

**SOUTH AMERICAN FROGS OF THE
HYLA ROSTRATA GROUP
(AMPHIBIA, ANURA, HYLIDAE)**

by

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With 3 text-figures and 3 plates

INTRODUCTION

Few groups of Neotropical anurans are so diverse and taxonomically puzzling as the *Hyla rubra* group (sensu lato). Within this complex which possibly is generically distinct from *Hyla*, there are several species groups: *Hyla strigilata* Spix and related taxa in eastern Brasil; *Hyla parkeri* Gaige and relatives that are widely distributed in South America; *Hyla catharinae* and related taxa in eastern Brasil; *Hyla acuminata* Cope and relatives in the Chacoan region of South America; *Hyla rostrata* Peters and allied taxa in lower Central America, northern South America, and the Amazon Basin; *Hyla rubra* Laurenti and many similar species that are widespread in Central and South America; and some species, such as *Hyla boesemani* Goin, that do not seem to be closely allied with any of the recognized groups.

The members of the *Hyla rostrata* group are treated in this paper. The earliest description of a species in this group is that of *Hyla rostrata* Peters (1863) named from Caracas, Venezuela. This name was not applied to known populations of frogs until Rivero (1968) used it for specimens from northern South America and Panamá; the Panamanian populations had been named as *Hyla foliamorta* by Fouquette (1958). In addition to synonymizing *Hyla foliamorta* with *Hyla rostrata*, Rivero also included *Garbeana garbei* Miranda-Ribeiro and *Hyla lutzi* Melin in the synonymy of *Hyla rostrata*.

Cope (1887) named *Scytopsis boulengeri* from Nicaragua; Günther (1901) and subsequent workers did not recognize *Scytopsis* and placed *boulengeri* in *Hyla*. Miranda-Ribeiro (1926) named a new genus and species, *Garbeana garbei* from Eirunepé, Amazonas, Brasil. Duellman (1970a) demonstrated that *Hyla lutzi* was a synonym of *Garbeana garbei*, a species of *Hyla* distinct from *Hyla rostrata*. Brongersma (1933) named a distinctive species, *Hyla proboscidea*, from Gran Río, Surinam, and Lutz (1968) named *Hyla eglerti* from Belém, Pará, Brasil.

The purposes of the present paper are to summarize the available data on members of this group, in order to form a basis for more refined systematic

studies, and to name a new species in the group. In so doing I am introducing much new data accumulated in the course of examining specimens in various museums and through my own field work in Central and South America. The new species named herein has a fleshy proboscis, as does *Hyla proboscidea* named by Brongersma; it seems appropriate to name a similar species in this volume dedicated to Prof. Brongersma.

Audiospectrograms were made on a vibralyzer (Kay Electric Company). Terminology and methods of measurements are those defined by Duellman (1970b); snout-vent length and head length do not include the fleshy proboscis, if present. The illustrations were executed by Linda Trueb, who has my sincere thanks for her skillful renderings. I thank the following persons for allowing me to examine specimens in their care; abbreviations for museum collections are given in parentheses (University of Kansas, Museum of Natural History is abbreviated KU): W. Frank Blair, Texas Natural History Collection (TNHC); Nelly Carrillo de Espinosa, Museo Javier Prado, Lima (MJP); Alice G. C. Grandison, British Museum (Natural History) (BMNH); Brigitta Hansson, Naturhistoriska Museet, Göteborg (NHMG); Walter Hellmich, Zoologische Sammlung, München (ZSM); D. Hillenius, Zoologisch Museum, Amsterdam (ZMA); M. S. Hoogmoed, Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Hymen Marx, Field Museum of Natural History (FMNH); Alan E. Leviton, California Academy of Sciences (CAS) and Stanford University (CAS-SU); Jean Lescure, Université de Paris (LG); Bertha Lutz, Museu Nacional, Rio de Janeiro (MNRJ); Charles W. Myers, American Museum of Natural History (AMNH); Craig E. Nelson (CEN); Günther Peters, Zoologisches Museum, Berlin (ZMB); James A. Peters, United States National Museum (USNM); Juan A. Rivero, University of Puerto Rico, Mayagüez (UPR-M); Dorothy M. Smith, University of Illinois, Museum of Natural History (UIMNH); Haydeé Solano, Universidad Central, Caracas (UCV); Paulo E. Vanzolini, Museo de Zoología, Universidade de São Paulo (MZUSP); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); John W. Wright, Los Angeles County Museum (LACM). I am grateful to Charles W. Myers, M. S. Hoogmoed, and Jean Lescure who provided photographs and recordings of, and data on, living frogs from Colombia, Surinam, and French Guiana, respectively, and to Linda Trueb for critically reviewing the manuscript.

TAXONOMIC TREATMENT

The *Hyla rostrata* Group

Definition. — Moderate-sized tree frogs (largest females 53 mm) having:
1) elongate pointed snouts, with snout projecting anteriorly beyond margin

of the jaw; 2) slightly depressed bodies, with or without tubercles on dorsum; 3) long digits with broad, truncate discs; 4) webbing absent or vestigial on hand; 5) toes webbed, except webbing absent between the first and second toes; 6) vocal sac single, median, subgular with laterad inflation; 7) palpebral membrane not pigmented; 8) a dark triangular cephalic marking with base lying between eyes and apex posteriorly; 9) posterior surfaces of thighs marked with bold dark and light mottling or broad vertical bars; 10) nasals large, comprising more than 40 per cent of length of skull and having long, pointed maxillary processes; 11) palatines slender; 12) quadratojugals slender and always articulating with maxillaries; 13) prevomerine teeth on transverse processes; 14) known tadpoles pelagic with deep bodies and fins, two upper and three lower rows of teeth, and median part of upper lip devoid of papillae; 15) mating call consisting of single or multiple, moderately long or short, low-pitched, well-pulsed notes.

Content. — Six species.

Distribution. — Lowlands of Central America from eastern Nicaragua southeastward; in South America: Pacific lowlands southward to northwestern Ecuador, Caribbean lowlands, Guianas, Orinoco and Amazon basins southward to Bolivia.

Remarks. — With the exception of *Hyla rostrata* which inhabits savannas and scrub forest, all members of the group live principally in tropical rain forest. All breed in ponds. Males characteristically call in a vertical position with the head down; usually they call from secluded places amidst low vegetation above, or adjacent to, water.

