pressure, that highlights the significance of larval gill-arch systems and fins in the discrimination of species and genera, and in categorizing ecological types, and simultaneously suggests the greatest caution in using them as indicators of phylogenetic relationship.

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Life History of *Phrynohyas venulosa* (Salientia: Hylidae) in Panamá

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Phrynohyas venulosa breeds in marshy ponds, laying its eggs in a surface film. In the laboratory, the eggs hatched in less than a day and metamorphosis commenced in 37 days. The manner of egg deposition and the presence in early larvae of extremely well-developed external gills are regarded as adaptations to the low oxygen tension prevalent in warm, standing waters. The larva is of the pond type, with globose body, lateral eyes, and well-developed tail fin. It appears to be unique among pond type hylid larvae in having a high number of labial tooth rows, 3/4 or 3/5, with the first upper row broadly interrupted and the labial fringe broken anteriorly. The mating call is a series of raucous, untrilled notes, each (at 27.6°C) lasting about 0.4 sec and separated by intervals of 0.4 to 0.5 sec. There is a broad band of pitch dominance from about 1,700 to 2,700 cps, with the pitch dropping about 300 cycles from beginning to end of call.

Frogs of the genus *Phrynohyas* have a wide distribution throughout tropical and subtropical regions from Mexico to Paraguay. Although some species are fairly well represented in research collections, little ecological information is on record. In his recent review of the genus, Duellman (1956) could present only meager information on the eggs of a single species, and the larva of none of the seven species has been described. Porter (1962) published the only objective data on the mating call of a *Phrynohyas*, but there is reason to question the accuracy of the description. Data gathered by me in Panamá during the summer of 1962 fill in some of the gaps in our knowledge.

The species discussed here was referred to by Duellman (1956) as *Phrynohyas zonata* (Spix) and by Rivero (1961) as *Hyla tibiatrix tibiatrix* Laurenti. I use the name *Phrynohyas venulosa* (Laurenti), following Opinion 520 of the International Commission on Zoological Nomenclature (Hemming 1958).

My observations were made in the vicinity

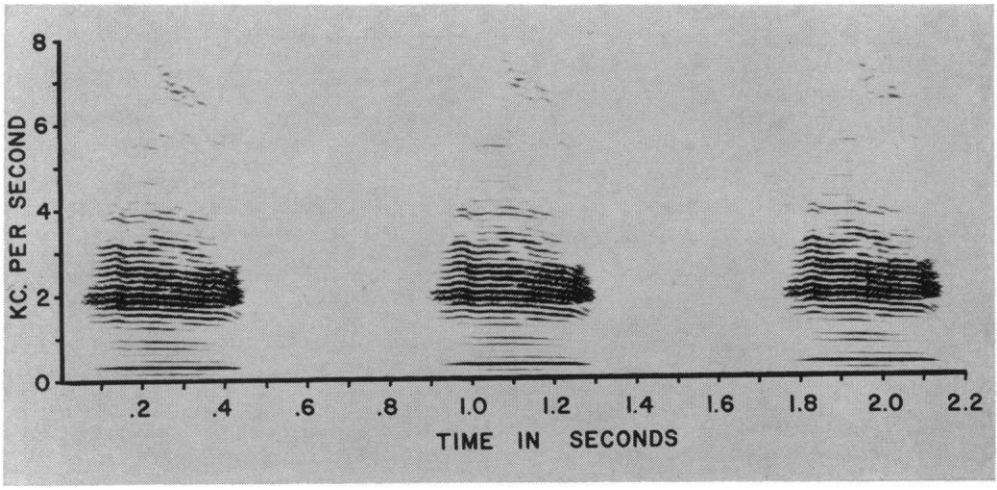

Fig. 1. Audiospectrogram (Sonagram) of mating call of *Phrynohyas venulosa* (AMNH 69807) recorded at a water temperature of 27.6°C on 1 July 1962, 1 mi WNW Nueva Gorgona, Panamá Prov., Panamá.

of the villages of Nueva Gorgona and Bejuco, Panamá Province, Panamá, about 40 miles (airline) southwest of Panamá City, where I spent several weeks in May, June, and July 1962. With the exception of a band of thorn forest fronting the ocean, the land is largely given over to agriculture. Presumably the native vegetation here was savanna. Rainfall at Nueva Gorgona during June 1962 totaled 7.48 in., an average of about 0.25 in. per day. Precipitation generally came in brief, hard showers, and on occasion there were several days in succession with no rain or only a trace of rain. The maximum daily air temperature in June (taken in the shade about 6 ft above the ground) ranged from 26.0° to 35.5°C, and the minimum ranged from 23.0° to 26.0°C.

