

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 96

**The Frogs of the Hylid Genus
Phrynohyas Fitzinger, 1843**

BY
WILLIAM E. DUELLMAN

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
February 21, 1956

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THE FROGS OF THE HYLID GENUS
PHRYNOHYAS FITZINGER, 1843*

INTRODUCTION

THE neotropical hylid frogs are extraordinarily diverse, and only in the last decade has sufficient material become available to make possible a critical analysis of the relationships and distribution of certain groups. This paper deals with the group commonly referred to the "species" *Hyla venulosa* (*auctorum*). This name, proposed nearly 200 years ago, has been subjected to misapplication and nomenclatural confusion ever since its first use. Taylor (1944), who has shown that the Mexican populations are composite, recognized three species, for which he used the generic name *Acrodytes*. While trying to allocate the Mexican specimens in the University of Michigan Museum of Zoology to the various species of *Acrodytes* and attempting to determine the status of the South American specimens, I became aware of the complexity of the situation and the need for systematic revision.

The results of the study as presented in this paper are the clarification of the status of the name *Hyla venulosa*, the characterization of the group under consideration as a distinct genus of hylid frogs, the establishment of the correct generic name for the group, the definition and description of the component species, and the analysis of the variation, distribution, and relationships of those species.

Many of the hylid genera are poorly defined and are of questionable status. This is due chiefly to the fact that they are based on superficial characters. In very few forms have gross anatomical structures been studied; also the ecology and modes of life history remain unknown for most species. The genus *Hyla* as now defined is a heterogeneous assemblage of species, many of which upon further study will fall into groups of related species. Whether or not these groups, like the one defined here, should be considered genera, subgenera, or *Artenkreise*, can be settled only after a great many more species have been adequately studied.

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Dr. Norman E. Hartweg and Dr. Laurence C. Stuart have greatly aided me in this work, not only by placing at my disposal the necessary facilities, but by offering constructive criticism throughout the course of the study. I am especially grateful to Dr. Charles F. Walker. Under his careful supervision many of my embryonic ideas have matured, and the less substantial ones have been cast aside. He has taken an interest in the problem from the beginning and has always willingly given his assistance.

MATERIALS AND METHODS

During the course of this study 532 alcoholic specimens have been examined, and the data on certain others have been made available by various museum curators. Nearly every specimen in North American herpetological collections was examined, as were those in the British Museum (Natural History) and the Instituto de La Salle, Colombia.

Eight measurements were taken on every suitable specimen; from these six proportions were calculated. The mean and range for each measurement and proportion were determined, and when the samples were of adequate size the standard error of the mean ($\sigma_{\bar{x}}$) was also calculated. The body length is the direct line distance from the tip of the snout to the posterior edge of the vent. The tibia length is the straight length of the tibia. The foot length is the distance between the proximal edge of the inner metatarsal tubercle and the tip of the longest (fourth) toe including the disc. The head width is the greatest width of the head at the position of the tympani.

The head length is the straight line distance between the posterior edge of the jaw articulation and the tip of the snout. The interorbital distance is essentially the width of the frontoparietals between the orbits. The internarial distance is that between the median borders of the external nares. The tympanum length is the greatest horizontal distance between the outer edges of the tympanic ring. The number of vomerine teeth is the total for both vomers.

All of the skeletal and cleared preparations were made from alcoholic specimens in the University of Michigan Museum of Zoology (UMMZ). The skeletons were cleaned by dermestids, and the cleared material was stained with alizarin red. The sections of the skin were cut at seven microns and stained with Mallory's Triple Stain.

GENUS *PHRYNOHYAS* FITZINGER, 1843

- Phrynohyas* Fitzinger, *Systema reptilium*, 1843, p. 30 (type *Hyla zonata* Spix by monotypy).
 ? *Acrodytes* Fitzinger (*nomen dubium*), *loc. cit.* (type "*Hyla venulosa*, Daudin" by monotypy = *Rana venulosa* Laurenti [*nomen dubium*]).
Acrodytes (*sensu* Fitzinger), Cope, *Nat. Hist. Rev.*, 5 (17) (1865): 109; Taylor, *Univ. Kans. Sci. Bull.*, 30 (6) (1944): 64.
Scytopsis Cope, *Proc. Acad. Nat. Sci. Phila.*, 14 (9) (1862): 354 (type *Scytopsis hebes* Cope by monotypy).

Historical Account

Fitzinger (*Systema Reptilium*, 1843) listed 11 generic names under the family name Hylae. One of these is *Phrynohyas*. Under it are placed four generic names as follows:

"*Phrynohyas*

Cephalophractus Fitz. — *Cephalo. galeatus* Fitz.

Trachycephalus Tschud. — *Trachy. nigromaculatus* Tschud.

Phrynohyas — *Hyla zonata* Spix

Acrodytes — *Hyla venulosa* Daudin"

In reviewing the status of the names given above, it was found that both *Cephalophractus* and *C. galeatus* are *nomina nuda*. The other names are tenable. *Trachycephalus*, with type species *T. nigromaculatus* Tschudi (1838), applies to a valid genus, for reasons given below. *Phrynohyas* has as its type species *Hyla zonata* Spix, a species occurring in the Amazon Basin. The type species of *Acrodytes* is *Hyla venulosa* Daudin which equals *Rana venulosa* Laurenti. Neither of these names applies to hylid frogs.

The reasoning involved in determining the status of *Hyla venulosa* Daudin and *Rana venulosa* Laurenti is as follows. It is evident from the examination of Fitzinger's work that the person's name following each specific name is usually the authority for the current generic and specific word combination, rather than the original describer of the species. Thus, since Daudin first used the combination *Hyla venulosa*, his name appears after

the specific name instead of that of the original describer of *venulosa*, namely, Laurenti. Although Daudin, both in 1802 when he referred *venulosa* to the genus *Rana* and in 1803 when he referred it to *Hyla*, described and figured (1802) a hyloid frog with paired lateral vocal sacs behind the angles of the jaws, he considered the specific name as that of Laurenti (1768). Laurenti based his description on a plate in Seba (1734, I: 115, Pl. 72, Fig. 4). This figure cannot, by any exercise of the imagination, conceivably be that of a hyloid frog. There are no webs or toe discs (Pl. I, Fig. 1); furthermore, there is a dorsolateral fold! Daudin was in error, therefore, when he used Laurenti's name *venulosa* for a hyloid frog with paired lateral vocal sacs. Unfortunately, this error has been perpetuated through the literature for the past 150 years. Since the name *Rana venulosa* Laurenti cannot be applied to any hyloid frog, and since neither the figure nor the description gives any possible clues to the identity of the frog figured by Seba, the name *Rana venulosa* must be considered a *nomen dubium*. It follows that the generic name *Acrodytes* (with *Rana venulosa* Laurenti [= *Hyla venulosa* Daudin] the type species by monotypy) also must be considered a *nomen dubium*. Thus, *Phrynohyas* (type species *Hyla zonata* Spix by monotypy) is the correct generic name for those hyloid frogs with paired lateral vocal sacs behind the angles of the jaws and without the skin of the head co-ossified with the skull.

Cope (1865: 109) was the first subsequent systematist to use the name *Acrodytes*, when he placed "*venulosa*" in it, in Fitzinger's sense. The name *Acrodytes* was not used again until 1944, when Taylor applied it to three species of Mexican frogs (*A. inflata*, *A. modesta*, and *A. spilomma*).

Cope (1862: 354) erected the genus *Scytopsis* (type *hebes*) characterized by the large parotoid glands on the anterior part of the back, a character that is common to *Phrynohyas*. *Scytopsis* is here considered a synonym of *Phrynohyas*, and *hebes*, the type species, a member of the genus *Phrynohyas*.

Hyla tibiatrix Laurenti, which customarily is carried as a synonym of *Hyla venulosa*, likewise should be treated as a *nomen dubium*. Laurenti's description of *Hyla tibiatrix* (1768: 34) also is based on a plate in Seba (1734, I, Pl. 71, Figs. 1-2). These figures show a frog with paired lateral vocal sacs and possibly a casque head. Daudin considered this species as a variety of "*Hyla venulosa*," although actually the name *tibiatrix* would have been much more credibly applied to his account of *venulosa*. Seba's figure shows no color pattern, the locality is given only as America, and the ambiguous figure might apply to any one of several species of frogs recognized in this paper. It is most logical, therefore, to consider *Hyla tibiatrix* Laurenti a *nomen dubium* and to apply only those specific names which can be assigned with reasonable certainty.

Generic Diagnosis

This genus of large, neotropical tree frogs may be distinguished by the following combination of characters: the males having paired, lateral, external vocal sacs formed by a posterolateral extension of the submaxillaris muscle and situated behind the angles of the jaws; skin not co-ossified with

the skull; skin of nape and shoulder region thickened by well-developed glands producing a volatile secretion that is irritating to mucous membranes (of humans, at least); teeth spatulate in form and bifid; adults without a frontoparietal fontanelle.

Frogs of this genus are widely distributed in the New World tropics. They are present in lowland areas from Tamaulipas and Sinaloa southward on both coasts of Mexico and Central America as far south as Nicaragua, beyond which in Central America they are found only on the Pacific side. In South America they occur along the Caribbean coast, in the Orinoco Basin, throughout the lowlands of the Guianas, in the Amazon Basin as far west as Bolivia and Ecuador, and southward into Paraguay and northern Argentina. They are also found on the islands of Trinidad and Tobago. Recently, a single specimen was collected on the Pacific coast of Ecuador.

Although this study deals only with those frogs previously known as *Hyla venulosa*, there are other species in South America that may be congeneric with *Phrynohyas*. These are *Hyla imitatrix* Miranda-Ribeiro, *H. mesophaea* Hensel, *H. quadrangulum* Boulenger, and *H. verrucigera* Peters. *H. buckleyi* Boulenger and *H. leprieweri* Duméril and Bibron may also be associated with this group. The genus *Trachycephalus* is close to *Phrynohyas*, from which it differs by having the skin of the head co-ossified with the skull to form a casque. Additional material for dissection and skeletal study is needed before the generic affinities of these frogs can be determined.

ANATOMICAL CONSIDERATION

Osteology

In studying the osteological characters of these frogs, two dried skeletons and one cleared and stained specimen of *Phrynohyas spilomma* and one dried skeleton of *Phrynohyas modesta* were used.

Phrynohyas has a broad, solidly roofed skull with no frontoparietal fontanelle. The nasals are large and in broad contact along the mid-line. The ethmoid is extensive and forms a flange laterally. A supraorbital cartilage encircles the orbit from the ventral edge of the nasals dorsally and then posteriorly to the anterior process of the squamosal. Near the anterior end of the orbit there is a calcified bar in the cartilage; this extends laterally from the ethmoid (Fig. 1). The anterior process of the squamosal does not reach the maxillary, thus leaving an incomplete arch; a quadrotjugal is present. The teeth are spatulate and bifid (Fig. 2).

The omosternum is calcified, ovoid, and longer than wide. The xiphisternum is calcified with a shallow indentation anterolaterally and a deep notch posteriorly. The sacral diapophyses are expanded; the anterior edge of the diapophysis is nearly at right angles to the vertebral column, but the posterior edge is strongly flared backward.

The swollen thumb region in the males is supported by a large bony prepollex; the spine, however, is not extruded as in *Plectrohyla*.

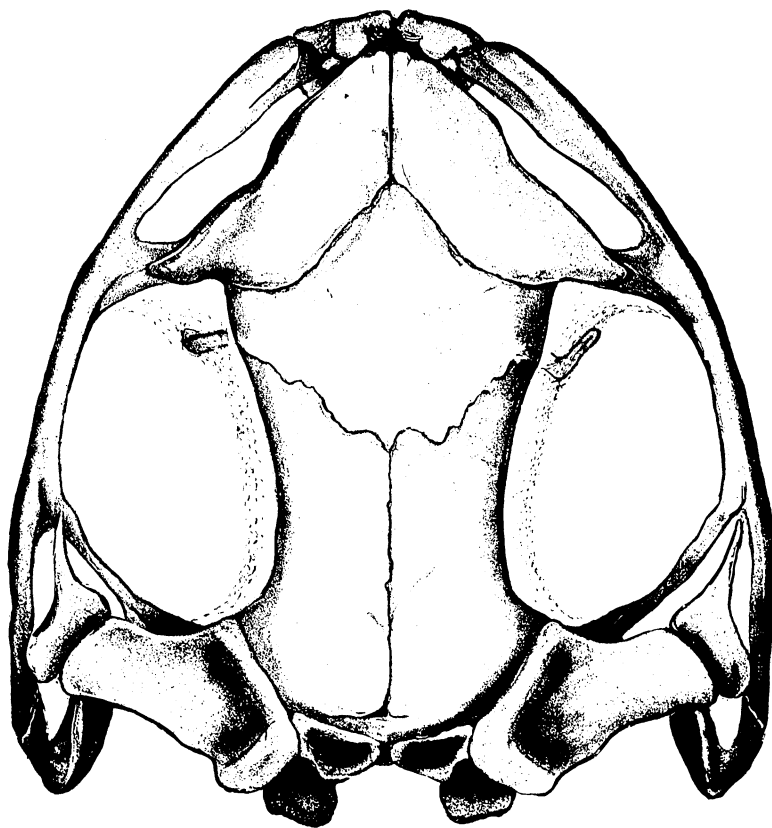


Fig. 1. Dorsal view of the skull of an adult male *Phrynohyas spilomma*.

Throat Musculature and Hyoid Apparatus

The frogs that comprise the genus *Phrynohyas* are characterized by paired, lateral vocal sacs behind the angles of the jaws in the males. Since the throat musculature of hylids with paired, lateral vocal sacs has never been described, I shall discuss the muscles and hyoid in detail. The following discussion is based upon dissections of two males and one female *Phrynohyas spilomma*.

The *M. submentalis* lies in the anterior angle of the lower jaw. It is quite thick and consists of transverse fibers extending between the dentary bones. The *M. submaxillaris* is a very thin muscle that arises from the whole of the inner surface of the lower jaw, except for the anterior angle occupied by the submentalis. Medially, it is attached to the hyoglossus and the geniohyoideus, which are dorsal to it. Posteriorly it folds slightly and is attached to the sternoradialis of the pectoral girdle (Fig. 3). The

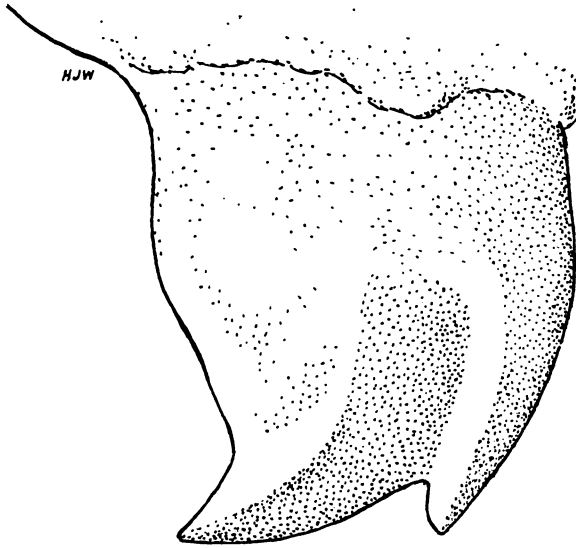


Fig. 2. Maxillary tooth of an adult male *Phrynohyas spilomma*, showing characteristic bifid condition.

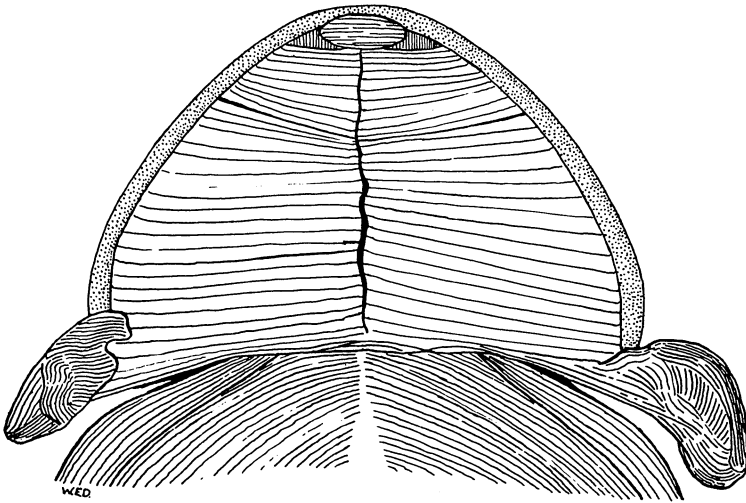


Fig. 3. Superficial throat musculature of an adult male *Phrynohyas spilomma*.

vocal sacs in the males are formed by a posterolateral extension of this muscle. The muscle forms a tube along the inner margin of the jaw and extends posteriorly behind the angle of the jaw. Here it expands into a pocket with many folds, the vocal sac. Dorsally, the vocal sac is attached to the muscles of the suprascapular region. A broad fan of connective tissue connects this part of the submaxillaris with the posterior part of the depressor mandibulae, and it also covers a considerable part of the latissimus dorsi (Fig. 5). In the females there is a narrow band of fascia extending posteriorly from the submaxillaris to the suprascapular region.

