POPULATIONAL VARIATION IN THE FROG GENUS *PHRYNOHYAS* FITZINGER IN MIDDLE AMERICA

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ABSTRACT: A detailed populational analysis indicates that *Phrynohyas latifasciata, inflata,* and *spilomma* are all representative of a single wide-ranging form, *Phrynohyas venulosa.* Important characteristics, including size, coloration, and skin texture, exhibit considerable variation and extensive overlap from population to population or within the same population.

The largest specimens of *Phrynohyas* occur in the more arid portions of its range. Large size is considered an important mechanism for increasing the frogs' efficiency in unfavorable habitats and allowing them to cope more effectively with the problems of desiccation. The degree of development of the dermal glands correlates with the annual climatic cycle characteristic of the wet and dry seasons in Costa Rica. Glandular secretions of *Phrynohyas venulosa* are considered a secondary adaptation against desiccation, as well as being important in deterring predators.

During the summer months of 1962, a field party from the University of Southern California conducted an extensive survey of the lowland amphibian and reptilian faunas of northwestern Mexico. On August 3 a series of nine large hylid frogs, genus *Phrynohyas,* was obtained from a rain-filled pond approximately 9 miles south of Escuinapa, Sinaloa. The frogs, eight males and one female, were located by their calls. Apparently this species was just initiating breeding activities, as only one pair was in amplexus. A second series of these frogs was collected on July 1 in Nayarit by a field party from California State College at Long Beach. This second series, 18 males and one female, was located by the loud chorus at a pond situated 0.1 mile west of the junction of Mexico Highway 15 and Highway 46, in Nayarit.

For the past eight years field parties from the University of Southern California have collected amphibians and reptiles in Costa Rica. In 1964, 1966, and again in 1967, I collected specimens of *Phrynohyas* in Guanacaste and Puntarenas Provinces of Costa Rica. Several of these specimens show striking similarities, particularly in color pattern, to specimens from western Mexico.

The results of a preliminary examination of the two series from Sinaloa and Nayarit indicate the need for a re-evaluation of the present understanding of the systematic arrangement of the genus in western Mexico. Also, with the availability of this additional material from Costa Rica, it seems appropriate to attempt to elucidate the relationships among the named populations of *Phrynohyas* in Middle America.

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HISTORICAL REVIEW

As Duellman (1956), in a monograph on the genus *Phrynohyas*, presented an historical account that included complete synonomies and literature references for each species, a review of material published prior to 1956 will not be repeated. Duellman (1956:8) proposed that *Phrynohyas* be used to refer to those frogs that possess "paired lateral vocal sacs behind the angles of the jaws and without the skin of the head co-ossified with the skull." The generic name *Phrynohyas* was adopted and, following Opinion 520 of the International Commission on Zoological Nomenclature (Hemming, 1958), has been used by most authors (Gans, 1960; Porter, 1962; Stuart, 1963; Zweifel, 1964; Savage, 1966). Rivero (1961:128-131) discussed Duellman's proposal at some length and presented an alternative for treatment of frogs referred to *Phrynohyas*. He suggested that the species be maintained in the genus *Hyla* (see Rivero, 1961, for additional discussion).

On the basis of the unique characters of the larvae of *Phrynohyas* (Zweifel, 1964:204-205) and the characters used by Duellman to diagnose this group of frogs, it seems reasonable to maintain the generic name *Phrynohyas*. For the sake of nomenclatural stability, in accordance with Opinion 520, those frogs referred to *Phrynohyas zonata* (Spix) by Duellman (1956), and to *Hyla tibiatrix* Laurenti by Rivero (1961), are assigned to *Phrynohyas venulosa* (Laurenti).

The five species of Middle American *Phrynohyas* recognized by Duellman (1956) are: *P. zonata* from Costa Rica, Panamá, and tropical South America; *P. spilomma* from southern Tamaulipas, Mexico, southward along the eastern coast of Central America to Nicaragua and along the Pacific coast from the Isthmus of Tehuantepec southward to Guatemala; *P. modesta* from El Salvador north along the Pacific coast of Chiapas through the region of the Isthmus of Tehuantepec into the Atlantic drainage; *P. inflata* from scattered localities along the Pacific coast of Mexico from central Guerrero north to Colima; and *P. latifasciata* from Presidio, Sinaloa, Mexico.

Shannon and Humphrey (1957) described *Phrynohyas corasterias* from a single young female collected 4.8 miles east of San Blas, Nayarit. This species was diagnosed on the basis of pattern and coloration. The only known specimen of *P. corasterias* was collected from a locality approximately midway between the northernmost locality for *P. inflata* and the type locality of *P. latifasciata*. Duellman (1961:45-46) discussed the characters used to diagnose *P. corasterias* and placed it in synonomy with *P. inflata*. He suggested that additional material from northwestern Mexico might show that *P. inflata* and *P. latifasciata* are conspecific (Duellman, 1956:21; 1961:45).

Examination of additional material from Guatemala convinced Duellman that the uniform brown or tan dorsum characteristic of *P. modesta* is only a color variant of *P. spilomma*, and accordingly he placed *P. modesta* in the synonomy of *P. spilomma* (Duellman, 1966:277).

METHODS AND MATERIALS

As presently understood, the species of *Phrynohyas* are distinguished by differences in size, body proportions, coloration, and pattern. To supplement the data gathered by Duellman from more than 350 specimens, I examined an additional 153 specimens of *Phrynohyas* from localities in western Mexico, Guatemala, Honduras, Costa Rica, and Panamá. Seven measurements, including body length, tibia length, foot length, head width, head length, interorbital distance, and internarial distance, were taken on each suitable specimen; five proportions were calculated from these measurements. These data are contained in Table 1. In order to standardize the measurements, only specimens larger than 45 mm in body length and capable of breeding are included. This procedure reduces the possibility of allometric growth in subadult stages confusing the data. The measurements taken are the same as those used by Duellman (1956:6-7). All measurements are in millimeters and were made with Helios dial calipers. Each available specimen was examined in detail with reference to skin texture, coloration, and pattern, because these characters, as presently understood, are the primary features used to distinguish between the species (see key to adult *Phrynohyas* in Duellman, 1956:43-44).

ANALYSIS OF THE POPULATIONS

Western Mexico.—The northernmost representatives of the genus were collected at Presidio, Sinaloa (Boulenger, 1882). Examination of these two specimens led Duellman (1956:24-25) to describe *P. latifasciata.* The Sinaloan species was described as being most closely related to *P. inflata,* a species known from six males collected from localities in Colima, Michoacán, and Guerrero to the south. The characters he used to distinguish between *P. latifasciata* and *P. inflata* were differences in size, skin texture, coloration, and pattern.

The utilization of size in diagnosing a species of frog known from only two specimens is open to criticism. Furthermore, in the case of *P. latifasciata,* there is no mention of the time of year the frogs were collected nor of the breeding condition of the specimens. The paratype of *P. latifasciata* is a young specimen. If it was collected at the same time as the holotype, as presumed by Duellman (1956:24), then I suspect that the specimens were taken before the breeding season. The holotype may be an adult, but if it is sexually mature, it probably is a young adult. This supposition is supported by the size range of males taken less than 50 miles to the south of the type locality (Table 1). At this locale, breeding males measuring from 74.2 to 90.2 mm were collected. In addition, a male (UMMZ 108019) referred to *P. inflata,* measures 63.5 mm, approximately 5 mm less than the type of *latifasciata.* The size of the vocal sacs as depicted in the illustration of the holotype of *P. latifasciata* (Duellman, 1956:pl. III, fig. 1), when compared to those of breeding males from Sinaloa

TABLE 1

Measurements and Proportion

	P. latifasciata[1]		Sinaloa		Nayarit		Colima-Guerrero		Oaxaca-Veracru	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀
Number of Specimens	1	0	6	1	17	1	5	0	4	
Body Length mm										
mean	—	—	80.9	—	84.9	—	80.3	—	65.6	54
range	68.0	—	74.2-90.2	89.0	81.1-92.6	95.8	63.5-92.0	—	55.9-69.0	47.4
Tibia Length mm										
mean	—	—	35.7	—	39.7	—	34.5	—	30.3	2
range	30.0	—	33.5-39.3	39.5	37.9-42.8	42.9	32.0-42.0	—	26.0-33.0	24.1
Foot Length mm										
mean	—	—	32.1	—	35.0	—	29.7	—	24.4	2
range	28.5	—	30.0-35.1	35.5	31.0-37.1	40.1	26.0-32.0	—	21.2-26.0	19.4
Head Length mm										
mean	—	—	23.8	—	25.0	—	23.6	—	19.5	1
range	20.5	—	22.5-26.2	25.7	23.0-26.6	28.1	20.0-27.0	—	15.8-21.0	15.4
Head Width mm										
mean	—	—	25.8	—	27.0	—	26.0	—	20.5	1
range	22.0	—	24.0-27.8	28.5	26.0-28.2	30.5	21.0-29.0	—	16.5-23.0	15.8
Interorbital Distance mm										
mean	—	—	7.5	—	7.8	—	7.5	—	5.7	5
range	6.0	—	6.9-8.2	9.5	7.0-9.4	8.8	5.5-9.0	—	4.6-7.0	5.1
Internarial Distance mm										
mean	—	—	5.6	—	6.2	—	6.2	—	4.9	4
range	4.0	—	4.9-6.1	6.2	5.5-6.7	6.5	5.5-7.0	—	4.1-6.0	3.9
% Tibia Length/Body Length										
mean	—	—	44.2	—	46.8	—	47.6	—	46.2	4
range	44.1	—	42.5-45.6	44.4	44.6-48.4	44.8	45.6-50.7	—	44.1-47.8	49.1
% Head Length/Body Length										
mean	—	—	29.5	—	29.4	—	32.5	—	29.6	3
range	30.1	—	27.6-31.5	28.8	28.0-31.3	29.3	31.5-33.3	—	28.3-30.4	32.8
% Head Width/Body Length										
mean	—	—	32.0	—	31.8	—	29.6	—	31.1	3
range	32.3	—	30.3-33.5	32.0	29.4-35.0	31.8	27.7-31.5	—	29.2-33.3	31.0
% Interorbital Distance/ Head Width										
mean	—	—	29.0	—	28.9	—	28.7	—	28.0	3
range	27.3	—	27.0-31.2	33.3	25.8-33.3	28.8	26.2-31.0	—	26.1-31.1	28.
% Internarial Distance/ Head Width										
mean	—	—	21.7	—	23.3	—	24.0	—	24.0	2
range	18.2	—	18.8-23.1	21.7	20.4-25.3	21.3	22.2-26.2	—	21.7-26.7	24.

