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A New Species of *Hyla* from Cerro Colorado, and Other Tree Frog Records and Geographical Notes from Western Panama

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ABSTRACT

Significant new records of tree frogs in western Panama include *Hyla graceae*, new species—a medium-sized (33–41 mm. SVL) brown frog with conspicuous white or yellow dorsolateral stripes. Adult and larval characters and breeding behavior seem to ally *H. graceae* with *H. angustilineata* and *H. pseudopuma*. The expanded *pseudopuma* group of *Hyla* is thus comprised of three generalized species, with a combined distribution in the highlands of Costa Rica and western Panama.

Hyla graceae evidently has a range comprising at least 50 km. along the western end of the Serranía de Tabasará, at elevations of 1100–1650 m. Its type locality is Cerro Colorado, situated to the west of the unexplored Cerro Santiago (of which a photograph is presented of the forested summit, showing this mountain to be much lower than previously supposed, about 2100 m. [below tree-line] vs. 2800 m.). Other notable hylids from Cerro Colorado are *Hyla rivularis*, with a range extended about 90 km. from extreme western Panama, and *Gastrotheca nicefori*, a South American species, whose range is extended by 450 km. from the nearest known locality in the Darién highlands of extreme eastern Panama.

Two names are resurrected from synonymy: *Hyla lythrodes* Savage, heretofore known only from the Costa Rican holotype and previously considered a junior synonym of *H. rufoculis*, is confirmed as a valid species of small, red-eyed frog having a changeably brown to green coloration; it occurs in wet forest at 170–800 m. on the Atlantic versant of southeastern Costa Rica and adjacent Panama.

Hyla palmeri Boulenger, is removed from the synonymy of the Amazonian-slope *H. albopunctulata*, for a moderate-sized, green tree frog having a range along the western foot of the northern Andes, and also known from one locality at 600 m. in west-central Panama. At the last locality, *Hyla palmeri* occurs sympatrically with *H. colymba*, the only other member of the *bogotensis* group of *Hyla* known to occur in Central America.

Other species discussed include *Smilisca sordida* and the rare *Agalychnis calcarifer*, from low elevations in Bocas del Toro, and six principally highland species from the Cerro Fortuna area: *Hyla debilis*, *H. lancasteri*, *H. miliaria*, *H. tica*, *H. uranochroa*, and the bromeliad-adapted *H. zeteki*. Except for the rare, giant fringe-limbed species (*H. miliaria*), the aforesaid records from Cerro Fortuna are of Talamancan species at or near the eastern limits of their ranges.

Cerro Fortuna guards the lower end of the high valley (~1000 m.) of the upper Río Chiriquí, which forms a conspicuous break in the mountainous backbone of Panama, as well as a convenient demarcation between the eastern end of the Cordillera de Talamanca and the western end of the Serranía de Tabasará. Although in the Pacific drainage, this highland valley supports extensive Lower Montane Rain Forest under essentially Temperate Wet (Cf) climatic conditions. The physical geography of the upper valley of the Río Chiriquí is briefly described in order to help understand the ecological geography of the herpetofauna.

INTRODUCTION

The Isthmus of Panama sustains a complex herpetofauna on a small land mass of relatively great climatic and topographical diversity. Many of the contained species are rare or secretive, have very small ranges, curious range disjunctions, or tangled taxonomy—or some combination of any or all of the preceding—which has been our excuse for continued collecting and deliberate delay in completing a catalogue of this fauna (Myers, 1972; Duellman and Myers, 1980). Our fieldwork in the late 1960s mainly involved establishing remote camps from boat or on foot in a country having few roads (e.g., see Duellman, 1970, pp. 16–17; Myers, 1969). This work was carried forward sporadically into the

1970s, a decade that provided unprecedented opportunity for reaching previously uncollected places by helicopter or on new roads to areas being opened for reservoirs or other purposes. Consequently, owing to economic development and to an increase in often correlated scientific activity (e.g., environmental surveys), more biologists than ever before have been poking about in places rarely seen by outsiders.

One such place is Cerro Colorado (fig. 1), the site of an enormous copper deposit (Clark, Farrar, and Kents, 1977; Linn et al., "1981"[1982]), situated in the Serranía de Tabasará just south of the continental divide at approximately 81°48' west longitude. This

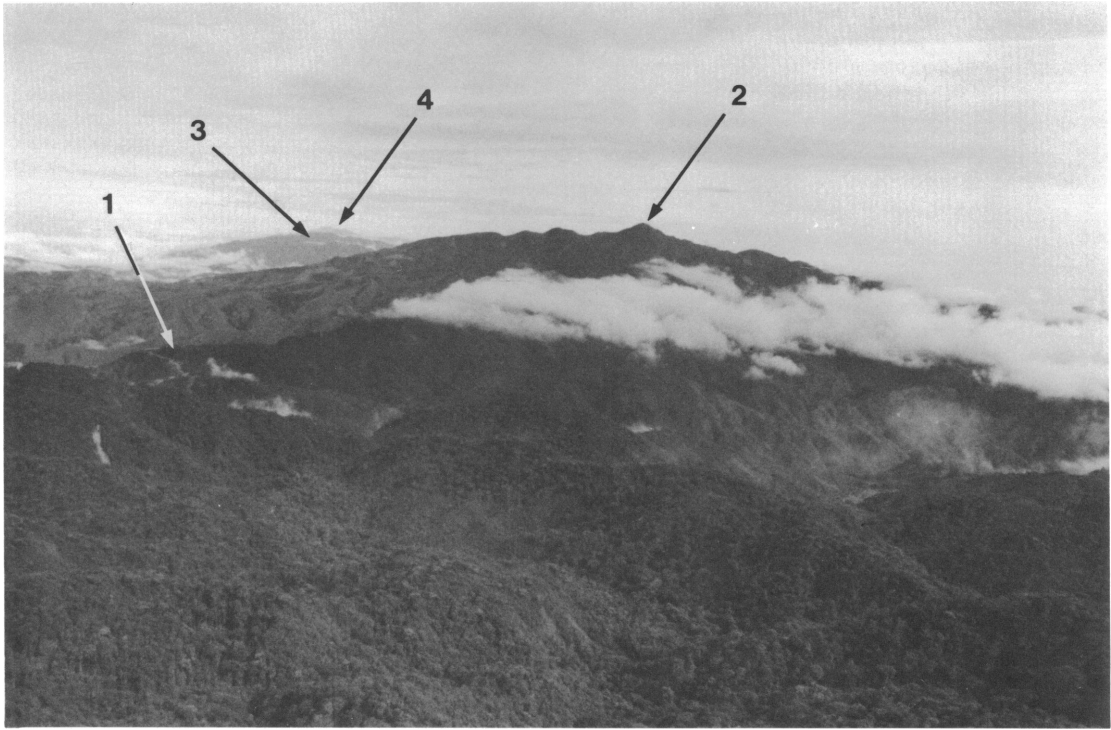


FIG. 1. Cerro Colorado area, Serranía de Tabasará, western Panama. Looking northwestward along continental divide, from a helicopter at an altitude of nearly 2000 m. Identifiable features include: 1. Cerro Colorado, at location of proposed open-pit copper mine; new access road from San Felix is visible in center left. 2. Cerro Sagui (C. Ratón), 2400 m., very likely the "cone-shaped peak" seen by members of an American Museum expedition in 1924 (see Myers, 1969, p. 32). 3. Cerro Chorchá, near western end of Tabasará range. 4. Volcán de Chiriquí (V. Barú) near eastern end of Cordillera de Talamanca. (Photograph by John S. Burt, August 6, 1980.)

section of the western highlands has been biologically unexplored, except for abortive attempts to reach Cerro Santiago³ a short dis-

³ See Myers (1969, pp. 3, 32–33). The unexplored Cerro Santiago was believed to be the second or third highest mountain in Panama, with an elevation of 2826 m. shown on recent maps. Even though uncontrolled map elevations in Panama often are inaccurate (*op. cit.*, p. 2), it was thought that Cerro Santiago would have a summit area above treeline. However, John S. Burt (*in litt.*, 1980–1982) and E. A. Wieselmann flew over the area in both a helicopter and a fixed-wing aircraft and concluded that there are no mountains higher than about 2400 m. in this part of the Serranía de Tabasará, and that Cerro Santiago itself is only about 2100 m. high (fig. 2), as also borne out by a preliminary (unpubl.) 1:50,000 topographic map. Mr. Burt described what he and Wieselmann identified as Cerro Santiago as "two high points on the continental divide, separated by a comparatively flat swale covered with an extremely dense canopy, in

tance to the east (fig. 2). Some herpetological materials are now available from Cerro Colorado. Grace M. Tilger obtained specimens for the American Museum in April 1978, and in April and August 1979, and a collection subsequently was made by Ronald H. Pine for the National Museum of Natural History, Smithsonian Institution.

Among the specimens obtained by Tilger is a distinctive new species of tree frog, which is the principal subject of this paper. We also comment on some other specimens obtained since the Middle American hylid fauna was surveyed by Duellman (1970), in order to add a few species to the Panamanian list, to call

an area that has obviously never heard the ring of a machete but which is only about five kilometers from the Cerro Colorado access road."