The *M. hyoglossus* is a paired median muscle that has its insertion in the fleshy tongue. The fibers bundle dorsally to the submentalis and extend posteriorly along the mid-line. In the throat region this muscle is attached ventrally to the submaxillaris. In a line approximately equal to the position of the angle of the jaw, the two halves of the muscle split and angle laterally. They pass ventrally to the geniohyoideus and dorsally to the sternohyoideus to attach on the inner side of the posterior part of the posterior bony cornu of the hyoid. The geniohyoideus arises on either side of the hyoglossus. The inner part of the muscle arises slightly above the submentalis, and the lateral part arises from the inner surface of the anterior part of the dentary. These flat muscles pass posteriorly, parallel to the hyoglossus. In the throat region they are connected by thin tissue to the submaxillaris. At a line equal to the posterior edge of the openings of the Eustachian tubes, the two components are separated by the intrusion of the sternohyoideus. The lateral part continues posteriorly and attaches on the ventral surface of the posterolateral cornu of the hyoid; the median part passes dorsally to the hyoglossus to insert on the inner surface of the bony posterior cornu (Fig. 4).

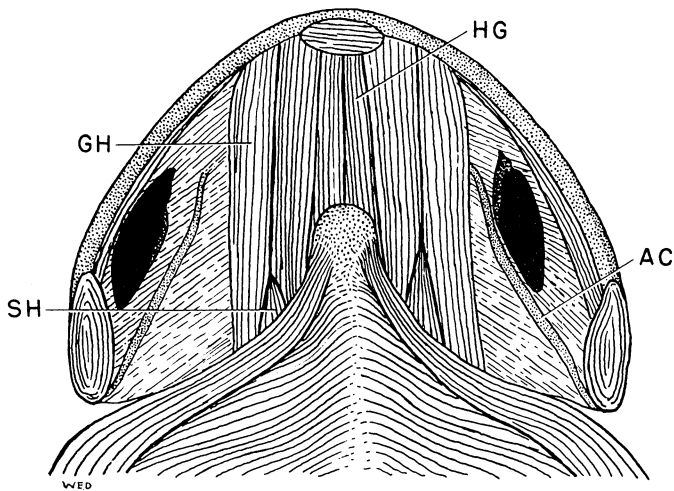


Fig. 4. Deep throat musculature of an adult male *Phrynohyas spilomma*. AC = anterior cornua of hyoid, GH = geniohyoideus, HG = hyoglossus, SH = sternohyoideus.

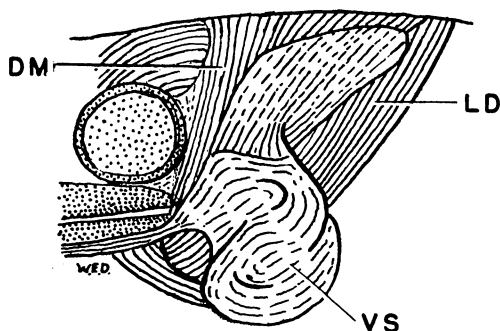


Fig. 5. Superficial shoulder musculature of an adult *Phrynohyas spilomma*, showing the location of the vocal sacs. DM = depressor mandibulae, LD = latissimus dorsi, VS = vocal sac.

The sternohyoideus is partly divided. The mesial part is firmly attached by connective tissue to the ventrolateral surface of the mesosternum; the lateral part is continuous with the rectus abdominus. The muscle passes ventrally to the hyoglossus and divides the geniohyoideus to insert on the ventrolateral surface of the hyoid plate. This insertion covers the edge of the plate from near the base of the posterolateral cornu to the ventral surface of the proximal part of the anterior cornu. Arising from the fascia on the back part of the skull, the petrohyoideus inserts on the lateral edge of the hyoid plate and the lateral edge of the proximal part of the anterior cornu. The omohyoideus arises from the inner, anterior surface of the scapula and passes anteromesially, partly dorsal to the sternohyoideus, to insert on the ventral surface of the hyoid plate between the bases of the posterolateral cornu and the posterior cornu (Fig. 6).

The hyoid plate is thin; in a male with a body length of 74 mm. it is 6 mm. wide and 4 mm. long. Nearly all of the posterior part of the plate and also parts of the anterior are calcified (Fig. 7). The bony posterior cornua (thyrohyales) extend backward and laterally at an angle of approximately 30° from the mid-line. These processes are about 10.5 mm. in length; however, the bony part measures only 8 mm. The posterolateral processes extend backward from the bases of the anterior cornua and measure only 3 mm. in length. There is a slight amount of calcification in the middle sections of these cornua. The anterior cornua extend almost directly forward for about 7 mm. from the anterolateral parts of the hyoid plate. They then loop laterally and extend posterolaterally to the angles of the jaws where they turn dorsad and attach to the posterior surface of the prootic.

Several other hylids were compared with *P. spilomma*. In most of them the submaxillaris arises from the inner surface of the lower jaw and completely covers the throat region. It is attached posteriorly to the deeper muscles of the throat and pectoral girdle. This is true in *Hyla boans*, *H. crepitans*, *H. versicolor*, *Agalychnis dacnicolor*, and *Pternohyla fodiens*,

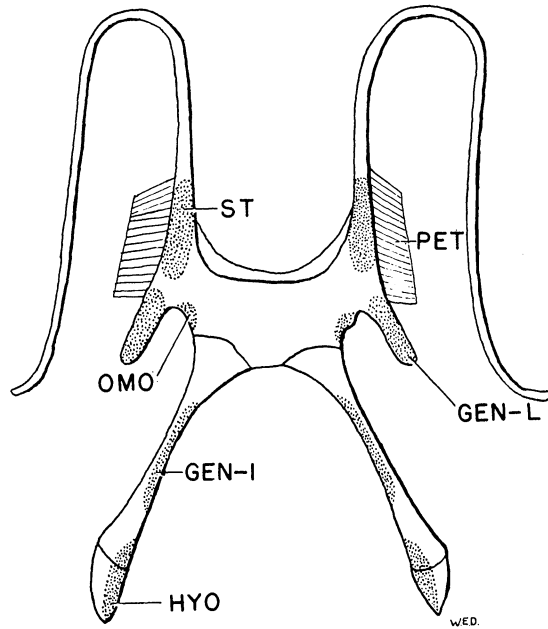


Fig 6. Hyoid apparatus of an adult male *Phrynohyas spilomma*, showing areas of muscle attachment. GEN-I = attachment of median component of the geniohyoideus, GEN-L = attachment of lateral component of the geniohyoideus, HYO = attachment of the hyoglossus, OMO = attachment of the omohyoideus, PET = petrohyoideus, ST = attachment of the sternohyoideus.

of those forms examined. A different situation is found in *Smilisca baudini*. In this form the vocal sacs are also paired, but they lie in the throat region. The submaxillaris is the same as in the forms mentioned above, except that there is a connection medially to the deeper throat musculature. There is considerable folding of the thin tissues of the submaxillaris to form the paired vocal sacs in the throat region. They are separated from each other only by the medial connection with the deeper throat muscles.

The hyoids of *Agalychnis dacnicolor* and *Smilisca baudini* were compared with that of *Phrynohyas spilomma*. The hyoid of *Agalychnis* consists of a very long plate with comparatively short posterior cornua, whereas that of *Smilisca* is similar to *Phrynohyas* but has a slightly wider plate and shorter posterior cornua. Trewavas (1933) discussed and illustrated the throat musculature and hyoids of two other American hylids—*Hyla rubra* and *H. versicolor*.

Dermal Glands

Many workers have mentioned the extremely heavy parotoid glands in these hylids. Whether or not the glandular development is homologous with

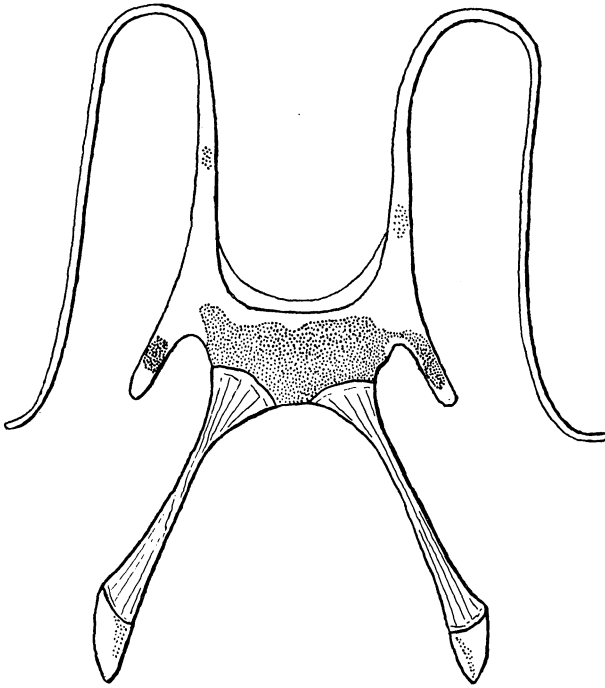


Fig. 7. The structure of the hyoid apparatus in an adult male *Phrynohyas spilomma*. The ossified areas are darkened.

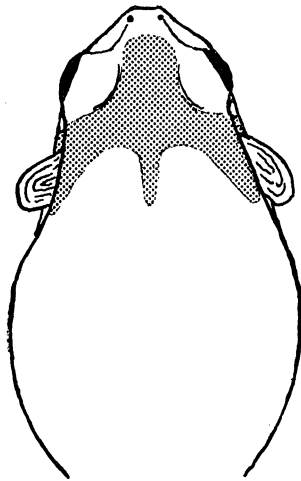


Fig. 8. Dorsal view of the body of an adult *Phrynohyas*, showing the area of normal parotoid development.

the parotoids of the bufonids is not known. Although the center of development is in the occipital region, the area covered is larger than that in *Bufo*. There is considerable variation in the development of the parotoids among the different species of *Phrynohyas*. Typically, the skin shows a thickened, glandular condition on the head between the orbits, in the occipital region, and in the supratympanic region. The glandular development continues posteriorly on the dorsum for a short distance (Fig. 8).

Sections of the skin from the neck of *Phrynohyas spilomma* show that there is a great development of the granular poison glands. These are much larger and much more numerous than the mucous glands. The small pustules on the dorsum of these frogs show the same type of glandular development. The skin between the pustules and away from the parotoid areas is much thinner and has fewer poison glands and more mucous glands.

Sections of the dorsal skin of *Agalychnis dacnicolor* and *Smilisca baudini* were compared with the sections from *Phrynohyas*. In neither of these two forms were the poison glands as well developed or as numerous. Phisalix (1922: 18) illustrated elongated, dorsolateral parotoid glands in *Phyllomedusa bicolor*.

The poisonous secretion of *Phrynohyas* has never been analyzed chemically, although that of a closely related genus, *Trachycephalus*, has been studied (Vellard, 1929). Lutz and Kloss (1952: 657) compared the effects of the secretions of "*Hyla venulosa*" and *H. imitatrix*. The effects of the volatile poison, which is apparently quite strong, are discussed under *Phrynohyas spilomma* and *P. zonata*.

SYSTEMATIC ACCOUNT OF THE SPECIES OF *PHRYNOHYAS*

Phrynohyas hebes (Cope)

Scytotis hebes Cope, *Proc. Acad. Nat. Sci. Phila.*, 14 (9) (1862): 354-55.

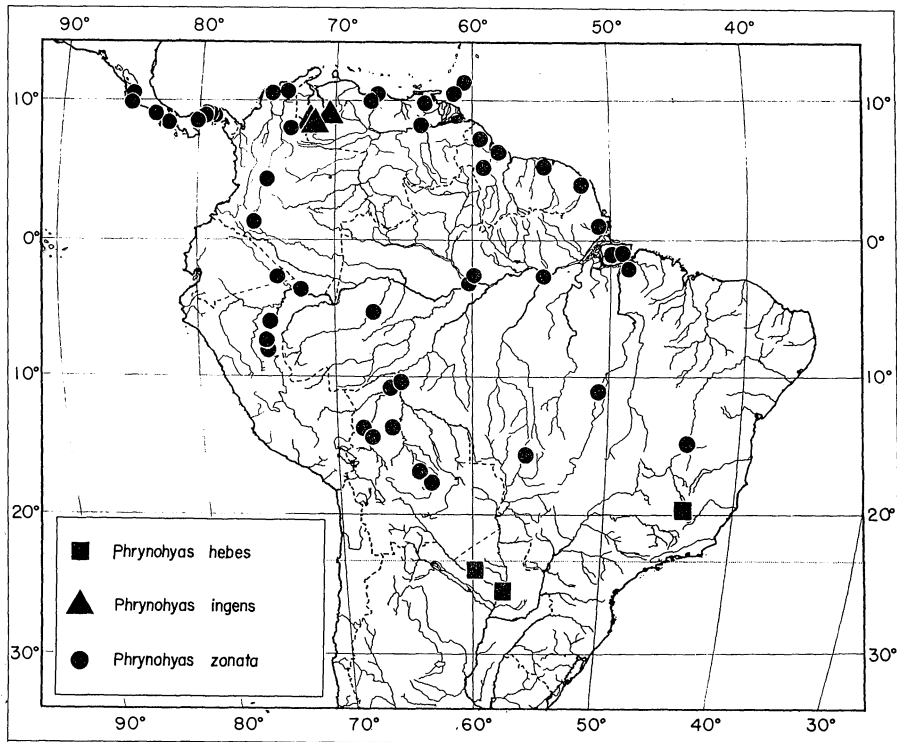
Hyla venulosa, Peracca, *Bol. Mus. Zool. Anat. Univ. Torino*, 10 (195) (1895): 29; Boulenger, *Ann. Mus. Genova*, 19 (2) (1898a): 126; Mähely, *Ann. Mus. Nac. Hungarici*, II (1904): 226; Müller and Hellmich, *Wiss. Ergeb. Deutsch. Gran Chaco-Exped. Amphib. and Rept.*, I (1936): 80-83; Lutz, *Copeia*, 3 (1946): 153; Vellard, *Acta. Zool. Lilloana*, V (1948): 149-50; Cochran, *Bull. U. S. Nat. Mus.*, 206 (1955): 62.

Type.—USNM 5837 listed from Paraguay. This specimen is one of many different species collected during a lengthy exploration of the Paraguay and Parana river systems. No definite locality can be given, but since the party was known to have collected in the vicinity of Asunción, Paraguay, I propose that the type locality be restricted to that place.

Since the type specimen is a badly faded female, one must depend largely upon Cope's original description, which I believe is applicable to the frogs under consideration.

Range.—This species occupies the southern extremities of the range of the genus, being found from the Rio São Francisco in Minas Gerais, Brazil, southward and westward through Paraguay and into northern Argentina (Map 1).

Description.—This moderate-sized species averages about 80 mm. in body length; the tibia is less than 50 per cent of the body length. There is



Map 1. Locality records for *Phrynohyas hebes*, *P. ingens*, and *P. zonata*.

no tarsal fold, and the subarticular tubercles are rounded. The inner metatarsal tubercle is roughly elliptical, the distal end slightly pointed, and the proximal end blunter. The discs of the toes are smaller than those of the fingers, which are equal to the diameter of the tympanum. The head is broad and flattened, and the snout is short and blunt. The canthus rostralis is rounded, and the loreal region is decidedly concave. The lips are flared. The tympanum is approximately three-fourths the diameter of the eye and is separated from it by a distance nearly equal to the diameter of the tympanum. The vomerine teeth range from 12 to 16 and average about 14. They are situated on two slightly curved ridges between the relatively large internal nares. The tongue is broadly cordiform and barely free behind.

The toes are webbed to the base of the disc, except for the fourth, which has the last two phalanges free. The fingers are webbed for about one-third of their length, but the web between the first and second digits is rudimentary. There is a well-developed parotoid in the head and neck region. The glandular development extends laterally to form a heavy fold above the tympanum, which it partly conceals. There are scattered pustules on the back; the throat, belly, and posterior surfaces of the thighs are granular.

