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**A REVIEW OF THE NEOTROPICAL FROGS
OF THE *HYLA BOGOTENSIS* GROUP**

By

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By comparison with the highlands of Central America, which are inhabited by a diversity of stream-breeding hylid frogs, the Andes in northwestern South America are characterized by a paucity of stream-breeding hylids. Duellman (1970:327) pointed out that one stream-breeder, *Hyla colymba*, in the highlands of Costa Rica and Panamá seemed to be related to the Colombian *Hyla bogotensis*, and he tentatively referred specimens from Ecuador to *Hyla colymba*. Recent field work in northwestern South America has resulted in the accumulation of series of specimens from many localities, tadpoles, and recordings of mating calls. Thus, it is now possible to review systematically six species that seem to form a natural unit—the *Hyla bogotensis* group.

The purposes of the present paper are to: 1) define the *Hyla bogotensis* group, 2) present the results of a multivariate analysis of characters, 3) diagnose the species, and 4) present the accumulated data on the biology of the species.

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MATERIALS AND METHODS

This investigation was based on the study of 149 preserved frogs (including the type specimens of all nominal taxa), 17 lots of tadpoles, two skeletons, nine radiographs, and eight tape recordings. For purposes of statistical analyses, 14 characters were recorded for 114 adult frogs. Of these characters, three are morphometric, eight are structural, and three are coloration. These data were subjected to a stepwise discriminant analysis by use of the BMDO7M Program (Dixon, 1971), which performs a multiple discriminant analysis in a stepwise manner, entering one variable at a time into a set of discriminating variables. The program computes canonical correlations and coefficients for canonical variables and plots the first two canonical variables in a two-dimensional matrix.

Individuals were grouped on the basis of geography and sex, as follows: Central America 6 ♂, 3 ♀; Pacific slopes of Ecuador 13 ♂, 15 ♀; Amazonian slopes of Ecuador and Perú 13 ♂, 3 ♀; Andes of central and southern Colombia 7 ♂, 4 ♀; Andes of western Venezuela 37 ♂, 11 ♀. One male and one female from northern Colombia were each treated as a group. Thus, the matrix for the discriminant analysis consisted of 14 variables and 12 groups.

Subsequently, the sexes were pooled, and each of the six groups was treated as an OTU in the NT-SYS Phenogram Program (Rohlf and Kishpaugh, 1966); in this program unweighted arithmetic character states were analyzed and plotted as a distance phenogram. For purposes of the Phenogram Program, 11 coded characters were

used (see following definition of characters). Five coded characters of tadpoles were analyzed by the Phenogram Program; again, groups (taxa) were treated as OTUs. Finally, the adult and tadpole characters were analyzed together by the Phenogram Program. All computations were done on a Honeywell 635 computer.

Recordings of the mating calls of three species are available. The calls of eight individuals were analyzed for seven characters: 1) notes per call group, 2) note repetition rate, 3) duration, 4) pulse rate, 5) number of harmonics, 6) fundamental frequency, and 7) dominant frequency (see Duellman, 1970, for methodology and terminology).

Definition of Characters

In the list of characters, those marked with an asterisk were used in the Phenogram Program; all characters of adults were used in the BMD07M Program.

*Snout-vent Length (SVL)**.—Measurement to nearest 0.1 mm of straight line distance from tip of snout to posterior edge of body; for NT-SYS coded: 1) ♂ <44 mm, ♀ <50 mm, 2) ♂ >44 mm, ♀ >50 mm.

Tibia Length (TL).—Measurement of length of tibia to nearest 0.1 mm; used as a ratio of snout-vent length.

Head Width (HW).—Measurement of greatest width to nearest 0.1 mm; used as a ratio of snout-vent length.

*Webbing on Hand (WEB)**.—The extent of webbing on the inner edge of the fourth finger coded with respect to the point of termination of the webbing with respect to the distal subarticular tubercle: 1) proximal to tubercle, 2) at tubercle, 3) distal to tubercle.

*Subarticular Tubercles (TUB)**.—The structure of the distal subarticular tubercles on the third and fourth fingers was coded: 1) conical, single, 2) conical, bifid, 3) flat, bifid.

*Ulnar Fold (ULN)**.—A dermal fold on the ventrolateral edge of the forearm was coded: 1) absent, 2) present.

*Tarsal Fold (TAR)**.—A dermal fold on the ventrolateral surface of the foot was coded: 1) absent, 2) present.

*Calcar (CAL)**.—A triangular dermal appendage projecting posteriorly from the upper edge of the heel was coded: 1) absent, 2) small, 3) large.

*Snout Profile (SNO)**.—The shape of the snout in lateral view coded: 1) round, 2) truncate, 3) anteriorly inclined.

*Tympanum (TYM)**.—The upper edge of the tympanum is covered by a supratympanic fold, but the tympanic ring below the fold coded: 1) distinct, 2) covered with undifferentiated skin.

Mental Gland (MEN).—A round glandular structure at the apex of the jaw was coded: 1) absent, 2) present.

*Dorsolateral Stripe (DST)**.—A pale stripe extending from the edge of the eyelid to a point on the side of the body was coded: 1) absent, 2) present.

*Tarsal Stripe (TST)**.—Longitudinal stripes on the outer edge of the foot were coded: 1) absent, 2) white, 3) white above and brown below.

*Anal Stripe (AST)**.—Transverse stripes above the anus were coded: 1) absent, 2) white, 3) white above and brown below.

*Tooth Rows (TOO)**.—The number of upper/lower rows of teeth in tadpoles was coded: 1) 4/5, 2) 5/7, 3) 6/9, 4) 7-8/10.

*Labial Papillae (LAB)**.—Labial papillae are continuous around the mouth in the tadpoles; the number of rows of papillae was coded: 1) one, 2) two.

*Serrations on Beak (SER)**.—The serrations on the cutting edge of the upper beak in tadpoles were coded: 1) none, 2) small, 3) medium, 4) large.

*Shape of Body (SHA)**.—The shape of the body of tadpoles in dorsal view was coded: 1) narrowly ovoid, 2) broadly ovoid, 3) narrow anteriorly and widening abruptly just anterior to eyes.

*Caudal Musculature (CAU)**.—The proportionate depth of the caudal musculature was coded: 1) <65%, 2) >65%.

RESULTS

For ease in discussion the nomenclature adopted in the following section on taxonomy is used throughout. The results of the discriminant analysis are discussed first, followed by the Phenogram Program and finally the mating calls.

Multiple Discriminant Analysis

Within-group Variation.—The amount of variation in snout-vent length is approximately the same in all species except *H. bogotensis* and *H. platydactyla* in which it is somewhat greater (Table 1). However, the amount of variation in the ratios of tibia length and head width to snout-vent length is no greater in these two species than in the others.

Variation of all structural features, except presence or absence of ulnar and tarsal folds, occurs within groups; likewise, color pattern characters show within-group variation (Table 2). Tarsal and anal stripes are either present or absent within a group; if present, there may be one or two stripes (*Hyla phyllognatha*). The presence of a mental gland is the most variable structural feature, displaying variation in five of the 12 groups. The amount of webbing is the next most variable character; variation occurs in four groups.

The variation within groups is not highly correlated with respect to the following characters—size, proportions, subarticular tubercles, snout shape, tympanum, and mental gland. Absolute positive cor-

TABLE 1.—Measurements and proportions of species in the *Hyla bogotensis* group.

(Mean and one standard deviation given below observed range.)

Species	Sex	N	Snout-vent Length	Tibia Length/ SVL	Head Width/ SVL
<i>H. alytolylax</i>	♂	13	32.1–37.0 34.85±1.51	0.443–0.525 0.474±0.024	0.298–0.331 0.316±0.010
	♀	15	37.2–43.9 40.38±2.23	0.462–0.532 0.496±0.021	0.296–0.331 0.310±0.010
<i>H. bogotensis</i>	♂	7	29.4–43.0 35.20±5.58	0.491–0.514 0.502±0.010	0.329–0.365 0.345±0.012
	♀	4	29.4–48.1 41.43	0.449–0.506 0.483	0.313–0.380 0.347
<i>H. colymba</i>	♂	6	31.9–37.0 34.65±2.29	0.452–0.514 0.481±0.023	0.302–0.327 0.318±0.010
	♀	3	31.4–39.1 36.23	0.486–0.493 0.490	0.310–0.340 0.325
<i>H. denticulenta</i>	♂	1	44.2	0.493	0.303
	♀	1	52.2	0.513	0.308
<i>H. phyllognatha</i>	♂	13	31.5–34.0 32.96±0.69	0.443–0.524 0.488±0.028	0.301–0.348 0.319±0.013
	♀	3	33.0–39.3 36.87	0.488–0.506 0.495	0.326–0.331 0.329
<i>H. platydactyla</i>	♂	37	26.5–39.4 34.36±3.05	0.464–0.540 0.488±0.016	0.323–0.383 0.347±0.014
	♀	11	30.6–42.3 38.41±3.64	0.457–0.506 0.491±0.016	0.333–0.356 0.342±0.009

relation exists between presence or absence of ulnar and tarsal folds, between tarsal folds and tarsal stripes, and between tarsal and anal stripes. Webbing is the most extensive and calcars are the largest in the species, *H. denticulenta*.

Sexual Dimorphism.—No sexual dimorphism is evident in proportions, amount of webbing, nature of folds or calcars, snout shape, or nature of tarsal and anal stripes. Minor sexual dimorphism occurs in the nature of the subarticular tubercles in *H. platydactyla*, in the tympanum in *H. bogotensis*, and in the dorsolateral stripe in *H. colymba* (Table 2). Snout-vent length is greater in females than in males; snout-vent lengths of 77 males is 26.5–44.2 (\bar{x} =34.43) mm, and of 37 females is 29.4–52.2 (\bar{x} =39.63) mm.

As noted above, the nature of the mental gland is highly variable. The gland is present in 44 of 77 (57.1%) males and in nine of 37 (24.3%) females. The structure and function of the mental gland are unknown; its development may be seasonal and associated with reproductive activity. Thus, its usefulness as a taxonomic character within the *Hyla bogotensis* group is questionable.

Interpopulational Variation.—The combination of the sexes in

TABLE 2.—Variation in structural characters and coloration in the *Hyla bogotensis* group.
(See Definition of Characters for abbreviations and coding; mean and one standard deviation given below observed range.)