FIG. 2. Cerro Santiago, Serranía de Tabasará, western Panama. Looking north over forested summit, from a helicopter at an altitude of about 2100 m. Valiente Peninsula (arrows) can be seen in background, behind Chiriquí Lagoon. The broad summit of Cerro Santiago might give the appearance of a volcano protruding above clouds, when a rare view can be gained from an ocean-going launch (Myers, 1969, p. 3), but it is considerably lower than shown on standard maps; see fn. 3. (Photograph by John S. Burt, August 6, 1980.)

attention to notable range extensions in the western half of the country, and to correct the taxonomic allocations of some populations. See Duellman (1970) for synonymies not given herein.

In addition to new data already presented on Cerro Santiago (fn. 3 and fig. 2), we shall take the occasion of this paper to summarize observations made by Myers on the physical geography of an unusual (for Panama) highland valley, which yielded a number of interesting specimens. The abbreviated discussion is pertinent to an understanding of the amphibian and reptile fauna of the area; additional information will be found in Adames (1977).

ACKNOWLEDGMENTS

We especially thank Ms. Grace M. Tilger for her efforts in obtaining specimens from

Cerro Colorado. Ms. Tilger's work was made possible and facilitated by Mr. John S. Burt, Environmental Officer, and Mr. E. A. Wieselmann, Chief Geologist, Texasgulf Panama, Inc., and Dr. Neal Griffith Smith, Smithsonian Tropical Research Institute. Officials of the Empresa de Cobre Cerro Colorado, S.A., are gratefully acknowledged for their interest and co-operation. Messrs. Burt and Wieselmann additionally shared their unparalleled knowledge of the Cerro Colorado-Cerro Santiago area and Mr. Burt provided the photographs reproduced here as figures 1 and 2. Dr. Smith made the photograph shown as figure 7. Miss Gretchen Bracher rendered the drawings reproduced as figures 4-6. Messrs. Karl-Heinz Jungfer and Wolfgang Utke provided transparencies in support of a range extension of the new frog.

For facilitating other fieldwork in Panama in the last decade, special thanks are due Drs.

Abdiel J. Adames, Pedro Galindo, and Eustorgio Méndez of the Gorgas Memorial Laboratory, Drs. Robert L. Dressler and A. Stanley Rand of the Smithsonian Tropical Research Institute, and Dr. Alwyn H. Gentry, Missouri Botanical Garden. Sincere debts of gratitude also are due Ing. José Arosemena III, General Manager of Petroterminal de Panamá, and Dr. Alberto Perdomo, Co-Director for ecological assessment of the Fortuna Hydroelectric Project for IHRE (Instituto de Recursos Hidráulicos y Electrificación). Licdos. Fernando Crastz and Víctor Martínez, of the University of Panama, helped to further work on the Fortuna Project—from which time the senior author reserves a special memory for the late Mr. Juan Landau, who shared his house and his knowledge in the high, wet valley of the Alto Río Chiriquí.

***Hyla graceae*, new species**

Figures 3–7

HOLOTYPE: AMNH 107966 (field no. 5499), an adult male obtained by Grace M. Tilger on August 23, 1979, near continental divide southeast of Cerro Colorado, approximately 1650 m. elev., Chiriquí Province, Panama. As plotted on an unpublished topographic map (1:20,000) of the area, the type locality lies on a rough construction road (from San Felix) at a point about 4 km. airline southeast of Cerro Colorado and about 0.6 km. due south of the continental divide (border of Bocas del Toro).

PARATYPES: AMNH 107957–107961, KU 192079–192080, all collected by G. M. Tilger on April 15, 1979, on the northern side of Cerro Colorado, near continental divide, 1500–1600 m., Bocas del Toro Province, Panama. An available map (see above) shows the paratypes to be from the drainage area of the Quebrada Alicia, which flows into Río Florez, one of the upper tributaries of the Río Cricamola.

ETYMOLOGY: The name honors Grace M. Tilger, first collector of the new species, in recognition of her many contributions to the collections of the American Museum of Natural History.

DIAGNOSIS: A medium-sized (about 33–41 mm. SVL) brown *Hyla* having a pair of con-

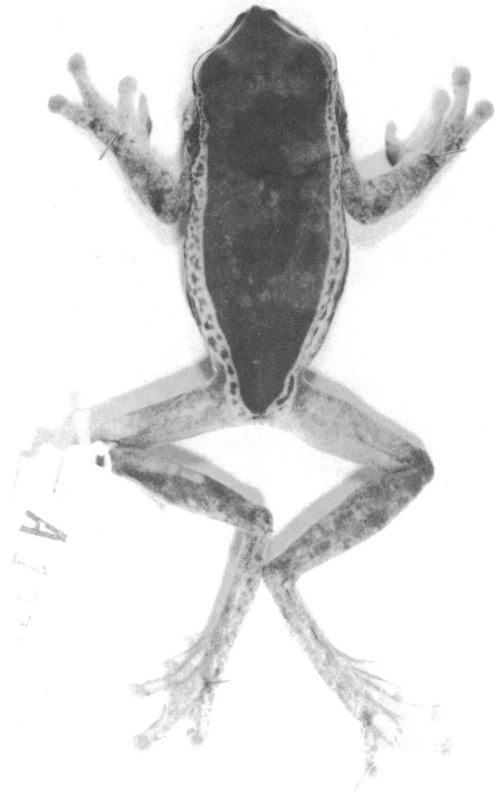


FIG. 3. *Hyla graceae*, new species. Holotype (AMNH 107966), $\times 1.4$.

spicuous white or yellowish dorsolateral stripes. A few other Middle American hylids have pale dorsolateral stripes or lines that extend the length of the body, but these are mostly small species with a yellow or tan dorsum. *Hyla angustilineata* of Costa Rica has a brown dorsum (green in juveniles) and approaches *H. graceae* in size, but it is readily distinguished by its narrower dorsolateral line (a pronounced stripe in *graceae*), by heavy brown flecking on the venter (immaculate in *graceae*), and by the absence of distinct finger webbing (thick basal webbing between fingers II–IV in *graceae*).

MEASUREMENTS (IN MM.) OF HOLOTYPE: Snout to vent 38.7; tibia 19.0; foot from proximal edge inner metatarsal tubercle to tip of longest toe 16.9; head length on the diagonal from tip of snout to angle of jaw 12.9; greatest head width (near angle of jaws) 13.4; width

TABLE 1
Measurements (in Millimeters) and Proportions
of *Hyla graceae*, New Species

Character	7 Males	1 Female
Snout-vent length (SVL)	33.5–38.7 (35.80) ^a	40.5
Tibia length/SVL	0.49–0.57 (0.536)	0.55
Foot length/SVL	0.44–0.50 (0.469)	0.46
Head length/SVL	0.33–0.35 (0.336)	0.34
Head width/SLV	0.34–0.37 (0.356)	0.36
Interorbital distance/ head width	0.30–0.36 (0.327)	0.42
Tympanum/eye	0.42–0.54 (0.490)	0.52

^a Range followed by mean. Measurements after Duellman (1970).

of upper eyelid and width of interorbital area each 4.0; internarial distance 2.5; rear edge naris to anterior corner of eye 3.4; eye opening from anterior to posterior corner 4.6; eye to tympanum 2.7; horizontal diameter of tympanum 2.5.

DESCRIPTION

Seven adult males 33.5–38.7 mm. SVL, one adult female 40.5 mm. SVL (see table 1). Head narrower than to slightly wider than body. In dorsal aspect, tip of snout extended past narial protuberances into a slight point, thus obscuring rounded profile of upper lip. The small tip of snout varying from weakly to noticeably pointed; snout tip tending to be confluent below with a weak vertical rostral keel (scarcely indicated on several specimens). Snout round to truncate in lateral profile. Nares directed dorsolaterally; internarial area nearly flat, not or but very slightly depressed; canthus rostralis angular; loreal region slightly concave; lips moderately thick but barely flared. Eyes directed anterolaterally, length greater than distance from nostril. Weak to moderate dermal fold extending posteriorly from eye, above tympanum, toward insertion of arm, this fold tending to obscure upper edge of tympanum. Tympanum directed slightly posterodorsally, its diameter 42–54 percent of eye length and \approx to distance between eye and tympanum.

Axillary membrane absent. Forearm only slightly swollen; ulnar ridge absent, but ventrolateral edge of forearm with a line of well-spaced, usually very weak tubercles; trans-

verse dermal fold present atop wrist. Hand large (fig. 4A), with moderately long and robust fingers bearing large discs; width of third finger disc \approx tympanum. Subarticular tubercles large, with rounded surfaces; distal subarticular tubercles tending to be bifid on fingers I, III, and IV. Supernumerary tubercles absent distally on fingers, but bases of fingers and palm dense with large, rounded tubercles, with consequently a palmar tubercle and elliptical pollical tubercle being not well differentiated. Prepollex moderately enlarged in males, bearing a generalized horny nuptial excrescence (comprised of minute spinules), extending to thumb disc in some individuals. Fingers with lateral fringes and with thick basal webbing between digits II–IV; webbing formula II 2–3 III 3–2½ IV.⁴

⁴ In this notational device, as originally defined by Savage and Heyer (1967, p. 116; see also 1969, p. 5), "Roman numerals represent fingers or toes [and] Arabic numerals represent the number of phalanges completely or partially free of webbing." Although not stated, it clearly was intended that metacarpals and metatarsals be counted as "phalanges" for this purpose.