KEY TO SPECIES IN THE *HYLA ROSTRATA* GROUP

1. Snout acutely rounded; row of tubercles lacking on lower jaw; skin on dorsum smooth or nearly so; throat in males dark grey or brown *Hyla rostrata*
- Snout acuminate; row of tubercles along edge of lower jaw; skin on dorsum tuberculate; throat in males pale with dark flecks or mottling 2
2. Posterior surfaces of thighs cream, yellow, or pale green with broad vertical dark brown or black bars about same width as interspaces 3
- Posterior surfaces of thighs mottled, or otherwise irregularly marked with blue, yellow, or pale green and black or dark brown 5
3. Fleshy proboscis present *Hyla proboscidea*
- No fleshy proboscis 4
4. Dorsum predominately green and black; small tubercles scattered on dorsum; one or two small tubercles on heel *Hyla boulengeri*
- Dorsum predominately brown and green; tubercles on dorsum concentrated on eyelids and supratympanic fold; one elongate tubercle on heel *Hyla garbei*
5. Posterior surfaces of thighs blue with black mottling *Hyla boulengeri*
- Posterior surfaces of thighs with irregular yellow or pale green and black or dark brown markings 6
6. Fleshy proboscis present; snout-vent length of males to 38 mm *Hyla epacrorrhina*
- No fleshy proboscis; snout-vent length of males to 30 mm *Hyla egleri*

Hyla boulengeri (Cope) (pl. I fig. 6)

Scytotis boulengeri Cope, 1887, Bull. U.S. Natl. Mus., 32: 12. — Holotype: USNM 13974, from "Nicaragua".

Hyla boulengeri; Günther, 1901, Biol. Centr.-Amer., Rept. & Batr.: 267.

Diagnosis. — This is the largest species in the group; males attain a snout-vent length of 48.7 mm and females, 52.8 mm; the species has the following characters: 1) skin on dorsum bearing small tubercles, sometimes forming a M-shaped mark in scapular region; 2) one row of low tubercles along edge of lower jaw; 3) one or two small tubercles on heel; 4) snout broad, acuminate, lacking fleshy proboscis; 5) dorsum mottled green and black; 6) posterior surfaces of thighs yellow or pale green with broad, vertical black bars or pale blue with black bars or mottling; 7) throat in breeding males white with grey flecks; 8) tadpoles silvery yellow with large black spots on the tail, having deep fins tapering sharply to terminal point; labial papillae long, present only laterally, third lower tooth row short, bearing long, curved teeth; 9) mating call consisting of single low-pitched note.

Hyla boulengeri can be distinguished from *epacrorrhina* and *proboscidea* by the absence of a fleshy proboscis in *boulengeri*. *Hyla rostrata* has a more blunt snout, smooth dorsum and dark throat. *Hyla garbei* and *egleri* are smaller; the former has an elongate tubercle on the heel, and the latter has an irregular mottling on the posterior surfaces of the thighs.

Distribution. — Caribbean lowlands of Central America from central Nicaragua to central Panamá; Pacific lowlands of southeastern Costa Rica, eastern Panamá, Colombia, and northwestern Ecuador.

Remarks. — Some, perhaps all, specimens from the Pacific lowlands of Colombia currently referred to *Hyla boulengeri* have blue and black markings on the thighs. Possibly these frogs represent only a geographical variant of *boulengeri*, or they may be specifically distinct from *boulengeri*.

The largest male from the Pacific lowlands of South America has a snout-vent length of 39.5 mm, and the largest female, 48.5 mm; these are notably smaller than specimens from Central America. The principal difference between Central American and Chocoan specimens is in coloration in life. The former are greyish tan or dull green with darker dorsal markings; the flanks are pale yellowish green, and the groin is pale green with black spots or mottling. The hidden surfaces of the thighs are greenish yellow or orange-yellow with vertical black bars; the iris is dull bronze. Coloration of living individuals (amplectant pair, AMNH 85373-4) from 2 kilometers above Playa del Oro, upper Río San Juan, Chocó, Colombia, was described by Charles W. Myers (field notes, 12 February 1971): "Male light yellowish brown with brown markings, and female light brown with dark brown mark-

ings. Male with a tinge of green around interorbital triangle, but in female the green is restricted to two small spots. Axilla, posterior flank through groin and anterior face of thigh, and posterior thigh sky blue with black markings. Also, some pale green suffused around the blue on the flanks (more extensive in female) and as a patch between first (proximal) pair of black markings on rear of thigh; but the blue is more extensive in total area. Venter white, turning pale blue on undersides of limbs; throat of female conspicuously dotted with brown but only weakly so in male. Iris pale grey in male and pale brown in female, both with narrow brown horizontal stripe through pupil and some sparse, fine black venation, which is not conspicuous".

A series of preserved specimens from central Chocó (LACM 46826-50) shows considerable variation in colour pattern. In some specimens the posterior surfaces of the thighs have distinct vertical dark bars, whereas in others the pattern is more diffuse or mottled; coloration in life is not known. The one available recording of the call of a Chocóan frog (AMNH 85373) shows that the call is similar to those of frogs from Central America (table 1); the Chocóan frog has a slightly longer call and only one, instead of two, emphasized harmonic.

Three specimens (FMNH 173966-8) from Santo Domingo de los Colorados, Pichincha Province, Ecuador, are like *Hyla boulengeri* in the coloration of the thighs but lack a distinct triangular mark on the head; furthermore, the snout is rounded, not pointed as in *boulengeri*. The largest individual, a gravid female, has a snout-vent length of 34.0 mm. These specimens definitely are not *Hyla boulengeri*. All other specimens from the Pacific lowlands are herein tentatively assigned to *Hyla boulengeri* until such time as more data on coloration in life and mating calls are available for a more meaningful comparison with samples from Central America.

***Hyla eglerti* Lutz (pl. 1 fig. 3)**

Hyla eglerti Lutz, 1968, Pearce-Sellards Ser. Texas Mem. Mus., 10: 8. — Holotype: MNRJ 4055, from Belém, Pará, Brasil.