1: Data from Duellman, 1956.

TABLE 1

ynohyas from Middle America

	. spilomma[1]		*P. modesta*[1]		Guatemala		Honduras		Costa Rica		Panama	
	♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
	9	85	13	14	53	20	1	4	2	9	4	1
	.7	67.7	63.7	63.5	63.6	64.6	—	66.2	81.5	77.5	88.9	—
4	87.0	56.0-86.5	54.0-69.5	52.0-80.5	54.5-71.1	60.5-79.3	67.0	62.7-68.5	74.3-88.6	54.5-94.1	84.0-92.0	82.0
	.8	32.6	31.0	31.7	30.2	31.1	—	32.9	38.1	37.2	41.8	—
2	40.0	27.0-41.0	25.5-33.5	26.0-40.0	28.0-34.2	28.8-36.4	31.3	30.9-34.0	34.4-41.7	29.6-45.8	40.6-43.5	39.4
	.9	27.8	25.5	26.5	24.8	25.8	—	27.3	32.6	31.7	35.9	—
1	35.0	22.5-34.5	20.5-29.0	21.5-32.5	22.5-30.2	23.5-30.8	26.5	24.5-28.4	29.6-35.5	26.0-35.7	32.5-38.3	34.5
	.7	20.7	19.5	19.5	19.2	19.8	—	20.0	24.0	23.8	25.2	—
1	26.0	16.5-27.0	16.5-22.5	17.0-23.0	17.3-21.9	18.8-21.7	20.8	19.1-20.9	22.4-25.5	18.9-27.7	23.5-26.0	23.8
	.2	22.3	20.8	20.9	19.3	20.2	—	20.7	25.1	25.4	27.0	—
1	27.0	19.0-27.0	17.5-23.0	18.0-26.0	17.5-21.4	18.5-22.8	20.8	20.1-21.4	22.5-27.7	19.8-30.0	25.0-28.6	25.3
	1	6.1	5.6	5.8	5.6	6.2	—	6.1	6.5	6.3	8.1	—
	8.0	5.0-7.5	4.5-6.5	5.0-7.0	4.5-6.6	5.4-7.8	5.5	5.9-6.6	6.0-7.0	4.0-7.0	7.5-9.2	7.5
	9	4.9	4.7	4.8	4.8	5.1	—	4.8	6.0	5.5	6.6	—
	6.5	3.5-6.0	4.0-5.0	4.0-5.0	4.2-5.8	4.5-5.8	4.7	4.7-5.1	6.0-6.0	4.5-6.5	6.5-7.0	5.9
	.8	47.7	48.7	49.9	48.5	48.2	—	49.7	46.7	48.2	47.0	—
4	-51.6	42.9-52.5	46.8-51.2	46.8-55.9	43.9-53.0	45.9-50.4	46.7	49.3-50.3	46.3-47.1	45.2-52.1	45.1-48.9	48.0
	.1	30.4	30.6	30.8	29.8	30.8	—	30.2	29.5	31.3	28.3	—
2	-33.3	27.0-33.1	28.8-32.6	28.6-32.8	27.7-32.8	26.0-32.7	31.0	29.2-32.0	28.8-30.1	26.9-43.1	27.6-29.0	29.0
	.4	32.6	32.6	32.9	30.0	31.3	—	31.3	30.8	33.5	30.4	—
2	-36.4	29.2-36.0	31.4-34.3	31.2-35.1	27.0-33.8	28.8-32.4	31.0	29.5-32.8	30.4-31.3	29.4-50.8	29.5-31.9	30.8
	.5	27.3	27.1	28.0	28.7	30.3	—	29.6	26.0	25.4	30.0	—
2	-33.3	22.2-34.3	25.6-30.6	25.5-32.4	24.2-34.1	25.9-35.1	26.4	28.0-32.7	25.3-26.7	14.4-29.8	26.2-34.6	29.6
	.0	21.9	22.8	22.9	25.0	25.1	—	23.4	24.2	22.1	24.6	—
1	-26.1	18.2-26.3	19.2-23.9	19.0-26.5	22.2-28.1	22.9-27.1	22.6	22.3-25.2	21.7-26.7	16.2-25.3	22.7-26.0	23.3

TABLE 1

TABLE 1

Measurements and Proportions of *Phrynohyas* from Middle America

	P. latifasciata[1]		Sinaloa		Nayarit		Colima-Guerrero		Oaxaca-Veracruz	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Number of Specimens	1	0	6	1	17	1	5	0	4	3
Body Length mm										
mean	—	—	80.9	—	84.9	—	80.3	—	65.6	54.7
range	68.0	—	74.2-90.2	89.0	81.1-92.6	95.8	63.5-92.0	—	55.9-69.0	47.4-60.9
Tibia Length mm										
mean	—	—	35.7	—	39.7	—	34.5	—	30.3	27.2
range	30.0	—	33.5-39.3	39.5	37.9-42.8	42.9	32.0-42.0	—	26.0-33.0	24.1-30.1
Foot Length mm										
mean	—	—	32.1	—	35.0	—	29.7	—	24.4	22.4
range	28.5	—	30.0-35.1	35.5	31.0-37.1	40.1	26.0-32.0	—	21.2-26.0	19.4-25.9
Head Length mm										
mean	—	—	23.8	—	25.0	—	23.6	—	19.5	17.4
range	20.5	—	22.5-26.2	25.7	23.0-26.6	28.1	20.0-27.0	—	15.8-21.0	15.4-18.9
Head Width mm										
mean	—	—	25.8	—	27.0	—	26.0	—	20.5	18.1
range	22.0	—	24.0-27.8	28.5	26.0-28.2	30.5	21.0-29.0	—	16.5-23.0	15.8-20.1
Interorbital Distance mm										
mean	—	—	7.5	—	7.8	—	7.5	—	5.7	5.5
range	6.0	—	6.9-8.2	9.5	7.0-9.4	8.8	5.5-9.0	—	4.6-7.0	5.1-5.8
Internarial Distance mm										
mean	—	—	5.6	—	6.2	—	6.2	—	4.9	4.4
range	4.0	—	4.9-6.1	6.2	5.5-6.7	6.5	5.5-7.0	—	4.1-6.0	3.9-4.9
% Tibia Length/Body Length										
mean	—	—	44.2	—	46.8	—	47.6	—	46.2	49.8
range	44.1	—	42.5-45.6	44.4	44.6-48.4	44.8	45.6-50.7	—	44.1-47.8	49.1-50.8
% Head Length/Body Length										
mean	—	—	29.5	—	29.4	—	32.5	—	29.6	33.0
range	30.1	—	27.6-31.5	28.8	28.0-31.3	29.3	31.5-33.3	—	28.3-30.4	32.8-33.3
% Head Width/Body Length										
mean	—	—	32.0	—	31.8	—	29.6	—	31.1	31.9
range	32.3	—	30.3-33.5	32.0	29.4-35.0	31.8	27.7-31.5	—	29.2-33.3	31.0-32.5
% Interorbital Distance/ Head Width										
mean	—	—	29.0	—	28.9	—	28.7	—	28.0	30.8
range	27.3	—	27.0-31.2	33.3	25.8-33.3	28.8	26.2-31.0	—	26.1-31.1	28.3-32.3
% Internarial Distance/ Head Width										
mean	—	—	21.7	—	23.3	—	24.0	—	24.0	24.5
range	18.2	—	18.8-23.1	21.7	20.4-25.3	21.3	22.2-26.2	—	21.7-26.7	24.4-24.7

