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SPECIATION IN FROGS OF THE *HYLA PARVICEPS*
 GROUP IN THE UPPER AMAZON BASIN

By

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As our knowledge of the amphibians in the upper Amazon Basin in South America increases, it becomes evident that the richness of the frog fauna is due to the occurrence there of representatives of many species groups and in some cases to the occurrence of several sympatric species belonging to one group. The latter phenomenon is especially noticeable in the *Hyla leucophyllata* and *Hyla parviceps* groups with five and three species, respectively. The present paper deals only with the latter group.

The primary purposes of this paper are to present analyses and interpretations of the morphological features of adults and tadpoles, mating calls, breeding behavior, and ecological relationships of the three species at Santa Cecilia in Amazonian Ecuador. However, as in most Amazonian frogs, some taxonomic problems must be dealt with before the biological problems can be discussed effectively. Thus, we also present here a systematic review of the entire *Hyla parviceps* group, as presently understood.

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Materials and Methods

The systematic aspects of this study are based on the examination of 720 preserved specimens, 26 cleared and stained specimens, and 19 lots of tadpoles. Recordings were made on a Uher-4000 Recorder and analyzed on a Vibralyzer (Kay Electric Company). All measurements of morphological characters and calls were taken in the manner described by Duellman (1970). Webbing formulae were determined in the manner described by Savage and Heyer (1967). Tadpoles were staged according to Gosner's (1960) system.

All specimens are referred to by the following abbreviations:

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CM	Carnegie Museum
FMNH	Field Museum of Natural History
KU	University of Kansas Museum of Natural History
LG	Lescure-Guiana (Jean Lescure, Paris)
LSU	Louisiana State University Museum of Zoology
NHMB	Naturhistorisches Museum Basel
SMF	Senckenbergische Museum Frankfurt
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology

USNM-GOV	United States National Museum (Gustavo Orcés V. collection)
WCAB	Werner C. A. Bokermann, São Paulo, Brasil
ZMB	Zoologisches Museum Berlin

SYSTEMATICS

The *Hyla parviceps* Group

Definition.—1) Great sexual dimorphism in size; snout-vent lengths to 25 mm in males, 32 mm in females; 2) snout short, blunt; 3) tympanum visible, but tympanic ring indistinct or absent; 4) hands and feet moderately webbed; 5) axillary membrane abbreviated; 6) thoracic glands absent; 7) calcars, ulnar and tarsal folds absent; 8) males having single, median, subgular vocal sac and no nuptial excrescences; 9) dorsum tan or brown with dark brown markings, with or without dorsolateral light stripes; 10) pale, vertical suborbital bars present; 11) thighs marked with cream, yellow, or orange spots; 12) anal, ulnar, and tarsal stripes absent; 13) iris pale gray with red ring around pupil; 14) nasals small, abutting or slightly overlapping sphenethmoid; 15) tectum nasi and septum nasi perichondrally ossified and synosteoically united with sphenethmoid; 16) frontoparietal fontanelle covered, or nearly so, by frontoparietals; 17) squamosals articulating with prootics; 18) quadratojugal reduced to small spur, or absent, not articulating with maxillary; 19) prevomerine teeth on posteromedially directed dentigerous processes between choanae; 20) presacral vertebrae nonimbricate, lacking neural crests, having transverse processes decreasing in length posteriorly (3,6 perpendicularly transverse; 4,5 inclined posteriorly; 7,8 inclined anteriorly); 21) sacral diapophyses expanded 53-77°, with convex edges; 22) tadpoles having ovoid bodies and xiphicercal tails with moderately deep fins not extending onto body; 23) larval mouths anteroventral with one row of large labial papillae laterally and ventrally, robust serrate beaks, and no more than one row of denticles; 24) mating call consisting of short, high-pitched notes, followed or not by shorter secondary notes; 25) diploid chromosome number 30.

Content.—Six species: *Hyla bokermanni* Goin, 1960; *H. brevifrons* new species; *H. luteocellata* Roux, 1927; *H. microps* Peters, 1872; *H. parviceps* Boulenger, 1882; *H. subocularis* Dunn, 1934.

Distribution.—The Amazon Basin, coastal lowlands and slopes of southeastern Brasil, northern South America from French Guiana to Colombia, and eastern Panamá.

Comment.—The *Hyla parviceps* group is one of four groups of small Neotropical frogs that share many of the characters noted above. The other groups are—the *Hyla leucophyllata* group with about six species in South America and one in Central America, the *Hyla microcephala* group with perhaps a dozen species in South and Central America, and *Hyla minuta*, a widespread South Amer-

ican "species" (see Cochran and Goin, 1970, for taxonomic comments). The *Hyla leucophyllata* and *microcephala* groups were defined by Duellman (1970).

Twelve of the 25 species in these four groups have a diploid number of 30 chromosomes (Duellman, 1970; Bogart, 1973); the chromosome numbers in the others are unknown. All known tadpoles (18 species) have xiphicercal tails and reduced mouth parts. In addition, the species in the four groups are consistent in characters 4, 7, 8, 18, 19, 20, and 22. Members of the *Hyla parviceps* group differ from all of the other three groups by having (numbers correspond to statements in preceding definition): 1) more pronounced sexual dimorphism in size; 2) shorter snout; 3) tympanic ring indistinct or absent; 5) much less extensive axillary membrane; 9) sexual dimorphism in width of dorsolateral stripes; 10) suborbital bars; 11) thighs patterned; 13) iris color; 15) more perichondral ossification in the tectum nasi and solum nasi; 17) squamosals articulating with prootics.

Although tadpoles of all of the groups have reduced mouth parts, there are consistent differences among the groups. Members of the *Hyla parviceps* and *minuta* groups have anteroventral mouths; there is one row of papillae in *parviceps* and two in *minuta*. Tadpoles of the *Hyla parviceps* group have no, or one, row of denticles below the beaks; *minuta* has one row. Tadpoles of the *Hyla leucophyllata* and *microcephala* groups have terminal mouths lacking rows of denticles; labial papillae are present in the former, absent in the latter.

The mating calls of members of the *Hyla leucophyllata* and *microcephala* groups, and *H. bokermanni* in the *parviceps* group consist of primary and secondary notes; the calls of *Hyla minuta* and other members of the *Hyla parviceps* group consist of series of short notes.

Cochran (1955) and Bokermann (1964) included *Hyla microps* in the *Hyla marmorata* group, although Bokermann (1964) defined the group in a more strict sense to include only four species (*Hyla acreana*, *marmorata*, *melanargyrea*, and *senicula*). These frogs differ from the groups discussed above by having more extensive webbing, well-developed ulnar and tarsal folds, less cranial ossification, and different kinds of mating calls. They are like the other groups in general larval and karyological features.

Other named taxa might be associated with the *Hyla parviceps* group or one of the other three groups; however, these species are too poorly known at the present time to be assigned to any group. These include:

Hyla schubarti Bokermann, 1963.—Rondônia, Brasil, and Amazonian lowlands of Perú.

Hyla leali Bokermann, 1964.—Rondônia, Brasil, and Amazonian lowlands of Ecuador and Perú.

Hyla grandisonae Goin, 1966.—Guyana.

Hyla oliveae Cochran and Goin, 1970.—Leticia, Colombia.

Hyla riveroi Cochran and Goin, 1970.—Amazonian Colombia, Ecuador and Perú.

Duellman (1969) named *Hyla carnifex* from the Pacific slopes of the Andes of Ecuador and placed the species in the *Hyla parviceps* group. Although there are superficial similarities in adult structure and coloration, tadpoles, and mating calls, *Hyla carnifex* seems to be related to *Hyla columbiana* and *variabilis* in Colombia and is now excluded from the *Hyla parviceps* group.

ANALYSIS OF CHARACTERS

Three categories of characters were analyzed in adult frogs—morphometric, structural, and coloration. In addition, characters of the mating calls and tadpoles were utilized.

Morphometric Characters

Seven measurements were taken on representative samples of the six species. From these, five proportions were calculated (Tables 1 and 2). Analyses of variance showed highly significant differences ($P \leq .001$) in both sexes among species for the following: snout-vent length, tibia length/snout-vent length, and head width/snout-vent length. Equally significant differences exist for head length/snout-vent length in females and for tympanum/eye in males. Significant differences ($P \leq .01$) were found for foot length/snout-vent length in males. The differences among species in foot length/snout-vent length and tympanum/eye in females, and in head length/snout-vent length in males were not significant.

Statistical comparisons of the sexes of three species revealed significant differences in snout-vent length between males and females of all three and in different proportions in different species (Table 1). Adult females of all six species are much larger than adult males; this is especially noticeable in *Hyla parviceps*, in which the smallest gravid females are larger than the largest males.

Structural Characters

The species comprising the *Hyla parviceps* group are alike in most structural features; those features that are constant, or nearly so, are listed in the definition of the group. The tongue is cordiform in all species, deeply notched posteriorly in *H. microps*, and shallowly notched in the others. Ulnar and tarsal tubercles are absent in all species, except females of *H. parviceps* and both sexes of *H.*

TABLE 1.—Measurements and proportions of three species of the *Hyla parviceps* group. All samples from Santa Cecilia, Ecuador.

Character	Males			Females			<i>t</i>		
	Range	\bar{X}	SD	SE	Range	\bar{X}		SD	
<i>Hyla brevifrons</i> 25 ♂, 11 ♀									
Snout-vent length (SVL)	17.00-21.40	18.570	0.970	0.190	20.1 -23.2	21.68	1.090	0.330	0.001
Tibia length/SVL	0.46- 0.51	0.484	0.015	0.003	0.45- 0.51	0.473	0.020	0.006	NS
Foot length/SVL	0.35- 0.46	0.416	0.027	0.005	0.38- 0.45	0.415	0.023	0.007	NS
Head length/SVL	0.28- 0.35	0.324	0.016	0.003	0.27- 0.34	0.315	0.018	0.005	NS
Head width/SVL	0.29- 0.33	0.308	0.012	0.002	0.29- 0.33	0.301	0.013	0.004	NS
Tympanum/Eye	0.36- 0.50	0.410	0.036	0.007	0.34- 0.44	0.379	0.033	0.010	0.05
<i>Hyla bokermanni</i> 25 ♂, 25 ♀									
Snout-vent length (SVL)	20.00-22.70	21.420	0.750	0.150	20.4 -25.6	23.48	1.300	0.260	0.001
Tibia length/SVL	0.46- 0.56	0.502	0.024	0.005	0.45- 0.53	0.494	0.023	0.005	NS
Foot length/SVL	0.38- 0.48	0.428	0.022	0.004	0.34- 0.46	0.420	0.028	0.006	NS
Head length/SVL	0.30- 0.38	0.329	0.018	0.004	0.29- 0.34	0.309	0.014	0.003	0.001
Head width/SVL	0.26- 0.32	0.298	0.017	0.003	0.27- 0.32	0.293	0.012	0.002	NS
Tympanum/Eye	0.33- 0.44	0.391	0.035	0.007	0.33- 0.56	0.413	0.056	0.011	NS
<i>Hyla parviceps</i> 25 ♂, 25 ♀									
Snout-vent length (SVL)	15.20-18.30	16.740	0.720	0.140	21.6 -26.1	23.45	0.970	0.190	0.001
Tibia length/SVL	0.44- 0.55	0.494	0.022	0.004	0.46- 0.55	0.506	0.025	0.005	NS
Foot length/SVL	0.38- 0.47	0.425	0.017	0.003	0.38- 0.46	0.424	0.021	0.004	NS
Head length/SVL	0.30- 0.35	0.328	0.014	0.003	0.28- 0.32	0.299	0.012	0.002	0.001
Head width/SVL	0.28- 0.33	0.308	0.012	0.002	0.26- 0.31	0.288	0.012	0.002	0.001
Tympanum/Eye	0.25- 0.45	0.328	0.042	0.008	0.34- 0.52	0.392	0.042	0.008	NS

TABLE 2.—Measurements and proportions of males of Non-Ecuadorian species in the *Hyla parviceps* group.
(See Table 1 for comparable statistics for Ecuadorian species.)

