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# THE GLADIATOR FROGS OF MIDDLE AMERICA AND COLOMBIA—A REEVALUATION OF THEIR SYSTEMATICS (ANURA: HYLIDAE)

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## INTRODUCTION

It seems appropriate to refer to the *Hyla boans* species group as the gladiator frogs in view of their extremely pugnacious behavior and the well-developed pre-pollical spines that they use when fighting. According to Duellman (1970, 1977), *boans* (Linnaeus), *circumdata* (Cope), *crepitans* Wied, *faber* Wied, *pardalis* Spix, and *rosenbergi* Boulenger constitute this natural assemblage. In the summer of 1975, I began a field study of the northern-most species, *boans, crepitans* and *rosenbergi,* in an attempt to determine the selective bases for the aggressive behavior exhibited by the males in defense of their mud nests (Breder, 1946; Lutz, 1960a, b). Eventually, the field work was focused on the forms occurring in Panamá, and the study of several of those marked populations is still in progress. It became clear from my earliest field research on the gladiator frogs that Duellman (1970) had overlooked a species in his monograph, "The Hylid Frogs Of Middle America". The following systematic review corrects that oversight and attempts to summarize the available data on the group's geographic distribution and phenotypic variation throughout Middle America and Colombia. It is not reasonable to treat all South American gladiator frogs at this time because the number

of samples and sample sizes of the more southern forms are too small, and I have too little knowledge of what these animals look and sound like in life.

## METHODS AND MATERIALS

Snout to vent length (SVL), head width at the angle of the jaws, tympanum width, and width of the toe pad of the third finger were measured in millimeters with vernier calipers on each well-preserved, reproductively mature specimen. SVL was used as the independent variable in all analyses of covariance (ANCOVA). Analysis of variance (ANOVA) was employed in the study of size variation (SVL). Computer programs (MIDAS) provided by the Statistical Research Laboratory of the University of Michigan were employed in all data analyses. The other characters examined are defined as follows: the calcar, a fleshy extension of the heel, was scored as absent (0) to well-developed (2); the degree of webbing between the third and fourth fingers was scored in five states—absent (0) to completely webbed (4), viz. to the base of the expanded toe discs; the palpebral membrane pigmentation was scored as completely transparent (0) to densely pigmented (2) and reticulated (3); the postauricular ridge, the fleshy fold immediately posterior to the tympanum, was considered absent (0) to well-developed (2). The Median Test (Siegel, 1956) was applied to the last four characters because of the ordinal scale in which their states are described. I have set the significance level at .05 for all statistical tests. In the species' accounts and Figure 8a and b, the average is given followed by one standard error of the mean in parentheses.

Two or more geographically contiguous sets of local samples of each species were used to assess geographic variation. The particular compositions are described in the sections on Geographic Variation. A gazetteer of the localities referred to in Appendix I can be obtained from the author.

## *HYLA PUGNAX O.* SCHMIDT
## A VALID SPECIES OF GLADIATOR FROG

Oscar Schmidt gave a brief Latin description of *Hyla pugnax* in 1857, and in the following year he provided a much longer characterization, in German, of his new species. Both descriptions appear to be based on the same individual (in fact the formal Latin diagnoses are nearly identical), which Schmidt said was collected by

the botanist J. von Warszewicz and deposited in the Krakau Museum (The Zoological Cabinet of Krakau). The type locality of *pugnax* was given (Schmidt, 1858) as "am Chiriquí-Flusse unweit Bocca del toro." Cope (1867) listed *pugnax* from Costa Rica and Günther (1858) and Brocchi (1882) cited it for Panamá (Chiriquí). There is no evidence that these three authors had additional material of *pugnax* before them.

Savage (1972) concluded that all the other amphibians collected by Warszewicz with the type locality of "Río Chiriquí near Bocas del Toro" (*Bufo simus, Hyla splendens, Hyla molitor* and *Hyla molitor marmorata)* came from South America, and in particular from Perú and Bolivia. The inference might be that *pugnax*'s type locality is also in error and that it too came from western South America. Furthermore, Duellman (1970; 1977) stated that the type locality of *pugnax* was in error. While the exact type locality may be incorrect (see below), it seems unlikely that the holotype could have come from the Perú-Bolivia area, which is the only part of the South American continent known to have been visited by Warszewicz, because *pugnax*'s distribution (see below) is almost certainly restricted to Panamá and eastern Colombia.

Subsequently, Savage stated (personal communication) that the type locality of *pugnax* "must be lowland, near Bocas del Toro. Several small streams along the north coast of what was then Chiriquí province, but is now Bocas del Toro province are called Río or Caño Chiriquí. The most likely candidate is the Río Chiriquí between the Rio Guarumo (Guarmo) and Chiriquí Grande. . . The village of Chiriquí is located on the west bank of this stream, near its mouth. Chiriquí Grande was established in the early 1900's by the Bananera (United Fruit) with a railhead (Eureka). On the other hand Flusse might mean streams. Perhaps Warszewicz just meant somewhere on the mainland across from Bocas del Toro. In that case the type is probably from near Róbalo, since he traveled by boat from there to Bocas del Toro." Contrary to Savage's conclusions, I believe restricting the type locality to the Caribbean drainage is unjustified given the general nature of the locality data provided by Schmidt, which I translate from the German as: along the Chiriquí rivers not far from Bocas del Toro. "Chiriquí rivers" could even refer to one of those around David, and possibly the Chiriquí River itself. I favor this interpretation because it is not inconsistent with the information provided by Schmidt, nor Warszewicz's itinerary, and it fits the Pacific lowland distribution of the species that I am calling *pugnax*.

Savage (1970) listed a specimen (1009/1339) in the Krakow Museum in the Department of Systematic Zoology, Jagellonian University as H. *pugnax*. He also stated (personal communication) that "Dunn saw the type in 1929—but his notes only list it as a synonym of *crepitans* without comment." Apparently, no other examples of *pugnax* were deposited at the other museums known to have received some of Warszewicz's amphibians and reptiles. Henryk Szarski, Professor of Comparative Anatomy, Jagellonian University, Krakow, kindly loaned me the only known specimen of *pugnax* collected by Warszewicz. Szarski stated (personal communication) that "One specimen of *Hyla pugnax* was found in our museum, signed KM 1009 and we hope that it is the holotype." Duellman (1970; 1977) claimed that the location of the holotype of *pugnax* is unknown. The only information accompanying the Jagellonian University specimen is written on the label glued to an isolated piece of glass. The label reads, "N.J. 1009. *Hyla pugnax* Nov. Granada." New Granada was the general term applied to the lower part of the Middle America that Warszewicz is known to have visited. The specimen KM 1009 agrees in all details with the type description of *pugnax*. In fact, my measurements (in parentheses) are nearly identical to those given by Schmidt: body 62 mm (62.1); foreleg 38 mm (37.1); hindleg 100 mm (100.0). There can be little doubt that KM 1009 is the specimen upon which Schmidt based his description of *pugnax,* and it seems to have been the only individual available to him. I conclude that KM 1009 is the holotype of *pugnax* and the only specimen of that species collected by Warszewicz.

Duellman (1970; 1977), as did Boulenger (1882), placed *pugnax* in the synonomy of *Hyla crepitans.* However, Duellman (1970) was aware of the existence of a local population at Río Bejuco, Panamá that is similar to *crepitans* and *rosenbergi*, but does not agree with either very well. He noted the large size (78.2 mm), absence of a dark dorsal body stripe and the reduced webbing between the fingers. A tape recording of the call of a frog from the Río Bejuco population had certain call similarities to both *rosenbergi* and *crepitans* (Figure 1), and Duellman concluded (1970: 257) that it might indicate the existence of hybridization between those two species. A Río Bejuco specimen (AMNH 69766) collected at the same time and place that the recording was made is similar to the holotype of *pugnax,* as is considerable material from elsewhere in Pacific Panamá and eastern Colombia (see *pugnax* locality records below). The fact that *pugnax* is never

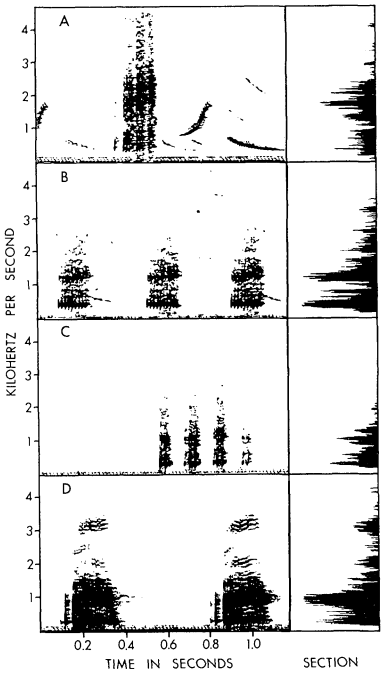


FIG. 1. Sonogram of (A) *crepitans,* (B) *pugnax,* (C) *rosenbergi,* and (D) *boans.* Modified after Duellman (1970).