In some frogs, the segment of the digit containing the terminal phalanx is expanded into a disc of rather complex morphology (Noble and Jaekle, 1928; Green, 1979; Emerson and Diehl, 1980). It would be arbitrary (and, considering intergroup variation, perhaps difficult) to define the disc apparatus so as to exclude the proximal part of the terminal segment, for which reason we suggest not following Savage and Heyer's notation that "0 indicates that the web reaches to the base of the finger or toe disc [and] 1 indicates that the web reaches the base of the terminal phalanx." To make the webbing formula universally applicable, we would reserve "0" for those frogs in which webbing extends to the very tip of a digit, as for example in some discoglossids and ranids (e.g., Inger, 1954, figs. 36, 49). We use "1" simply to mean that the disc or the entire terminal segment is free of web.

A "1-" might suffice for what Savage and Heyer originally intended to convey by "0," since they suggested using superscript + or - if the web reaches, respectively, the proximal or distal margins of a subarticular tubercle. However, most frogs lack a tubercle at the distal phalangeal articulation (although a distinct subarticular swelling is present in the phyllomedusines for which the webbing formula was originally developed). In any case, such precision is of little value whenever there is an element of subjectivity. Determining degree of webbing sometimes amounts to assigning a point on a smooth curve, as when a deeply emarginate web curves up to join a fringed digit near its tip.

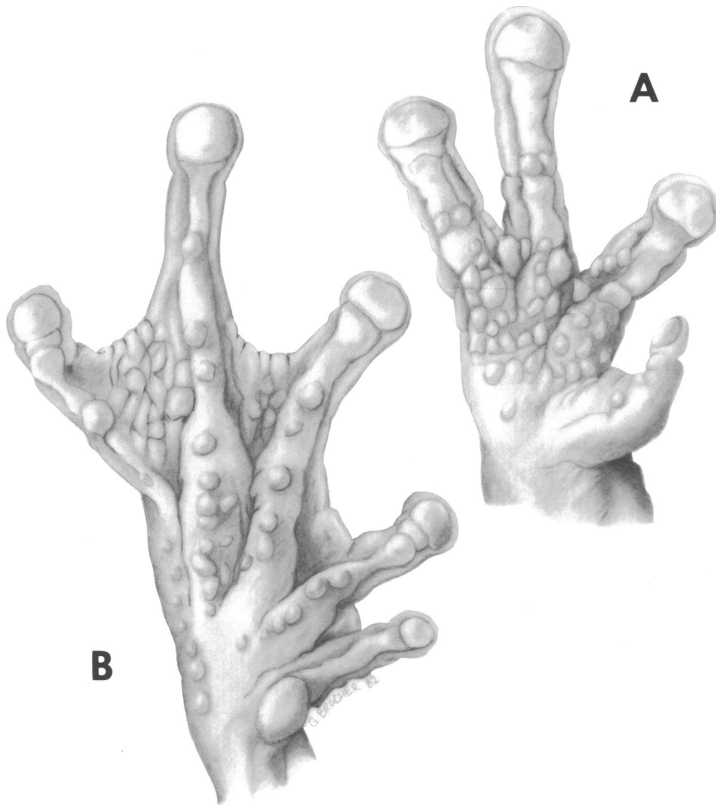


FIG. 4. Hand (A) and foot (B) of *Hyla graceae* (holotype), $\times 5$.

Hind limbs moderately long and slender; tibia 49–57 percent of SVL; foot 44–50 percent of SVL; toe discs slightly smaller than those on fingers. Heel and inner ventrolateral edge of tarsus feebly to moderately tuberculate, lacking distinct tarsal fold. Prominent inner metatarsal tubercle a raised ovoid (but flattened and with free edge on right foot only of holotype); outer metatarsal tubercle absent or not differentiated from small supernumerary tubercles covering bases of toes and plantar surface. Subarticular tubercles large, with rounded surfaces, usually single although sometimes bifid on toes IV and V. Toes with lateral fringes and about one-half webbed (fig. 4B), except web between first and second toes is vestigial; modal webbing formula (with variation in parentheses) I 2–2½ II 1½–3 III 1½(1½–2)–3 IV 3(2½–3)–1½ V.

Skin on venter and proximal posteroventral surfaces of thighs strongly and coarsely granular, becoming weakly granular or feebly

tuberculate on sides of body and sometimes atop arms; skin of dorsum and limbs otherwise smooth; vocal pouch of males coarsely granular like chest, but throat of single female smooth. Anal opening directed posteroventrally from just below level of upper surfaces of thighs, which are coarsely granular below opening; small dermal flap above anal opening. Tongue ovoid to weakly cordiform, not or barely free behind. Prevomerine dentigerous processes narrowly separated, positioned transversely between and well separated from rear margins of ovoid choanae; each process bearing 3–7 teeth in seven males ($\bar{x} = 5.4$), and 6–7 teeth in one female. Vocal slits extending from midlateral or postero-lateral edge of tongue to angle of jaws. Vocal pouch single, subgular, and moderately distensible.

Dorsum and sides of body light to dark grayish brown, unicolor or with some vague dark blotches, and with pair of conspicuous



FIG. 5. Tadpole of *Hyla graceae*, AMNH 107964; total length 28.5 mm.

white or pale grayish dorsolateral stripes, extending from upper edges of eyes and converging to meet on anal flap at end of body. The dorsolateral stripes vary in width from narrow (\approx one-half length of tympanum) to wide ($>$ tympanum length); stripes of some specimens immaculate, in others enclosing small, ill-defined dusky spots (most evident in holotype, fig. 3). Some specimens with a vague pale canthal line, extending along edge of upper eyelid to fuse with body stripe. A dark brown stripe extending along side of head from tip of snout through eye and enclosing tympanum. Upper lip pale grayish to yellowish brown. Limbs paler brown than body (darkest atop shanks), either lacking definite markings or with several irregular and widely separated dark brown crossbands (fig. 7). Groin and rear of thighs unmarked, very pale brown like upper surfaces of thighs. Ventral surfaces white, the venter immaculate but underside of head and palms and soles with a fine dusting of melanophores.

In life, according to color transparencies and collector's notes, the dorsolateral stripes varied from white to pale yellowish on a light to medium bronzy brown body; venter yellow; iris chestnut brown.

TADPOLES

Three tadpoles (AMNH 107964; figs. 5, 6) from the Quebrada Alicia drainage (see Natural History) are in Gosner's developmental stage 25. Their body lengths are 11.3, 10.3, and 9.5 mm. and total lengths are 28.5, 27.2, and 24.0 mm., respectively. The body is robust, widest at midlength, and only slightly wider than deep. In dorsal view the snout is round, and in profile it is inclined anteroventrally from the nostrils. The eyes are small, widely separated, and directed laterally. The nostrils are situated at a point about 40 per-

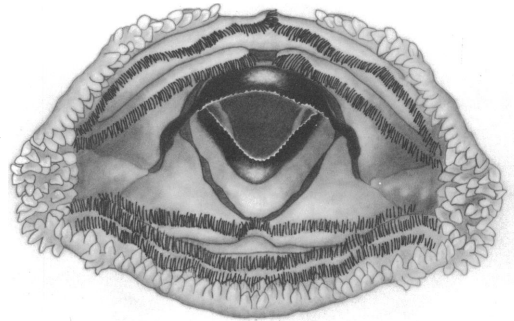


FIG. 6. Mouth of tadpole of *Hyla graceae*, AMNH 107964; width of oral disc 3.3 mm.

cent of the distance from the eyes to the tip of the snout. The opening of the sinistral spiracle is directed posteriorly, just below the midline at about two-thirds of the distance from the snout to the end of the body. The anal tube is short and dextral. The caudal musculature is relatively slender and terminates gradually just short of the tip of the rounded caudal fin. The caudal fins are equal in depth throughout the proximal two-thirds of the tail; each fin is about equal in depth to the caudal musculature. The dorsal fin does not extend onto the body.

In preservative, the body is dark brown above and grayish tan below. The caudal musculature is cream, and the fins are translucent. Numerous dark brown blotches are present on the caudal musculature and dorsal fin, and a few dark flecks are present on the ventral fin.

The mouth is ventral and directed anteroventrally. The mouth is relatively small and has weak lateral folds. The median part of the upper lip is bare; otherwise the lips are bordered by two irregular rows of small papillae. Additional papillae are present in the lateral folds. The well-developed beaks bear extremely fine serrations. The upper beak is in the form of a broad arch with long lateral processes, and the lower beak is broadly V-shaped. There are two upper and three lower rows of denticles. The first upper row is arched outward medially so as to extend onto the anteromedial lip; the second upper row is narrowly interrupted medially. The lower rows are complete and nearly as long as the upper rows.

NATURAL HISTORY

The collector's observations show that *Hyla graceae* is at times active by day. Diurnality is quite unusual among *Hyla*, even in such cool, wet habitats as occupied by this species. The type specimens are from an area of montane rain forest, the character of which in western Panama is profoundly influenced by elevation and orographic rain and mist from the windward (Atlantic) side of the central cordilleras, causing development of "ridge-top cloud forest" along the continental divide (Myers, 1969).

One paratype was in a puddle on a muddy road by day. The frogs were breeding during the late morning of April 15, at a small headwater stream of the Quebrada Alicia, in forest just below the continental divide, as evidenced by an amplexing pair (fig. 7) and two males sitting in the stream. The breeding site was a narrow stream with a clay and gravel bottom of low gradient. Eggs (AMNH 107964) thought by the collector to belong to this species were attached to emergent vegetation at the edge of the stream, where several tadpoles also were collected. On a return visit in August, the breeding site was found to have been greatly disturbed by forest clearing resulting in siltation from the adjacent construction road (G. M. Tilger, personal commun.).

