracruz, for arranging for field work in northern Oaxaca in 1959; Walter Hannstein and Lothar Menzel for the use of facilities at Finca La Paz, Guatemala, in 1960; Alan Hempstead for the use of facilities at Finca Los Alpes, Guatemala in 1960 and 1961; and Julio Aguirre C. of the Instituto Tropical de Investigaciones Científicas, San Salvador, El Salvador, for providing comfortable working quarters and transportation and guides to the mountains in northern El Salvador. Without the cheerful efforts of Jorge A. Ibarra, Director of the Museo Nacional de Historia Natural in Guatemala, my field work would have been greatly restricted during politically precarious times in that country. Permits to collect in México were furnished by the late Luis Macías Arellano of the Dirección General de Caza. Each of these individuals has my profound thanks for his indispensable aid.

Field work on hylid frogs in Middle America has been supported by the National Science Foundation, Grant NSF-G9827, and this is the 9th publication on the results of study of the material from America.

Materials and Methods

During the course of this study I have examined 247 frogs that I assign to the genus *Ptychohyla*, plus 40 lots of tadpoles and 12 skeletal preparations. Furthermore, I have examined all of the type specimens. I have studied each of the species and subspecies in the field and have examined from seven (*P. euthysanota macrotympanium*) to 33 (*P. spinipollex*) living individuals of each species.

Measurements given in the analysis of data and in the descriptions of the species are those described by Duellman (1956). In the descriptions of living colors the capitalized names are from Ridgway (1912). All interpretations of osteological characters are based on specimens cleared in potassium hydroxide and stained with alizarin red.

ANALYSIS OF DATA

Data that are used to arrive at a systematic arrangement of the species of *Ptychohyla* are analyzed and discussed below for the values inherent in the analysis. These data are of some value also in the recognition of species and subspecies but if employed for that purpose the data must be used in combination with the keys and the diagnoses of the individual species and subspecies.

External Morphology

Each of the external morphological characters used in the systematic treatment of *Ptychohyla*, as well as the nature of the tongue, is discussed below.

SIZE AND PROPORTIONS.—Comparisons of size and certain proportions are given in [Table 1](#). Frogs of this genus are small; the largest specimen examined is a female of *P. euthysanota euthysanota* having a snout-vent length of 53.3 mm. The species comprising the *Ptychohyla schmidtorum* group are smaller; the largest specimen examined is a female of *P. schmidtorum schmidtorum* having a snout-vent length of 38.0 mm. An analysis of the various measurements and proportions shows few constant differences. *Ptychohyla ignicolor* differs from all of the other species in having the head slightly wider than long and the tympanum noticeably less than half the size of eye. *Ptychohyla spinipollex* has a relatively narrow interorbital distance, approximately equal to the width of the eyelid, whereas in all of the other species that distance is much more than the width of the eyelid.

SNOUT.—All species have a blunt snout. In *P. leonhardschultzei* and *P. ignicolor* the snout is nearly square in lateral profile; in *P. schmidtorum* the snout is slightly rounded above and below, and in the other species it is rounded above. *Ptychohyla leonhardschultzei* and *P. spinipollex* have a vertical fleshy rostral keel on the snout; in these [species](#), because of this keel, the snout in dorsal profile is pointed. The nostrils are slightly protuberant in all species, and in *P. schmidtorum* the internarial region is slightly depressed.

TABLE 1.—VARIATION IN CERTAIN CHARACTERS IN THE SPECIES OF PTYCHOHYLA. (MEANS ARE IN PARENTHESES BELOW THE RANGES.)

Species	Sex	Number of specimens	Maximum snout-vent length	Tibia length	Tympanum	Vomerine teet
				Snout-vent length	Eye	
<i>P. euthysanota euthysanota</i>	♂	17	38.1	44.4-55.0 (48.7)	48.6-63.8 (56.3)	4-6 (5.1)
	♀	15	53.3	46.5-56.6 (51.4)	42.9-56.4 (51.4)	6-18 (9.6)
<i>P. euthysanota macrotympanum</i>	♂	5	38.0	48.8-52.0 (50.2)	50.0-57.1 (54.1)	0-4 (2.6)
	♀	5	44.8	46.4-54.1 (50.2)	48.7-58.9 (53.7)	8-10 (9.2)
<i>P. leonhardschultzei</i>	♂	16	35.6	48.8-56.1 (51.2)	48.7-61.9 (52.1)	6-9 (6.5)
	♀	3	41.6	52.3-59.5 (54.7)	47.5-48.6 (48.1)	7-12 (9.5)
<i>P. spinipollex</i>	♂	32	41.2	46.9-53.1 (49.0)	45.0-55.2 (49.5)	3-7 (4.9)
	♀	6	44.6	46.1-50.2 (48.8)	47.7-53.8 (50.4)	6-10 (7.6)
<i>P. schmidtorum schmidtorum</i>	♂	25	32.8	45.3-52.4 (48.1)	51.5-59.3 (54.7)	5-11 (6.2)
	♀	9	38.0	46.5-49.1 (47.7)	51.3-58.3 (54.9)	7-11 (8.7)
<i>P. schmidtorum chamulae</i>	♂	40	30.5	46.0-51.9 (48.2)	48.2-65.6 (54.9)	4-6 (4.7)
	♀	4	31.8	48.1-52.4 (50.5)	51.4-61.7 (55.7)	4-9 (6.2)
<i>P. ignicolor</i>	♂	13	30.5	45.9-52.2 (49.6)	37.1-47.1 (43.2)	3-9 (6.1)

HAND.—The species in the *Ptychohyla euthysanota* group have a vestige of web between the first and second fingers; the other fingers are about one-third webbed. Breeding males have a cluster of horny nuptial spines on the thumb. The spines are largest in *P. spinipollex* ([Fig. 1](#)) and vary in number from 35 to 66 (average 47.4) on each thumb. In the other species of the *Ptychohyla euthysanota* group the spines are smaller and usually more numerous; the numbers of spines on each thumb (means in parentheses) in members of this group are: *P. euthysanota euthysanota*, 44-143 (83.8); *P. euthysanota macrotympanum*, 40-110 (63.0); *P. leonhardschultzei*, 24-80 (54.7). The species in the *Ptychohyla schmidtorum* group have no web between the first and second fingers and only a vestige of web between the other fingers. Furthermore, these species lack nuptial spines in breeding males. Like the usual horny [excrescences](#) on the thumbs of many species of frogs, the horny spines on the thumbs of members of the *Ptychohyla euthysanota* group are seasonal in development.

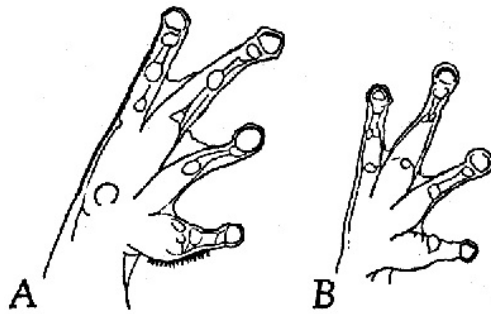


FIG. 1. Palmar views of right hands of (A) *Ptychohyla spinipollex* (KU 58054) and (B) *Ptychohyla schmidtorum schmidtorum* (KU 58043). $\times 4$.

Many workers have used the presence of a bifid subarticular tubercle beneath the fourth finger as a diagnostic character of certain species of hylids. Examination of the subarticular tubercles in *Ptychohyla* reveals considerable intraspecific variation. Bifid tubercles beneath the fourth finger are found in all species except *P. ignicolor*, which is known from only two specimens. In *P. euthysanota euthysanota* nearly 60 per cent and in *P. schmidtorum schmidtorum* about 90 per cent of the specimens have a bifid tubercle beneath the fourth finger on one or both hands. All specimens of *P. leonhardschultzei* have either a bifid or double tubercle beneath the fourth finger, and some have a bifid distal tubercle beneath the third finger.

FEET.—Members of the *Ptychohyla euthysanota* group have a weak tarsal fold, whereas in the species comprising the *Ptychohyla schmidtorum* group the tarsal fold is absent. Webbing on the foot extends to the discs of the third and fifth toes and to the base of the penultimate phalanx of the fourth toe, except in *P. ignicolor*, which has less webbing.

VENTROLATERAL GLANDS.—Breeding males develop thickened, pigmented glandular areas on the sides of the body. In living specimens of *P. schmidtorum* and *P. ignicolor* the glands are not readily visible, but in preservative they show as distinctive orange-colored areas. These glands are most distinct in *P. euthysanota*; in many specimens of this species the glands are elevated above the surrounding skin. The extent of the glands is variable (Fig. 2); probably this variability is due to different degrees of development in individual frogs rather than to interspecific differences. All *Ptychohyla ignicolor* and some *P. schmidtorum chamulae* have a small, round glandular area on the chin; to my knowledge this does not occur in the other species. Superficial examination of microscopic preparations of the glands reveals no histological differences between species. The glands occupy most of the thickened area and have narrow ducts leading to the exterior. Detailed studies of the histology will be reported elsewhere. Since the glands are developed only in breeding males, it is surmised that the glands are associated with some phase of the breeding activity.

[Pg 306]

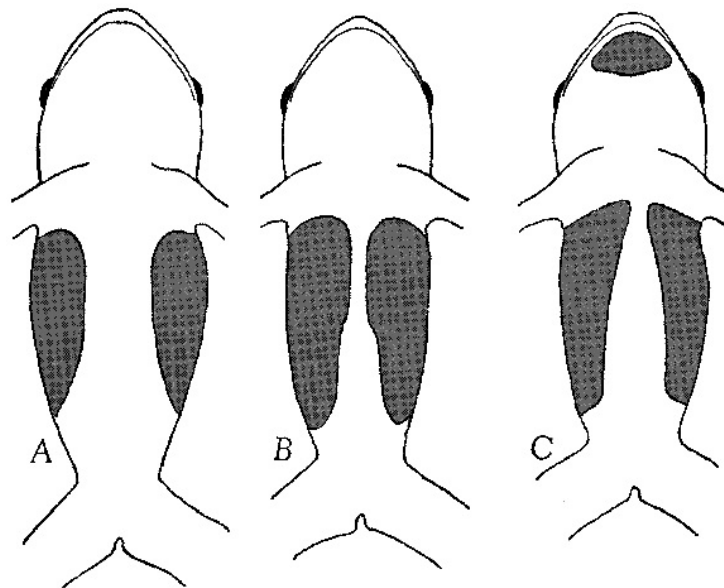


FIG. 2. Normal extent of ventrolateral glands in (A) *Ptychohyla euthysanota euthysanota* (KU 58008), (B) *Ptychohyla schmidtorum schmidtorum* (KU 58037), and (C) *Ptychohyla ignicolor* (UMMZ 119603). $\times 2\frac{1}{4}$.

TONGUE.—The shape of the tongue varies intraspecifically. Usually the tongue is ovoid; in some specimens it is barely notched posteriorly, whereas in others it is deeply notched, making the tongue cordiform. Deeply notched cordiform tongues are found in *P. leonhardschultzei* and *P. schmidtorum*; with the exception of these two species, some individuals of all species have emarginate tongues. Some individuals of all species have tongues that are shallowly notched posteriorly.

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Color and Pattern

The dorsum in living frogs of the genus *Ptychohyla* is primarily yellowish or reddish brown, except in *P. schmidtorum chamulae* and *P. ignicolor* in which it is green. Usually there are some darker blotches or reticulations on the dorsum. The venter usually is white; in *P. ignicolor* it is yellow. The venter is spotted in all members of the *Ptychohyla euthysanota* group; the species, arranged from least to most spotting ventrally, are: *P. euthysanota euthysanota*, *P. euthysanota macrotympanum*, *P. leonhardschultzei*, and *P. spinipollex*. The last two species also have bold dark spots on the flanks. *Ptychohyla schmidtorum* lacks spots on the venter, whereas *P. ignicolor* has small dark flecks ventrally.

Ptychohyla euthysanota and *P. schmidtorum* have white stripes on the upper lips and on the flanks. All species have some form of a pale stripe above the anus and usually rather distinct white or pale stripes along the ventrolateral edges of the tarsi and forearms. There are no bright or boldly marked flash-colors (colors that are revealed only when the hind limbs are extended), except in *P. ignicolor*, which has bright red flash-colors in the groin and on the thighs. In life the iris varies from several different shades of bronze color to deep red in *P. schmidtorum schmidtorum*.

The degree of metachrosis is moderate. Usually any change of color in life consists only of change in the intensity of color. At times when the over-all coloration is darkened some markings are obscured.

Osteology

The following description of the skull, hyoid, sternum, and prepollex is based on a male specimen of *P. spinipollex* (KU 68632) that has been cleared and stained. The broad, flat skull (Fig. 3) has a large frontoparietal fontanelle. The ethmoid is large and has a flange laterally. The nasals are of moderate size and in broad contact with the ethmoid, but are separated from one another medially. The anterior half of the maxillary bears a thin, high flange. The anterior process of the squamosal is short and widely separated from the maxillary. The quadratojugal is a small spine-shaped element projecting anteriorly from the ventral base of the quadrate; the quadratojugal does not articulate with the maxillary.

[Pg 308]

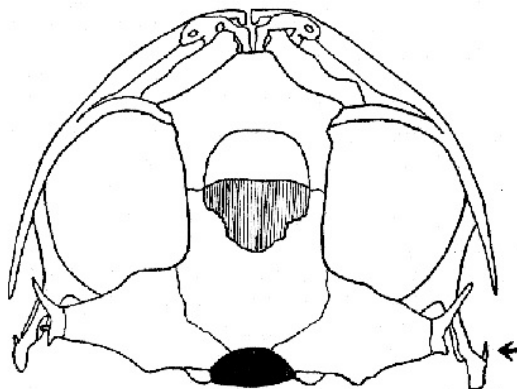


FIG. 3. Dorsal aspect of skull of *Ptychohyla spinipollex* (KU 68632). Arrow indicates reduced quadratojugal. $\times 6$.

The posteromedian part of the hyoid plate is calcified; from this plate the long bony, posterior cornua (thyrohyales) extend posterolaterally.

The omosternum is calcified, widest anteriorly, and has a convex anterior edge. The calcified xiphisternum is roughly bell-shaped having short lateral processes anteriorly and a deep notch posteriorly.

The swollen thumb is supported by a dorsoventrally flattened spine that does not extrude through the skin.

VARIATION.—In general, the skull varies little. Usually the quadratojugal is present only as a short element attached to the quadrate, but in one specimen of *P. spinipollex* the quadratojugal articulates with the maxillary and forms a complete quadratojugal-maxillary arch on each side of the skull. One specimen of *P. leonhardschultzei* has a complete arch on one side and an incomplete arch on the other.

Only *P. spinipollex* has lateral processes anteriorly on the xiphisternum; in the other species the xiphisternum is deeply bell-shaped.

Ptychohyla schmidtorum and *P. ignicolor* have slightly longer premaxillaries than the other species. The longer premaxillary is reflected in the larger number of teeth on the bone—9 to 11 (average 10) in four specimens of *P. schmidtorum* and 10 teeth in one *P. ignicolor*, as compared with 6 to 10 (average 7.9) in seven specimens of the other species. The number of maxillary teeth in the various species are: *P. euthysanota euthysanota*, 43; *P. euthysanota macrotympanum*, 38; *P. leonhardschultzei*, 38 and 40; *P. spinipollex*, 34 and 40; *P. schmidtorum schmidtorum*, 37 and 43; *P. schmidtorum chamulae*, 40 and 41; *P. ignicolor*, 43. The teeth on the premaxillary and anterior part of the maxillary are long, pointed, and terminally curved backwards. Posteriorly on the maxillary the teeth become progressively shorter and blunter.

[Pg 309]

Variation in number of vomerine teeth is shown in Table 1.

Tadpoles

[Pg 310]

Tadpoles of the genus *Ptychohyla* are adapted to live in mountain streams. The bodies are streamlined, and the tails are long and have low fins (Figs. 4 and 5). The mouths are large and directed ventrally. Tadpoles of the two groups of species have strikingly different mouthparts.

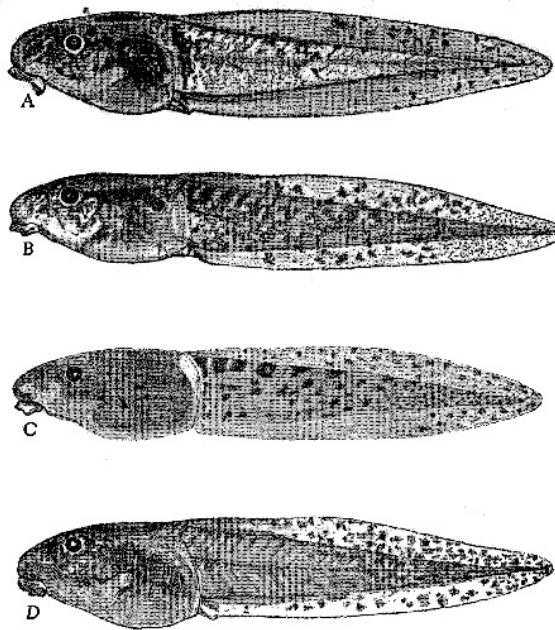


FIG. 4. Tadpoles of the *Ptychohyla euthysanota* group: (A) *P. euthysanota euthysanota* (KU 60042), (B) *P. euthysanota macrotympanum* (KU 60049), (C) *P. leonhardschultzei* (KU 68556), and (D) *P. spinipollex* (KU 60053). $\times 2\frac{1}{2}$.