TABLE 1

PLACES OF LOCAL SYMPATRY IN GLADIATOR FROGS

| | | | |
|---|---|---|---|
| *crepitans* | 1,2 | | |
| *pugnax* | | 4,5,14 | |
| *rosenbergi* | 12,13 | 6,7,8*,9,10,11 | 3 |
| | *boans* | *crepitans* | *pugnax* |

*personal field observations

1. Guaicaramo, Boyacá, Colombia
2. Villavicencio, 489 m, Meta, Colombia
3. Socorre, upper Río Sinu, 100–150 m, Córdoba, Colombia
4. Finca El Aranar, near Bonda, Magdalena, Colombia
5. Fundación, Magdalena, Colombia
6. Alhajuela, Canal Zone, Panamá
7. Camp Chagres Boy Scout Camp, 120 m, Canal Zone, Panamá
8. Chiva Chiva Road Quarry, Canal Zone, Panamá
9. Madden Dam, Canal Zone, Panamá
10. San Pablo, Canal Zone, Panamá
11. Summit Gardens, 100 m, Canal Zone, Panamá
12. Río Frijoles, Canal Zone, Panamá
13. Río Tuira at Río Mono, 130 m, Darién, Panamá
14. Tonosí, 40 m, Los Santos, Panamá

in sympatry with both *crepitans* and *rosenbergi* and only rarely so with either of them alone (Table 1) forces me to reconsider Duellman's interpretation of a hybrid origin for the *pugnax* morphotype. The following diagnoses and descriptions of geographic variation lend additional support to my hypothesis that four species of gladiator frogs, *boans, crepitans, pugnax* and *rosenbergi,* occur in Middle America and Colombia.

## SPECIES ACCOUNTS

### *Hyla boans* (Linnaeus)

*Rana boans* Linnaeus. 1758, Syst. Nat., ed. 10, 1:213. Type locality: "America".

DIAGNOSIS–Within the gladiator group, *boans* is the largest species, and it exhibits no significant size (SVL) sexual dimorphism (Figure 8a). It is unique within the group in possessing a golden reticulated palpebral membrane, and it is further diagnosed by its darkly pigmented color pattern of bars on the side of the body and anteroventral surface of the thigh, nearly completely webbed fingers, and usually well-developed calcar.

GEOGRAPHIC DISTRIBUTION–*Boans* appears to be restricted to lowlands of northeastern Panamá and western and southern Colombia. The discontinuous distribution of *boans* in Panamá is probably due to lack of collecting; however, its absence from the Río Magdalena drainage of Colombia can not be related to the lack of such effort (Figure 6). *Boans* is locally sympatric with *crepitans* and *rosenbergi* (Table 1).

DESCRIPTION–Snout-vent length 97.3 (±1.78); head width 32.4 (±.90); typanum width 4.7 (±.12); width of toe pad at the end of the third finger 4.9 (±.16); calcar 1.75 (±.07); webbing 3.8 (±.04); palpebral membrane 2.9 (±.05); postauricular ridge .10 (±.03).

SEXUAL DIMORPHISM– None of the variables was found to be significantly different between the sexes when geographic origin was ignored.

GEOGRAPHIC VARIATION– The *boans* from the Amazonas and Orinoco drainages (N=11♂♂, 8♀♀), departments of Amazonas, Boyacá, Caquetá, Meta and Vaupés, were compared to all others (N=44♂♂, 11♀♀).The ANCOVA revealed significant differences in only the tympanum width regressions when the males and females were considered separately; the Amazonas-Orinoco samples tend to be relatively larger. When the sexes were lumped and the males

considered alone they were also found to have significantly different toe pad regressions, those from the Amazonas-Orinoco drainages usually being smaller. Among the ordinal variables, webbing was found to be significantly different, and it was so only in the males (the Amazonas-Orinoco sample has less).

ONTOGENETIC VARIATION–Recently metamorphosed *boans* have a well-developed palpebral reticulation; however, unlike adults, those same individuals have greatly reduced webbing and numerous small dark spots on the dorsal body surface.

## *Hyla crepitans* Wied

*Hyla crepitans* Wied. 1824, Abbild. Naturgesch. Brasil., Weimar, p. 47, pl. 48, fig. 1. Type locality: Tamburil, Jiboya, Arrayal da Conquista, Bahia, Brasil (restricted to Tamburil, Condeubas, Bahia, Brasil, by Bokermann, 1966).

DIAGNOSIS–Within the gladiator group, *crepitans* is the smallest (SVL) species, and females are considerably larger than males (Figure 8b). It usually possesses a densely pigmented palpebral membrane, lightly pigmented lateral body color pattern (Figure 2), very little webbing between the fingers (Figure 4); it does not possess an obvious color pattern of dark bars on the anteroventral surface of the thigh (Figure 3), nor does it exhibit a well-developed calcar.

GEOGRAPHIC DISTRIBUTION–*Crepitans* has a discontinuous geographic distribution in Panamá and Colombia (Figure 7). It is widespread throughout the Pacific lowlands of central Panamá (Canal Zone and the provinces of Cocle, Los Santos and Panamá), but it is unknown from the Darién. In Panamá, *crepitans* usually breeds in disturbed environments, particularly shallow, temporary pools at the margins of forest. In Colombia, it is widespread throughout the Magdalena River basin and it is also known from several minor river systems that independently empty into the Caribbean. In addition, there are a few locality records for this species from the Orinoco drainage (Boyaco and Meta departments). *Crepitans* ranges from sea level to 1580 meters. The geographic ranges of *crepitans* and *pugnax* are extremely similar and the two species are locally sympatric at three localities (Table 1). *Crepitans* is frequently found with *rosenbergi* and occasionally with *boans*.

DESCRIPTION–Snout-vent length 55.6 (±.38); head width 18.6 (±.13); tympanum width 4.2 (±.03); width of toe pad at end of third finger 2.6 (±.05); calcar .03 (±.01); webbing 1.6 (±.02); palpebral membrane 1.6 (±.04); postauricular ridge 2.

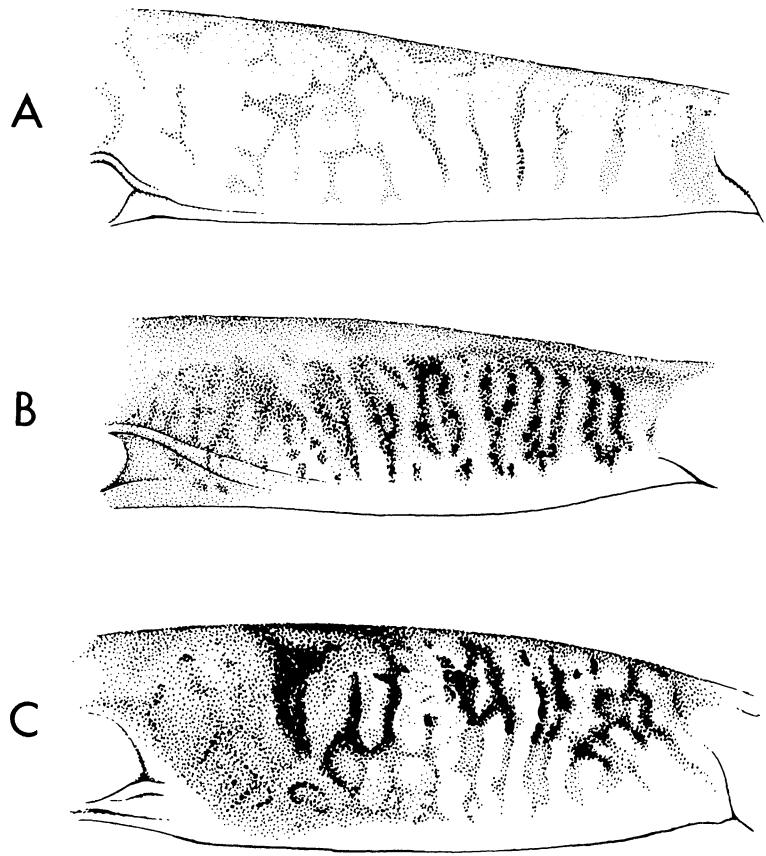


FIG. 2. Left lateral view of the body showing the color pattern and its intensity in (A) *crepitans* X3, (B) *pugnax* X2, and (C) *rosenbergi* X2.