Two paratypes were found at night at the edge of a second small headwater stream of the Quebrada Alicia. The holotype was found by day, hidden in a bromeliad on the ground.

It seems that the breeding season must be long (or sporadic). At a site some 50 km. northwest of the type locality, where breeding was observed in April, two male *Hyla graceae* were found calling on the night of October 11, 1981. The calling frogs were sitting at the edges of two small pools (~50 cm. in diameter, 6–7 cm. deep), which appeared to be part of a small stream at times of heavy rain (*vide* Karl-Heinz Jungfer, *vide infra*).

RELATIONSHIPS AND DISTRIBUTION

Frogs of the genus *Hyla* are represented by many species in the highlands of Costa Rica and Panama. Most of these breed in streams and have tadpoles with either enlarged mouths with numerous and/or extensive rows



FIG. 7. *Hyla graceae*, new species, $\times 1$. Paratype specimens (AMNH 107957 δ , 107958 ♀) found in amplexus by day. From color transparency by Neal Griffith Smith.

of denticles (*Hyla rivularis*, *pictipes*, *salvadorensis*, and *bogotensis* groups) or funnel-shaped mouths and long slender tails (*Hyla uranochroa* group). Members of the *Hyla zeteki* group breed in arboreal bromeliads and have tadpoles with reduced mouthparts. The scarcity of standing water for breeding probably precludes many lowland species that normally breed in temporary or permanent ponds from invading higher elevations. Only one group of *Hyla* does breed in quiet water at moderate elevations in Costa Rica and western Panama; this is the *Hyla pseudopuma* group, comprised of *Hyla pseudopuma* and *H. angustilineata* (Duellman, 1970, p. 261), to which we now add *Hyla graceae*. Natural ponds are few and far between in the narrow and steep Serranía de Tabasará, but it may be pertinent that breeding sites of *H. graceae* included a nontorrential, low-gradi-

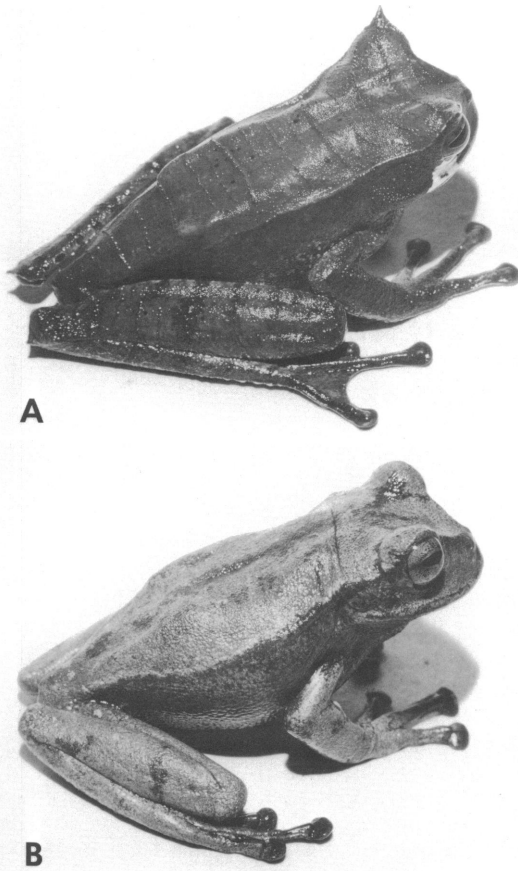


FIG. 8. Central American species of *Gastrotheca* (marsupial frogs). A. *Gastrotheca ceratophrys* (AMNH 90980, Cerro Malí, Darién), a species widespread in Panama and probably also occurring in southeastern Costa Rica. B. *Gastrotheca nicefori* (AMNH 90986, Cerro Tacarcuna, Darién), a South American species that also occurs in the Darién highlands and at Cerro Colorado in western Panama.

ent section of a small headwater stream, and small isolated pools in an intermittent streamlet. It would not seem a great ecological shift from these situations to highland ponds. In any case, *Hyla graceae* does appear to be a member of the *Hyla pseudopuma* group.⁵

⁵ There is an error in the definition of the *Hyla pseudopuma* group; Duellman (1970, p. 262) stated: "A distinct tarsal fold is present . . ." However, in the descriptions of the species the tarsal fold was characterized as weak or absent, as it is in *Hyla graceae*.

The general size, habitus, skin texture, amount of webbing, and nature of nuptial excrescences in the males of *Hyla graceae* are all similar to the conditions known for *H. pseudopuma* and *H. angustilineata*. Furthermore, the well-ossified skull, with quadra-tojugals present, allies it with the group. The tadpoles are nearly identical with those of *H. pseudopuma*, except for the anterior projection of the first row of denticles onto the upper lip.

The *Hyla pseudopuma* group contains generalized highland species. The group is defined by character states that are primitive in comparison with those states that define other groups in Central America. As such, the group is definable phenetically but not cladistically. A plesiomorphic group may of course be a monophyletic group even if synapomorphies seem to be lacking or have not been identified. We think that the *Hyla pseudopuma* group probably does form a monophyletic assemblage and that *Hyla graceae* is a member of that assemblage, but these are matters that deserve critical attention whenever additional comparisons can be made.

As final typescript was being prepared for this paper, we received for identification transparencies of *Hyla graceae* from Karl-Heinz Jungfer, who reported (letters, Feb. 2, March 3, 1982) that he and Wolfgang Utke had found the species some 50 km. northwest of the type locality, at an elevation of 1100 m. in the highland valley of the Río Chiriquí (for a description of this valley, see section on the Geography of the Cerro Fortuna Area). Thus, the range of *Hyla graceae* includes at least the western end of the Serranía de Tabasará (as defined herein, see fn. 8). As presently understood, *Hyla graceae* is distributed allopatrically to other members of its group, although *H. pseudopuma* occurs as far east as Boquete, less than 25 km. northwest of the new locality provided by Messrs. Jungfer and Utke.

OTHER NOTEWORTHY HYLIDS FROM CERRO COLORADO

In addition to the type series of *Hyla graceae*, Tilger obtained specimens of three other montane species. One is the curious horned frog, *Hemiphractus fasciatus* W.

Peters, previously discussed by Myers (1966) and Duellman (1970) under the name *Cerathyla*, or *Hemiphractus panamensis* Stejneger (synonymy after Trueb, 1974, pp. 28–29⁶). This frog—notable for its bizarre appearance and propensity to bite—is now known to be widely distributed in wet upland forest throughout Panama. It is expected but not yet found in Costa Rica, occurring from extreme western Panama to northwestern Ecuador.

The remaining two species, discussed below, represent substantial range extensions, one from extreme eastern Panama and the other from the extreme western part of the country. Such records are indicative of the complicated mixing of Central American and South American elements on the Isthmus of Panama, and should not be used to attribute particular biogeographic significance to single localities.

Gastrotheca nicefori Gaige

Figure 8B

Originally described from Colombia, this frog was thought to enter Central America only in the Darién highlands of extreme eastern Panama, where specimens were collected by Myers between 800 and 1100 m. in the Serranía de Pirre and the Cordillera de Juradó southeast of Serranía del Sapó (see Duellman, 1970, pp. 158–160) and, more recently, at 1540–1660 m. on Cerro Tacarcuna in the Serranía del Darién (AMNH 90986–90987). Consequently, a specimen caught by Grace M. Tilger at Cerro Colorado came as a considerable surprise. This record from the Serranía de Tabasará represents a straight line (over the Gulf of Panama) range extension of about 450 km. westward from the nearest locality in eastern Panama.

We have not heard the call⁷ of this species

⁶ The species *H. fasciatus* was originally described from Amazonian Ecuador, but Trueb (*loc. cit.*) believed that the type locality must be in error. If that view is correct, the type specimen might well have been obtained in western Panama, where the purported collector—Moritz Wagner—traveled extensively (other discussion and citations in Myers, 1982, p. 8).

⁷ The call of *Gastrotheca nicefori* is a drawn out, chicken-like “bruck,” followed by two or usually three similar but shorter notes, with the call from one indi-

vidual sometimes seeming to trigger a “chorus” that may pass wavelike through a local population (e.g., up a mountain gully). Thus, the call is quite different from that of Panamanian *G. ceratophrys*, whose call, usually heard at lower elevations, is a loud “bop” (audiospectrograms in Duellman, 1970, pl. 36).

in the intervening territory of central Panama, although we would not now be surprised to find the species in any wet upland, particularly in the few areas above 800 m. As now known, *Gastrotheca nicefori* and *G. ceratophrys* are broadly sympatric in Panama, although some elevational separation seems evident, with *ceratophrys* occurring at known elevations of 40 to 910 m. and *nicefori* at 800 to 1660 m. These are brown frogs of distinctive appearance (fig. 8). The enigmatic *Hyla splendens* O. Schmidt (1857)—purportedly collected in western Panama by Warszewicz ca. 1850—has been assigned to *Gastrotheca* by Duellman (1970, p. 651). Although *G. splendens* probably is a South American frog whose identity is to be determined (Savage and Heyer, 1969, p. 63; Duellman, *loc. cit.*), the possibility cannot be completely excluded that *Gastrotheca splendens* represents a third species of the genus in Panama. If so, *G. splendens* presumably would be immediately distinguishable from brown *G. nicefori* and *G. ceratophrys* by a metallic green or yellowish green color (in life, “auf dem Rücken ein gelbgrünlicher Metallschimmer” [Schmidt, 1858, p. 245]).