Diagnosis. — This is the smallest species in the group; males attain a snout-vent length of 29.9 mm and females, 39.4 mm; the species has the following characters: 1) skin on dorsum bearing small tubercles, especially prevalent on head; 2) one indistinct row of small tubercles on edge of lower jaw; 3) one or two small tubercles on heel; 4) snout narrow, acuminate, lacking fleshy proboscis; 5) dorsum tan or olive-brown with darker brown diagonal marks; 6) posterior surfaces of thighs mottled dark brown and yellow or pale green, mottling not forming distinct, broad vertical bars (fig. 1B); 7) throat in breeding males white with brown flecks; 8) tadpoles pale green with black spots, having deep fins and xiphicercal tail; labial

papillae small, present ventrally; third lower tooth row same length as others; 9) mating call consisting of series of short, pulsed notes.

Hyla egléri can be distinguished from other members of the group, except *epacrorrhina*, in lacking broad vertical light and dark bars on the posterior surfaces of the thighs. *Hyla epacrorrhina* differs from *egleri* by having a fleshy proboscis.

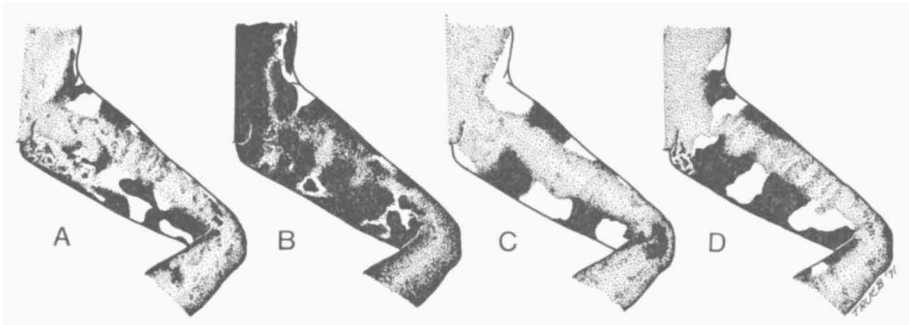


Fig. 1. Colour pattern of thighs of members of the *Hyla rostrata* group. A, *Hyla epacrorrhina*, KU 139247; B, *Hyla egléri*, KU 128366; C, *Hyla garbei*, KU 125604; D, *Hyla proboscidea*, RMNH 12517. The patterns of *Hyla boulengeri* and *rostrata* are like C and D.

Distribution. — The Guianas southeastward in coastal lowlands to Alagoas, Brasil.

Remarks. — *Hyla egléri* is extremely abundant in the vicinity of Belém, Brasil, where it breeds in ponds at the edge of the forest. Early reports of *Hyla acuminata* Cope from northeastern Brasil and the Guianas apparently were based on examples of *Hyla egléri*. I have not seen specimens from areas southeast of Belém; the species was reported from Alagoas and Paraiba, Brasil by Lutz (1968).

***Hyla epacrorrhina* spec. nov. (pl. 1 fig. 1)**

Holotype. — KU 139247 from Pilcopata, Departamento Cuzco, Perú, 13°05'S, 71°12'W, elevation 750 m, one of a series collected by William E. Duellman and Thomas H. Fritts on 15 January 1971.

Paratopotypes. — KU 139242-45, 139249, AMNH 85382, RMNH 16922, same data as holotype.

Diagnosis. — The largest male has a snout-vent length of 37.8 mm and the only female, 40 mm; the species has the following characters: 1) skin on dorsum bearing many small, low tubercles; 2) one row of distinct tubercles along edge of lower jaw; 3) one large triangular tubercle on heel; 4) snout narrow, acuminate, bearing flattened, triangular fleshy proboscis (fig. 2);

5) dorsum tan with narrow, diagonal brown marks; 6) posterior surfaces of thighs dark brown with yellow spots and mottling (fig. 1A); 7) throat in breeding males white with black flecks; 8) tadpoles unknown; 9) mating call consisting of long primary note followed by one or two secondary notes.

Hyla epacrorrhina differs from all other members of the group, except *proboscidea*, in having a fleshy proboscis. *Hyla proboscidea* has broad, vertical light and dark bars on the posterior surfaces of the thighs, whereas *epacrorrhina* has dark and light mottling.

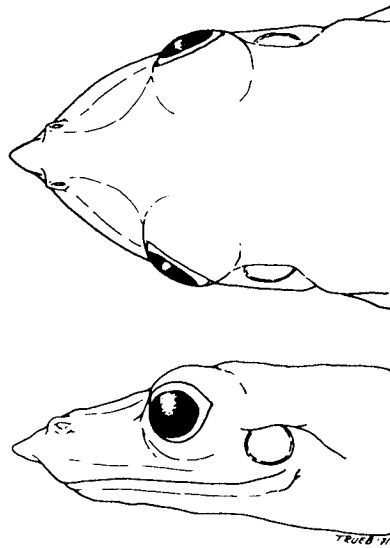


Fig. 2. Dorsal and lateral views of the head of *Hyla epacrorrhina*, KU 139247-holotype. $\times 3$.

Description of holotype. — An adult male; body slender; head longer than wide; snout acuminate in dorsal and lateral views; fleshy triangular proboscis present; snout projecting well beyond margin of lip; canthus rostralis angular; loreal region slightly concave, oblique; nostrils protuberant dorsolaterally; internarial region depressed; lips thick, flared; top of head flat; tympanum distinct, separated from eye by distance equal to about one-half diameter of tympanum; supratympanic fold weak, covering upper edge of tympanum, extending to point just posterior to angle of jaw. Axillary membrane absent; forearm more robust than upper arm, lacking ulnar fold; fingers long, slender, bearing truncate discs; length of fingers from shortest to longest 1-2-4-3; width of disc on third finger equal to three-fourths diameter of tympanum; subarticular tubercles small, conical; distal tubercle on fourth finger bifid; subarticular tubercles small, conical, present only on

proximal segments of digits; palmar tubercle trifold; prepollical tubercle elongate; nuptial excrescences absent; webbing absent. Hind limbs moderately long, slender, one large triangular tubercle and several small tubercles on heel; tarsal fold absent; inner metatarsal tubercle small, elliptical, not visible from above; outer metatarsal tubercle half as large as inner, conical; toes moderately long, slender; length from shortest to longest 1-2-5-3-4; discs notably smaller than those on hand; subarticular tubercles large, round; supernumerary tubercles small, conical; webbing absent between first and second toes, extending from distal end of penultimate phalange of second to base of penultimate phalange of third, from distal end of penultimate phalange of third to distal end of antepenultimate phalange of fourth and on to distal end of penultimate phalange of fifth toe. Skin on belly and proximal posteroventral surfaces of thighs granular; skin on other ventral surfaces smooth; skin on dorsum smooth, except for tubercles on head and in scapular region; row of low, conical tubercles along margin of lower jaw; anal opening directed ventrally at mid-level of thighs, bordered laterally by heavy dermal fold and ventrolaterally by small tubercles; dentigerous processes of prevomers small, transverse at level of posterior margins of large, ovoid choanae, bearing 6-6 teeth; tongue cordiform, half again as long as wide, shallowly notched and barely free posteriorly; vocal slit extending from mid-lateral base of tongue to angle of jaw; vocal sac single, posteromedian, sub-gular with slight lateral protrusions.