SEXUAL DIMORPHISM– Females are significantly larger than males (SVL $\bar{x}_{\delta}$ = 54.4; $\bar{x}_{\varphi}$ = 61.2). None of the other variables differed significantly when geographic variation was ignored.

GEOGRAPHIC VARIATION– The *crepitans* were divided into the following three samples for the purpose of studying geographic variation: (1) Orinoco drainage (N = 27 ♂♂; 14 ♀♀), departments of Boyacá and Meta, (2) all other Colombian material (N = 59♂♂; 14♀♀), and (3) Panamá (N = 31♂♂; 9♀♀). The Colombian (2) samples of males and females were significantly smaller (SVL $\bar{x}_{\delta}$ = 53.0; $\bar{x}_{\varphi}$ = 58.2) than those from Panamá and Orinoco; the latter are lumped in Figure 8b ($\bar{x}_{\delta}$ = 55.0; $\bar{x}_{\varphi}$ = 62.8). In the case of males alone, the Colombian (2) sample is significantly different

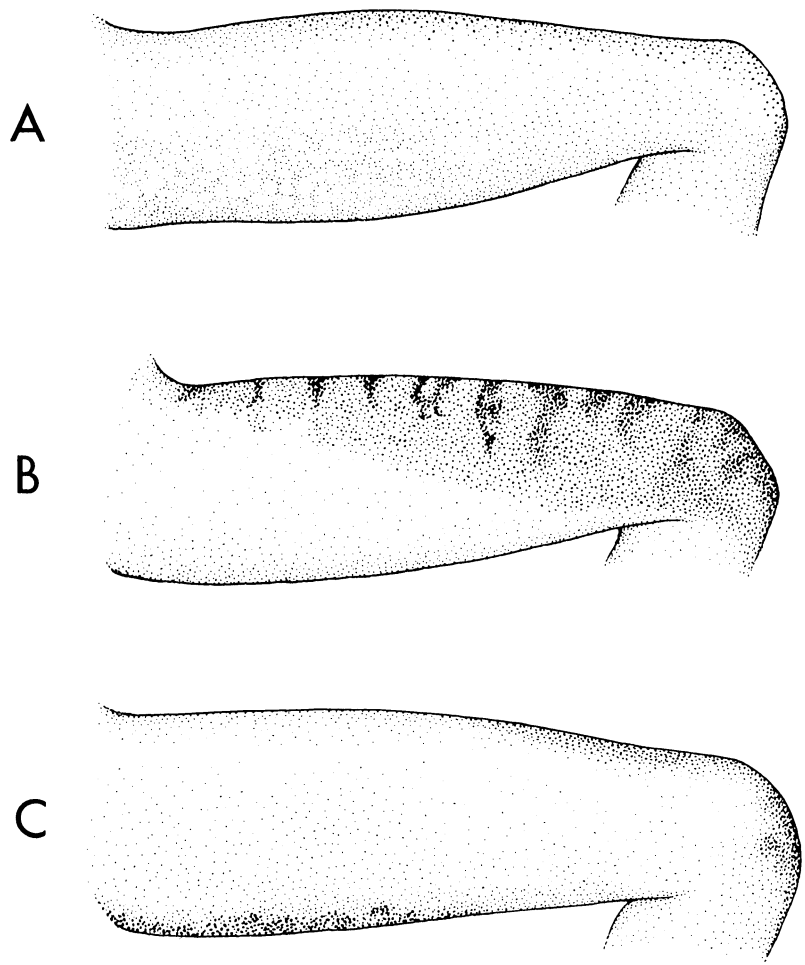


FIG. 3. Ventral view of left thigh showing the extent of the color pattern in (A) *crepitans* X3, (B) *pugnax* X2, and (C) *rosenbergi* X2.

in having a narrower head, whereas the Panamá material is different in possessing a wider tympanum. Where females are analyzed separately, all three samples differ significantly in head width; Panamá specimens average the largest and Colombia the smallest. When the morphometric variables are not separated by sex there are significant differences in all three. All three geographic samples differ significantly in head and tympanum size; Panamá is the largest and Colombia the smallest. In the case of the toe pad variable, the Orinoco sample is significantly larger than the Panamanian

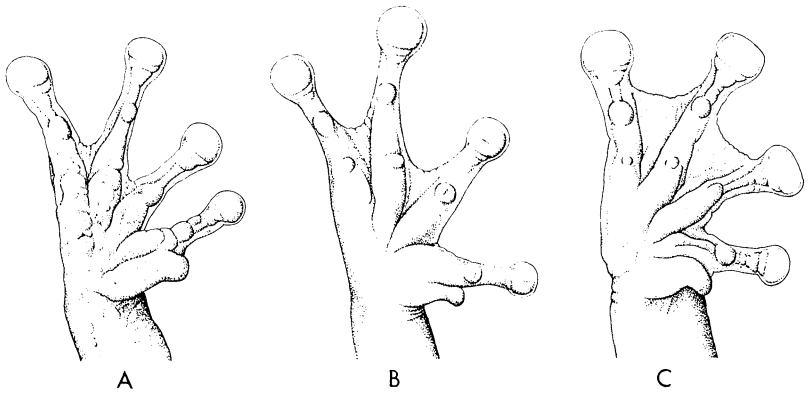


FIG. 4. Ventral view of the right hand showing the extent of webbing in (A) *crepitans* X4, (B) *pugnax* X2, and (C) *rosenbergi* X2.5.

and Colombian. Among the ordinal variables there are some interesting patterns of significant differences in webbing. When the sexes are analyzed separately, males from the Orinoco show less webbing than those from Panamá and Colombia. However, it is only the females from Panamá that are significantly different from those from Colombia; the former have less webbing. When the data set is not separated by sex, all three samples are significantly different; Panamá has the least webbing and Orinoco the most.

REMARKS–Duellman (1977) stated that AMNH 785 is a syntype of Wied's (1824) *crepitans*. While this specimen is part of the Wied collection purchased by the American Museum of Natural History, there is nothing in the register accompanying the material to indicate that AMNH 785 is a type of *crepitans*. In fact, the register does not note the type status of any of the purchased specimens. I have examined AMNH 795, which is in extremely poor condition, and I find it to be similar to Wied's original description and plate. It is a female, 66.0 mm SVL. Wied's plate shows no evidence of the enlarged prepollical spine characteristic of male gladiator frogs, and the author gave the length of the species as "2 zoll 6 linien" which is about 64 mm. The lateral body and anteroventral thigh color patterns of conspicuous dark bars in AMNH 785 are very similar to the specimen Wied illustrated. Moreover, the uncommon dorsal body spotting and discontinuous nature of the middorsal stripe are nearly identical in the specimen and illustration. These numerous similarities lead me to conclude that AMNH 785 formed the basis of Wied's original description of *crepitans* and I designate it the lectotype.

The name *crepitans* clearly applies to Brasilian populations; however, they are probably not the same species that I am calling *crepitans* from Middle America and Colombia. Immediately southeast of Colombia there exists a complex of *crepitans*-like forms, almost certainly representing more than two species, which differ in color, pattern, size, advertisement call and breeding biology. The lectotype of *crepitans* is similar to one of the forms that does not appear to intergrade with the Colombia-Panamá species that I am referring to as *crepitans.*

Duellman (1970) suggested that the *crepitans* from Tela, Honduras (AMNH 45997) might represent a valid record because at least one other predominantly South American species, *Cnemidophorus lemniscatus,* is known to have a similarly exceptional disjunct distribution in Middle America. The lizard and frog comparison does not form the basis for a particularly compelling argument. Aside from the fact that one species is dry-adapted and the other wet, their distributions are hardly similar. *Lemniscatus* is much more widely distributed in Middle America; it is known from the Atlantic versant from Guatemala to Nicaragua and from Panamá to Brasil (Meyer and Wilson, 1973). Meyer and Wilson (1971), in their review of the Honduras herpetofauna, referred to the Tela record for *crepitans* as erroneous, and I accept their conclusion in the absence of direct evidence to the contrary.