Species	Sex	N	WEB	TUB	ULN	TAB	CAL	SNO	TYM	MEN	DST	TST	AST
<i>H. alytolylax</i>	♂	13	2-3	1	2	2	1	1	1	2	2	2	2
			2.538	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
			0.519	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	♀	15	2-3	1	2	2	1-2	2	1	1	2	2	2
			2.867	-----	-----	-----	1.067	-----	-----	-----	-----	-----	-----
			0.352	-----	-----	-----	0.258	-----	-----	-----	-----	-----	-----
<i>H. bogotensis</i>	♂	7	2	2	1	1	1	2	1-2	1-2	1	1	1
			-----	-----	-----	-----	-----	-----	1.571	1.143	-----	-----	-----
			-----	-----	-----	-----	-----	-----	0.535	0.378	-----	-----	-----
<i>H. colymba</i>	♀	4	2	2	1	1	1	2	2	1	1	1	1
			-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
			-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	♂	6	2	1	2	2	1	1	1	2	2	2	2
			-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
			-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	♀	3	2	1	2	2	1	1	1	1-2	1-2	2	2
			-----	-----	-----	-----	-----	-----	-----	1.667	1.667	-----	-----
			-----	-----	-----	-----	-----	-----	-----	0.577	0.577	-----	-----
<i>H. denticulenta</i>	♂	1	3	3	2	2	3	3	1	1	1	3	3
			-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
			-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	♀	1	3	3	2	2	3	3	1	1	1	3	3
			-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
			-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>H. phyllognatha</i>	♂	13	1-2	1	2	2	1-2	1-2	1	2	1	2-3	2-3
			1.077	-----	-----	-----	1.308	1.077	-----	-----	-----	2.538	2.538
			0.277	-----	-----	-----	0.480	0.277	-----	-----	-----	0.877	0.877
	♀	3	1-2	1	2	2	1-2	1-2	1	1-2	1	2-3	2-3
			1.667	-----	-----	-----	1.667	1.333	-----	1.333	-----	2.333	2.333
			0.577	-----	-----	-----	0.577	0.577	-----	0.577	-----	1.155	1.155
<i>H. platydactyla</i>	♂	37	1	1-2	1	1	1	2	1-2	1-2	1-2	1	1
			-----	1.892	-----	-----	-----	-----	1.162	1.297	1.162	-----	-----
			-----	0.315	-----	-----	-----	-----	0.374	0.463	0.374	-----	-----
	♀	11	1	2	1	1	1	2	1-2	1-2	1-2	1	1
			-----	-----	-----	-----	-----	-----	1.091	1.545	1.091	-----	-----
			-----	-----	-----	-----	-----	-----	0.302	0.522	0.302	-----	-----

the geographic samples provides an assessment of populational differences for taxonomic distinction. Each of the 14 characters, in combination with others, serves to distinguish one population from another, but, with the exception of snout-vent length in *H. denticulenta*, no one character distinguishes one population from all of the others. The stepwise discriminant analysis provided a multivariate analysis of 14 characters in the 12 groups (males and females were treated separately in each of the geographic samples) and produced a two-dimensional plot of the first and second canonical variables (Fig. 1). The first canonical variable is weighted primarily on webbing, secondly on subarticular tubercles, and lastly on ulnar and tarsal folds, whereas the second canonical variable is weighted on snout-vent length, calcar, and dorsolateral stripe, in descending order. The plot clearly shows the clustering of samples and the overlap (in most cases) of the sexes within the samples. Thus, on the basis of adult morphology, the samples can be treated as different taxa.

Distance Phenograms

In an attempt to determine the phenetic relationships of the six geographic samples, each of the six was treated as an OTU. Mean values for each of 11 characters (sexes pooled) were used. Body ratios and the nature of the mental gland were excluded from the analysis. The resultant distance phenogram (Fig. 2A) shows the separation of the phenetically similar *H. bogotensis* and *H. platydactyla* from the other taxa. *Hyla denticulenta* is separated from the remaining three species clumped in the middle of the phenogram. The arrangement of the taxa is compatible with the plot of the canonical variables (Fig. 1). Thus, the results of the Phenogram Program supports the results of the multiple discriminant analysis.

The previous analyses were based on characters of the adult frogs. Tadpoles are available for all six geographic samples; these have been associated with adults on the basis of morphological characteristics of the metamorphosing young. The most obvious inter-populational differences are evident in the structures of the mouths (Fig. 3). The distribution of character states of five characters is shown in table 3. For purposes of analysis, the mean ratio of depth of caudal musculature to total caudal depth was used; the other characters are constant within populations and were coded. The phenogram of populations as OTUs differs only slightly from the arrangement based on adults (Fig. 2B). The major difference is that *H. alytolylax* is clustered with *H. denticulenta*, whereas in the phenogram based on adults *H. alytolylax* is grouped with *H. colymba* and *H. phyllognatha*.

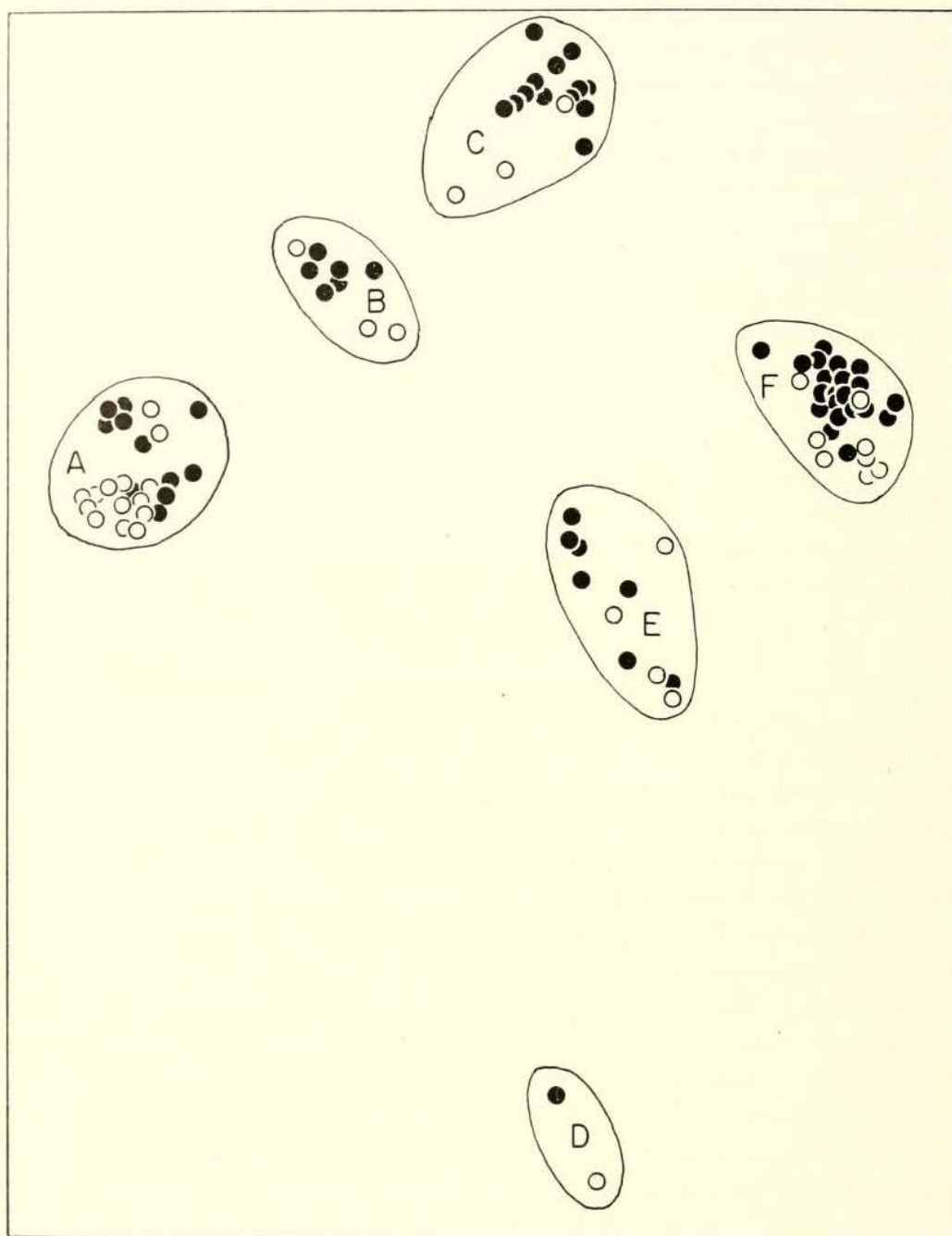


FIG. 1.—Plot of first (horizontal axis) and second (vertical axis) canonical variables; solid dots are males and open circles are females. A. *Hyla alytolylax*. B. *H. colymba*. C. *H. phyllognatha*. D. *H. denticulenta*. E. *H. bogotensis*. F. *H. platydactyla*.

A final analysis of both adult and larval characters produced a phenogram somewhat intermediate between the first two (Fig. 2C). Here it can be seen that *H. bogotensis* and *H. platydactyla* are divergent from the other taxa and that *H. colymba* and *H. phyllognatha* are close to *H. alytolylax*, whereas *H. denticulenta* is more distant.

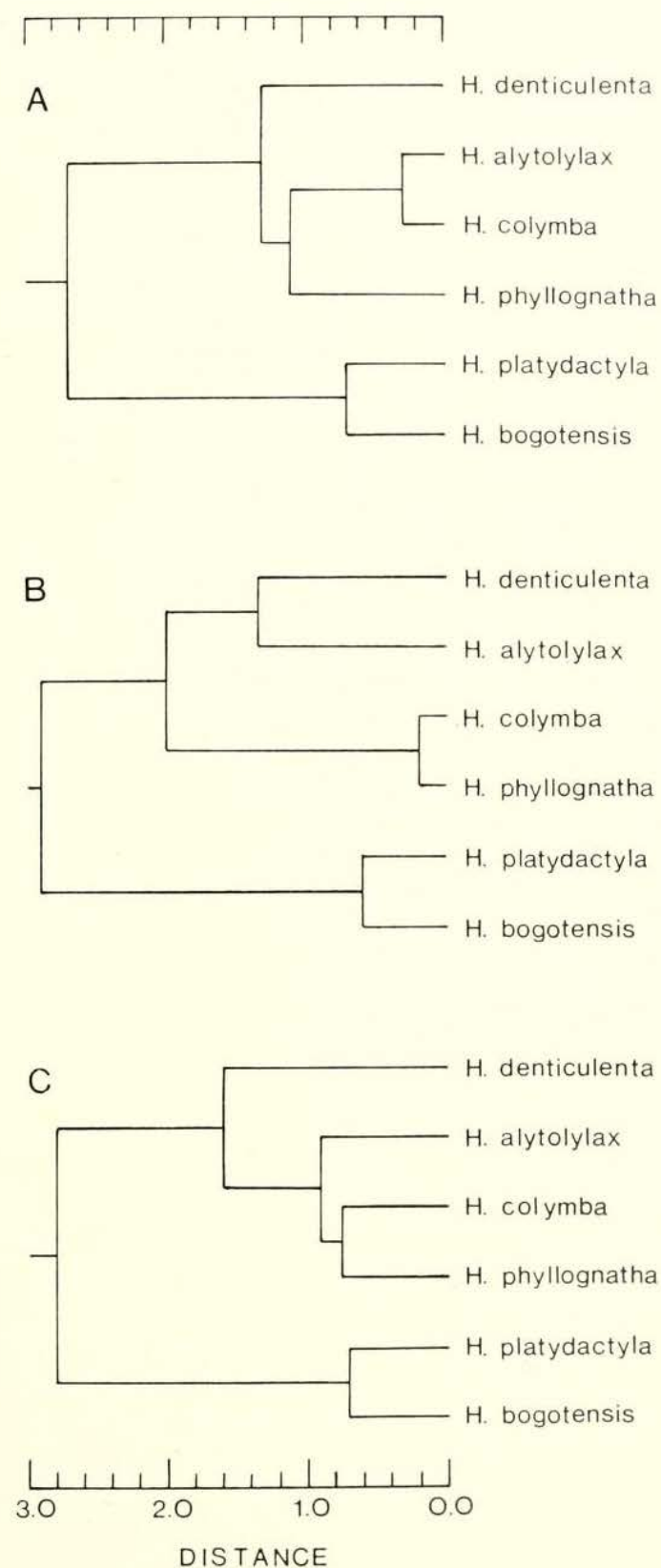


FIG. 2.—Distance phenogram of *Hyla bogotensis* group based on unweighted analysis of 11 adult and five larval characters. A. Adult characters. B. Larval characters. C. Adult and larval characters.