	P. spilomma[1]		*P. modesta*[1]		Guatemala		Honduras		Costa Rica		Panama	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Number of Specimens	109	85	13	14	53	20	1	4	2	9	4	1
Body Length mm												
mean	68.7	67.7	63.7	63.5	63.6	64.6	—	66.2	81.5	77.5	88.9	—
range	48.0-87.0	56.0-86.5	54.0-69.5	52.0-80.5	54.5-71.1	60.5-79.3	67.0	62.7-68.5	74.3-88.6	54.5-94.1	84.0-92.0	82.0
Tibia Length mm												
mean	32.8	32.6	31.0	31.7	30.2	31.1	—	32.9	38.1	37.2	41.8	—
range	22.5-40.0	27.0-41.0	25.5-33.5	26.0-40.0	28.0-34.2	28.8-36.4	31.3	30.9-34.0	34.4-41.7	29.6-45.8	40.6-43.5	39.4
Foot Length mm												
mean	27.9	27.8	25.5	26.5	24.8	25.8	—	27.3	32.6	31.7	35.9	—
range	19.0-35.0	22.5-34.5	20.5-29.0	21.5-32.5	22.5-30.2	23.5-30.8	26.5	24.5-28.4	29.6-35.5	26.0-35.7	32.5-38.3	34.5
Head Length mm												
mean	20.7	20.7	19.5	19.5	19.2	19.8	—	20.0	24.0	23.8	25.2	—
range	16.0-26.0	16.5-27.0	16.5-22.5	17.0-23.0	17.3-21.9	18.8-21.7	20.8	19.1-20.9	22.4-25.5	18.9-27.7	23.5-26.0	23.8
Head Width mm												
mean	22.2	22.3	20.8	20.9	19.3	20.2	—	20.7	25.1	25.4	27.0	—
range	16.0-27.0	19.0-27.0	17.5-23.0	18.0-26.0	17.5-21.4	18.5-22.8	20.8	20.1-21.4	22.5-27.7	19.8-30.0	25.0-28.6	25.3
Interorbital Distance mm												
mean	6.1	6.1	5.6	5.8	5.6	6.2	—	6.1	6.5	6.3	8.1	—
range	4.0-8.0	5.0-7.5	4.5-6.5	5.0-7.0	4.5-6.6	5.4-7.8	5.5	5.9-6.6	6.0-7.0	4.0-7.0	7.5-9.2	7.5
Internarial Distance mm												
mean	4.9	4.9	4.7	4.8	4.8	5.1	—	4.8	6.0	5.5	6.6	—
range	3.5-6.5	3.5-6.0	4.0-5.0	4.0-5.0	4.2-5.8	4.5-5.8	4.7	4.7-5.1	6.0-6.0	4.5-6.5	6.5-7.0	5.9
% Tibia Length/Body Length												
mean	47.8	47.7	48.7	49.9	48.5	48.2	—	49.7	46.7	48.2	47.0	—
range	44.1-51.6	42.9-52.5	46.8-51.2	46.8-55.9	43.9-53.0	45.9-50.4	46.7	49.3-50.3	46.3-47.1	45.2-52.1	45.1-48.9	48.0
% Head Length/Body Length												
mean	30.1	30.4	30.6	30.8	29.8	30.8	—	30.2	29.5	31.3	28.3	—
range	27.9-33.3	27.0-33.1	28.8-32.6	28.6-32.8	27.7-32.8	26.0-32.7	31.0	29.2-32.0	28.8-30.1	26.9-43.1	27.6-29.0	29.0
% Head Width/Body Length												
mean	32.4	32.6	32.6	32.9	30.0	31.3	—	31.3	30.8	33.5	30.4	—
range	29.1-36.4	29.2-36.0	31.4-34.3	31.2-35.1	27.0-33.8	28.8-32.4	31.0	29.5-32.8	30.4-31.3	29.4-50.8	29.5-31.9	30.8
% Interorbital Distance/ Head Width												
mean	27.5	27.3	27.1	28.0	28.7	30.3	—	29.6	26.0	25.4	30.0	—
range	23.8-33.3	22.2-34.3	25.6-30.6	25.5-32.4	24.2-34.1	25.9-35.1	26.4	28.0-32.7	25.3-26.7	14.4-29.8	26.2-34.6	29.6
% Internarial Distance/ Head Width												
mean	22.0	21.9	22.8	22.9	25.0	25.1	—	23.4	24.2	22.1	24.6	—
range	19.1-26.1	18.2-26.3	19.2-23.9	19.0-26.5	22.2-28.1	22.9-27.1	22.6	22.3-25.2	21.7-26.7	16.2-25.3	22.7-26.0	23.3

1: Data from Duellman, 1956.

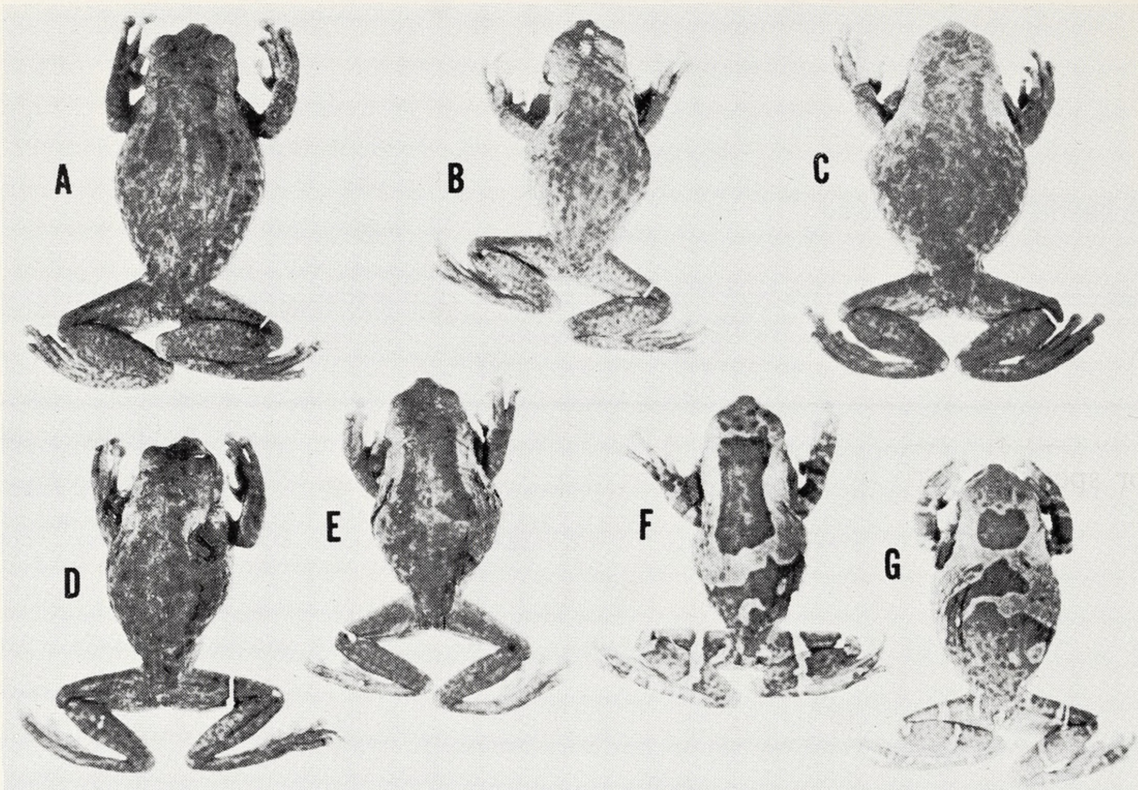

Figure 1. Series of *Phrynohyas venulosa* collected 9.4 miles south of Escuinapa, Sinaloa, Mexico. These frogs exhibit both unicolor and blotched color patterns.

and Nayarit, also suggests that the specimen is a young male. If the Sinaloan specimens referred to *P. latifasciata* represent a population distinct from *P. inflata*, then differences in proportions might be anticipated. It is apparent from Table 1 that the additional material from southern Sinaloa and Nayarit is intermediate between *P. latifasciata* and *P. inflata* in measurable characters. Although only two adult females of *Phrynohyas* are known from western Mexico, data suggest that females attain a larger size than males.

The development of the dorsal pustules in the *Phrynohyas* from Sinaloa and Nayarit varies considerably. The series includes animals with a nearly smooth dorsum, animals with moderately developed pustules, and animals with well developed pustules. The range of variation in this character encompasses the differences attributed to *latifasciata* and *inflata.* A specimen from Nayarit (CSCLB 641) that was preserved in alcohol has a relatively smooth skin. Additional specimens (CSCLB 625-640) collected from the same locality and on the same night were fixed in ten percent formalin and then preserved in alcohol. These specimens exhibit a wide range of variation in skin texture but in all cases are more rugose than the specimen initially preserved in alcohol. This suggests that the type of *latifasciata* was fixed in alcohol, apparently a common practice in the late 1800s.