TABLE I
SUMMARY OF MEASUREMENTS AND PROPORTIONS
OF EIGHT ADULT *PHRYNOHYAS HEBES*

Character	Mean		Range	
	♂	♀	♂	♀
Number of specimens	3	5	3	5
Body length	80.3	80.3	73.0-86.0	68.0-84.0
Tibia length	37.7	37.8	34.0-40.0	34.0-39.5
Per cent tibia/body length	46.9	47.2	46.5-47.6	45.2-50.0
Foot length	32.2	32.0	27.5-35.0	27.0-34.0
Head length	23.7	24.9	22.0-24.5	22.0-26.5
Per cent head/body length	29.5	31.1	28.5-30.1	28.7-32.4
Head width	26.3	26.4	24.0-28.5	23.0-28.5
Per cent head width/body length	32.8	32.9	32.3-33.1	30.5-34.5
Interorbital distance	7.3	7.8	6.5- 9.0	6.5- 9.0
Per cent interorbital/head width	27.7	29.5	24.5-31.6	27.5-32.1
Internarial distance	5.7	5.4	5.0- 6.5	5.0- 6.0
Per cent internarial/head width	21.6	20.5	20.8-23.2	17.9-22.2
Tympanum length	5.0	5.5	4.0- 5.5	5.0- 6.0
Per cent tympanum/head length	21.0	22.1	18.2-22.4	20.8-23.1
Vomerine teeth	13.3	14.8	12-16	14-16

Coloration.—There is a tawny brown patch that begins on the eyelids and continues posteriorly. This is usually outlined in a darker brown. The snout is either cream or light tan, a color that persists as a dorsolateral band on either side of the dorsal dark patch (Pl. I, Fig. 2). Just anterior to the tympanum there begins a lateral dark brown band that passes over the tympanum and onto the flank. In some specimens there are spots of darker brown in the lighter dorsolateral band. There are transverse bands on the limbs that are about twice the width of the interspaces. The color of the bands is the same as that of the dorsal patch, and the color of the interspaces is the same as that of the dorsolateral band. There are dashes or dots of dark brown in the light interspaces. The belly and other under-surfaces are cream or sometimes tinged with tan.

Remarks.—One immature individual from Patino, Paraguay, is tentatively referred to this species. The specimens described by Müller and Hellmich (1936: 80-83) from the Gran Chaco resemble those that I have examined. Unfortunately, their specimens were destroyed during World War II.

Affinities.—This species is very close to *P. zonata*, and it is given specific rank only because of the absence of intermediate specimens. Three specimens from Chapada, Mato Grosso, Brazil (BMNH 1903.3.26.54-6), somewhat resemble *P. hebes* in their dorsal color pattern, but in most other respects they are like *P. zonata*. I have considered them *P. zonata*.

Specimens examined.—9, as follows:

BRAZIL: *Minas Gerais*: Piraporinha—USNM 98536-7.

ARGENTINA: USNM 73523.

PARAGUAY: AMNH 19916-7, 19919, USNM 5837 (holotype); Asunción—BMNH 94.3.14.168; Patino—CNHM 10799; Puerto 14 de Mayo, Bahia Negra—BMNH 98.6.3.19.

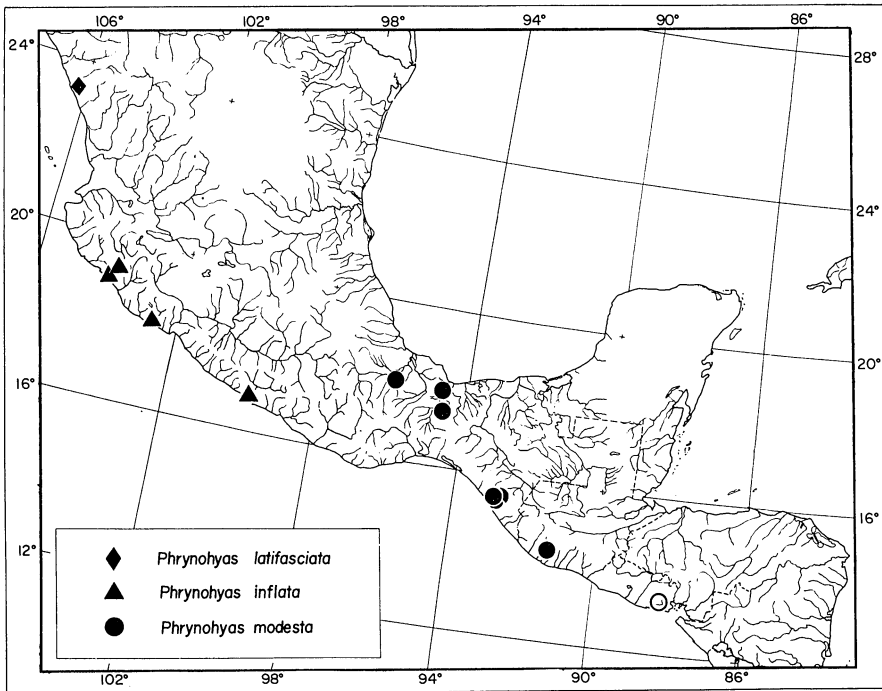
Phrynohyas inflata (Taylor)

Hyla venulosa, Oliver, *Occ. Papers Mus. Zool. Univ. Mich.*, No. 360 (1937): 7.

Acrodytes inflata Taylor, *Univ. Kans. Sci. Bull.*, 30, I (6) (1944): 63-68, Pl. IX; Smith and Taylor, *Bull. U. S. Nat. Mus.*, No. 194 (1948): 74; Peters, *Occ. Papers Mus. Zool. Univ. Mich.*, No. 554 (1954): 7.

Type.—EHT-HMS No. 17890 from near La Venta, Guerrero, collected by E. H. Taylor.

Range.—Known only from a few localities along the Pacific coast of Mexico from Colima to central Guerrero. It is quite probable that the species ranges northward into Nayarit, southward into Oaxaca, and possibly into Chiapas. It may also occur in the Balsas Basin (Map 2).



Map 2. Locality records for *Phrynohyas inflata*, *P. latifasciata*, and *P. modesta*.

Description.—This is a large species, the males attaining a body length of 95 mm. The hind limbs are comparatively short; three large males have an average tibia/body length ratio of 44.97 per cent. One smaller male from Colima, however, with a body length of 70 mm. has a tibia/body length ratio of 51.4 per cent. Thus, it seems safe to assume that in this species as in *P. spilomma* the smaller individuals have on the average a proportionately longer tibia than do the larger individuals. There is no distinct tarsal fold. The inner metatarsal tubercle is large and flat, and the subarticular tubercles are large, flattened, and subelliptical. In four males the hind feet

average 33.4 mm. in length. The head is broader than long and is flattened, its width averaging 32.7 per cent and its length 30.2 per cent of the body length. The snout is rounded and blunt, and there is an abrupt slope downward from the nostrils to the tip of the snout. The canthus rostralis is rounded but distinct. The loreal region is very noticeably concave, and the upper lips are distinctly flared. The tympanum is quite small, being about one half the diameter of the eye. It is separated from the eye by a distance less than the diameter of the tympanum. The eyes do not appear to be as large as they are in most of the species in this genus; their diameter is approximately equal to their distance from the nostrils.

The vomerine teeth normally range from 12 to 22, with a mean of 17.5, and are situated on two highly projecting ridges at the level of the posterior border of the internal nares. The ridges are widely separated in the mid-line with the medial parts of the series slightly posterior to the lateral parts. In one specimen, UMMZ 104814, the vomerine projections are broad and are not separated in the mid-line. The medial part is anterior to the lateral parts. There are 24 teeth, most of which are situated in one long, curved row, but medially there are four teeth in a cluster posterior to the primary row. There is also a secondary row of teeth paralleling the left wing of the primary row. In all of the specimens the tongue is circular, barely notched behind, and only slightly free along its posterior border.

The fingers are less than half webbed. The web between the thumb and first finger is vestigial; that between the first and second fingers connects them at the position of the proximal subarticular tubercles. Between the second and third fingers the web is better developed, connecting them at the second subarticular tubercles. The webbing of the foot is well developed. All of the digits are webbed to the disc except the fourth toe, which is webbed to the base of the penultimate phalanx. The skin above is rather thick and has many large, round, flat pustules on the back, especially posteriorly. The development of the parotoid glands, not so extensive as in *P. ingens*, *P. spilomma*, and *P. zonata*, is found only in the neck and shoulder regions. There is a heavy fold extending posteriorly from the eye, above the tympanum, and terminating at a point above the vocal sacs. The skin on the ventral surfaces of the body is granular, a condition which is especially pronounced in the throat region. The posteroventral surfaces of the thighs are also granular; otherwise, the ventral surfaces of the limbs are smooth.

Coloration.—As described by Taylor (1944: 66), the ground color above is usually reddish brown, fading to a lighter tan color on the limbs. Superimposed upon this ground color posteriorly is a dark patch, which extends from the vent to the sacral region and laterally onto the flanks. This posterior patch is separated by a broad band of ground color from an anterior patch, which begins on the upper eyelids and extends posteriorly with nearly straight sides. This anterior patch may or may not be solid brown. In some specimens there are small spots of ground color interrupting the continuity of the dark patch. There are scattered darker flecks on the reddish brown ground color, and there is a weakly defined dark bar extending posteriorly from the eye to the vocal sac. This bar is interrupted by the tympanum, which is light reddish brown.

There are two transverse dark bands on the thighs, two on the tibia, two or three on the tarsus, and usually one on the foot. These bands are dark brown or dark reddish brown and are slightly wider than the interspaces. They may or may not be outlined with a darker color. In some individuals the interspaces are marred with a few dark flecks. One or two bands of similar nature are on the arms, and usually there is a narrow, incomplete band on the hand. The bands on the arms are narrower than the interspaces. The vocal sacs are brownish gray. Ventrally the color is a dirty cream, the undersurfaces of the limbs being slightly lighter than that of the belly. The undersurfaces of the feet are colored like the belly.

UMMZ 104814 from Michoacán shows basically the same color pattern, but it differs decidedly from the preceding description. The ground color is a yellowish gray. The dorsal patches and the transverse leg bands are gray and are outlined in black. All of the dark markings have superimposed upon them fine reticulations of black. There are a few scattered black flecks on the dorsal ground color. The under parts are cream, and the vocal sacs are dark gray. The eye in life showed a black horizontal bar, separating a dorsal and a ventral dark field with vivid golden markings (Pl. II, Fig. 1).

Remarks.—Only males of this species are known. Taylor gave the length of the body of the type specimen as 95 mm., and the specimens examined by me are all quite large and robust. It is to be assumed that the females may be considerably larger and may possibly attain a greater size than the females of *P. ingens*, the largest known member of the genus.

The distribution of this species appears to be restricted to the subtropical forests of the Pacific coast of Mexico. Taylor found the type series in a forest. Oliver (1937: 7) reported a specimen from the vicinity of the city of Colima as found "about forty feet above the ground at the base of a palm frond in a coconut tree." I found one individual in the Barranca de Bejuco near the mouth of the Río Nexpa in Michoacán. It was on a horizontal limb about seven feet above the ground in a tropical deciduous forest, composed of, among others, *Castilla*, *Licania*, *Monstera*, *Plumeria*, and many Leguminosae. Reptiles and amphibians collected at the same locality include *Bufo horribilis*, *Bufo marmoratus*, *Anolis nebulosus*, *Ctenosaura pectinata*, *Sceloporus siniferus siniferus*, *Ameiva undulata sinistra*, and *Cnemidophorus guttatus immutabilis*. Taylor found his specimens calling in rain pools at night.

Affinities.—*Phrynohyas inflata* is quite distinct from all other Central American and Mexican forms of this genus. Only by the South American species, *P. ingens* and *P. zonata*, is it rivaled in size. The character of the broad band of ground color separating a large posterior and a large anterior dorsal patch, plus the small size of the tympanum, combined with the over-all large size, are sufficient to identify this species. Geographically, *P. inflata* is situated between *P. latifasciata* to the north in Sinaloa and *P. modesta* to the southeast in Chiapas. There is a possibility that *P. inflata* and *P. latifasciata* are subspecifically related, but unless intermediate specimens are found they should be considered as distinct species. To the south and east the range of *P. inflata* may overlap that of *P. modesta*. These frogs are dissimilar in their coloration and in certain structural characters.

Specimens examined.—5, as follows:

MEXICO: *Colima*: 1 mi. N. Colima—UMMZ 80018; Paso del Río—UMMZ 108019; *Guerrero*: near La Venta—EHT-HMS 17889, 17891 (paratypes); *Michoacán*: Barranca de Bejuco—UMMZ 104814. One other specimen, the type, EHT-HMS 17890 from near La Venta, Guerrero, was not examined by me.

Phrynohyas ingens, new species

(Pl. II, Fig. 2)

Holotype.—UMMZ 55570, an adult female from La Fria, Pueblo Nuevo, Depto. Zulia, Venezuela, collected April 20, 1920, by H. B. Baker.

Paratopotypes.—UMMZ 55567-55569 collected with the holotype.

Range.—Known only from three closely approximated localities in the lowlands south of Lake Maracaibo in northern Venezuela (Map 1).

Diagnosis.—A gigantic member of the genus characterized by a comparatively small head, a high number of vomerine teeth, relatively long legs, and a dull brown dorsal coloration.

Description of holotype.—A female measuring 105 mm. in body length; tibia 54.5 mm., being 51.9 per cent of the body length; length of foot 44 mm.; foot/body length ratio 41.9 per cent; head width 33.5 mm.; head width/body length ratio 31.9 per cent; head length 30.0 mm.; head length/body length ratio 28.6 per cent. Snout short and rounded; canthus rostralis rounded, and loreal region slightly concave; internarial distance 7 mm.; interorbital distance 9 mm.; eyes comparatively small, being equal to their distance from the nostrils; tympanum large, 6.5 mm., two-thirds the diameter of the eye, and separated from the eye by a distance less than the diameter of the tympanum. A heavy supratympanic fold extends from the posterior edge of the eyelid above the tympanum and then downward behind it. The parotoid glands are very heavy in the neck region; the skin of the back has a leathery texture. The fingers are only slightly webbed; the web between the first and second digits is vestigial, whereas those between the second and third and the third and fourth digits connect them for about one-third their length. The toes are more completely webbed; the membrane extends to the base of the disc of the first, second, third, and fifth toes, but the distal and penultimate phalanges of the fourth toe are free. The discs of the fingers are slightly larger than the tympanum, but the discs of the toes are only about half as large. There is no tarsal fold; the subarticular tubercles of the fingers and toes are rounded but not flattened. The distal subarticular tubercles on the fourth finger and fifth toe are bifid. There are 19 vomerine teeth situated on two nearly straight ridges at the level of the posterior edge of the internal nares. The ridges are only narrowly separated in the mid-line. The tongue is rounded, shallowly notched posteriorly, and only slightly free behind. The skin dorsally is heavy and smooth; that of the belly and throat is granular.

Coloration.—The dorsal color is a dusky brown, which becomes lighter on the flanks, and tannish cream on the belly. The throat is pinkish buff.

TABLE II
SUMMARY OF MEASUREMENTS AND PROPORTIONS
OF SIX ADULT *PHRYNOHYAS INGENS*

Character	Mean		Range	
	♂	♀	♂	♀
Number of specimens	4	2	4	2
Body length	84.0	108.8	75.0-88.0	105.0-112.5
Tibia length	39.5	55.5	36.0-41.5	54.5- 56.0
Per cent tibia/body length	47.0	50.9	45.9-48.0	49.8- 51.9
Foot length	33.4	45.3	31.0-35.0	44.0- 46.6
Head length	24.6	31.0	23.5-25.5	30.0- 32.0
Per cent head/body length	29.4	28.5	27.8-31.3	28.4- 28.6
Head width	26.1	35.3	24.0-27.0	33.5- 37.0
Per cent head width/body length	31.1	32.4	30.0-32.0	31.9- 32.9
Interorbital distance	6.8	9.0	6.5- 7.0	9.0
Per cent interorbital/head width	25.9	25.6	24.5-27.1	24.3- 26.9
Internarial distance	5.3	7.0	5.0- 5.5	7.0
Per cent internarial/head width	20.1	19.9	18.9-20.8	18.9- 20.9
Tympanum length	5.3	6.8	4.5- 6.0	6.5- 7.0
Per cent tympanum/head length	21.3	21.8	18.4-24.0	21.7- 21.9
Vomerine teeth	18	19	17-19	19

There are small, scattered, darker brown dots on the back, especially posteriorly. On the flanks these form interrupted vertical and longitudinal streaks. There is a dark brown band extending from the posterior edge of the tympanum onto the flank. The dark brown spots are especially apparent on the dorsal surfaces of the hind limbs, where some of them are fused into dark streaks. The posterior parts of the thighs are light tan (Pl. II, Fig. 2).

Variation.—In the other known specimens of *P. ingens* the belly color is more of a dirty cream, a color that is slightly lighter than that described for the holotype. The dorsal color pattern is essentially the same in all of the specimens. One male is lighter than the others, the color on the flanks being a light gray. In this specimen the dots on the legs have formed better developed transverse streaks, and in this respect it resembles the species with the transverse limb bands. In three of the specimens the dark band behind the tympanum is very indistinct or lacking. The vocal sacs in the males are dark brown.

One paratype, UMMZ 55567, a female, has a body length of 112.5 mm. This huge individual has discs on the fingers 8 mm. in diameter. Two specimens do not have the distal subarticular tubercles of the fourth finger and fifth toe showing a bifid condition.

Remarks.—In his field notes Baker made the following statements concerning the type series, which he collected at La Fria: "Two pairs of these big frogs were copulating in a peccary wallow pond near a big tree. The male makes a loud noise like dropping a rock into a vessel partially filled with water. After heavy rains eggs on surface (of water) formed films two or three feet across." These interesting but meager notes constitute the total amount of information available concerning the life history and habitat of the species.

Affinities.—Undoubtedly, *P. ingens* is closely related to *P. zonata*, from which it differs principally by having a more or less unicolor dorsum and

by being of a greater size. *P. ingens* probably differentiated from *P. zonata* through isolation in the Maracaibo Basin.