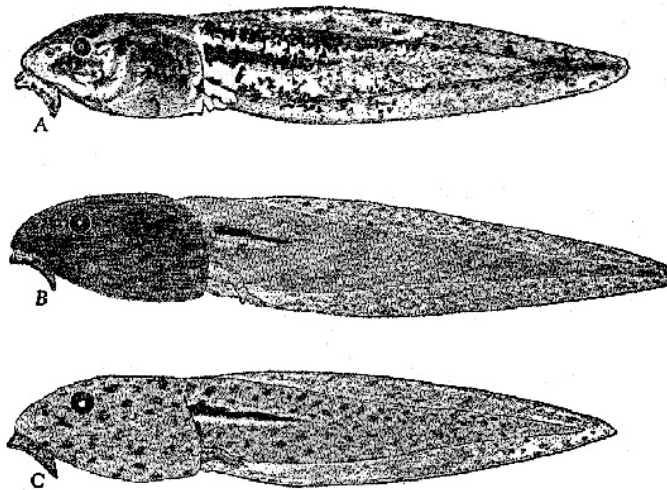


FIG. 5. Tadpoles of (A) *Ptychohyla schmidtorum schmidtorum* (KU 60051), (B) *P. schmidtorum chamulae* (KU 58199), and (C) *P. ignicolor* (KU 71716). $\times 2\frac{1}{2}$.

Lips of tadpoles of the *Ptychohyla euthysanota* group (Fig. 6 A-D) are folded laterally; there are $\frac{4}{6}$ or sometimes $\frac{4}{7}$ tooth-rows. A lateral "wing" projects on either side of the upper beak. The beaks have blunt, peglike serrations. Lips of tadpoles of the *Ptychohyla schmidtorum* group (Fig. 6 E-G) are greatly expanded and form a funnel-shaped disc; there are $\frac{3}{3}$ short tooth-rows. There is no lateral projection or "wing" on either side of the upper beak. The beaks have long, pointed serrations.

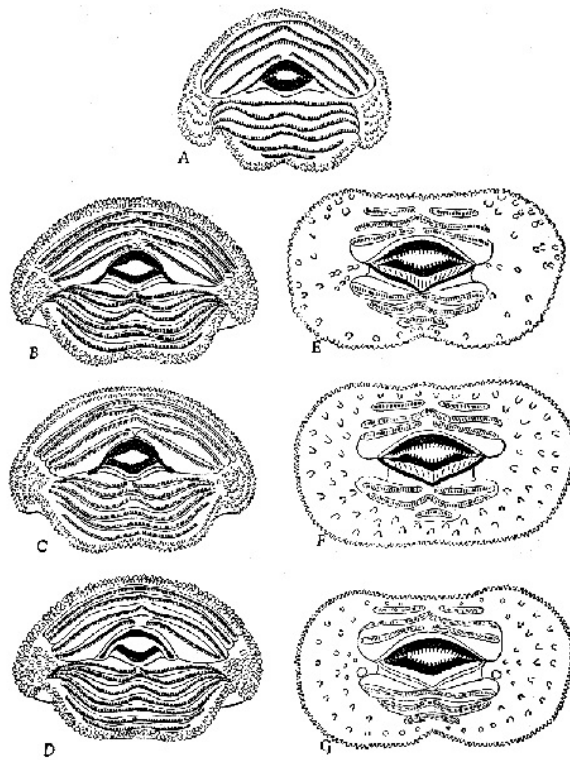


FIG. 6. Mouthparts of tadpoles of *Ptychohyla*: (A) *P. euthysanota euthysanota* (KU 60042), (B) *P. euthysanota macrotympaanum* (KU 60049), (C) *P. leonhardschultzei* (KU 68556), (D) *P. spinipollex* (KU 60053), (E) *P. schmidtorum schmidtorum* (KU 60051), (F) *P. schmidtorum chamulae* (KU 58199), and (G) *P. ignicolor* (KU 71716). $\times 10$.

Variation in certain structural details and in coloration is discussed for each species and subspecies in the systematic accounts that follow. Sizes, proportions, and numbers of tooth-rows are tabulated in [Table 2](#).

TABLE 2.—COMPARISON OF CERTAIN LARVAL CHARACTERS IN THE SPECIES OF PTYCHOHYLA. (MEANS ARE IN PARENTHESES BELOW THE RANGES.)

[Pg 312]

Species	Number of specimens	Maximum length	$\frac{\text{Head length}}{\text{Total length}}$	Tooth-rows
<i>P. euthysanota euthysanota</i>	23	40.8	30.9-37.3 (33.5)	$\frac{4}{6}$
<i>P. euthysanota macrotympaanum</i>	13	43.3	30.6-33.4 (32.7)	$\frac{4}{6}$
<i>P. leonhardschultzei</i>	7	47.5	29.2-32.7 (31.1)	$\frac{4}{6}$
<i>P. spinipollex</i>	32	45.0	30.2-35.9 (33.0)	$\frac{4}{7}$
<i>P. schmidtorum schmidtorum</i>	14	42.5	28.9-31.2 (29.9)	$\frac{3}{3}$
<i>P. schmidtorum chamulae</i>	4	45.0	26.9-29.3 (27.8)	$\frac{3}{3}$
<i>P. ignicolor</i>	2	39.6	29.6-29.8 (29.7)	$\frac{3}{3}$

Evidence on the pattern of development of tooth-rows indicates that the inner rows develop first. A small tadpole of *P. euthysanota euthysanota* has six lower rows and three fully developed upper rows and only the beginning of the first (outer) upper row. A small tadpole of *P. euthysanota macrotympaanum* has four upper rows and five lower rows. In a small tadpole of *P. leonhardschultzei* the three upper and four lower tooth-rows are well developed; the first upper and fifth lower rows are beginning to develop, and the sixth lower row is absent. In small tadpoles of *P. spinipollex*, the sixth lower row is poorly developed, and the seventh row is absent; large individuals normally have seven lower rows. A small tadpole of *P. schmidtorum chamulae* has $\frac{3}{2}$ tooth-rows.

Breeding Call

Breeding calls of all species and subspecies of *Ptychohyla* were recorded in the field. Obtaining series of calls of *Ptychohyla* is difficult because these frogs call mostly from vegetation along roaring mountain streams and only by locating a calling frog some distance from the water or along a quiet stretch of the stream can good recordings be obtained. For example, four individuals of *P. spinipollex* were recorded, but only one recording was sufficiently free of background noise to be analyzed.

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Analysis of breeding calls supports the division of the genus *Ptychohyla* into two groups of species. The call of each member of the *Ptychohyla euthysanota* group consists of a single long note, whereas the call of species in the *Ptychohyla schmidtorum* group consists of a series of short notes. Since no differences were found between the calls of subspecies of any given species, the following discussion of breeding calls pertains to species. These calls are described briefly below and at greater length in the systematic accounts farther on. Audiospectrographs of the breeding calls are shown in [Plate 11](#), and comparisons of the characteristics of the calls are given in [Table 3](#).

TABLE 3.—COMPARISON OF THE BREEDING CALLS OF PTYCHOHYLA

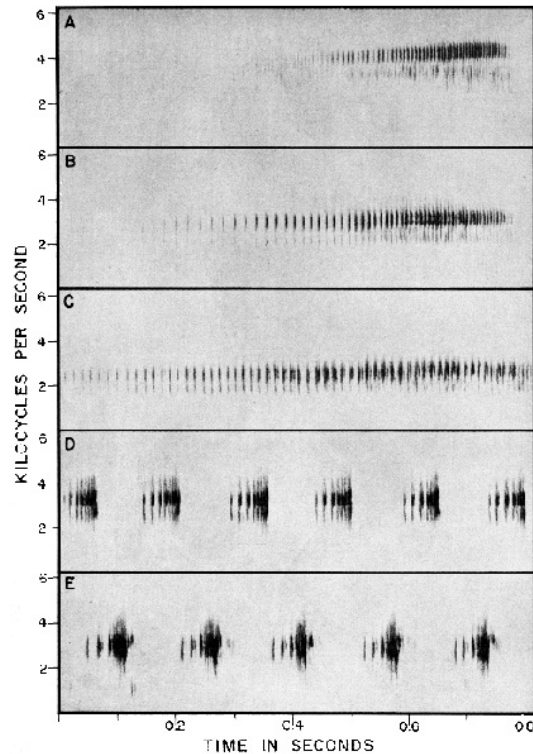
	Notes per	Duration of	Pulses per	Frequency	Dominant
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Species	Number	call group	note (seconds)	second	range (cps)	frequency (cps)
<i>P. spinipollex</i>	1	1	46	147	3000-5100	4300
<i>P. euthysanota</i>	7	1	62 (.60-.65)	95.3 (91-102)	1800-4200	3070 (3000-3200)
<i>P. leonhardschultzei</i>	2	1	79 (.62-.95)	77 (76-78)	1500-3500	2750 (2700-2800)
<i>P. schmidtorum</i>	6	8.5 ^[A] (8-9)	.064 (.054-.070)	110 (96-121)	1400-5800 (3350-3450)	3400.
<i>P. ignicolor</i>	2	12 ^[A] (11-13)	.079 (.078-.080)	126 (123-129)	1000-5000	3150 (3100-3200)

[A] Only an analysis of the long series of calls is given here; see text for explanation.

Plate 11.

[Pl 11]



Audiospectrographs of the breeding calls of the five species of

Ptychohyla

: (A)

P. spinipollex

(KU Tape No. 41), (B)

P. euthysanota macrotympanum

(KU Tape No. 48), (C)

P. leonhardschultzei

(UMMZ Tape No. 525), (D)

P. schmidtorum chamulae

(KU Tape No. 52), (E)

P. ignicolor

(UMMZ Tape No. 526).

P. spinipollex (Pl. 11A).—One long note is repeated at intervals of 45 seconds to four minutes and has an average dominant frequency of 4300 cycles per second.

P. euthysanota (Pl. 11B).—One long note is repeated six to nine times at intervals of 2.7 to 3.4 seconds and has an average dominant frequency of 3070 cycles per second.

P. leonhardschultzei (Pl. 11C).—One long note is repeated once after 10 to 13 seconds and has an average dominant frequency of 2750 cycles per second.

P. schmidtorum (Pl. 11D).—The complete call consists of one short series of notes alternating with two long series. Numbers of notes per series in one individual having a typical call were 5-8-8-3-9-9. The average dominant frequency of notes in the short and long series alike is 3400 cycles per second.

P. ignicolor (Pl. 11E).—The complete call consists of a short series of notes alternating with a long series. In one complete recording the numbers of notes in these series were 4-13-3-11. The notes in the short series have an average dominant frequency of 2100 cycles per second, whereas the notes in the long series have an average dominant frequency of 3150 cycles per second. The four series of notes were given in one minute and 15 seconds.

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SYSTEMATIC ACCOUNTS

The museum catalogue numbers of the specimens examined, together with the localities from which they came, are listed at the end of the account of each subspecies or monotypic species. The localities that are represented by symbols on the distribution map (Fig. 7) are in roman type; those that are not represented on the map, because overlapping of symbols would have occurred, are in italic type.

Ptychohyla Taylor, 1944

Ptychohyla Taylor, Univ. Kansas Sci. Bull., 30:41, May 15, 1944. Type, *Ptychohyla adipoventris* Taylor, 1944 [= *Hyla leonhardschultzei* (Ahl), 1934].

Diagnosis.—Small hylids having stream-adapted tadpoles and differing from other hylid genera in having large ventrolateral glands in breeding males.

Composition.—Five species, two of which are made up of two subspecies, arranged in two groups of species on the basis of morphological characters of adults and tadpoles and on the basis of breeding calls.

Distribution.—Moderate elevations from southern Guerrero and northern Oaxaca, México, to northern El Salvador and central Honduras.

KEY TO ADULTS

1. A weak tarsal fold; outer fingers one-third webbed; males having spiny nuptial tuberosities; color in life tan or brown with blotches or reticulations, never green; iris bronze color *P. euthysanota* group—2
No tarsal fold; outer fingers having only vestige of web; males lacking nuptial tuberosities; color in life green or brown; iris red or golden color *P. schmidtorum* group—5
2. Chest, throat, and flanks usually having brown or black spots; no distinct white stripe on upper lip or on flanks; a faint white line usually present above anal opening; a rostral keel 3
Chest, throat, and flanks usually unspotted; distinct white line on upper lip and on flank present or not; white line above anal opening faint or well defined; no rostral keel 4
3. Interorbital region much wider than eyelid; spots on throat and chest black; spots only occasionally present on belly; flanks marbled with black and white; nuptial spines small, as many as 80 on one thumb *P. leonhardschultzei*
Interorbital region about as wide as eyelid; spots on chest and throat brown or black; spots usually present on belly; flanks having round brown or black spots; nuptial spines moderate in size, conical, seldom more than 60 on one thumb *P. spinipollex*
4. A distinct, broad, white lateral stripe usually present; usually a distinct white line above anal opening; a distinct white stripe on upper lip *P. euthysanota euthysanota*
No white lateral stripe; a faint white stripe above anal opening; no distinct white stripe on upper lip *P. euthysanota macrotympanum*
5. A distinct, broad, lateral stripe; a white stripe on upper lip expanded to form a large spot below eye; hidden surfaces of thighs and webs of feet not red in life; internarial region slightly depressed; diameter of tympanum greater than one-half diameter of eye 6 [Pg 315]
No lateral white stripe; no stripe on upper lip; in life dorsum green, hidden surfaces of thighs and webs of feet orange tan to bright red, and eye golden color; internarial region flat; diameter of tympanum less than one-half diameter of eye *P. ignicolor*
6. Webs of feet and posterior surfaces of thighs pale cream color; dorsum in life reddish brown; iris bright red *P. schmidtorum schmidtorum*
Webs of feet and posterior surfaces of thighs pale brown; dorsum in life green; iris reddish bronze color *P. schmidtorum chamulae*

KEY TO TADPOLES

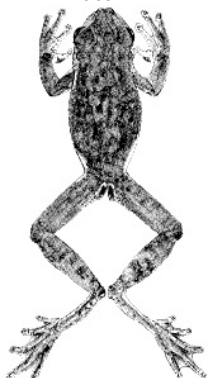
1. Lips greatly expanded forming a funnel-shaped mouth; tooth-rows $\frac{3}{3}$ *P. schmidtorum* group—2
Lips folded laterally, not forming a funnel-shaped mouth; tooth-rows $\frac{4}{6}$ or more *P. euthysanota* group—4
2. Belly and mouth mottled; tail cream color heavily blotched with brown 3
Belly dark gray; tail cream color with dense brown flecking, giving brown appearance *P. schmidtorum chamulae*
3. Belly cream color with brown mottling; no large tubercle at each end of first lower tooth-row *P. schmidtorum schmidtorum*
Belly grayish green with brown mottling; a large tubercle at each end of first lower tooth-row *P. ignicolor*
4. Tooth-rows $\frac{4}{6}$; cream-colored crescent-shaped mark on posterior part of body bordered posteriorly by large brown mark 5
Tooth-rows usually $\frac{4}{7}$ (sometimes $\frac{4}{6}$); cream-colored crescent-shaped mark on posterior part of body usually indistinct, not bordered posteriorly by large brown mark *P. spinipollex*
5. Caudal musculature uniformly flecked with brown; lower tooth-rows 1-4 about equal in length to upper rows *P. euthysanota euthysanota*
Caudal musculature having brown square blotches dorsally on anterior one-half of tail; lower tooth-rows 1-4 usually slightly shorter than upper rows 6
6. Dorsal caudal blotches well defined and extending onto sides of tail; moderately large brown flecks on caudal fin; eye in life pale reddish brown *P. leonhardschultzei*
Dorsal caudal blotches faint, not extending onto sides of tail; small brown flecks on caudal fin; eye in life silvery bronze *P. euthysanota macrotympanum*

Three species in group; adults having moderate amount of webbing between fingers, and tarsal fold; breeding males having spinous, horny, nuptial tuberosities on pollex; mouths of tadpoles having lateral folds in lips and $\frac{1}{6}$ or $\frac{4}{7}$ tooth-rows; breeding call consisting of one long note.

Ptychohyla euthysanota

Diagnosis.—Rostral keel absent; nuptial spines in males small; interorbital region much wider than eyelid.

Plate 12



Click to View Larger.

Ptychohyla euthysanota euthysanota (Kellogg)

- Hyla euthysanota* Kellogg, Proc. Biol. Soc. Washington, 41:123-124, June 29, 1928 [Holotype.—USNM 73296 from Los Esemiles, Depto. Chalatenango, El Salvador; Ruben A. Stirton collector]. Mertens, Senckenbergiana, 33:169-171, June 15, 1952; Abhand. Senckenbergische Naturf. Gesell., 487:29, December 1, 1952. Stuart, Proc. Biol. Soc. Washington, 67:169, August 5, 1954.
- Hyla rozellae* Taylor, Univ. Kansas Sci. Bull., 28:78-80, pl. 9, fig. 1, May 15, 1942 [Holotype.—USNM 115039 from Salto de Agua, Chiapas, México; Hobart M. and Rozella Smith collectors]. Taylor and Smith, Proc. U. S. Natl. Mus., 95:587, June 30, 1945. Smith and Taylor, Bull. U. S. Natl. Mus., 194:86, June 17, 1948. Stuart, Proc. Biol. Soc. Washington, 67:169, August 5, 1954.
- Ptychohyla bogerti* Taylor, Amer. Mus. Novitates, 1437:13-16, fig. 5, December 7, 1949 [Holotype.—AMNH 51847 from Río Grande, Oaxaca, México; Thomas MacDougall collector]. Stuart, Proc. Biol. Soc. Washington, 67:169, August 5, 1954.
- Ptychohyla euthysanota*, Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:351, April 27, 1961.