Mating Call

On the evening of 4 June, following a day of intermittent rain in which 0.85 in. fell, I encountered a chorus of *Phrynohyas* 3 mi south of Bejuco. The frogs were calling from a weedy roadside pond that evidently (from earlier and subsequent observations) held water throughout the rainy season, but may not have been perennial. The water was about 8 in. in maximum depth, and, owing to the abundant emergent vegetation, had little free surface area. Some individuals I saw were sitting on partly submerged twigs or branches, although others called while floating. None was seen or heard in the small trees or bushes fringing part of the pond. The paired lateral vocal sacs each inflate to a volume as great as or greater than that of the head, looking like a pair of "water wings" that cause the calling frog to float high in the water. Gans (1960:302) described the call as "similar to the roar of a bull." The call is quite loud, and in my first encounters I consistently estimated my distance from the frogs as only about one-third of what it actually was. Several other species of frogs contributed to the din: *Hyla microcephala, Hyla staufferi, Eupemphix pustulosus, Leptodactylus labialis, Bufo granulosus,* and *Elachistocleis pearsei.* The first four of these could be found calling around this and similar ponds virtually every night, whereas the last two (and *Phrynohyas*) appeared less regularly.

The call of an individual (AMNH 69807), tape-recorded 1 mile west–northwest of Nueva Gorgona on the evening of 1 July 1962 (a day with 1.13 in. of rain), is illustrated (Fig. 1) by a sound spectrogram (Sonagram). The frog was calling while floating in a flooded area in a cornfield, water temperature 27.6°C. The call consists of a monotonously repeated series of rather raucous notes, each approximately 0.4 sec in length and separated by intervals of 0.4 to 0.5 sec. The repetition rate was about 67 per min. As is typical of such noisy (as opposed to more musical) calls, the energy

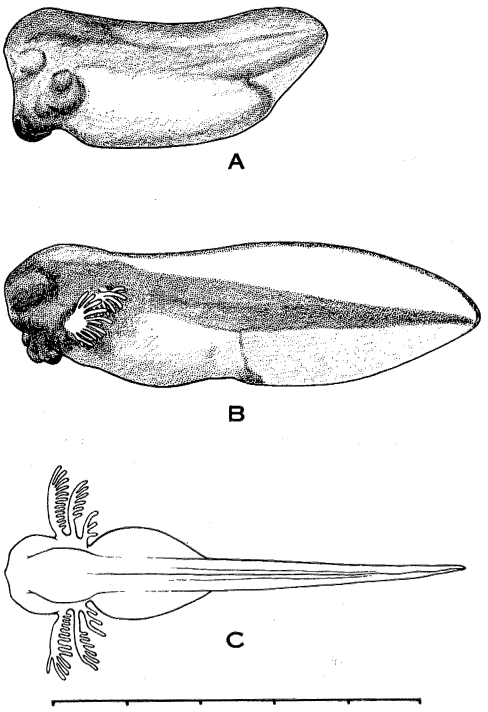

Fig. 2. Early larval stages of *Phrynohyas venulosa*. A. Early stage 18, lateral view (hatching stage). B. Early stage 21, lateral view. C. Early stage 21, dorsal view, pigment not indicated. Elapsed time between stages shown, 14 hr. Scale line indicated relative length of 5 mm.

is broadly distributed throughout the frequency spectrum. The region of frequency dominance spreads from about 1,700 to 2,700 cycles per second (cps) but is not sharply defined. The pitch of the call wavers slightly and drops about 300 cycles between beginning and end.