Specimens examined.—6, as follows:

VENEZUELA: *Trujillo*: Savana de Mendoza—UMMZ 57397; *Zulia*: La Fria, Pueblo Nuevo—UMMZ 55567-70 (type series); Oropo—CNHM 2604.

Phrynohyas latifasciata, new species

(Pl. III, Fig. 1)

Hyla vemulosa, Boulenger, *Ann. Mag. Nat. Hist.*, ser. 5, X (1882): 327-28; Gadow, *Proc. Zool. Soc. London*, 1905, p. 207; Kellogg, *Bull. U. S. Nat. Mus.*, 160 (1932): 176-79.

Holotype.—BMNH 83.2.7.1, an adult male collected at Presidio, Sinaloa, Mexico, in 1882, by Alphonso Forrer.

Paratype.—BMNH 83.4.5.5, from Presidio and presumably collected with the holotype.

Range.—At present known only from the type locality. It probably ranges along the west coast of Sinaloa and possibly into Nayarit, where it may or may not intergrade with *P. inflata* (Map 2).

Diagnosis.—A small frog characterized by the presence of three large brown spots on the anterior part of the back, very wide transverse bands on the hind limbs, black vocal sacs, and relatively smooth, nongranular skin.

Description of holotype.—A male measuring 68 mm. in body length; tibia 30 mm., or 44.1 per cent of the body length; length of foot 28.5 mm.; foot/body length ratio 41.9 per cent; head width 22 mm.; head length 20.5 mm., or 30.1 per cent of the body length. Head blunt and rounded, snout slightly pointed; canthus rostralis rounded but distinct; internarial distance 4 mm.; interorbital distance 6 mm.; eyes large, twice the diameter of the tympanum and equal to their distance from the nostrils. A well-defined, but not excessively heavy supratympanic fold extends backward from the posterior edge of the eyelid, above the tympanum, to a point above the protrusion of the vocal sacs. The development of the parotoid glands is restricted to the head and nuchal region. The fingers are only slightly webbed, the web between the first and second fingers being rudimentary, whereas those between the second and third and the third and fourth connect the fingers for about one-third of their length. The toes are more completely webbed, the web extending to the base of the distal phalanx (disc) of the first, second, third, and fifth toes; the last two phalanges of the fourth toe are free. The discs of the fingers are as large as the tympanum; those of the toes are scarcely half as large. There is no tarsal fold, and the subarticular tubercles of the fingers and toes are rounded and flat. Sixteen vomerine teeth are situated on two slightly curved ridges at the level of the posterior edge of the internal nares. The median part of the vomerine series is slightly anterior to the lateral parts, and the ridges are separated in the mid-line. The tongue is rounded and very slightly notched behind; the posterior edge is barely free. Dorsally the skin is smooth except for a few indistinct pustules posteriorly. The ventral surfaces of the belly and thighs are slightly granular; the granular condition is more pronounced on the throat.

The dorsal ground color is a pinkish buff. On the back between the vocal sacs is a large square patch of chestnut brown. Posterior to this but anterior to the sacral hump are two smaller, elongated brown spots separated in the mid-line by a strip of ground color in which there are three small dashes of brown in a longitudinal row. The posterior part of the trunk is covered with a large brown patch, which is slightly lighter than the smaller anterior patches. There is a dark brown band extending posteriorly from the eye, narrowing above the tympanum, and ending just back of the vocal sacs. There are two wide brown bands on the thighs and one nearly the whole extent of the tibia. These are separated by narrow interspaces of cream. There is one wide dark band on each segment of the forelimbs. The vocal sacs are black, and the belly and other undersurfaces are cream.

Remarks.—The paratopotype is a young specimen 46 mm. in body length; tibia 20.5 mm.; foot 16 mm.; head width 15.5 mm.; head length 15.5 mm. There are 14 vomerine teeth. The dorsal ground color is faded, but there are visible spots as described in the holotype. The limb bands are not quite as wide as those in the holotype, and, as is true of all small individuals of this genus, the skin is very pustulate.

Boulenger (1882a: 327-28) gave a description of the living specimen here designated as the holotype. This was brought to him from Presidio by Forrer. The description is as follows:

Upper surfaces light brown, with large chestnut-brown spots; these occupy entirely the hinder part of the back and the hind limbs; upon the latter the lighter ground-colour appears in the form of transverse lines; on the flanks the spots are bordered with pure white; lower surfaces of a rather dirty white, the throat with brown vermiculations. The eye is very beautiful, the iris being golden with black reticulations, and a vertical and a horizontal black bar, forming a cross. The vocal bladders are black; they cannot be retracted, as in the *Ranae* with external vocal sacs; and when empty they hang on each shoulder like a cutaneous lobe.

Concerning the secretion of this species Boulenger stated (1882a):

It is by no means shy, but, when handled, exudes a great quantity of poisonous fluid, more so than any Batrachian I have had before. Besides, this fluid, of a milky appearance, coagulates instantaneously, sticking to the fingers in a very disagreeable manner; it has a strong odour, resembling that of peaches, and affects very disagreeably the mucous membrane of the nostrils, causing a strong itching.

Affinities.—This species is closest geographically to *P. inflata*, the northernmost record for which is Colima, Colima. It differs from *inflata* in being of smaller size, having a dorsal pattern anteriorly of brown spots instead of the large brown or gray blotch. The skin is without the well-developed pustules of *inflata*, and the ventral surfaces are relatively smooth, not highly granular as in most other species of *Phrynohyas*. The vocal sacs are black, not brown or gray as in *P. inflata*.

Specimens examined.—2, as follows:

MEXICO: *Sinaloa*: Presidio—BMNH 83.2.7.1, 83.4.5.5.

Phrynohyas modesta (Taylor and Smith)

Hyla venulosa, Nieden, *Das Tierreich - Anura*, I (1923): 244-45; Kellogg, *Bull. U. S. Nat. Mus.*, 160 (1932): 176-79.

Acrodyles modesta Taylor and Smith, *Proc. U. S. Nat. Mus.*, 95 (1945): 594-96, Pl. 27, Fig. 2, Pl. 28, Figs. 2-3; Smith and Taylor, *Bull. U. S. Nat. Mus.*, 194 (1948): 74.

Hyla modesta, Mertens, *Abhand. Senck. Naturf. Gesell.*, 487 (1952): 30, Pl. 10.

Type.—USNM 115013 from Cruz de Piedra near Acacoyagua, Chiapas, Mexico, collected by Hobart M. Smith.

Range.—Known from scattered localities along the Pacific slopes from El Salvador through Chiapas. It occurs in the Atlantic drainage only in the region of the Isthmus of Tehuantepec in the states of Oaxaca and Veracruz, Mexico (Map 2).

Description.—This is a rather small species. The largest individual examined is a female measuring 80.5 mm. in body length. The average length is considerably less, 63 mm. The tibia is rather long and is nearly 50 per cent of the body length in adults. The variation in measurements and proportions is given in Table III. There is no tarsal fold. The inner metatarsal tubercle is rounded and subelliptical; the subarticular tubercles are rounded. The discs of the fingers are larger than those of the toes and are equal to the diameter of the tympanum. The head is broad, and the snout is short and rounded. The canthus rostralis is rounded; the loreal region is slightly concave. The lips tend to be flared. The tympanum is about two-thirds the diameter of the eye and is separated from it by a distance less than the diameter of the tympanum. The eyes are rather large, and are greater in diameter than their distance from the nostrils. The vomerine teeth range from 10 to 23 and average about 16. They are situated on two highly projecting ridges at the level of the posterior borders of the internal nares. The ridges are narrowly separated in the mid-line. The tongue is cordiform, only slightly notched posteriorly, and barely free behind. The toes are webbed to the base of the disc, except the fourth toe which is enclosed to the base of the penultimate phalanx. The fingers are half webbed; the membrane between the thumb and the first finger is vestigial.

TABLE III
SUMMARY OF MEASUREMENTS AND PROPORTIONS
OF TWENTY-SEVEN ADULT *PHRYNOHYAS MODESTA*

Character	Mean		$\pm 2\overline{\sigma_x}$		Range	
	♂	♀	♂	♀	♂	♀
Number of specimens	13	14	13	14	13	14
Body length	63.7	63.5	3.03	4.66	54.0-69.5	52.0-80.5
Tibia length	31.0	31.7	1.38	2.38	25.5-33.5	26.0-40.0
Per cent tibia/body length	48.7	49.9	.83	1.16	46.8-51.2	46.8-55.9
Foot length	25.5	26.5	1.27	1.99	20.5-29.0	21.5-32.5
Head length	19.5	19.5	.86	1.20	16.5-22.5	17.0-23.0
Per cent head/body length	30.6	30.8	.64	.81	28.8-32.6	28.6-32.8
Head width	20.8	20.9	1.01	1.47	17.5-23.0	18.0-26.0
Per cent head width/body length	32.6	32.9	.46	.55	31.4-34.3	31.2-35.1
Interorbital distance	5.6	5.8	.30	.36	4.5- 6.5	5.0- 7.0
Per cent interorbital/head width	27.1	28.0	.79	.94	25.6-30.6	25.5-32.4
Internarial distance	4.7	4.8	.22	.28	4.0- 5.0	4.0- 5.0
Per cent internarial/head width	22.8	22.9	.85	1.34	19.2-23.9	19.0-26.5
Tympanum length	4.2	4.3	.28	.33	3.5- 4.5	3.5- 5.5
Per cent tympanum/head length	21.7	22.2	1.27	1.00	19.4-24.2	18.2-24.4
Vomerine teeth	14.7	16.7	1.69	1.77	12-23	10-21

The dorsal surface is covered with scattered, small, round pustules. The development of the glandular condition of the skin is considerably less than in *P. ingens*, *P. spilomma*, and *P. zonata*; it is restricted to the neck region and the fold above the tympanum. The skin of the throat, belly, and posterior surfaces of the thighs is granular.

Coloration.—In preservative the dorsal ground color is a medium brown to a lavender brown. The ventral surfaces are a dirty cream or a light brown. Dorsally there are scattered black dots on the back. On the limbs these dots usually form thin, broken, transverse lines. Five specimens from Mazatenango, Guatemala, display a coloration somewhat different from that of specimens from Mexico. Three of the specimens are very heavily dotted dorsally. The dots on the limbs extend onto the feet and even to the discs. In two of the individuals the dots form short, thin, broken, dorsolateral lines. In all of the Mexican specimens the venter is unspotted, but four of the specimens from Mazatenango have the ventral surfaces of the hind limbs spotted. One of these also has the throat and belly heavily spotted. There may or may not be a dark line bordering the upper edge of the tympanum, which is colored like the dorsum. The vocal sacs are brown (Pl. III, Fig. 2).

Remarks.—Six juveniles collected in the autumn of 1937 in the vicinity of Escuintla, Chiapas, Mexico, range in body length from 26 to 33 mm. (average 29.6). They are colored like the adults save for the lack of black dots on the dorsal surfaces that are characteristic of the larger individuals.

Several specimens of *P. spilomma* superficially resemble this species. Most of these are badly faded individuals in which the dorsal dark patch is not readily apparent.

There is little known of the habitat and habits of this species. Males collected at Mazatenango, Guatemala, on July 29, 1924, are in breeding condition and have brown, horny nuptial rugosities on the thumbs. Taylor and Smith (1945: 596) stated: "During the wet season in Chiapas specimens were found calling at night in a tree about 12 feet above the ground. The call is a loud, raucous, grinding noise that lasts perhaps a second. It is sometimes repeated twice or thrice, and then follows a long period of silence."

Affinities.—Although structurally *P. modesta* closely resembles *P. spilomma*, they must be regarded as distinct species. The ranges of the two forms overlap on the Pacific slopes from the Isthmus of Tehuantepec to Guatemala. In coloration *P. modesta* resembles the brown form of *P. zonata* from the upper Amazon Basin. The latter, however, can easily be distinguished from *P. modesta* by the shorter tibia and lack of black dots dorsally.

Specimens examined.—37, as follows:

GUATEMALA: *Suchitepeque*: Mazatenango—CAS 69726-30.

MEXICO: *Chiapas*: Colonia Soconusco—USNM 115024-5; Cruz de Piedra—USNM 115013-19, 115021-3; Escuintla—UMMZ 88270 (10); La Esperanza—UMMZ 87849-50, USNM 115010-12; *Oaxaca*: Tuxtepec—USNM 46917; *Veracruz*: Jesús Carranza—UK 27392-4; Minatitlan—AMNH 52147.

Mertens (1952: 30) reported two specimens of this species from Laguna de Jocotal, San Miguel, El Salvador. They were not examined by me.

Phrynohyas spilomma (Cope)

- Hyla lichenosa* Günther, *Cat. Batr. Sal.*, 1858, p. 102, Pl. 8, Fig. c; Brocchi, *Miss. Sci. Mex. L'Amer. Cent.*, 3 (2) (1881): 33; Sumichrast, *La Naturleza*, 6 (1882): 81.
- Hyla spilomma* Cope, *Proc. Amer. Phil. Soc.*, 17 (1877): 86; Brocchi, *op. cit.*, 1881, pp. 39-40; Boulenger, *Cat. Batr. Sal.*, 1882b, pp. 402-3; Sumichrast, *op. cit.*, 1882; Cope, *Bull. U. S. Nat. Mus.*, 29 (1887a): 15; Günther, *Biol. Cent. Amer.*, 1901, pp. 282-83; Nieden, *Das Tierreich - Anura*, I (1923): 247.
- Hyla paenulata* Brocchi, *Bull. Soc. Philom. Paris*, 7, III (1) (1879): 21; Brocchi, *op. cit.*, 1881, pp. 45-46.
- Hyla nigropunctata* Boulenger, *op. cit.*, 1882b, p. 366; Garman, *Bull. Essex Inst.*, 16 (1884): 45; Ferrari-Perez, *Proc. U. S. Nat. Mus.*, 9 (1886): 198.
- Scytotis venulosus*, Cope, *op. cit.*, 1887a, p. 12.
- Hyla venulosa*, Günther, *op. cit.*, 1901, pp. 272-73; Gadow, *Proc. Zool. Soc. London*, 1905, p. 207; Nieden, *op. cit.*, 1923, pp. 244-45; Kellogg, *Bull. U. S. Nat. Mus.*, 160 (1932): 176-79; Dunn and Emlen, *Proc. Acad. Nat. Sci. Phila.*, 84 (1932): 24; Stuart, *Misc. Publ. Mus. Zool. Univ. Mich.*, No. 29 (1935): 39; Gaige, *Carnegie Inst. Wash. Publ.*, 457 (1936): 293-94; Smith, *Occ. Papers Mus. Zool. Univ. Mich.*, No. 388 (1938): 12; Smith, *Chicago Nat.*, 4 (2) (1941): 38.
- Acrodytes spilomma*, Taylor, *Univ. Kans. Sci. Bull.*, 30, I (6) (1944): 64; Taylor and Smith, *Proc. U. S. Nat. Mus.*, 95 (1945): 593-94; Smith and Taylor, *Bull. U. S. Nat. Mus.*, 194 (1948): 75; Taylor, *Univ. Kans. Sci. Bull.*, 33, I (2) (1949): 176; Reese and Firschein, *Trans. Kans. Acad. Sci.*, 53 (1) (1950): 52; Werler and Smith, *Texas Journ. Sci.*, 4 (4) (1952): 552.

History.—Günther (1858: 102) based his description of *Hyla lichenosa* on ten specimens, seven of which were young or half-grown individuals from Mexico; the other three were noted as "South America, Amazons, America." He failed to designate a type, and I assume that they all represent syntypes. The figured specimen (1858, Pl. 8, Fig. c.) also is not designated. Boulenger (1882b: 366) described *Hyla nigropunctata* on the basis of the seven Mexican syntypes of *lichenosa*, plus two others from the same country. By using Günther's Mexican syntypes of *H. lichenosa* as part of his type series of *H. nigropunctata* Boulenger thus by inference restricted the name *lichenosa* to the South American specimens. The other three syntypes of *H. lichenosa* are listed under *H. venulosa* in Boulenger's catalogue, and he placed *Hyla lichenosa* in part as a synonym of *Hyla venulosa* and in part as a synonym of *Hyla nigropunctata*. Prior to this, however, Cope (1877: 86) had described *Hyla spilomma* from an immature specimen collected at Cosamalapa, Veracruz, by Sumichrast. His description fits the frogs found in eastern Mexico as well as do the descriptions of *Hyla lichenosa* and *Hyla nigropunctata*. Smith and Taylor (1948: 75, footnote 32) explicitly restricted the name *lichenosa* to the South American frogs by designating the specimen listed by Günther from "Amazons" as the lectotype. It was supposedly collected by Bates and was presented to the British Museum (Natural History) by Günther. I have examined this specimen, which has been reregistered under the number BMNH 1936.12.3.119, and find it to be an immature *Phrynohyas zonata*; therefore, *Hyla lichenosa* is, in part, a synonym of both *Phrynohyas spilomma* and *Phrynohyas zonata*, Alice G. C. Grandison compared recent Veracruz specimens with the existing syntypes of *Hyla lichenosa* and *Hyla nigropunctata* and has kindly informed me that they are identical in their diagnostic characters. The same conclusion was reached by Kellogg (1932: 176-77), who examined the syntypes of *H. lichenosa* and *H.*

nigropunctata and considered them conspecific with the species found in Veracruz, which he called *Hyla venulosa*. Of the three names that are applicable in their descriptions to the species occurring in eastern Mexico, the specific name *spilomma* must be applied.