Measurements (in mm): snout-vent length 36.6, tibia length 21.0, foot length 16.0, head length 12.8, head width 19.9, interorbital distance 4.0, internarial distance 3.0, eyelid 3.1, eye 3.8, tympanum 2.8, eye-nostril 4.5.

Colour in alcohol: dorsum greyish tan with dark brown triangle between eyes with apex posteriorly, dark brown spot and diagonal mark above insertion of arm, and brown chevron mark in sacral region; limbs coloured like body with narrow darker transverse bars; anterior and posterior surfaces of thighs cream with bold black mottling; flanks creamy tan; webbing dark brown; venter cream with brown spots on shanks and brown flecks laterally on belly and on throat.

Variation. — Structurally all of the specimens are alike, except that in two males and one female the proboscis is poorly developed. The single female has a snout-vent length of 40.0 mm; eight males have snout-vent lengths of 34.4-37.8 (mean 35.1) mm. The total number of prevomerine teeth in males is 8-13 (11.3) and 9 in one female.

In life individuals from *Pilcopata* were tan to brown with darker brown dorsal markings. The upper parts of the flanks and narrow transverse marks on the dorsal surfaces of the thighs were pale green. The lower flanks and

anterior and posterior surfaces of the thighs were yellow orange with black marks on the thighs. The throat was greyish brown with cream flecks, and the belly was cream. The iris was creamy grey with brown triangular marks anterior and posterior to the pupil.

The pattern on the posterior surfaces of the thighs is most prominent distally. In four specimens the pattern consists of irregular mottling; in five individuals the pattern consists of an irregular longitudinal pale area surrounded by black. In no case is there a tendency towards vertical dark and light bars.

Distribution. — In addition to the type locality in southern Perú, the species also is known from near Chipiriri, Departamento Cochabamba, Bolivia, elevation 260 m. Both localities are in the headwaters of the Río Madeira drainage system.

Remarks. — At Pilcopata the frogs were calling at night in dense, herbaceous vegetation at the edge of a shallow pond in second growth tropical rainforest. Most males were oriented head-down on branches or leaves. The one specimen from Bolivia was found on the night of 15 February 1970; it was sitting on a low shrub in primary tropical rainforest.

The specific name is derived from the Greek *epakros*, meaning pointed at the end, and the Greek *rhinos*, meaning nose; the name *epacrorhina* alludes to the pointed fleshy tip to the snout.

Hyla garbei (Miranda-Ribeiro) (pl. 1 fig. 2)

Garbeana garbei Miranda-Ribeiro, 1926, Arch. Mus. Nac. Rio de Janeiro, 27: 96. — Holotype: MZUSP 277, from Eirunepé, Amazonas, Brasil.

Hyla lutzii Melin, 1941, Göteborgs Kungl. Vetensk.-och Vitterh.-Sam. Handl. (B), 1 (4): 36. — Lectotype: NHMG 481, from Maráos, Amazonas, Brasil (synonymy fide Duellman, 1970a: 536).

Hyla (Garbeana) garbei; Lutz & Kloss, 1952, Mem. Inst. Osw. Cruz, 50: 648.

Osteocephalus garbei; Goin, 1961, Ann. Carnegie Mus., 36: 13.

Hyla garbei; Duellman, 1970a, Copeia, 1970 (3): 536.

Diagnosis. — Males of this species attain a snout-vent length of 42.8 mm and females, 46.3 mm; the species has the following characters: 1) skin on dorsum nearly smooth, except for small tubercles on eyelid, supratympanic fold, and above insertion of arm; 2) one row of conical tubercles along edge of lower jaw; 3) one elongate tubercle on heel; 4) snout narrow, acuminate, lacking fleshy proboscis; 5) dorsum dull brown, with streaks of dull green in some individuals, with dark brown markings; 6) posterior surfaces of thighs yellow or orange with broad, vertical black or dark brown bars (fig. 1C); 7) throat in breeding males white with grey flecks; 8) tad-

poles unknown; 9) mating call consisting of one single moderately short note with medium pitch.

Hyla garbei can be distinguished from *epacrorrhina* and *proboscidea* by lacking a fleshy proboscis. *Hyla rostrata* has a more blunt snout, smooth dorsum, and dark throat, and *egleri* has mottling on the posterior surfaces of the thighs. *Hyla boulengeri* is larger and lacks an elongate tubercle on the heel.

Distribution. — Upper Amazon Basin in southern Colombia, Ecuador, northern Perú, and western Brasil; upper Orinoco Basin in Venezuela.

Remarks. — The synonymy and variation in this species have been discussed in detail by Duellman (1970a), who noted that two specimens from Mitú, Vaupés, Colombia, had mating calls different from Ecuadorian *Hyla garbei*. Subsequently, I have seen some uncatalogued specimens (AMNH) from the vicinity of Leticia, Amazonas, Colombia, that have a different colour pattern on the thighs and lack long tubercles on the heels. Werner C. A. Bokerman informed me (in litt.) that he has a specimen of *Hyla garbei* from Maranhão, Brasil. All of these facts indicate that much remains to be learned about the systematics of this group of frogs.

Hyla proboscidea Brongersma (pl. 1 fig. 5)

Hyla proboscidea Brongersma, 1933, Zool. Anz., 103 (9/10): 267. — Holotype: ZMA 5710, from Upper Gran Rio, Surinam.

Diagnosis. — Males attain a snout-vent length of 39.8 mm, and the only known female has a snout-vent length of 37.0 mm; the species has the following characters: 1) skin on dorsum bearing small tubercles, especially prevalent in M-shaped mark in scapular region; 2) one row of small tubercles along edge of lower jaw; 3) one small, short tubercle on heel; 4) snout narrow, acuminate, having a long, triangular fleshy proboscis; 5) dorsum dark brown with darker brown markings; 6) posterior surfaces of thighs yellow with broad, vertical dark brown bars (fig. 1D); 7) throat in both sexes white with brown flecks; 8) tadpoles unknown; 9) mating call consisting of one to three polyphasic notes with a rapid pulse rate.