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Diagnosis.—Dorsum tan to reddish brown; venter white; rarely flecked with brown or black; a white stripe on upper lip, on flank, and usually above anus.

Description.—The following description is based on KU 58008 from Finca La Paz, Depto. San Marcos, Guatemala (Pl. 12). Adult male having a snout-vent length of 35.0 mm.; tibia length, 16.5 mm.; tibia length/snout-vent length, 47.1 per cent; foot length, 14.2 mm.; head length, 11.0 mm.; head length/snout-vent length, 31.4 per cent; head width, 10.7 mm.; head width/snout-vent length, 30.6 per cent; diameter of eye, 3.3 mm.; diameter of tympanum, 1.8 mm.; tympanum/eye, 54.5 per cent. Snout in lateral profile nearly square, slightly rounded above, and in dorsal profile bluntly rounded; canthus pronounced; loreal region moderately concave; lips thick, rounded, and slightly flaring; nostrils protuberant; internarial distance, 3.0 mm.; top of head flat; interorbital distance, 4.1 mm., and approximately a third broader than width of eyelid, 2.9 mm. Moderately heavy dermal fold from posterior corner of eye above tympanum to point above insertion of forelimb, covering upper edge of tympanum; tympanum round, its diameter slightly more than its distance from eye. Forearm moderately robust, having distinct dermal fold on wrist; dermal fold, but no row of tubercles along ventrolateral surface of forearm; pollex only slightly enlarged, bearing triangular shaped patch of small horn-covered spines (128 on right, 134 on left); second and fourth fingers equal in length; subarticular tubercles round, distal one on fourth finger bifid; discs moderate in size, that of third finger equal to diameter of tympanum; no web between first and second fingers; other fingers one-third webbed. Heels broadly overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; low rounded tarsal fold; inner metatarsal tubercle large, elliptical, and flat; outer metatarsal tubercle small and round; low dermal fold from heel to disc of fifth toe; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third and fifth toes webbed to base of disc; fourth toe webbed to proximal end of penultimate phalanx; thin dermal fold from inner metatarsal tubercle to disc of first toe; disc smaller than on fingers. Anal opening at the level of the upper edge of thighs; anal flap short; anal opening bordered above by thin transverse dermal fold and laterally by heavy dermal fold. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands moderately developed, not reaching axilla or groin and broadly separated midventrally. Tongue ovoid, emarginate, and only slightly free posteriorly; vomerine teeth 2-2, situated on small triangular elevations between ovoid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

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Dorsal ground-color of head, body, and limbs dull reddish brown with irregular dark brown reticulations on head and body and dark brown transverse bands on limbs; dorsal surfaces of first and second fingers and webbing on hand cream color; dorsal surfaces of third and fourth fingers dull brown; anterior surfaces of thighs dull creamy yellow; posterior surfaces of thighs dull brown; tarsi and toes tan with brown flecks; webbing of feet brown; faint creamy white stripe along lateral edges of tarsi and forearms; thin white line along edge of upper lip; distinct white stripe above and beside anal opening; axilla white; throat, chest, belly, and ventral surfaces of forelimbs creamy white; flanks white, separated from pale venter by a row of partly connected dark brown spots; ventral surfaces of thighs dull creamy yellow; feet grayish brown; ventrolateral glands pale grayish brown; small brown flecks on periphery of chin.

In life the dorsal ground-color was pale reddish brown (Orange-Cinnamon); dorsal reticulations dark brown (Chocolate); dorsal surfaces of first and second fingers and webbing on hands creamy tan (Light Pinkish Cinnamon); posterior surfaces of thighs reddish brown (Vinous-Tawny); webbing of feet gray (Deep Mouse Gray); throat and belly grayish white (Pale Gull Gray); ventral surfaces of hind limbs creamy white (Marguerite Yellow); spots on flanks dark brown (Warm Sepia); iris reddish bronze (Apricot Orange).

Variation.—No geographic variation in structural characters is discernible; variation in size and proportions is given in Table 1. Of 32 adults examined, seven have the tongue shallowly notched posteriorly; in the others the tongue is emarginate. Twenty specimens have a bifid subarticular tubercle beneath the fourth finger; in the others there are no bifid tubercles.

The coloration described above is typical of the 16 specimens available from Finca La Paz. The living coloration at night, when the frogs were collected, was somewhat darker than the living colors described above, which were recorded for the frogs the morning after collection, at which time one individual had a pale reddish brown dorsum (Orange-Cinnamon) with dull olive green (Deep Grape Green) reticulations on the back and transverse bands on the limbs; the dorsal surfaces of the first and second fingers and the discs on the third and fourth fingers were orange (Mikado Orange).

More than half of the specimens from Finca La Paz agree in all essential characters with the description given above. The distinctness of the white stripe on the upper lip is variable; in two individuals the stripe is barely discernible. Likewise, in some individuals the white stripe on the flanks is not distinct, either because there are few or no brown spots separating the stripe from the pale venter, or because the ventrolateral gland has diffused the pale color on the flanks. There is some noticeable variation in dorsal coloration, either through a greater or lesser development of dark pigment. One specimen (KU 58007) is grayish tan above with dark brown markings; the posterior surfaces of the thighs are dull grayish yellow; the first and second fingers and the webbing on the hands are pale yellowish gray; the belly and throat are dusty white; the flecks on the throat are gray; the ventral surfaces of the feet are grayish brown. Dark individuals, such as KU 58009 have a uniform dark brownish black dorsum; the belly is cream; the first and second fingers and the webbing on the hands are dull creamy tan; the dorsal and ventral surfaces of the feet are dark brown. In KU 58013 there is a heavy suffusion of brown on the throat and flanks. Two specimens have scattered white flecks on the dorsum.

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The reddish brown dorsal ground-color with dark brown reticulations on the head and body and dark brown transverse bands on the limbs seems to be rather constant throughout the range of the subspecies. Likewise, the presence of the white stripe on the upper lip and the white stripe around the anal opening are present on most specimens. In breeding males having well-developed ventrolateral glands the lateral white stripe often is obliterated.

Description of Tadpole.—The following description is based on KU 60042 from Finca La Paz, Depto. San Marcos, Guatemala (Figs. 4A and 6A). No limb buds; total length, 35.8 mm.; body length, 11.2 mm.; body length/total length, 31.3 per cent. Body moderately depressed, slightly wider than deep, ovoid in dorsal profile; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils slightly protuberant and directed anteriorly, closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral.

Caudal fin low, rounded posteriorly; depth of caudal musculature about one-half greatest depth of caudal fin; musculature extends nearly to tip of tail.

Mouth large; lips having deep lateral folds; two complete rows of papillae on lips; five to six rows of papillae laterally. Beaks moderately developed, bearing peglike serrations; slender lateral projections on upper beak; tooth-rows $\frac{4}{6}$; upper rows subequal in length, second longest; fourth row interrupted medially; lower rows complete; lower rows 1-4 equal in length to upper rows; fifth lower row somewhat shorter; sixth lower row short.

Body brown above; tip of snout cream color; grayish cream color below; caudal musculature creamy tan; caudal fin transparent; cream-colored crescent-shaped mark on posterior edge of body and anterior part of caudal musculature, bordered posteriorly by dark brown blotch; scattered brown flecks on caudal musculature and posterior part of caudal fin. Eye bronze color in life.

Variation.—The variation in size and proportions is given in [Table 2](#). In some specimens the first upper tooth-row is irregular, sometimes broken, and often shorter than other upper tooth-rows. Usually the fourth upper and first lower, and sometimes the sixth lower, tooth-rows are interrupted medially. One specimen has a short, irregular, seventh lower tooth-row; all others have six.

The cream-colored crescent-shaped mark usually is distinct. The brown blotch posterior to this mark is variously shaped ranging from a narrow vertical bar to a triangular blotch. Brown flecks seldom are present on the anterior part of the ventral caudal fin.

Comparisons.—Aside from the characters given in the diagnosis, *P. euthysanota euthysanota* can be distinguished from both *P. spinipollex* and *P. leonhardschultzei* by the absence of bold black and white marbling on the flanks; furthermore, from the former it can be distinguished by having more and smaller horny nuptial spines and from the latter by having the snout, in lateral profile, rounded above and not acutely angulate. *Ptychohyla euthysanota euthysanota* differs from *P. euthysanota macrotympaum* by normally having a darker dorsal color, broader stripe on upper lip, and a distinct lateral stripe.

Occurring sympatrically with *Ptychohyla euthysanota euthysanota* are several species of *Plectrohyla*, all of which differ in having a bony prepollex, rather rugose skin on the dorsum, and more squat bodies. Other sympatric species are *Ptychohyla schmidtorum schmidtorum*, which lacks a tarsal fold and nuptial spines and has a red eye in life, *Hyla salvadorensis*, which has a green dorsum and lacks spinous nuptial tuberosities, and *Hyla sumichrasti*, a small yellow frog usually lacking vomerine teeth.

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Life History.—This subspecies breeds in clear, swift mountain streams. Males call from stems and leaves of plants at the edge of, or overhanging, the streams. The breeding call consists of a soft "wraack," repeated at intervals of three to four seconds. Each note has a duration of 0.60 to 0.65 seconds and has 91 to 102 pulses per second; the dominant frequency falls between 3000 and 3200 cycles per second.

Tadpoles in various stages of development were found at Finca La Paz, Guatemala, in late July. This indicates that there is either extreme differential growth, or, more probably, an extended breeding season. A tadpole having a body length of 6.8 mm. and a total length of 19.1 mm. has a short median first upper tooth-row; lower tooth-rows 3-6 are only two-thirds as long as lower rows 1 and 2. Two recently metamorphosed young have snout-vent lengths of 14.2 and 14.8 mm.; they are colored like the adults.

Remarks.—The type specimen of *Hyla euthysanota* Kellogg (1928:123) is a female; therefore, when Taylor (1944) proposed the name *Ptychohyla* for hylids having ventrolateral glands in breeding males, he was unaware that *Hyla euthysanota* was a member of this group. In his description of *Hyla rozellae*, Taylor (1942) did not compare his specimens with *Hyla euthysanota*, but instead placed *H. rozellae* with *H. loquax* and *H. rickardsi*. The type series of *H. rozellae* consists of one large adult female and several metamorphosing young. Taylor (1949:16) based the description of *Ptychohyla bogerti* on two males and compared these specimens with *P. adipoventris* Taylor [= *P. leonhardschultzei* (Ahl)]. Thus, in a period of 22 years the females of this species were given two names and the male another. Stuart (1954:169) suggested that *Hyla euthysanota* and *Hyla rozellae* were *Ptychohyla*. Now that sufficient specimens are available from throughout the range it is possible to determine that the various named populations are conspecific.

Distribution.—This subspecies inhabits cloud forests at elevations of 660 to 2200 meters on the Pacific slopes of the Sierra Madre from extreme eastern Oaxaca and western Chiapas, México, through Guatemala to northern El Salvador; probably it occurs also in southwestern Honduras. Aside from the specimens listed below, three in the Frankfurt Museum from Depto. Santa Ana, El Salvador (44571, Hacienda San José; 43040, Hacienda Los Planes; 65119, Miramundo) are listed by Mertens (1952:29).

Specimens examined.—MEXICO: *Chiapas: Cascarada, 30 km. W of Ciltapec*, UMMZ 87851-2; Cerro Ovando, UMMZ 87853-4; Chicomuselo, UMMZ 94439-40; Finca Juárez, 28 km. N of Escuintla, USNM 115052-5; *Las Nubes, Cerro Ovando*, USNM 115030-8; Salto de Agua, USNM 115039-51. *Oaxaca: Cerro Pecho Blanco*, UIMNH 40963; between La Gloria and Cerro Azul, UIMNH 40976-7; Río Grande, AMNH 51847-8; Santo Tomás Tecpan, UIMNH 41071.

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GUATEMALA: *San Marcos: Finca La Paz, 2 km. W of La Reforma*, KU 58001-14, 59937 (skeleton), 60042-3 (tadpoles), 60044 (4 young), MCZ 34997, UMMZ 107739, 123151-7 (tadpoles); Finca Pirineos, Río Samalá, CNHM 35066. *Santa Rosa: Finca La Gloria*, UMMZ 123148 (tadpoles), 123150 (tadpoles). *Sololá: Finca Santo Tomás*, UMMZ 123149 (tadpoles); Olas de Mocá, near Mocá, CNHM 20208.

EL SALVADOR: *Chalatenango: Los Esemiles*, USNM 73296. *Santa Ana: Miramundo*, CNHM 65120.

Plate 13



Click to View Larger.

***Ptychohyla euthysanota macrotympaum* (Tanner)**

Hyla macrotympaum Tanner, Great Basin Nat., 17:52-53, July 31, 1957 [Holotype.—AMNH 62141 (formerly BYU 13752) from 10 miles east of Chiapa de Corzo, Chiapas, México; Robert Bohlman collector].

Ptychohyla macrotympaum, Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:351, April 27, 1961.

Diagnosis.—Dorsum usually pale tan; venter white with scattered brown or black flecks; a thin white stripe on upper lip and another above anal opening; no distinct white stripe on flanks.

Description.—The following description is based on KU 58049 from Linda Vista, Chiapas, México ([Pl. 13](#)). Adult male having a snout-vent length of 38.0 mm.; tibia length, 19.5 mm.; tibia length/snout-vent length, 51.3 per cent; foot length, 15.7 mm.; head length, 11.8 mm.; head length/snout-vent length, 31.1 per cent; head width, 11.7 mm.; head width/snout-vent length, 30.8 per cent; diameter of eye, 3.8 mm.; diameter of tympanum, 2.1 mm.; tympanum/eye, 55.2 per cent. Snout in lateral profile nearly square, slightly rounded above, and in dorsal profile bluntly rounded; canthus pronounced; loreal region concave; lips thick, rounded, and slightly flaring; nostrils protuberant; internarial distance, 3.1 mm.; top of head flat; interorbital distance, 3.8 mm., and approximately a fourth broader than width of eyelid, 3.1 mm. A moderately heavy dermal fold from posterior corner of eye above tympanum to point above insertion of forelimb, covering upper edge of tympanum; tympanum round, its diameter equal to its distance from eye. Forearm moderately robust, having a distinct dermal fold on wrist; dermal fold, but no row of tubercles along ventrolateral surface of forearm; pollex only slightly enlarged, bearing triangular patch of small horn covered spines (94 on right, 100 on left); fourth finger slightly longer than second;

subarticular tubercles round, none bifid; discs moderate in size, that of third finger equal to diameter of tympanum; vestige of web between first and second fingers; other fingers one-third webbed. Heels broadly overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; weak tarsal fold on distal two-thirds of tarsus; inner metatarsal tubercle large, elliptical, and flat; outer metatarsal tubercle small and round; no dermal fold from heel to disc of fifth toe; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third toe webbed to base of disc; fifth toe webbed to middle of penultimate phalanx; fourth toe webbed to proximal end of penultimate phalanx; no fold of skin from inner metatarsal tubercle to base of disc on first toe; discs much smaller than on fingers. Anal opening near upper edge of thighs; short anal flap bordered above by thin dermal fold; small tubercles and heavy dermal fold lateral to anal opening. Skin of dorsum and ventral surfaces of fore limbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands weakly developed, not reaching axilla or groin and broadly separated midventrally. Tongue ovoid, shallowly notched posteriorly, and barely free behind; vomerine teeth 2-2, situated on small triangular elevations between ovoid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

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Dorsal ground-color of head, body, and limbs pale pinkish tan with the greatest part of head and body covered by large gray interconnected blotches; black flecks over most of dorsum; grayish brown transverse bands on shanks; dorsal surfaces of first and second fingers pale grayish yellow; dorsal surfaces of third and fourth fingers and webbing on hand pale grayish tan; anterior surfaces of thighs pale flesh-color; posterior surfaces of thighs pale grayish yellow; dorsal surfaces of tarsi and toes pale grayish tan with black flecks; webbing of feet pale gray; faint creamy white stripes along ventrolateral edges of tarsi and forearms; a very thin white line along edge of upper lip; a narrow grayish white stripe above anal opening; axilla gray; throat, chest, belly, and ventral surfaces of forelimbs pale grayish white; ventral surfaces of hind limbs cream color; flanks gray flecked with brown; ventral surfaces of feet grayish tan; ventrolateral glands pinkish tan; anterior one-half of chin flecked with brown.

In life the dorsum was pale tan (Pinkish Buff); the dark markings on dorsum dull brown (Tawny-Olive); tarsi pale tan (Pale Pinkish Buff); flanks pinkish tan (Pale Cinnamon-Pink); iris coppery bronze (Capucine Orange).

Variation.—The few specimens from a limited geographic region preclude any analysis of geographic variation. All specimens, except the one described above, have the fifth toe webbed to the base of the disc. Many individuals have a bifid subarticular tubercle beneath the fourth finger. The shape of the posterior edge of the tongue varies from nearly straight and shallowly notched to bluntly rounded and emarginate. Two females (KU 58050-1) have more pointed snouts in dorsal profile than do males.

Some specimens, such as KU 58048, are notably darker than the specimen described above; in dark specimens the dorsum is brown with dark brown markings; all fingers and the webbing on the hand are brown. The tarsi and feet are like those in the specimen described above, but the posterior surfaces of the thighs are yellowish tan heavily suffused with brown; the venter is cream color. In life KU 58048 had a brown (Verona Brown) dorsum with dark brown (Chocolate) markings. KU 58047 is slightly darker than KU 58048 and has scattered small white flecks on the dorsum. All specimens have the thin white line on the upper lip, but in some individuals it is indistinct. The grayish white line above the anus is present in all specimens.