NEW RECORD: AMNH 106564, eastern slopes Cerro Colorado, 1600 m., near continental divide, Bocas del Toro, Panama.

Hyla rivularis Taylor

Figure 9

A specimen from Cerro Colorado, Serranía de Tabasará, extends the range about 90 km. eastward from localities in the Cordillera de Talamanca of extreme western Panama (Duellman, 1970, map on p. 288). It was found at night in low vegetation along a forest trail, at about the same place as the preceding specimen of *Gastrotheca nicefori*.

The specimen assigned to *H. rivularis* is an immature male of 24.5 mm. SVL. In life, it was blue-green above and yellow below (G. M. Tilger, field notes). Except for a few dark dots, the body in preservative is uniformly

vidual sometimes seeming to trigger a “chorus” that may pass wavelike through a local population (e.g., up a mountain gully). Thus, the call is quite different from that of Panamanian *G. ceratophrys*, whose call, usually heard at lower elevations, is a loud “bop” (audiospectrograms in Duellman, 1970, pl. 36).

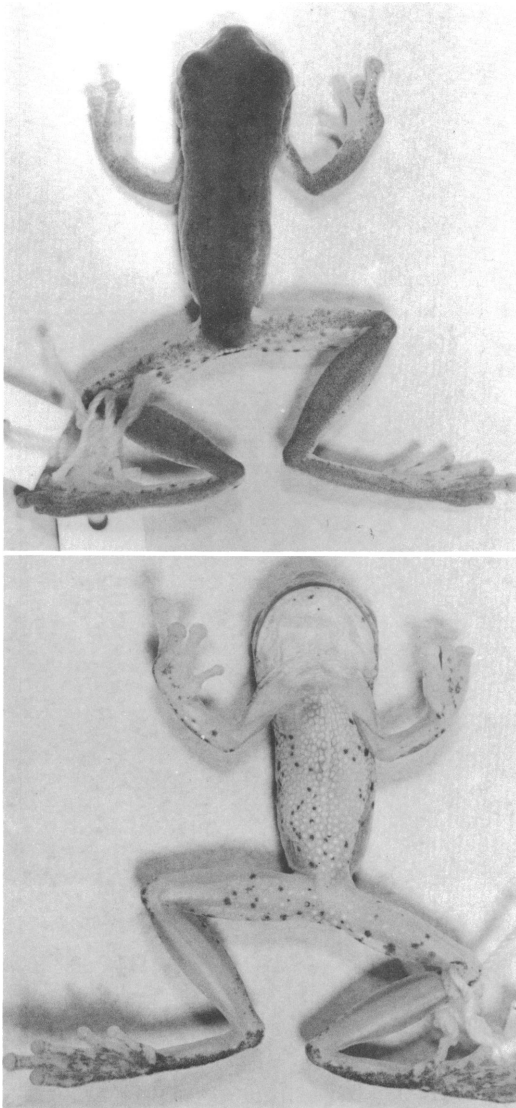


FIG. 9. *Hyla rivularis*, dorsal and ventral views of immature specimen (AMNH 107965) from Cerro Colorado.

bluish gray and the limbs light brown; the supra-anal warts are white, forming a transverse white line; the thighs above and below, and the venter, are conspicuously dotted with dark brown; the palms and especially the soles have a suffusion of dark pigment.

Hyla rivularis is normally a tan or brown frog in life (Duellman, 1970, p. 286, color pl. 53), although areas of green pigmentation have been observed on some individuals

(Savage and Heyer, 1969, p. 30). We do not know whether the blue-green body of the present specimen is correlated with immaturity or geography.

NEW RECORD: AMNH 107965, eastern slopes Cerro Colorado, 1600 m., near continental divide, Bocas del Toro, Panama.

GEOGRAPHY OF CERRO FORTUNA AREA, UPPER RÍO CHIRIQUÍ

In February 1976, one of us (CWM) participated in an environmental survey involving the Fortuna Hydroelectric Project (Adames, 1977). Work was conducted principally on the northeastern base of Cerro Fortuna, at a proposed dam site on the upper Río Chiriquí (about 23 km. NNE Gualaca, Chiriquí Prov.), at about 1000 m. above sea level. From this point, the Chiriquí River skirts the northern side of Cerro Fortuna and then rushes southward down open, sun-exposed slopes to the lowlands, discharging into the Pacific Ocean southeast of David. Before commenting on the species collected in the wet forest at 1000 m. and above, it is pertinent to discuss briefly the physical geography and ecology of the upper valley of the Río Chiriquí.

The upland valley (fig. 10) of this river, particularly the westerly aligned section from 82°08' to 82°17'W, forms a pronounced break in the mountainous backbone of Panama. The subdivisions of the central cordillera are not well established cartographically or even locally, but the high valley of the Río Chiriquí might conveniently be considered to delimit the eastern end of the Cordillera de Talamanca and the western end of the Serranía de Tabasará⁸—which end-to-end carry the

⁸ This two-part division of the central cordillera is suggested as probably being adequate for most biogeographic considerations, although there is little precedence for using the name "Serranía de [or del] Tabasará" so far to the west. Terry (1956, pp. 9–10) terminated the Talamanca Range with the Volcán de Chiriquí at 82°30'W; he defined a "central part" of the cordillera (including the highland valley in question) as extending east to the 82nd meridian; the designation "Serranía de Tabasará," a name derived from the Río Tabasará in eastern Chiriquí, was thus used in its original sense for the more eastern portion of the western cordillera (including the Cerro Colorado–Cerro Santiago area, figs. 1–2).



FIG. 10. View across narrow, downstream end of upper valley of the Río Chiriquí—looking northwest toward eastern end of Cordillera de Talamanca. This highland valley (about 1000 m. above sea level) forms a break between the Talamanca Range and more eastern parts of the central cordillera, including the Serranía de Tabasará (see fn. 8), which carries the continental divide toward central Panama. (Photograph by C. W. Myers, March 4, 1976, from 1170 m. elev. on east slope Cerro Fortuna; conical hill on left is Cerro Pinola.) See also figure 24.

continental divide through western Panama. These mountains are virtually unbroken up to the 1200-m. contour, but the continental divide dips lower due north of the broad, upper part of the high Río Chiriquí valley, which then narrows funnel-like downstream toward the dam site at the northern base of Cerro Fortuna. This aspect of the topography profoundly influences the climate and vegetation of the upland valley. Ascending air currents on the Atlantic versant spill over the low section of the continental divide before losing most of their moisture orographically, and this moist air is funneled westward with increasing force through the upper Río Chiriquí valley. The dynamic interaction of winds and topography was easily visualized at the lower, narrow end of the Fortuna Valley. At

ground level, prevailing winds were blowing consistently from the east, often in strong gusts. These winds carried frequent *bajareque* (wind-driven mist characteristic of some highlands), and even the heavier rainfall had a strong horizontal component as it drifted down valley from the east, that is, from the direction of the low continental divide at the upper end of the valley. In contrast, that part of the divide adjacent to (due north of) the lower end of the valley is relatively high (1900–2000 m.), and clouds spilling over this part of the divide were moving southward, at a right angle to the ground-level winds. These clouds, which had already lost much moisture on the Atlantic versant, frequently tended to dissipate as they crossed above the

Chiriquí Valley, bringing only a rare shower in February.⁹

Preliminary data for the dam site indicate a high average rainfall in excess of 4000 mm., with an average temperature of about 16°C. in a range of about 11–23°C. (Adames, 1977, p. 23). Apparently, there is no real dry season. Rain fell daily at the dam site in February 1976, at a time when the adjacent Pacific lowlands were sun-exposed and in the midst of the annual dry season. Occasional days were clear and sunny, with precipitation falling only as *bajareque* in late afternoon, but usually there were also spells of cold, drenching rain. This climate is classifiable as Temperate Wet (*Cf*) under the Köppen system, in contrast to the Temperate Wet and Dry (*Cw*) conditions that prevail in most montane areas of Pacific-western Panama. Quite in keeping with the *Cf* climatic conditions, the forest of this high, Pacific-drainage watershed is physiognomically classifiable as Lower Montane Rain Forest, which, in western Panama, is found mainly on the Atlantic drainage. The forest is comprised of tall, straight-boled trees, with a high canopy approaching 30 m. on favorable slopes. Buttressed roots are common but of smaller average size than is characteristic of Lowland Rain Forest; large stilt roots and spiny trunks are decidedly uncommon. Vascular epiphytes are abundant, even growing low on the tree trunks in some areas, but the tree trunk "moss" layer is relatively sparse. On gentle slopes, the forest tends to be fairly open, with few saplings and treelets but with a dense ground cover of ferns and herbaceous vegetation growing to a height of about 1 m.; but in many places, particularly on steep slopes, there is a much denser woody undergrowth and passage is difficult. Tree ferns and palms are scattered, with some palms penetrating the high canopy. However, compared with the situation usually encountered (in Panama) in both higher

and lower-elevation wet forest, palms are relatively scarce, growing densely only in apparently rare groves of "*guagara*" palm. This forest is replaced on the summit of Cerro Fortuna (1400–1500 m.) by a denser, more luxuriant cloud forest, which has a lower canopy and a rather stunted and twisted aspect, physiognomically approaching Montane Thicket.