### *Hyla pugnax* O. Schmidt

*Hyla pugnax* O. Schmidt. 1857, S. Ber. k. Akad. Wiss., math.-nat. Cl., Wien, 24:11. Type locality: Along the Chiriquí rivers not far from Bocas del Toro, Panamá.

DIAGNOSIS–Within the gladiator group, *pugnax* (Figure 5) is a medium-sized (SVL) species, and it exhibits no sexual dimorphism in snout-to-vent length (Figure 8b). It usually possesses a clear palpebral membrane, darkly pigmented color pattern of bars on the side of the body (Figure 2) and anteroventral surface of the thigh (Figure 3), very little webbing between the fingers (Figure 4), and no well-developed calcar.

GEOGRAPHIC DISTRIBUTION–*Pugnax* has a discontinuous distribution much like that of *crepitans* (Figure 7). While *pugnax* is known from only a few scattered specimens in central Panamá it is locally common and widespread in northeastern Colombia. Most of the Colombia records are from the Río Magdalena drainage. Unlike *crepitans, pugnax* does not appear to live above a

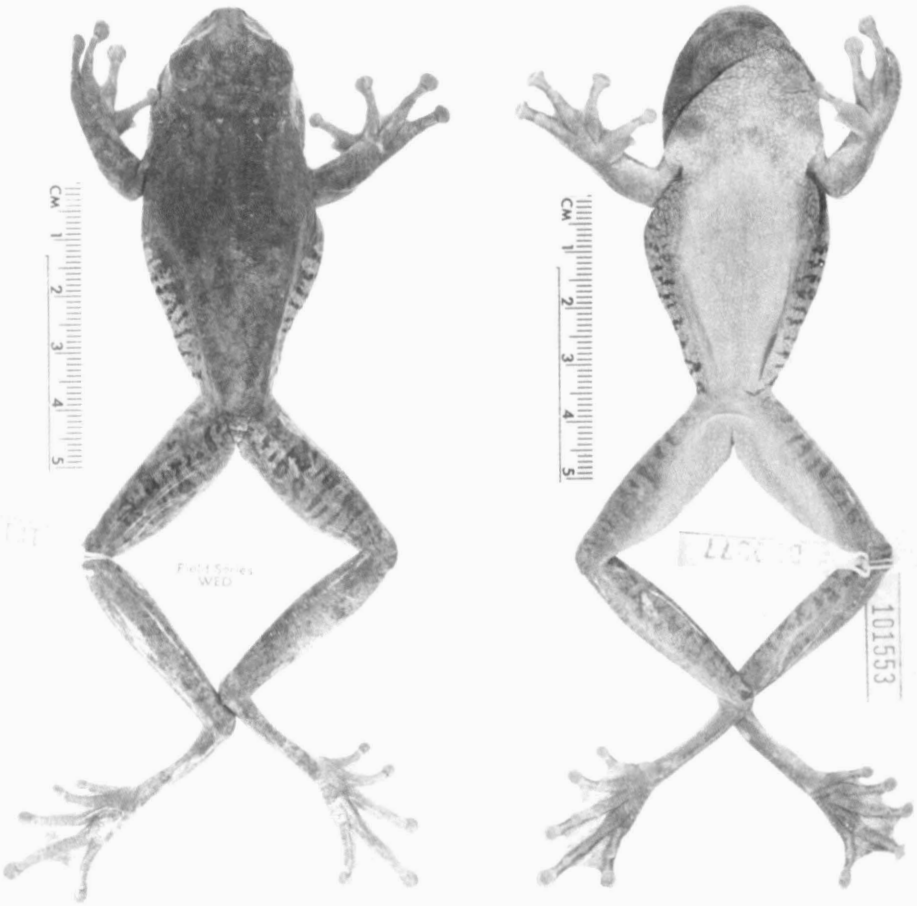


FIG. 5. Dorsal (A) and ventral (B) views of *pugnax* (KU 101553) from Tonosı, 40 m, Los Santos, Panamá.

few hundred meters elevation. *Pugnax* is locally sympatric with *crepitans* and *rosenbergi* but not *boans* (Table 1).

DESCRIPTION–Snout-vent length 70.7 (±.55); head width 22.4 (±.33); tympanum width 4.6 (±.07); width of toe pad at end of third finger 3.4 (±.06); calcar .20 (±.04); webbing 2.0 (±.03); palpebral membrane .23 (±.05); postauricular ridge 1.97 (±.03).

SEXUAL DIMORPHISM–None of the variables was found to be significantly different.

GEOGRAPHIC VARIATION–The *pugnax* were divided into Panamá (N = 6♂♂; no♀♀) and Colombia (N = 43♂♂; 32♀♀) subsamples. The only variable that was found to be significantly different was tympanum width; the Panamá sample was the narrower.

REMARKS–MCZ 16078 is a typical female *pugnax* in all diagnostic characters, except the usually conspicuous pattern of bars on the anteroventral margin of the thigh is absent. This specimen is suppposed to have been collected at Garagoa, Colombia, and it is the only record of *pugnax* that I know of from the entire Orinoco drainage. MCZ 16078 is one of several lower vertebrates that were given to the Museum of Comparative Zoology by Nicéforo María, and in a letter to Thomas Barbour he listed only one tagged frog (field no. 121) from Garagoa. MCZ 16079, which is a *boans,* bears that tag. All other frogs included in the gift from Nicéforo María were untagged, and he collectively referred them to the Garagoa locality. I have not included the Garagoa record in my estimate of the geographic range of *pugnax* (Figure 7) because of its uncertain origin and exceptional appearance.

USNM 151982 is recorded as having been collected at the Virology Field Station, Río Raposo, Valle Province, Colombia at 1500-2000 meters by Wm. Al. Kyburg on March 12, 1962. This is the only specimen of *pugnax* from the Pacific versant of Colombia and I am reasonably certain that its locality data are erroneous. The United States National Museum has only one series of six gladiator frogs that is known to have been collected at the Virology Field Station. These are *rosenbergi* collected by W. A. Thornton and V. H. Lee during May, 1962, on June 25, 1962 and October 28, 1963 (USNM 151385-90). The Virology Station is near sea level and the collecting of vertebrate material by Thornton was not initiated before April 14, 1962 (Thornton, 1965). To complicate matters further, Cochran and Goin (1970) listed USNM 151982 twice under the specimens of *crepitans* examined by them (they did not recognize *pugnax*). Their two different sets of locality data are near Villavicencio, Meta Province, and near Bitaco, on the way to Dagua, Valle Province. The latter locality is near the Virology Station, but much below 1500 meters and still well outside the geographic ranges of *crepitans* and *pugnax*. The former locality is not within the well-documented range of *pugnax* and the given altitude of 1500-2000 meters is

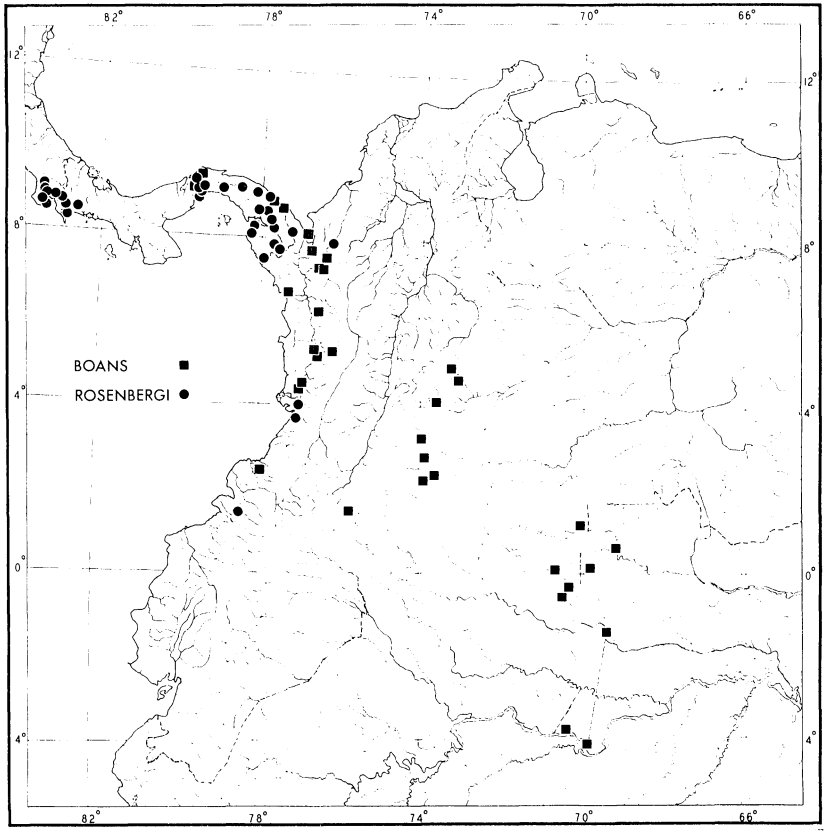


FIG. 6. The geographic distribution of *boans* and *rosenbergi* in Middle America and Colombia. Extralimital material is not plotted. See Appendix I for place names.

inconsistent with that around Villavicencio (approximately 600 meters) as well as the known altitude range of the species.