Description of Tadpole.—The following description is based on KU 60049 from Río Hondo, 9.5 kilometers south of Pueblo Nuevo Solistahuacán, Chiapas, México (Figs. 4B and 6B). No limb buds; total length, 36.2 mm.; body length, 11.1 mm.; body length/total length, 30.6 per cent. Body moderately depressed, slightly wider than deep, ovoid in dorsal profile; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils slightly protuberant and directed anteriorly, somewhat closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Caudal fin low, acutely rounded posteriorly; depth of caudal musculature slightly more than one-half greatest depth of caudal fin; caudal musculature extending nearly to tip of tail.

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Mouth large; lips having deep lateral folds; two complete rows of papillae on lips; five or six rows of papillae laterally. Beaks moderately developed, bearing small peglike serrations; moderately wide lateral projections on upper beak; tooth-rows $\frac{5}{6}$; upper rows subequal in length; fourth row interrupted medially; length of lower rows 1-4 subequal to upper rows; fifth and sixth lower rows decreasing in length; first lower row interrupted medially.

Body brown above; tip of snout cream color; venter creamy white; caudal musculature creamy tan; caudal fin transparent; cream-colored crescent-shaped mark on posterior edge of body and anterior part of caudal musculature, bordered posterodorsally by dark brown blotch; four dark brown blotches on dorsum of anterior part of caudal musculature; scattered brown flecks on caudal musculature and fin; eye silvery bronze in life.

Variation.—The variation in size and proportions is given in Table 2. All specimens have $\frac{5}{6}$ tooth-rows; in some the first lower row is interrupted medially. Specimens from Jacaltenango and two kilometers west of San Pedro Necta, Depto. Huehuetenango, Guatemala, have weakly developed sixth lower tooth-rows.

The cream-colored crescent-shaped mark is distinct in all specimens; the dorsal blotches on the anterior part of the caudal musculature are narrow and do not extend far onto the sides of the tail. The blotches are most distinct in small tadpoles and sometimes indistinct in large ones.

Comparisons.—*Ptychohyala euthysanota macrotympaum* can be distinguished from both *P. spinipollex* and *P. leonhardschultzei* by the absence of bold black and white marbling on the flanks, as well as by the characters given in the diagnosis; furthermore, from the former it differs in having more and smaller horny nuptial tuberosities and from the latter by having the snout, in lateral profile, rounded above instead of angulate. *Ptychohyala euthysanota macrotympaum* differs from *P. e. euthysanota* by normally having a paler dorsum, narrower stripe on upper lip, and no distinct lateral stripe.

Ptychohyala euthysanota macrotympaum occurs sympatrically with *Plectrohyla guatemalensis* and *P. matudai matudai*. Each of the last two has a bony prepollax, rather rugose skin on the dorsum, and more squat body. Other sympatric species are *Hyla walkeri*, which has a green dorsum with brown markings and a rather pointed snout, and *Hyla sumichrasti*, a small yellow frog usually lacking vomerine teeth.

Life History.—This species breeds in clear mountain streams in mixed pine and broad-leafed forest. Males call from trees and bushes along the streams. The breeding call consists of a soft "wraack," repeated three to nine times with intervals of 2.7 to 3.4 seconds between notes. Each note has a duration of 0.60 to 0.65 second, and a rate of 92 to 100 pulses per second; the dominant frequency falls between 3000 and 3200 cycles per second (Pl. 11B). The call is indistinguishable from that of *P. e. euthysanota*.

Tadpoles in various stages of development were found in the Río Hondo, Chiapas, on June 16, 1960. The smallest tadpole has a total length of 24.1 mm.; in this individual the sixth lower tooth row has barely started to develop. A metamorphosing frog taken at the same time has a snout-vent length of 19.8 mm., a short remnant of the tail, and the mouth and tongue developed, whereas another individual having a snout-vent length of 17.8 mm. and a tail 31.0 mm. in length still has larval teeth. Three completely metamorphosed juveniles collected by L. C. Stuart at Jacaltenango, Guatemala, on June 6 and 7, 1955, have snout-vent lengths of 16.0, 16.0, and 16.1 mm.

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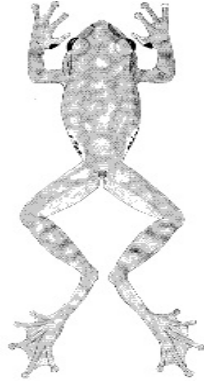
Remarks.—Tanner (1957:52) based the description of *Hyla macrotympaum* on a single female, which, of course, lacked the characters diagnostic of *Ptychohyala*. On the basis of general external characters Tanner suggested that *Hyla macrotympaum* was related to *H. miotympaum*, from which it differed in having a larger tympanum and a bifid subarticular tubercle beneath the fourth finger. The collection of additional females, together with males of the species, has shown that *Hyla macrotympaum* is a *Ptychohyala*.

Intergradation between *Ptychohyala euthysanota* and *P. macrotympaum* has not been demonstrated. Currently their ranges are separated by the dry valleys of the Río Grijalva and Río Cuilco. The similarity in structure of the adults and tadpoles and the indistinguishable breeding calls are the basis for considering the two populations subspecies.

Distribution.—This species occurs in mixed pine and broad-leafed forests at elevations of 700 to 1700 meters on the southern slopes of the Chiapan Highlands and Sierra de Cuchumatanes, in Guatemala. These forests are on the south facing slopes north of the valleys of the Río Grijalva and Río Cuilco.

Specimens examined.—MEXICO: Chiapas: 6 km. NE of Chiapa de Corzo, TCWC 16183; 16 km. E of Chiapa de Corzo, AMNH 62141; Linda Vista, 2 km. NW of Pueblo Nuevo Solistahuacán, KU 58049-51, 59939 (skeleton); Río Hondo, 9.5 km. S of Pueblo Nuevo Solistahuacán, KU 58047-8, 60046-7, 60048-9 (tadpoles); San Fernando, MZTG 15, 17; Tonina (ruins), KU 41592.

GUATEMALA: Huehuetenango: Jacaltenango, UMMZ 123139 (tadpoles); 0.5 km. E of Jacaltenango, UMMZ 123142-3; 2 km. S of Jacaltenango, UMMZ 123141; 2 km. W of San Pedro Necta, UMMZ 123140 (tadpoles).

***Ptychohyla leonhardschultzei* (Ahl)**

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- Hyla leonhard-schultzei* Ahl, Zool. Anz., 106:185-186, fig. 1, April 15, 1934 [Holotype.—ZMB 34353 from Malinaltepec, Guerrero, México; Leonhard Schultze collector]. Smith and Taylor, Bull. U. S. Natl. Mus., 184:87, June 17, 1948.
- Hyla godmani*, Ahl, Zool. Anz., 106:186, April 15, 1934.
- Hyla pinorum* Taylor, Proc. Biol. Soc. Washington, 50:46-48, pl. 2, fig. 2, April 21, 1937 [Holotype.—UIMNH 25049 from Agua del Obispo, Guerrero, México; Edward H. Taylor collector]. Smith and Taylor, Bull. U. S. Natl. Mus., 194:87, June 17, 1948.
- Ptychohyla adipoventris* Taylor, Univ. Kansas Sci. Bull., 30:41-45, May 15, 1944 [Holotype.—UIMNH 25047 from Agua del Obispo, Guerrero, México; Edward T. Taylor collector]. Smith and Taylor, Bull. U. S. Natl. Mus., 194:91, June 17, 1948. Taylor, Amer. Mus. Novitates, 1437:16, December 7, 1949. Stuart, Proc. Biol. Soc. Washington, 67:169, August 5, 1954.
- Hyla milleri* Shannon, Proc. U. S. Natl. Mus., 101:473-477, figs. 92b, 93a-c, May 17, 1951 [Holotype.—USNM 123700 from San Lucas Camotlán, Oaxaca, México; Walter S. Miller collector].
- Ptychohyla leonhard-schultzei*, Duellman, Herpetologica, 16:191-197, figs. 1-3, September 23, 1960; Univ. Kansas Publ. Mus. Nat. Hist., 13:351, April 27, 1961.

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Diagnosis.—Rostral keel present; snout in lateral profile not rounded above; interorbital region much broader than eyelid; distal subarticular tubercle beneath fourth finger bifid or double; no white stripe on edge of upper lip; flanks white with black spots.

Description.—The following description is based on KU 64117 from Vista Hermosa, Oaxaca, México (Pl. 14). Adult male having a snout-vent length of 35.6 mm.; tibia length, 18.0 mm.; tibia length/snout-vent length, 50.5 per cent; foot length, 14.3 mm.; head length, 10.7 mm.; head length/snout-vent length, 30.1 per cent; head width, 10.6 mm.; head width/snout-vent length, 29.8 per cent; diameter of eye, 3.6 mm.; diameter of tympanum, 1.8 mm.; tympanum/eye, 50.0 per cent. Snout in lateral profile square, not rounded above, and in dorsal profile rounded with pointed tip resulting from vertical rostral keel; canthus pronounced; loreal region barely concave; lips thick, rounded, and barely flaring; nostrils protuberant; interocular distance, 3.2 mm.; top of head flat; interorbital distance, 3.8 mm., and approximately a fifth broader than width of eyelid, 3.2 mm. A moderately heavy dermal fold from posterior corner of eye above tympanum and curving ventrad to anterior edge of insertion of forelimb, covering upper edge of tympanum; tympanum round, its diameter equal to its distance from eye. Forearm moderately robust, having distinct dermal fold on wrist; row of small, low, rounded tubercles along ventrolateral surface of forearm; pollex only slightly enlarged, bearing triangular patch of small horn-covered spines (56 on right, 62 on left); second finger noticeably shorter than fourth; subarticular tubercles round, distal ones on third and fourth toes bifid; discs moderate in size, that of third finger slightly larger than diameter of tympanum; no web between first and second fingers; other fingers one-third webbed. Heels broadly overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; a low rounded tarsal fold on distal half of tarsus; inner metatarsal tubercle elevated, flat, and elliptical; outer metatarsal tubercle at base of fourth toe, round; row of low, sometimes indistinct, tubercles from heel to base of fifth toe; subarticular tubercles round; length of digits from shortest to longest 1-2-3-5-4, third and fifth being about equal in length; third and fifth toes webbed to base of disc; fourth toe webbed to base of penultimate phalanx; discs of toes much smaller than on fingers. Anal opening near dorsal surface of thighs; short anal flap; opening bordered laterally by heavy dermal fold and ventrolaterally by large tubercles. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands moderately developed, reaching axilla but not to groin and broadly separated midventrally. Tongue cordiform, shallowly notched behind and barely free posteriorly; vomerine teeth 4-3, situated on transverse elevations between ovoid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

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Dorsal ground-color of head, body, and limbs pale tan with large interconnected dark brown blotches on head and body and broad dark brown transverse bands on limbs; dorsal surfaces of first and second fingers and of webbing of hands pale brown; dorsal surfaces of third and fourth fingers dark brown; anterior surfaces of thighs flesh-color; posterior surfaces of thighs brown; dorsal surfaces of tarsi and feet dark brown; narrow white stripe along ventrolateral edges of forearms and tarsi; a faint creamy white stripe above anal opening; axilla white; flanks creamy white, boldly spotted with black; throat and chest white; ventral surfaces of tarsi and feet dark brown; other ventral surfaces dusty cream color; large brown spots on chin and anterior part of abdomen.

In life the dorsum was reddish brown (Orange-Cinnamon) with dark brown (Chocolate) blotches; first and second fingers and webbing on hand pale reddish brown (Cinnamon); webbing on feet dark brown (Clove Brown); flanks pale creamy white (Pale Olive Buff) with dark brown (Bone Brown) spots; iris reddish bronze (Apricot Orange).

Variation.—No noticeable geographic variation is apparent in the few available specimens; variations in proportions are given in Table 1. The distal subarticular tubercle of the fourth finger is either bifid or double in all specimens; that on the third finger usually is bifid, sometimes single. The vertical rostral keel is prominent in all freshly preserved specimens; in some older specimens it is indistinct. The tongue always is notched posteriorly; in some individuals the notch is shallow; in others it is deep.

Some specimens are paler and less boldly marked than the specimen described above. All specimens from Agua del Obispo and some specimens from the northern slopes of the Sierra Madre Oriental in Oaxaca have a pale tan dorsum with brown markings. In most individuals the white color in the axilla extends onto the posterior edge of the upper arm. The creamy white color of the flanks is constant and usually extends slightly dorsad in the inguinal region. The white stripe above, and sometimes continuing down beside, the anal opening varies from a thin indistinct line or row of flecks to a distinct continuous stripe. Two specimens have dark brown spots on the belly; in the others the spots are confined to the flanks and throat.

Description of tadpole.—The following description is based on KU 68556 from 7.5 kilometers south of Yetla, Oaxaca, México (Figs. 4C and 6C). No limb buds; total length, 37.3 mm.; body length, 12.2 mm.; body length/total length, 32.7 per cent; body slightly depressed, barely wider than deep, ovoid in dorsal profile; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant and directed anterolaterally, about midway between snout and eye; spiracle sinistral and posteroventrad to eye; anal tube dextral. Caudal fin low, bluntly rounded posteriorly; greatest depth of caudal musculature about one-half depth of caudal fin; musculature extends nearly to tip of tail.

Mouth large; lips having deep lateral folds; two complete rows of papillae on lips; five to seven rows of papillae laterally; beaks moderately developed, bearing short peglike serrations; moderately wide lateral projections on upper beak; tooth-rows $\frac{1}{6}$; upper rows subequal in length; fourth row interrupted medially; length of lower rows 1-4 equal to upper rows; fifth and sixth lower rows shorter; first lower row interrupted medially.

[Pg 326]

Body brown above; tip of snout brown; venter creamy gray; caudal musculature creamy tan; caudal fin transparent; cream-colored crescent-shaped mark on posterior edge of body; dark brown flecks on caudal musculature and all except anterior two-thirds of ventral caudal fin; large brown square blotches on dorsum of caudal fin; eye reddish brown in life.

Variation.—The variation in size and proportions is given in Table 2. With the exception of one specimen having a short, broken, seventh tooth-row, all specimens have $\frac{1}{6}$ tooth-rows that are like those described above. In some specimens the brown blotches on the dorsum of the caudal musculature are fused and marked with cream-colored flecks.

Comparisons.—*Ptychohyla leonhardschultzei* differs from all other members of the *Ptychohyla euthysanota* group in having a square snout, and further differs from *P. spinipollex* in more numerous and smaller nuptial spines and in transverse, instead of posteromedially slanting, vomerine processes between the inner nares. *Ptychohyla leonhardschultzei* differs from *P. euthysanota* in having a rostral keel and in having white flanks boldly spotted with black.

All small hylids that are sympatric with *Ptychohyla leonhardschultzei* are either yellow (*Hyla dendroscarta* and *H. melanomma*) or green (*Hyla erythromma*, which has a red eye, *Hyla hazelae*, which has a black line on the canthus, and *Ptychohyla ignicolor*, which has red flash colors on the thighs).

Life History.—This frog has been found along streams in cloud forests and in pine-oak forest. Males call from vegetation along the stream or from rocks in and at the edge of the stream. The call is a single, long, soft "wraack," repeated at intervals of anywhere from several seconds to three or four minutes. Each note has a duration of 0.62 to

0.95 of a second and a rate of 76 to 78 pulses per second; the dominant frequency falls between 2700 and 2800 cycles per second (Pl. 11C).

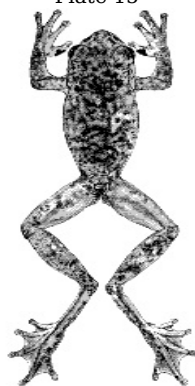
Tadpoles were found in several streams in northern Oaxaca. A tadpole having a total length of 21.1 mm. has three upper and four lower tooth-rows well developed; the fourth upper and fifth lower rows are weakly present, and the sixth lower row has not started to develop. Two metamorphosed young have snout-vent lengths of 15.2 and 15.5 mm.

Remarks.—Four specific names have been applied to this species. Ahl (1934:185) based his description of *Hyla leonhardschultzei* on a small, poorly preserved female. Taylor (1944:41) proposed the generic name *Ptychohyla* for a species (named therein as *P. adipoventris*) of hylid having ventrolateral glands and horn-covered nuptial spines. Obviously, Taylor was unaware that *Hyla leonhardschultzei* was the same species. Earlier Taylor (1937:46) described *Hyla pinorum*. The types of all of these species came from the Pacific slopes of the Sierra del Sur in Guerrero. Examination of the types and other available specimens shows that they are representatives of a single species. The type of *Hyla pinorum* is an immature male having a snout-vent length of 26.7 mm. All of these specimens have the square snout and black and white flanks characteristic of *Ptychohyla leonhardschultzei*. Although Shannon (1951:473) based his description of *Hyla milleri* on a male having well-developed ventrolateral glands, he overlooked the presence of these glands in his description and discussion of relationships. The acquisition of more specimens from northern Oaxaca has shown that *Hyla milleri* is the same as *Ptychohyla leonhardschultzei*. [Pg 327]

Distribution.—This species is known from pine-oak forest and cloud forest on the Pacific slopes of the Sierra Madre del Sur in Guerrero and Oaxaca and from the Atlantic slopes of the Sierra Madre Oriental in northern Oaxaca. Specimens have been collected at elevations between 700 and 1650 meters. Probably the species occurs in humid forests at similar elevations around the eastern end of the Mexican Highlands in Oaxaca.