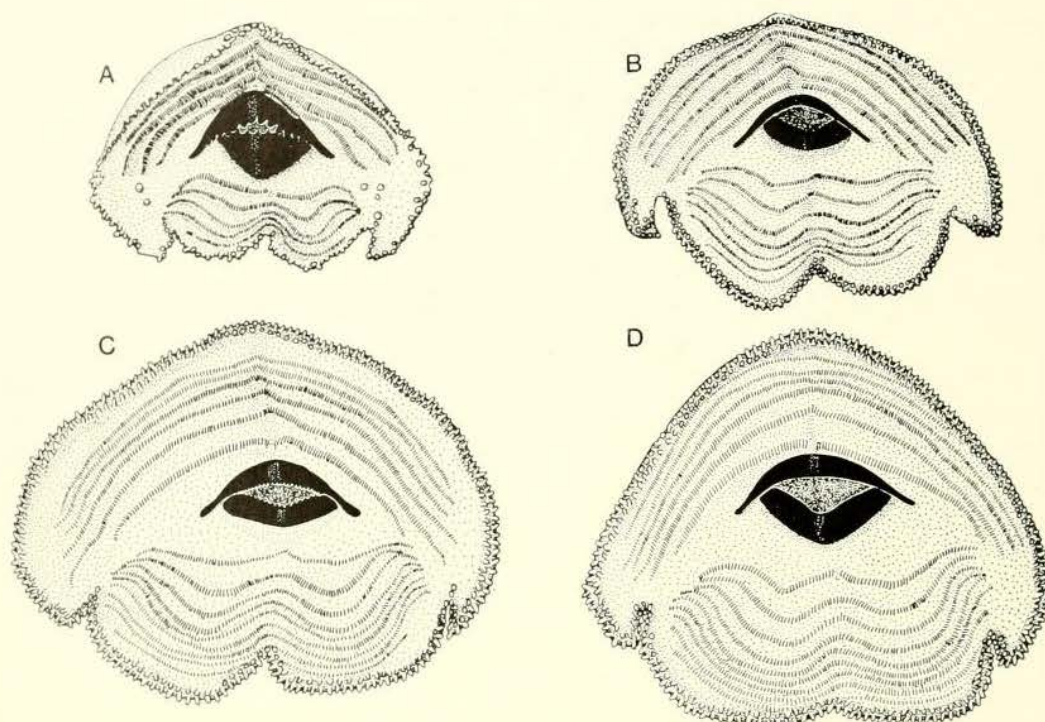


FIG. 3.—Mouths of tadpoles of *Hyla bogotensis* group. A. *H. platydactyla*, KU 139521. B. *H. alytolylax*, KU 112358. C. *H. phyllognatha*, KU 143542. D. *H. denticulenta*, KU 139531. $\times 8$. The mouth of the tadpole of *H. bogotensis* is like that of *H. platydactyla* except that the former has much smaller serrations on the beaks; the mouth of the tadpole of *H. colymba* is like that of *H. phyllognatha* (see Duellman, 1970:330).

Mating Calls

The mating calls are known for all species, except *H. bogotensis* and *H. denticulenta*; the calls consist of a series of short, loud peeps. Analysis of tape recordings of calls of three species reveals noticeable differences in several parameters of the calls (Table 4, Fig. 4). *Hyla colymba* has the most distinctive call, differing from the others in notes per call group, duration of notes, pulse rate, and pitch; the second harmonic is dominant. The calls of *H. phyllognatha* and *H. platydactyla* are more nearly alike in having only one har-

TABLE 3.—Characteristics of tadpoles of *Hyla bogotensis* group.

Species	Tooth Rows	Labial Papillae	Serrations on Beak	Total Length/ Body length	Caudal Musculature/ Caudal Depth
<i>H. alytolylax</i>	5/7	2	small	30.2%	63.1%
<i>H. bogotensis</i>	4/5	1	medium	32.3%	66.7%
<i>H. colymba</i>	6/9	2	small	35.6%	61.1%
<i>H. denticulenta</i>	7-8/10	2	none	35.3%	57.2%
<i>H. phyllognatha</i>	6/9	2	small	35.2%	60.0%
<i>H. platydactyla</i>	4/5	1	large	39.5%	80.0%

monic and fewer, but longer, notes per call group. However, their calls differ in note repetition rate, pulse rate, and pitch. The absence of analyzable recordings of the other three species precludes a complete biosonic analysis of the group. Nevertheless, the differences in the parameters of the calls of the three species are of the magnitude separating both sympatric and allopatric species in other Neotropical hylids [see Duellman (1963), Duellman and Trueb (1966), Duellman and Fouquette (1968), and Duellman (1972) for examples].

TABLE 4.—Comparison of mating calls of species in the *Hyla bogotensis* group.

Character N ^a	<i>H. colymba</i> 3/9	<i>H. phyllognatha</i> 4/13	<i>H. platydactyla</i> 1/16
Notes per Call Group	12–104 (40.3)	2–12 (5.5)	7–10 (8.8)
Note Repetition Rate (min)	123–236 (179)	120–360 (210)	540
Duration (sec)	0.05 -----	0.11–0.13 (0.12)	0.09–0.17 (0.14)
Pulses per Second	120–160 (138)	260–280 (279)	170–180 (177)
Harmonics	4	1	1
Fundamental Frequency (Hz)	1760–1820 (1796)	2550–2620 (2588)	2700–2860 (2790)
Dominant Frequency (Hz)	3520–3640 (3592)	2550–2620 (2588)	2700–2860 (2790)

^a N=individuals/notes.

DISCUSSION

The grouping of specimens into geographic samples provided an *a priori* assumption that the groups represented different taxa. This assumption was tested by discriminant analysis of 14 characters in adults. The results were re-tested by subsequent independent and combined analyses of 11 characters of adults and five of tadpoles by means of the distance phenogram program. The conclusions are supported by data on mating calls. Although it is possible that some of the taxa (*H. bogotensis* and *H. platydactyla*; *H. colymba* and *H. alytolylax*) might be geographical variants (subspecies), there exists no evidence for gene flow between populations. Consequently, the six recognized taxa are treated as species.

The distributions of the species are broadly allopatric (Fig. 5). Two species, *H. bogotensis* and *H. platydactyla*, occur in the Andes at elevations of 2500–2900 m and 1600–2700 m, respectively. *Hyla colymba* inhabits both Caribbean and Pacific slopes at elevations of 560–1410 m in Costa Rica and Panamá. The other species occur on Andean slopes: *H. alytolylax* at 800–1460 m on Pacific slopes,

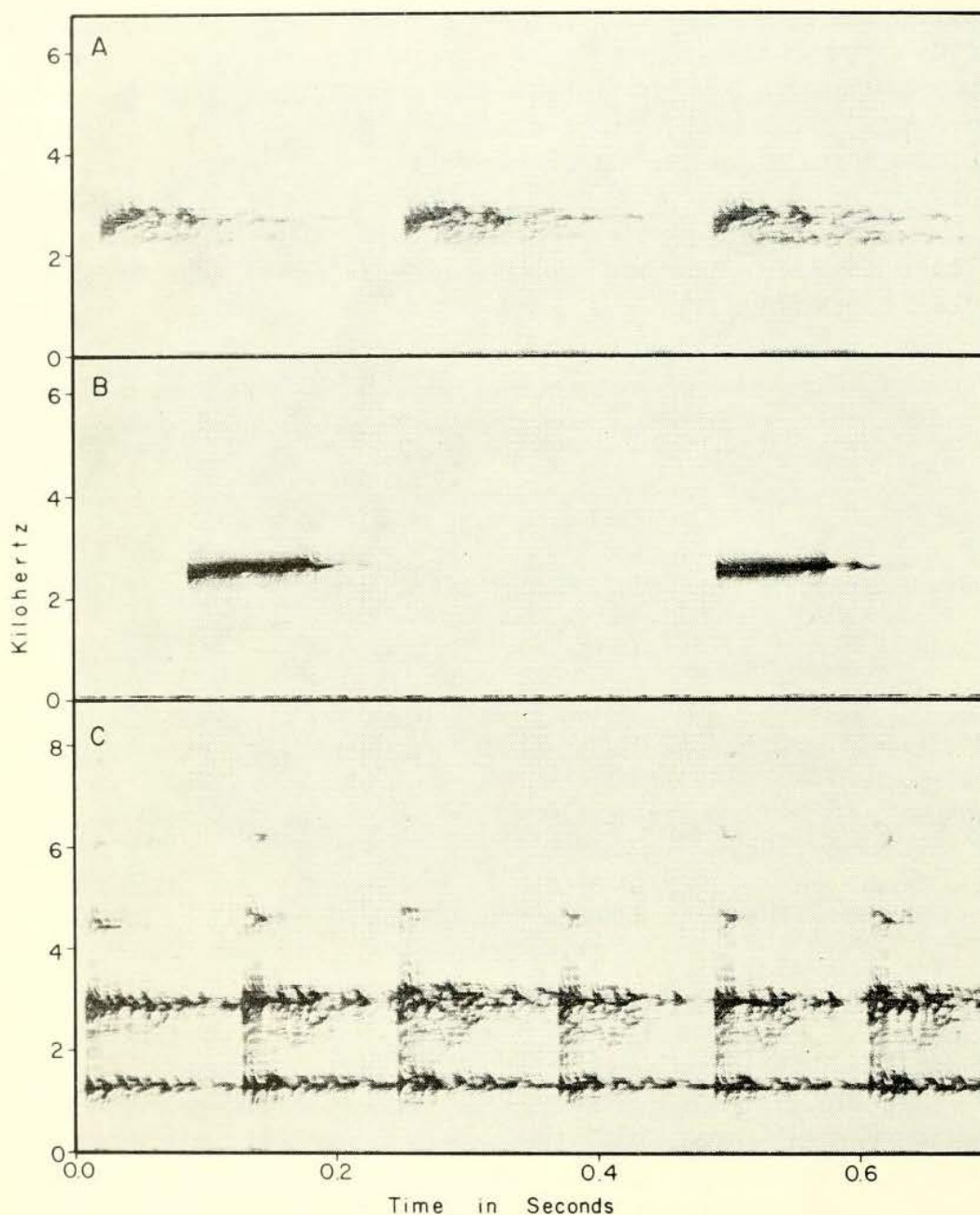


FIG. 4.—Audiospectrograms of mating calls. A. *Hyla platydactyla*, KU Tape 1029; 15-20 km NW Mérida, Mérida, Venezuela; temperature unknown. B. *H. phyllognatha*, KU Tape 1166; Río Azuela, Napo, Ecuador; 18° C. C. *H. colymba*, KU Tape 599; ridge between Río Jaqué and Río Imamadó, Darién, Panamá; 19° C. Band width 20 Htz.