The differences in coloration and pattern between species of *Phrynohyas*, as pointed out by Duellman (1956), include the nature of the dorsal color pattern and the arrangement and size of the transverse leg bands. These differences also form the primary basis for the key to the adult *Phrynohyas* (Duellman, 1956:43-44). A series of seven specimens from Sinaloa (LACM 6314-19, 7245) exhibits a range of variation in dorsal color pattern encompassing three of the nominal species of *Phrynohyas* from Mexico (Fig. 1). Five of the specimens have a pattern similar to the unicolor form of *P. spilomma*, originally considered distinct and referred to *P. modesta* by Duellman (1956). Dorsally these specimens are mottled brown on tan, or dark brown on brown. Two of the specimens (D and E) show a slight indication of a darker middorsal color, a condition considered intermediate between the unicolor phase and the blotched forms (F and G). The upper surface of the thighs is unicolor or speckled dark brown (A through E). Duellman (1956:27) pointed out that the unicolor brown dorsum and the speckled condition of the hind legs is typical of specimens of *P. modesta* found in southern Mexico and Guatemala. A second dorsal color pattern (F) consists of a light brown ground color with a large chocolate brown patch extending posteriorly from behind the eyes to near mid-body. A broad band of ground color bounds a posterior brown patch that continues to the vent and onto the dorsal surface of the thighs. The brown bands on the legs are separated by tan interspaces. This color pattern is typical of the specimens from Colima and Guerrero referred to *P. inflata* and shows striking similarities to the specimen from Michoacán figured by Duellman (1956:pl. II, fig. 1). Specimen G has a dorsal color pattern similar to specimen F but differing in having the anterior dorsal patch olive brown and broken into two parts rather than forming a continuous central patch. The middle spot is connected by a narrow band to the posterior blotch. The presence of two or more anterior dorsal spots is characteristic of the nominal species *Phrynohyas latifasciata* (Duellman, 1956:25, pl. III, fig. 1). The bands on the legs are not as wide as in the type of *latifasciata* (three times the width of the interspaces) but rather are very much like the condition of specimen F and the type of *P. inflata.* The vocal sacs of the Sinaloan frogs in life varied from chocolate brown to dark olive. With the differences in coloration of the vocal sacs noted in the Sinaloan series, it is not surprising to find that Boulenger (1882:327-328) described the type of *P. latifasciata* as possessing black vocal bladders. In life, the ventral surfaces of the *Phrynohyas* from Sinaloa vary from a dirty white to brownish white. The throat is usually creamy white with or without brown vermiculations.

In the series of specimens from Nayarit (Fig. 2), the anteriodorsal blotch is generally continuous in most specimens. However, one individual (A) has the anterior blotch broken into two parts. The nature of this break in the blotch is easily traced to the solid blotched pattern through intermediate specimens (B, C, G). In addition to the split of the anterior central patch, there is considerable variation in other specimens in the shape of the blotch. Certain individuals have a rectangular shaped blotch (E, H); some exhibit an hourglass-shaped blotch (J, N). Some have posterior indentations of the blotch (K, L), anterior indentations of the blotch (B, G), or both (C, I, M). The color of the blotch varies from a uniform chocolate (E) to a mottled light brown blotch that is darker laterally (N). Some individuals have isolated circles of ground color within the blotch (F, G). In two specimens (M and N) the anterior and posterior blotches connect, while in others (L and O) the two dorsal blotches are almost completely fused.

In addition to the variation in dorsal pattern, the Nayarit series (Fig. 2) also exhibits a wide range of variation in color pattern of the legs. Some specimens have continuous bands on the femur and tibia of both hind legs (A, E, N). In some the bands are four times the interspace width (J, O); in some they are only twice the interspace width (B, C). There are progressive stages from specimens with nearly unicolor legs (L) through an individual with one tibia solid and one banded (H), or both tibiae solid (F, G), to specimens on which the interspaces do not meet across the face of the tibia on

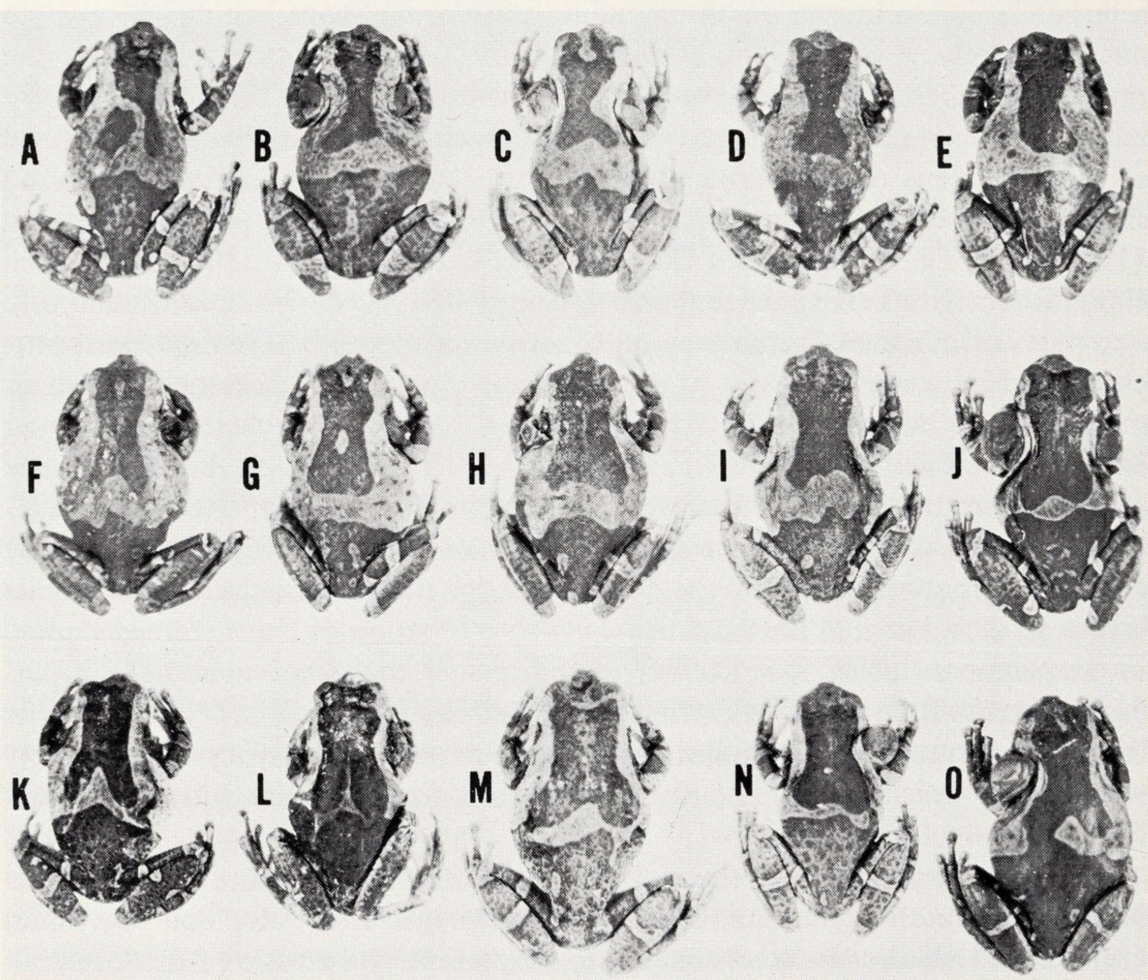

Figure 2. Selected individuals from a series of *Phrynohyas venulosa* collected 0.1 mile west of the junction of Mexico Highway 15 and Highway 46 (=22.9 miles east of San Blas), Nayarit, Mexico. The specimens show variation in dorsal color pattern and leg pattern.

either one side (K) or both sides (J). The leg markings vary from nearly unicolor (D, O) to a banded condition with varying degrees of spotting or marbling with a darker color (I, K). Most, but not all, of the leg bands are edged in dark brown. The Nayarit specimens possess a brownish white to creamy white venter, generally with some brown marking on the chin. The vocal sacs vary from light brown and olive to dark brown.

I examined the six specimens previously called *P. inflata* from western Mexico and found no differences between these specimens and the Nayarit or Sinaloa material, either in measurements or in proportions (Table 1). In terms of coloration and pattern, the six known specimens of *P. inflata* are almost exactly duplicated in the series from Nayarit. A single specimen (KU 73879) taken approximately halfway between the localities of the Nayarit and Sinaloan series possesses characteristics typical of some of the Nayarit specimens as well as of one of the Sinaloan specimens.

The description and illustration of *P. corasterias* (Shannon and Humphrey, 1957:15-18) indicate that this nominal species shares characters of color and pattern with some of the Nayarit material. In addition, the condition of the subarticular tubercle on the penultimate joint of the fourth finger (toe) varies from a bifid condition to a typical round condition in both the Nayarit and Sinaloan material. The webbing characters appear to be constant in all specimens examined from western Mexico and, in general, are the same as the illustration of the hand and foot of *P. corasterias* (Shannon and Humphrey, 1957:17, fig. 2). The other characters supposedly diagnostic of *P. corasterias* are well within the range of variation found in the Nayarit and Sinaloan series. Duellman (1961:45-46) considered the holotype of *P. corasterias* as a representative from the population of frogs from Colima, Michoacán, and Guerrero. The new material from Sinaloa and Nayarit indicates that there is extensive overlap between the characters used to distinguish between *P. latifasciata* and *P. inflata* and argues for recognition of but a single species of *Phrynohyas* in western Mexico.