Specimens examined.—MEXICO: Guerrero: Agua del Obispo, CNHM 123489-90, 126651, 106300, MCZ 29639, UIMNH 25047, 25049, USNM 114551; Malinaltepec, ZMB 34351, 34353. Oaxaca: 2.5 km. N of La Soledad, KU 58061; San Lucas Camotlán, UIMNH 3201, USNM 123700-1; Vista Hermosa, KU 64116-7, 64119, 68560 (tadpoles), 71344, 71717-8 (tadpoles), UMMZ 119604; 5 km. S of Yetla, KU 60045 (tadpoles); 7.5 km. S of Yetla, KU 64118, 68556-7 (tadpoles), 68559 (tadpoles), 68561 (2 young), 68630 (skeleton), UMMZ 115514-5, 118863 (tadpoles); 9 km. S of Yetla, KU 68558 (tadpoles).

Plate 15



Ptychohyla spinipollex (Schmidt)

Hyla euthysanota, Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:25, March 22, 1932.

Hyla spinipollex Schmidt, Proc. Biol. Soc. Washington, 49:45-46, May 1, 1936 [Holotype.—MCZ 21300 from the mountains behind Ceiba, Depto. Atlantidad, Honduras; Raymond E. Stadelman collector]. Stuart, Misc. Publ. Mus. Zool. Univ. Michigan, 69:32-34, figs. 5-6, June 12, 1948; Contr. Lab. Vert. Biol. Univ. Michigan, 45:22, 52, 54, 57, May, 1950; Proc. Biol. Soc. Washington, 67:169, August 5, 1954.

Ptychohyla spinipollex, Stuart, Contr. Lab. Vert. Biol. Univ. Michigan, 68:48, November, 1954. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:351, April 27, 1961.

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Diagnosis.—Rostral keel present; snout in lateral profile rounded above; eyelid nearly as wide as interorbital region; flanks white with brown spots; belly spotted; nuptial spines pointed and moderate in size.

Description.—The following description is based on KU 58054 from Finca Los Alpes, Depto. Alta Verapaz, Guatemala (Pl. 15). Adult male having a snout-vent length of 37.7 mm.; tibia length, 18.2 mm.; tibia length/snout-vent length, 48.2 per cent; foot length, 15.8 mm.; head length, 11.7 mm.; head length/snout-vent length, 31.0 per cent; head width, 11.7 mm.; head width/snout-vent length, 31.0 per cent; diameter of eye, 3.6 mm.; diameter of tympanum, 1.9 mm.; tympanum/eye, 52.7 per cent. Snout in lateral profile nearly square, slightly rounded above, and in dorsal profile rounded with a pointed tip resulting from vertical rostral keel; canthus pronounced; loreal region barely concave; lips thick, rounded, and barely flaring; nostrils protuberant; internarial distance, 3.0 mm.; top of head flat; interorbital distance, 3.7 mm., about equal to width of eyelid, 3.6 mm. A heavy dermal fold from posterior corner of eye above tympanum to point above insertion of forearm, covering upper edge of tympanum; tympanum round, its diameter equal to its distance from eye. Forearm moderately robust, having faint dermal fold on wrist; row of low, rounded tubercles along ventrolateral edge of forearm; pollex only slightly enlarged, bearing triangular patch of moderate-sized, pointed, horn-covered spines (38 on right, 43 on left); second finger noticeably shorter than fourth; subarticular tubercles round, distal one on fourth finger bifid; discs of fingers of moderate size, that of third finger slightly smaller than diameter of tympanum; vestigial web between first and second fingers; other fingers one-third webbed. Heels broadly overlapping when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; distinct, but low, tarsal fold extending length of tarsus; inner metatarsal tubercle elevated, flat, and elliptical; outer metatarsal tubercle small and round, near base of fourth toe; row of low indistinct tubercles from heel to base of fifth toe; subarticular tubercles round; length of toes from shortest to longest 1-2-3-5-4, the third and fifth being about equal in length; third and fifth toes webbed to base of disc; fourth toe webbed to base of penultimate phalanx; discs of toes slightly smaller than those on fingers. Anal opening near upper edge of thighs; opening bordered laterally by moderately heavy dermal folds and ventrolaterally by tubercles. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands barely evident. Tongue ovoid, barely notched behind and slightly free posteriorly; vomerine teeth 2-3, situated on V-shaped elevations between round inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus. [Pg 328]

Dorsal ground-color of head, body, and limbs grayish tan with dark brown reticulations on head and body and dark brown transverse bars or spots on limbs; first and second fingers cream color; third and fourth fingers and webbing on hands pale grayish brown; anterior surfaces of thighs reddish tan; posterior surfaces of thighs yellowish tan; tarsi and toes pale grayish tan with brown flecks; webbing on foot pale brown; faint white stripe along ventrolateral edges of tarsi and forearms; narrow white line above and beside anal opening; no white stripe on edge of upper lip; axilla pale flesh-color; throat, chest, and ventral surfaces of limbs pale creamy gray; belly white with scattered brown flecks; flanks grayish white with dark brown flecks; ventral surfaces of tarsi dark brown; ventrolateral glands grayish tan.

In life the dorsal ground-color of the head, body, fore limbs, and thighs was yellowish tan (Pinkish Buff); dorsal surfaces of shanks and tarsi pale yellowish tan (Pale Pinkish Buff); markings on head and back brown (Snuff Brown) to dark brown (Chocolate); dark bands on limbs brown (Tawny-Olive); first and second fingers creamy tan (Light Pinkish Cinnamon); posterior surfaces of thighs creamy tan (Light Pinkish Cinnamon); third and fourth fingers and webbing on hand grayish brown (Avellaneous); webbing on feet dark brown (Olive Brown); axilla pale pink (Hydrangea Pink); flanks buff (Cream-Buff) becoming yellow (Lemon Chrome) in groin; spots on flanks dark brown (Clove Brown); iris dull grayish bronze (Orange-Citrine). [Pg 329]

Variation.—The distal subarticular tubercle beneath the fourth finger is bifid in about two-thirds of the specimens; in the rest it is round. The posterior edge of the tongue varies from being emarginate to shallowly notched. In most specimens the row of tubercles along the outer edge of the tarsus is made up of discrete tubercles, but in some individuals the tubercles form a nearly continuous dermal fold. Most specimens have the vomerine teeth situated on V-shaped elevations, but in some individuals the elevations are more nearly transversely situated between the inner nares.

All 42 specimens from Finca Los Alpes, Guatemala, have dark brown spots and flecks on the venter. Some individuals have only a few flecks on the throat and a few large spots on the flanks, as does KU 64125. Other specimens, such as KU 64132, have dense

spotting over the entire venter. The color of the dorsum varies from pale tan to dark brown with darker brown markings; the white line above the anus is present in all specimens, but in some it is indistinct. KU 58053 and 64127 have a dark brown dorsum with large pale tan, square blotches; in life the blotches were pale tan (Pinkish Buff); the rest of the dorsum was dark brown (Sayal Brown). KU 58052 is dark brown with many small white flecks on the dorsum; in life the dorsum was deep olive brown (Dark Olive).

Aside from the differences mentioned above, all specimens from Guatemala are similar in coloration. Three specimens from Honduras (MCZ 21300 and UMMZ 113102-3) have unspotted white venters. MCZ 21300, the holotype of *P. spinipollex*, lacks a white stripe above the anal opening, whereas the stripe is indistinct in UMMZ 113102-3.

Description of tadpole.—The following description is based on KU 60053 from Fina Los Alpes, Depto. Alta Verapaz, Guatemala (Figs. 4D and 6D). No limb buds; total length, 37.2 mm.; body length, 12.2 mm.; body length/total length, 32.8 per cent. Body rounded, not depressed, as wide as deep, ovoid in dorsal profile; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant and directed anterolaterally, somewhat closer to eye than snout; spiracle sinistral and posterovertrally to eye; anal tube dextral. Caudal fin low, bluntly rounded posteriorly; greatest depth of caudal musculature about one-half depth of caudal fin; musculature extends nearly to tip of tail.

Mouth large; lips having deep lateral folds; two complete rows of papillae on lips; six or seven rows of papillae laterally; beaks moderately developed, bearing fine blunt serrations; slender lateral projections on upper beak; tooth-rows $\frac{4}{4}$; upper rows subequal in length; fourth row interrupted medially; lower rows 1-4 equal in length to upper rows; lower rows 5-7 decreasing in length; first lower row interrupted medially.

Top of head and tip of snout brown; venter creamy gray; caudal musculature tan; caudal fin transparent; faint cream-colored, narrow, crescent-shaped mark on posterior edge of body, not bordered posteriorly by dark brown mark; brown flecks scattered on caudal musculature and caudal fin; only a few flecks on anterior half of ventral caudal fin; eye bronze-color in life.

Variation.—The variation in size and proportions as compared with tadpoles of other species is given in Table 2. Of the 57 tadpoles of this species that I have examined, 21 have only six lower tooth-rows, although in some of these specimens a faint ridge for a seventh row is present. In those specimens having seven lower rows, the seventh often is broken.

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There is considerable variation in coloration. None has a distinct cream-colored, crescent-shaped mark bordered posteriorly by a dark brown bar or triangle, as in the other species in the *Ptychohylla euthysanota* group. Most specimens have a rather indistinct crescent; some have no crescent. In a few specimens there is a weakly outlined dark mark posterior to the crescent. Some specimens in a series of tadpoles from 32 kilometers north of Morazán, Baja Verapaz, Guatemala, have faint dorsal blotches on the dorsal musculature, much like those in tadpoles of *Ptychohylla leonhardschultzei*.

Comparisons.—*Ptychohylla spinipollex* differs from all other species in the genus by having moderate-sized, instead of small, pointed nuptial spines; also it has fewer spines than the other species (see discussion of this character in Analysis of Data). The nearly equal interorbital breadth and width of the upper eyelid also is diagnostic of this species.

Other hylids sympatric with *Ptychohylla spinipollex* include three species of *Plectrohyla*, each of which has a bony prepollex, heavy body, and rugose skin on the dorsum. The only other sympatric hylid that could be confused with *Ptychohylla spinipollex* is *Hyla bromeliacea*, which has a round snout and yellowish tan dorsum not marked with dark brown.

Life History.—At Finca Los Alpes, Guatemala, in July, 1960, and in August, 1961, calling males were found on bushes and trees along cascading mountain streams. The breeding call consists of a soft "wraack," repeated at intervals of 45 seconds to four minutes. Each note has a duration of about .46 of a second and a rate of 147 pulses per second. The dominant frequency is 4300 cycles per second (PL 11A).

Tadpoles have been found in cascading mountain streams. Two metamorphosed young have snout-vent lengths of 15.0 and 15.5 mm.

Remarks.—There is little doubt that all of the specimens herein referred to *Ptychohylla spinipollex* are conspecific. However, the three specimens from Honduras, including the type of *Ptychohylla spinipollex*, differ from Guatemalan specimens in lacking all dark spotting on the venter. Additional specimens from Honduras and eastern Guatemala may show that two subspecies are recognizable, in which case the nominal subspecies will be the population in Honduras.

Distribution.—This species lives in cloud forests at elevations of 800 to 1700 meters on the Atlantic side of the Guatemalan Highlands from the Sierra de Cuchumatanes in western Guatemala eastward to central Honduras.

Specimens examined.—GUATEMALA: *Alta Verapaz*: Finca Chichén, UMMZ 90876 (tadpoles); Finca Los Alpes, KU 58052-60, 59939 (skeleton), 60053 (tadpoles), 64122-41, 68562, 68563 (tadpoles), 68631-2 (skeletons), MCZ 35000-1, UMMZ 90873, 90874 (3), 90875 (tadpoles); La Primavera, UMMZ 90877 (tadpoles); Panzamalá, UMMZ 90878 (tadpoles). *Baja Verapaz*: 32 km. N of Morazán, KU 68564 (tadpoles); *Santa Elena*, UMMZ 98119, 98120 (2). *Huehuetenango*: 1 km. E of Barillas, UMMZ 123136-7 (tadpoles). *Progreso*: Finca Bucaral, UMMZ 106783 (3), 123138 (tadpoles), S-1292 (skeleton).

[Pg 331]

HONDURAS: *Atlántida*: Mountains behind Ceiba, MCZ 21300. *Morazán*: Cerro Uyuca, UMMZ 123102-3.

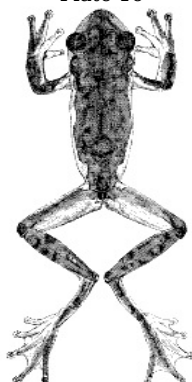
The *Ptychohylla schmidtorum* Group

Two species in group; adults having only vestige of web between fingers and lacking tarsal fold; pollex of breeding males lacking spinous, horny, nuptial tuberosities; mouth of tadpole greatly expanded, funnel-shaped, lacking lateral folds, and having $\frac{3}{3}$ tooth-rows; breeding call consisting of series of short notes.

Ptychohylla schmidtorum

Diagnosis.—Diameter of tympanum more than half of diameter of eye; internarial region depressed; toes three-fourths webbed; no red flash-colors on thighs.

Plate 16



Ptychohylla schmidtorum schmidtorum Stuart

Ptychohylla schmidtorum Stuart, Proc. Biol. Soc. Washington, 67:169-172, August 5, 1954 [Holotype.—CNHM 27055 from El Porvenir (17 kilometers air-line west of San Marcos), Depto. San Marcos, Guatemala; Karl P. Schmidt collector]. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:351, 355, April 27, 1961.

Diagnosis.—Vomerine teeth 5-11; dorsum dark brown; white spot below eye; eye red in life.

Description.—The following description is based on KU 58043 from Finca La Paz, Depto. San Marcos, Guatemala (Pl. 16). Adult male having snout-vent length of 31.6 mm.; tibia length, 15.0 mm.; tibia length/snout-vent length, 47.5 per cent; foot length, 12.5 mm.; head length, 10.2 mm.; head length/snout-vent length, 32.3 per cent; head width, 9.9 mm.; head width/snout-vent length, 31.3 per cent; diameter of eye, 3.4 mm.; diameter of tympanum, 1.8 mm.; tympanum/eye, 52.9 per cent. Snout in lateral profile nearly square, slightly rounded above and below, and in dorsal profile bluntly squared; canthus pronounced; loreal region concave; lips thick, rounded, and flaring; nostrils protuberant; internarial distance, 2.2 mm.; internarial region depressed; top of head flat; interorbital distance, 3.4 mm., much greater than width of eyelid, 2.5 mm. Thin dermal fold from posterior corner of eye above tympanum to insertion of forelimb, covering upper edge of tympanum; tympanum round, its diameter equal to its distance from eye. Forearm slender, lacking distinct dermal fold on wrist; row of low rounded tubercles along ventrolateral edge of forearm; pollex slightly enlarged; no nuptial spines; second and fourth fingers about equal in length; subarticular tubercles small and round, distal one beneath fourth finger bifid; discs small, that of third finger noticeably smaller than tympanum; no web between first and second fingers; vestige of web between other fingers. Heels overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; no tarsal fold; inner metatarsal tubercle large, flat, and elliptical; outer metatarsal tubercle small, ovoid, slightly more distal than inner; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third and fifth toes webbed to base of discs; fourth toe webbed to base of penultimate phalanx; discs of toes smaller than on fingers. Anal opening directed posteriorly at upper edge of thighs; no anal flap; pair of large tubercles below anal opening and smaller tubercles farther below. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of belly and ventral surfaces of thighs granular. Ventrolateral glands well developed, reaching axilla and groin and narrowly separated on chest. Tongue ovoid, emarginate posteriorly, and only slightly free behind; vomerine teeth 3-3, situated on small triangular elevations between ovid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus. [Pg 332]

Dorsum of head, body, and limbs reddish brown with indistinct, irregular darker brown markings on body and dark brown transverse bands or spots on limbs; first and second fingers creamy white; third and fourth fingers brown; dorsal surfaces of tarsi and third, fourth, and fifth toes tan with brown spots; first and second toes and webbing on feet creamy tan; enamel-white stripe along edge of upper lip continuing over, and on posterior edge of, forearm to groin, expanded to form spot below eye; belly white, unspotted; ventrolateral glands pale brown; ventral surfaces of hind limbs and anterior and posterior surfaces of thighs cream color; enamel-white stripe on heel; creamy white stripe along ventrolateral edges of tarsi and forearms.

In life dorsum reddish brown (Terra Cotta) with dark brown (Burnt Umber) markings; first and second fingers and first and second toes orange-yellow (Light Orange-Yellow); posterior surfaces of thighs pale reddish tan (Ochraceous-Salmon); webbing on feet yellowish tan (Deep Colonial Buff); belly white; iris red (Nopal Red).

Variation.—Little variation in structural characters was observed. All but five specimens have bifid subarticular tubercles beneath the fourth finger. Three specimens have cordiform tongues, and in four others the tongue is ovoid and shallowly notched behind; all other specimens have an emarginate ovoid tongue.

Some individuals when active at night had a pale brown (Ochraceous-Tawny) dorsum with dull olive green (Dark Olive Buff) markings. Otherwise there was no noticeable variation in color.

Description of tadpole.—The following description is based on KU 60051 from Finca La Paz, Depto. San Marcos, Guatemala (Figs. 5A and 6E). Small hind limbs; total length, 37.9 mm.; body length, 11.6 mm.; body length/total length, 30.6 per cent. Body only slightly depressed, nearly as deep as wide, in dorsal profile ovoid, widest just posterior to eyes; in lateral profile snout rounded; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant, directed anteriorly, somewhat closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Tail long and slender; caudal fin low and rounded posteriorly; depth of caudal musculature one-half greatest depth of caudal fin; musculature not extending to tip of tail.