Character	Range	\bar{X}	SD	SE
<i>Hyla luteocellata</i> 9 ♂♂				
Snout-vent length (SVL) ..	20.00-23.10	21.720	1.260	0.420
Tibia length/SVL	0.47- 0.50	0.483	0.014	0.005
Foot length/SVL	0.39- 0.45	0.417	0.017	0.006
Head length/SVL	0.31- 0.35	0.326	0.013	0.004
Head width/SVL	0.31- 0.33	0.319	0.008	0.003
Tympanum/Eye	0.36- 0.45	0.397	0.035	0.012
<i>Hyla microps</i> 25 ♂♂				
Snout-vent length (SVL) ..	18.30-23.20	21.110	1.340	0.270
Tibia length/SVL	0.45- 0.55	0.499	0.025	0.005
Foot length/SVL	0.41- 0.46	0.437	0.018	0.004
Head length/SVL	0.30- 0.34	0.320	0.014	0.003
Head width/SVL	0.29- 0.34	0.318	0.014	0.003
Tympanum/Eye	0.37- 0.52	0.454	0.037	0.007
<i>Hyla subocularis</i> 25 ♂♂				
Snout-vent length (SVL) ..	20.50-23.10	21.720	0.730	0.150
Tibia length/SVL	0.48- 0.55	0.509	0.015	0.003
Foot length/SVL	0.38- 0.45	0.426	0.018	0.004
Head length/SVL	0.29- 0.34	0.320	0.011	0.002
Head width/SVL	0.32- 0.34	0.328	0.007	0.001
Tympanum/Eye	0.26- 0.44	0.365	0.041	0.008

microps. In the latter, small tubercles are present on the eyelid in most specimens (see Lutz, 1973, for discussion of variation).

The webbing is slightly variable within all species (Table 3): *H. parviceps* has slightly more webbing than any of the others. Females generally have slightly more webbing than do males; this is especially noticeable in *H. parviceps*, which has the greatest sexual dimorphism in size.

Coloration

Five aspects of color pattern were analyzed on 408 preserved adults, representing both sexes of all species, except *H. luteocellata* and *microps*, for which only males were used. However, partial data were utilized for two female *H. microps*; the pattern of female *H. luteocellata* was described by Rivero (1969).

Dorsal Body Pattern.—This is the most intraspecifically variable pattern character (Table 4). *Hyla bokermanni* is the most variable species.

Dorsolateral Stripes.—These stripes are absent in *H. microps* and *parviceps*, and most males of *H. brevifrons*. In males of the other species a narrow cream or pale yellow stripe extends from

TABLE 3.—Variation in webbing in members of the *Hyla parviceps* group.
(Roman numerals = digits; Arabic numerals = number of free phalanges.)

Species	N	Hand	Foot
<i>H. bokermanni</i>	20	II (1½-2⁻) - (2¾-3) III (2⁺-2¾) - (2⁻-2¼) IV 1 (1½-2) - (2-2⁺) II (1-1½) - 2 III (1⁺-1½) - 2 IV (1½-2) - (1-1½) V	
<i>H. brevifrons</i>	20	II (2⁻-2) - (2½-2¾) III (2¼-2¾) - (2-2) IV 1 (2⁻-2) - (2-2⁺) II (1¼-1½) - (2-2¼) III (1⁺-1½) - 2 IV 2 - (1¼-1½) IV	
<i>H. luteocellata</i>	5	II 2⁻ - (2¾-3) III 2½ - (2-2⁺) IV 1 (1¾-2) - (2-2) II (1⁺-1½) - 2 III (2⁺-2¼) - (2-2½) IV (2-2½) - (1¼-1½) V	
<i>H. microps</i>	8	II (2⁻-2½) - (2½-3) III (2½-3) - 2 IV 1 (1¼-2) - (2-2⁺) II (1⁺-1¼) - (2⁻-2¼) III (1-1½) - (2-2⁺) IV (2⁻-2⁺) - (1¼-1½) V	
<i>H. parviceps</i>	20	II (1½-2⁻) - (2¼-3) III (2-2⁺) - (2-2⁺) IV 1 (1¼-1¾) - (2-2⁺) II (1-1½) - (2-2⁺) III (1-1½) - (2-2⁺) IV (2-2⁺) - (1-1½) V	
<i>H. subocularis</i>	20	II (1¾-2⁻) - (2¾-3) III (2⁺-2½) - (2⁻-2⁺) IV 1 (1¾-2) - (2-2⁺) II (1-1½) - (1½-2½) III (1-2) - (2-2⁺) IV (2-2⁺) - (1-1½) V	

the cyclid or supratympanic region to the sacral region. In females of these species the stripe is broad and well defined; the stripe angles posterolaterally onto the flank in *H. brevifrons* but continues posteriorly in the other species.

TABLE 4.—Variation in dorsal color pattern in the *Hyla parviceps* group. (Numbers are percentages.)

Pattern	<i>H. bokermanni</i>	<i>H. brevifrons</i>	<i>H. luteocellata</i>	<i>H. microps</i>	<i>H. parviceps</i>	<i>H. subocularis</i>
N	93	111	9	25	114	56
Plain	20	—	—	36	—	18
Flecks	19	3	—	—	—	—
Longitudinal marks	11	—	—	—	—	—
Median blotch anteriorly; paired marks posteriorly	9	—	—	—	—	—
Transverse bars	41	97	—	—	—	—
X anteriorly; paired spots posteriorly	—	—	100	—	—	—
λ-shaped mark	—	—	—	—	76	—
Median blotch anteriorly; trans. bar posteriorly	—	—	—	—	24	—
X anteriorly	—	—	—	—	—	20
X anteriorly; transverse bar posteriorly	—	—	—	—	—	62
Irregular dashes	—	—	—	64	—	—

Head Markings.—All species have vertical, cream or yellow sub-orbital bars, although the bars are absent in 5 percent of the *H. parviceps*. Normally there are two bars in *H. bokermanni*, *brevifrons*, and *subocularis*, and only one bar in the other species. The bars are much broader in *H. microps* than in the other species. Canthal and rostral stripes are absent in *H. microps* and *parviceps*. Stripes are present in varying percentages of the other species (Table 5). The stripes are cream or pale yellow. A canthal stripe

TABLE 5.—Variation in head stripes in the *Hyla parviceps* group. (Numbers are percentages.)

	<i>H. bokermanni</i>	<i>H. brevifrons</i>	<i>H. luteocellata</i>	<i>H. subocularis</i>
N	93	111	9	56
Canthal only	41	8	—	29
Canthal & rostral	51	30	—	62
Rostral only	—	29	100	—
None	8	33	—	9

extends along the canthal ridge from the anterior corner of the orbit to the nostril; in some individuals the stripes meet on the snout or fuse with the upper end of the vertical rostral keel on the snout.

Hind Limb Markings.—Important interspecific differences are evident in the coloration of the thighs. All individuals of *H. luteocellata* and *subocularis* and 80 percent of the *H. bokermanni* have a large black-bordered, deep yellow spot on the anterior surface of the thigh. The anterior surfaces of the thighs are unmarked in all *H. brevifrons* and *microps* and in 20 percent of the *H. bokermanni* and 11 percent of the *H. parviceps*; in the rest of the *H. parviceps* (89%) there are one or two small cream spots on the anterodorsal surface of the thigh, which otherwise is black. The dorsal surface of the thigh is dark brown or black with 1-3 small cream or yellow spots in *H. bokermanni* (91%), *brevifrons* (94%), *luteocellata* (100%), *parviceps* (3%), and *subocularis* (91%); in all *H. microps*, 97 percent of the *H. parviceps* and less than 10 percent of the other species, pale spots are absent. The posterior surface of the thigh is dark brown in *H. brevifrons*, black with or without small cream spots in *H. parviceps*, and usually yellow or tan with or without black mottling in *H. bokermanni*, *luteocellata*, and *subocularis*. On the posterior surface of the thigh in *H. microps* there is a large black-bordered, orange spot. The dorsal surface of the shank has transverse dark markings. These consist of 3-4 narrow bars in the *H. bokermanni*; 3 broad bars in *H. brevifrons*, *microps*, *subocularis*, and *parviceps* (median bar wider than others), or faint lines in *H. luteocellata*.

Ventral Coloration.—In *H. parviceps* the venter is dark gray fading to white medially on the throat and anterior belly; the ventral surface of the shank is gray with a bright orange spot proximally. In the other species the venter is cream; gray flecks are present on the anterior edge of the chin in *H. brevifrons* (75%), *luteocellata* (100%), and *microps* (100%), and gray flecks are present on the belly in 32 percent of *H. microps*.

Mating Calls

We have analyzed tape recordings of four species (Table 6), and Rivero (1969) provided an audiospectrogram of *H. luteocellata*. The call of *H. microps* has not been analyzed, but Lutz (1973) described the call as "the chirping of a cricket." The calls of all of the species consist of short, high-pitched, insect-like notes. The call of *H. parviceps* is much higher pitched than the others, and the call of *H. bokermanni* is distinctive in having secondary notes (Fig. 1). The release call of *H. luteocellata* illustrated by Rivero (1969) may be a series of secondary notes.

TABLE 6.—Comparison of mating calls of members of the *Hyla parviceps* group. (N = individuals/notes; means in parentheses below ranges.)