Hyla proboscidea differs from all other members of the group, except *epacrorrhina*, by having a fleshy proboscis. *Hyla epacrorrhina* has dark and light mottling on the posterior surfaces of the thighs, whereas *proboscidea* has broad, vertical dark and light bars.

Distribution. — Southwestern Guiana through southern and central Surinam to central French Guiana.

Remarks. — This species remains rare in collections; seven specimens

are known from four localities. Six males have snout-vent lengths of 33.0-39.8 (mean 37.4) mm. All individuals have a well-developed proboscis and broad vertical dark bars on the thighs. According to Lescure (in litt.), the specimen from Saül, French Guiana, had bright green flanks in life.

Hyla rostrata Peters (pl. 1 fig. 4)

Hyla rostrata Peters, 1863, M. Ber. k. Preuss. Akad. Wiss. Berlin, 1863: 466. — Holotype: ZMB 3175, from Caracas, Venezuela.

Hyla foliamorta Fouquette, 1958, Herpetologica, 14: 125. — Holotype: TNHC 23109, from 11 kilometers north of Miraflores Locks, Canal Zone, Panamá (synonymy fide Rivero, 1968: 133).

Hyla rostrata; Rivero, 1968, Acta Biol. Venezuel., 6 (3/4): 133.

Diagnosis. — This is a large species; males attain a snout-vent length of 45.7 mm, and the largest female is 48.0 mm in snout-vent length; the species has the following characters: 1) skin on dorsum nearly smooth, bearing a few low tubercles; 2) no tubercles along edge of lower jaw; 3) no tubercles on heel; 4) snout broad, acutely rounded, lacking fleshy proboscis; 5) dorsum tan or brown with darker brown markings; 6) posterior surfaces of thighs orange or dark yellow with broad, vertical dark brown bars; 7) throat in breeding males brown or dark grey; 8) tadpoles greenish yellow with black spots; fins deep; tail xiphicercal; labial papillae present ventrally; third lower tooth row subequal in length to others and bearing small teeth; 9) mating call consisting of single moderately long, low-pitched note.

Hyla rostrata differs from all other members of the group by having a smooth dorsum, dark throat, rather blunt snout, and no row of tubercles on the margin of the lower jaw.

Distribution. — Sub-humid, non-rainforest environments from central Panamá across northern South America to French Guiana; Cauca Valley in Colombia and llanos of Colombia and Venezuela.

Remarks. — Rivero (1968) and Duellman (1970a) discussed the synonymy and distribution of the species in South America, and Duellman (1970b) presented detailed data on the species in Panamá. Notes on one Venezuelan specimen (KU 133443) show the coloration in life to be similar to that of specimens from Panamá: "Dorsum tan; interorbital triangle darker brown; bright yellow on anteroventral thigh with black bars on thigh; throat dark grey; belly white with small grey flecks. Iris silvery gold with fine black flecks" (Stephen R. Edwards, field notes, 27 May 1970).

DISCUSSION

Each of the six species is distinguished by structural features, coloration, and mating call. Usually these differences are not correlated. For example,

a fleshy proboscis is present in two species, *H. proboscidea* and *epacrorrhina*, but the latter and *egleri* differ from the other species by having mottled, instead of barred, thighs. A phenetic analysis of characters 1-7 in the preceding diagnoses reveals that *H. rostrata* differs from the other species in 4-6 (mean 5.0) characters; values for the other species are lower: *H. boulengeri* 1-4 (2.0), *egleri* 1-5 (2.4), *epacrorrhina* 2-6 (3.2), *garbei* 1-4 (2.4), and *proboscidea* 1-6 (2.8).

Analyses of mating calls indicate that interspecific differences occur in various parameters; for example, the calls of *H. garbei* and *proboscidea* are alike in duration and pulse note, but notably different in note repetition rate and pitch of emphasized harmonics, whereas *boulengeri* and *rostrata* have the same note repetition rate but differ in duration, pulse rate, and pitch (table 1, plates 2 and 3).

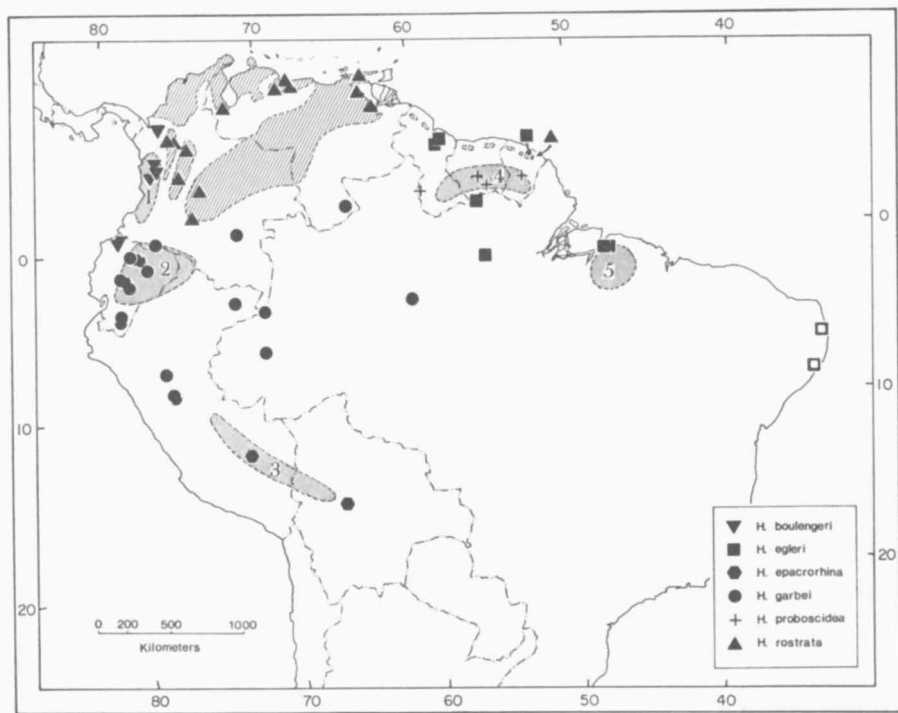


Fig. 3. Distribution of the members of the *Hyla rostrata* group in South America. Solid symbols indicate localities from which specimens were examined; open symbols are literature records. See Duellman (1970b, figs. 78 and 79) for distributions in Central America. Hypothesized Pleistocene forest refugia are shaded: 1 = Chocó, 2 = Napo, 3 = Perú, 4 = Guiana, 5 = Belém. Non-forest environments in northern South America are indicated by diagonal lines (Haffer, 1967).