H. phyllognatha at 610-1740 m on Amazonian slopes, and *H. denticulenta* at 1400-2400 m on Caribbean slopes. The principal habitat requirement seems to be cool, rocky streams for development of the tadpoles.

Due to lack of substantive information on direction of evolutionary change in many of the characters utilized, no quantitative phyletic analysis (Kluge and Farris, 1969) was attempted. The

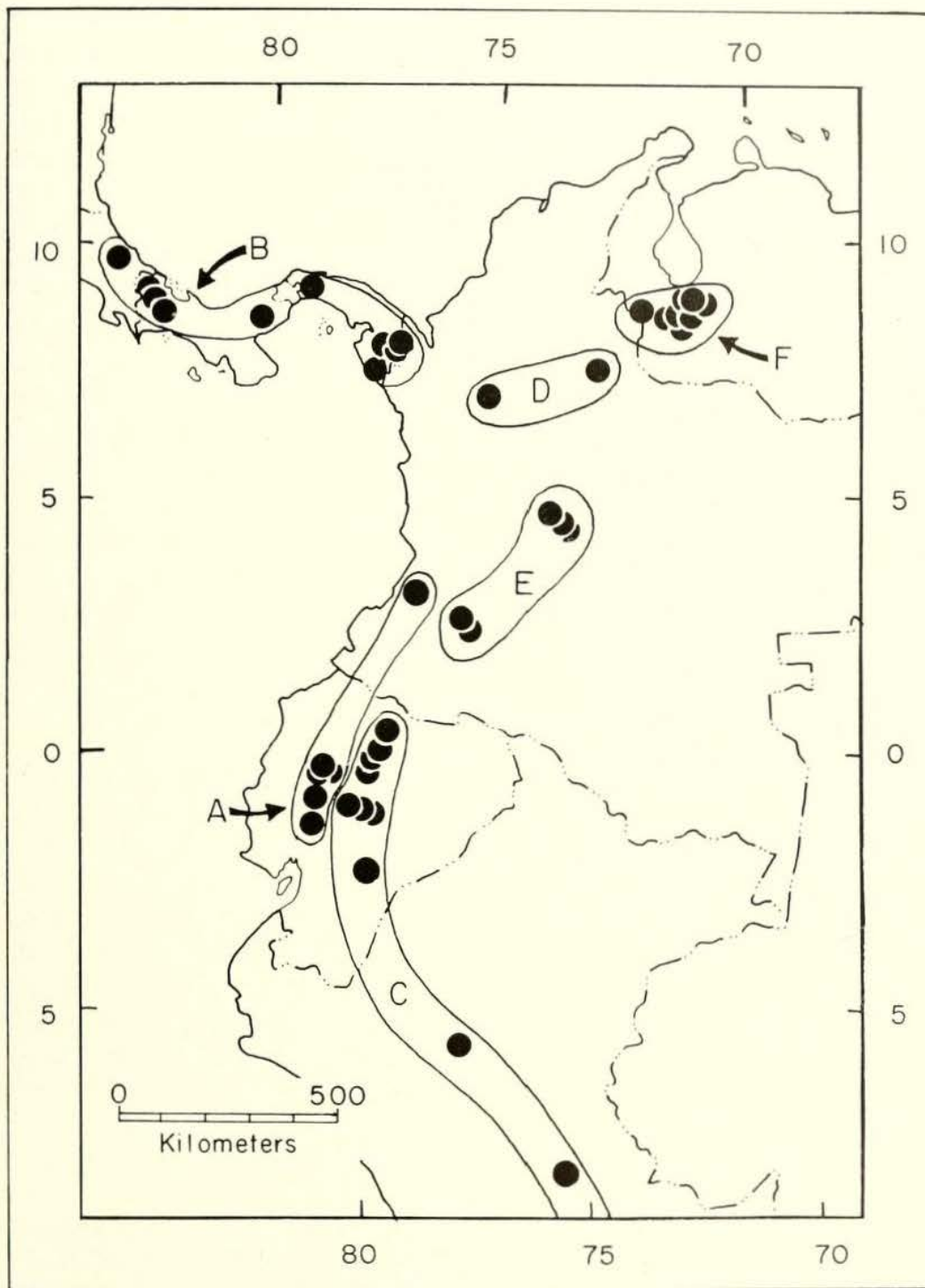


FIG. 5.—Distributions of the species in the *Hyla bogotensis* group. A. *H. alytolylax*. B. *H. colymba*. C. *H. phyllognatha*. D. *H. denticulenta*. E. *H. bogotensis*. F. *H. platydactyla*. Lines enclose approximate known ranges, within which specific localities are indicated by dots; the range of *H. phyllognatha* extends to southern Perú.

presence of dermal folds and calcars in adults and proliferation of tooth rows in tadpoles are certainly derived states (Duellman, 1970). The occurrence of extensive webbing and bifid subarticular

tubercles are probably derived character states. Furthermore, it seems that the presence of two tarsal stripes may have evolved from a condition in which one stripe was present. Other characters of structure and coloration remain evolutionarily enigmatic. All evidence points to *H. bogotensis* and *H. platydactyla* being the most generalized species, that is, having fewest derived character states. *Hyla denticulenta* possesses an array of derived states in both larvae and adults and seems to be the most advanced species in the group. The remaining three species seem to be closely related and phylogenetically intermediate between the primitive *H. bogotensis* and *H. platydactyla* and the advanced *H. denticulenta*.

Evidence from a variety of sources points to considerable Pleistocene climatic fluctuation and concomitant shifts in vegetation in the northern Andes (see Vuilleumier, 1971, for summary). This climatic fluctuation, together with orogenic changes in the Andes during the Pleistocene and volcanic activity to the Present, provided ample opportunity for isolation of populations on different slopes of the Andes (*H. alytolylax*, *H. denticulenta*, and *H. phyllognatha*), in disjunct interandean basins (*H. bogotensis* and *H. platydactyla*), and dispersal across presently uninhabited lowlands (*H. colymba*).

TAXONOMY

The inclusion of six species in the *Hyla bogotensis* group necessitates a modification of the definition of the group as given by Duellman (1970:327). The group can now be defined: 1) moderate-sized, stream-breeding frogs with males attaining snout-vent lengths of 45 mm and females 53 mm; 2) dorsum pale green or brown with or without dark flecks; 3) digits bearing small discs; 4) toes about three-fourths webbed; 5) axillary membrane absent; 6) quadratojugal articulating with maxillary; 7) sphenethmoid broad, not ossified anteriorly; 8) nasals small, widely separated medially; 9) frontoparietal fontanelle large; 10) tadpoles having long muscular tails, low fins, ventral mouths completely bordered by papillae, and 4/5—8/10 tooth rows; 11) mating calls consisting of series of short, loud peeps.

Distribution.—The combined distributions of the six species include the Andes and interandean valleys of western Venezuela and central and southern Colombia, Pacific and Amazonian slopes of Andes in Ecuador, Amazonian slopes in Perú, Caribbean slopes in northern Colombia, and Caribbean and Pacific slopes of highlands in Costa Rica and Panamá, with an elevational range of 560 to 2900 m (Fig. 5).

Remarks.—Members of the *Hyla bogotensis* group superficially resemble another group of species inhabiting lower Andean slopes in Ecuador, Colombia, and Venezuela (*H. palmeri* Boulenger, *H. albopunctata* Boulenger, and *H. lascinia* Rivero). These frogs lack mental glands; the mating calls and tadpoles are unknown.

KEY TO THE SPECIES IN THE *HYLA BOGOTENSIS* GROUP

1. Tarsal and ulnar folds and tarsal and anal stripes present; distal subarticular tubercle on fourth finger single, conical (if bifid, flat, not conical) 2
 Tarsal and ulnar folds and tarsal and anal stripes absent; distal subarticular tubercle on fourth finger bifid, conical 5
2. Distal subarticular tubercle on fourth finger single, conical; calcar, if present, small; snout round or truncate; tarsal and anal stripes single or double 3
 Distal subarticular tubercle on fourth finger bifid, flat; calcar large; snout anteriorly inclined; tarsal and anal stripes double, light above, dark below *H. denticulenta*
3. Dorsolateral stripe absent; webbing in males not extending to distal subarticular tubercle on fourth finger, reaching tubercle in females *H. phyllognatha*
 Dorsolateral stripe usually present; webbing in both sexes extending to or beyond subarticular tubercle on fourth finger 4
4. Dark pigment fine, scattered on dorsum; webbing usually extending beyond distal subarticular tubercle on fourth finger *H. alytolylax*
 Dark pigment coarse, dense on dorsum; webbing extending to distal subarticular tubercle on fourth finger *H. colymba*
5. Webbing extending to distal subarticular tubercle on fourth finger; dorsolateral stripe absent; dark pigment usually fine and scattered on dorsum *H. bogotensis*
 Webbing not extending to distal subarticular tubercle on fourth finger; dorsolateral stripe present or absent; dark pigment on dorsum forming discrete spots in adults *H. platydactyla*

***Hyla alytolylax* new species**

Figure 6A

Holotype.—KU 111903 from Tandapi, Provincia Pichincha, Ecuador, 1460 m, obtained on 22 July 1967, by John D. Lynch.