Species (N)	Note Repetition Rate	Duration (secs)	Pulses per Second	Secondary Notes	Dominant Frequency (Hertz)
<i>H. bokermanni</i> (4/12)	5-19 (12.2)	0.23-0.28 (0.259)	100-190 (132.5)	2-5 (3.3)	4000-4652 (4478)
<i>H. brevifrons</i> (9/25)	26-46 (36.8)	0.43-0.49 (0.467)	30- 40 (38.9)	0	4152-5115 (4625)
<i>H. parviceps</i> (1/3)	54.5	0.12-0.14 (0.13)	140	0	6072-6341 (6221)
<i>H. subocularis</i> (2/4)	3-20	(0.53)	(43)	0	2200

Tadpoles

The tadpoles of *H. luteocellata* are unknown. The tadpole of *H. microps* was described by Bokermann (1963b) and that of *H. subocularis* by Duellman (1970). The mouthparts of the tadpoles are alike in having robust, finely serrated beaks, bare upper lips and one row of labial papillae laterally and ventrally. In *H. bokermanni* and *subocularis* the papillae lateral to the mouth are partially fused in the form of a vertical fold. The mouth is small and directed anteroventrally; the body is ovoid with blunt snout in dorsal view. The caudal fin does not extend onto the body, and the tail is xiphicercal (Fig. 2). The spiracle is sinistral and lateral, and the anal tube is dextral. Rows of denticles are absent in all except *H. microps*, which has a single row of small denticles below the lower beak.

Tadpoles of this group are brightly colored and patterned. Longitudinal cream stripes are present on the dorsal surface of the body of *H. microps* and *subocularis*, and on the snout of *H. bokermanni*. Two broad cream transverse bars are present on the body of *H. parviceps*, and broad yellowish-tan dorsolateral stripes on the body and a red streak on the dorsal fin characterize the tadpole of *H. brevifrons*.

KEY TO THE SPECIES

1. Dorsolateral light stripe absent 2
 Dorsolateral light stripe present, narrow in males, broad in females 4
2. Venter gray, white medially; small orange spot proximally on ventral surface of shank *Hyla parviceps*
 Venter cream or white, with or without small gray flecks; no orange spot on ventral surface of shank 3

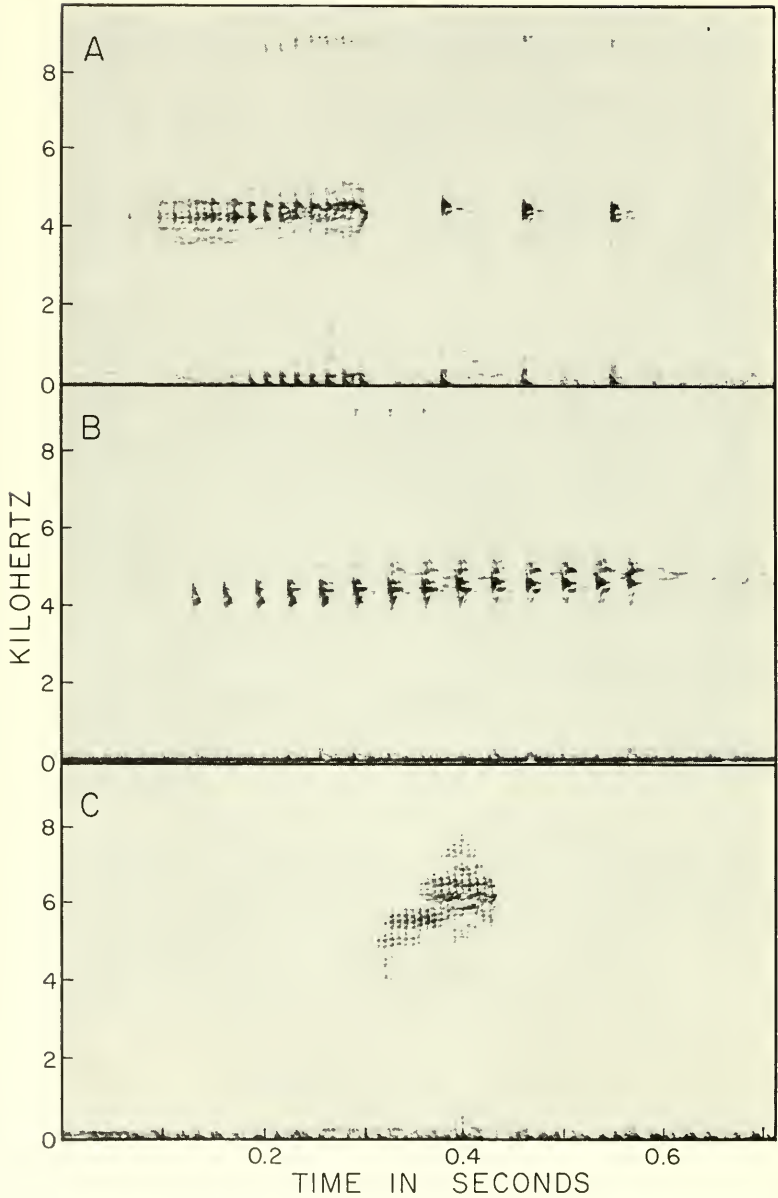


FIG. 1. Audiospectrograms of mating calls of members of the *Hyla parviceps* group at Santa Cecilia, Ecuador. A. *Hyla bokermanni* (KU Tape 688). B. *H. brevifrons* (KU Tape 1176). C. *H. parviceps* (KU Tape 1178).

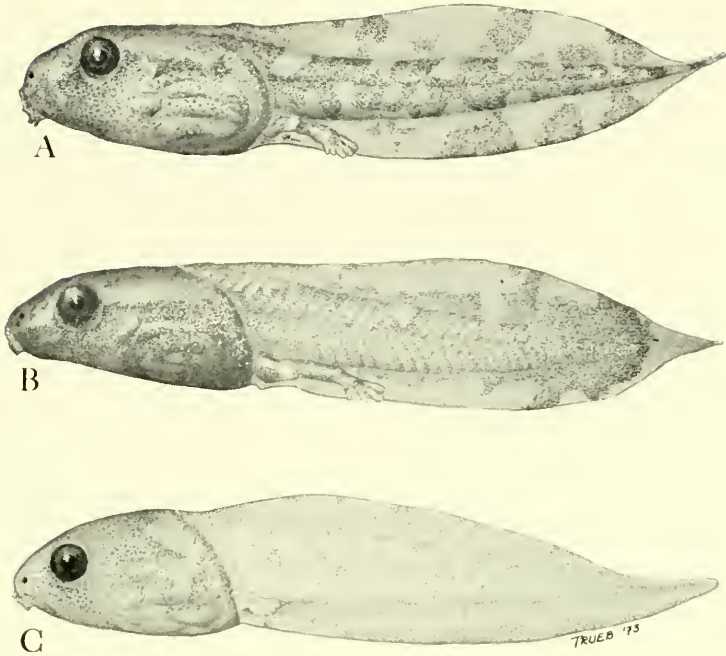


FIG. 2. Tadpoles of members of the *Hyla parviceps* group at Santa Cecilia, Ecuador. A. *Hyla bokermanni* (KU 124193). B. *H. brevifrons* (KU 125899). C. *H. parviceps* (KU 146791). $\times 5$.

- 3. No spots on dorsal surface of thigh; large orange spot on posterior surface of thigh *Hyla microps*
 Two small creamy yellow spots on dorsal surface of thigh; no large orange spot on posterior surface of thigh
 *Hyla brevifrons* (♂♂)
- 4. Anterior surface of thigh dark *Hyla brevifrons* (♀♀)
 Anterior surface of thigh tan, usually with large, black-bordered spot 5
- 5. One suborbital white bar *Hyla luteocellata*
 Usually two suborbital white bars 6
- 6. Dorsum plain, flecked, or usually marked with large median dark blotch or transverse bar anteriorly *Hyla bokermanni*
 Dorsum marked with a dark X-shaped pattern anteriorly
 *Hyla subocularis*

SPECIES ACCOUNTS

In the following accounts, the major distinguishing features are enumerated in the diagnoses. Sizes given in diagnoses are maximum snout-vent lengths. With the exception of one new species, detailed descriptions are omitted. Variation of characters is treated in the preceding analysis of characters. Colors are of living frogs and tadpoles. The statements of distribution are based on the localities in the list of specimens examined.

Hyla bokermanni Goin

(Figure 3)

Hyla bokermanni Goin, 1960:721 [Holotype.—WCAB 2881 from Tarauacá, Território do Acre, Brasil; W. C. A. Bokermann collector].

Hyla rondoniae Bokermann, 1963a:247 [Holotype.—WCAB 7845 from Rondônia, Território do Rondônia, Brasil; A. Machado collector]. New synonym.

Diagnosis.—1) Snout-vent length 22.7 mm in males, 25.6 mm in females; 2) webbing on hand II 2-3- III 2⁺-2 IV, on foot I 2-2 II 1 $\frac{1}{4}$ -2 III 1 $\frac{1}{4}$ -2 IV 2-1⁺ V; 3) ulnar and tarsal tubercles absent; 4) canthal and rostral stripes (50%) or canthal stripes only (41%) present; 5) two suborbital bars (98%); 6) dorsum plain, flecked, or marked with three transverse bars or one blotch anteriorly and one bar posteriorly; 7) dorsolateral light stripe present, broad in females; 8) thigh usually (80%) having large black-bordered yellow spot anteriorly and 1-3 small yellow spots dorsally; 9) all ventral surfaces uniform cream.

Hyla bokermanni, *luteocellata*, and *subocularis* all have dorsolateral light stripes and large yellow spots on the anterior surfaces of the thighs. *Hyla bokermanni* differs from *H. luteocellata* in usually having canthal stripes and two, instead of one, suborbital bars; *H. subocularis* differs from *H. bokermanni* by having an X-shaped pattern anteriorly on the dorsum, instead of a large blotch, transverse bar, or no markings.

Coloration.—At night, the dorsum is pale yellowish tan; the dorsal markings and dorsolateral stripes are barely discernable. By day, the dorsum is tan, and the dorsal markings are dark brown. The dorsolateral stripe is creamy yellow in males and creamy white in females. The large spot on the anterior surface of the thigh is bright yellow, and the small spots on the dorsal surface of the thigh are creamy yellow. The iris is silvery gray with a narrow red ring around the pupil. Males have a yellow vocal sac; otherwise the venter is creamy white.

Tadpoles.—A tadpole in stage 36 has a body length of 7.2 mm and a total length of 19.8 mm. The body is dark brown with two short, broad, longitudinal yellowish tan bars on the snout. Prox-



FIG. 3. *Hyla bokermanni*, female, 24.4 mm SVL (KU 126552).

imally the caudal musculature and fins are pale orange, unpigmented distally, except for broad gray vertical marks. The iris is red medially and silver peripherally.

Distribution.—Lowlands (< 1000 m) of upper Amazon Basin in Ecuador and extreme western Brasil, and presumably in the intervening area of northeastern Perú.

Remarks.—We have examined the holotype of *H. rondoniae* (WCAB 12148) and compared it with the figure of the holotype of *H. bokermanni* and series of specimens from Ecuador. As suggested by Rivero (1969), the name *H. bokermanni* is based on a female and *H. rondoniae* on a male of the same species.

Hyla brevifrons new species (Figures 4 & 5)

Holotype.—KU 126370, an adult male, from Santa Cecilia, Provincia Napo, Ecuador, obtained on 16 May 1969, by William E. Duellman and Linda Trueb.