TABLE I
 Characteristics of Mating Calls of Frogs in the *Hyla rostrata* Group. (N = number of individuals/number of notes; observed ranges in parentheses below means; means only given for note repetition rate and emphasized harmonics)

Species	N	Notes per Call Group	Note Repetition Rate (min.)	Duration (sec.)	Pulse Rate	Emphasized Harmonics (Hz)
<i>H. bouleengeri</i> Central America	8/22	1	0.5	0.35 (0.24-0.47)	101 (80-120)	1600 + 2800
<i>H. bouleengeri</i> Chocó	1/1	1	---	0.50	120	----- 3250
<i>H. eglerei</i>	2/7	4-7 (5.4)	39.5	0.16 (0.13-0.20)	58 (55-60)	720 + 1050
<i>H. epaerorhina</i>	2/5	1	9.8	0.72 (0.65-0.80)	68 (65-70)	1740 + 3760
<i>H. garbei</i>	8/25	1	140.0	0.21 (0.16-0.26)	215 (195-240)	----- 3244
<i>H. proboscidea</i>	1/4	1-3 (1.3)	28.0	0.24 (0.21-0.30)	215 (205-230)	----- 2012
<i>H. rostrata</i>	7/20	1	0.5	0.69 (0.23-0.86)	51 (50-60)	920 + 3050

The uncorrelated nature of the interspecific differences suggests that the species differentiated through isolation in disjunct geographic areas. It is noteworthy that the ranges of five of the species correspond with hypothesized Pleistocene forest refugia in South America (Haffer, 1969, 1970; Vuilleumier, 1971): *H. eglerti* in the Belém refugium; *epacrorrhina* in the eastern Perú refugium; *garbei* in the Napo refugium; *proboscidea* in the Guiana refugium; *boulengeri* in the Chocó refugium and apparently also in the Caribbean Costa Rica refugium. These are the six primary refugia as defined by Haffer (1970). *Hyla rostrata* inhabits subhumid regions of northern South America and has a typical "non-forest" distribution (Haffer, 1967). Conceivably the species of the *Hyla rostrata* group differentiated in the aforementioned forest refugia (*rostrata* being isolated in non-forest environments) during arid phases of the Pleistocene; present patterns of distribution, including one case of sympatry, are the result of expanding humid forests and their anuran inhabitants (fig. 3). *Hyla rostrata* probably invaded Central America during an arid phase, whereas *boulengeri* probably invaded during an earlier humid phase.

If characters such as the fleshy proboscis, tubercles on the heels, and tubercles on the jaws are considered to be derived, *Hyla rostrata* seems to be the most primitive member of the group. *Hyla proboscidea* and *epacrorrhina* possess the largest number of derived character states, whereas the other three species are intermediate. However, until the larval and osteological characters are known for all members of the group and the taxonomy of related groups is thoroughly investigated, a phyletic scheme is not feasible.

SPECIMENS EXAMINED

All specimens examined from South America are listed below; literature references for specimens from other localities and not examined by me are given in parentheses. In addition to 318 specimens from South America, I have examined 228 specimens from Central America. Localities for Central American specimens were given by Duellman (1970b: 699, 711).

Hyla boulengeri. — COLOMBIA: *Chocó*: Andagoya, FMNH 81854-5, LACM 46826-9, near Playa del Oro, upper Río San Juan, LACM 46842; 2 km above Playa del Oro, upper Río San Juan, AMNH 85373-4; Quibdó, LACM 46830-41; Tado, Río San Juan, LACM 46843-50. *Cordoba*: Río Manso, BMNH 1964.942. ECUADOR: *Esmeraldas*: Carondelet, UIMNH 53584; San Javier, UIMNH 55653-4.

Hyla eglerti. — BRASIL: *Alagoas*: Rio Largo (Lutz, 1968: 10). *Pará*: Belém, MNRJ 4055; Ipean, 3 km E Belém, KU 127565-617, 128365-81, 130030, 130154 (tadpoles); Óbidos, KU 130031-6; Utinga, 5 km E Belém, KU 127618-30, 127988-9 (skeletons), 127992-3 (skeletons), 128386. *Paraíba*: Mamanguape (Lutz, 1968: 10). FRENCH GUIANA: *Inini*: Crique Gabrielle, LG 676. GUYANA: *East Demerara*: Djakara Creek, near Atkinson

Field, CEN 68/58-60; 5 km E Soesdyke, CEN 68/71. SURINAM: *Nickerie*: Sipaliwini, RMNH 16908.

Hyla epacrorhina. — BOLIVIA: *Cochabamba*: 6.5 km N Chipiriri, KU 136310. PERÚ: *Cuzco*: Pilcopata, AMNH 85382, KU 139242-5, 139247, 139249, RMNH 16922.

Hyla garbei. — BRASIL: *Amazonas*: Maráos, NHMG 481; Rio Jurua, Eirunepé, MZUSP 277. COLOMBIA: *Amazonas*: Leticia, KU 124788. *Putumayo*: Puerto Asís, USNM 152278. *Vaupés*: Río Piraboton, FMNH 82008. ECUADOR: *Napo*: Limón Cocha, KU 99194-6, UIMNH 64857, 90065, 90801; Puerto Libre, Río Aguarico, KU 123118-9; Puerto Ore, Río Aguarico, KU 123120; Santa Cecilia, KU 104846-7, 109358-60, 111680-3, 123114-7, UMMZ 129319 (4). *Pastaza*: Mera, KU 120981-1001; Sarayacu, KU 120977-80; Shell Mera, CAS 94223, KU 99193. *Zamora-Chinchipe*: 2 km SW Cumaraza, KU 121002-7; Zamora, KU 121008-9. PERÚ: *Huánuco*: Tingo María, CAS 85153, MJP 654, USNM 193106 (4), 193107 (2), 193108-10; 4 km S Tingo María, USNM 193111; Tocache, Río Huallaga, MJP 646. *Loreto*: Pebas, CAS-SU 3156, 6324, 12643; Transval, near Pebas, CAS-SU 3157. VENEZUELA: *Amazonas*: Costa del Iguapo, Alto Orinoco.