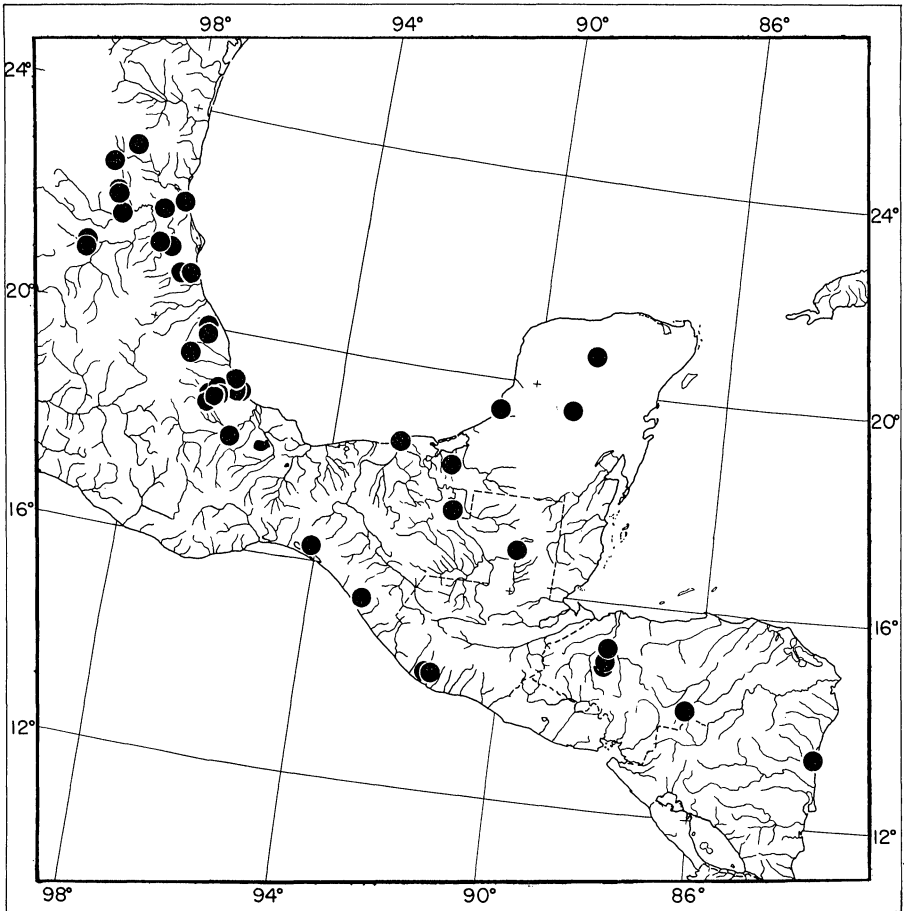
Type.—Apparently lost (*vide* Kellogg). It is not on record in the Academy of Natural Sciences of Philadelphia or in the United States National Museum. According to Cope (1877: 86) it was collected at Cosamaloapam, Veracruz, Mexico, by Francis Sumichrast.

Range.—Savannas and tropical forested areas from sea level to an elevation of 4,000 feet, southern Tamaulipas and San Luis Potosí southward and eastward into the Yucatán Peninsula,¹ through the lowlands of El Petén, Guatemala, and eastern Honduras, terminating in the coastal lowlands of eastern Nicaragua; on the Pacific coast from the Isthmus of Tehuantepec southward along the coastal lowlands of Oaxaca and Chiapas to Guatemala (Map 3).

Description.—This is a medium-sized member of the genus, with an average body length of 68 mm., although a few much larger individuals occur, the largest having a body length of 87 mm. Such large specimens are rare, however, as most adults range from 60 to 75 mm. The legs are rather long, the tibia/body length ratio averaging 47.5 per cent. The head is broader than long; the head width/body length ratio averages 32.5 per cent. The snout is short and blunt. The canthus rostralis is rounded and usually is distinct. The loreal region may be noticeably concave and, therefore, gives the lips a flared appearance, or there may be merely a straight slope from the canthus to the mouth. The nostrils are well separated and are situated near the tip of the snout. There is an abrupt downward slope from the nostrils to the tip of the snout. The eye is large and its diameter is equal to or slightly exceeds its distance from the nostrils. The tympanum is also large and is equal to two-thirds the diameter of the eye. This ratio is not constant, as many females and most juveniles seem to have proportionately smaller tympana. The length of the tympanum is always equal to or greater than the distance of the tympanum from the eye.

There is no tarsal fold. The inner metatarsal tubercle is large and elliptical in shape. The webbing of the foot is well developed; the membrane extends to the base of the distal phalanx (disc) of the first, second, third, and fifth toes and to the base of the penultimate phalanx of the fourth toe. There is little variation in the webbing of the feet; an occasional specimen may have all of the toes webbed to the distal phalanx; in another a toe other than the fourth may possess two free phalanges. The fingers have less webbing than the toes. The web between the thumb and first finger is rudimentary. In most of the specimens examined the other fingers are webbed for approximately one-third their length. In several individuals the membrane extends as far as the middle of the penultimate phalanx of the third digit; in a few, the digits are not webbed for even one-third their length. The subarticular tubercles of the feet are flattened and slightly elliptical

¹Ferrari-Perez (1886) reported two specimens from Teziutlán, Puebla, a record which seems improbable on the basis of altitude alone (6500 feet); the specimens probably originated in the lowlands to the east.



Map 3. Locality records for *Phrynohyas spilomma*.

in shape; those of the hands are round and less flattened. In some individuals the distal subarticular tubercle of the fourth digit of the hand is slightly bifurcated but still round in general shape, so that it appears heart-shaped. The discs of the fingers, slightly smaller than the diameter of the tympanum, are larger than those of the toes.

The number of vomerine teeth ranges from 9 to 22 and averages about 15. They are situated on two transverse projections between the inner nares and at a level with the posterior border of the nares. The ridges may be rather rounded or quite thin and long, the latter condition being the most common. They are usually broadly separated in the mid-line, although occasional specimens show no separation whatsoever. The ridges may be straight, but normally they are somewhat curved, their lateral parts being slightly posterior to the median parts. The internal nares are rather triangular in shape with the inner posterior angle at nearly 90° . The tongue

is thick and either round or slightly elongated. There is a slight notch in the posterior border, which is barely free.

The skin above is pustulate. In young individuals these pustules are round and high and close together, giving a definite warty appearance. In the larger individuals the pustules are flattened and are well developed only on the back. The greatest concentration of pustules is always posterior to the sacrum, and in many individuals none is present elsewhere. Usually, however, they are scattered over the dorsal surface, with a few on the flanks. The skin is granular on the throat, belly, and posteroventral surface of the thighs, but the rest of the ventral surface is smooth. The parotoid glands are well developed. The skin of the head, neck, and shoulder region is thickened by the glandular development, which may extend half-way down the back. There is a heavy fold that extends from the eye to a point above the insertion of the forearm. In many individuals this fold obscures part or all of the tympanum.

Coloration.—Although the coloration varies extensively, there is a general basic pattern. As in most other forms, the limbs are banded. The dorsal pattern consists of a middorsal dark blotch which may extend solidly from the eyelids to the vent, or may be broken up longitudinally or transversely. It may be solid dark brown or grayish brown and outlined with darker brown or black. The dorsal patch may give way posteriorly to fine black spotting, or it may be well defined. The dark transverse limb bands may be solid, or they may be brown outlined with a darker brown, a color which intrudes upon the band as small flecks. The ventral surfaces are usually a cloudy cream, but sometimes may be pure cream. As often as not the venter is speckled with small black dots, and in some individuals there are fine brownish or grayish reticulations on the throat. Bordering the dorsal dark blotch on either side is a reddish brown, yellowish brown, or fawn-colored stripe. This extends from the head, which is the same color as the stripe, and continues to the flank. Behind the eye is another dark band which goes through the tympanum and continues to the axilla. In occasional individuals, however, this stripe stops at the protrusion of the vocal sacs or continues farther posteriorly onto the flanks.

Thirty specimens from the vicinity of La Libertad, Guatemala, may be described as follows: Dorsally the color pattern consists of some form of dark patch extending from the eyelids to the vent. It may be either continuous or broken by a wavy transverse band of ground color. The dorsal patch may be chocolate brown, reddish brown, or grayish brown. The dark markings are superimposed upon a ground color of yellowish tan or pinkish tan. The ground color becomes lighter on the sides, fading to a buff, cream, or white on the belly, throat, and underside of the thighs. There are dark transverse bands on the limbs, usually two on the femur, two on the tibia, and three on the tarsus; there is usually one band on each segment of the forearm. The bands are slightly wider than the interspaces of ground color. In nearly half of the specimens the dorsal patch and dark limb bands are not a solid color, but instead are outlined by a darker color and show a stippled or dashed effect. This is particularly evident on the transverse limb bands. There may be a small dark spot in front of the eye, but usually a dark bar extends from the eye, above the tympanum and vocal sac, to the axilla (Pl. IV, Fig. 2).

In comparison, nine specimens from Potrero Viejo, Veracruz, may be described thus: Dorsally there is a patch of dark brown or blackish extending from the eyelids to the vent. In six individuals this dark patch is split anteriorly by an intervening wide longitudinal stripe of ground color. In two others the patch is nearly separated posteriorly by a transverse intrusion of ground color. In the other individual there is a square of ground color in the sacral region that is completely surrounded by the dark color of the dorsal patch. The dorsal ground color is a light reddish brown to fawn, becoming a dirty cream on the ventral surfaces. There are dark transverse bands on the limbs; these bands are usually slightly wider than the interspaces. All of the bands are brown, but superimposed upon them are small black flecks, giving the limb bands a stippled appearance. All nine specimens have a dark brown band, either solid or stippled, extending from the eye to the axilla. In five of the specimens this band extends onto the flanks. Five individuals are spotted posteriorly on the flanks, three have the ventral surfaces of the thighs spotted with black, and two are heavily spotted over the entire ventral surface (Pl. IV, Fig. 1).

Variation.—In color pattern the specimens from the Yucatán Peninsula most closely resemble those from La Libertad, Guatemala, Honduras, and Nicaragua. None of these shows any ventral spotting, a character which seems to be more prevalent in central Veracruz, but even there it is absent as often as present. The west coast specimens most closely resemble those from Veracruz, but lack the black stippling on the belly, although some have the brown throat reticulations, again a character that is most prevalent in individuals from central Veracruz. In color and pattern individuals from San Luis Potosí and Tamaulipas closely approach the ones from central Veracruz.

TABLE IV
SUMMARY OF MEASUREMENTS AND PROPORTIONS
OF 194 ADULT *PHRYNOHYAS SPILOMMA*

Character	Mean		$\pm 2\overline{\sigma}_x$		Range	
	♂	♀	♂	♀	♂	♀
Number of specimens	109	85	109	85	109	85
Body length	68.7	67.7	1.33	1.97	48.0-87.0	56.0-86.5
Tibia length	32.8	32.6	.61	.64	22.5-40.0	27.0-41.0
Per cent tibia/body length	47.8	47.7	.32	.44	44.1-51.6	42.9-52.5
Foot length	27.9	27.8	.52	.58	19.0-35.0	22.5-34.5
Head length	20.7	20.7	.36	.43	16.0-26.0	16.5-27.0
Per cent head/body length	30.1	30.4	.23	.28	27.9-33.3	27.0-33.1
Head width	22.2	22.3	.38	.41	16.0-27.0	19.0-27.0
Per cent head width/body length	32.4	32.6	.27	.33	29.1-36.4	29.2-36.0
Interorbital distance	6.1	6.1	.06	.15	4.0- 8.0	5.0- 7.5
Per cent interorbital/head width	27.5	27.3	.43	.53	23.8-33.3	22.2-34.3
Internarial distance	4.9	4.9	.10	.10	3.5- 6.5	3.5- 6.0
Per cent internarial/head width	22.0	21.9	.30	.37	19.1-26.1	18.2-26.3
Tympanum length	4.3	4.1	.09	.09	3.0- 6.0	3.5- 5.5
Per cent tympanum/head length	20.6	20.0	.32	.37	16.7-27.3	15.9-23.9
Vomerine teeth	14.6	16.0	.51	.41	9-22	10-22

There is also considerable variation in the measurements and proportions of the specimens examined (Table IV); however, no definite trend in the variation of any one character or combination of characters has been detected. For example, the average number of vomerine teeth in adult males from Honduras is 18, the same as for those from Tamaulipas. Those from La Libertad, Guatemala, the Yucatán Peninsula, and San Luis Potosí average 15; those from central Veracruz average 13. Likewise, the lowest tibia/body length ratio is found in specimens from Honduras and San Luis Potosí; the ratios in specimens from Guatemala, Yucatán, Veracruz, and Tamaulipas are close to one another but slightly higher than those from Honduras and San Luis Potosí. The largest specimens are from San Luis Potosí and Yucatán. Those from La Libertad, Guatemala, average slightly larger than those from Veracruz and Honduras, but are much smaller than those from Yucatán.

Growth and sexual dimorphism.—This is the only species of the genus for which there is sufficient material to justify statistical analysis. All of the measurements, counts, and proportions were compared for the two sexes, and only in the number of vomerine teeth was there found to be a significant difference (at the 95 per cent level); the females have an average count of 16.1 and the males 14.6.

There is a definite ontogenetic change in tibia/body length ratio. Only in the small adults and juveniles does the tibia exceed 50 per cent of the body length (Fig. 9). As mentioned previously, the pustules on the dorsum are much more evident in juvenile specimens, in which they are high, round, and close together, presenting a definitely warty appearance.

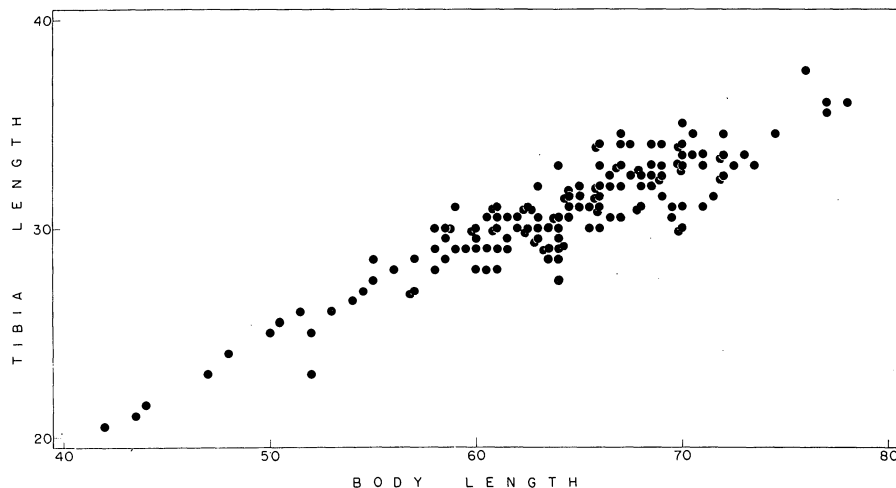


Fig. 9. Body length plotted against tibia length (in mm.) for 147 *Phrynohyas spilomma* from central Veracruz, Mexico.

Remarks.—This is one of the few forms of the genus for which there is information concerning habits and habitat. Taylor and Smith (1945: 594) told of finding this species in bromeliads and banana plants during the dry season, and Smith (1941: 38) said it was commonly found in bromeliads. A series from Potrero Viejo, Veracruz, was taken from banana plants in March, 1949. Dr. Archie Carr (*in litt.*) stated that he had found *P. spilomma* in Honduras in mesic woodlands of edaphic origin—the gallery forests such as river fringe woodland and ravine forest. Stuart (1935: 39) found this species in patches of bushes on the savannas in El Petén, Guatemala, after the first rains of the season, and later at breeding pools there. The one specimen from the Pacific Coast of Guatemala was found about ten feet above the ground in a palm tree. Dr. Walter Dalquest, who collected many of the specimens that are now in the collection of the University of Kansas, stated (*in litt.*):

P. spilomma is rarely found on the ground or level, except for the horizontal leaves of bananas or other plants. At night one usually finds them on vertical surfaces of trees, cliffs, or buildings, and usually less than ten feet above the ground. . . . In the daytime they hide on a vertical surface and under cover. I found most of my specimens under the loose, outer leaves of banana trees, and especially the red banana, Platino morado, as it is called in Veracruz. I also found the frog common in the tufts of thread-like roots suspended from the ends of the aerial roots of *Ficus*. I have also found them under loose pieces of bark, under roofing tiles when these are almost vertical, in caves and crevices, under layers of moss on cliffs, in bromeliads, and in similar places. The hiding places are always dark, damp, and with vertical or almost vertical walls. . . . It is quite a solitary species. Usually one finds only one frog in a certain daytime hiding spot, and almost always they are alone at night. . . . The general habitat of this species is the tropical forest. In Veracruz they are most abundant at 1700 to 4000 feet elevation, but along rivers where there are woods, they go down to sea level.