Allotype.—KU 126371, an adult female, same data as holotype.

Paratopotypes.—KU 111786-802, 123049-50, 123059, 123072-88, 126342-61, 126363-69, 126546, 126548-51, 136298, 143189, 146281-87, 146413, 146415-18.

Diagnosis.—1) Snout-vent length 21.4 mm in males, 23.2 mm in females; 2) webbing on hand II 2-2½ III 2½-2 IV, on foot I 2-2 II 1½-2 III 1½-2 IV 2-1¼ V; 3) ulnar and tarsal tubercles absent; 4)

canthal and rostral stripes usually present (one or both in 66%); 5) two suborbital bars (95%); 6) dorsal pattern consisting of broad transverse bars; 7) dorsolateral light stripe absent in males, broad in females; 8) thigh dark brown anteriorly, having 1-3 small yellow spots dorsally; 9) venter uniformly cream, except for gray flecks on chin (78%).

Hyla brevifrons differs from those other members of the group having dorsolateral light stripes by lacking a large black-bordered yellow spot on the anterior surface of the thigh.

Description.—The following description is based on the holotype and allotype; where differences occur, the characters of the allotype are in parentheses. Snout-vent length 19.1 mm (23.0 mm); snout short, truncate in dorsal view, inclined posteroventrally in profile; canthus rounded; loreal region slightly concave; lips rounded; internarial area depressed; nostrils slightly protuberant anterolaterally; supratympanic fold weak; tympanic ring indistinct. Axillary membrane extending one-fourth length of upper arm; forearm lacking folds or tubercles; fingers moderately short, bearing small discs; webbing on hand II 2-2½ III 2½-2 IV (II 2-2½ III 2¼-2 IV); webbing on foot I 2-2+ II 1½-2 III 1½-2 IV 2-1½ V (I 2-2 II 1¼-2¼ III 1¼-2 IV 2-1½ V). Anal flap short, opening at upper level of thighs; skin on belly and proximal posteroventral surfaces of thighs granular; skin on other surfaces smooth. Prevomerine teeth 2-2 (3-4) on processes posteromedially inclined between posterior margins of ovoid choanae; tongue cordiform, shallowly notched posteriorly; vocal slit extending from midlateral base of tongue to angle of jaw (absent).

Color (in alcohol): Dorsum tan (grayish tan) with brown markings—blotch in occipital region, square blotch in scapular region, and transverse blotch in sacral region extending onto flanks; dorsolateral stripe absent (distinct, broad, creamy white, extending



FIG. 4. *Hyla brevifrons*, holotype, male, 19.1 mm SVL (KU 126370).



FIG. 5. *Hyla brevifrons*, allotype, female, 23.0 mm SVL (KU 126371).

from eyelid to transverse sacral blotch and thence laterad onto flanks, bordered below by broad brown mark); one (two) suborbital white bar; forearms and shanks tan with two and three transverse brown bars; thighs pale brown with two creamy yellow spots on dorsal surfaces; venter white with brown flecks on chin.

Coloration.—The dorsum is olive-tan with brown markings and, in females, distinct creamy tan dorsolateral stripes. The thighs are dark brown; the spots on the thighs and the suborbital bars are creamy yellow. The venter is unpigmented except for the pectoral region and chin (in females), which is white; males have a pale yellow vocal sac. The iris is red medially and silvery gray peripherally.

Tadpoles.—A tadpole in stage 39 has a body length of 7.6 mm and a total length of 22.2 mm. In dorsal view the body is dark brown medially and pale brown laterally. The venter and sides of the body are dark brown with cream flecks. The tail is tan with dark brown mottling and a bright red streak on the dorsal fin. The iris is gray-bronze with a red ring around the pupil.

Distribution.—The upper Amazon Basin in Ecuador, Perú, and probably western Brasil, to elevations of about 1300 m on the eastern slopes of the Andes. Additionally, the species is known from French Guiana and Belém, Brasil; it probably occurs throughout the Amazon Basin.

Etymology.—The specific name is derived from the Latin *brevis*

meaning short, and the Latin *frons*, meaning brow. The name is used in allusion to the short head of the species.

Hyla luteocellata Roux

Hyla luteo-ocellata Roux, 1927:260 [Holotype.—NHMB 3900 from El Mene, Estado Falcón, Venezuela; Kugler and Vonderschmidt collectors].

Diagnosis.—1) Snout-vent length 23.1 mm in males, 28.0 mm in females (Rivero, 1969:132); 2) webbing on hand II 2⁻-3 III 2½-2 IV, on foot I 2-2 II 1½-2 III 2⁺-2 IV 2⁺-1¼ V; 3) ulnar and tarsal tubercles absent; 4) canthal stripes absent, rostral stripe present; 5) one suborbital bar; 6) dorsal pattern consisting of X-shaped mark anteriorly and pair of dashes posteriorly; 7) dorsolateral light stripe present, broad in females; 8) thigh having large black-bordered yellow spot anteriorly and 1 or 2 small yellow spots dorsally; 9) venter uniformly cream, except for gray flecks on chin.

Hyla luteocellata is like *H. bokermanni* and *subocularis* in having dorsolateral light stripes and a large yellow spot on the anterior surface of the thigh. It differs from these species by lacking canthal stripes and in having only one suborbital bar. Furthermore, it differs from *H. bokermanni* by having an X-shaped dorsal marking anteriorly, instead of a median blotch or transverse bar, and from *H. subocularis* by having paired longitudinal markings posteriorly on the dorsum instead of no markings or a transverse bar.

Coloration.—Rivero (1969:128) described the suborbital bar as cream or yellow, the spot on the anterior surface of the thigh orange, spots on the dorsal surface of the thigh greenish yellow, brownish, or dirty white.

Distribution.—Northern Venezuela from Lago Maracaibo to the Unare Depression (Rivero, 1969:130). The species also occurs near Brownsweag and in the Kayser Mountains in Surinam (M. S. Hoogmoed, pers. comm.).

Hyla microps Peters

Hyla microps Peters, 1872:682 [Holotype.—ZMB 7472 from Novo Friburgo, Estado do Rio de Janeiro, Brasil; Salmin collector].

Hyla hilli Boulenger, 1920:123 [Holotype.—BMNH 1914.3.20.9 (RR 1947.2.24.10) from Teresópolis, Estado Rio de Janeiro, Brasil; J. P. Hill collector]. Synonymy *vide* Cochran (1955:177).

Hyla giesleri Mertens, 1950:185 [Holotype.—SMF 41217 from Barro Branco, Estado do Rio de Janeiro, Brasil; P. Giesler collector]. Synonymy *vide* Bokermann (1966:51).

Diagnosis.—1) Snout-vent length 24.6 mm in males, 31.3 mm in females; 2) webbing on hand II 2¼-2¾ III 2¾-2 IV, on foot I 2-2 II 1⁺-2 IV 2-1¼ V; 3) ulnar and tarsal tubercles low in both sexes; 4) canthal and rostral stripes absent; 5) one broad suborbital bar; 6) dorsum plain or marked with irregular dashes; 7) dorsolateral

light stripe absent; 8) thighs yellow anteriorly, brown dorsally, having large black-bordered orange spot posteriorly; 9) venter cream with gray flecks on chin (100%) and on belly (32%).

This species differs from all other members of the group, except *H. parviceps*, in lacking dorsolateral light stripes; it differs from *H. parviceps* by having a cream venter and a large orange spot on the posterior surface of the thigh and a black mark in the axilla. *Hyla parviceps* has a gray venter with an orange spot on the proximal ventral surface of the shank and cream spots anterodorsally on the thigh.

Coloration.—Lutz (1973:95) described specimens from Serra da Bocaina, Brasil, as brown above with darker brown dorsal markings. The spots on the thighs and the webs between the inner toes are bright orange. The axilla is black, and the belly is greenish yellow.

Tadpoles.—Bokermann (1963b) described tadpoles from Campo Grande, São Paulo, Brasil. The body is dark olive with dorsolateral and lateral light stripes.

Distribution.—Coastal lowlands and lower slopes of the highlands in southeastern Brasil from Espírito Santo to Paraná.

Remarks.—Lutz (1973) mentioned a specimen 38 mm in length from Angra dos Reis, Rio de Janeiro, Brasil. Although we have not seen the specimen, we are dubious of the identification reported by Lutz because of the reported size and coloration.

Duellman examined the holotypes of *Hyla hilli* and *Hyla giesleri* and concluded as did Cochran (1955) and Bokermann (1966) that they are representatives of *Hyla microps*. In addition to the localities given in the specimens examined, Cochran (1955) reported the species from Rio Novo, Espírito Santo, and from several localities in Rio de Janeiro and Santa Catarina.

Hyla parviceps Boulenger (Figure 6)

Hyla parviceps Boulenger, 1882:393 [Holotype.—BMNH 80.12.5.214 (RR 1947.2.13.5) from Sarayacu, Provincia Pastaza, Ecuador; Mr. Buckley collector].

Diagnosis.—1) Snout-vent length 18.3 mm in males, 26.1 mm in females; 2) webbing on hand II $1\frac{3}{4}$ -2 $\frac{3}{4}$ III 2-2 IV, on foot I $1\frac{1}{2}$ -2 II 1^+ -2 III $1\frac{1}{4}$ -2 IV 2- $1\frac{1}{4}$ V; 3) ulnar and tarsal tubercles low on females, absent on males; 4) canthal and rostral stripes absent; 5) usually (92%) one suborbital bar; 6) dorsal markings usually (76%) a λ -shaped mark, or (24%) median blotch anteriorly and transverse bar posteriorly; 7) dorsolateral stripe absent; 8) thigh usually (92%) having one or two small cream spots anteriorly and uniform dark dorsally; 9) throat and belly gray, white medially; ventral surface of shank gray with orange spot proximally.



FIG. 6. *Hyla parviceps*, female, 24.5 mm SVL (KU 126476).

Hyla parviceps differs from all other species in the group, except *H. microps*, in lacking dorsolateral light stripes; it differs from *H. microps* by having a dark venter with an orange spot on the proximal ventral surface of the shank and cream spots anterodorsally on the thigh. *Hyla microps* has a cream venter and a large orange spot on the posterior surface of the thigh.

Coloration.—The dorsum is tan with faintly darker markings at night. By day the dorsum is orange-tan, reddish brown, or brown with darker brown markings. The flanks are dark brown or black and white. The thighs are dark brown or black with creamy-yellow spots. The suborbital bar is creamy white. The venter is gray or white with gray or black suffusion most prominent laterally on the throat and belly. The ventral surfaces of the limbs are gray with an elongate bright orange spot proximally on the shank. Some individuals also have a small orange spot in the axilla. The iris is red medially and silvery gray peripherally.

Tadpoles.—The body is dark brown with two broad, transverse cream bars dorsally (snout and posterior to spiracle). The tail is pinkish orange or orange-tan with dark brown mottling.