Hyla proboscidea. — FRENCH GUIANA: *Inini*: Saül, LG 622. GUYANA: *Rupununi*: Shudi-kar-wau, AMNH 49248-9, 49254, KU 140900. SURINAM: *Brokopondo*: Upper Gran Rio, ZMA 5701. *Marowijne*: Paloemeu, RMNH 12517.

Hyla rostrata. — COLOMBIA: *Antioquia*: Caceras, Río Cauca, ZMB 9514; El Real, USNM 127865-6. *Meta*: Boca del Cano Losada, USNM 152186-8; Puerto Lopez, AMNH 75698. *Santander*: Cimitarra, Río Guayabito, USNM 152285. *Tolima*: Mariquita, FMNH 81824-5. FRENCH GUIANA: *Inini*: Crique Gabrielle, LG 675. SURINAM: no specific locality, ZMB 7727. VENEZUELA: *Aragua*: Maracay, ZSM 163/26 (28), 266/29 (10), 267/29, (11), 268/29, 300/29, 104/30 (4), 105/30 (2), 85/34. *Carabobo*: Puerto Cabello, ZMB 3175. *Monagas*: Barrancas, UIMNH 61489, 61995; 13 km S Maturín, KU 129844. *Sucre*: between Tunapui and Bojoral, KU 133443. *Tachira*: between Apure and Tachira, UPR-M 2723-5.