Southern Mexico-Northern Central America.—The *Phrynohyas* from southern and eastern Mexico and northern Central America were considered by many workers to represent two species, *P. spilomma* and *P. modesta* (Smith and Taylor, 1948; Duellman, 1956, 1960; Neill and Allen, 1959a, 1959b; Neill, 1965; Stuart, 1963). Recently, Duellman (1966:277) presented evidence to show that *P. modesta* was a color variant of *P. spilomma.* Examination of material from Mexico, Guatemala, and Honduras augments the conspecificity of *P. modesta* and *P. spilomma.*

In his monograph of the genus in 1956, Duellman examined 335 specimens of *P. spilomma.* I have examined an additional 85 specimens. The measurements and ratios for the adult specimens are listed in Table 1. It is immediately obvious from the measurements that presumed *P. spilomma* generally average smaller than specimens of *Phrynohyas* from western Mexico.

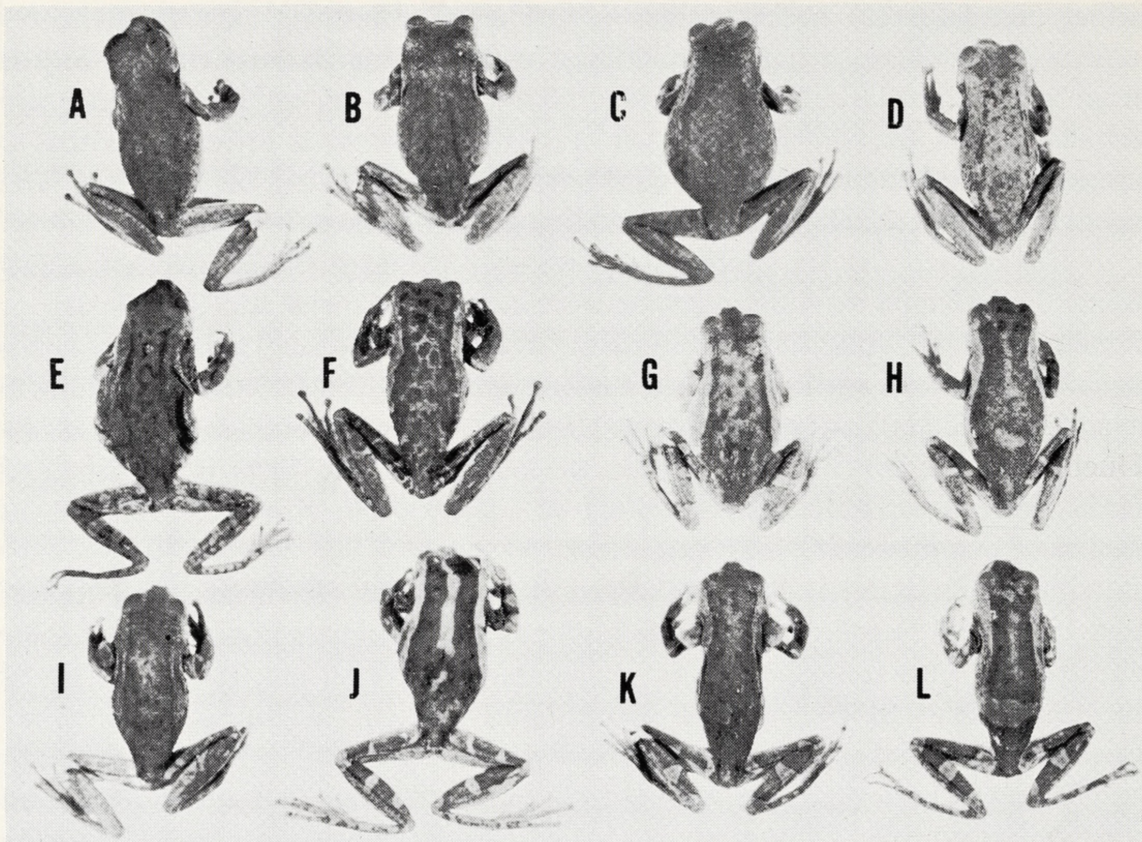

Figure 3. Part of a large series of *Phrynohyas venulosa* from Cuyuta, Guatemala. These specimens show a gradation from unicolor to blotched dorsal pattern.

However, it should be pointed out that there is overlap in the ranges of all measurements of the frogs from southern and eastern Mexico and west Mexican *Phrynohyas*. In addition, the averages of the ratios are nearly the same from Sinaloa, Mexico to Honduras. While there is considerable variation in the measurements and proportions of this sample, there is no consistent geographic variation within the sample. Besides the overlap in measurements and proportions, there is a wide range of variation in skin texture. No consistent differences in skin texture or glandular development exist to aid in distinguishing the west Mexican individuals from those referred to *P. spilomma*.

The primary characters, other than overall size, that have been used to distinguish between eastern Mexican and Central American *Phrynohyas* and the *Phrynohyas* from western Mexico are differences in coloration and pattern. Examination of a large series of *Phrynohyas* from Cuyuta, Guatemala (AMNH 74377-90, +58) indicates that all the pattern types characteristic of *Phrynohyas* from Mexico and northern Central America may be present in a single breeding population. Selected individuals in this series (Fig. 3) exhibit a gradation from unicolor to blotched pattern. Some possess a unicolor brown dorsum with various degrees of spotting on the back and legs (A and B);

some have faint traces of a dorsal pattern and leg barring (C and D); three individuals (E, F, and G) are heavily mottled dorsally, tending towards a uniform dorsal blotch similar to those frogs referred to *P. spilomma*, as figured by Duellman (1956:pl. IV, figs. 1 and 2); others (H, I, and J) exhibit various modifications of a dorsal pattern and barred legs; and two specimens (K and L) are nearly identical in pattern with specimens from Nayarit, Mexico (Fig. 2, D, F, N). Ventral coloration in these 12 specimens is uniform white or dirty white with some brown mottling on the throat, or white with numerous brown spots.

Others have mentioned the color patterns characteristic of populations in a single area (Neill, 1965:88). Honduranean specimens were described by Duellman (1956:32) as closely resembling those from La Libertád, Guatemala (Duellman, 1956:pl. IV, fig. 2) and considered typical of the nominal *P. spilomma.* Meyer (1966:173) reported five specimens from Honduras, all of which were unicolor. Thus in Honduras, as in Guatemala, British Honduras, and Mexico, *Phrynohyas* exhibits a wide range of color pattern within a single population or between populations.

Costa Rica and Panamá.—Material from lower Central America, although scanty, provides a basis for further understanding of the relationships between the populations of this wide ranging hylid frog. As previously mentioned, both unicolor and blotched forms are known from Honduras. The only

Figure 4. Costa Rican specimens of *Phrynohyas venulosa* showing the variation in coloration and size.

known specimen from Nicaragua has a blotched pattern typical of some of the Guatemalan individuals. All previously known specimens from Costa Rica and Panamá exhibited a blotched dorsal pattern and banded legs. These frogs were assigned to *Phrynohyas venulosa* by Taylor (1952:800) and Zweifel (1964:201), and to *Phrynohyas zonata* by Duellman (1956:37). Several additional specimens from Costa Rica closely resemble the individual illustrated by Duellman (1956:pl. V, fig. 2) from Palmar, Puntarenas Province, Costa Rica, and the individual illustrated by Zweifel (1964:206, fig. 5) from Nueva Gorgona, Panamá Province, Panamá. Thus it appeared that lower Middle American *Phrynohyas* were generally consistent in their color pattern and large size and possibly represented a species distinct from the *Phrynohyas* from Honduras and areas to the north.

In late May, 1964, four unicolor specimens of *Phrynohyas* were collected in the Atlantic drainage at Los Chiles, Alajuela Province, Costa Rica. These specimens are smaller than other Costa Rican individuals but larger than most specimens from Honduras and Guatemala. The measurements and proportions of all the specimens examined from Costa Rica and Panamá are listed in Table 1. The specimens from lower Central America are generally larger than individuals of *Phrynohyas* to the north, but, as was true with the forms already discussed, there is overlap with the northern Central American forms in most of the measurements and very little difference, if any, among the ratios.

Ten of the Costa Rican specimens that were examined are pictured (Fig. 4). The four Los Chiles specimens, three females and one male, range from dark brown to brownish tan dorsally (A through D). Three specimens have unicolor legs, while the fourth possesses many dark spots on the hind legs. Ventrally they are yellowish white with a faint brown mottling on the throat and belly. The dorsal pattern of the remaining six adults from Costa Rica consists of a wide dark brown blotch beginning between the eyes and extending along the lateral edge of the dorsal blotch to about mid-body. The width of the lateral band varies from a narrow line (E and F) to a wide band (I and J) and determines the shape of the dorsal blotch. The legs of all the specimens are variously crossed by solid bands or a series of broken bands which give the legs an overall mottled appearance. Ventrally, these frogs are yellowish white with a faint brown mottling on the throat or covered with numerous brown spots. The skin texture varies from nearly smooth (A, C, and I) to very rugose and pustulate (B, E, and G). The ventral surfaces also show some variation in pustulation.

The Panamanian specimens examined exhibit the pattern (Fig. 5) characteristic of most of the Costa Rican frogs. The dorsal blotches are somewhat narrower than in some of the Costa Rican individuals and the lateral bands from the eyes are correspondingly wider. Ventrally, these frogs show varying degrees of faint brown mottling.