Paratopotypes.—KU 111892-6, 111898-902, 111906, John D. and Marsha Lynch, 15-24 July 1967; KU 117982-4, John D. Lynch, 1-3 March 1968; KU 120851-60, John D. Lynch and Gerald R. Smith, 27-28 July 1968; KU 132425-6, John D. Lynch, 6 August 1970.

Diagnosis.—1) Webbing extending to or beyond distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers single, conical; 3) ulnar and tarsal folds present; 4) calcar absent in males, absent or small in females; 5) snout in profile round in males, truncate in females; 6) tympanum distinct; 7)

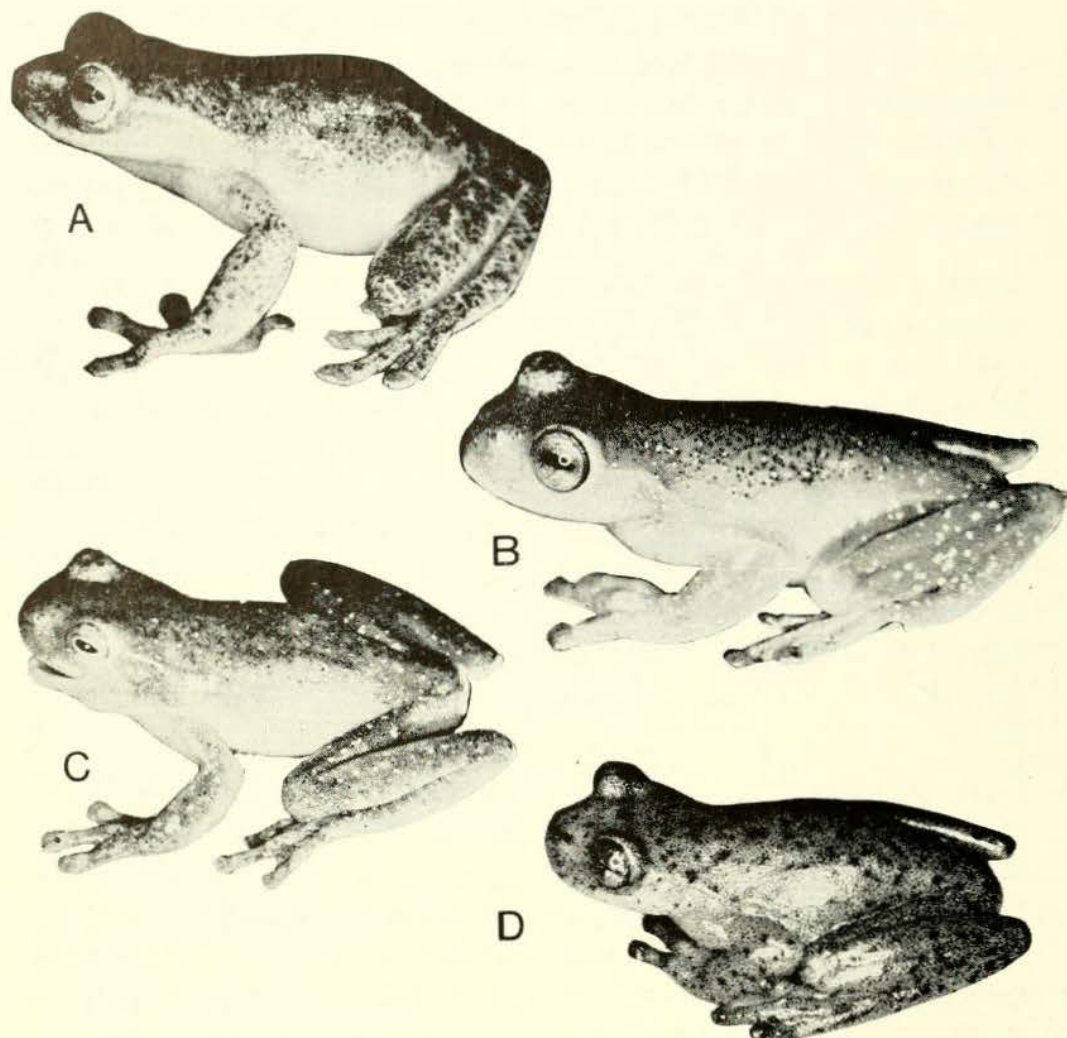


FIG. 6.—Frogs of the *Hyla bogotensis* group. A. *H. alytolylax*, KU 111900, ♀, 39.6 mm SVL. B. *H. denticulenta*, KU 133451, ♂, 44.2 mm SVL. C. *H. phyllognatha*, KU 143197, ♂, 33.3 mm SVL. D. *H. platydactyla*, KU 133433, ♂, 36.5 mm SVL.

mental gland present in males, absent in females; 8) dorsolateral light stripe present; 9) tarsal and anal stripes white; 10) tadpoles having 5/7 tooth rows, two rows of labial papillae, and small serrations on beaks.

Hyla alytolylax most closely resembles *H. colymba*, from which it differs by having slightly more webbing and less dense flecking on the dorsum; furthermore, the tadpoles of *H. alytolylax* have fewer tooth rows and a narrower snout. *Hyla alytolylax* also resembles *H. phyllognatha*, from which it differs by having more webbing, no or smaller calcars, and a dorsolateral light stripe; furthermore, the tadpoles of *H. phyllognatha* have more tooth rows and a broader snout.

Description.—N=13 ♂♂, 15 ♀♀; pertinent measurements and proportions given in table 1. Head slightly narrower than body; snout moderately short, round in dorsal aspect, round in profile in

males, truncate in females; nostrils four-fifths distance from eye to tip of snout, not protuberant; internarial area slightly depressed; canthus round; loreal region concave; lips thin, round; top of head flat; eyes not greatly protuberant; supratympanic fold weak, curved downward toward angle of jaw, obscuring upper edge of tympanum; tympanic ring evident ventrally; tympanum slightly less than one-half diameter of eye (0.382-0.484, \bar{x} =0.434, N=13 ♂♂; 0.425-0.500, \bar{x} =0.457, N=15 ♀♀), separated from eye by distance slightly greater than diameter of tympanum.

Axillary membrane absent; forearm robust, bearing ulnar fold; prepollical tubercle large, elliptical; palmar tubercle large, bifid; distal subarticular tubercle on fourth finger conical, single; supernumerary tubercles small, indistinct; fingers short, bearing small discs (that on third finger slightly larger than tympanum); length of fingers from shortest to longest 1-2-4-3; webbing vestigial between first and second fingers, extending from base of penultimate phalange of second finger to middle of antepenultimate phalange of third, from base of penultimate phalange of third to base or middle of penultimate phalange of fourth finger. Hind limb moderately robust; dermal fold on knee; calcar usually absent; inner tarsal fold absent; outer tarsal fold extending entire length of tarsus; inner metatarsal tubercle elliptical, barely visible from above; outer tarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles minute, present proximally; toes long; length of toes from shortest to longest 1-2-3-5-4; discs slightly smaller than those of fingers; webbing extending to base of penultimate phalange of fourth toe, to discs on other toes.

Anal opening directed posteriorly at upper level of thighs in both sexes; skin on belly and proximal posteroventral surfaces of thighs weakly granular; skin on other surfaces smooth; mental gland present in males. Tongue cordiform, shallowly notched posteriorly, barely free behind; dentigerous processes of prevomers antero-medially inclined posterior to small ovoid choanae; total number of prevomerine teeth 15-22 (\bar{x} =18.8, N=13 ♂♂), 20-24 (\bar{x} =21.8, N=15 ♀♀); vocal slit extending from midlateral base of tongue to angle of jaw; vocal sac bilobate, subgular.

Coloration.—In life, adults have a greenish dorsum varying from pale green to greenish yellow, greenish gray, or greenish brown. In some individuals the anterior part of the dorsum is darker than the posterior part, and the loreal region usually is dark green. A cream line extends along the canthus, edge of eyelid, and supratympanic fold; a narrow white tarsal stripe and white anal stripe are present. The dorsal surfaces of the body and limbs have small scattered brown or black flecks and, in some individuals, minute white flecks. In some specimens faint cream reticulations are present on the dorsal surfaces of the body and thighs. The groin and concealed surfaces of the limbs are not pigmented. The

venter is white, and in males the vocal sac is bluish green. The iris is creamy white.

In preservative, the dorsum is creamy tan with black flecks, varying from few to many, scattered over the dorsum. Dorsolateral, tarsal, and anal white stripes are evident. The groin, hidden surfaces of thighs, and all ventral surfaces are cream. Pale reticulations are evident posteriorly in some specimens.

Tadpoles.—A typical tadpole in developmental stage 27 from Tandapi, Ecuador, has a body length of 15.2 mm and a total length of 42.6 mm. Body ovoid, widening abruptly just anterior to eyes, three-fourths as deep as wide; nostrils about midway between eyes and tip of snout; spiracle sinistral; spiracular opening directed posteriorly at a point just below midline about two-thirds length of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually, extending nearly to tip of pointed tail; depth of caudal musculature at one-third length of tail 63 percent of total depth of tail. Mouth moderately large; lips indented posterolaterally, completely bordered by two rows of small labial papillae; five upper and seven lower rows of teeth; fifth upper row narrowly interrupted medially; beaks slender; lateral processes not expanded distally; upper beak bearing small peglike serrations; lower beak having small pointed serrations (Fig. 3B).

In preservative, the body is dark brown above and dull gray below; the caudal musculature is cream with brown flecks or reticulations laterally. The dorsal musculature is cream with transverse brown bars. The fins are transparent, except for a few brown flecks on the outer edge of the dorsal fin. In life, the body is pale brown above and dark brown below; the caudal musculature is pale cream with brown mottling laterally and blotches dorsally. The iris is silvery cream.

Etymology.—The specific name is derived from the Greek *alytos* meaning continuous, and the Greek *lylax* meaning babbler; the name is applied in reference to the long continuous calls of the species.

Distribution.—*Hyla alytolylax* is definitely known from elevations of 800 to 1460 m on the Pacific slopes of the Cordillera Occidental in Ecuador and southeastern Colombia. The northern localities in Ecuador are along the Río Pilatón, a tributary of the Río Toachi, and the southern localities are in the Río Playas drainage.

Remarks.—At Tandapi, Ecuador, males were calling from vegetation over, and boulders in, cascading mountain streams in cloud forest in July 1967 and in March and July 1968. Gravid females were found on bushes along streams. Tadpoles were obtained from gravel-bottomed pools in fast-flowing streams. Metamorphosing young were found on low vegetation along streams in July 1967, and two metamorphosed on 14 September from tadpoles obtained on 17 July 1967. Five young have snout-vent lengths of

17.6-20.4 (\bar{x} =18.4) mm. In life, the dorsal surfaces were pale green with a middorsal brown streak, expanded anteriorly into an interorbital bar in one individual.

The mating call consists of a long series of short, loud whistles, reminiscent of the call of *Hyla colymba*. Analyzable recordings are not available.