Distribution.—The upper Amazon Basin in western Brasil, southern Colombia, Ecuador, and Perú, to elevations of 1300 m on the eastern slopes of the Andes.

Remarks.—In addition to the localities given in the specimens examined, Melin (1941) reported the species from Taracuá, Ama-

zonas, Brasil, and Cochran and Goin (1970) reported it from Río Apoporis, Amazonas, and Ceilán, Caquetá, both in Colombia, and from Acre, Brasil.

Hyla subocularis Dunn

Hyla subocularis Dunn, 1934:2 [Holotype.—AMNH 41117 from Río Chucunaque at first creek above Río Tuquesa, Provincia Darién, Panamá; Charles M. Breder collector].

Diagnosis.—1) Snout-vent length 23.1 mm in males, 26.1 mm in females; 2) webbing on hand II 2-3 III 2½-2 IV, on foot I 2-2 II 1¼-2¼ III 1+2 IV 2+1¼ V; 3) ulnar and tarsal tubercles absent; 4) canthal and rostral stripes (64%) or canthal stripes only (29%) usually present; 5) one (14%) or two (86%) suborbital bars; 6) dorsal markings consisting of X-shaped mark anteriorly (83%) with or without transverse bar posteriorly; 7) dorsolateral light stripe present, broad in females; 8) thigh having one large black-bordered yellow spot anteriorly, and usually (91%) one small yellow spot dorsally; 9) ventral surfaces uniform cream.

Hyla subocularis is like *H. bokermanni* and *luteocellata* in having dorsolateral light stripes and a large yellow spot on the anterior surface of the thigh. *Hyla subocularis* differs from *H. luteocellata* in usually having canthal stripes and two, instead of one, suborbital bars; *H. bokermanni* differs from *H. subocularis* in having a large median dark blotch, transverse bars, or no markings anteriorly on the dorsum, instead of an X-shaped mark.

Coloration.—Duellman (1970:236) described the color of *Hyla subocularis*. The dorsum is yellowish tan with brown markings. The suborbital bars and dorsolateral stripes are creamy white or creamy yellow. The spots on the thigh are yellow. The iris is rose-pink medially and pale silver peripherally.

Tadpoles.—The tadpoles were described by Duellman (1970:237), who noted that the body and tail are black with a dorsolateral tan stripe on the body and irregular tan vertical marks on the tail.

Distribution.—Lowlands to 800 m in Darién, Panamá, and northwestern Colombia.

ECOLOGY

All the members of the *Hyla parviceps* group inhabit wet lowland tropical forest. Information on the habitat of *Hyla luteocellata* was provided by Rivero (1969), of *H. subocularis* by Duellman (1970), and of *H. microps* by Lutz (1973). We are concerned here with the three sympatric species in the upper Amazon Basin (*H. bokermanni*, *H. brevifrons*, and *H. parviceps*). The following observations resulted from intensive field studies from June 1971

through July 1972 at Santa Cecilia, Provincia Napo, Ecuador. Santa Cecilia is situated at 76°58' W, 00°02' N at an elevation of 340 m on the northern bank of the Río Aguarico, which flows into the Río Napo, a major tributary of the Río Amazonas.

At Santa Cecilia the three sympatric species utilize different breeding sites. Males of each species occasionally were found calling in swamps in open, disturbed areas; no females were found in such habitats. *Hyla parviceps* seems to be a habitat generalist, breeding in great abundance in both forest-edge and forest swamps. This species calls and breeds sympatrically and synchronously with either of the other species. On the other hand, *H. bokermanni* and *H. brevifrons* only rarely were observed together. *Hyla bokermanni* breeds mainly in forest swamps, but occasionally in forest-edge situations. *Hyla brevifrons* breeds mainly in forest-edge swamps and only occasionally in forest swamps.

The calling sites of the three species are similar. Males call from vegetation usually 1-2 m above the water. *Hyla bokermanni* and *H. brevifrons* call from stems, branches, or leaves, whereas *H. parviceps* almost always calls from leaves. *Hyla bokermanni* usually calls from emergent vegetation, whereas the other two species also call from vegetation peripheral to the water.

There is distinct segregation in egg deposition sites. *Hyla bokermanni* and *H. brevifrons* deposit eggs in clumps on leaves overhanging the water. Egg clutches of the former were found at heights from 50 cm-160 cm (\bar{x} = 104.0 cm; N = 14), and those of the latter at heights from 52 cm-100 cm (\bar{x} = 75.4 cm; N = 5) above water. On the other hand, *H. parviceps* deposits eggs in water.

Breeding Patterns at One Study Site

The breeding patterns and relative abundances of the species were studied during 10-day intervals at a forest swamp from July 1971 to July 1972. Most observations were made between 1900 and 2400 hrs. The swamp is approximately 15 m by 50 m and is choked with large-leaved *Heliconia* plants. Twenty-two species of frogs were found at the swamp, but no more than 12 were there at any given time.

All three species of the *Hyla parviceps* group were found at the site, although *Hyla brevifrons* was observed only rarely. Several males of that species were present in August, whereas only five were present in October; none was calling. One gravid female was there in March. There were many *H. bokermanni* calling whenever *H. brevifrons* were found.

Throughout the year *H. bokermanni* and *H. parviceps* were observed calling in great numbers (more than 50 and 20 respectively).

Gravid females and/or amplexant pairs of both species were found on the same nights in November, March, and June. On only one occasion was the population of *H. parviceps* estimated to be greater than 50 individuals; in July 1972, about 100-150 calling males were present. Approximately 20 gravid females were found; this is about twice the number found on any other evening. The same evening 30-50 calling *H. bokermanni* were found; no females were observed. The water depth at this time was about 1 m in the middle of the swamp. Generally, when the two species were found calling synchronously, *H. bokermanni* was more than twice as abundant as *H. parviceps* (30-100 versus 10-35). *Hyla bokermanni* calls from *Heliconia* leaves and stems 1-2 m above the water surface. *Hyla parviceps* calls from the same sites, but usually at least one-third of them call at about the same heights from vegetation at the edge of the swamp. *Hyla bokermanni* was rarely found at the edge of the swamp.

Hyla bokermanni had two peaks of breeding activity at the swamp: October-November and February-April. These periods coincided with the times of greatest water depth in the swamp. On several occasions density of calling males was estimated between 300-500. Once in late March, the number of gravid females was estimated at 30-50; usually no more than 10-15 were found in one evening. Occasionally, when the swamp was dry, numerous egg clutches of *H. bokermanni* were hanging from the vegetation, and males were calling.

In contrast, male *H. parviceps* were observed calling only when there was at least 30 cm of water in the swamp. Generally, the more water, the greater the number of calling individuals. Breeding activity of *H. parviceps* reached a peak in October-November (coinciding with that of *H. bokermanni*) and again in June-July.

The breeding population of *H. bokermanni* generally seems to be larger than that of *H. parviceps* at any given time at the swamp. Apparently, there is no species replacement, for both species breed at the same time. This is probably due to differences in mating calls and in egg deposition sites.

Reproduction

Two modes of reproduction are represented in the *Hyla parviceps* group. *Hyla parviceps* deposits its eggs directly in the water, whereas both *H. bokermanni* and *H. brevifrons* deposit their eggs on leaves over water; upon hatching the tadpoles drop into the water where they complete development (Table 7).

The eggs of *H. parviceps* are small (1.0-1.2 mm) and heavily pigmented black and creamy white. The ovarian complement (120-395) is more than twice that of either *H. bokermanni* or *H. brevi-*

TABLE 7.—Summary of Reproductive Data for three species in the *Hyla parviceps* group at Santa Cecilia.
(Means and sample sizes are in parentheses below observed ranges.)

	<i>H. bokermanni</i>	<i>H. brevifrons</i>	<i>H. parviceps</i>
Snout-vent length (mm)	22.5-25.5	18.0-23.5	20.0-25.5
of gravid females	(23.9, n=29)	(20.9, n=15)	(23.3, n=101)
Number of mature ovarian eggs	65-135 (98.3, n=29)	48-114 (79.1, n=15)	120-395 (234.1, n=101)
Volume (ml) of gravid female	0.9-1.1 (1.0, n=5)	0.9-1.2 (1.1, n=6)
Volume (ml) of mature ovarian eggs	0.1 (n=5)	0.1-0.2 (0.1, n=6)
% Egg volume of total volume of ♀	9.1-11.1 (10.5, n=5)	8.3-22.2 (11.2, n=6)
Clutch size	60-196 (116.8, n=53)	48-91 (70.0, n=6)	165-385 (302.8, n=15)
.....	1.5-1.8	1.2-1.6	1.0-1.2
Ovum size	(1.6, n=53)	(1.3, n=6)	(1.1, n=15)
Number of days until hatching	4.0-5.3 (4.4, n=20)	6.3 (n=1)	1.3-2.3 (1.9, n=13)
Total length (mm) of hatchling	4.0-4.5 (4.2, n=20)	6.0 (n=1)	4.0-4.5 (4.1, n=13)

frons. A correlation analysis was run on 112 females with mature ovarian eggs in order to determine the relationship between snout-vent length and fecundity (both variables were normally distributed). The correlation coefficient was significant at the .01 level. Therefore, on the basis of this sample, it is concluded that larger female *H. parviceps* produce more eggs at a given breeding time. *Hyla parviceps* has a slightly greater percent volume of eggs relative to its total body volume than does *H. bokermanni*. The eggs develop rapidly under laboratory conditions (1.3-2.3 days). The range of variation of total length of the hatchlings (4.0-4.5 mm) is the same as that of *H. bokermanni*. Gravid females were found in every month of the year, indicating that breeding is continuous. Of 146 females found, 125 (85.6%) were gravid.

Hyla bokermanni deposits the largest eggs (1.5-1.8 mm) of the three species. The eggs are lightly pigmented tan and cream. The ovarian complement ranges from 65-135. A correlation analysis run on 29 females of this species (both variables normally distributed) indicated no significant correlation between snout-vent length of the female and the number of mature ovarian eggs. Thus, it seems as though there is no selective advantage for female *H. bokermanni* to increase in size in order to increase fecundity. It is suggested that perhaps larger females produce larger eggs. Under laboratory conditions the eggs took from 4.0-5.3 days to hatch. As previously indicated, although the eggs are larger to begin with and require more than twice as long to hatch, the size range of the

hatchlings is the same as that of *H. parviceps*. Gravid females were found October-November 1971 and throughout January-June 1972. Of 92 females found, 85 (92.4%) were gravid.

Hyla brevifrons, the smallest of the three species, deposits the intermediate-sized eggs (1.2-1.6 mm). The eggs are lightly pigmented tan and cream, similar to those of *H. bokermanni*. The species has the lowest ovarian complement (48-114). Only one clutch of eggs hatched in the laboratory; the eggs hatched in 6.3 days, and the hatchlings were 6.0 mm in length. Gravid females were found in July, October, and December 1971, and January, March, and June 1972. Of 13 females found, 10 (76.9%) were gravid.