## *Hyla rosenbergi* Boulenger

*Hyla rosenbergi* Boulenger. 1898, Proc. zool. Soc. London, 1898:123. Type locality: Cachabe, Esmeraldas Province, Ecuador.

DIAGNOSIS–Within the gladiator group, *rosenbergi* is a medium size species, and females are usually slightly larger (SVL) than males (Figure 8a). It often possesses a lightly pigmented palpebral membrane, and it almost always has a darkly pigmented color pattern of bars on the side of the body (Figure 2), no pattern of

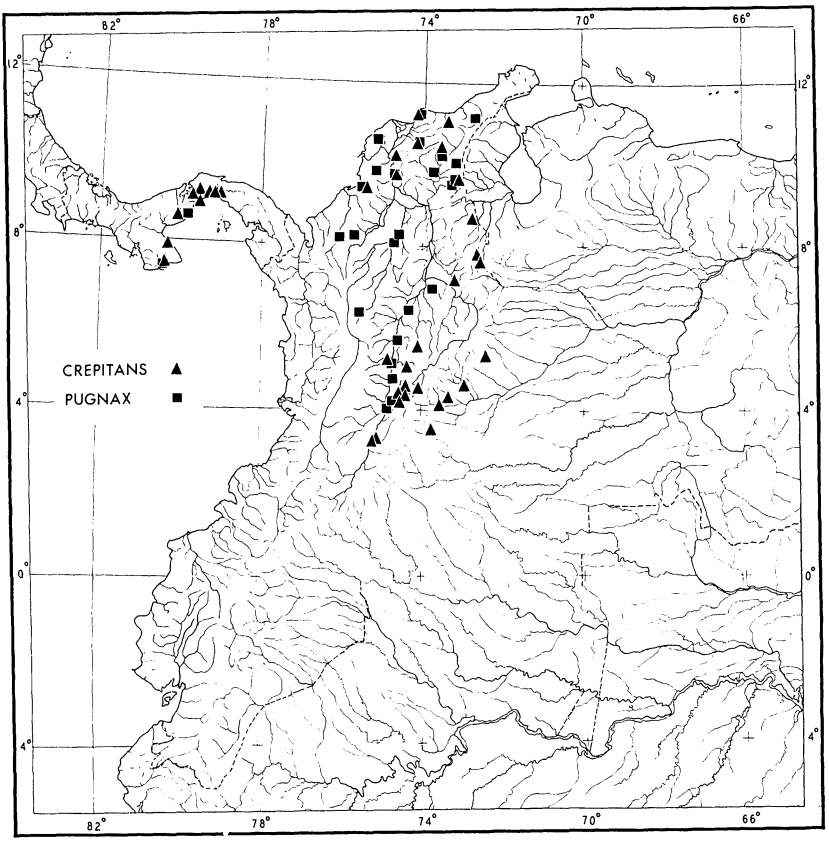


FIG. 7. The geographic distribution of *crepitans* and *pugnax* in Middle America and Colombia. Extralimital material is not plotted. See Appendix I for place names. The *crepitans* from Tela, Honduras (AMNH 45997) and the *pugnax* from Garagoa (MCZ 16078) and the Virology Field Station on the Río Raposo (USNM 151982), Colombia are not plotted. The questionable type locality of *pugnax* has also been omitted; see the Remarks sections in the individual species accounts.

bars on the anteroventral surface of the thigh (Figure 3), extensive webbing between the fingers (Figure 4), and occasionally a weakly-developed calcar.

GEOGRAPHIC DISTRIBUTION–*Rosenbergi* is found in the lowlands of southeastern Costa Rica, southwestern and eastern Panamá and western Colombia. The distribution of *rosenbergi* is noticeably discontinuous in western Panamá and in Colombia (Figure 6). This disjunction is almost certainly not due to lack of collecting.

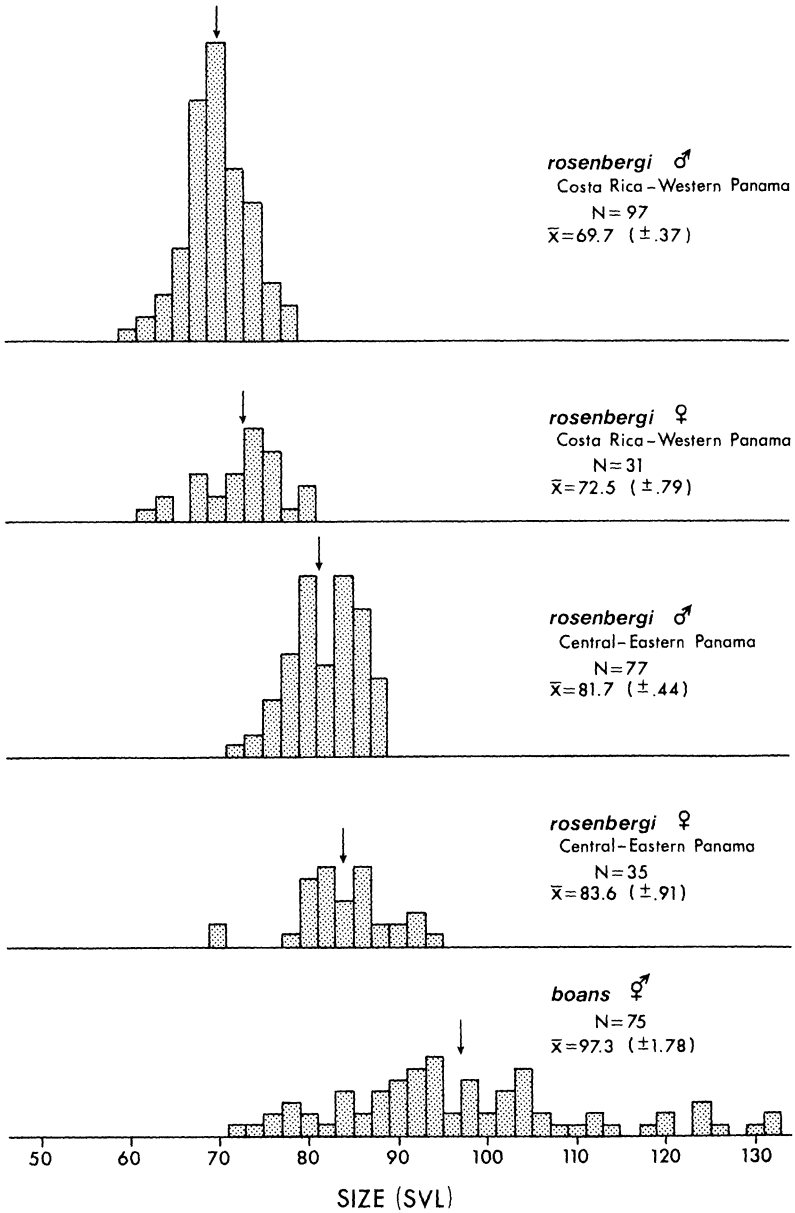


FIG. 8a. Size (SVL) histograms for each species broken down by sex and geographic region where significantly different. Only reproductively mature individuals considered. An arrow denotes the average. See individual species accounts for discussion of geographic origin and statistical significance of samples.