The intermediate size of the Los Chiles specimens and the presence of

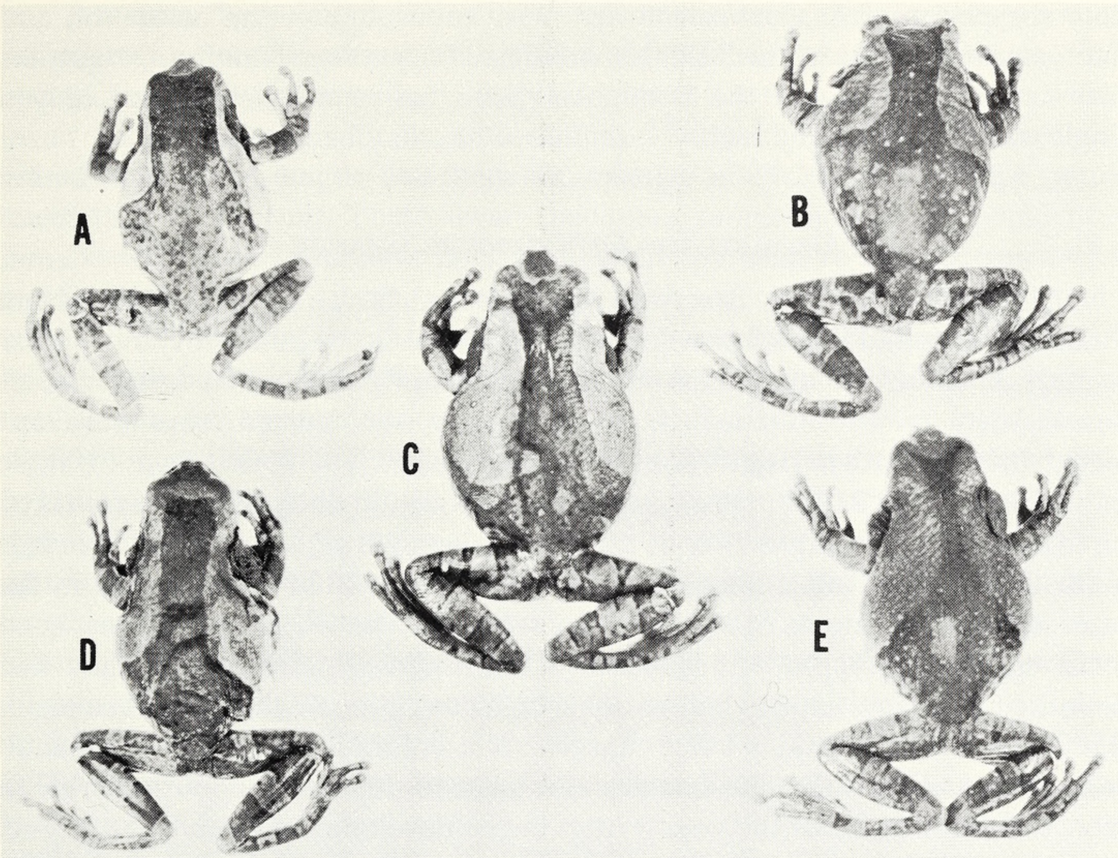

Figure 5. Panamanian specimens of *Phrynohyas venulosa* illustrating the lateral restriction of the dorsal blotch.

both color patterns in Costa Rica suggest that there is a very close relationship between the Panamanian and Costa Rican *Phrynohyas* and those to the north. Analyses of several characters of specimens from the entire range of the genus in Mexico and Central America indicate that there are no consistent differences among the populations studied. The characteristics utilized by Duellman (1956) to distinguish between species of *Phrynohyas* have been shown to exhibit considerable variation within each population and extensive overlap among several populations.

Based on the preceding discussion and analysis, I consider all known specimens of frogs of the genus *Phrynohyas* from Mexico and Central America as representative of a single, wide-ranging, variable species. All Middle American specimens presently referred to *Phrynohyas latifasciata, P. inflata, P. spilomma, P. modesta,* and *P. zonata* are regarded as representatives of *P. venulosa.*

Some comments concerning the South American species seem appropriate. Duellman discussed the relationship of *P. hebes* and *P. ingens. Phrynohyas hebes* is very close to *P. zonata* and Duellman (1956:42) suggested that they may be subspecifically related. *Phrynohyas ingens* differs from *P. venulosa* primarily in coloration and size, and Rivero (1961:131) considered *ingens* to be a subspecies of *P. venulosa.* Based on a knowledge of the coloration and size variation found in the Middle American *Phrynohyas venulosa,* I suspect that detailed analysis of the South American forms will reveal that only a single, wide-ranging, and highly variable species may be involved.

GROWTH AND ONTOGENETIC CHANGE

Zweifel (1964:201) described the eggs and larvae of *P. venulosa* from Panamá. He found that the larvae metamorphosed in the laboratory in approximately 37 days, and suggested that under natural conditions a faster rate of development might be expected. Several newly transformed frogs were collected in Costa Rica from June 18 to September 18, 1964. Two of these individuals (CRE 8178), measuring 26 and 27 mm in body length, were taken on the road about 12 miles NW of Liberia on the night of July 26. Field records indicate that three adult females (CRE 8102, 8105, 8121) were taken in the same area on the nights of June 29 and June 30. The retention of a few scattered eggs in the reproductive tracts of these frogs indicates that they had deposited their eggs shortly before being collected, probably the previous night. Both juveniles had attained the characteristic coloration typical of the adult frogs. If we assume that the females had finished depositing eggs just prior to their collection and that the young frogs began development at about that time, then the period from egg to frog encompassed thirty or more days. Zweifel (1964:205) pointed out that the characteristic adult pattern is not reached until several days after metamorphosis appears complete. The evidence, while circumstantial, suggests that under natural conditions the rate of development probably is faster than in the laboratory. In either case, the inferences concerning the length of time from egg laying to metamorphosis generally support Zweifel's findings. Other recently metamorphosed frogs from Parrita and Rincón de Osa, Costa Rica, are between 13 and 17 mm body length and do not exhibit the adult pattern. These specimens are assignable to *Phrynohyas venulosa* by their possession of green bones and the leg stripe characteristic of the recently transformed frogs (Zweifel, 1964:205).

Duellman (1956:33) mentioned the presence of ontogenetic change in the tibia/body length ratios of *Phrynohyas* from central Veracruz, Mexico. He stated that "Only in the small adults and juveniles does the tibia exceed 50 percent of the body length", and he refers to a graph of body length plotted against tibia length. All that can be determined from these data (Duellman, 1956:33, fig. 9) is that specimens above 60 mm body length generally have a shorter tibia and show a lower percent tibia/body length than do specimens below 60 mm. While there is no way to determine at what size (body length) he considered specimens to represent small adults and juveniles, it can be seen from his graph that there are specimens over 60 mm body length which have a tibia/body length ratio greater than 50 percent.

The tibia/body length ratios for 72 specimens from Guatemala show that ratios greater than 50 percent are found in six specimens ranging between 54.5 and 66.3 mm. The average body length for these six frogs is 60.7 mm, a value lower than the average for the total sample (Table 1). There are seven individuals with body lengths less than the average of 60.7 mm that have ratios lower than 50 percent. These seven specimens range between 58.7 and 60.5 mm ($\bar{x} = 59.7$ mm) and have tibia/body length percents ranging between 47.9 and 49.3 ($\bar{x} = 48.7$). It can be seen that there are about as many specimens with a tibia/body length ratio greater than 50 percent as there are with a tibia/body length ratio less than 50 percent at the same or larger body length. For the total sample this means that, proportionally, some of the smaller frogs have a slightly longer tibia than the larger frogs. These findings generally are supported by the few smaller individuals from other populations. In these instances the higher tibia/body length ratios are found in the smaller specimens. As Duellman and, to a degree, my data indicate, there is ontogenetic change in tibia length so that the smaller the individual, the relatively longer the tibia. The data presented by Duellman in support of this change are for animals greater than 40 mm in body length. Apparently, he did not have specimens smaller than 40 mm from central Veracruz, Mexico. A series of 20 specimens (TCWC 16782-91, 16800-09) from Zacapa, Santa Rosa Department, Guatemala, has body lengths between 24.4 and 30.1 mm ($\bar{x} = 26.3$ mm); the tibia length ranges between 11.5 and 14.1 mm ($\bar{x} = 12.6$ mm); and the percents of tibia/body length range between 44.6 and 51.5 ($\bar{x} = 47.9$). Unfortunately, no adults are available from this locality. A graph plotting body length against tibia length for these specimens (Fig. 6) exhibits the same distribution in reference to the 50 percent line as Duellman found for the adults from central Veracruz, Mexico. The majority of the specimens lie below the 50 percent line. These results indicate that a parabolic curve rather than a sigmoid curve of tibia/body length ratios would be found in a given population.

Two juvenile frogs (26 and 27 mm) and five adults (78.5 to 94.1 mm) from the same general locality in Costa Rica exhibit similar patterns. The smallest and the largest specimens have comparable ratios which are slightly lower than the intermediate sized specimens. Again the sample size, degree of differences among the ratios, and the lack of specimens from 30 to 70 mm body length do not allow for a meaningful analysis and only suggest the parabolic oscillation in ratios for a given population.