An ovarian size factor³ was calculated from means of egg clutches deposited in the laboratory. *Hyla parviceps* has the largest value (13.38), *H. brevifrons* the smallest (4.42), and *H. bokermanni* an intermediate value (7.05). The reproductive strategy of *H. parviceps* is to produce many small eggs, deposited in open water. The species is a habitat generalist, breeding both in forest and forest-edge situations. The other two species are more restricted: *H. bokermanni* breeds mainly in the forest, and *H. brevifrons* in forest-edge swamps and ponds. The last two species lay relatively few, large eggs, and have more specialized egg deposition sites on vegetation above the water. The nearly identical utilization of egg deposition sites perhaps explains why these species generally do not breed at the same swamps. Neither *H. bokermanni* nor *H. brevifrons* was found to be gravid throughout the year. Perhaps these factors are indicative of more critical requirements for breeding than those of *H. parviceps*. Observations on the relationship between egg deposition sites and sunlight are inconclusive. It is suggested, however, that differences in pigmentation of the eggs may be explained by their exposure to different amounts of solar radiation. The darkest eggs are those of *H. parviceps* (deposited in water); perhaps these are subject to more solar radiation than those of *H. bokermanni* and *H. brevifrons* (deposited on leaves above water) which are protected by surrounding vegetation.

Food

Stomach contents of adults of both sexes of the three species at Santa Cecilia were analyzed. Ten orders of arthropods were found in 66 stomachs. Treating males and females separately, niche over-

³ The ovarian size factor is calculated by the formula $CS(OD)/SVL$, where CS = the mean clutch size, OD = the mean ovum diameter, and SVL = the mean snout-vent length of the females depositing the clutches. This provides an index for comparing fecundity and egg size relative to adult body size.

lap scores were calculated by the method suggested by Colwell and Futuyama (1971). Niche overlap scores varied from 0.13 to 0.76 (1.0 is complete overlap). The lowest scores are those of female *H. brevifrons* in which the sample consisted of only two specimens. Analysis of variance within groups (males and females) and between groups (males versus females) revealed no significant difference. The average niche overlap scores for food is 0.451, indicating a moderate amount of overlap between sexes in a given species and between species. The niche overlap values must be considered maximal to actual overlap because 1) small sample sizes (2-23) minimize overlap, and 2) only gross identifications (to order) were made on the food items. Because of the fragmentary nature, and/or degree of decomposition, of the food, insufficient data were obtained on prey size. However, individuals of all three species, including both sexes, contained caterpillars that were nearly as long as the frogs that had eaten them.

PHYLOGENETIC RELATIONSHIPS

In deducing phylogenetic relationships, it is customary to establish criteria for primitiveness. We have relied on the criteria used by Wagner (1961) (see Kluge and Farris, 1969, and Trueb, 1973, for discussions). Utilizing these criteria, primitive character states of a particular group are: 1) likely to be present in many closely related groups; 2) more likely to be widespread within a group than is any one derived state; and 3) likely to be associated with other primitive characters.

As a basis for phylogenetic analysis, we are assuming that the small, primarily Amazonian *Hyla* having a diploid number of 30 chromosomes and tadpoles with reduced mouthparts and xiphicerical tails are more closely related to one another than any is to any other group. Thus, we recognize the *leucophyllata*, *microcephala*, *minuta*, and *parviceps* groups of *Hyla*. Eleven structural and color pattern characters that are variable within the *Hyla parviceps* group and present in the other groups were analyzed. Of these 11 characters, the primitive states of eight are present in all three of the other groups, two in two groups, and one in one group.

In the following list of characters, the primitive state is number 0; states 1 and 2 are derived in succession, except F and G, in which the advanced states (1 and 2) are probably independently derived.

- A. Sexual dimorphism in size:
 - 0. ♂ > 90% ♀
 - 1. ♂ = 80-90% ♀
 - 2. ♂ < 80% ♀
- B. Ulnar and tarsal tubercles:
 - 0. Absent
 - 1. Present

- C. Suborbital bars:
 - 0. Absent
 - 1. One
 - 2. Two
- D. Canthal stripes:
 - 0. Absent
 - 1. Present
- E. Rostral stripes:
 - 0. Absent
 - 1. Present
- F. Dorsolateral stripes:
 - 0. Absent in both sexes
 - 1. Absent in males; present in females
 - 2. Present in both sexes
- G. Anterior thigh:
 - 0. Unicolor
 - 1. Small yellow spots
 - 2. Large yellow spot
- H. Dorsal thigh:
 - 0. Unicolor
 - 1. Small yellow spots
- I. Posterior thigh:
 - 0. Unicolor
 - 1. Large orange spot
- J. Venter:
 - 0. Plain
 - 1. Patterned
- K. Denticles (larvae):
 - 0. One lower row
 - 1. Absent

The distribution of character states within the *Hyla parviceps* group reveals variation from 6 to 11 derived characters (Table 8). The greatest number of primitive states occurs in *H. microps*, followed by *H. parviceps* and *brevifrons*; *H. bokermanni*, *luteocellata*, and *subocularis* have the fewest primitive states.

A phylogenetic arrangement (Fig. 7) was constructed by a method proposed by Camin and Sokal (1965). The branching sequence defines one group having few derived characters (*H. microps* and *parviceps*) and another with many derived characters (*H. luteocellata*, *bokermanni*, and *subocularis*). *Hyla brevifrons* is intermediate between these two groups.

Although reproductive data are incomplete, the existing information supports the proposed phylogeny. *Hyla microps* and *parviceps* deposit eggs in water, whereas the other species (unknown for *H. luteocellata*) deposit eggs on vegetation above water. Quantitative data on reproduction of three species in Ecuador reveal that in most features *H. brevifrons* is intermediate between *H. bokermanni* and *parviceps*. If the reproductive mode of *H. luteocellata* is the same as that for *H. bokermanni* and *subocularis*, a phylogenetic construct based on reproductive characters would approximate the arrangement based on morphological features.

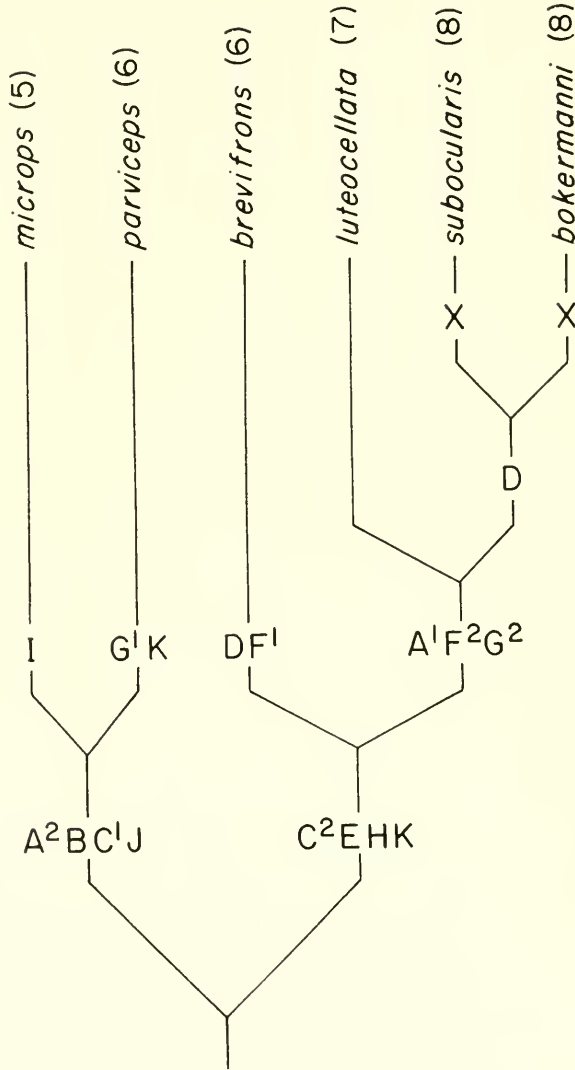


FIG. 7. Most parsimonious phylogenetic arrangement of species in *Hyla parviceps* group, based on 26 states of 11 characters. Letters indicate shifts from primitive to derived character states; superscripts indicate direction of change or degree of change in those characters represented by more than two states; X = change in dorsal pattern not accompanied by shifts in any one of the 11 characters; numbers in parentheses are numbers of evolutionary steps in each line. See Table 8 and text for character states and explanation.

TABLE 8.—Character states of 11 characters in species in the *Hyla parviceps* group.
(0 = primitive state; 1 and 2 = derived states; see text for list of characters and explanation.)

Character	<i>H. bokermanni</i>	<i>H. brevifrons</i>	<i>H. lutocollata</i>	<i>H. microps</i>	<i>H. parviceps</i>	<i>H. subocularis</i>
A	1	0	1	2	2	1
B	0	0	0	1	0.5 ^a	0
C	2	2	2	1	1	0
D	1	1	0	0	0	1
E	1	1	1	0	0	1
F	2	1	2	0	0	2
G	2	0	2	0	1	2
H	1	1	1	0	0	1
I	0	0	0	1	0	0
J	0	0	0	1	1	0
K	1	1	1	0	1	1
Total	11	7	10	6	6.5	11

^a Females only.

The presence of a row of denticles in the tadpoles of *Hyla microps* is the only larval character that can be determined as primitive in the group. Otherwise, the known tadpoles differ from one another principally in coloration. We have no bases for deducing evolutionary change in the coloration. We have incomplete data on mating calls, but the calls of *H. parviceps* and *brevifrons* consist of series of uniform notes, whereas *H. bokermanni* produces primary and secondary notes. Presumably the complex call of *H. bokermanni* is derived from the simple call of the others, a conclusion compatible with the phylogenies deduced from morphological and reproductive data.

Zoogeography

Recent works on distributional patterns in the tropical lowlands of South America emphasize Quarternary climatic fluctuations and the existence of forest refugia during times when climatic conditions were drier than present (Müller, 1968; Haffer, 1969; Vanzolini and Williams, 1970). Müller and Schmithusen (1970) and Vuilleumier (1971) summarized Pleistocene climatic changes and interglacial sea transgressions in South America. Haffer (1969) provided evidence from avian distributions and differentiation for six forest refugia in Amazonian South America. Vanzolini and Williams (1970) proposed four core areas for the differentiation of

populations of *Anolis chrysolepis* and hypothesized an evolutionary model of three expansions and two contractions of forest environments resulting in isolation, differentiation, and introgression of *Anolis chrysolepis*.

Accepting the preceding phylogenetic arrangement as a reasonable approximation of the actual evolutionary sequences of morphological characters in the *Hyla parviceps* group, we can superimpose the cladistics of the frogs on the biogeographical patterns in the lowland tropics. Our paleogeographic evolutionary model of the *Hyla parviceps* group is predicated on cyclic alternation of wetter and drier climates in the Pleistocene and Holocene, resulting in expansion and contraction of lowland tropical forests, and the existence of forest refugia during the drier periods (see Moreau, 1966, for paleogeographic evidence from Africa; Vanzolini and Williams, 1970, for a survey of the literature documenting changes in South America; and Van der Hammen and Gonzalez, 1960, for dating of palynological data). Duellman (1972) and Heyer (1973) suggested probable evolutionary histories of groups of South American hyliid and leptodactylid frogs with respect to vicissitudes of Quaternary climates.