Some 50 species of amphibians and reptiles were sampled in the area. Only two have primarily Pacific-drainage distributions (*Smilisca sila*, *Oxybelis fulgidus*). The majority are species occurring widely at low to moderate elevations, although, in western Panama, many of these are principally Caribbean-slope animals, a few of which had not previously been found in Chiriquí Province (e.g., *Colostethus pratti*). The remaining species, representing over a fourth of the total, are Talamancan forms, with highland distributions in Costa Rica and/or western Panama. Some of these had not previously been taken so far to the east in Panama (e.g., *Dendrobates speciosus*, *Rhadinaea pulveriventris*). Six species of *Hyla* were obtained, all Talamancan species, with only one (*H. miliaria*) being presently known from a locality farther to the east. Brief accounts for these six species follow. In addition, specimens of the herein newly described *Hyla graceae* (*q.v.*, Relationships and Distribution) and *Hyla colymba* (see fig. 19C) were obtained in the area late in 1981 by Karl-Heinz Junger (*in litt.*, 1982) and Wolfgang Utke. Other species to be expected certainly include *Hyla rivularis* (*q.v.*), now known from Cerro Colorado. The only other hylids collected in the Fortuna area in 1976 are three species that range the length of Panama in suitable habitat, namely *Smilisca phaeota*, *Smilisca sila*, and *Phyllomedusa lemur* (specimens reported in Canatella, 1980).

This highland valley was moderately undisturbed in 1976, when it was accessible only on foot or by helicopter, but there is now a road from Gualaca.

Hyla debilis Taylor

Figure 11

These frogs were found by night on low vegetation in the forest and along a small

⁹ Owing to prevailing northerly winds throughout the year, cloud formation and precipitation are heaviest and most constant on the north-facing (Atlantic) slopes of the central cordillera of western Panama. This pattern normally holds true even during the period from December to April, when the strong northeast trade winds lose most of their limited moisture before bringing a pronounced dry season to the Pacific versant (Myers, 1969).

rocky stream in upland pasture, not far from the forest edge. Calling males and other specimens were perched on leaves from about 10 cm. to 1 m. aboveground, close to the stream. Unlike *Hyla uranochroa* (q.v.), they seemed to avoid the more open stretches of stream, being found only in an area where the stream entered a dense, meter-high stand of ferns and herbaceous vegetation. The call is a harsh, insect-like chirp or very brief nonmusical "trill." Sound spectrograms of AMNH 94904, recorded in light rain at an air temperature of 15.0°C., show the call to be comprised of a group of 7–9 closely spaced and slightly ascending notes, with the call group having a duration of only 0.2 second and repeated at half-second intervals; maximum energy output occurs at about 5200–5300 Hz (slightly rising with each note except the last one or two). Except for being of slightly longer duration, the call group is similar to that described and illustrated by Duellman (1970, p. 291, pl. 21), from a recording made at 18°C. on Cerro Pando, near the Costa Rican border.

Six adult males have snout–vent lengths of 25.2–26.8 (\bar{x} = 25.9) mm.; one gravid female, 30.0 mm.; two juveniles, 18.2 and 22.2 mm. These males are slightly smaller than those from Cerro Pando in Bocas del Toro (26.1–29.5, \bar{x} = 27.5 mm., N = 9; Duellman, 1970, p. 289). The coloration in life also is slightly different from the Cerro Pando specimens, which were basically brown with green and darker brown flecks dorsally.

In the Fortuna area, specimens of *Hyla debilis* appeared grayish green by night, turning green or (usually) dark bluish green by day, with the body being nearly uniform in color or with spots of lighter green and mottling of vague blackish gray. Other color notes on these specimens are: Limbs usually mottled brown, with small patches of green. Head with blackish brown stripe, which may be edged with blue, from tip of snout to eye and continuing vaguely from eye through tympanum (in juveniles, the postocular stripe is blue with an upper brown edge); a golden yellow to very pale yellow subocular mark. A usually distinct pale lateral stripe, ranging from golden yellow to white. Groin, anterior and posterior surfaces of thigh and adjacent part of shank bright yellow (pale in one), with

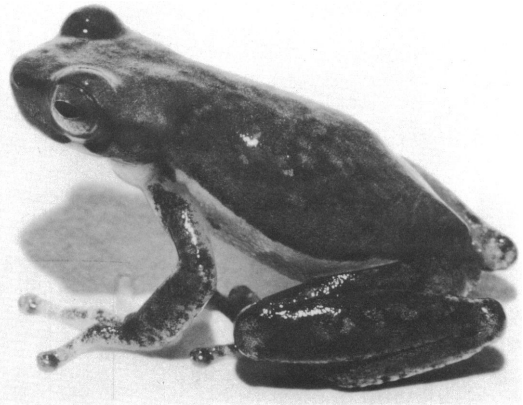


FIG. 11. *Hyla debilis* (AMNH 94904) from Cerro Fortuna, Chiriquí.

underside of limb being mostly unpigmented; webs clear or with some brown pigmentation. Underside of head and venter white. Iris ranging from bronzy tan or bronzy gray to pale yellow with brown suffusion; palpebrum clear. Bones white. The dorsal coloration of *H. debilis* seems less variable in Panamanian populations than in central Costa Rican populations (based on this account and Duellman, 1970, as compared with Savage and Heyer, 1969).

We previously collected *Hyla debilis* at 910–1450 m. elevation in lower montane rain forest, on the Atlantic versant of extreme western Panama, and a specimen from Boquete was tentatively assigned to this species, otherwise known from the Atlantic side of central Costa Rica (map in Duellman, 1970, pp. 292–293). Thus, the present material supports the assignment of the Boquete specimen and provides a short range extension to the southeast.

NEW RECORDS: AMNH 94903, upper Río Chiriquí, Fortuna Dam Site, 1000 m., and AMNH 94904–94911, east slope Cerro Fortuna, 1170 m., Chiriquí, Panama.

Hyla lancasteri Barbour
Figure 12

This species was known only from the Atlantic versant of central Costa Rica until 1966, when, together with Linda Trueb, we obtained samples along a vertical transect in extreme western Panama, on the Atlantic

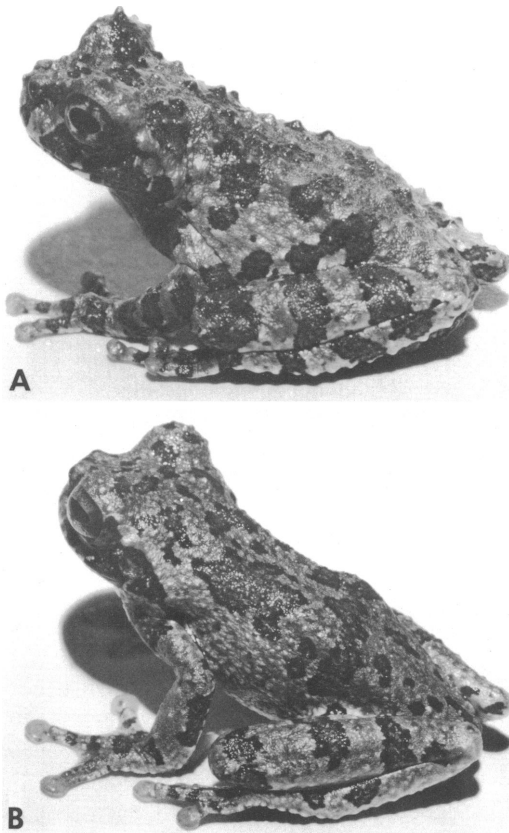


FIG. 12. Intermediate highland and low-elevation morphs of *Hyla lancasteri*. A. East slope Cerro Fortuna, 1170 m., Chiriquí (AMNH 94882). B. Río Changuinola near Quebrada El Guabo, 90 m., Bocas del Toro (AMNH 107259).

slopes of Cerro Pando, from 1920 m. down to 650 m. Recent specimens from lower in the same drainage system (Río Changuinola) extend the vertical range down to 90 m. above sea level, near the edge of the Atlantic coastal plain. Specimens from 1170 m. on Cerro Fortuna extend the horizontal range some 50 km. to the southeast.

Trueb (1968) described in detail the altitudinal clinal variation—especially striking in degree of tuberosity—discovered on the Cerro Pando expedition. The new specimens, albeit few, suggest that the altitudinal variation analyzed by Trueb may be generally descriptive of this species throughout the mountains of western Panama.

The Changuinola specimens from 90–170

m. have relatively smooth (granular) skin dorsally (fig. 12B) and are relatively large (length from snout to vent 29.8–30.8 mm., \bar{x} = 30.3 mm., in 3 δ , 41.5 mm. in 1 ♀). Their dorsal color ranges from mostly light brown (one specimen), to brown with blackish brown blotches and the whole overlain with small patches of bright green; the white venters are nearly immaculate; there are bright yellow and black flash marks in the groin, rear of thigh and concealed part of shank.

In contrast, the frogs from 1170 m. on Cerro Fortuna are conspicuously tuberculate (fig. 12A) and are slightly smaller on the average (28.5–30.9 mm., \bar{x} = 29.5 mm., in 4 adult δ). Their color also differs from that of the low-elevation frogs, varying from mostly light metallic brown to overall bright metallic green, with brown spots; there are numerous small black spots on the venters; yellow flash marks are lacking (the groin and leg areas being grayish white with some black markings). The Cerro Fortuna specimens most closely resemble those from the same vegetational zone (lower montane rain forest at 1450 m.) on the Cerro Pando transect. The Fortuna frogs do not attain the extreme tuberosity seen in the montane rain forest at elevations above 1800 m. on Cerro Pando (compare fig. 12A with Trueb [1968, fig. 2a] or Duellman [1970, pl. 54, fig. 4]). As indicated by Trueb, the extraordinary elevational changes in *Hyla lancasteri* seem to be associated with environmental changes in temperature and habitat; see Myers (1969, figs. 16–17) for illustrations of the pronounced vegetational differences between lower montane and montane rain forests in western Panama.