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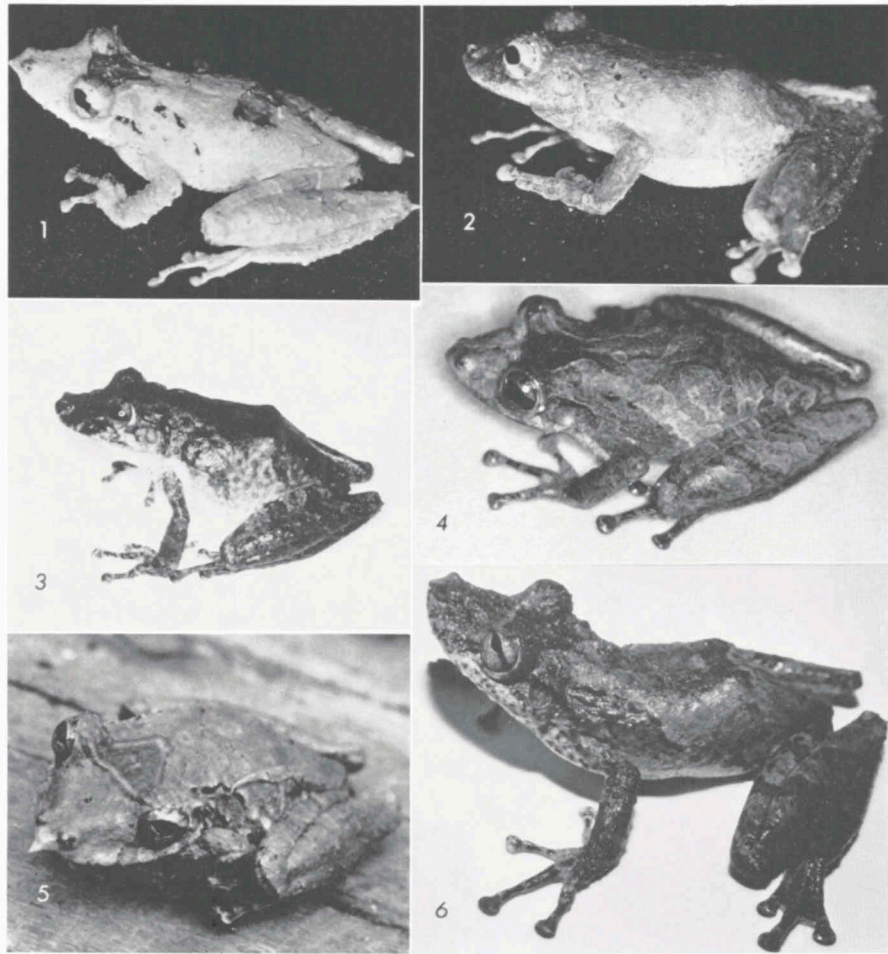
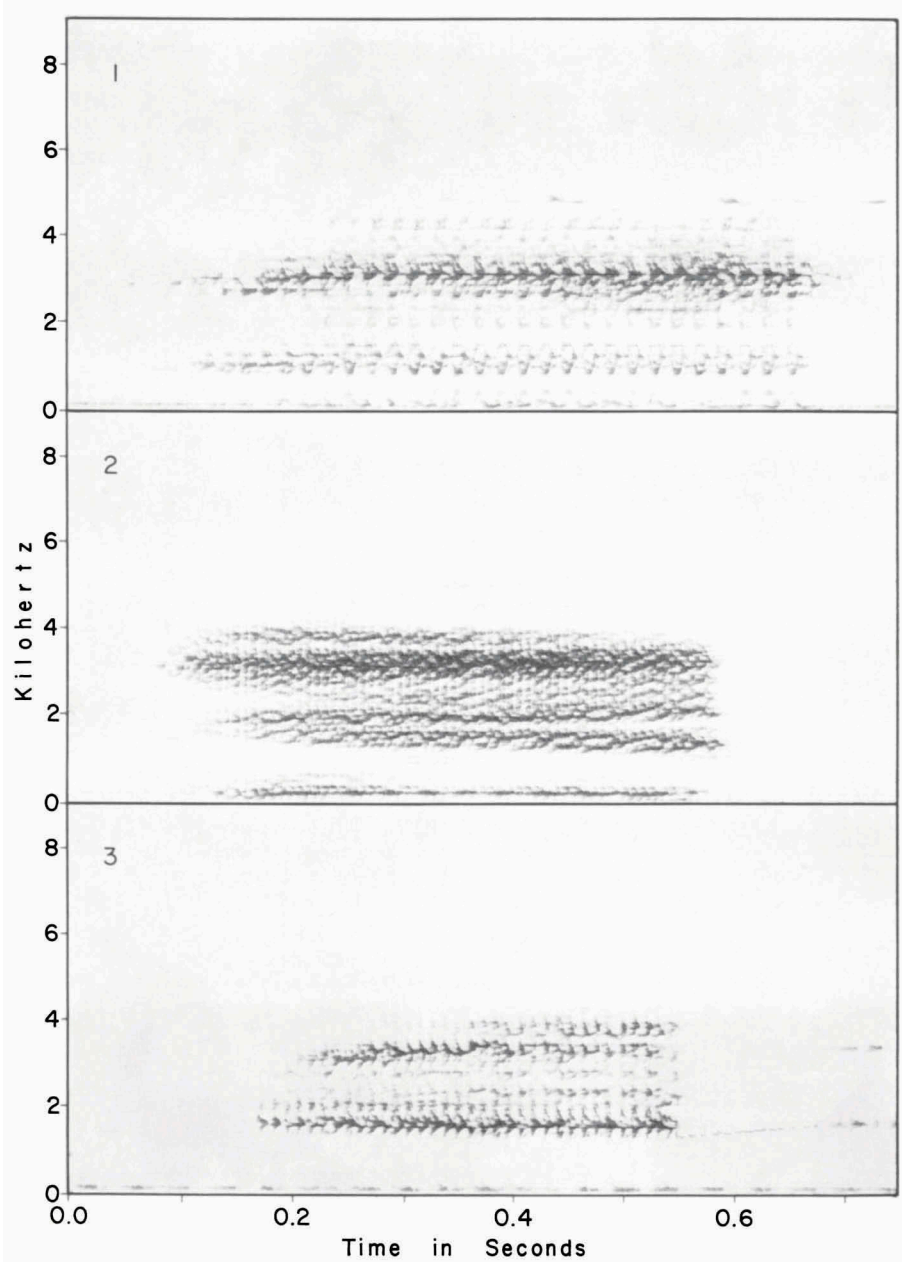
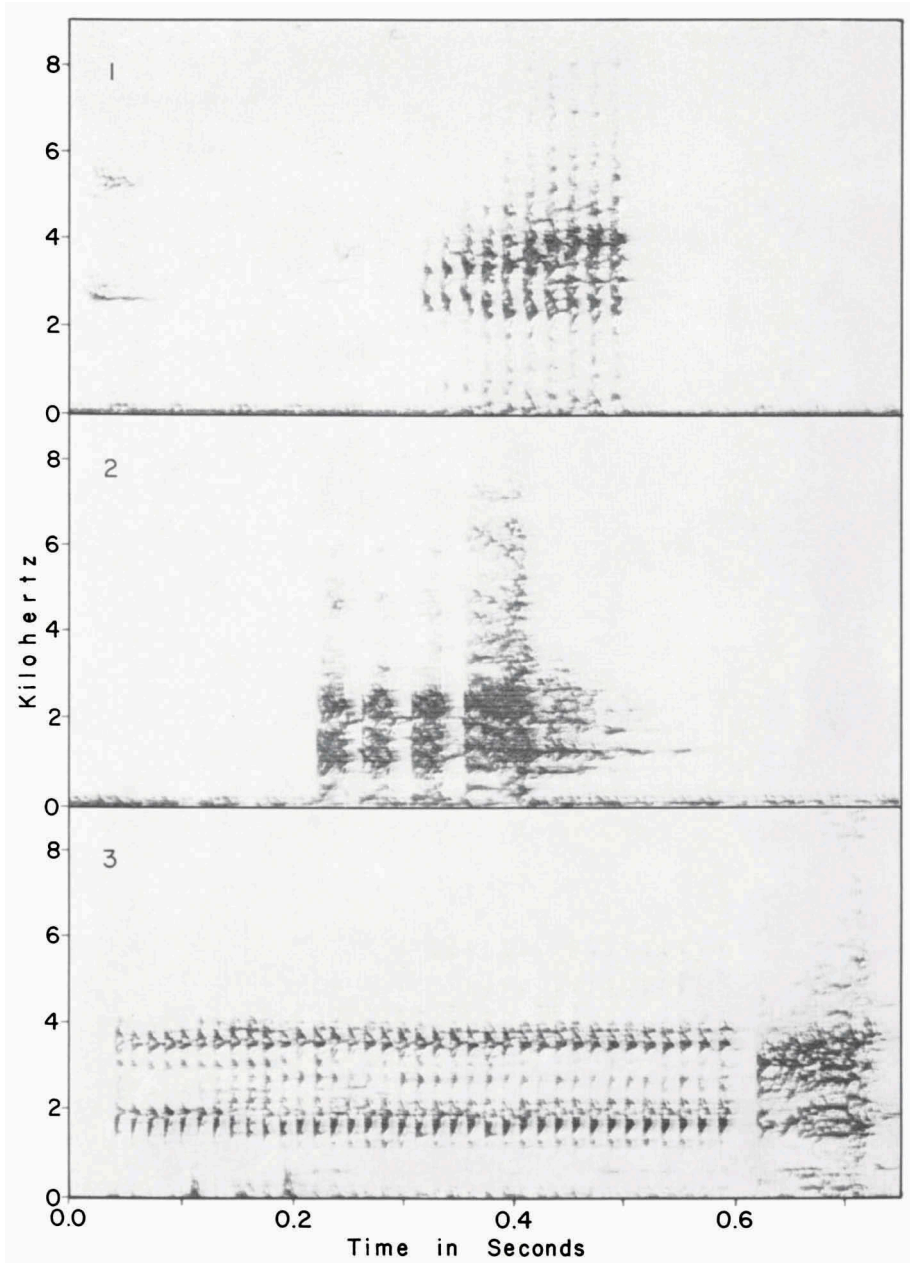


Fig. 1. *Hyla epacrorrhina*, KU 139242; fig. 2. *Hyla garbei*, KU 111680; fig. 3. *Hyla egleri*, KU 128365; fig. 4. *Hyla rostrata*, KU 77164; fig. 5. *Hyla proboscidea*, LG 622; fig. 6. *Hyla boulengeri*, AMNH 85373. All approx. 1.5 X.



Audiospectrograms of mating calls of the *Hyla rostrata* group: fig. 1. *Hyla rostrata*, KU Tape 288; fig. 2. *Hyla boulengeri*, AMNH 85373; fig. 3. *Hyla garbei*, KU Tape 683. Narrow band analysis.



Audiospectrograms of mating calls of the *Hyla rostrata* group: fig. 1. *Hyla egleri*, KU Tape 907; fig. 2. *Hyla proboscidea*, LG 622; fig. 3. *Hyla epacrorhina*, KU Tape 1077. Narrow band analysis.