There is also an indication of ontogenetic change in the number of vomerine teeth. All juvenile frogs smaller than 30 mm body length that were examined averaged 4 to 5 fewer teeth than the adults from the same areas. Again the lack of sufficient material from the same population makes it difficult to evaluate these differences adequately.

Color pattern is the only other character which shows a well defined ontogenetic change. Recently metamorphosed frogs maintain the hind leg

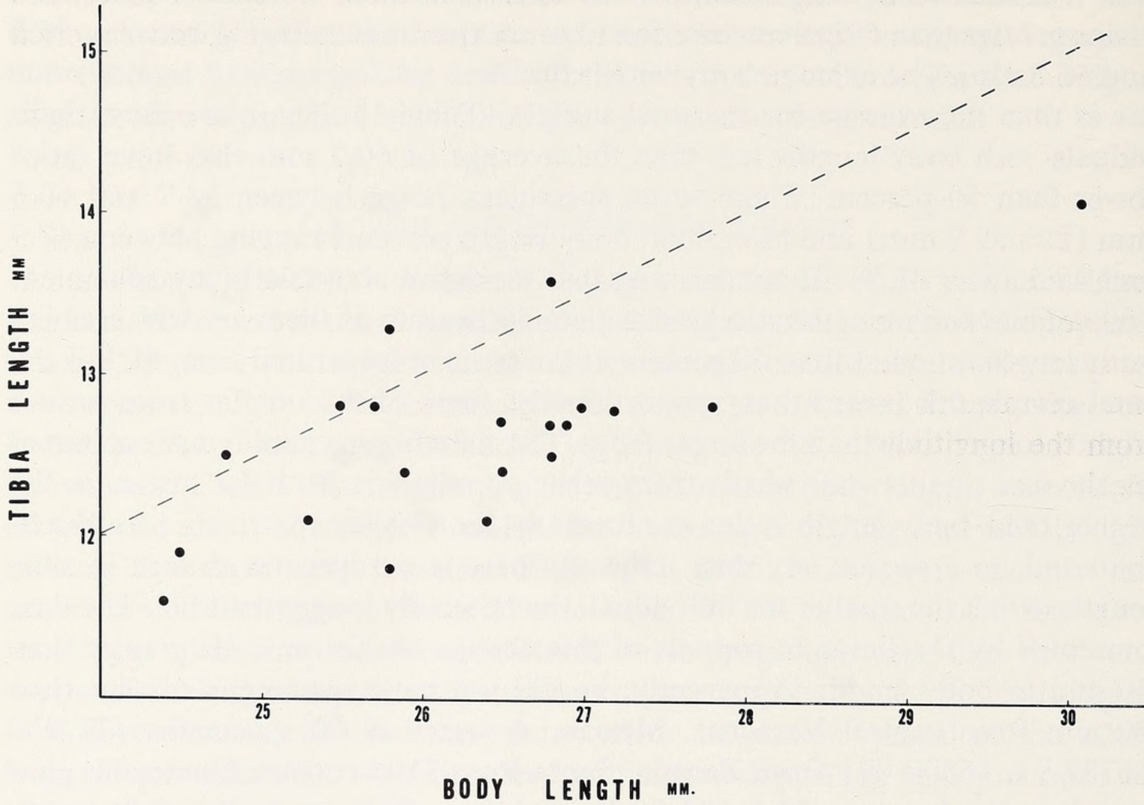

Figure 6. Graph plotting body length against tibia length for 20 small specimens of *Phrynohyas venulosa* from Zacapa, Guatemala. The 50 percent index is indicated by the dashed line.

stripe of the tadpoles for a few days after transformation. Zweifel (1964:205) described this characteristic coloration, and my material supports his findings. By the time the frogs reach 24 mm body length, they have attained the adult color pattern.

DISCUSSION

During the course of this study, several evolutionary trends among the different populations of *Phrynohyas* became obvious. I have already shown that color patterns, once thought to be consistent for each population, exhibit a wide range of variation from sample to sample or within a single population. The arrangement of the dorsal coloration in specimens from Mexico and Guatemala exhibits a clinal trend. All of the lower Middle American patterned specimens examined exhibit a single dorsal blotch. Most of the Guatemalan individuals possess a single dorsal blotch that extends from between the eyes to the vent. A single specimen from western Guatemala has the two blotched dorsal pattern characteristic of the western Mexican specimens. Individuals from Colima and Guerrero to the north exhibit a pattern of two blotches. In some specimens from the northern portion of the range of the genus along the west coast of Mexico, the dorsal pattern consists of three blotches. The trend is towards a fragmentation of the dorsal blotch from northern Central America northward along the Pacific coast of Mexico.

In addition to the fragmentation of the dorsal pattern into two or three blotches, the anterior dorsal blotch tends to split along the longitudinal axis of the body. The split appears first in the Nayarit series and becomes prevalent in the southern Mexican and Guatemalan populations. There is no indication of a longitudinal split in dorsal patterns of specimens from Costa Rica and Panamá. The dorsal blotch is constricted in Panamanian and Costa Rican specimens, but most marked in the former. The lateral constriction narrows the dorsal blotch and decreases the amount of dark dorsal coloration, but in a different manner from the longitudinal splitting of the dorsal blotch found in the Guatemalan specimens.

The blotched dorsal coloration is considered the primitive condition. In the southern Mexican and Guatemalan populations, completely gradating series from blotched to unicolor forms are known. Apparently, the unicolor condition is a local variant, perhaps the result of a single gene mutation, which is distributed throughout the range of the species. The unicolor pattern may occur in all known specimens from a single locality, as is the case for the populations from near La Lima, Honduras, and Los Chiles, Costa Rica, or may appear with typical blotched forms without obvious intermediates, as in the population from near Escuinapa, Sinaloa.

Of primary importance to a discussion of the relationships among the major populations of *Phrynohyas* in Middle America is an understanding of the differences in sizes of the individuals from different populations. The data (Table 1) indicate that *Phrynohyas* from two areas are similar in size. The largest frogs are found in the terminal portions of the range of the species in Middle America, along the northwest coast of Mexico and in Costa Rica and Panamá. The central portion of the range is occupied by smaller frogs. In the past these differences have been interpreted as favoring the recognition of three species. As previously pointed out, there is complete overlap in the measurements from population to population and only slight differences between the ratios. Further, an examination of material from Central America clearly indicates a clinal gradation in body length for frogs from Guatemala (about 64.0 mm average size), Honduras (about 66.4 mm average size), Los Chiles, Costa Rica (about 70.5 mm average size), other Costa Rican specimens (about 83.0 mm average size), and Panamanian specimens (about 87.0 mm average size). This gradation generally is reflected in all other measurements as well (Table 1).

If a clinal trend in size does exist in western and southern Mexico, it is not immediately obvious for two reasons. First, there is insufficient material from Nayarit southward to Chiapas for adequate analysis. Secondly, the data for the southern and eastern Mexican populations, presented by Duellman (1956) and included in Table 1, are lumped for all populations. It is obvious from these data that there is variation in size, sometimes marked and sometimes clinal, from population to population throughout the range of *Phrynohyas venulosa* in Middle America.

The larger specimens of *Phrynohyas* generally are found in areas of low mean annual rainfall, characterized by definite wet and dry seasons. The largest specimens were collected in western Mexico and along the Pacific coasts of Costa Rica and Panamá. Rainfall data from the major localities reveal that the largest individuals of the genus come from areas which have between 200 and 400 mm of precipitation in September and that the smaller individuals come from areas which have between 300 and 500 mm of precipitation in the same month (Vivo Escoto, 1964:200, fig. 11). Duellman (1956: 33) presented evidence which supports the proposed correlation between large size and drier environments. He recorded the largest specimens of his *Phrynohyas spilomma* from San Luis Potosí and Yucatan (mean monthly precipitation for September, between 100 and 300 mm). Frogs of intermediate size were taken from La Libertad, Guatemala (300 to 400 mm precipitation), while the smallest specimens are from Veracruz, Mexico (300 to 500 mm precipitation). This evidence indicates that there is a correlation between the size of the *Phrynohyas* and the amount of annual precipitation as evaluated by the mean monthly precipitation in September, the peak of the rainy season. Rainfall data for March (Vivo Escoto, 1964:202, fig. 12), the driest month of the year, also correlate with the sizes of the individuals from different populations. The largest specimens come from areas characterized by less than 25 mm precipitation in March, while the smallest specimens come from areas where the mean March precipitation exceeds 50 mm.

There are several selective forces that may operate to regulate an animal's size relative to the amount and distribution of the precipitation in a given habitat. The primary factor favoring large size in a dry habitat is water economy. The primary site of water loss in terrestrial and arboreal frogs is the skin. It has been well established that water loss via the skin is reduced in environments of high humidity and increased in environments of low humidity (Prosser and Brown, 1962:32). Thorson (1955:100-116) demonstrated that, within a species, small individuals lose water at a more rapid rate than large individuals. Schmidt-Nielsen (1964:23-32) discussed the advantage of a large body size in arid environments as an adaptation to cope with the continual problems of overheating and desiccation. Bogert and Cowles (1947:33) found that reptiles which live in moist environments lose moisture at a more rapid rate (in terms of the percentage of their original body weight) than those that are found in dry environments. They also point out that there is a definite correlation between habitat selection and ability to resist desiccation. Based on this evidence, it seems that the correlation between size and habitat in *Phrynohyas* represents an adaptive response to the environment. The occurrence of the largest specimens in the driest areas suggests that the osmo-regulatory powers of *Phrynohyas* are increased in drier environments by large size.