The only sound spectrogram published so far for a member of the genus *Phrynohyas* is of *P. spilomma*, a Mexican species (Porter 1962). The appearance of this spectrogram differs so widely from that for *P. venulosa* that I suspect some error. The duration of call shown is similar, approximately 0.5 sec, but the dominant pitch is between 6,000 and 7,000 cps. Porter (1962: 170) wrote that the pitch "is surprisingly high in consideration of the large size of the species." This is, perhaps, an understatement. The highest-pitched call I find recorded in the literature is that of the tiny *Hyla ocularis*, for which Blair ("1958" [1959]:83) recorded a dominant pitch of about 7,000 cps. It seems most unlikely that a mating call described as "a loud, nasal 'grawl'" (Duellman 1960a:66) would have a dominant frequency as high as that of *Hyla ocularis* and several other tiny frogs with high-pitched squeaking or peeping calls. Perhaps an electronic or even a simple mechanical inversion of the spectrogram took place, for it much more closely resembles my spectrograms of *P. venulosa* when inverted.

Eggs and Larvae

On the evening of 1 July 1962, while recording the call discussed above, I heard another individual calling in the distance. The frog stopped calling shortly before I reached the pond where I supposed it to be, but I saw there a mated pair of *Phrynohyas* which eluded capture. The next morning I found and collected eggs where the frogs had been seen. The following descriptions of eggs and larvae are based on individuals from that collection. The identity of the eggs as those of *Phrynohyas* was confirmed by raising several of the larvae through metamorphosis. The developmental series upon which the following descriptions are based is No. 69808 in the amphibian collection of the American Museum of Natural History.

Eggs.—The eggs are deposited as a surface film, with a distance of about 1.5 cm between eggs. In the single instance observed, the clutch was confined to an area of about 1.5 m^2, although it did not cover the entire area, being interrupted by emergent clumps of grassy vegetation. Duellman (1956:23) recorded a similar manner and area of deposition for *Phrynohyas ingens*, a form that Rivero (1961:131) regarded as a subspecies of the present species. When I collected the eggs, they had already developed past the stage where an accurate measurement of the diameter of the vitellus could be made. The diameter of the outer jelly coat is approximately 3.5 mm.

Larval development.—Unless specified otherwise, the following descriptions are based on specimens preserved in formalin. Staging of larvae follows the system of Pollister and Moore (1937) as extended by Limbaugh and Volpe (1957) and Gosner (1960). Because I could not make microscopic observations on the living young larvae, staging is based on general morphology rather than on more precise criteria like heartbeat and gill circulation.

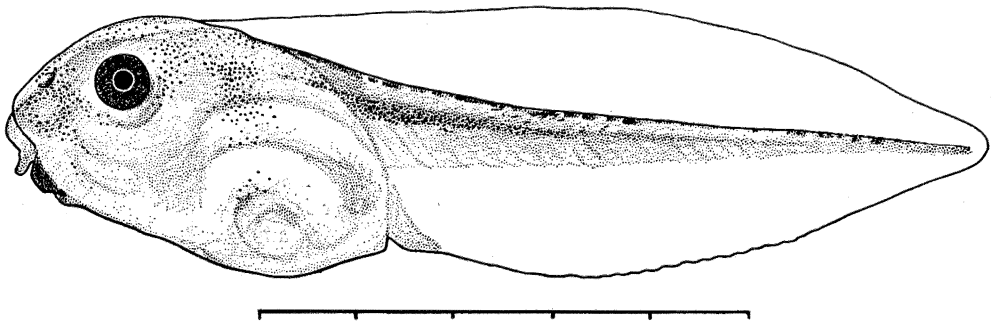

Fig. 3. Larva of *Phrynohyas venulosa*, stage 25. Scale line indicates 5 mm.

Hatching occurs early in stage 18 (Fig. 2A). Five individuals preserved at hatching range from 3.8 to 4.4 mm total length, mean 4.1 mm. By early stage 21 (Figs. 2B, C) the larvae reach an average length of 6.5 mm (range 6.0 to 6.6 mm in 10 specimens), and the external gills are extremely well developed. In these early stages there is no pattern to the distribution of brown pigment other than a slight accumulation along the edge of the dorsal fin in stage 21.

Ten specimens in stage 25 (Fig. 3) average 10.0 mm total length, range 9.5 to 10.5 mm. A few deep melanophores are present on the body, and those present on the tail musculature are organized into a diffuse lateral line and a series of dorsal spots. The lungs are conspicuous in the living tadpoles. The adhesive organs are still evident at this stage and are dark in color.