Two specimens (LACM 73000-1) from Camino de Yupe, Chocó, Colombia (420 m), possibly are referable to *Hyla alytolylax*, but because of certain differences, they have not been included in the analysis nor in the description. Both are males having snout-vent lengths of 39.0 mm and large mental glands. The dorsolateral stripe is absent, but tarsal and anal stripes are present; on either side of the anus is a triangular dermal flap, larger than the calcar. Perhaps these specimens represent an undescribed species that is intermediate in certain characters between *H. alytolylax* and *H. denticulenta*.

Duellman (1970:331) referred specimens of *H. alytolylax* to *H. colymba*.

***Hyla bogotensis* (Peters)**

Hylonomus bogotensis Peters, 1882a:107 [Holotype.—ZMB 10209 from Bogotá, Departamento Cundinamarca, Colombia; Möschler collector].

Hyloscirtus bogotensis Peters, 1882b:127.

Hyla bogotensis—Duellman, 1970:327.

Diagnosis.—1) Webbing extending to distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers bifid, conical; 3) ulnar and tarsal folds absent; 4) calcar absent; 5) snout in profile truncate; 6) tympanum distinct or covered in males, covered in females; 7) mental gland present or absent in males, absent in females; 8) dorsolateral light stripe absent; 9) tarsal and anal stripes absent; 10) tadpoles having 4/5 tooth rows, one row of labial papillae, and medium-sized serrations on beaks.

Hyla bogotensis is like *H. platydactyla* in having bifid, conical subarticular tubercles, no ulnar and tarsal folds, no tarsal and anal stripes, and tadpoles with 4/5 tooth rows and one row of labial papillae; these characters distinguish these two species from other members of the group. *Hyla bogotensis* can be distinguished from *H. platydactyla* by the presence of more webbing and finer dorsal flecking in the former; moreover, the tadpoles of *H. bogotensis* have smaller serrations on the beaks than do those of *H. platydactyla*.

Coloration.—I have not seen living individuals of this species, so I must rely upon descriptions given by others. Cochran and Goin (1970:315) noted that a specimen from Bogotá, Colombia, was "... a yellowish brown with a definite pattern of more or less uniformly distributed pencil-like black spots on all the dorsal surfaces. All ventral surfaces were a dirty gray without pattern, except for faint pepper-like flecks under the throat and a yellowish tinge to the under-margin of the jaws." Philip A. Silverstone (field notes,

6 January 1966) described a specimen (LACM 50562) from Páramo de Puracé, Colombia, as "Green all over; yellowish tinge on flanks and ventral surfaces of thighs. Blue on ankle and sole; web orange." Juan A. Rivero (pers. com.) stated that a specimen (UPR-M 1800) from Páramo de Palacio was solid brown above in life, but that the freshly preserved specimen was chartreuse above with dark brown dots; there was some yellow on the throat and ventral surfaces of the thighs.

In preservative, most specimens are creamy tan with or without scattered dark flecks on the dorsum. Two individuals (FMNH 81916 and UPR-M 1800) have many larger black dots on the dorsum.

Tadpoles.—A single tadpole (CAS-SU 22971) in developmental stage 37 has a body length of 21.0 mm and a total length of 68.0 mm. Body ovoid, two thirds as deep as wide; nostrils slightly closer to eye than to tip of snout; spiracle sinistral; spiracular opening directed posterodorsally on midline at about midlength of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually; extending nearly to tip of pointed tail; depth of caudal musculature at one-third length of tail 66.7 percent of total depth of tail. Mouth moderately large; lips indented posterolaterally, completely bordered by single row of labial papillae; four upper and five lower rows of teeth; fourth upper row narrowly interrupted medially; beaks massive; lateral processes expanded distally; beaks bearing medium-sized serrations.

In preservative the body is pale brown above and cream below. The caudal musculature is pale brown with a dorsolateral dark brown stripe on the proximal half of the tail.

Distribution.—This species is known from subpáramo regions in the Bogotá Valley in the Cordillera Oriental and in the highlands east of Popoyán in the Cordillera Central in Colombia. All recorded elevations are between 2500 and 2900 m.

Remarks.—For many years this species was regarded as being generically distinct from *Hyla* on the basis of having rounded, instead of dilated, sacral diapophyses. Duellman (1970:328) noted that the type (ZMB 10209) actually had expanded sacral diapophyses. Subsequent examination of additional specimens supports the contention that the sacral diapophyses are not round in this species.

The mating call is unknown. Dunn (1944:79) noted that a specimen was found in a bromeliad at Boquerón, Colombia. Philip A. Silverstone (field notes, 6 January 1966) found one individual on a leaf near a stream in subpáramo by day. Notes by Anne Funkhouser accompanying a tadpole and partially metamorphosed young (CAS-SU 22970-1) state: "Fast mountain stream on road to Choachí from Bogotá. Fairly common in area collected. Adults were never found, but young kept for several months were bright grass green above with random dark spots; turquoise shading to

yellow ventrally; iris gold." The metamorphosing young (CAS-SU 22970) has a snout-vent length of 22.0 mm and a tail stub of 7.2 mm; in preservative, it is creamy tan with scattered brown flecks on the dorsum.

Hyla colymba Dunn

Hyla colymba Dunn, 1931:400 [Holotype.—MCZ 10234 from La Loma, Provincia Bocas del Toro, Panamá; Chester Duryea and Emmett R. Dunn collectors].

Hyla alvaradoi Taylor, 1952:882 [Holotype.—KU 30886 from Moravia, Provincia Cartago, Costa Rica; Edward H. Taylor collector]. Synonymy fide Duellman (1966:267).

Diagnosis.—1) Webbing extending to distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers single, conical; 3) ulnar and tarsal folds present; 4) calcar absent; 5) snout in profile round; 6) tympanum distinct; 7) mental gland present in males, present or absent in females; 8) dorsolateral light stripe present in males, present or absent in females; 9) tarsal and anal stripes white; 10) tadpoles having 6/9 tooth rows, two rows of labial papillae, and small serrations on beaks.

Hyla colymba most closely resembles *H. alytolylax*, from which it differs by having slightly less webbing and more dense flecking on the dorsum; furthermore, the tadpoles of *H. colymba* have more tooth rows and a broader snout. *Hyla colymba* differs from *H. phyllognatha* by having more webbing and usually a dorsolateral light stripe; the structure of the tadpoles of the two species is identical, but dark transverse blotches are present on the dorsum of the tail in *H. phyllognatha*, whereas the tail in *H. colymba* is nearly uniform brown.

Coloration.—In life, most individuals are pale green with faint yellow flecks or scattered brown flecks on the dorsum. A faint creamy yellow stripe extends from the canthus, along the edge of the eyelid and on the supratympanic fold to a point above the arm. The anal, ulnar, and tarsal stripes are pale creamy yellow. The ventral surfaces of the limbs are pale green, and the throat is pale bluish green. The belly and chest are white, and the mental gland is white or creamy yellow. Some individuals are pale tan with brown flecks. The iris is pale brown.

In preservative, the dorsum is pale creamy white, creamy tan, or pale brown. Minute dark flecks are present dorsally; usually these are most numerous on the head and middorsally on the body. The stripes are white, and the venter is creamy white.

Tadpoles.—A typical individual in developmental stage 25 from Darién, Panamá, has a body length of 15.1 mm and a total length of 37.3 mm. Body ovoid, four-fifths as deep as wide; nostrils midway between eyes and tip of snout; spiracle sinistral; spiracular opening directed posteriorly just below midline at midlength of

body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually, extending nearly to tip of pointed tail; depth of caudal musculature at one-third length of tail 61 percent of total depth of tail. Mouth large, ventrals; lips deeply indented posterolaterally, completely bordered by two rows of labial papillae; six upper and nine lower rows of teeth; sixth upper and first lower rows narrowly interrupted medially; outermost three lower rows shorter than others; upper beak broadly arched, bearing long slender lateral processes; lower beak broadly V-shaped; both beaks bearing small, blunt serrations.

In preservative, the body is brown with faint white flecks. The caudal musculature is creamy tan; brown flecks are present on the musculature and dorsal fin. In life, the dorsum of the body is bronze-tan with golden lichenous flecks; the sides of the body are brown with gold flecks. The caudal musculature is tan; dark brown spots are present on the musculature and dorsal fin. This iris is dull bronze.

Distribution.—This species occurs in cloud forest and lower humid montane forest at elevations of 610-1200 m on the Caribbean slopes of the Cordillera Talamanca in Costa Rica and Western Panamá and 560-1410 m on the Pacific slopes of the highlands in central and eastern Panamá.

Remarks.—Duellman (1970:328) gave a detailed account of *H. colymba* and discussed the nomenclatural history of the species; his reference to the occurrence of the species in Ecuador was based on material herein assigned to *H. alytolylax*.

The mating call consists of a series of short high-pitched, cricket-like chirps. Calls have as many as 104 notes produced at a rate of 123-236 notes per minute. The second harmonic at about 3600 Hertz is dominant (Fig. 4C).

Adults have been found on vegetation along streams, and males were found calling beneath boulders in streams. Tadpoles have been found in quiet pools in small rocky streams.

***Hyla denticulenta* new species**

Figure 6B

Holotype.—KU 133451 from Charta, Departamento Santander, Colombia, 2400 m, obtained on 15 July 1970, by Stephen R. Edwards.

Paratype.—KU 133452 from Valdivia, Departamento Antioquia, Colombia, obtained on 3 August 1970, by Stephen R. Edwards.

Diagnosis.—1) Webbing extending beyond distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers bifid, flat; 3) ulnar and tarsal folds present; 4) calcar large; 5) snout in profile anteriorly inclined; 6) tympanum distinct; 7) mental gland absent; 8) dorsolateral stripe absent; 9) tarsal and

anal stripes white above, brown below; 10) tadpoles having 7-8/10 tooth rows, two rows of labial papillae, and no serrations on beaks.

Hyla denticulenta differs from all other members of the group by its large size, bifid and flat subarticular tubercles, large calcars, and anteriorly inclined snout; also, the presence of 7-8/10 tooth rows and absence of serrations on the beaks distinguish the tadpoles from all others.

Description.—N=1 ♂ (holotype), 1 ♀ (paratype); pertinent measurements and proportions given in table 1. Head as wide as body; snout moderately short, round in dorsal aspect, anteriorly inclined in profile (especially in female); nostrils three-fourths distance from eye to tip of snout, not protuberant; internarial area flat; canthus round; loreal region concave; lips thin, round; top of head flat; eyes not greatly protuberant; supratympanic fold weak, curved downward toward angle of jaw, obscuring upper part of tympanum; tympanic ring distinct; tympanum one-half diameter of eye, separated from eye by distance equal to half again diameter of tympanum.