There are other factors which should be considered in a discussion of the correlation between the frog's size and habitat. It is generally true that species reach their highest population density in areas of most favorable habitat. As a corollary, it may be assumed that the species probably is less successful in an unfavorable as opposed to a favorable habitat. Success in a less favorable habitat may involve some biological adaptation. In the long term this might lead to a gradual morphological modification through natural selection toward a closer adaptation to the specific habitat. An immediate measure advantageous to the species in an unfavorable habitat would be an increase in size. Salt (1962: 912) has pointed out that large size is a factor in certain avian species to increase their chance of success in unfavorable habitats as a temporary adaptation pending the eventual evolution of specific adaptations to the new habitat. Salt has shown that under some circumstances larger birds are more efficient than smaller individuals. For example, large birds can support a larger amount of tissue without a proportional increase in food requirement. If a large animal can feed at less energy output per gram than a small animal, then the large animal is more efficient, and greater efficiency has a selective value. A selective advantage could give the larger animal more latitude in moving into new habitats than the smaller animal. On this basis it is anticipated that the well adapted smaller form will occur in the favorable habitat, that is, the area occupied for the longest time. Conversely, the largest individuals are to be expected in unfavorable habitats, peripheral to the ecologic and distributional center of the species.

An examination of the distributions of the various *Phrynohyas* populations supports this suggestion. The most favorable habitat, as determined by species density based on collecting records, is in southeastern Mexico and northern Central America and is occupied by small individuals. That all the basic color patterns are represented in the populations from this area adds support to my contention that this area represents the possible center of dispersal of the species in Middle America. The Middle American center of dispersal for *Phrynohyas* is not necessarily the center of evolutionary origin for the species. I suggest that the general habitat now found in southeastern Mexico and northern Central America is similar to the habitat where *Phrynohyas* originated. In an historical sense, one would expect the best ecological fit between a species and its habitat to be in the area where adaptive evolution is most complete. In peripheral populations the degree of adaptation to the habitat is lower because there has been less time for evolutionary change.

An interesting sideline to this argument is that peripheral, drier environments, for several reasons, may not be able to support the same number of individuals as more mesic areas. This could explain the apparent greater density of smaller frogs in the more favorable humid habitats. If the populations of larger frogs in dry regions are composed of fewer individuals than are the populations of smaller frogs, as is indicated by locality records, then another factor might favor a large size frog in drier areas. A large male potentially can call louder and attract more females from a wider area than can a small male at the same site. If the population density of *Phrynohyas* in dry environments is lower than in wet environments, then it would be advantageous to breeding males to be larger and have a louder call. Small males would not face the same problems in the more mesic environments where the population density is higher.

Bogert and Cowles (1947:33) found a rough correlation between the ability of representatives of a species to resist desiccation and the vagility of the species. The populations that exhibit wide latitudes in terms of physiological or ecological parameters usually have the greatest distribution and make the best colonizers. If it is assumed that the frog population that originally moved into peripheral habitats evolved a larger size to counteract suboptimal conditions in the new habitat, and that this larger size was also secondarily advantageous as a water conserving mechanism, then, after a given period of time, it might be expected that further adaptive modifications would appear. In the *Phrynohyas* from Costa Rica such an adaptation exists in the development of the dermal glands.

In specimens collected in late June and July, during the rainy season, the dermal glands in the neck region show relatively little development; the glands of specimens collected during the dry season, in February and March, show extensive development (Fig. 7). In many of the dry season specimens, glandular development is so extensive that parts of the tympanum are concealed (A). The tympanum is never concealed in Costa Rican specimens taken during the rainy season (B). Duellman (1956:31, 38) mentioned that many individuals of his *Phrynohyas spilomma* and *P. zonata* possess heavy glandular folds which obscure part or all of the tympanum. Because of the effects that the apparent

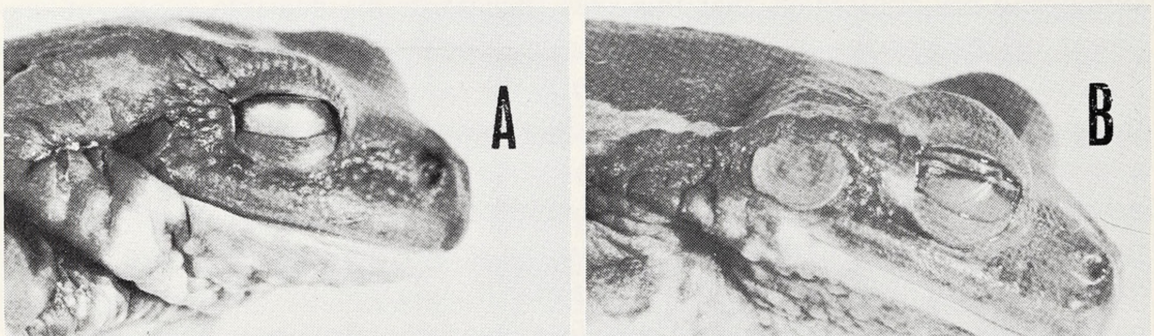

Figure 7. Lateral view of the heads of two Costa Rican *Phrynohyas venulosa* from Guanacaste Province showing the development of the dermal glands in the region of the tympanum. Specimen A was collected in February during the dry season; specimen B was collected in June during the rainy season.

seasonal variation in glandular development has on tympanum size, I did not consider tympanum size in the populational analysis. Small frogs have proportionally larger tympanums than larger frogs, and this difference is ontogenetic. Duellman (1956:39) mentioned a small form of his *Phrynohyas zonata* with a larger tympanum than in typical *P. zonata.*

The secretions of the dermal glands apparently are volatile and poisonous. The effectiveness of this secretion in deterring collectors (Smith, 1941:38; Duellman, 1956:41; Shannon and Humphrey, 1957:18; Neill and Allen, 1959: 26; Janzen, 1962:651) is well attested. It probably is very effective on natural predators, as well. Although differential predation on *Phrynohyas* in the dry season may account for the seasonal variation in glandular development, another explanation seems more plausible.

Slime secretion may be a factor decreasing skin permeability to water (Prosser and Brown, 1962:32). The use of slime secretion as a mechanism to prevent desiccation is well documented in lungfish (Herald, 1961:290; Smith, 1961:77-78). Vellard (1948:143) regarded the thick skin of the frog *Leptodactylus bufonius,* which is very rich in cutaneous glands, as protection against desiccation. McClanahan (1967:88) mentioned the appearance of dark, keratinized skin on *Scaphiopus* while the frog is hibernating, a change in integument effective in reducing water loss through the skin. Robert Stebbins (pers. comm.) reported the appearance of a cellophanelike membrane in *Pyxicephalus adspersus,* an African frog which is especially successful in arid environments. Stebbins wrote that whenever he wished to show the formation of this membrane, in which the frog completely encases itself, he merely placed the animal in a dry container for a few days. Neill and Allen (1959a:25) proposed that the slime of *Phrynohyas* might serve to prevent desiccation in addition to lessening predation. These authors point out that viscous organic liquids are comparatively resistant to evaporation. I have found that this secretion is water insoluble and is difficult to remove when dried. McConkey (*in* Duellman, 1956:41) mentioned that a collecting sac used to carry the frogs became stiff as a board a day or so after the secretion had dried. Vellard (1948:150) reports that in northern Argentina, these frogs use this cutaneous secretion to line the cavities of trees in which they seek refuge. If this is a response to aridity, then this peculiar behavior suggests that *Phrynohyas* has developed a modification to decrease water loss, which is similar to that mechanism utilized by lungfish.

All *Phrynohyas venulosa* examined have these glands, whether the frogs are from areas with a definite wet-dry season or from areas where there is some precipitation throughout the year. Frogs from the dry forests of Costa Rica, where there is a marked wet-dry season, apparently exhibit a change in the glandular development from season to season. It is suggested that the greater development and subsequent secretion of the glands in the dry season is produced as an adaptive response to arid environments. Additional investigation with other populations of *Phrynohyas* is needed to corroborate the evidence. Similar adaptations may occur in other genera of frogs inhabiting arid environments.

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SPECIMENS EXAMINED

MEXICO

Sinaloa: 9.4 mi S. Escuinapa (LACM 6314-19, 7245).
Nayarit: 46.5 mi S. Escuinapa (KU 73879); 22.9 mi E. San Blas (KU 74339, CSCLB 625-31, 633-41).
Colima: 1 mi N. Colima (UMMZ 80018); Paso del Río (UMMZ 108019).
Michoacán: Barranca de Bejuco (UMMZ 104814).
Guerrero: near La Venta (FMNH 10046, 10835, 10836).
Oaxaca: Temascal (LACM 28215-16, 36220-21).
Veracruz: 44 km S. Tampico (JLC 903-04); Salinas (TCWC 19103).

GUATEMALA

Escuintla: Cuyuta (AMNH 74377-90 +58).
Santa Rosa: 45 km S. Guatemala City (LACM 8442); 23 km W. Zacapa (TCWC 16782-91, 16800-09).