The evolutionary model is outlined, as follows:

1. The prototype of the *Hyla parviceps* group was widespread in Amazonia during a wetter period. This prototype had the primitive states of the characters listed in the preceding section, aquatic eggs, and a simple mating call.

2. Climatic desiccation resulted in contraction of forests and isolation of two populations: 1) the *H. microps-parviceps* stock in an Amazonian refugium; 2) the *H. brevifrons-bokermami-luteocellata-subocularis* stock in an upper Amazonian refugium (Napo or Peruvian refugia of Haffer). The former stock developed more sexual dimorphism in size, ulnar and tarsal tubercles in females, one suborbital bar, and gray flecks on the venter. The second stock developed two suborbital bars, rostral stripes, yellow spots on the dorsal surfaces of the thighs; retained moderate sexual dimorphism in size; and lost the larval denticles.

3. During the subsequent pluvial period both stocks spread through the Amazon Basin; the *H. microps-parviceps* group expanded into eastern and southeastern Brasil, and the other stock invaded the coastal lowlands of northern South America and eastern Panamá.

4. Climatic desiccation resulted in the isolation of two populations of the *H. parviceps-microps* group (*H. microps* in the Serra do Mar refugium of Müller in southeastern Brasil and *H. parviceps* in an Amazonian refugium). The other stock was separated into four isolates. The prototypes of *H. bokermami* and *H. brevifrons* were isolated in separate refugia (probably Haffer's Napo and

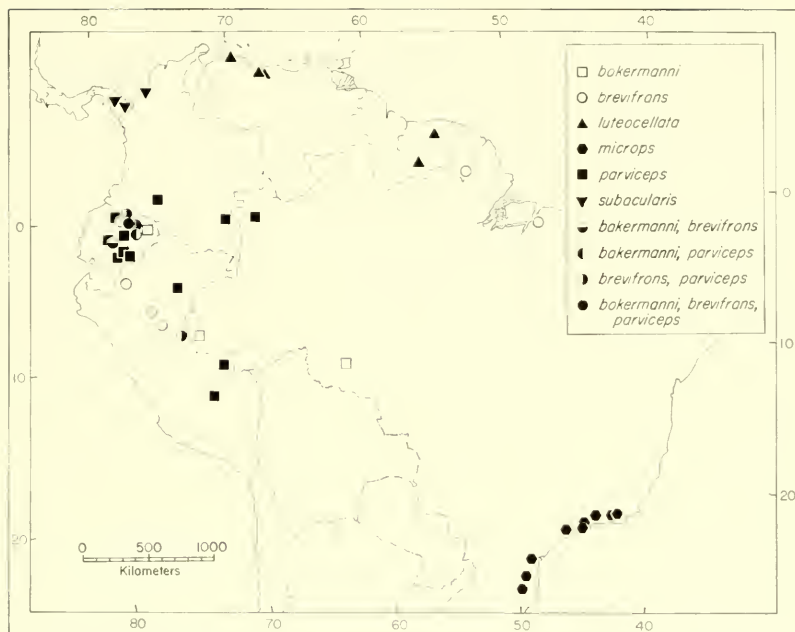


FIG. 8. Distribution of species in the *Hyla parviceps* group.

Peruvian refugia); *H. luteocellata* was isolated in the Cordillera de la Costa in northern Venezuela (a core area proposed by Vanzolini and Williams, 1970), and *H. subocularis* was restricted to one or more of the small refugia in northwestern Colombia (Chocó, Nechi, or Catatumbo refugia of Haffer, 1969).

5. The development of more equable climates resulted in the expansion of the Amazonian forests and of the ranges of the six populations of frogs. However, due to the dry *caatinga* and *cerrado* of eastern Brasil, *H. microps* remained restricted to southeastern Brasil. *Hyla luteocellata* expanded its range eastward into the Guianas, and *H. subocularis* moved into Panamá. In the Amazon Basin, the ranges of three species (*H. bokermanni*, *brevifrons*, and *parviceps*) expanded from their respective refugia and became sympatric in the upper part of the basin (Fig. 8).

EVOLUTION IN THE SYMPATRIC SPECIES

If we accept the proposed phylogenetic arrangement and the suggested paleogeographic model, we are forced to hypothesize that the three species now occurring in sympatry in the upper Amazon Basin evolved through geographic isolation at different times (*H. parviceps* versus *H. brevifrons* and *bokermanni*) and in

different places (*H. brevifrons* and *bokermanni*). Presumably, genetic differences that evolved when the populations were isolated have been reinforced through selection in sympatric populations. Due to lack of data on any one of the species where it occurs in the absence of the other two, we are unable to determine if there is any character displacement.

According to Van der Hammen and Gonzalez (1960), the climate in northern South America has been becoming progressively wetter for the past 4000 years, thus, it is possible that the three species in the upper Amazon Basin have been sympatric for less than 4000 years, before which time they were isolated in forest refugia (Haffer, 1969).

We are concerned here with those mechanisms which are operant in maintaining the specificity of the sympatric populations. Following Müller's (1942) classification of isolating mechanisms, as modified by Fouquette (1960), we recognize three major categories of isolating mechanisms—anti-mating, courtship, and post-mating. The last category includes gametic incompatibility, hybrid inviability, and hybrid sterility; we have no information on these factors and no evidence of hybridization, so they are not considered here.

Of the five kinds of anti-mating mechanisms, one (geographic isolation) has already been accounted for by the hypothesized differentiation through geographic isolation. Data on the others can be summarized, as follows:

Habitat isolation.—Relative to breeding activities, *H. parviceps* is a habitat generalist, usually present at sites where the other species breed. *Hyla bokermanni* and *brevifrons* usually breed at different sites.

Seasonal isolation.—Synchronous breeding activity is common, but at least *H. bokermanni* and *H. parviceps* have some different periods of intense breeding activity.

Temporal isolation.—All three species are nocturnal breeders.

Climatic isolation.—All three species have a positive response to periods of heavy rainfall.

Fouquette (1960) recognized only two categories of courtship isolating mechanisms, whereas we recognize three; oviposition sites are considered:

Auditory isolation.—The mating calls of three species are distinctly different in note repetition rate and duration of notes; furthermore, the call of *H. brevifrons* is distinctive in pulse rate, that of *H. parviceps* in dominant frequency, and that of *H. bokermanni* in the presence of secondary notes (Table 6).

Mechanical isolation.—Because the females of the three species have nearly identical snout-vent lengths, difference in size might be an effective mechanical isolating mechanism only in *H. parvi-*

ceps, the males of which are much smaller than males of the other species.

Ovipositional isolation.—*Hyla parviceps* deposits its eggs in water and the other species place their eggs on vegetation over water. The apparent behavioral and probable physiological differences of females and eggs, respectively, are potentially important factors in isolation.

The three species broadly overlap in most categories of potential isolating mechanisms, but there are distinct differences in two categories, ethological and ovipositional. Fouquette (1960) found that the mating call was the primary isolating mechanism operant in three sympatric species of *Hyla* in Panamá. Duellman (1967) reached the same conclusion in a study of a breeding community of ten species of hylids in Costa Rica. Martof and Thompson (1958) and Littlejohn and Michand (1959) provided experimental evidence demonstrating that females respond positively to the calls of the males and that females can discriminate between calls of males of their own and other species. Littlejohn (1964, 1965) presented evidence on evolution of differences in mating calls through geographic isolation and reinforcement of these differences in sympatric populations. We conclude that at least some of the differences in mating calls in the three species of the *Hyla parviceps* group evolved at times when the populations were geographically isolated from one another; furthermore, these differences may have been reinforced through selection upon subsequent geographical sympatry.

The differences in oviposition sites involve a modification in reproductive strategy from the presumed primitive strategy of placing eggs in water (*H. parviceps*) to a derived strategy of placing eggs on vegetation over water (*H. bokermanni* and *brevifrons*). Salthe and Duellman (1973) showed that within a given anuran reproductive mode there exist positive correlations between ovum size, clutch size and female snout-vent length, and negative correlations between clutch size and ovum size and between ovum size and rate of development. Among the three species under consideration, *Hyla parviceps* with aquatic eggs has the largest clutch size, smallest ova, and shortest duration of development (Table 7). Females of the other species are no larger than *H. parviceps*; thus, as concluded by Salthe and Duellman (1973), the achievement of a larger ovum in *H. bokermanni* and *brevifrons*, without an increase in body size of the females, was by selection for a change in the site of intraovular development, in this case vegetation over water. Larger eggs produce larger hatchlings better adapted to make the transition from leaf to water. Because the reproductive modes are different in the two lineages in the group, it is most reasonable to assume that this differentiation took place only once and that by

the time the three species became sympatric in the upper Amazon Basin the differences in reproductive strategy were already in existence. However, the differences are important aspects of resource partitioning in synchronously breeding frogs within one community.

Salthe and Duellman (1973) noted that in small anurans: “. . . it seems to be more advantageous to maintain a certain minimal number of eggs in the clutch than it is to maintain the size of the hatchling. Presumably, clutch sizes are already at, or near, a lower limit allowable for the production of an adequate amount of genetic variability per unit time. Thus, in general, selection in small species seems to function by maintaining minimal clutch sizes and maximizing the sizes for relatively tiny hatchlings.” Our reproductive data indicate that despite differences in mode of reproduction and ovum size, the hatchlings are about the same size in *H. bokermanni* and *parviceps*, but larger in *H. brevifrons*, which has the smallest clutches (Table 7).

The problem of production of an adequate amount of genetic variability, as related to fecundity, per unit time perhaps is an important factor in the great amount of sexual dimorphism in size in the *Hyla parviceps* group. At Santa Cecilia, the three species in the group occur in swamps inhabited by many other species, of which 17 *Hyla* are known to breed in the same ponds or swamps as do members of the *Hyla parviceps* group. All of these are larger than the species in the *Hyla parviceps* group. Selection might favor reduction in size in response to competition for food, calling sites, and oviposition sites. However, reduction in size of the females is more restricted than in males due to the limitations imposed by egg-carrying capacities. Schoener (1967, 1969, 1970) documented evidence for sexual selection in size of West Indian *Anolis*, noting that extremes of sexual dimorphism in size are reached on islands inhabited by only one species of *Anolis*; on these islands the sexes exist ecologically as two species using different resource states, such as perches and food. However, in the *Hyla parviceps* group, the presence of many other species utilizing a variety of resource states negates the hypothesis of intraspecific selection in size solely for resource partitioning and suggests that the reproductive necessities of the females balance selection for small size, which is evident in males.