At the Changuinola locality, *Hyla lancasteri* was found in April perched on low vegetation in company with *H. lythrodes*, at the edge of a small ridgetop stream in lowland rain forest (fig. 18). At Cerro Fortuna in February, *Hyla lancasteri* was calling microsymbatrically with *H. uranochroa*, in low (<0.5 m.) vegetation along the edge of a stream in a montane pasture (fig. 10). The insect-like call at this locality consists of one or two drawn out notes, which are harsh and poorly modulated. Recordings and sound spectrograms (AMNH reel 208, 15.2°C.) show repetition rates of about 1.8–4.8 notes per



FIG. 13. *Hyla miliaria* (AMNH 94887), a species of giant, fringe-limbed tree frog. This specimen, a subadult female from Fortuna Dam Site, was marked with green (dark areas) on pale brown.

minute, with the notes being given either singly or paired (with a half-second separation); the notes have durations of 0.20–0.35 sec. and rates of roughly 90 pulses/sec.; maximum energy output occurs at a dominant frequency of about 3000–3200 Hz, with an essentially co-dominant fundamental frequency at about 1500–1600 Hz. One individual produced a normal note and then a series of notes of different quality, while it shifted about on its perch; the last notes are of similar duration but are more squeaklike, seemingly due to more rapid pulsation (pulses not resolvable on wide-band spectrograms).

Trueb (1968) and Duellman (1970) discussed altitudinal variation in the call of *Hyla lancasteri*. At 1170 m. on Cerro Fortuna, the call of this frog is reminiscent of lower-elevation (<1000 m.) populations in that the notes are occasionally paired, but the calls more closely resemble higher-elevation (>1400 m.) populations in that the notes are long and slowly pulsed. Audiospectrograms from Cerro Fortuna show notes similar to those produced at 1450 m. on Cerro Pando, as illustrated in Trueb (1968, fig. 8A) and

Duellman (1970, pl. 24, fig. 2). Considering that the notes also are often uttered singly at Cerro Fortuna, the vocalization correlates with degree of skin tuberosity (fig. 12A), body size, and coloration—causing the Cerro Fortuna frogs to closely resemble those from the same vegetational zone (lower montane rain forest) on Cerro Pando, some 50 km. to the northwest.

NEW RECORDS: AMNH 94882–94885, east slope Cerro Fortuna, 1170 m., Chiriquí, Panama. AMNH 107259–107262, above Río Changuinola near Quebrada El Guabo, 90–170 m. (16 km. airline W Almirante), Bocas del Toro, Panama.

Hyla miliaria (Cope)

Figure 13

A specimen of this large, fringe-limbed frog was taken from the mouth of a snake (*Chironius* sp.¹⁰), which was found on the forest

¹⁰ It is a currently unrecognized northern species (or population) of *Chironius*, easily distinguished in life from other Central American species by bright green dorsal



FIG. 14. *Hyla tica* (AMNH 94913 above, 94914 below), showing pattern variation in specimens from Fortuna Dam Site, 1000 m., Chiriquí.

floor by day, but whether the snake had found the frog in a terrestrial or in an arboreal situation is not known. This rare tree frog has a broad distribution from Nicaragua to Colombia, but the only previous Panamanian specimens are from two widely separated localities in the western half of the country (map in Duellman, 1970, p. 351). The new specimen of *Hyla miliaria* is from an intervening locality, suggesting that the species may be at least continuously distributed in the central cordillera of western Panama.

The specimen (fig. 13) is a subadult female with a snout-vent length of 86.2 mm. In general habitus the specimen agrees with the descriptions given by Duellman (1970, p.

coloration and yellow venter, and a conspicuously displayed orange-red tongue (gray on tips of fork). This snake ranges from Costa Rica to South America, with a spotty montane distribution on the Isthmus of Panama. Its taxonomic disposition is presently in the hands of Dr. John A. Wiest.

352), but the skin on the dorsum is less tubercular than in the two specimens from Finca Santa Clara, Chiriquí, and the holotype of *Hyla immensa* (= *H. miliaria*, *vide* Duellman, *loc. cit.*) from Costa Rica. The prepollical spine does not protrude on the left thumb and only the tip protrudes on the right thumb. The proportions of this female are within the ranges of variation given for four males by Duellman (*loc. cit.*).

In life, the overall color of the Fortuna frog was light brown, with grayish green blotches atop the head and front of body; loreal region bright green. Upper surface of arm and fingers III-IV mostly green; hind limbs broadly banded with green on pale brown; webs of hands and feet light brown with small green patches. Axilla, groin, and rear of thighs dull brown, with irregular areas of pale brown on rear of thigh. Ventral surfaces, including hands and feet, brown, with small blotches of white on belly and under thighs; subanal warts very pale tan. Iris rich, dark brown. Lower half of palpebrum solid tan, upper half clear, with flecks of bronzy tan.

NEW RECORD: AMNH 94887, upper Río Chiriquí, Fortuna Dam Site, 1000 m., Chiriquí, Panama.

Hyla tica Starrett

Figure 14

Three specimens were found by night: one was on a rock at the edge of a torrential stream in heavy forest; two were perched in low brush (<0.5 m.) amongst boulders in a more open stream, where *Smilisca sila* was breeding. Coloration is highly variable. When found at night, one individual (fig. 14, bottom) was a mottled green overall, with green limb bands, but by day it had turned tan with dark brown markings that were only slightly tinged or edged with green. The other specimens were tan by day and night, being either nearly unicolor (fig. 14, top), or having a dark grayish brown hourglass marking anteriorly on body and head, with narrow gray bands on the limbs. In all, the axilla, groin, anterior and posterior surface of thigh, and adjacent part of shank, were bright orange-yellow. Venter white. Iris gray or pale grayish brown, with fine black venation.

Two adult males and one gravid female

have snout-vent lengths of 30.0, 30.9, and 37.0 mm., respectively. These measurements are near the mean sizes given for the species by Duellman (1970, p. 280). The coloration of these frogs is generally like that described by Duellman (1970, p. 282), except that the hidden surfaces of the limbs (anterior and posterior surfaces of the thighs and posteroventral surfaces of the shanks) were bright orange-yellow in life, instead of brown or orange-brown as in western Panama or tan or yellowish tan as in central Costa Rica. Also, the night to day color change described above is just the reverse of the change described by Duellman, although such metachrosis conceivably might be influenced by factors other than light (e.g., temperature).

Hyla tica was known to occur from northern Costa Rica to the slopes of Volcán de Chiriquí in western Panama, where the range is now extended a short distance to the southeast.

NEW RECORD: AMNH 94912-94914, upper Río Chiriquí, Fortuna Dam Site, 1000 m., Chiriquí, Panama.

Hyla uranochroa Cope

Figure 15

Calling males were found by night on low vegetation along a small rocky stream in upland pasture (near foreground in fig. 10). They occurred microsymbatrically with *Hyla lancasteri* (q.v.) along fairly open stretches of stream bank, and also occurred with *Hyla debilis* (q.v.) in a more densely vegetated section of the same stream. They also were heard calling at a small stream in dense forest near the Río Chiriquí. The call of *Hyla uranochroa* is a single, high-pitched melodic note, which separates on spectrograms into a few well-spaced harmonics. Duellman (1970, pp. 305-306) described two kinds of note trains at air temperatures of 18-20°C., namely a *fast call* at localities in Costa Rica (notes of 0.03-0.04 sec. duration produced at a rate of >200/min.), and a *slow call* from Cerro Pando in extreme western Panama (notes of 0.05-0.06 sec. duration produced at rates of 50-60/min.). Specimens recorded at a still cooler temperature (15°C.), in light rain on Cerro Fortuna, were slow callers; they produced long notes (~0.06 sec.), sometimes

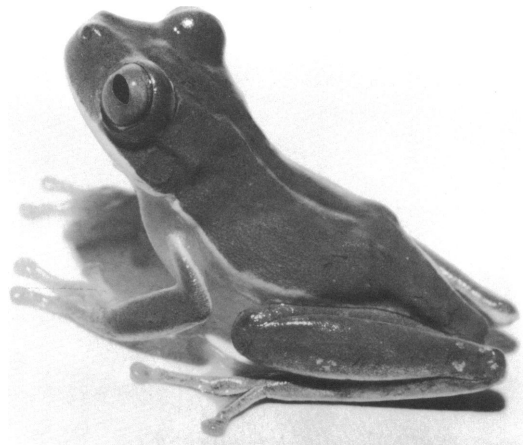


FIG. 15. *Hyla uranochroa* (AMNH 94888), a red-eyed, green tree frog from Fortuna Dam Site, 1000 m., Chiriquí.

giving a few notes at intervals of only 0.5 or 0.6 sec. but with individual frogs seeming to produce no more than about 20 notes/min. (AMNH reel 208, segments 1, 3).