Axillary membrane absent; forearm robust, bearing ulnar fold; prepollical tubercle large, elliptical; palmar tubercle large, bifid; distal subarticular tubercle on fourth finger flat, bifid; others round; supernumerary tubercles small, indistinct; fingers short, bearing small discs (that on third finger slightly larger than tympanum); length of fingers from shortest to longest 1-2-4-3; webbing vestigial between first and second fingers, extending from base of penultimate phalange of second to distal end of antepenultimate phalange of third, from base of penultimate phalange of third to base (male) or middle (female) of penultimate phalange of fourth finger. Hind limb moderately robust; dermal fold on knee; calcar prominent, triangular; inner tarsal fold absent; outer tarsal fold extending length of tarsus; inner metatarsal tubercle elliptical, visible from above; outer tarsal tubercle absent; subarticular and supernumerary tubercles about equal in size, small, round; toes long; length of toes from shortest to longest 1-2-3-5-4; discs slightly smaller than those on fingers; webbing extending to base of penultimate phalange of fourth toe, to discs on other toes.

Anal opening directed posteroventrally at midlevel of thighs (male), posteriorly at upper level of thighs (female); skin on belly and proximal posteroventral surfaces of thighs weakly granular; skin on other surfaces smooth. Tongue broadly cordiform, shallowly notched posteriorly, barely free behind; denticigerous processes of prevomers slightly anteromedially inclined posterior to small ovoid choanae, bearing 21 (male), 20 (female) teeth; vocal slit extending from posterolateral base of tongue to angle of jaw; vocal sac subgular, possibly bilobate.

Coloration.—In life, the male holotype had a pale green dorsum covered with many small white flecks; black flecks were present

on the head and back. The flanks were creamy yellow; the throat, chest, groin, anterior surfaces of the thighs, and ventral surfaces of the shanks were bluish green. The belly was creamy yellow, and the iris was reddish gold. The female had a green dorsum with a white margin to the lips and white anal, ulnar, and tarsal stripes. The axilla, groin, and ventral surfaces of the thighs were blue-green; the flanks were yellow-orange. The throat and belly were greenish white, and the iris was dark gold with black reticulations.

In preservative, all pigment is lost, except for many small brown flecks on the head and anterior two-thirds of the back in the male and a few scattered flecks on the eyelids, head, and middorsum of the female. Also, white flecks are apparent dorsolaterally in the male. In both specimens narrow white anal, ulnar, and tarsal stripes are bordered below by a narrow line of brown pigment, which is expanded on the palm and sole.

Tadpoles.—Five tadpoles (KU 139531) are from the type locality. The smallest individual is in developmental stage 25 and has a body length of 17.5 mm and a total length of 51.5 mm; the largest is in stage 38 and has measurements of 22.0 and 65.5 mm. Body ovoid, four-fifths as deep as wide, widening and deepening abruptly just anterior to the eyes; nostrils midway between eyes and tip of snout; spiracle sinistral; spiracular opening directed posteriorly just below midline at about midlength of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, gradually tapering, extending nearly to tip of pointed tail; depth of musculature at one-third length of tail 57 percent of total depth of tail. Mouth large, ventral; lips deeply indented posteriolaterally, completely bordered by two rows of small papillae; seven or eight upper and ten lower rows of teeth; proximal upper row narrowly interrupted medially; upper beak slender with long, tapering lateral processes; lower beak broadly V-shaped; both beaks smooth or bearing minute serrations (Fig. 3D).

In preservative, the body is dark brown above and dull gray below; the caudal musculature is cream with dense brown pigment laterally, forming distinct transverse bars, separated by narrow cream interspaces, dorsally. The fins are transparent, except for a few flecks on the dorsal fin. In life, the body is pale gray; the tail is distinctly mottled black, gray, and white, and the fins are transparent.

Etymology.—The specific name is derived from the Latin *denticulus* meaning with small teeth, and the Latin *lentus* meaning full of; the name refers to the many rows of teeth in the tadpoles.

Distribution.—This species is known from only two localities: Charta at an elevation of 2400 m on the northern slope of the Cordillera Central, and Valdivia at an elevation of 1400 m on the northern slope of the Cordillera Central. These localities are separated by the low Río Magdalena Valley. It is unlikely that gene

flow exists between the populations; thus, it is possible that additional material will reveal differences between the populations.

Remarks.—At Charta the frogs were found along a shallow river south of the village. The river, a tributary of the Río Suratá, flows through pasture land with a few scattered trees. Tadpoles and a metamorphosing young having a snout-vent length of 24.6 mm and a tail stub of 10.4 mm were found in pools in the river bed. The holotype was found by day under a large rock in a small stream cascading into the river bed. The adult female was found in the town of Valdivia, where it was perched on a leaf of a large herb 2 m above the ground on a steep bank at night. The mating call is unknown.

Hyla phyllognatha Melin

Figure 6C

Hyla phyllognatha Melin, 1941:30 [Holotype.—NHMG 474 from Roque, Departamento San Martín, Perú; Douglas Melin collector].

Diagnosis.—1) Webbing not extending to, or just extending to, distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers single, conical; 3) ulnar and tarsal folds present; 4) calcar absent or small; 5) snout in profile round or truncate; 6) tympanum distinct; 7) mental gland present in males, present or absent in females; 8) dorsolateral light stripe absent; 9) tarsal and anal stripes absent or white; 10) tadpoles having 6/9 tooth rows, two rows of labial papillae, and small serrations on beaks.

Hyla phyllognatha is like *H. colymba* and *H. alytolylax* but has less webbing and no dorsolateral stripe. In some specimens of *H. phyllognatha* a calcar is present, but this is smaller than the calcars in *H. denticulenta*, which further differs by having bifid subarticular tubercles, anteriorly inclined snout, and more webbing. The tadpoles of *H. phyllognatha* have 6/9 tooth rows, a character shared with *H. colymba*, the tadpoles of which differ from those of *H. phyllognatha* by not having transverse brown blotches on the dorsal caudal musculature.

Coloration.—In life, the dorsum is olive-green anteriorly changing to olive-tan posteriorly; the dorsal surfaces of the limbs are green. Minute black flecks are present on the head and middorsal part of the body, and small white flecks are scattered on the body and limbs. The margin of the lip is yellow, and the anal and tarsal stripes are pinkish white. The hidden surfaces of the limbs are dull green. The belly is creamy yellow, and the webbing is dull yellow. The vocal sac is green, and the lining of the mouth is bluish green. The iris is dull bronze with black reticulations. One female found by day was bright green with bluish white flecks.

In preservative, the dorsum is cream to grayish brown with scattered dark flecks apparent in paler specimens. The venter and hidden surfaces of the thighs are cream.

Tadpoles.—A typical tadpole in developmental stage 27 from 16.5 km NNE of Santa Rosa, Ecuador, has a body length of 16.5 mm and a total length of 50.3 mm. Body ovoid, slightly wider than deep; nostrils slightly closer to tip of snout than to eyes; spiracle sinistral; spiracular opening directed posteriorly just below midline about two-thirds length of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually, extending nearly to tip of pointed tail; depth of musculature at one-third length of tail 60 percent of total depth of tail. Mouth large, lips indented posterolaterally, completely bordered by two rows of small labial papillae; six upper and nine lower rows of teeth; sixth upper row narrowly interrupted medially; beaks moderately slender, bearing small, blunt serrations; upper beak arched with lateral processes barely expanded distally; lower beak broadly V-shaped (Fig. 3C).

In preservative, the body is dark brown above and gray below; the caudal musculature is cream with dense brown flecking laterally and dark brown transverse bars anterodorsally. The fins are transparent with brown flecks, except anteriorly on ventral fin. In life, the body is dark brown with small green, lichenous flecks. The caudal musculature is tan with brown blotches; the fins are clear with orange spots. The iris is dark bronze.

Distribution.—*Hyla phyllognatha* is known from elevations of 610-1740 m on the Amazonian slopes of the Cordillera Oriental of the Andes and associated ranges, such as the Cordillera del Dué and Cordillera Carabaya, from northern Ecuador to southern Perú.

Remarks.—Males call from low bushes over torrential mountain streams; calling males have been found in April, July, August, and October. Gravid females have been found in October. The tadpoles live in gravel-bottomed pools in the streams. Recently metamorphosed young have been found on vegetation along streams at night and in bromeliads by day. Four young have snout-vent lengths of 18.4-20.3 (\bar{x} =19.5) mm; in life, the dorsum is green with black flecks middorsally.

The mating call consists of a series of short, loud whistles, repeated at a rate of about 210 notes per minute. The notes have about 280 pulses per second; the fundamental frequency at about 2560 Hertz is dominant (Fig. 4B).

No information has been published on *Hyla phyllognatha* since Melin's (1941) original description. The holotype (NHMG 474) is an adult male having a snout-vent length of 32.3 mm and a mental gland. The specimen compares favorably with series of fresh specimens from Ecuador and three individuals from southern and central Perú.

Hyla platydactyla Boulenger

Figure 6D

Hyla platydactyla Boulenger, 1905:183 [Holotype.—BMNH 1904.6.30.17 (RR 1947.2.13.14) from Mérida, Estado Mérida, Venezuela; Briceño collector].

Hyla paramica Rivero, 1961:112 [Holotype.—UMMZ 59016 from Escorial, Estado Mérida, Venezuela; received from W. F. H. Rosenberg]. New synonymy.

Hyla jahni Rivero, 1961:113 [Holotype.—UMMZ 46465 from Escorial, Estado Mérida, Venezuela; presented by A. G. Ruthven]. New synonymy.

Diagnosis.—1) Webbing not extending to distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers single or bifid in males, bifid and conical in females; 3) ulnar and tarsal folds absent; 4) calcar absent; 5) snout in profile truncate; 6) tympanum distinct or covered; 7) mental gland present or absent in both sexes; 8) dorsolateral stripe present or absent; 9) tarsal and anal stripes absent; 10) tadpoles having 4/5 tooth rows, one row of labial papillae, and large serrations on beaks.

Hyla platydactyla is like *H. bogotensis* in having bifid, conical subarticular tubercles, no tarsal or anal stripes, no ulnar or tarsal folds, and tadpoles with 4/5 tooth rows and one row of labial papillae; these characters distinguish these two species from other members of the group. *Hyla platydactyla* can be distinguished from *H. bogotensis* by having less webbing and, in large adults, discrete dark spots dorsally. Also, the tadpoles of *H. platydactyla* have larger serrations on the beaks than do those of *H. bogotensis*.

Coloration.—In life, specimens from a locality 15-20 km NW of Mérida, Venezuela, had reddish brown dorsal surfaces with many small black spots on the back. The throat was greenish tan, and the belly was white. The iris was copper with fine black reticulations. Through the courtesy of Juan A. Rivero, I have seen colored photographs of individuals having olive-tan dorsal coloration and creamy yellow dorsolateral stripes. Rivero stated (pers. com.) that some individuals are dark brown above and that in most specimens the anterior and posterior surfaces of the thighs are orange.