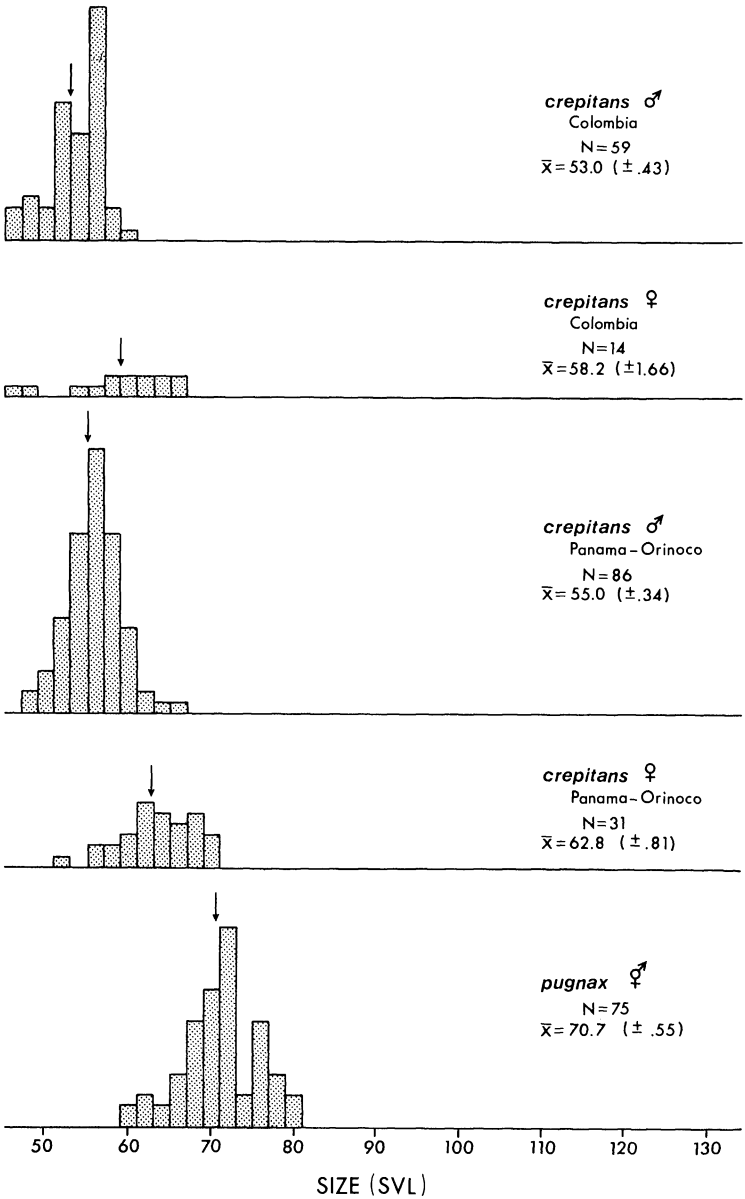


FIG. 8b. Size (SVL) histograms for each species broken down by sex and geographic region where significantly different. Only reproductively mature individuals considered. An arrow denotes the average. See individual species accounts for discussion of geographic origin and statistical significance of samples.

DESCRIPTION–Snout-vent length 76.0 (±.47); head width 24.8 (±.19); tympanum width 5.5 (±.06); width of toe pad at end of third finger 4.3 (±.05); calcar .06 (±.06); webbing 3.3 (±.02); palpebral membrane 1.2 (±.06); postauricular ridge 1.99 (±.01).

SEXUAL DIMORPHISM– Females tend to be slightly, but significantly, larger than males, except in central Panamá. Females have significantly wider heads and tympanums.

GEOGRAPHIC VARIATION–The *rosenbergi* were divided into the following four samples: (1) Costa Rica and Western Panamá, Chiriquí Province (N = 63♂♂; 23♀♀), (2) central Panamá, Canal Zone, and Colón and Panamá Provinces (N = 17♂♂; 9♀♀), (3) eastern Panamá, Darién Province (N = 22♂♂; 17♀♀), and (4) Colombia (N = 6♂♂, no♀♀). Frogs of the Costa Rica-Chiriquí sample are conspicuously smaller (SVL $\bar{x}_{♂}$ = 69.7, $\bar{x}_{♀}$ = 72.5) than all others (the combined SVL $\bar{x}_{♂}$ = 82.9, $\bar{x}_{♀}$ = 83.3). The small Colombia sample of six males (no females were available) appear to be significantly larger than the central Panamá and Darién material; however, additional specimens must be studied before this conclusion can be considered with any confidence. Among the morphometric variables analyzed without respect to sex, the width of the tympanum and toe pad were found to have the same pattern of significant geographic variation; the Costa Rica-Chiriquí sample was smaller than the central Panamá and it in turn was smaller than the remaining two sets of specimens (they not being significantly different from each other). The Costa Rica-Chiriquí sample had the smallest tympanum width in both males and females and the smallest toe pad width in males alone. Further, the central Panamá female subsample had a significantly smaller toe pad width than the Darién material. The Costa Rica-Chiriquí collection, males and females separated or not, usually had the calcar more frequently present than all other samples but the Colombia. The Colombia sample exhibited the calcar more frequently than the Darién, and it also has more extensive webbing than the central Panama and Darién samples when males are studied separately or the sexes are lumped. Curiously, females from Costa Rica-Chiriquí have more webbing than do either of the other Panamanian samples; however, there are no such significant differences when the males are considered.

## INTERSPECIFIC DIFFERENCES

The species treated in this review are readily distinguished from one another in several characteristics, even if one ignores the confounding geographic and sexual variation described above. One

of the most conspicuous interspecific differences is in size; *boans* is approximately twice as long as *crepitans,* whereas *pugnax* and *rosenbergi* are intermediate (Figure 8a and b). Size differences are not only evident in the averages but also in the sample variances; *boans* is significantly more variable than all other species. I believe this difference to be the case at the local population level of sampling, and I predict that it is related to *boans* being much longer lived than the other species. Differences are also evident in degree of size sexual dimorphism; female *crepitans* are much larger than males, whereas females are usually only slightly larger in *rosenbergi.* No significant size differences between the sexes were noted in *boans* and *pugnax* (Figure 8a and b).

All possible interspecific comparisons involving head, tympanum and toe pad widths were significantly different except the following: *pugnax* compared to *crepitans* and *rosenbergi* in head width, and *pugnax* compared to *crepitans* in toe pad width. All species exhibit significant differences in calcar development; *boans* almost always has a large calcar whereas *crepitans* rarely exhibits even a trace of such a projection. *Pugnax* and *rosenbergi* occasionally have a poorly-developed calcar present. Similarly, all species exhibit significant differences in degree of webbing (only reproductively mature adults can be considered because of marked ontogenetic variation); *boans* has nearly fully webbed hands and *rosenbergi* only slightly less. *Pugnax* possesses a little webbing whereas *crepitans* has even less. *Boans* is unique in possessing a reticulated palpebral membrane. The other species are significantly different in degree of palpebral pigmentation; *pugnax* very rarely has any, whereas *crepitans* possesses a little more than *rosenbergi.* Again, *boans* is peculiar in not having the well developed postauricular ridge that the other three species nearly always possess.

In summary, *boans* is quite different from the other three species; *rosenbergi* is probably more similar to *boans* than are *pugnax* and *crepitans. Pugnax* appears to be intermediate between *rosenbergi* and *crepitans.*

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## LITERATURE CITED

BOKERMANN, W. C. A. 1966. Lista anotada das localidades tipo de anfibios Brasileiros. Sao Paulo, R.U.S.P., pp. 1-183.

BOULENGER, G. A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum (Natural History). Second edition. London, Taylor and Francis, pp. i-xvi+1-503.

BREDER, C. M., JR. 1946. Amphibians and reptiles of the Rio Chucunaque drainage, Darien, Panama, with notes on their life histories and habits. Bull. Am. Mus. nat. Hist., 86(8):375-436.

BROCCHI, P. 1882. Etudes de batraciens de l'Amerique Centrale, p. 1-122. *In:* Mission Scientifique au Mexique et dans l'Amerique Centrale, Recherches Zoologiques. Paris, 3(2).

COCHRAN, D. M. and C. J. GOIN. 1970. Frogs of Colombia. Bull. U.S. natn. Mus., 288:1-655.

COPE, E. D. 1867. On the families of the raniform Anura. J. Acad. nat. Sci. Philad., 6(4):189-206.

DUELLMAN, W. E. 1970. The hylid frogs of Middle America. Univ. Kans. Monogr. Mus. nat. Hist., 1:1-427.

DUELLMAN, W. E. 1977. Liste der rezenten Amphibien und Reptilien. Hylidae, Centrolenidae, Pseudidae. Tierreich, 95:1-225.

GÜNTHER, A. 1858. Catalogue of the Batrachia Salientia in the collection of the British Museum. London, Taylor and Francis, pp. i-xvi+1-160.