Mouth large; thin fleshy lips greatly expanded and forming large funnel-shaped disc; width of mouth two-thirds greatest width of body; outer edge of lips having one row of small papillae; inner surfaces of mouth smooth; scattered large papillae forming one nearly complete row around teeth; other large papillae laterally; beaks moderately developed, bearing long, pointed denticulations; no lateral projections on upper beak; tooth-rows $\frac{3}{3}$, all short; second and third upper rows subequal in length; first upper row shorter; first and third upper rows interrupted medially; first lower row interrupted medially, equal in length to second and third upper rows; second lower row slightly shorter; third lower row shortest. [Pg 333]

Body mottled brown and creamy gray above and below; mouth colored like body; caudal musculature creamy tan; caudal fin transparent; dark brown streak mid-laterally on anterior third of caudal musculature; rest of tail and all of caudal fin heavily flecked with brown; eye red in life.

Variation.—The third upper tooth-row is interrupted in all specimens; in some individuals the first upper and first lower rows are complete. The variation in size and proportions is given in Table 2. The dark brown lateral streak on the anterior part of the caudal musculature is distinct on most specimens; the only other variation in coloration is in the amount of brown flecking on the caudal musculature and fin.

Comparisons.—*Ptychohyla schmidtorum schmidtorum* differs from *P. schmidtorum chamulae* as stated in the diagnosis and in having pale creamy tan, as opposed to dark brown, webbing on the feet; and from *P. ignicolor* in having a depressed, as opposed to a flat, internarial region. Tadpoles of *P. s. schmidtorum* have a mottled appearance, as opposed to the more uniform brown color of *P. s. chamulae*.

Ptychohyla schmidtorum schmidtorum and several species of *Plectrohyla* are sympatric. All species of the latter genus have a bony prepollex, rugose skin on the dorsum, and heavy body; also sympatric is *Ptychohyla e. euthysanota*, which has a tarsal fold and in breeding males spinous nuptial tuberosities.

Life History.—This species breeds in clear mountain streams where males call from vegetation along the stream. The call consists of series of short notes, three to nine notes per series, sounding like "raa-raa-raa." The duration of each note is approximately .065 of a second, and has a rate of 96 to 119 pulses per second; the dominant frequency is about 3400 cycles per second. The call is almost indistinguishable from that of *Ptychohyla schmidtorum chamulae*.

Tadpoles and metamorphosing young were found at Finca La Paz, Guatemala, in late July, 1960. Two young lacking tails but not having completely developed mouths have snout-vent lengths of 14.2 and 14.6 mm. L. C. Stuart collected four metamorphosing young at Finca La Paz on May 6, 1949. By May 10 the frogs were completely metamorphosed, at which time they had snout-vent lengths of 15.5 to 17.0 (average 16.1) mm.

Remarks.—There is no doubt that this frog is most closely related to *Ptychohyla schmidtorum chamulae*, even though the ranges of the two subspecies are separated by the interior depression of Chiapas. Since at least at Finca La Paz, Guatemala, *P. s. schmidtorum* occurs with *P. e. euthysanota*, it is surprising that the former species has not been found at more localities along the Pacific slopes on northern Central America. At Finca La Paz in July, 1960, *P. s. schmidtorum* was more abundant than *P. e. euthysanota*. [Pg 334]

Distribution.—This species is known only from a limited area at elevations between 1300 and 2200 meters on the Pacific slopes of the Sierra Madre in extreme eastern Chiapas and western Guatemala.

Specimens examined.—MEXICO: Chiapas: Finca Irlandia, UMMZ 105429-30.

GUATEMALA: San Marcos: El Porvenir, CNHM 20755, 20761, 69904, UMMZ 80918; Finca La Paz, 2 km. W of La Reforma, KU 58016-44, 59940-2 (skeletons), 60050 (3 young), 60051 (tadpoles), 60052 (4 young), MCZ 34998-9, UMMZ 123144-7 (tadpoles).



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***Ptychohyla schmidtorum chamulae* Duellman**

Ptychohyla chamulae Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13: 354-357, pl. 25, fig. 2, April 27, 1961 [Holotype.—KU 58063 from 6.2 kilometers south of Rayón Mescalapa, Chiapas, México; William E. Duellman collector].

Diagnosis.—Vomerine teeth 4-6; dorsum bright green; white lateral stripe; eye reddish bronze in life.

Description.—The following description is based on KU 58069 from 6.2 kilometers south of Rayón Mescalapa, Chiapas, México (PL 17). Adult male having a snout-vent length of 27.6 mm.; tibia length, 13.0 mm.; tibia length/snout-vent length, 47.1 per cent; foot length, 10.8 mm.; head length, 9.6 mm.; head length/snout-vent length, 34.7 per cent; head width, 9.2 mm.; head width/snout-vent length, 33.1 per cent; diameter of eye, 3.0 mm.; diameter of tympanum, 1.6 mm.; tympanum/eye, 53.3 per cent. Snout in lateral profile nearly square, slightly rounded above and below, and in dorsal profile blunt, almost square; canthus pronounced; loreal region concave; lips thick, rounded and flaring; nostrils protuberant; internarial distance, 2.5 mm.; internarial region slightly depressed; top of head flat; interorbital distance, 3.3 mm., much greater than width of eyelid, 2.5 mm. Thin dermal fold, from posterior corner of eye above tympanum to insertion of fore limb, covering upper edge of tympanum; tympanum nearly round, its diameter equal to its distance from eye. Forearm slender, lacking distinct fold on wrist; row of low, rounded tubercles on ventrolateral surface of forearm; pollex slightly enlarged, without nuptial spines; second and fourth fingers equal in length; subarticular tubercles round, that under fourth finger bifid; discs small, that of third finger noticeably smaller than tympanum; no web between first and second fingers; vestige of web between other fingers. Heels overlapping when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; no tarsal fold; inner metatarsal tubercle large, flat, and elliptical; outer metatarsal tubercle small, elliptical, slightly more distal than inner; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third and fifth toes webbed to base of disc; fourth toe webbed to base of penultimate phalanx; discs smaller on toes than on fingers. Anal opening directed posteriorly at upper edge of thighs; no anal flap; pair of large tubercles below anal opening. Skin of dorsum and of ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands well developed, not reaching axilla or groin and broadly separated midventrally. Tongue cordiform, shallowly notched behind and only slightly free posteriorly; vomerine teeth 2-3, situated on small triangular elevations between ovoid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

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Dorsum of head, body and limbs reddish brown with dark purplish brown markings on back and shanks; first finger creamy tan; other fingers pale brown; dorsal surfaces of tarsi, third, fourth, and fifth toes dull tan with brown spots; first and second toes creamy tan; webbing on feet brown; anterior and posterior surfaces of thighs tan; faint creamy white stripe along ventrolateral edges of tarsi and forearms; enamel-white stripe on heel; axilla and groin gray; enamel-white stripe on edge of upper lip, continuing onto proximal upper surfaces of forelimb and on flanks to groin, widened under eye to form large spot, and bordered below on flanks by dark brown stripe; white stripe above and white spots below anal opening; throat and chest white; belly and ventral surfaces of limbs cream color; brown dash on either side of chin and brown spot on throat near angle of jaws; few brown flecks on belly; ventrolateral glands orange-tan; ventral surfaces of tarsi and feet brown.

In life, dorsal surfaces of head, body, and limbs bright green (Shamrock Green); first and second fingers pale orange (Apricot Yellow); stripe on upper lip and spot below eye enamel-white; stripe on flanks silvery white, bordered below by brown (Saccardo's Umber) brown; anterior and posterior surfaces of thighs yellowish brown (Old Gold); webbing of feet dull brown (Brownish Olive); belly deep yellow (Amber Yellow); iris reddish bronze (English Red).

Variation.—Tubercles beneath the fourth fingers are bifid in 20 specimens and rounded in all others. The tongue is emarginate in 12 specimens and cordiform in all others. In most specimens the white stripe on the upper lip continues onto the flanks and to the groin; in five specimens the stripe terminates above the forearm, and in three it terminates at mid-flank. The lateral stripe is absent in two specimens. All specimens were uniform green above when found at night; later some changed to pale green (Light Oriental Green) on the dorsum with irregular yellowish tan (Naples Yellow) blotches. Most males have brown flecks on the throat and ventrolateral gland, but some specimens are immaculate below, and one has dark brown mottling on the throat. Several males have a round, orange-tan glandular area on the chin, as does *P. ignicolor*.

Description of tadpole.—The following description is based on KU 58199 from 6.2 kilometers south of Rayón Mescalapa, Chiapas, México (Figs. 5B and 6F). Hind limbs small; total length, 39.0 mm.; body length, 10.5 mm.; body length/total length, 26.9 per cent. Body barely depressed, only slightly wider than deep, widest just posterior to eyes; in dorsal profile ovoid; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant, directed anterodorsally, slightly closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Tail long and slender; caudal fin low, rounded posteriorly; depth of caudal musculature one-half greatest depth of caudal fin; musculature not extending to tip of tail.

Mouth large; thin fleshy lips greatly expanded and forming funnel-shaped disc; outer edge of lips having one row of small papillae; inner surfaces of mouth smooth; scattered large papillae forming nearly one complete row around teeth; other papillae laterally; beaks moderately developed, bearing long, pointed denticulations; no lateral projections on upper beak; tooth-rows $\frac{3}{3}$, all short; second and third upper rows subequal in length; first upper row shorter; first and third upper rows interrupted medially; first lower row interrupted medially, equal in length to second and third upper rows; second lower row slightly shorter; third lower row shortest.

[Pg 336]

Body dark brown above and dark gray below; fleshy part of mouth creamy gray mottled with dark brown; caudal musculature pale tan with heavy suffusion of brown flecks; caudal fin transparent with brown spots; dark brown streak mid-laterally on anterior one-fifth of caudal musculature, bordered below by cream-colored spot; eye brown in life.

Variation.—The third upper tooth-row is interrupted in all specimens, but in some individuals the first upper row and first lower row are complete. The only noted variation in color is the intensity of brown pigmentation on the caudal musculature, which in most specimens is sufficiently dense to make the tail look brown. In some specimens the mid-lateral streak is indistinct, and the pale spot below the streak is absent.

Comparisons.—Aside from the characters listed in the diagnosis, *Ptychohyla schmidtorum chamulae* differs from *P. schmidtorum schmidtorum* by having dark brown webbing on the feet, instead of pale creamy tan webbing, and in having in life a yellow venter, instead of a white venter. *Ptychohyla ignicolor* also is green in life, but has red flash-colors on the thighs, red webbing on the feet, and lacks the white lateral stripe diagnostic of *P. schmidtorum chamulae*.

Plectrohyla matudai matudai and *P. guatemalensis* are sympatric with *Ptychohyla schmidtorum chamulae*. Each of the first two has a bony prepollex, rugose skin on the dorsum, and heavy body. Also living with *Ptychohyla chamulae* are *Hyla chaneque*, a large species having a tuberculate dorsum and webbed fingers, and *Hyla bivocata*, a small yellow species having a broad, flat head, small indistinct tympanum, and an axillary membrane.

Life History.—Calling males were found on leaves of herbs and bushes by cascading streams in cloud forest. The call consists of series of short notes, three to nine notes per series, sounding like "raa-raa-raa." The duration of each note is .054 to .070 of a second, and has a rate of 96 to 110 pulses per second. The dominant frequency falls between 3350 and 3450 cycles per second (PL 11D). The call is almost indistinguishable from that of *Ptychohyla schmidtorum schmidtorum*.

Tadpoles were found in the cascading streams; the smallest tadpole has a total length of 17.2 mm. and has only $\frac{3}{2}$

tooth-rows. At a stream 6.2 kilometers south of Rayón Mescalapa, Chiapas, metamorphosing young were found on June 16 and August 5, 1960. Each of two completely metamorphosed young has a snout-vent length of 15.7 mm. Another having a snout-vent length of 16.2 mm. has a tail stub 2 mm. long and a completely metamorphosed mouth. Two others have snout-vent lengths of 13.6 and 14.1 mm. and tail lengths of 11.5 and 8.1 mm. respectively; in these the mouth parts are incompletely metamorphosed.

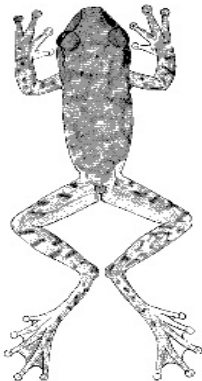
Remarks.—Duellman (1961:354) described *Ptychohyala chamulae* and stated that it probably was most closely related to *P. schmidtorum*. Further study has revealed additional resemblance in morphological and behavioral details. It is concluded that the two populations are more realistically treated as subspecies than as species. The geographic ranges, as now known, are disjunct. *Ptychohyala schmidtorum chamulae* inhabits cloud forest on the Atlantic slopes of the Chiapan Highlands, whereas *P. s. schmidtorum* lives in cloud forest on the Pacific slopes of the Sierra Madre in Chiapas and Guatemala. Between their known geographic ranges are the pine clad Sierra Madre and Chiapan Highlands, and intervening sub-humid Grijalva Valley.

Distribution.—This species is known only from elevations between 1500 and 1700 meters on the Atlantic slopes of the Chiapan Highlands; it is to be expected in cloud forests on the northern slopes of the Sierra de Cuchumatanes in Guatemala.

Specimens examined.—MEXICO: Chiapas: 15 km. N of Pueblo Nuevo Solistahuacán, UMMZ 123325 (4); 16.5 km. N of Pueblo Nuevo Solistahuacán, UMMZ 123322 (10); 18 km. N of Pueblo Nuevo Solistahuacán, UMMZ 121395-9, 123324 (8), 123326 (5); 18.6 km. N of Pueblo Nuevo Solistahuacán, UMMZ 123323 (4); 5.6 km. S of Rayón Mescalapa, KU 58062, 58200 (tadpoles); 6.2 km. S of Rayón Mescalapa, KU 58063-74, 58199 (tadpole), 58234-8, 59936 (skeleton).

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Plate 18



Ptychohyala ignicolor Duellman

Ptychohyala ignicolor Duellman, Uni. Kansas Publ. Mus. Nat. Hist., 13:352-353, pl. 25, fig. 1, April 27, 1961 [Holotype.—UMMZ 119603 from 6 kilometers south of Vista Hermosa, Oaxaca, México; Thomas E. Moore collector].

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Diagnosis.—Diameter of tympanum less than one-half diameter of eye; internarial region flat; 3-7 vomerine teeth; toes one-half webbed; no white spot below eye; no lateral white stripe; in life dorsum green; groin and thighs having bright red flash-colors.

Description.—The following description is based on UMMZ 119603 from 6 kilometers south of Vista Hermosa, Oaxaca, México (Pl. 18). Adult male having a snout-vent length of 30.0 mm.; tibia length, 14.6 mm.; tibia length/snout-vent length, 48.7 per cent; foot length, 12.3 mm.; head length, 9.2 mm.; head length/snout-vent length, 30.7 per cent; head width, 9.3 mm.; head width/snout-vent length, 31.0 per cent; diameter of eye, 3.2 mm.; diameter of tympanum, 1.3 mm.; tympanum/eye, 40.6 per cent. Snout in lateral profile square, and in dorsal profile rounded; canthus pronounced; loreal region slightly concave; lips moderately flaring; top of head flat; nostrils protuberant; internarial distance, 2.8 mm.; internarial region flat; interorbital distance, 3.3 mm., much broader than width of eyelid, 2.8 mm. A heavy dermal fold from posterior corner of eye above tympanum to insertion of forelimb, covering upper edge of tympanum; tympanum elliptical, its greatest diameter equal to its distance from eye. Forearm moderately robust having distinct dermal fold on wrist; pollex moderately enlarged without nuptial spines; second and fourth fingers equal in length; subarticular tubercles round, none is bifid; discs on fingers moderate in size, that on third finger slightly larger than tympanum; no web between first and second fingers; vestige of web between other fingers. Heels overlap when hind limbs adpressed; tibiotarsal articulation extends to anterior corner of eye; no tarsal fold; inner metatarsal tubercle large, flat, and elliptical; outer metatarsal tubercle near inner one and triangular in shape; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third toe webbed to proximal end of penultimate phalanx; fourth toe webbed to distal part of antepenultimate phalanx; fifth toe webbed to middle of penultimate phalanx; discs on toes smaller than on fingers. Anal opening directed posteriorly at upper edge of thighs; no anal flap; pair of large tubercles below anal opening; small tubercles ventral and lateral to these. Skin of dorsum and ventral surfaces of limbs smooth; that of throat and belly granular. Ventrolateral glands noticeably thickened, extending from axilla nearly to groin and only narrowly separated midventrally on chest; skin of anterior part of chin thickened and glandular. Tongue cordiform, shallowly notched behind and only slightly free posteriorly; vomerine teeth 0-3, situated on rounded elevations between somewhat larger, round inner nares; openings to vocal sac large, one situated along posterior margin of each mandibular ramus.

[Pg 338]

Dorsal ground-color of head, body, and limbs dull brown with dark brown reticulations on head and body and dark brown transverse bands or spots on limbs; first and second fingers cream color; third and fourth fingers dull tan; anterior surfaces of thighs pale brown; posterior surfaces of thighs cream color with heavy suffusion of brown; dorsal surfaces of tarsi and third, fourth, and fifth toes dull brown with dark brown spots; first and second toes creamy white; webbing on foot brown; axilla and groin cream color; flanks brown; no white stripes on edge of upper lip or on flank; faint, barely discernible tan streak above anal opening; faint creamy tan line on ventrolateral edges of tarsi; throat, belly, ventral surfaces of limbs, inner edges of tarsi, and first toes cream color; outer ventral surfaces of tarsi and other toes brown; chest and throat spotted with brown; ventrolateral and chin glands orange-brown.