Dalquest also stated that *Smilisca baudini* is almost always found with *P. spilomma*.

Near La Libertad, Guatemala, Stuart found *P. spilomma* breeding on June 1, 1933; previous to that date he collected specimens from trees at the same locality. Two transforming individuals were also found there on July 8. One specimen with a rudimentary tail has an over-all length of 31 mm., with a body length of 15 mm. The other individual has a body length of 14 mm. Dalquest (*in litt.*) stated that in Veracruz *P. spilomma* comes to the breeding pools late in the season. Bryce C. Brown found the species calling at dusk from the main lower branches of strangler figs along a river bank near Valles, San Luis Potosí, on June 24, 1942. The males collected during the breeding season have well-developed horny rugosities on the pollex. The vocal sacs are very distended and when filled, they extend laterally and dorsally.

The volatile, poisonous secretion of this species has been noticed in particular. The secretion appears first on the nape as a white slime; if the frog is irritated, the fluid is secreted from the entire back but always more profusely from the nape. Reports from various collectors indicate that the secretion produces effects very much like hay fever, causing a severe irritation of the mucous membranes of the eyes and nose. Sometimes temporary blindness may result. Certain people have developed a rash after handling these frogs. Smith (1941: 38) stated:

When picked up these frogs (*P. spilomma*) invariably secreted a white, viscous substance that quickly came off on our hands and dried. Our relation with them did not end as they were placed in the bag, for the secretion on our hands, finding its way after a time to our nostrils, caused a violent catarrh lasting four or five hours. Some of the men with us became so sensitive to these secretions that they began to sneeze as soon as they became within a few feet of the frogs. This peculiar, poisonous characteristic accounts for the fact that our collection contains few of the offending species, even though we found many of them. Not only did the frogs themselves make our lives miserable, while we collected and carried them in the field, but the very sacks in which they were carried could not be used again for several days without causing violent sneezing and much blowing of the nose.

Unfortunately, the peculiar volatile poison has never been analyzed chemically.

Affinities.—Doubtless this frog is closely related to *P. modesta*, from which it differs primarily in coloration. The relationship of *P. spilomma* with *P. zonata* is not certain; they are very similar in their general color pattern.

Specimens examined.—298, as follows:

GUATEMALA: *El Petén*: La Libertad—CNHM 27082-3, MCZ 21457, UMMZ 75301-9 (28), 75336 (2), USNM 25141-2; *Retalhuleu*: Hacienda Casa Blanca—UMMZ 107996; Caballo Blanco—CNHM 1813.

HONDURAS: *Comayagua*: La Misión, 3-1/2 mi. N. Siquatepeque—AMNH 54910, MCZ 26426; 8 km. above La Misión—MCZ 26450; *Cortez*: Rancho Agua Azul—AMNH 54915-6; El Paraiso, Valle de Jamastran—AMNH 54799.

MEXICO: *Campeche*: Becan—UMMZ 76116; Champoton—MCZ 21450, UMMZ 73170-1 (4); Tres Brazos—EHT-HMS 12694, UI 25373; *Chiapas*: Lake near Acacoyagua—USNM 115020; *Oaxaca*: Tepanatepec—MCZ 15771-3; *San Luis Potosí*: Pujal—LSUMZ 531; 1 km. E. Naranjo—UMMZ 107997-8; Río Coy near Pujal—USNM 114979; Tamazunchale—UMMZ 80954; 4 km. N. Tamazunchale—UMMZ 104040; 8 mi. S. Valles—BCB 6011-7; 10 mi. S. Valles—AMNH 52954; *Tabasco*: Frontera—BMNH 1901.12.19.57-9; Tenosique—USNM 115009; *Tamaulipas*: Río Sabinas, + 5 mi. NE. Gómez Farías—UMMZ 104096; Tampico—BMNH 1901.12.19.48-52; *Veracruz*: 5 km. SW. Boca del Río—UI 25079, 28083-6; Cordoba—USNM 38264, 38303; Cuautlapam—EHT-HMS 24664-5, UI 25376, UK 25942-92, UMMZ 85460-3 (50); Hacienda El Potrero—MCZ 24738-9; Jalapa—BMNH 81.10.31.20 (syntype of *Hyla nigropunctata*); La Laja—UI 3627-46, 3648-9; 4 mi. W. Martínez de la Torre on Nautla-Tezuitlan Rd.—UI 3650; Misantla—BMNH 1901.12.19.53-6 (5); Panuco—MCZ 9761; Paraje Nuevo—UMMZ 85459, 85464 (15); Paso del Macho—UMMZ 88796 (4); Potrero Viejo—CNHM 38663, UI 25374-5, UK 25920, 25922-8, 25941, UMMZ 88797 (5), 88798, 89283 (7), 102061 (10); Rodríguez Clara—EHT-HMS 1430; Tierra Colorado—EHT-HMS 1426, UI 25372; Toxtlacuaya—EHT-HMS 1427, 1429; Veracruz—AMNH 6300; *Yucatán*: Chichén Itzá—CNHM 26929-33, 36558, UMMZ 83914 (2).

NICARAGUA: *Bluefields*: Wounta Haulover—ANSP 15430.

Phrynohyas zonata (Spix)

Hyla zonata Spix, *Species novae test. et ranarum*, 1824, p. 41, Pl. 12, Fig. 1; Peters, *Akad. Wiss. Berlin*, 1872a, p. 219.

Hyla bufonia Spix, *op. cit.*, 1824, p. 42, Pl. 12, Fig. 2; Peters, 1872a, *op. cit.*

Hyla venulosa, Duméril and Bibron, *Erpétologie générale*, 8 (1841): 560-63; Guichenot, *Animaux nouveaux*, 1855, p. 84; Lichtenstein, *Nomenc. Rept. et Amphib.*, 1856, p. 37; Günther, *Cat. Batr. Sal.*, 1858, p. 104; Steindachner, *Novara-exped.*, Zool. Theil., Bd. I (1867), Amphib., pp. 58-59; Peters, *Akad. Wiss. Berlin*, 1872b, p. 771; Boulenger, *Cat. Batr. Sal.*, 1882b, pp. 364-65; Boettger, *Kat. Batr. Mus. Senck. Naturf. Gesell.*, 1892, p. 40; Boulenger, *Ann. Mus. Genova*, 19 (2) (1898b): 133; Stejneger, *Proc. U. S. Nat. Mus.*, 24 (1248) (1901): 180; Peracca, *Bol. Mus. Zool. Anat. Univ. Torino*, 19 (465) (1904): 37; Baumann, *Zool. Jahrb.*, 33 (2) (1912): 103-5; Proctor, *Ann. and Mag. Nat. Hist.*, 8 (7) (1921): 189-92; Nieden, *Das Tierreich - Anura*, I (1923): 244-45; Mirando-

- Ribeiro, *Gymnobatrachios (Anura) Brasileiros*, 1926, pp. 76-77, Fig. 43; Cott, *Proc. Zool. Soc. London*, 1926, pp. 1164-68, Pl. 4; Roux, *Ann. Soc. Zool. Suisse*, 33 (4) (1926): 97; Lutz, *Mem. Oswaldo Cruz*, 20 (1) (1927): 64-65; Maria, *Rev. Soc. Colombiana Cien. Nat.*, IV (105)(1930): 53, *ibid.*, (106): 104; Parker, *Trop. Agric.*, 10 (1) (1933): 6; Santos, *Anfíbios e Répteis do Brasil*, 1942, pp. 102-4, Figs. 29-30; Beebe, *Zoologica*, 37 (13) (1952): 174; Lutz and Kloss, *Mem. Inst. Oswaldo Cruz*, 50 (1952): 655-57; Cochran, *Bull. U. S. Nat. Mus.*, 206 (1955): 62.
- Hyla vermiculata* Duméril and Bibron, *Erpétologie générale*, 8 (1841): 563.
- Phrynohyas* (= *Hyla zonata*) Fitzinger, *Systema reptilium*, 1843, p. 30.
- Hyla lichenosa* Günther, *Cat. Batr. Sal.*, 1858, p. 102, Pl. VIII, Fig. c; Brocchi, *Miss. Sci. Mex. et Amer. Cent.*, 3 (2) (1881): 33.
- Scytopus venulosus*, Cope, *Journ. Acad. Nat. Sci. Phila.*, new ed., 6, Pt. I (2) (1866): 85; Cope, *Bull. U. S. Nat. Mus.*, 32 (1887a): 12.
- Hyla coriacea* Peters, *Akad. Wiss. Berlin*, 1867, p. 711; Boulenger, *Cat. Batr. Sal.*, 1882b, p. 367; Mole and Urich, *Journ. Trinidad Field Nat. Club*, 2 (3) (1894): 89; Nieden, *Das Tierreich - Anura*, I (1923): 309.
- ? *Hyla pardalis*, (non Spix) Garman, *Bull. Essex Instit.*, 19 (1887): 16.
- Hyla resinificatrix* Goeldi, *Proc. Zool. Soc. London*, 1907, pp. 135-40, Figs. 56-59; Baumann, *Zool. Jahrb.*, 33 (2) (1912): 105-7, Pl. 4, Fig. 4; Nieden, *Das Tierreich - Anura*, I (1923): 303.
- Acrodytes venulosa*, Taylor, *Univ. Kans. Sci. Bull.*, 35, Pt. I (5) (1952): 799-801.

History.—The paucity of material from the vast reaches of tropical South America and the wide variation displayed by the existing specimens pose a vexatious problem for the systematist. The great amount of variation is reflected in the number of names that have been proposed by earlier workers. The synonymy shows that no fewer than six specific names have been attributed to different variants of "*Hyla venulosa*" in tropical South America.

The variation shown by the specimens included under the name *Phrynohyas zonata* is as great as that displayed by all the other members of the genus. Only the southernmost specimens from South America — Minas Gerais in Brazil, Paraguay, and Argentina — and those from the Maracaibo Basin of Venezuela possess sufficiently stable characters to entitle them to consideration as specific taxonomic units. To the former the name *P. hebes* (*Scytopus hebes* Cope, 1862) has been applied, and for the latter the name *P. ingens* has been proposed. Spix's specific name *zonata* has been used for the remaining specimens from South America, because it is the earliest available name with an accompanying description which adequately applies to the majority of the specimens examined. Spix's plate (bearing the name *Hyla zonalis*) is typical of the frogs from the Amazon Basin of Brazil, the region from which he obtained his material.

Doubtless there is more than one form represented in the material here lumped under one name, but in working with such a small amount of preserved material it has not been possible to delimit the variants; therefore, the various names that have been proposed and their possible application to the frogs in question will be discussed.

Hyla bufonia was described by Spix in 1824 from *Ecga* (= *Eca*), Amazonas, Brazil. This locality is near the Rio Teffé where it empties into the Rio Solimões. Specimens resembling the description and plate of *Hyla bufonia* are found in the upper Amazon Basin in Bolivia, Peru, and Brazil. Typical *P. zonata* are found in the same localities, and intermediate specimens are also found there.

Hyla vermiculata Duméril and Bibron was based upon a single specimen given to the authors by Harlan. Duméril and Bibron believed it to be a North American form (*Erpétologie générale*, 8: 563). Jean Guibé has examined the type of this species (Museum National d'Histoire Naturelle, No. 4797), and from his description, added to that given by Duméril and Bibron, it is most likely that the frog came from eastern Venezuela or the Guianas, since several specimens from that area show characteristics that are essentially those of *Hyla vermiculata*.

Günther described *Hyla lichenosa* from several juvenile specimens, one of which is from Amazonas, Brazil (BMNH 1936.12.3.119), and has been designated as the lectotype for that name by Smith and Taylor (1948: 75, footnote 32).

Hyla coriacea of Peters appears to have been based upon a rather faded specimen of "*Hyla vermiculata*" Duméril and Bibron. I have examined only one specimen that was previously designated as *H. coriacea* (BMNH 70.3.10.69 from Surinam). It is so poorly preserved that the color characters are unusable. For the time being the name should be considered a synonym of *P. zonata*.

Goeldi described *Hyla resinificatrix* from Pará, Brazil, principally upon his assumption that these frogs were unique in building "nests" in hollow trees. This fact has never again been demonstrated.² Since nothing is known of the breeding habits of *P. zonata*, and since *H. resinificatrix* is morphologically identical with *P. zonata*, they should be considered the same species.

Type.—Originally deposited in the Munich Museum but now apparently lost. Dr. Cochran informed me that although she examined many Spix types at Munich, that of *Hyla zonata* was not among them. Dr. Hellmich informed me that he does not know the type. The type locality was given as "*in arbustis et arboribus ad flumen Teffé*," and is here restricted to Lago Teffé at the mouth of the Rio Teffé, where it empties into the Rio Solimões, Amazonas, Brazil.

Range.—The Pacific coastal lowlands from Costa Rica southward through Panamá and along the coast of Venezuela and Colombia, the Río Magdalena drainage of Colombia, the islands of Trinidad and Tobago, B.W.I. It ranges also into the Orinoco Basin, the Guianas, and the Amazon Basin as far west as southern Colombia and Ecuador and south into Bolivia and Mato Grosso, Brazil (Map 1). A specimen has recently been found on the Pacific coast of Ecuador.

Description.—The following discussion is based upon specimens that are here considered to be typical *Phrynohyas zonata* from the lower Amazon Basin. In this moderate- to large-sized species the males average 69.3 mm. in body length and the females average 74.9 mm. The tibia/body length ratio averages 46.6 per cent. The head is relatively narrow, and the snout is blunt but rather rounded. The nostrils are widely separated, and the canthus rostralis is distinct and rounded; the loreal region is slightly concave, and the upper lips are flared. The tympanum is large,

²Vellard (1948: 150) mentioned that "*Hyla venulosa*" takes refuge in cavities in trees in the Argentine Chaco.

being equal to one-half to two-thirds the diameter of the eye, from which it is separated by a distance less than the diameter of the tympanum. The diameter of the eye is equal to its distance from the nostril. There is no tarsal fold; the inner metatarsal tubercle is large and elliptical, the proximal end being very blunt, the distal more pointed. The subarticular tubercles are hemispherical, except for the distal tubercles of the fourth finger and fifth toe, which are flattened and may be bifurcate. There is a rudimentary web between the first two digits of the hand, but the other digits are webbed for nearly half of their length, the membrane extending to the distal subarticular tubercle of the third digit. The toes are webbed to the base of the disc, except for the fourth toe, which is enclosed only to the distal subarticular tubercle. The skin of the head and shoulder region is thickened by the well-developed parotoid glands. These form heavy ridges from the posterior edge of the eye above the tympanum and down to a point above the position of the vocal sacs. The heavy ridge often conceals part of the tympanum. There are pustules scattered over the dorsum; the skin of the belly and throat is highly granular. The vomerine teeth range from 12 to 24 and average 16.7. They are situated on rather stout, highly projecting ridges between the inner nares. These are normally widely separated medially, but in some individuals they are only narrowly separated or are in contact. The tongue is heart-shaped and only slightly free behind.

Coloration.—There is a dark brown to blackish dorsal patch beginning on the eyelids and extending for the length of the body. Posteriorly, it extends onto the flanks, and it may be broken by patches of lighter ground color. The snout is a lighter brown. Extending posteriorly and laterally along the sides of the dorsal dark patch are lighter brown bands beginning on the eyelids and passing onto the flanks. There is a dark bar extending from the eye through the tympanum and to the axilla. The width of the dark, transverse limb bands is approximately equal to the width of the lighter interspaces. The bands are outlined with a still darker brown. There may be dashes or a network of darker color in the interspaces. The ventral surfaces are a dirty cream; the vocal sacs are grayish brown to dark brown.

Through the courtesy of James A. Peters I was able to examine a living specimen of this species which he collected at Hacienda San Miguel, Milagro, Guayas Province, Ecuador. The specimen, a large adult male, had a dorsal ground color of golden brown; the dorsal dark patch was light chocolate brown tending toward a dark chocolate brown on the edges. The ground color of the limbs was somewhat darker than that of the dorsum; the transverse limb bands were dark chocolate brown. A dark brown postorbital bar reached the axilla. The throat was cream, and the belly, a dirty cream. The tympanum was golden brown; iris flecked with golden.

Variation.—The only large series of this species available is from Trinidad, and the variation in measurements and proportions in this series is given in Table V.

The frogs on the Caribbean coast and on the islands of Trinidad and Tobago are essentially the same as those from the Amazon Basin (Pl. V, Fig. 1). Some of the individuals from the Guianas and Trinidad have the

dorsal dark patch narrowed, especially anteriorly. This condition is most extreme in certain individuals from Costa Rica and Panamá, in which the dorsal patch is narrowed until it is only a longitudinal line (Pl. V, Fig. 2). These frogs also have a lighter ground color, yellowish tan to pinkish tan. They average larger in body length, 79.3 mm., and the tibia/body length ratio is higher, 49.1 per cent. The average number of vomerine teeth is 19.6. These frogs possibly represent an undescribed subspecies, but until additional material is available not only from Costa Rica and Panamá, but also from Colombia, their systematic status cannot be determined.