The average total length of six specimens in stage 26 is 14.6 mm, range 13.6 to 15.8 mm. Melanic pigmentation is considerably denser than in the previous stage. The dark streak on the side of the tail musculature extends forward onto the body, separating the relatively pale dorsal surface from the paler abdominal wall. There is a faint stippling of melanophores in the upper tail fin, but the intensity of the melanic edging of the fin is reduced. The position of the adhesive organs is made evident by accumulations of melanin, but the organs themselves are virtually gone.

Eight specimens in stages 27 and 28 range in total length from 17.6 to 19.0 mm (mean 18.3 mm), and in body length from 6.8 to 7.5 mm (mean 7.0 mm). The height of the tail fin from edge of ventral to edge of dorsal fin 4.1 to 4.6 mm, and the ratio of fin height to body length ranges from 0.59 to 0.66, mean 0.62. Pigmentation is similar to that described for stage 26. The dark lateral band on the proximal third of the tail musculature passes upward distally to join the dark dorsal edge of the musculature. A continued increase in the amount of dark pigment on the body leads to a reduction in the striped appearance of earlier larvae. There is no dark pigment ventrally on the abdomen. The dorsal tail fin shows a stippling of melanophores, some of which anastomose into a dendritic pattern.

Five tadpoles in stages 35 and 36 range in total length from 34.0 to 43.5 mm, and in body length from 11.4 to 14.4 mm. Fin height is 7.2 to 9.8 mm, giving a ratio of fin height to body length of 0.63 to 0.74, mean 0.68. This indicates a slight increase in relative fin height as the tadpoles grow. The appearance of specimens preserved in formalin differs from that of the earlier stages only in the presence of melanophores in the lower tail fin. Notes on color in life were made for four individuals in stages 35 and 36. The dorsal ground color of the body is golden brown with no evident pattern other than an accumulation of clumps of golden cells along the lateral-line system. Under magnification, the superficial pigmentation resolves into an even scattering of brown and golden cells, with the former more numerous. The deeper layer of pigment is similar, but contains more melanophores. The deep abdominal layer is golden, and the chest has more gold than is present dorsally, but some melanophores are present also. There is a ragged lateral stripe of melanophores on the proximal third of the tail musculature, but it fades distally. The upper and lower fins show a stippling of melanophores and golden cells with occa-

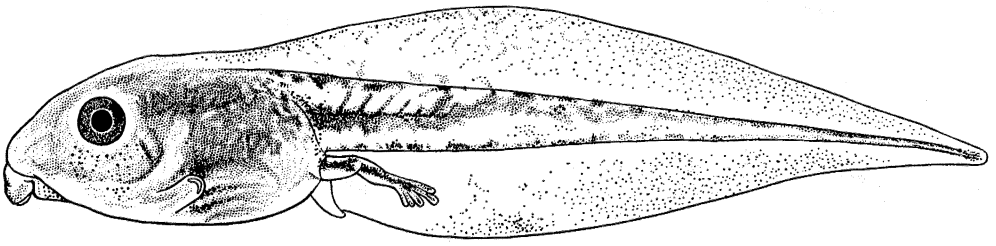

Fig. 4. Larva of *Phrynohyas venulosa*, stage 38. Total length 42 mm.

sional slight accumulation along blood vessels. The typical appearance of a large tadpole (stage 38) is illustrated in Fig. 4.

The largest tadpole preserved is in stage 41 and has a total length of 49.4 mm, body length 15.5 mm, and fin height 10.4 mm. The larva of *Phrynohyas venulosa* is typical in body form of pond type tadpoles with deep, tapered fin, mouth directed forward, and eyes placed laterally so that they are visible from both above and below. The spiracle is on the left side of the body. Although hylid frogs commonly have a dextral anal tube, in this species it is median, appearing as if the thin tail fin were split at the base to form the tube.

Metamorphosis takes place at a body length of about 15 to 16 mm. The characteristic pattern of the adult frog is not assumed until several days after metamorphosis appears complete. The dark longitudinal stripe so evident on the hind leg of the large tadpole (Fig. 4) persists in the newly transformed frog and the variable dark figure on the back is slow to appear, so that for a few days the young frog, with unicolored back and striped legs, looks quite unlike the boldly patterned adult (Fig. 5).

Mouthparts.—The mouthparts in my specimens are quite variable, even among individuals of the same general size and stage of development. A somewhat idealized, fully developed condition is illustrated (Fig. 6). The labial fringe is consistently interrupted anteriorly. It is single on the anterior edge of the mouth, somewhat irregularly double on the posterior edge, and multiple in the corners of the mouth. Not infrequently there is a deep indentation in the middle of the lower lip; the fringe is continuous through this indentation.