LUTZ, B. 1960a. Nocão de território em anfíbios anuros *Hyla faber* Wied. Annls. Acad. Bras. Ciênc., 32:143-5.

LUTZ, B. 1960b. Fighting and incipient notion of territory in male treefrogs. Copeia, 1960(1):61-3.

MEYER, J. R. and L. D. WILSON. 1971. A distributional checklist of the amphibians of Honduras. Los Angeles County Museum. Los Angeles. Contr. Sci. 218:1-47.

MEYER, J. R. and L. D. WILSON. 1973. A distributional checklist of the turtles, crocodilians, and lizards of Honduras. Los Angeles County Museum. Los Angeles. Contr. Sci., 244:1-39.

SAVAGE, J. M. 1970. On the trail of the golden frog: with Warszewicz and Gabb in Central America. Proc. Calif. Acad. Sci., 38(14):273-88.

SAVAGE, J. M. 1972. The systematic status of *Bufo simus* O. Schmidt with description of a new toad from western Panama. Jour. Herpetology 6(1):25-33.

SCHMIDT, O. 1857. Diagnosen neuer Frosche des zoologischen Cabinets zu Krakau. Sber. Akad. Wiss., Wien, 24(1):10-15.

SCHMIDT, O. 1859. Deliciae herpetologicae. Denkschr. Akad. Wiss., Wien, 14:1-22.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill, pp. i-xvii+1-312.

THORNTON, W. A. 1965. A new frog of the genus *Eleuthrodactylus* from the coastal rain forest of Colombia. Copeia, 1965(4):425-7.

WIED, M. 1824. Abbildungen zur Naturgeschichte Brasiliens. Weimar.

## APPENDIX I

## SPECIMENS EXAMINED

*Hyla boans*—COLOMBIA, *Amazonas:* Cano Guacaya, tributary lower Río Apoporis (USNM 152130); Leticia (USNM 146263); Puerto Nariño (KU 153349, USNM 152128-29); Raudal Jirijirimo, upper Río Apoporis (MCZ 28051, USNM 152132-33); Río Apoporis (USNM 152135); Río Popayaca, tributary lower Río Apoporis (USNM 152131). *Antioquia:* Belen, Río Arquia (LACM 45453-54, 59-60, 45463, 47194); Chigorodo, nr. Turbo (AMNH 76185); Finca Chibugui, Río Arquia (LACM 45456-58); Finca Los Llanos, Río Arquia (LACM 45455); Mutatá (KU 140387); nr. Puerto Palacios, Río Arquia (LACM 45407-11); Urabá, Río Currulao (FMNH 63894-96); Villa Arteaga, nr. Turbo (FMNH 78143-44). *Boyaca:* Guaicaramo (KU 150752, USNM 152101-04); Macanal (UMMZ 71216). *Caldas:* Santa Cecilia, Pueblo Rico (FMNH 54785-91). *Caqueta:* Morelia (ANSP 25314). *Cauca:* Guapi (KU 145070). *Choco:* Boca de Raspadura, upper

Quito (AMNH 13690); Quebrada Decordo, bet. Cucurrupi & Noanama on Río San Juan (CAS 119743); Quebrada Tapparral, c. 20 KM N Palestina on Río San Juan (CAS 119910); Quita Creek, Las Animas (AMNH 13596); Tado, Río San Juan (LACM 45462); Upper Río Napipi, below mouth Río Merendo (LACM 45461). *Cordoba:* c. 25 KM mouth Río Esmeralda (NS 16-17). *Meta:* El Refugio, bet. Río Macarana & Río Guayabero (USNM 152194); Los Micos (USNM 152200); nr. Mouth Cano Losada, upper Río Guayabero (USNM 152189-90); Serrania de la Macarena (USNM 152630-31); Villavicencio, 498 M (MCZ 11622-23). *Vaupes:* Alto Río, Río Cuduairi (AMNH 6055); Río Cuduairi (USNM 152319); Río Fatima (USNM 193873); Río Vaupés (USNM 193872 a-b). PANAMÁ, *Canal Zone:* Río Frijoles (AK 1834, UMMZ 145577-79, 146747). *Darien:* Jaque at jct. Río Jaque & Río Imamado (USNM 161211); Río Tuira at Río Mono, 130 M (KU 96013-14). *Panamá:* Candelaria, Peluca Stations, nr. Boqueron (AMNH 53716-17). *San Blas:* Armila (USNM 150068-69); Camp Sasardí, 12 M (KU 108839-51, 116778a-b).

*Hyla crepitans*—COLOMBIA, *Boyaca:* Guaicaramo (UMMZ 78303a-d); Muzo (MCZ 24917); Yopal (USNM 153927); Bogotá (AMNH 39775-80); Finca El Cuchero, nr. Tocaima (USNM 152182-83); Fusagasuga, 1580 M (CAS 22972); La Mesa, 1000-1300 M (USNM 152179-80); Las Mesitas del Colegio (AMNH 84042-45); Monte Redondo (USNM 152185); Pueblo Nuevo, nr. Nilo (USNM 153946); San Javier, 1000-1100 M (USNM 152181); Villeta (MCZ 20940). *Huila:* Cerbatana, 5 KM N Villavieja, 427 M (MVZ 63234-43); 16 KM NE Villavieja, 498 M (MVZ 63232); 7 KM E Villavieja, 427 M (MVZ 63233). *Magdalena:* El Rincon, c. 10-12 KM E Becerril, 250-280 M (AMNH 84384-85); Finca el Aranar, nr. Bonda (USNM 152717-33); Fundación (UMMZ 46913); Guatapuri River, nr. Ariguani, Santa Marta Mts. (UMMZ 85599); La Concepción, 900 M (MCZ 2324-25); Palomina (UMMZ 48302); Parque Nacional Tayrona, trail between Canaveral & El Pueblito (NS 80); Parque Nacional Tayrona, within 2 KM El Cedro Station (NS 179-87); Pueblo Bello (CAS 116214-20); Sta. Marta Dist. (MCZ 2327-30); Zarate (KU 150754). *Meta:* between Río Macarana & Río Guayabero (USNM 152195); Granada on Río Ariari (USNM 151946-61); nr. Villavicencio (USNM 151943); Villavicencio, 498 M (AMNH 20376-80, 20420-23, 43848, FMHN 81781-82, KU 110495-96, MVZ 63244-50, USNM 146264a-b, 152209-14, FMNH 121616-17); 5 KM SE Villavicencio, 480 M (KU 110497); 7 KM NE Villavicencio (USNM 152628). *Norte de Santander:* Chinacota (KU 150753); Finca Miramonte, 15 KM N Tibu (USNM 152263-76); La Selva (USNM 152115). *Santander:* Lebrija (USNM 152284). *Sucre:* 4 KM NW Toluviejo (NS 59-62). *Tolima:* Boquerón, Cundinamarca boundary (LACM 47152); Mariquita (FMNH 81821, USNM 152286-87); Melgar (USNM 152640). HONDURAS, *Atlantida:* Tela (AMNH 45997). PANAMÁ, *Canal Zone:* Alhajuela (CM 7387, UMMZ 75993a-g); Camp Chagres Boy Scout Camp, 120 M (AK 1-8, KU 77018-33, UMMZ 135399); Chiva Chiva Road Quarry (AK 1-5); Curundú (GML unnumbered a-b); K2 along Canal (SR unnumbered); Madden Dam (UMMZ 78482); nr. Venado Beach (USNM 193332a-b); San Pablo (AMNH 6731, MCZ 26963, UMMZ 47209, 60290); Summit (FMNH 83558, MCZ 17971, FMNH 22983-84); Summit Gardens, 100 M (ANSP 23357-59); 2.8 KM SW Fort Kobbe, Venado Beach area, 5 M (KU 116360). *Cocle:* El Valle, 560 M (CAS 97924, KU 77035). *Los Santos:* Jagoa (SR unnumbered); Tonosi, 40 M (KU 77703). *Panamá:* Cerro Azul (FMNH 161481, GML unnumbered); Chepo (GML unnumbered); Chilibre (USNM 139698); El Cangrejo, Panama City, 40 M (KU 116358); Finca la Sumbadora, 570 M (KU 80456-58); La Carrasquilla (GML unnumbered); Las Cumbres (AMNH 69767); Los Angeles (GML unnumbered); Panama Hilton, Panama City (AMNH 77702); Río Abajo, Panama City (KU 116359); Río Mamoní, 5 KM E Chepo (KU 77034); 17.7 KM E Tocuman (MVZ 78661); 3 KM WSW Chepo, 20 M (KU 101550-52); 6.4 KM NE Cerro Azul (FMNH 161480).