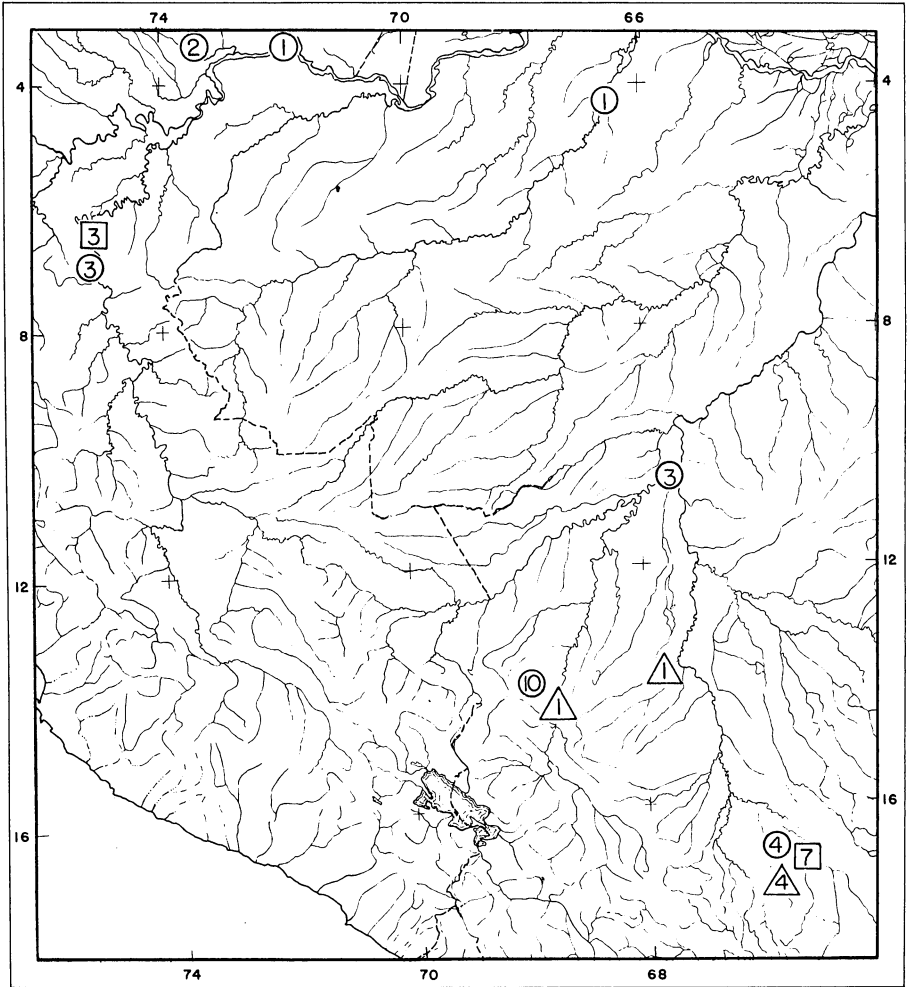
TABLE V
SUMMARY OF MEASUREMENTS AND PROPORTIONS
OF THIRTY-ONE ADULT *PHRYNOHYAS ZONATA* FROM TRINIDAD, B.W.I.

Character	Mean		$+2\sigma_x$		Range	
	♂	♀	♂	♀	♂	♀
Number of specimens	25	6	25	6	25	6
Body length	74.9	67.8	1.34	-	67.0-82.0	65.0-72.5
Tibia length	36.0	33.9	.53	-	33.0-38.5	32.5-36.0
Per cent tibia/body length	48.1	50.1	.50	-	45.7-49.7	46.9-52.9
Foot length	29.8	27.8	.62	-	27.0-33.0	26.0-29.0
Head length	22.4	20.1	.45	-	21.0-25.0	19.5-21.0
Per cent head/body length	29.9	29.6	.45	-	28.0-32.1	27.5-31.5
Head width	23.2	20.7	.52	-	21.0-26.5	19.5-21.5
Per cent head width/body length	31.0	30.5	.46	-	29.2-33.6	29.0-31.6
Interorbital distance	6.7	5.8	.22	-	5.5- 8.0	5.0- 6.0
Per cent interorbital/head width	28.9	28.3	.65	-	25.0-31.8	24.4-30.8
Internarial distance	5.3	4.8	.16	-	4.5- 6.0	4.0- 5.0
Per cent internarial/head width	22.7	23.0	.53	-	20.8-26.1	19.5-24.4
Tympanum length	4.8	4.2	.18	-	4.0- 6.0	4.0- 4.5
Per cent tympanum/head length	21.5	20.7	.69	-	17.4-24.0	19.0-23.1
Vomerine teeth	16.1	15.7	1.14	-	12-20	13-18

Six specimens from Caicara, Venezuela, and four others from scattered localities in Venezuela and the Guianas are here considered to be what Duméril and Bibron described as *Hyla vermiculata*. These are relatively smaller frogs than the typical *P. zonata* and are distinguished by the vermiculated condition of the dorsal patch and transverse limb bands (Pl. VI, Fig. 2). Intermediate specimens from the Guianas and Venezuela indicate that *vermiculata* may be only a color phase of *P. zonata*, although extensive series might establish their specific identity. Since typical *P. zonata* has been collected with *P. vermiculata* the latter cannot be considered a subspecies of that form.

The most striking variant is a smaller, brown form with its center of distribution in the upper Amazon Basin. This is probably what Spix described as *Hyla bufonia*. In nearly every character it is distinct from *P. zonata*, yet several specimens are intermediate. Since typical *zonata* has been taken with this brown form, they cannot be considered as two subspecies (Map 4). They are thus considered as variants. This smaller frog is characterized by a slightly more pointed snout, a larger tympanum,

and a lower number of vomerine teeth than has typical *P. zonata* in the lower Amazon Basin. The dorsum is unicolor tawny brown, and the venter is cream. On the flanks are fine black vermiculations, which often extend onto the thighs (Pl. VI, Fig. 1).



Map 4. Distributional records of two color varieties of *Phrynohyas zonata* in the upper Amazon Basin. Circles = small brown variety, squares = typical *zonata*, triangles = intermediate specimens; numbers in symbols refer to the number of specimens of each type from that locality.

Remarks.—Information concerning the habits and habitat of this species was supplied by Mr. Edwin H. McConkey, who collected a large series on Trinidad. On April 26, 1952, and again on June 10, he heard them calling in a shallow ditch. Only one clasping pair was found. McConkey described

the voice as a deep moan when heard at a distance, but the voice of a single individual singing close by sounded more like the bleating of a sheep. *Ela-chistocleis ovale* was found chorusing with *P. zonata*. Kloss (in Lutz and Kloss, 1952: 656) stated: "*Hyla venulosa* [= *Phrynohyas zonata*] seems quite frequent on the Upper Amazonas and the Itacoai. They are called 'boatman frogs' because their croaks imitate the tapping of the oars against the side of the canoes, which are used by the Indians to maintain the rhythm of the stroke when rowing. . . Our three specimens were all collected at night on branches of trees on the banks of a small stream."

This species has well-developed parotoid glands. McConkey (*in litt.*) related his experiences with their secretion: "The secretion is very heavy. The bag in which I collected the twenty was stiff as a board a day or so later when the stuff had time to dry. It is white and sticky when fresh, and if there is a lot of it, gives you the urge to sneeze, even though you do not get closer than two feet to it." Kloss (1952: 656) stated: "When seized they [*P. zonata*] release a milky secretion all over the body which becomes brown after drying and is very difficult to remove. I passed a hand over an eye while some of this secretion was sticking to my hands. Ten minutes later the eye was inflamed and I was unable to see. This continued all night and was followed the next day by a terrific headache." Vellard (1948: 150), however, stated that the formidable cutaneous secretion from these frogs lines the cavities in trees where "*Hyla venulosa*" seeks refuge and is valued by quack doctors for the curing of headaches and neuralgia!

Affinities.—*Phrynohyas zonata* is here considered to be composed of several varieties, the relationships of which are obscure. The typical form found in the Amazon Basin and along the Caribbean coast of South America has differentiated slightly on the Pacific coast of lower Central America, giving rise to a population that may be worthy of subspecific designation. The small, vermiculated form in Venezuela and the Guianas and the small, unicolor form in the upper Amazon Basin may represent distinct species, but at the present time there is too little material to justify such conclusions. Lying adjacent to the range of *P. zonata* are *P. hebes* and *P. ingens*. The former quite likely is only a subspecies of *P. zonata*, whereas the latter certainly appears to be specifically distinct.

Specimens examined.—175, as follows:

BOLIVA: *Beni*: Esperanza—BMNH 1920.11.29.15-16; *La Paz*: Ixiamas—MCZ 10087, UMMZ 57529 (4), 57530 (3); Rurrenabaque—UMMZ 57528, 57531 (2); Santa Ana de Movimas—BMNH 98.6.9.38; *Santa Cruz*: Buenavista—BMNH 1927.8.1.85-6, CM 2582, 3828, 3892, 3971, 3974, 3986, 4467-8, UMMZ 60526, 63960 (2), 66559-60; Santa Cruz—BMNH 1904.10.29.177, 1907.10.31.72, 1927.8.1.87, CM 2514.

BRAZIL: San Goncallo—MCZ 1531; *Amazonas*: BMNH RR1936.12.3.119 (lectotype of *Hyla lichenosa*); Lower Amazonia—USNM 28926-7; Manaus—AMNH 51755, UMMZ 66647; Rio Jurua—BMNH 1904.11.4.12; Santarem—BMNH 56.3.25.14 (2); *Mato Grosso*: Barra do Tapiripe, Rio Araguaya—SU 12304-12; Chapada nr. Cuyaba—BMNH 1903.3.26.54-6; San Luis de Caceres—SU 12298-9; Villa Murinho—UMMZ 56770; *Minas Gerais*: Manga Rio São Francisco—UMMZ 108894; *Pará*: Belem—SU 12390-3; Bosqus—BMNH 1926.5.26.4; Liveramento—SU 12383-7; Marajo Island—BMNH 1923.11.9.26; *Pará*—BMNH 45.8.25.143, 96.1.7.2; *Pernambuco*: BMNH 58.11.28.48; Bonita—MCZ 4998.

BRITISH GUIANA: Better Hope—BMNH 80.11.22.5-6; Georgetown—MCZ 2618, UMMZ 80495; Kaieteur—AMNH 23128; Santa Rosa Island, Moruka River—UMMZ 55834.

BRITISH WEST INDIES: *Tobago*: Milford Bay—MCZ 4087; Whim—BMNH 1926.1.19.1; *Trinidad*: CNHM 41683, MCZ 3517, 5971; Oarino River—BMNH 1929.11.25.4; Churchill-Roosevelt Highway—AMNH 55712-5 (16), 55717-9 (6); Fyzabad—BMNH 1929.11.25.5-6; Imp. Coll. Trop. Agric.—BMNH 1932.9.16.41; Mt. Harris—CNHM 49701; Mt. Tabor—CM 5257; St. Augustine—AMNH 55716.

COLOMBIA: *Caqueta*: Morelia—ANSP 25313; *Cundinamarca*: Honda—ILS 1-2; *Magdalena*: Barranquilla—ILS 3; Fundación—UMMZ 48263; *Norte de Santander*: Río Zulia N. of Cucuta—ILS 4.

COSTA RICA: Bebedero—BMNH 94.11.15.31; Las Huecas, Guanacaste, Nicoya Peninsula—UMMZ 71211; Palmar—UK 31862-3.

ECUADOR: USNM 14054; *Guayas*: Hac. San Miguel, Milagro—James A. Peters; *Napo-Pastaza*: Montalvo, Río Bobonaza—SU 10318-9.

FRENCH GUIANA: Cayenne—BMNH 53.2.4.89-90.

NICARAGUA: USNM 13975-6.

PANAMA: Punta Paitilla—MCZ 10160; Tapia—AMNH 18927; *Coclé*: Santa Clara—CNHM 57535; *Canal Zone*: MCZ 15283; Ancon—ANSP 23154; La Pita—MCZ 17377; Río Chagres, Madden Dam—SU 9743.

PERU: *Ucayali*: Orellana—USNM 127168-9, 127180; Pevas—SU 12622; Río Ucayali—CNHM 3562, UMMZ 48210; Roabaya—AMNH 43316, 43534.

SURINAM: BMNH 70.3.10.68-9, USNM 14618; Paramaribo—AMNH 4009, ANSP 2161-70, BMNH 1946.4.2.24-5, MCZ 7662, USNM 13820-1.

VENEZUELA: Las Canales—USNM 128792; *Amzatequi*: Carapa—USNM 80612; *Aragua*: Maracay—EHT-HMS F1383; *Distrito Federal*: La Guaira—USNM 22545, 27797; *Monagas*: Caicara—AMNH 16904-6, 16911-12, USNM 36377.

Through the courtesy of Dr. Walter Hellmich I have had available the data and photographs of two other specimens: Munich Museum 23/1924 — Brazil, Amazonas, Manacapurú on the Rio Solimões, and Munich Museum 120/1911 — Brazil, Pará, Cachoeira on Marajo Island.

DISCUSSION OF THE RELATIONSHIPS OF THE SPECIES

The various species described above can be segregated into different groupings on the basis of several characters. *P. spilomma* and *P. modesta* are similar in most of their morphological characters, but differ considerably in color pattern, *modesta* showing a reduction. As stated previously, *P. zonata* and *P. hebes* are similar in many respects and may be subspecifically related. That *P. spilomma* and *P. zonata* are not too distantly related is shown by their similar color pattern and development of the parotoid glands. They occupy separate ranges, one in northern Central America and Mexico, and the other in extreme lower Central America and South America. Possibly they differentiated at the time of the conjectured open sea portal in lower Central America in Miocene or Pliocene time. *P. ingens* probably differentiated from a stock resembling *zonata* through isolation in the Maracaibo Basin, whereas *P. inflata* possibly diverged from an early *spilomma* stock and became isolated on the narrow Pacific lowlands of Mexico, where it gave rise to *P. latifasciata* in the northern part of its range. My idea of the relationships of the species of *Phrynohyas* is given in Figure 10.

The origin of the group still remains a problem. I consider the paired, lateral vocal sacs behind the angles of the jaws in the males to be an advanced specialization. To determine the affinities of the genus, it is necessary to take into consideration the other known hylids with similarly situated vocal sacs. The frogs of the genus *Trachycephalus* are most

similar to *Phrynohyas*. These frogs possess paired, lateral vocal sacs that are essentially the same as those of *Phrynohyas*. There is a slight gular extension of the sacs, however, which may indicate that *Trachycephalus* is closer to the frogs with paired gular vocal sacs. *Trachycephalus* also has well-developed parotoid glands. On the basis of these characters I believe that *Phrynohyas* and *Trachycephalus* evolved from a common ancestral stock; *Trachycephalus* developed a casque head, *Phrynohyas* did not. Because the development of the casque head changes with ontogeny and shows sexual dimorphism, the disposition of the vocal sacs seems to be a more stable character in determining relationships.

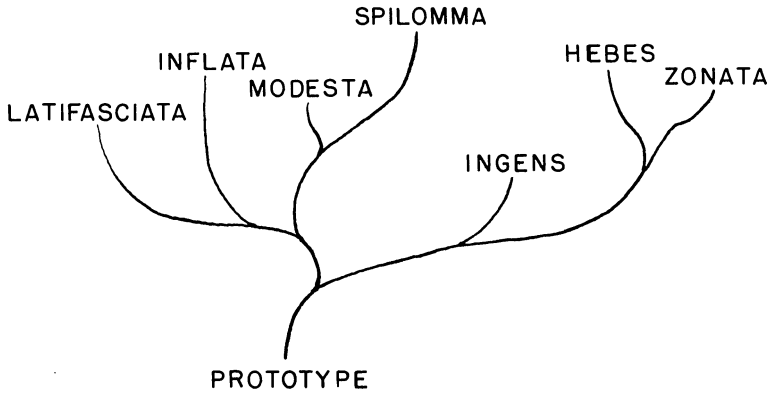


Fig. 10. Relationships of the various species of *Phrynohyas*.

The ancestral stock may have had paired subgular vocal sacs much like those found in *Smilisca*. It is doubtful that *Smilisca* is related to this ancestral stock. *Smilisca* has a frontoparietal fontanelle, a bony squamosal-maxillary arch, small nasals not meeting in the mid-line, and a postorbital extension of the frontoparietal. All of these characters are unlike those in *Phrynohyas*.