The anterior (upper) rows of labial teeth are fairly constant in length and continuity. The first row is broadly interrupted, the second complete, and the third interrupted but with a smaller gap than the first. In many instances the first row is weakly developed. The lower rows of labial teeth are variable in number and continuity. Five rows may be present, but more often there are only four. As a rule, the fourth row is complete, but the others usually are interrupted, often without regard to symmetry. Most of the larger tadpoles, stage 35 and up, have the upper beak poorly developed, as if metamorphic changes were taking place at an early stage. Younger specimens show complete beaks.

The mouthparts are relatively small. In 15 specimens the width of the oral disc is 41 to 47% of the width of the body, mean 44%. The anterolateral edges of the disc are capable of folding toward the midline, in effect closing the mouth and giving a triangular shape to the mouthparts.

Rate of development.—I assume that the mated pair of frogs observed on the evening of 1 July were the parents of the eggs collected at the same spot the following morning. If this is so, the eggs were deposited later than 8:30 PM on 1 July and commenced hatching about 5:30 PM on 2 July, a period of less than 21 hr. Judging from water temperatures taken earlier in the evening, the eggs were deposited at about 27°C. In the course of development they may have been exposed to temperatures as low as 25°C and as high as 33°C, the minimum and maximum air temperatures recorded on 2 July. The eggs were collected early in the morning before being heated directly by the sun and were kept indoors, so they probably did not reach the extreme of 33°C.

The first tadpole metamorphosed on 6 August, at an age of 37 days. Considering that the tadpoles were kept under what were possibly unfavorably crowded conditions, a faster rate of development is possible. The tadpoles fed ravenously on

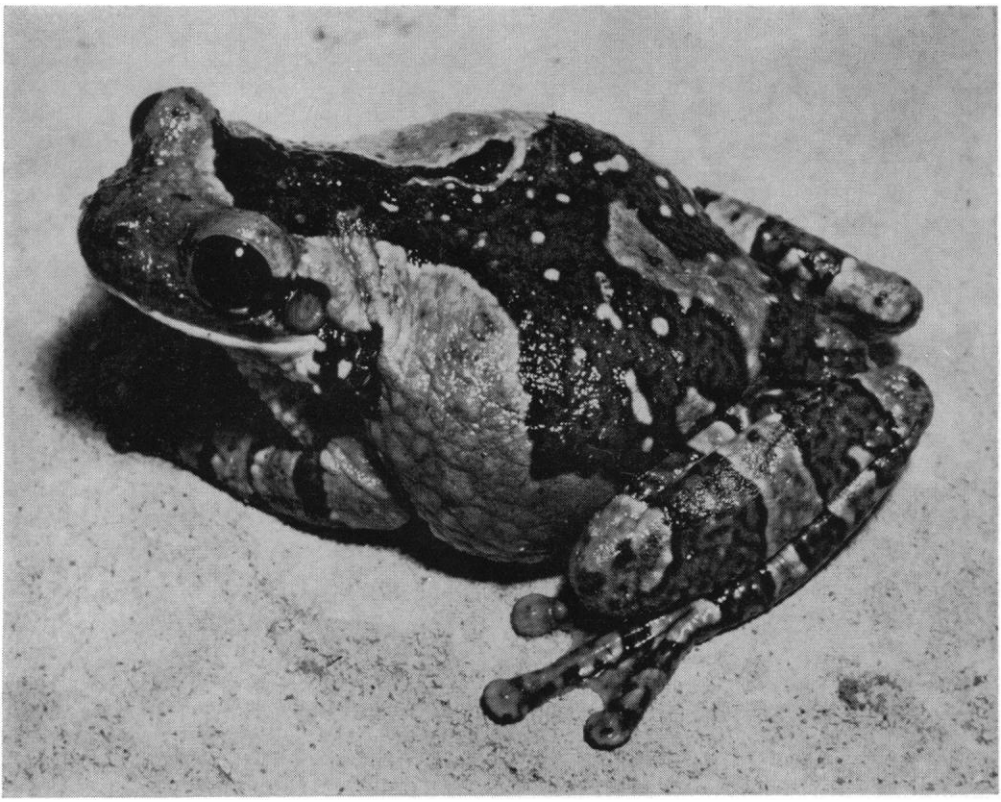

Fig. 5. Adult female *Phrynohyas venulosa*, AMNH 69805, from Nueva Gorgona, Panamá.

canned spinach supplemented occasionally by boiled lettuce.