*Hyla pugnax*—COLOMBIA, *Antioquia:* Alto de Quimari (FMNH 61751); Nechi (FMNH 54778-82); Puerto Berrio (AMNH 39013, 15, 21-25, UMMZ 56506); San Pedro, nr. Medellin (MCZ 7777). *Atlantico:* Los Pendales (USNM 152142). *Bolivar:* La Raya (USNM 127863-64); 1 KM N San Cristobal (KU 158582-84). *Boyacá:* Garagoa (?) (MCZ 16078); Puerto Boyacá (USNM 152144). *Cesar:* Finca El Diamante, 15 KM S Bosconia (NS 110-15, 17, 19-22); La Jagua, 15 KM S Becerril (CAS 116294). *Córdoba:* Catival, upper Río San Jorge (FMNH 61169-70); Socorre, upper Río Sinu, 100-150 M (FMNH 61168); Tierra Alta, 40 M (FMNH 61752, UMMZ 135336a-1). *Cundinamarca:* Beltran, upper Río Magdalena (USNM 152611-12); Girardot (AMNH 20424). *La Guajira:* Río Barbacoa, Arroyo de Arenas (UMMZ 54619). *Magdalena:* Aracataca (ANSP 19779); Becerril (CAS 116280); Curumani (MCZ 21475-79, 21483); Finca El Aranar, nr. Bonda (USNM 152715-16); Fundación (UMMZ 46908-12, 14-21); nr. Río Frio (MCZ 16051); Plato, 25 M (AMNH 71042). *Santander:* El Centro, 112 M (AMNH 71043). *Sucre:* Hacienda la Estanzuela, 4 KM E Tolu (NS 42, 43, 240-42). *Tolima:* Espinal, Magdalena Valley (MCZ 15063-64); Honda (USNM 152121-22, 156888). *Vaupés:* Río Vaupés (USNM 151982). PANAMÁ, *Chiriquí:* along the Chiriquí Rivers, not far from Boca del Toro (KM 1009). *Los Santos:* Guanico, Arriba Río Guanico, 60 M (KU 116361); Tonosi, 40 M (KU 101553-55). *Panamá:* Bejuco, Rio Bejuco (AMNH 69766).

*Hyla rosenbergi*—COLOMBIA, *Córdoba;* Socorre, upper Río Sinu, 100-150 M (FMNH 61167). *Narion:* La Guayacana, 250 M (KU 145072). *Valle:* Lower Río Calima (USNM 152313-15); Río Raposo (USNM 151385-90). COSTA RICA, *Puntarenas:* bet. Julieta & Quebrada Palma (UCR 4791); brook nr. Rincon Airstrip (UCR 4588-89); c. 7.3 KM S Rincon (UMMZ 126013a-b); Camp Seattle (UMMZ 123616a-d); Canas Blancal, E Palmar Norte (UCR 5774); Finca Los Angeles (UCR 3895-99, 4380); Golfito (KU 31841-55, 34849, UMMZ 123625, 126012a-b); Golfito, Hotel Balneario, 4 M (CRE 706, 7231-32 a-d); nr. Rincon (CRE 6391a-d); nr. Rincon Airstrip (UCR 2000, 3837); Pacific Road, Osa Peninsula (UCR 4580); Palmar Sur, 45 M (KU 31839-40, 95450); Puerto Cortes (UCR 5486, 5726); Puerto Jiménez (UCR 2406); Quebrada Benjamin, 200 M (AK 1-5, 99999); Rincon, 30 M (CRE 7248, LACM 114296, UCR 2245-48, 3834, 4046); Río Ferruviosa, 7.2 KM S Rincon (CRE 7235); Río Rincon (CRE 6027-29); Río Riyito (W bank), 8 KM SW Rincon (CRE 9531-32); Savage Woods, 6 KM SW Rincon (9415); TSC Field Stn., Rincon (LACM 114295, UCR 765); Villa Neilly, 15 M (KU 103744); 1.1 KM NW Villa Neilly (CRE 8002); 1.6 KM S Compania, Rincon (LACM 54001-03); 10.5 KM WNW Villa Neilly, 25 M (KU 65015-16); 12.9 KM N Golfito (LACM 60501); 2 KM NE Jaco, Cerro Puntado (CRE 7139); 2.4 KM NW Camp Seattle (CRE 705a-d); 2.5 KM SE Palmar Sur, 15 M (KU 93965-67); 2-10 KM ESE Villa Neilly (KU 129841-43); 21.8 KM NW Villa Neilly, nr. KM Post 29 (CRE 8005a-e); 3 KM E Golfito, 10 M (KU 86443-46); 3 KM SSW Rincon (CRE 8314); 3 KM W Rincon Airstrip (CRE 3112a-b, 6567); 3 KM WSW Rincon (CRE 9293-95, 9656); 3 KM WSW Rincon Airstrip (CRE 9545); 4 KM ESE Palmar Sur, 15 M (KU 65017-18); 4.5 KM W Rincon (KU 102259-62, UCR 1107-8); 4.8 KM S Rincon (UCR 1162-63); 7 KM NW Villa Neilly (CRE 8003a-b); 7.5 KM SW Rincon on Pacific Rd. (CRE 9601); 8 KM SSW Rincon on Pacific Rd. (CRE 3108a-b); 9 KM SSW Rincon on Pacific Rd. (CRE 3141); 9.6 KM ESE Golfito, 100 M (CRE 7105). PANAMÁ, *Canal Zone:* Alhajuela (CM 7418-19, UMMZ 75994); Camp Chagres Boy Scout Camp, 120 M (KU 77291-98); Ft. Clayton (FMNH 130965); Lighthouse Trail, 4 KM NWW Bohio Peninsula (USNM 196302); Madden Dam (UMMZ 78482a-b); nr. Coclí (SR unnumbered); Rodman (GML unnumbered); San Pablo (MCZ 1731); Summit Gardens, 100 M (KU 96045); 0.32 KM E Gaillard Hwy. on Chiva Chiva Rd. (UF 29101); 0.8 KM S Juan Mina (FMNH 67822); 2.7 KM E Gaillard Hwy. on Chiva Chiva Rd. (UF 29102); 4.7 KM NW Gamboa P. O. on Pipeline Rd. (UMMZ 135406); 5 KM NW Gamboa, 90 M (KU 107433); 6.3 KM NW Summit Gardens entrance on

Gaillard Hwy. (UMMZ 135385a-b); 9°7′ N and 79°41′30″ W on Gaillard Hwy. (UMMZ 135397a-d). *Chiriquí:* Puerto Armuelles (AMNH 58707, ASNP 21598-99); San Miguel District of Bugaba (GML unnumbered). *Colón:* La Hoya (ANSP 25124-25). *Darien:* c. 10 KM below Río Subcuti on Río Chucunaque, 120 M (KU 107427-29); c. 7 KM above Río Mortí on Río Chucunaque, 150 M (KU 107430-32); camp above mouth Río Sansan (AMNH 40650); Camp Creek (AMNH 79913a-j); Camp Townsend, Camp Creek (AMNH 40924, 41015-18, 41024-26, 41060, 41071-73, 41148-51, 41158-63, 41723, 41767); Cana, 609 M (USNM 50209); Chalichmans Creek, Río Sucubti (AMNH 41057); mouth Río Membrillo (AMNH 40550); nr. intersect. Chucunaque & Ucurganti Rivers (USNM 140614-15); nr. mouth Río Canclón (UMMZ 135951-52); Río Tuira at Río Mono, 130 M (KU 96046-67); Samba Valley, Río Esnape (MCZ 9173); Santa Fe Camp (FMNH 170440); SgVIII Site (FMNH 170429); Tacarcuna, 550 M (GML unnumbered a-d, KU 77300-05, USNM 141793-94); Three Falls Creek (AMNH 41010, 41683); 0.5 hr. below jct. Río Jaque & Río Imamado (USNM 151212). *Panamá:* Capitana, nr. Chepo (USNM 192618a-b); Johnsons Place, Río Bayano (FMNH 16547); Las Sabanas, Panamá City (MCZ 17583); Majé (SR unnumbered); 6 KM WSW Chepo, 15 M (KU 77299); 6 KM WSW Chepo, 20 M (KU 107434-36).

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