KEY TO THE IDENTIFICATION OF ADULT *PHRYNOHYAS*

- 1. Dorsal ground color brown; no darker central patch 2
 Dorsal color not uniform brown; usually some form of a darker central patch with lighter dorsolateral bands; limbs with transverse bands 4
- 2. Large; females attaining a length of 110 mm.; skin of dorsum thick and glandular *ingens*
 Smaller; skin of dorsum less glandular and thinner 3
- 3. Usually many scattered, small black dots on dorsum and upper surfaces of thighs *modesta*
 Upper surfaces uniform brown; no black dots; fine reticulations on flanks . . . *zonata*

4. Usually one continuous dark patch (wide or narrow) from the eyelids or occiput to vent; transverse limb bands not more than twice the width of the interspaces. . . . 5
Dorsal dark patch interrupted by a transverse band of ground color; limb bands more or less than twice the width of the interspaces 7
5. A light tan or cream band from the upper eyelids onto the flanks; interspaces between solid transverse limb bands with dark dashes or dots *hebes*
Dorsal color pattern not as above, or if so, no dark dashes in the interspaces between limb bands. 6
6. Some form of dark patch on dorsum bordered on either side by a lighter color; limb bands usually outlined with a darker color (Costa Rica southward). . . . *zonata*
As above, but limb bands solid, or if outlined with a darker color, they are stippled with the same color (Mexico and northern Central America). *spilomma*
7. Size large; an anterior dark patch separated from a posterior one by a band of ground color in the sacral region; tympanum small *inflata*
Size smaller; anterior dark patch broken into two or more smaller spots; limb bands three times the width of the interspaces *latifasciata*

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PLATE I

Fig. 1. Copy of the figure upon which the description of *Rana venulosa* was based (Seba, 1734, Vol. I, Pl. 72, Fig. 4).

Fig. 2. *Phrynohyas hebes* (Cope). USNM 98536 from Piraporhina, Mato Grosso, Brazil; ♀ body length 82.5 mm.

PLATE I



Fig. 1

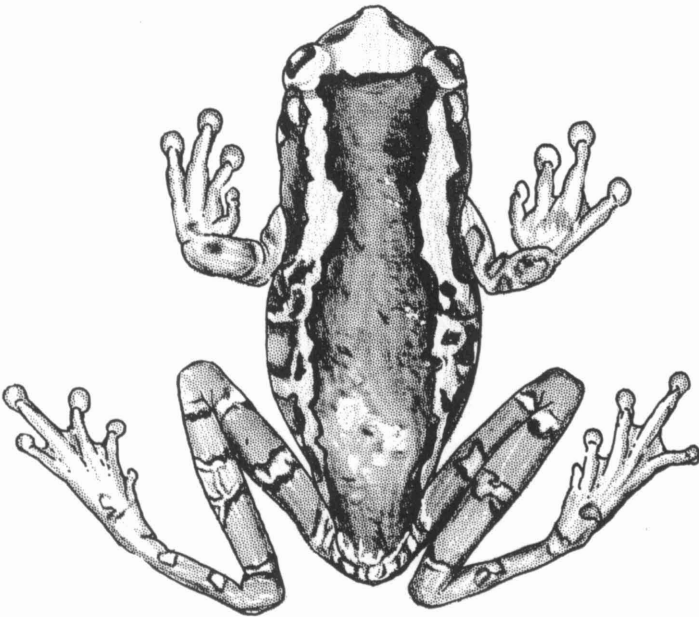


Fig. 2

PLATE II

Fig. 1. *Phrynohyas inflata* (Taylor). UMMZ 104814 from Barranca de Bejuco, Michoacán, Mexico; ♂ body length 93 mm.

Fig. 2. *Phrynohyas ingens*, new species. Holotype, UMMZ 55570 from La Fria, Venezuela; ♀ body length 105 mm.

PLATE II



Fig. 1

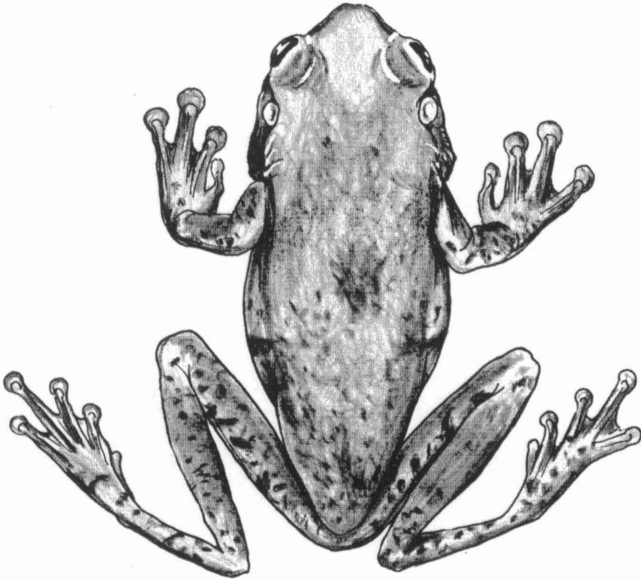


Fig. 2

PLATE III

Fig. 1. *Phrynohyas latifasciata*, new species. Holotype, BMNH 83.2.7.1 from Presidio, Sinaloa, Mexico; ♂ body length 68 mm.

Fig. 2. *Phrynohyas modesta* (Taylor and Smith). UMMZ 88270, ♂ from Escuintla, Chiapas, Mexico; body length 64 mm.

PLATE III

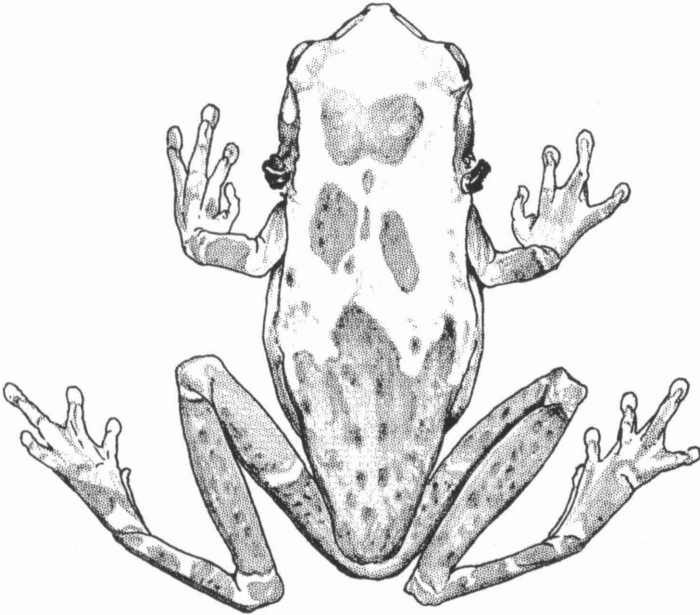


Fig. 1

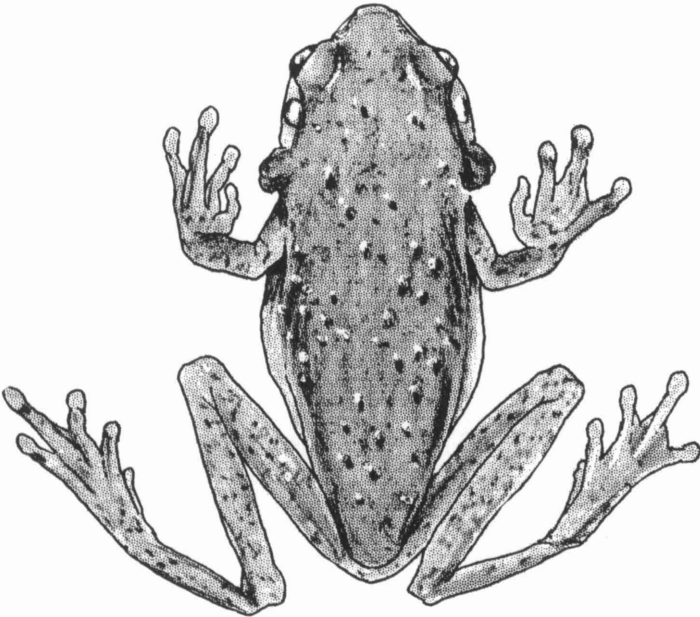


Fig. 2

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PLATE IV

Fig. 1. *Phrynohyas spilomma* (Cope). UMMZ 102061, ♂ from Potrero Viejo, Veracruz, Mexico; body length 71 mm.

Fig. 2. *Phrynohyas spilomma* (Cope). UMMZ 75308, ♂ from La Libertad, Guatemala; body length 75 mm.

PLATE IV

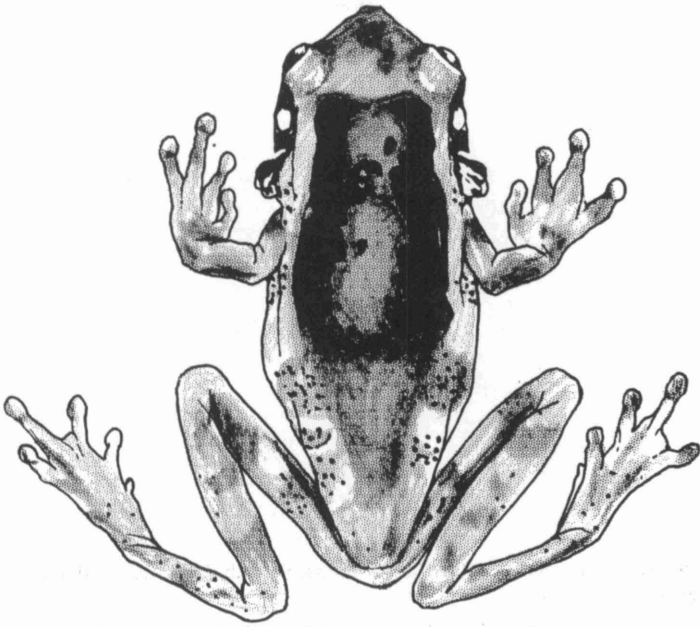


Fig. 1

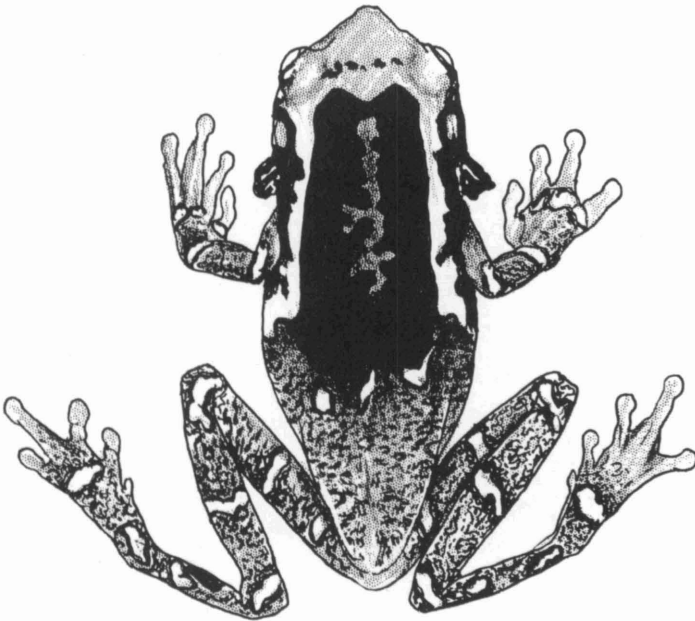


Fig. 2

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PLATE V

Fig. 1. *Phrynohyas zonata* (Spix) UMMZ 55834, ♀ from Santa Rosa Island, British Guiana; body length 93 mm.

Fig. 2. *Phrynohyas zonata* (Spix) UK 31862, ♀ from Palmar, Costa Rica; body length 81 mm.

PLATE V

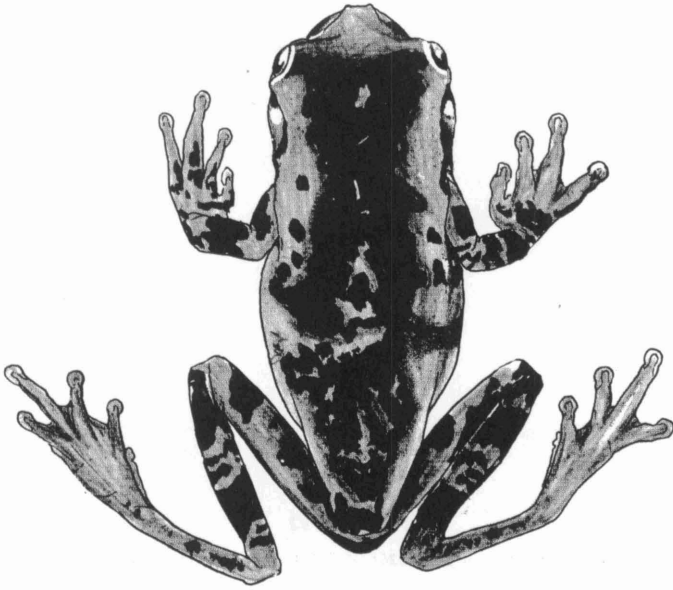


Fig. 1

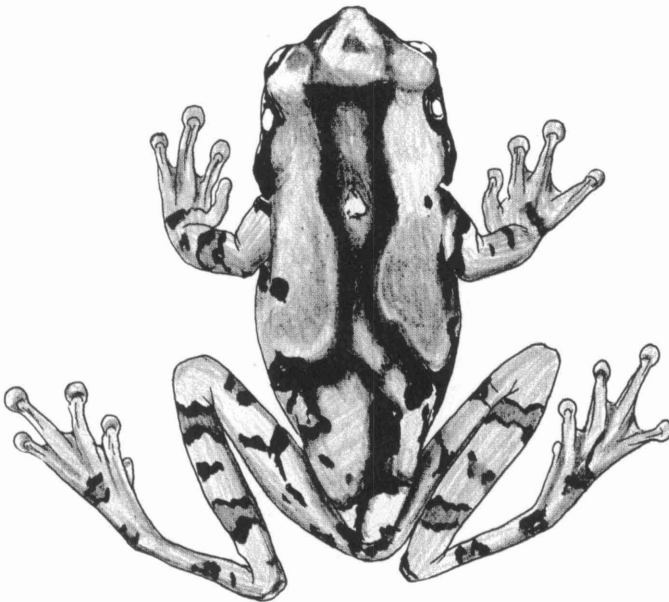


Fig. 2

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PLATE VI

Fig. 1. *Phrynohyas zonata* (Spix) UMMZ 57530, ♂ from Ixiamas, Bolivia; body length 73 mm.

Fig. 2. *Phrynohyas zonata* (Spix) USNM 36377, ♀ from Caicara, Venezuela; body length 74 mm.

PLATE VI

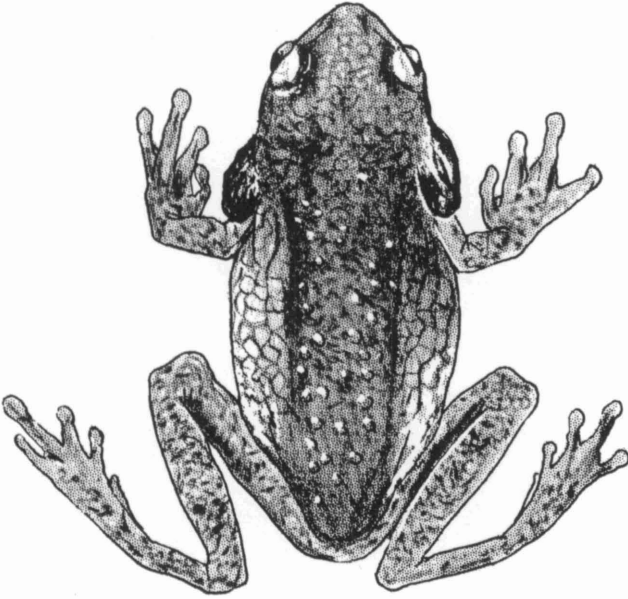


Fig. 1

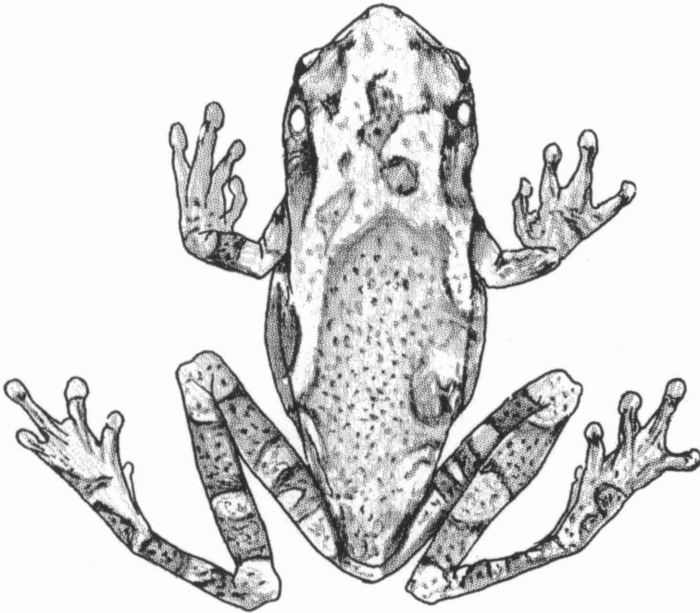


Fig. 2

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- No. 32. Following Fox Trails. By Adolph Murie. (1936) Pp. 45, 6 plates, 6 figures
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