Adaptations of the eggs and larvae.—*Phrynohyas venulosa* is clearly well adapted to spend its early life in warm, stagnant waters. The surface film type of egg mass is an adaptation to the relatively low oxygen tension present in warm, standing water (Moore 1940). Tadpoles at stage 21 (Figs. 2B, C) were observed to hang vertically with their large external gills spread out at the surface of the water. The significance of such gills for tadpoles living where dissolved oxygen may be in short supply was discussed by Noble (1927:98) and Savage (1961:22). The presence of conspicuous lungs in the young (stage 25) *Phrynohyas* tadpole probably is also an adaptation to life in warm, stagnant waters, in accord with the interpretations of Savage (1961: 54–55).

Comparison with other hylid tadpoles.—Although published descriptions of hylid tadpoles reveal a wide range of variation in body form and morphology of mouthparts, the larva of *Phrynohyas venulosa* appears unique in the following combination of characters: pond type larva with deep, tapered tail fin, globose body, and laterally placed eyes; oral disc directed forward, small, less than half the width of the body; labial fringe interrupted on the anterior edge of the mouth; labial teeth in 3 upper and 4 or 5 lower rows, the first upper row being broadly interrupted and most of the lower rows generally irregularly broken; median rather than dextral cloacal tube.

The tooth-row formula most often encountered in hylid larvae is 2/3. This formula occurs in all *Hyla* and *Pseudacris* of the United States (*H. crucifer* is sometimes 2/2) and in many species of *Hyla* in Latin America as well. The larvae of several species of *Phyllomedusa* are known (Starrett 1960), and all have the 2/3 formula except the peculiar funnel-mouthed *P. guttata* (Lutz and Lutz 1939). Among other genera, *Smilisca baudini* (Stuart 1948), *Pternohyla fodiens* (Webb 1963), *Plectrohyla* (sev-

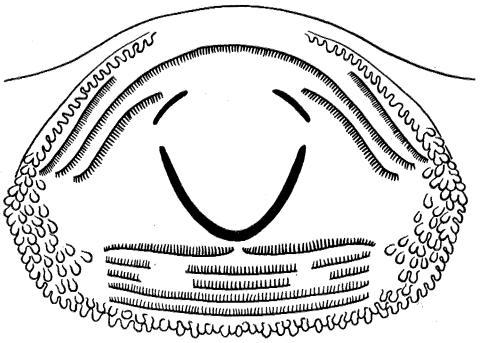

Fig. 6. Generalized appearance of mouthparts of mature larva of *Phrynohyas venulosa*. The beak may be more or less complete than shown, and the lower rows of labial teeth may be extensively interrupted. The degree of development shown is reached by stage 27 or 28.

eral species: Hartweg and Orton 1941, Stuart 1942), and *Triprion petasatus* (Maslin 1963) are 2/3.

Higher tooth-row formulae do occur frequently in hylid species, but almost invariably (the exception is *Phrynohyas*) appear to be associated with adaptation to life in swiftly moving waters. Examples are *Hyla colymba* (Dunn 1924, 1931), *Hyla* (*Hylella*) *smaragdina* (McDiarmid 1963), *Hylella sumicrasti* (Starrett 1960), *Ptychohyla spinipollex* (Stuart 1948), *Ptychohyla leonhardschultzei* (Duellman 1960b), *and Ptychohyla schmidtorum chamulae* (Duellman 1961). These tadpoles have the depressed body and low tail fin commonly found in stream type tadpoles, together with a large oral disc directed more or less ventrally. The papillary border is complete, not interrupted anteriorly as it is in *Phrynohyas*, and the first upper row of labial teeth is not broadly interrupted.

If the distinctness of the tadpole of *Phrynohyas venulosa* proves to be typical of other species of *Phrynohyas* as well, it might be advisable to include the characters of the tadpole in the definition of the genus. Rivero (1961:127–131) questioned the adequacy of the diagnostic characters attributed to *Phrynohyas* by Duellman and referred the Venezuelan species to the genus *Hyla*.

Acknowledgments

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