SUMMARY

Among the small Neotropical *Hyla* having a diploid number of 30 chromosomes and reduced mouth parts in the tadpoles, one group of six species is characterized by great sexual dimorphism in size, more cranial ossification, and aspects of coloration (patterned thighs, suborbital bars, and iris color). Six species are included in

the group: *H. bokermanni* Goin, *H. brevifrons* new species, *H. luteocellata* Roux, *H. microps* Peters, *H. parviceps* Boulenger, and *H. subocularis* Dunn. *Hyla rondoniae* Bokermann, 1963, is placed in the synonymy of *Hyla bokermanni* Goin, 1960. The group is widespread in the Amazon Basin, southeastern Brasil, northern lowlands of South America and eastern Panamá.

Although interspecific differences exist in size, proportions, amount of webbing, and tubercles, the principal taxonomic characters are in the coloration. These include the number of pale suborbital bars, presence or absence of canthal and rostral stripes, presence and width of dorsolateral stripes, and pattern on the dorsum, venter, and especially the thighs. All of the tadpoles have one row of labial papillae. Tadpoles of *H. microps* have one row of denticles; denticles are absent in the others. The known tadpoles are brightly colored and have different patterns of transverse bars or longitudinal stripes. The mating calls consist of series of short, high-pitched notes; *H. bokermanni* produces primary notes followed by shorter secondary notes.

It is suggested that the species arose through isolation in forest refugia in the tropical lowlands during dry periods in the Pleistocene. The proposed phylogeny indicates that the two most primitive species now occupy different regions—*H. microps* in southeastern Brasil and *H. parviceps* in the upper Amazon Basin. The three most advanced species also have allopatric distributions—*H. bokermanni* in the upper Amazon Basin, *H. luteocellata* in coastal northern South America, and *H. subocularis* in eastern Panamá and northwestern Colombia.

Three species (*H. bokermanni*, *brevifrons*, and *parviceps*) occur at Santa Cecilia in Amazonian Ecuador. Intensive field studies there continuously for 13 months revealed slight differences in habitat and seasonal activity. One species (*H. parviceps*) lays eggs in the water, whereas the other two place eggs on vegetation over the water. Clutch size is larger and ovum size is smaller in *H. parviceps* than the others.

It is suggested that differences in mating calls and oviposition sites are the primary isolating mechanisms operating in the sympatric species. Furthermore, it is suggested that natural selection for small size in comparison with many sympatric congeners is balanced in females by the necessity for maintaining an adequate number of eggs to insure genetic variability in the population. In the absence of such pressure in the males, they have become much smaller than the females.

RESUMEN

Entre las pequeñas ranas neotropicales del género *Hyla* con un número diploide de 30 cromosomas y renacuajos con bocas de

estructuras pequeñas, un grupo de seis especies se caracteriza por el gran dimorfismo sexual de su tamaño, mayor osificación craneal, y algunos aspectos de su coloración (diseños en los muslos, barras suborbitales, y color del iris). Las seis especies incluidas en el grupo son: *H. bokermanni* Goin, *H. brevifrons* nueva especie, *H. luteocellata* Roux, *H. microps* Peters, *H. parviceps* Boulenger, y *H. subocularis* Dunn. *Hyla rondoniae* Bokermann, 1963, se pone en el sinonimia de *Hyla bokermanni* Goin, 1960. Este grupo se encuentra difundido en la Cuenca Amazónica, el sureste brasileño, las tierras bajas del norte de Suramérica, y el este panameño.

Aun cuando existen diferencias interespecíficas de tamaño, proporciones, extensión de las membranas interdigitales, y tubérculos, las principales características taxonómicas giran alrededor de la coloración. Esto incluye el número de barras suborbitales claras, la presencia o ausencia de las rayas cantales y rostrales, la presencia y ancho de las rayas dorsolaterales, y el diseño dorsal, ventral, y especialmente de los muslos. Todos los renacuajos tienen una fila de papilas labiales. Los renacuajos de *H. microps* tienen una fila de denticulos que no existe en los otros. Los renacuajos que se conocen son de coloración luminosa y tienen distintos diseños de barras transversales y rayas longitudinales. La llamada de reclamo consiste de series de notas cortas y altas; *Hyla bokermanni* produce notas primarias seguidas de notas secundarias más cortas.

Se sugiere que estas especies surgieron como resultado de su aislamiento en refugios en la selva de la tierra tropical baja durante los períodos secos del Pleistoceno. La filogenia propuesta sugiere que las dos especies más primitivas ocupan ahora regiones distintas—*H. microps* ocupa el sureste brasileño y *H. parviceps* la parte superior de la Cuenca Amazónica. Las tres especies más evolucionadas también tienen distribuciones alopátricas—*H. bokermanni* en la parte superior de la Cuenca Amazónica, *H. luteocellata* en la costa norte de Suramérica, y *H. subocularis* en el este panameño y noroeste colombiano.

Tres especies (*H. bokermanni*, *brevifrons*, y *parviceps*) se encuentran en Santa Cecilia en la Amazonia Ecuatoriana. Estudios continuos e intensivos de campo durante un período de 13 meses revelan pequeñas diferencias en su "habitat" y en la actividad estacional. Una de las especies (*H. parviceps*) pone sus huevos en el agua, mientras que las otras dos los ponen en la vegetación sobre el agua. En *H. parviceps* el número de huevos es mayor y el tamaño de los huevos es menor que en las otras especies.

Se sugiere que diferencias en las llamadas de reclamo y los lugares de oviposición son los mecanismos principales de aislamiento en las especies simpátricas. Se sugiere además que la selección natural a favor de un tamaño pequeño en estas especies en comparación con muchos otros congéneres simpátricos está con-

trarestada en las hembras por la necesidad de mantener un número adecuado de huevos con lo que asegura la variabilidad genética de la población. En la ausencia de esta presión, los machos se han mantenido mas pequeños.

SPECIMENS EXAMINED

Hyla bokermanni

BRASIL: *Acre*: Cruzeiro do Sul, WCAB 12148. *Rondônia*: Rondônia, WCAB 7845.

ECUADOR: *Napo*: Limón Cocha, UIMNH 64799-800, 90069; Santa Cecilia, KU 104432-3 (skeletons), 105118-9, 105121-2, 105125-6, 105131, 105189, 109355-7, 109452, 109468, 123051-8, 123060, 123062-71, 123089-91, 124193 (tadpoles), 126362, 126541-5, 126547, 126552-5, 143131, 143188, 146288-95, 146414, 146419, 146800-1 (tadpoles), 150026-51, 152290-1 (tadpoles), 152419-28, 152535, 152750-3 (skeletons), UMMZ 129325 (4). *Pastaza*: 3 km S Puyo, KU 127087.

Hyla brevifrons

BRASIL: *Pará*: IPEAN, 5 km E Belém, KU 127846.

COLOMBIA: *Putumayo*: Santa Rosa de Sumbios, AMNH 88068-80.

ECUADOR: *Napo*: Lago Agrio, 126556-8; Puerto Libre, KU 123092-4; Santa Cecilia, KU 105063, 105107-11, 105120, 105127-30, 105132-4, 105190, 107003-4, 109449-51, 109453-67, 111786-802, 112341 (eggs), 123049-50, 123059, 123072-88, 125899-900 (tadpoles), 126342-61, 126363-71, 126546, 126548-51, 136298, 143189, 146281-7, 146413, 146415-8, 150052-74, 152429-32, 152536-7 (tadpoles), 152754-8 (skeletons), UMMZ 129324 (2). *Pastaza*: Puyo, CAS 85142.

FRENCH GUIANA: *Inini*: Crique Eleupocigne, Upper River Oyapak, LG 1119, 1308, 1311-12.

PERÚ: *Loreto*: Pampa Hermosa, Río Cushabatay, AMNH 42358; Río Utoquinia-Río Tapiche, AMNH 43576; Tacsha Huachiyacu, Río Morona, AMNH 43045; Yurimaguas, Río Hnallaga, BMNH 84.2.18.53.

Hyla luteocollata

VENEZUELA: *Aragua*: Cumboto, UMMZ 113890 (2); Monte Oscuro, BMNH 1968.73-4, KU 125861-5, UMMZ 130085-6.

Hyla microps

BRASIL: *Paraná*: Curitiba, UMMZ 104118 (2), 104129 (6), 104130, 104160. *Rio de Janeiro*: Barro Branco, SMF 41217; Novo Friburgo, ZMB 7472; Teresópolis, BMNH 1947.2.11.10. *São Paulo*: Campo Grande, Santo Andre, KU 74266-8, 74269 (skeleton), 92073-7, 92078 (skeleton); Campos de Jordão, KU 112398 (tadpoles); 10 km W Casa Grande, KU 129838. *Santa Catarina*: UMMZ 58515; Humboldt, AMNH 15373-82.

Hyla parviceps

COLOMBIA: *Putumayo*: Santa Rosa de Sumbios, AMNH 88081-2.

ECUADOR: *Napo*: Bermejo No. 4 (well site), Sierra Umbaqui, KU 122963; Cuyabeno, UIMNH 54134-6, 54172, 59625-8, 90108-9; Dureno, KU 105113-4; Lago Agrio, KU 126480; Limón Cocha, KU 99223-8, 99229 (skeleton), UIMNH 64805, 90076; Santa Cecilia, KU 104428-31 (skeletons), 105046-62, 105064-106, 105112, 107048-9, 109433-46; 11764-84, 112339-40 (tadpoles), 122925-62, 123061, 126462-79, 143167-73, 146307-11, 146790-1 (tadpoles), 150309-56, 152303-4 (tadpoles), 152547 (tadpoles), 152759-63 (skeletons), UMMZ 129279 (9); Tena, UIMNH 59628, 90059-64; UMMZ 123903. *Pastaza*: Abitagua, UMMZ 90416-7; Chontoa, KU 120910-13,

121407; Mera, KU 120909; 3 km S Puyo, KU 127086, 127090; 25 km NNE Puyo, KU 146792 (tadpoles); Río Conambo, mouth of Río Shione, USNM-GOV 7143; Río Oglan, upper Río Curaray, USNM-GOV 9526; Sarayacu, BMNH 1947.2.13.51. *Tungurahua*: Llanganate area, FMNH 23522-3; Mirador, BMNH 99.10.30.49; Río Negro, KU 120913-14, 121408.

PERÚ: *Cuzco*: Pilcopata, KU 139228. *Loreto*: Balta, Río Curanja, LSU 25719-57; Iquitos, AMNH 42086; headwaters Río Utoquinia, AMNH 43314.

Hyla subocularis

COLOMBIA: *Córdoba*: Río Manso, CM 50447-50.

PANAMÁ: *Darién*: Laguna, KU 77348-59, 77620; Río Chucumaque, AMNH 51777; Río Chucumaque at first creek above Río Tuquesa, AMNH 41117; Río Ueurganti, 7 km above mouth, KU 116785, 116784 (tadpoles); Tacarcuna, KU 77360-403, 77621, 77688-90 (skeletons), UMMZ 124780.

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