In life the dorsum was uniform green (Cosse Green) becoming paler green (Bright Green-Yellow) on flanks, later changing to paler green (Javel Green) on dorsum with irregular darker green (Lettuce Green) markings and greenish yellow (Green-Yellow) on flanks; anterior and posterior surfaces of thighs, ventral surfaces of shanks, anterior surfaces of tarsi, and upper proximal surfaces of first, second, and third toes red (Coral Red); venter pale creamy yellow (Sulfur Yellow); iris pale golden color (Aniline Yellow).

Variation.—Of 13 specimens, six have a cordiform tongue; the others have an emarginate tongue. Five specimens have round subarticular tubercles beneath the fourth fingers; six specimens have a bifid tubercle on one hand, and two specimens have bifid tubercles on both hands. A round gland is present on the chin of all specimens; in some the gland is barely visible, but in others it is large and distinct. In two specimens the ventrolateral glands are weakly developed; in the others the glands are well developed and orange-tan. The white anal stripe varies from a thin line to a series of white flecks. Dark brown or black flecks are present on the throat, chest, and flanks of all specimens. In some the flecks are small and widely scattered; in others the flecks are larger and more numerous. All specimens were pale green above when calling at night; later they changed to dull green with darker green reticulations. The flash-colors on the thighs and in the groin vary from red to orange-red or brownish red.

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Description of tadpole.—The following description is based on KU 71716 from Vista Hermosa, Oaxaca, México (Figs. 5C and 6C). Hind limbs small; total length, 39.6 mm.; body length, 11.8 mm.; body length/total length, 29.8 per cent. Body moderately depressed, only slightly wider than deep, in dorsal profile ovoid, widest just posterior to eyes; in lateral profile snout rounded; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant, directed anteriorly, somewhat closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Tail long and slender; caudal fin low and rounded posteriorly; depth of caudal musculature about one-half greatest depth of caudal fin; musculature not extending to tip of tail.

Mouth large; thin fleshy lips greatly expanded and forming large funnel-shaped disc; width of mouth about two-thirds greatest width of body; outer edge of lips having one row of small papillae; inner surface of mouth smooth; scattered large papillae forming one nearly complete row around teeth; other papillae laterally; one large papilla just above each end of first lower tooth-row; beaks moderately developed bearing long, pointed denticulations; no lateral projections on upper beak; tooth-rows $\frac{3}{4}$, all short; second and

third upper rows subequal in length; first upper row shorter; first lower row equal in length to second and third upper rows; second lower row slightly shorter; third lower row shortest.

Body creamy gray with dark brown flecks above and below; mouth colored like body; caudal musculature creamy tan; caudal fin transparent; dark brown streak on anterior third of caudal musculature; rest of tail and all of caudal fin, except anterior two-thirds of ventral fin, heavily flecked with brown; iris silvery bronze color in life.

Variation.—The only other known tadpole, which was collected with the individual described above, differs in having only two upper tooth-rows. The first upper tooth-row seems not to have developed.

Comparisons.—From *P. schmidtorum chamulae* and *P. s. schmidtorum*, *P. ignicolor* differs as follows: Tympanum smaller; snout more nearly square; less webbing on toes; internarial region flat instead of depressed; white lateral stripes lacking.

Ptychohyla ignicolor and several small and moderate sized hylids are sympatric. From *P. ignicolor* these hylids can be distinguished as follows: *Hyla dendroscarta* has a round snout and yellow dorsum; *Hyla erythromma* has a round snout, green dorsum, white flanks, and a red eye; *Hyla hazelae* has a tarsal fold, green dorsum, and a black line on the canthus; and *Ptychohyla leonhardschultzei* has a tarsal fold, brown dorsum, black and white flanks, and horny nuptial spines in breeding males.

Life History.—At Vista Hermosa, Oaxaca, males were calling on vegetation above small streams on March 30, 1959, and on June 28, 1962; males were found on vegetation overhanging a stream 6 kilometers south of Vista Hermosa on June 27 and July 3, 1962. The call consists of a series of short notes, three to thirteen notes per series, sounding like "raa-raa-raa." The duration of each note is about .08 of a second and has a rate of 123 to 129 pulses per second. The dominant frequency of notes in short series is about 2100 cycles per second, whereas the dominant frequency of notes in long series is about 3150 cycles per second (Pl. 11E).

On June 28, 1962, two tadpoles of this species were found in a quiet pool in a spring-fed rivulet at Vista Hermosa, Oaxaca. Females are unknown.

Remarks.—The absence of a tarsal fold and of nuptial spines in breeding males, the nature of the breeding call, and the form of tadpole are characters that place *Ptychohyla ignicolor* in the *P. schmidtorum*-group.

Distribution.—This species is known from only two localities at elevations of 1500 and 1850 meters in the cloud forest on the northern (Atlantic) slopes of the Sierra Madre Oriental in northern Oaxaca.

Specimens examined.—MEXICO: Oaxaca: Vista Hermosa, KU 71334, 71716 (tadpoles), UMMZ 119602; 6 km. S of Vista Hermosa, KU 71335-42, 71343 (skeleton), UMMZ 119603, 123327 (2).

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DISTRIBUTION AND ECOLOGY

Geographic Distribution of the Species

The distribution of species of *Ptychohyla* reflects the distribution of cloud forest in southern México and northern Central America. The frogs are restricted to mountainous areas, usually at elevations higher than 1000 meters above sea level. *Ptychohyla* does not range to great heights in the mountains, where west of the Isthmus of Tehuantepec the mountain streams are inhabited by frogs of the *Hyla bistincta* group, and in Chiapas and Guatemala by species of *Plectrohyla*.

Frogs of the *Ptychohyla euthysanota* group have a greater combined geographic range than the species comprising the *Ptychohyla schmidtorum* group (Fig. 7). No two species in the same group are sympatric, but members of different groups are sympatric in at least parts of their ranges. Apparently *P. leonhardschultzei* ranges around the southern edge of the Mexican Highlands, where the species occurs on both Atlantic and Pacific slopes; as can be seen from the distribution map, there are many gaps in the known range of this species. The range of *P. euthysanota euthysanota* is along the Pacific slopes of the Sierra Madre in Chiapas, Guatemala, and El Salvador, whereas that of *P. euthysanota macrotympanum* is along the southern interior slopes of the Central Highlands of Chiapas and the Sierra de Cuchumatanes in Guatemala. *Ptychohyla spinipollex* occurs on the wet Atlantic slopes of the Guatemalan and Honduran Highlands; the range of the species in Honduras is poorly known.

[Pg 341]

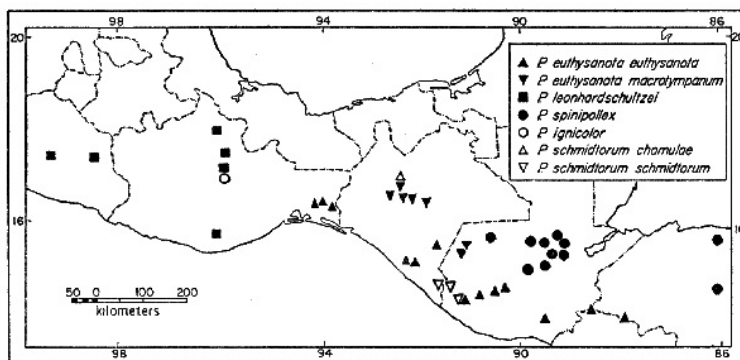


FIG. 7. Map showing locality records for the species and subspecies of *Ptychohyla*.

The frogs of the *Ptychohyla schmidtorum* group have more restricted geographic ranges than members of the former group. *Ptychohyla schmidtorum schmidtorum* occurs on the Pacific slopes of the Sierra Madre in Chiapas and Guatemala, where it occurs with *P. euthysanota euthysanota*; *P. schmidtorum chamulae* is known from only two localities on the Atlantic slopes of the Central Highlands of Chiapas, where it occurs close to, but as now known not with, *P. euthysanota macrotympanum*. On the Atlantic slopes of the Sierra Madre Oriental in northern Oaxaca *P. ignicolor* occurs with *P. leonhardschultzei*.

In the Sierra de los Tuxtlas in southern Veracruz and in the cloud forests along the eastern slopes of the Sierra Madre Oriental northward to Nuevo León, *Hyla miotympanum* seems to be the ecological replacement of *Ptychohyla*. On the Pacific slopes north of Guerrero, México, humid forests in which there are cascading mountain streams are absent; consequently, no *Ptychohyla* are known from that region. In the mountains of El Salvador *Ptychohyla euthysanota euthysanota* occurs sympatrically with another small stream-breeding hylid, *Hyla salvadorensis*. To the south of Honduras the highlands diminish into the lowlands of Nicaragua, where habitat suitable for *Ptychohyla* apparently does not exist. In the mountains of Costa Rica and Panamá, the habitats occupied by *Ptychohyla* in northern Central America are filled by a variety of stream-breeding *Hyla*, such as *Hyla legleri*, *H. rivularis*, *H. ruficulis*, *H. alleei*, and *H. uranochroa*.

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Although members of the genus *Ptychohyla* occur in the southern part of the Mexican Highlands to the west of the Isthmus of Tehuantepec, the greater distribution and differentiation in the genus is in the Chiapan-Guatemalan Highlands. In this respect *Ptychohyla* is a counterpart of *Plectrohyla*.

Habitat Preference

Frogs of the genus *Ptychohyla* are ecologically associated with mountain streams at elevations between 650 and 2200 meters; in the geographic region where these frogs occur the vegetation between those elevations consists of cloud forest or pine-oak forest. In some places the frogs have been found in a mixture of oak and semi-deciduous scrub forest. At Vista Hermosa, Oaxaca, *P. leonhardschultzei* and *P. ignicolor* were found in cloud forest, whereas at Agua del Obispo, Guerrero, the former species was found in pine-oak forest. *Ptychohyla schmidtorum* is known only from cloud forest; *P. euthysanota euthysanota* and *P. spinipollex* generally are found in cloud forest, but in some places they live in pine-oak forest. *Ptychohyla euthysanota macrotympanum* has been found in pine-oak forest and in a mixture of oak and semi-deciduous scrub forest. With the possible exception of the members of the *Ptychohyla schmidtorum* group, which has been found only in cloud forest, it seems as though the type of vegetation is not the controlling factor in the ecological distribution of these frogs.

Ptychohyla has been found only where there are clear, cascading streams overhung by vegetation, on which adults and young perch at night, or even by day. The presence of these streams, in which the tadpoles live, seems to be an important factor in the distribution of *Ptychohyla*. As has been shown previously, the tadpoles of *Ptychohyla* are adapted for existence in torrential streams, where the water is cool, and the amount of oxygen is high. Clearly these tadpoles are unsuited for life in ponds or sluggish streams in the lowlands, where the temperature of the water is high, a layer of silt on the bottom is deep, and the amount of oxygen is low. The tadpoles cling to rocks on the bottom of the streams; there they move slowly across the rocks, apparently feeding on the thin covering of algae. Tadpoles were not observed on rocks having a thick covering of algae or moss. The tadpoles were observed to swim against the current in torrential streams, in which no fishes were found. Therefore, it seems as though the presence of the stream-habitat for the tadpoles is a significant factor in the ecological distribution of the species of *Ptychohyla*.

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Interspecific Competition

At localities where two species of *Ptychohyla* occur sympatrically (*P. ignicolor* and *P. leonhardschultzei* at Vista Hermosa, Oaxaca, and *P. euthysanota euthysanota* and *P. schmidtorum schmidtorum* at Finca La Paz, Depto. San Marcos, Guatemala) effort was made to determine what, if any, ecological interspecific relationships existed. Although adults of the sympatric species were found on adjacent leaves or branches of bushes overhanging the streams at both localities, segregation at the time of breeding seems to be maintained by the notably different breeding calls in sympatric species (see discussion of breeding calls). Thus, as has been shown by Blair (1956), Fouquette (1960), and others working on a variety of pond-breeding frogs and toads, the breeding call in *Ptychohyla* acts as an important reproductive isolating mechanism.

At no locality were *Ptychohyla* and associated species of hylids found so abundantly as were species of pond-breeding hylids in the lowlands. Apparently reproductive activity is not concentrated in a short breeding season, and it is highly doubtful if the populations of these frogs are as large as those of the lowland pond-breeders. The continual humid conditions and abundance of insect food throughout the year in the cloud forest are perhaps indicative of little interspecific competition among adults of *Ptychohyla* and other sympatric hylids.

At Finca La Paz, Guatemala, tadpoles of two species of *Ptychohyla* were ecologically segregated. The tadpoles of *P. euthysanota euthysanota* were found in riffles in the streams, whereas those of *P. schmidtorum schmidtorum* were found in slower water, chiefly in small pools in the streams. At Vista Hermosa, Oaxaca, tadpoles of *P. leonhardschultzei* were found in riffles, and tadpoles of the sympatric *P. ignicolor* were found in a small pool in a stream. Similar ecological relationships were observed for several species of Costa Rican hylids. Throughout the range of *Ptychohyla* east of the Isthmus of Tehuantepec, members of the genus occur with species of *Plectrohyla*, all of which are larger than *Ptychohyla*, and all of which have tadpoles that live in torrential streams. Tadpoles of *Ptychohyla spinipollex* have been found in streams inhabited by the tadpoles of *Plectrohyla guatemalensis* and *P. quecchi*; tadpoles of *Ptychohyla euthysanota euthysanota* and *P. schmidtorum schmidtorum* were found in streams inhabited by tadpoles of *Plectrohyla guatemalensis*, *P. matudai*, and *P. sagorum*. In some streams great numbers of tadpoles occur. The habitat is rather restricted, and the food supply is limited. Consequently, interspecific competition among the various species of hylids whose tadpoles live in the torrential streams probably is highest during the larval stage. Unfortunately, this aspect of salientian population ecology has received no intensive study.

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Reproduction and Development

Since the cloud forests inhabited by *Ptychohyla* are daily bathed in clouds and have a fairly evenly distributed rainfall throughout the year, the frogs living in these forests are active throughout the year. At least some of the species evidently have a long breeding season, for I found calling males of *P. leonhardschultzei* in February, March, and August, and found tadpoles in February, March, June, and August. Tadpoles of the various species have been obtained throughout much of the year, as follows: *P. euthysanota euthysanota*, February, March, May, and July; *P. euthysanota macrotympanum*, March, June, and August; *P. spinipollex*, February, March, April, June, July, and August; *P. schmidtorum schmidtorum*, March, May, June, July, and August; *P. schmidtorum chamulae*, June and August; *P. ignicolor*, June. I suspect that this temporal distribution more accurately reflects the seasonal activities of collectors than of the frogs.

Calling frogs usually are on vegetation adjacent to or overhanging streams; some calling males of *P. spinipollex* were on rocks in or by streams. Claspings pairs of *P. euthysanota* and *P. schmidtorum* were observed on vegetation by streams. Despite intensive search, no eggs were found. It is doubtful if *Ptychohyla* deposit eggs on vegetation overhanging streams, as do centrolenids and *Phyllomedusa*, for egg-clutches of these frogs are easily found. Possibly the eggs are laid separately on vegetation above the stream, in which case they could be overlooked easily. In streams where *Ptychohyla* and other hylid tadpoles occur, empty egg capsules have been found on the lee sides of rocks, but there is no way to determine which species laid the eggs.

Numbers of eggs were counted in gravid females; the largest eggs have diameters ranging from 2.5 to 3.0 mm. The smaller species, comprising the *Ptychohyla schmidtorum* group, have fewer eggs than do the larger species. Numbers of eggs found in females of the various species are: *P. euthysanota euthysanota*, 108; *P. euthysanota macrotympanum*, 136, 160; *P. leonhardschultzei*, 141; *P. spinipollex*, 119, 134, 143; *P. schmidtorum schmidtorum*, 59, 61, 90; *P. schmidtorum chamulae*, 60, 71, 89.

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Duration of the larval stage is unknown. Metamorphosing young have been found from May through August. From two to six completely metamorphosed young are available for each of the species, except for *P. ignicolor* of which none is available. The smallest young frog is a *P. euthysanota* having a snout-vent length of 14.2 mm.; the largest young frog is a *P. schmidtorum schmidtorum* having a snout-vent length of 17.0 mm.

PHYLOGENY OF PTYCHOHYLA

The preceding data on morphology, life histories, and behavior form the basis for the following interpretation of the phylogeny of *Ptychohyla*. Additional data are needed to support some of the ideas discussed below; many of the data that are available for *Ptychohyla* are lacking for other, possibly related, hylids. The family Hylidae is composed of several hundred species, and most of the species are poorly known. Consequently, any attempt to place *Ptychohyla* in the over-all scheme of hylid phylogeny would be premature at this time. But, as between the five species of two species-groups here recognized as constituting the genus *Ptychohyla*, some estimate of relationships can be made. First, it is necessary to determine the validity of the genus itself.

***Ptychohyla* as a Natural Assemblage**

As stated in the diagnosis of the genus, the only character that sets this group of species apart from other hylids is the presence of ventrolateral glands in the breeding males. To many systematists the thought of being able to identify to genus only breeding males is sufficiently disturbing to cause them to view with disfavor the recognition of the genus. Nonetheless, the question is raised: Do the five species herein placed in the genus *Ptychohyla* constitute a natural assemblage? If the genus is considered to be more than a category of convenience, that is to say, a group of related species having a common origin, the primary problem is to determine whether or not the five species form a phylogenetic unit.