In preservative, in adults the dorsal surfaces of the head, body, forearms, and shanks are tan to brown with small dark brown to black spots present in most specimens. The dorsolateral stripe, thighs, and ventral surfaces are cream.

Tadpoles.—In a series from 15-20 km NW of Mérida, Venezuela, the smallest tadpole is in developmental stage 25 and has a body length of 8.5 mm and a total length of 26.5 mm; the largest tadpole (stage 37) has measurements of 23.0 and 60.5 mm. Body ovoid, three-fourths as deep as wide; nostrils slightly closer to eyes than to tip of snout; spiracle sinistral; spiracular opening directed posteriorly on midline about midlength of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust,

tapering gradually, extending nearly to tip of pointed tail; depth of caudal musculature at one-third length of tail 80 percent of total depth of tail. Mouth moderately large; lips deeply indented posterolaterally, completely bordered by one row of labial papillae; four upper and five lower rows of teeth; fourth upper row narrowly interrupted medially; fifth lower row short; upper beak moderately massive, arched, with robust lateral processes and large, pointed serrations; lower beak massive, broadly V-shaped, bearing large blunt serrations (Fig. 3A).

In preservative, the body is dark brown above and paler brown below; the caudal musculature is creamy tan with a heavy suffusion of brown laterally and two or three distinct longitudinally rectangular blotches on the dorsum, separated by narrow cream interspaces. The dorsal fin and posterior one-third of ventral fin are heavily flecked with brown.

Distribution.—This species is known only from the Mérida Andes in western Venezuela, where it occurs at elevations from 1600 to at least 2500 m, inhabiting subtropical and temperate areas.

Remarks.—Rivero (1961:115) diagnosed *Hyla paramica* from *H. jahni* by the former having a “. . . rounded snout, less defined canthus and in lacking supratympanic fold, canthal, palpebral, and supratympanic lines and closely set dark dots above.” He (1961:116) stated that *Hyla platydactyla* differed from *H. jahni* “. . . in the shorter snout and less defined canthus, absence of a light canthal and supratympanic line, narrower interorbital space, more vertical loreal region and different coloration [no dorsal spots].” Rivero based his descriptions of *H. paramica* on five specimens and of *H. jahni* on seven, all of which are rather poorly preserved; he examined no specimens of *H. platydactyla*.

I have examined all of the specimens studied by Rivero and the holotype of *H. platydactyla*, together with several series from western Venezuela (total of 59 adults and subadults). I find no consistent structural differences, such as snout shape, definition of canthal ridge, or inclination of loreal region, by which to distinguish more than one taxon in western Venezuela. The dorsolateral stripe (canthal, palpebral, and supratympanic lines of Rivero) is variable; a stripe is evident in the supratympanic region in slightly more than half of the specimens; in some of these it extends posteriorly to the axilla. Also, in some of these specimens no stripe is evident on the canthus. On the basis of preserved specimens alone, there seems to be a continuum from well-defined to no stripes. Thus, only one species, *H. platydactyla*, can be recognized.

The mating call consists of a series of short notes repeated at a rate of 540 notes per minute; the pulse rate is about 177 pulses per second, and the fundamental frequency at about 2790 Hertz is dominant (Fig. 4A).

At a locality 15-20 km NW of Mérida, Venezuela, adults were found at night on leaves of herbs on a steep bank over a roadside ditch. Tadpoles were found in quiet pools in a cascading stream. Juan A. Rivero stated (pers. com.) that adults are found in bromeliads by day and that males call from bushes over streams at night. He also noted that the frogs produce a smelly exudate when handled.

Cochran and Goin (1970:256) proposed the name combination *Hyla labialis platydactyla*; the name was used for the population of frogs in the eastern Andes of Colombia that is referable to the highly variable *Hyla labialis*, a species quite distinct from *H. platydactyla*.

RESUMEN

Las ranas del grupo *Hyla bogotensis* se crían en los arroyos de las vertientes de los Andes en el occidente de Venezuela, Colombia, Ecuador, y Perú, y en las sierras de Costa Rica y Panamá. Las ranas de este grupo se caracterizan por: 1) su tamaño moderado (longitud de cabeza-cuerpo de los machos hasta 45 mm, en las hembras hasta 53 mm); 2) el dorso de color verde opaco o carmelita con manchas pequeñas oscuras espaciadas en él; 3) los dedos con tres cuarta partes cubiertos por la membrana interdigital; 4) la glándula del mentón en el ápice de éste; 5) membrana axilar ausente; 6) el cuadratoyugal articulado con el maxilar; 7) los nasales pequeños, separados ampliamente en el medio; 8) la fontanela frontoparietal grande; 9) renacuajos con colas musculares, largas, la boca ventral grande, completamente bordeada por papilas labiales, con 4/5—8/10 hileras de dientes.

Se analizaron 14 caracteres de ranas adultas por medio del programa de computación de análisis discriminante multiple; los seis grupos resultantes fueron tratados como OTUs en los programas de NT-SYS, en el cual 11 caracteres de adultos y cinco de los renacuajos constituyeron los datos básicos para la construcción de los fenogramas. Los resultados de estos análisis son sostenidos por el análisis de las llamadas de reclamo de tres especies.

Se reconocen seis especies en el grupo: 1) *H. alytolylax* especie nueva, laderas del Pacífico de los Andes en Ecuador; 2) *H. bogotensis* (Peters, 1882), Andes del centro y sur de Colombia; 3) *H. colymba* Dunn, 1931, sierras de Costa Rica y Panamá; 4) *H. denticulenta* especie nueva, laderas del Caribe de los Andes en el norte de Colombia; 5) *H. phyllognatha* Melin, 1941, laderas amazónicas de los Andes en Ecuador y Perú; 6) *H. platydactyla* Boulenger, 1905, Andes del occidente de Venezuela. *Hyla paramica* Rivero, 1961, y *Hyla jahni* Rivero, 1961, son colocadas en sinónimia de *Hyla platydactyla* Boulenger, 1905.

SPECIMENS EXAMINED

Hyla alytolylax.—COLOMBIA: *Chocó*: Camino de Yupe, 420 m, LACM 73000-1. *Valle*: Anchicayá, KU 148703-4. ECUADOR: *Bolívar*: Balsabamba, 800 m, KU 132432, 132545 (tadpoles). *Cotopaxi*: 20.3 km W Pilaló, 830 m, KU 142857 (tadpoles). *Pichincha*: 3.7 km E. Dos Ríos, 1190 m, KU 142856 (tadpoles); Las Palmas, 920 m, KU 132427; Tandapi, KU 111892-903, 111904 (skeleton), 111905-10, 112357-8 (tadpoles), 112359 (young), 117982-4, 118123 (tadpoles), 120851-60, 132425-6.

Hyla bogotensis.—COLOMBIA: *Cauca*: Moscopán, 2500 m, UMMZ 121032. *Cundinamarca*: Bogotá, 2630 m, CAS-SU 22970 (tadpole), 22971 (young), KU 125363, UMMZ 123946-8, ZMB 10209; Boquerón, 2900 m, FMNH 81916; Páramo de Palacio, Siberia, UPR-M 1800. *Huila*: east of Páramo de Puracé, 2500 m, LACM 50562.

Hyla colymba.—COSTA RICA: *Cartago*: Moravia, 1200 m, KU 30886, 31864, 31865 (skeleton). PANAMÁ: *Bocas del Toro*: La Loma, 610 m, MCZ 10234-5; Río Changena, 650 m, KU 104237 (young); Río Changena, 830 m, KU 104236 (tadpoles). *Coclé*: El Valle, 560 m, AMNH 59606. *Darién*: Cerro Citurio, Serranía de Pirre, 1100 m, KU 116357; Cerro Malí, 1410 m, GML 4-00426; Laguna, 820 m, KU 77414; ridge between Río Jaqué and Río Imamadó, 730 m, KU 116779 (tadpoles), 116780-1 (young). *Panamá*: Altos de Pacora, 740 m, KU 95979.

Hyla denticulenta.—COLOMBIA: *Antioquia*: Valdivia, 1400 m, KU 133452. *Santander*: Charta, 2400 m, KU 133450-1, 139531 (tadpoles).

Hyla phyllognatha.—ECUADOR: *Morona-Santiago*: Macas, AMNH 33911. *Napo*: Bermejo No. 4 (oil well site), 15 km ENE Umbaqui, 720 m, KU 123130-2; Río Azuela, 1740 m, KU 143199-204, 143543 (young), USNM 193349-50; Río Salado, 1 km upstream from Río Coca, 1410 m, KU 146794 (tadpoles); Salto de Agua, 2.5 km NNE Río Reventador, 1660 m, KU 143205, 143544 (young), 146793 (tadpoles); San José, AMNH 22164; 16.5 km NNE Santa Rosa, 1700 m, KU 143197-8, 143542 (tadpoles). *Pastaza*: Mera, 1140 m, KU 121418 (tadpoles), 121419 (young); Puyo, 960 m, FMNH 172632; Río Alpayacu, 1 km E Mera, 1100 m, KU 121040. *Tungurahua*: 18.5 km E Baños, 1600 m, KU 141596 (young). PERÚ: *Junín*: Perene, AMNH 17260, 17277. *Puno*: La Unión, Río Huacamayo, Carabaya, 610 m, BMNH 1907.5.7.36. *San Martín*: Roque, NHMG 471.

Hyla platydactyla.—VENEZUELA: *Mérida*: Camino de La Culata, UPR-M 2763, 2765; Carretera La Azulita, PUR-M 2762; Escorial, 2500+ m, FMNH 3567-8, NHMW 6397 (4), 6398, UMMZ 46465, 59016, 105439, UPR-M 3158-62; La Culata, 2700 m, AMNH 10636-40, BMNH 1905.5.31.83-87, NHMW 6396 (3), UPR-M 3150-2, 3932-5, 4330; La Mucuy, 2500 m, UPR-M 4321-2; Mérida, 1620 m, BMNH 1909.4.30.81-83, 1912.11.1.83, 1947.2.13.14, MCZ 2523; 15-20 km NW Mérida, road to La Azulita, 1700 m, KU 133430-3, 139521 (tadpoles); 32 km NW Mérida, road to La Azulita, 2010 m, KU 139522 (tadpoles); Río Albarregas, 2400 m, UPR-M 2767-70; Río Chama, Mérida, 1620 m, UMMZ 95310 (tadpoles). *Tachira*: 15 km from Delicias, to Rubio, 1800 m, UPR-M 2249-50, 2766; Guacharaquita, near La Grita, UPR-M 4858.

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