The species of *Ptychohyla* are divided into two groups on the basis of external morphology, breeding calls, and tadpoles. The *Ptychohyla euthysanota* group seems to be a natural group composed of three species, all of which are more closely related to one another than to any other hylid. Likewise, the species comprising the *Ptychohyla schmidtorum* group seem to represent a natural unit. If the presence of ventrolateral glands in breeding males is ignored, a student of salientian systematics might derive the *Ptychohyla euthysanota* group from a hylid stock containing *Hyla miotympanum* and *Hyla mixomaculata*. Likewise, *Ptychohyla schmidtorum* could be placed with *Hyla uranochroa* and related species in Costa Rica. Nonetheless, the fact remains that all of the species assigned to the genus *Ptychohyla* have ventrolateral glands in the breeding males; furthermore, ventrolateral glands are unknown in other hylids. If the *P. schmidtorum* group and the *P. euthysanota* group each evolved from separate hylid stocks, then the ventrolateral glands must have developed independently in both groups. That ventrolateral glands developed independently in five species of frogs in southern México and northern Central America and not in any of the other approximately 500 species of hylids in the world is untenable. It is more logical to assume that the development of the glands took place only once in a stock of hylids that gave rise to the five species herein recognized as members of the genus *Ptychohyla*.

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Generic Relationships

The affinities of *Ptychohyla* apparently are not with any of the other groups that have been generically separated from *Hyla*. Of the daughter genera in Middle America only *Plectrohyla* has stream-adapted tadpoles, but these large frogs are not closely related to *Ptychohyla*. Stuart (1954:169) suggested that certain montane species of *Hyla* in lower Central America and *Hyla salvadorensis* in El Salvador may be related to *Ptychohyla* or even congeneric. I have had experience with most of these species in the field and believe that Stuart was correct in his suggestion of relationships. The species concerned are four red-eyed stream-breeding *Hyla* in Costa Rica—*H. alleei*, *H. legleri*, *H. rufioculis*, and *H. uranochroa*, plus *Hyla salvadorensis* in the mountains of El Salvador. Morphologically all of the species are similar; *Hyla uranochroa*, *H. legleri*, and *H. rufioculis* have a lateral white stripe that is expanded to form a spot beneath the eye, as in *Ptychohyla schmidtorum*. The tadpoles of *Hyla rufioculis* and *H. uranochroa* have large funnel-shaped mouths and long slender tails like those of *Ptychohyla schmidtorum*. Lips of the tadpoles of *H. legleri* and *H. salvadorensis* are folded laterally, in this respect resembling those of the *Ptychohyla euthysanota* group. I do not know the tadpoles and the breeding call of *Hyla alleei*. The breeding calls of *Hyla rufioculis* and *H. uranochroa* consist of high melodious notes; the calls of *H. legleri* and *H. salvadorensis* consist of series of short notes that have the general characteristics of the call of *Ptychohyla schmidtorum*. Affinities of the genus *Ptychohyla* seem to me to be with the red-eyed species forming the *Hyla uranochroa* group in Costa Rica. All of the species in the *Hyla uranochroa* group have large frontoparietal fontanelles, rather small ethmoids, and small nasals that are not in contact with one another or with the ethmoid. Some species have a complete quadratojugal-maxillary arch; others do not. Assuming that the parental stock that gave rise both to the *Hyla uranochroa* group and to *Ptychohyla* was widespread in Central America at a time of cooler, more humid conditions, it is possible that with subsequent warming temperatures and seasonal rainfall in the lowlands the parental stock was restricted to the Costa Rican highlands, where the *Hyla uranochroa* group developed, and to the Chiapas-Guatemala highlands, where *Ptychohyla* evolved.

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Interspecific Relationships

Ptychohyla schmidtorum is thought to resemble more closely the parental stock of the genus than does any other species of *Ptychohyla* now extant. This parental stock is discussed above in the account of the generic relationships. *Ptychohyla schmidtorum* has a red eye, white lateral stripe, frontoparietal fontanelle, funnel-shaped mouth in tadpoles, and lacks nuptial spines; in all of these characters it resembles members of the *Hyla uranochroa* group. Probably during times of glaciation during the Pleistocene, when climates in México and Central America were depressed, the *Ptychohyla* stock was more widespread than it is now. Subsequent elevation of climatic zones during interglacial periods would have isolated populations as they are today in regions of cloud forests. Thus, through geographic isolation populations could have differentiated and evolved into the present species. Climatic fluctuation in the Pleistocene must have been of sufficient magnitude to permit the spread of cool, moist forests containing *Ptychohyla* across the Isthmus of Tehuantepec into the mountains of Oaxaca.

Because of its small nuptial spines, small triangular vomers, coloration, and absence of a rostral keel, *Ptychohyla euthysanota*, more than any of the other species in the *P. euthysanota* group, resembles *P. schmidtorum*. At the present time *P. euthysanota* and *P. schmidtorum* are sympatric.

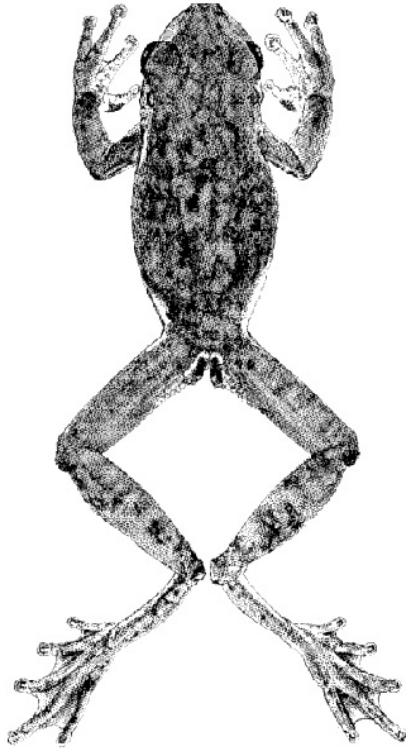
As I have mentioned previously, ecological segregation and interspecific competition probably is highly developed in the tadpoles of *Ptychohyla*. If this ecological segregation resulted from intraspecific competition in a stock of *Ptychohyla*, possibly *P. euthysanota* and *P. schmidtorum* differentiated sympatrically in this way. Specific identity is maintained, at least in part, by different breeding calls in males.

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Ptychohyla spinipollex and *P. leonhardschultzei* seem to be more closely related to one another than either is to *P. euthysanota*. Probably a stock of *P. euthysanota* was isolated on the Atlantic slopes of northern Central America from *P. euthysanota* on the southern slopes. The frogs on the Atlantic slopes differentiated and spread into the mountains of Oaxaca, where through isolation by the barrier of the Isthmus of Tehuantepec they developed into *P. leonhardschultzei*, while the stock on the northern slopes of Central America evolved into *P. spinipollex*. Subsequent to the differentiation of *P. leonhardschultzei* and *P. spinipollex* from *P. euthysanota* and during a time of cooler more equable climate than exists now, *P. euthysanota* and *P. schmidtorum* invaded the Central Highlands of Chiapas. Subsequent climatic changes isolated populations of each in the Central Highlands, where *P. euthysanota macrotympanum* and *P. schmidtorum chamuluae* evolved. *Ptychohyla ignicolor* probably represents stock of *P. schmidtorum* that crossed the Isthmus of Tehuantepec and became isolated in Oaxaca on the western side of the isthmus.

PLATE 12

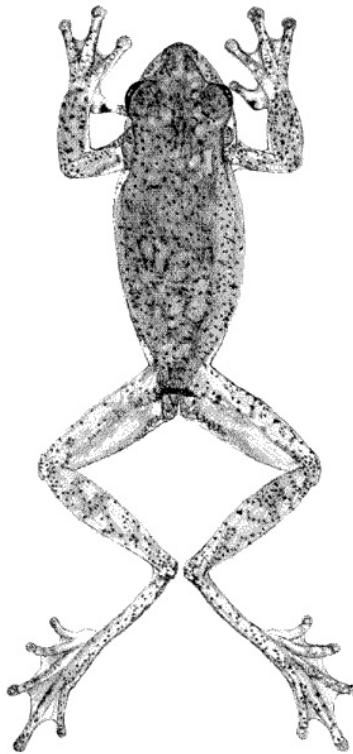
[Pl 12]



Ptychohyla euthysanota euthysanota (KU 58008). × 2.

PLATE 13

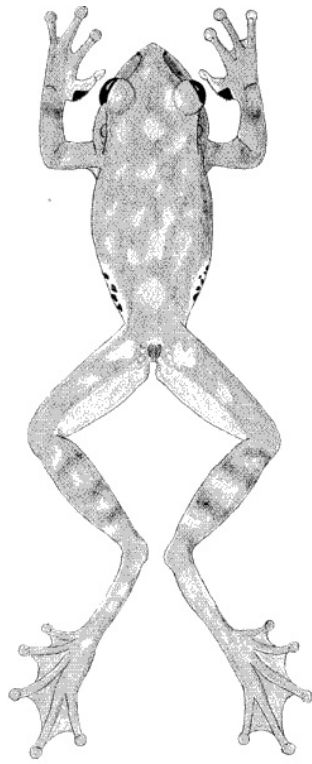
[Pl 13]



Ptychohyla euthysanota macrotympaum (KU 58049). × 2.

PLATE 14

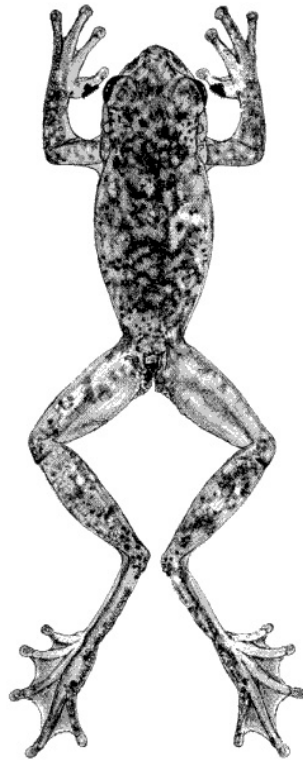
[Pl 14]



Ptychohyla leonhardschultzei (KU 64117). × 2.

PLATE 15

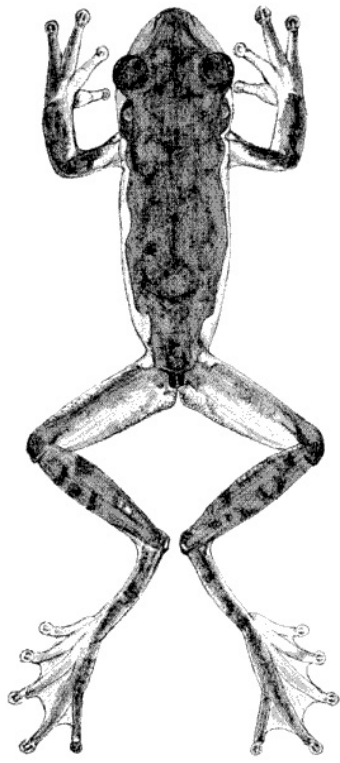
[PI 15]



Ptychohyla spinipollex (KU 58054). × 2.

PLATE 16

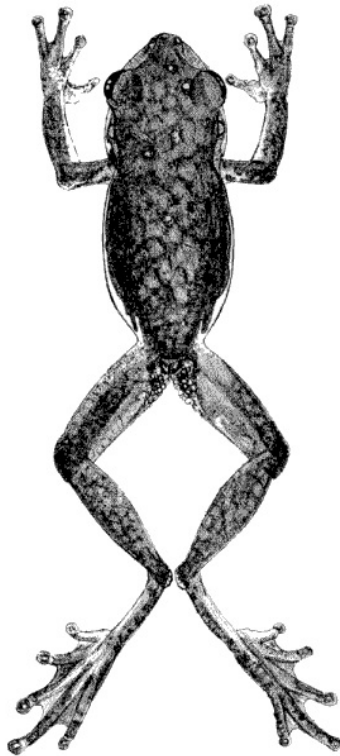
[PI 16]



Ptychohyla schmidtorum schmidtorum (KU 58043). × 2.

PLATE 17

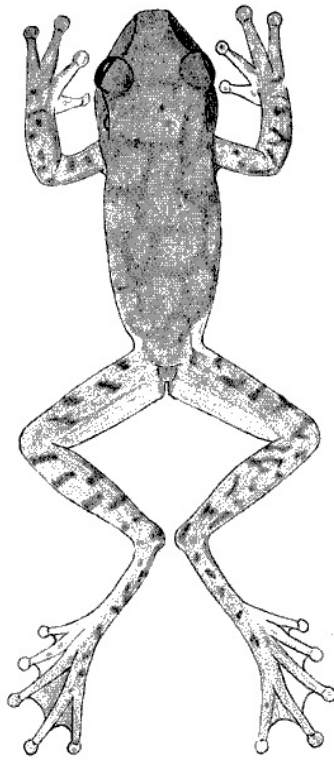
[Pl 17]



Ptychohyla schmidtorum chamulae (KU 58069). × 2.

PLATE 18

[Pl 18]



Ptychohyla ignicolor (UMMZ 119603). × 2.

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*4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr., and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.

Index. Pp. 651-681.

*Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. Nos. 1-15 and index. Pp. 1-651, 1952-1955.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. *1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.

2. Additional records and extension of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.

3. A new long-eared myotis (*Myotis evotis*) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.

4. Subspeciation in the meadow mouse, *Microtus pennsylvanicus*, in Wyoming. By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.

5. The condylarth genus *Ellipsodon*. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.

6. Additional remains of the multituberculate genus *Eucosmodon*. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.

7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.

8. Comments on the taxonomic status of *Apodemus peninsulae*, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.

9. Extensions of known ranges of Mexican bats. By Sydney Anderson. Pp. 347-351. August 15, 1956.

10. A new bat (Genus *Leptonycteris*) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.

11. A new species of pocket gopher (Genus *Pappogeomys*) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-

361. January 21, 1957.
12. Geographic variation in the pocket gopher, *Thomomys bottae*, in Colorado. By Phillip M. Youngman. Pp. 363-387, 7 figures in text. February 21, 1958.
 13. New bog lemming (genus *Synaptomys*) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388. May 12, 1958.
 14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396. December 19, 1958.
 15. New subspecies of the rodent *Baiomys* from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.
 16. Mammals of the Grand Mesa, Colorado. By Sydney Anderson. Pp. 405-414, 1 figure in text, May 20, 1959.
 17. Distribution, variation, and relationships of the montane vole, *Microtus montanus*. By Sydney Anderson. Pp. 415-511, 12 figures in text, 2 tables. August 1, 1959.
 18. Conspicuity of two pocket mice, *Perognathus goldmani* and *P. artus*. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14 1960. [Pub_2]
 19. Records of harvest mice, *Reithrodontomys*, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.
 20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.
 21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.
 22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
 23. Speciation and evolution of the pygmy mice, genus *Baiomys*. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.
- Index. Pp. 671-690
- Vol. 10.
1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
 2. Comparative breeding behavior of *Ammospiza caudacuta* and *A. maritima*. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
 3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
 4. Aspects of reproduction and development in the prairie vole (*Microtus ochrogaster*). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.
 5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.
 - *6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
 7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.
 8. Natural history of the salamander, *Aneides hardyi*. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
 9. A new subspecies of lizard, *Cnemidophorus sacki*, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.
 10. A taxonomic study of the middle American snake, *Pituophis deppei*. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.
- Index. Pp. 611-626.
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- Vol. 12.
1. Functional morphology of three bats: *Sumops*, *Myotis*, *Macrotus*. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
 - *2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
 3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
 - *4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.
 5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
 6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
 7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
 8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.
- More numbers will appear in volume 12.
- Vol. 13.
1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
 2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960.
 3. A new subspecies of the slider turtle (*Pseudemys scripta*) from Coahuila, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.
 4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.
 5. Occurrence of the garter snake, *Thamnophis sirtalis*, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
 6. Fishes of the Wakarusa river in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
 7. Geographic variation in the North American cyprinid fish, *Hybopsis gracilis*. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.
 8. [Descriptions](#) of two species of frogs, genus *Ptychohyla*; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961. [Pub_3]
 9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figs. August 11, 1961.
 10. Recent soft-shelled turtles of North America (family Trionychidae). By Robert G. Webb. Pp. 429-611, pls. 31-54, 24 figures in text, February 16, 1962.

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- Vol. 14.
1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
 2. Geographic variation in the harvest mouse. *Reithrodontomys megalotis*, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
 3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1 and 2, 3 figures in text. July 24, 1961.
 4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall and Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
 5. North American yellow bats, "*Dasypterus*," and a list of the named kinds of the genus *Lasiurus* Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
 6. Natural history of the brush mouse (*Peromyscus boylii*) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-111, 1 figure in text. December 29, 1961.
 7. Taxonomic status of some mice of the *Peromyscus boylii* group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 113-120, 1 figure in text. December 29, 1961.
 8. A new subspecies of ground squirrel (*Spermophilus spilosoma*) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
 9. Taxonomic status of the free-tailed bat, *Tadarida yucatanica* Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
 10. A new doglike carnivore, genus *Cynaretus*, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
 11. A new subspecies of wood rat (*Neotoma*) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143. April 30, 1962.
 12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.
 13. A new bat (*Myotis*) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
 14. The mammals of Veracruz. By E. Raymond Hall and Walter W. Dalquest. Pp. 165-362, 2 figures. May 20, 1963.
 15. The recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963.

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- Vol. 15.
1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figures in text. December 20, 1961.
 2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
 3. A new species of frog (Genus *Tomodactylus*) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
 4. Type specimens of amphibians and reptiles in the Museum of Natural History, the University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
 5. Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, pls. 7-10, 6 figures in text. October 4, 1963.
 6. A revision of snakes of the genus *Conophis* (Family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figures in text. October 4, 1963.
 7. A review of the Middle American tree frogs of the genus *Ptychohyla*. By William E. Duellman. Pp. 297-349, pls. 11-18, 7 figures in text. October 18, 1963.

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References to [Plate 11](#) (Audiograms): Pl. 1A, Pl. 1B, ...=> Pl. 11A, Pl. 11B, ...
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Page 301, Paragraph 1: [know](#) => [known](#)
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