Nine adult males from the Fortuna area have snout-vent lengths of 32.6-35.4 (\bar{x} = 34.1) mm., with the same mean as in a larger sample from Cerro Pando (Duellman, 1970, p. 302). Coloration in life of the Fortuna sample seems characteristic of *Hyla uranochroa*: Dorsal surfaces were light, bright green, with or without white or pale yellow flecks; a conspicuous white line around the lip, continuing posteriorly to groin as a usually distinct low lateral line (fig. 15); also white lines on rear of arm, foot, and above cloacal opening; digit tips, webs, anterior and posterior surfaces of thighs, and ventral surfaces of limbs and body, all bright yellow, usually a paler yellow under head; iris bright orange-red, unmarked or with a faint horizontal streak of gray; upper edge and lower third of palpebrum green like body, upper two-thirds clear with white flecks.

The specimens listed below place *Hyla uranochroa* in the Pacific drainage at the eastern end of its known range. The elevation is low for the Pacific versant (Duellman, 1970, p. 306), but, as already stressed, the upper valley of the Río Chiriquí has an Atlantic-slope environment. The species has long been

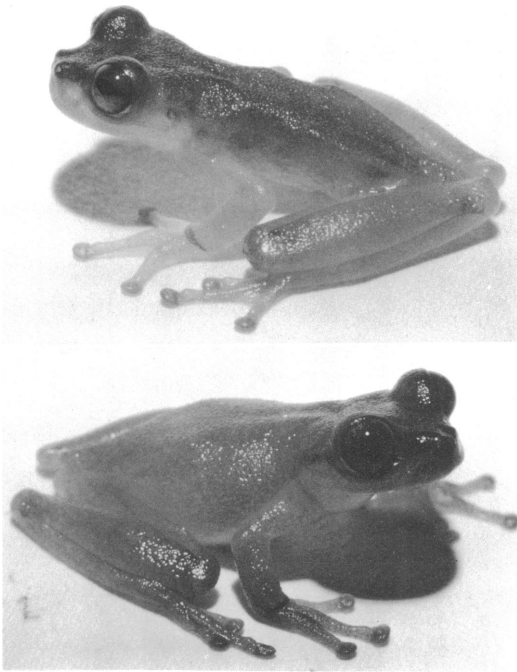


FIG. 16. *Hyla zeteki* (AMNH 94899 above, 94901 below), a small bromeliad frog from Fortuna area, 1000–1170 m., Chiriquí.

known from La Loma, a locality about 13 km. to the northeast of the present records. La Loma (=Buena Vista), a Dunn locality, has been assigned several incorrect elevations in the literature; it lies near the edge of the Atlantic coastal plain, 15 km. airline southwest of Chiriquí Grande, at only about 300 m. above sea level. Thus, *Hyla uranochroa* seems to attain the lowest elevations at the southern (eastern) end of its range—300 m. on the Atlantic side and 1000 m. on the Pacific versant.

NEW RECORDS: AMNH 94888, upper Río Chiriquí, Fortuna Dam Site, 1000 m., and AMNH 94889–94898, east slope Cerro Fortuna, 1170 m., Chiriquí, Panama.

Hyla zeteki Gaige
Figure 16

Only three specimens of this tiny tree frog were obtained. Two adult males (snout–vent lengths 21.1, 21.6 mm.) were in bromeliads,

and a subadult (19.3 mm.) was out by night, perched in low vegetation at the brushy edge of an upland pasture (near foreground in fig. 10). Previous specimens of *Hyla zeteki*, including eggs and larvae, were found in bromeliads, to which the tadpole seems adapted by virtue of morphological peculiarities and possibly specialized feeding (egg-eating) habits.

The adult frog also seems morphologically and behaviorally suited to an existence in bromeliads. Various kinds of frogs seek shelter in bromeliads, with many species leaping out if the plant is being seriously disturbed. But with its small, flattened body, *Hyla zeteki* is able to slide backward down between the basal parts of the leaves of the bromeliad, submerging completely in water held in the base of the plant. Two of the three specimens have a suffusion of dark pigment on the anterior part of the iris, adjacent to the darkened canthal region (fig. 16, bottom), which may serve as a subtle way of disrupting the outline of the eye—remembering that potential predators will get a head-on view of the resting frog.

The head and body were light brown, yellowish brown, or pale yellowish green, turning darker on the snout and lighter on the limbs; there is a conspicuous black mark across the wrist (fig. 16). The unpigmented venters appeared silvery white owing to an underlying silvery peritoneum; throat pale green; undersides of limbs, hands, and feet pale yellow or yellowish green. Iris light, dull red or pinkish bronze, with a gray or black suffusion anteriorly, fine black lines radiating from pupil, and a thin, horizontal gray streak; or iris light red and lacking horizontal line and anterior suffusion of dark pigment. Palpebrum clear, unmarked. Bones white.

These specimens extend the range a short distance southeastward from the type locality above Boquete, and provide a second Panamanian locality. They agree with Costa Rican specimens in lacking dorsal red coloration that was present in the type specimens (summary in Duellman, 1970, p. 325).

NEW RECORDS: AMNH 94901, upper Río Chiriquí, Fortuna Dam Site, 1000 m., and AMNH 94899–94900, east slope Cerro Fortuna, 1170 m., Chiriquí, Panama.

ADDITIONAL RECORDS, INCLUDING TWO *HYLA* NEW TO PANAMA

Four other records of tree frogs in western Panama are treated in the following accounts. New specimens of *Smilisca sordida* and the heretofore rarely collected *Agalychnis calcarifer* provide museum documentation of predicted occurrence in the Atlantic lowlands. Other specimens require resurrection from synonymy of the names *Hyla lythrodes* and *Hyla palmeri*; these specimens represent new country records of frogs previously reported only from Costa Rica (*H. lythrodes*) or Colombia (*H. palmeri*).

Hyla lythrodes Savage

Figure 17

Hyla lythrodes Savage, 1968, p. 1, fig. 1B (lateral profile head). Holotype: Los Angeles County Mus. 26766, an adult male obtained March 20, 1964 by Jay M. Savage and Norman J. Scott, Jr., at Alta Talamanca, 800 m., 21 km. SW Amubri at confluence Río Lari and Río Dipari, Limón Prov., Costa Rica. Savage and Heyer, 1969, p. 34. Savage, 1980, p. 31 (in key).

Hyla rufiocularis: Duellman, 1970, p. 307 (*H. lythrodes* placed in synonymy).

Hyla lythrodes was described on the basis of a single specimen from a locality at 800 m. elev. on the Atlantic versant of extreme southeastern Costa Rica. Three additional males, collected in April 1980, serve to validate the species and extend its range about 58 km. east-southeast to the middle Río Changuinola drainage in northwestern Panama; the elevational range is lowered by about 600 m., nearly to the edge of the Atlantic coastal plain. The new locality is a ridgetop in rain forest (fig. 18) at 170 m. above sea level, or about 130 m. above low-water level of the nearby Río Changuinola. The frogs were found at night perched in low vegetation on the banks of shallow headwater streams, in company with a normally montane tree frog, *Hyla lancasteri*¹¹; a principally lowland



FIG. 17. *Hyla lythrodes* (AMNH 107263), a changeably brown to green tree frog with red eyes, from ridge above Río Changuinola near Quebrada El Guabo, 170 m., Bocas del Toro.

species, *Agalychnis calcarifer* (fig. 20), was common in the canopy above. Hylids found closer to the Río Changuinola were species that could be expected in lowland forest below 100 m. elevation (*Agalychnis callidryas*, *Gastrotheca ceratophrys*, *Hyla ebraccata*, *H. elaeochroa*, *Smilisca phaeota*, *S. sordida*).

Hyla lythrodes is not always a brown frog as indicated in the original description. The Panamanian specimens exhibited metachrosis, with the frogs being individually changeable from brown to light green. There was a conspicuous white labial line, including an expanded subocular section, and also a sharply defined transverse white line above the anal region; white lines along the lower sides of the body and along the outer edges of the forearm and foot were less sharply defined. All ventral surfaces were yellow; both anterior and posterior sides of the thighs also were yellow, lacking dark pigmentation. The iris was bright red. The three specimens are adult males (vocal slits present) 30.0, 30.2, and 32.6 mm. SVL.

Savage (1980, p. 31) has maintained *Hyla lythrodes* in a checklist and key, stressing (in couplets 28–29) characters of heavy pigmentation on the sole of the foot and lack of such pigmentation on the rear of the thigh to separate it from *H. rufiocularis*. The present specimens have the lateral plantar surfaces only slightly to moderately suffused with dark and the medial sides pale. The rear of the thighs

¹¹ *Hyla lancasteri* is generally found above 600 m. elevation, although at this locality a specimen (fig. 12B) was found as low as 90 m. above sea level. The species is discussed further in the Cerro Fortuna section of this paper.



FIG. 18. Head of small stream (lower center from between trees), in rain forest on ridge above Río Changuinola, near Quebrada El Guabo, 170 m. elev., Bocas del Toro. *Hyla lancasteri* (fig. 12B) and *Hyla lythrodes* (fig. 17) were found on low vegetation along this streamlet, and *Agalychnis calcarifer* (fig. 20) was abundant in the canopy above. (C. W. Myers, April 27, 1980.)

is immaculate as stressed by Savage, but Duellman (1970, p. 310) had already stated that this is not a reliable character for separating *lythrodes* from *rufioculis*, which is highly variable in thigh coloration. Savage (1968, pp. 5–6) had described the call of the *lythrodes* holotype as a burst of 5–7 notes, each “a weak bell-like ping,” and the call of *rufioculis* as a differing “single non-melodic scraape” (a “short rattle . . . of three or four short notes” *vide* Duellman, 1970, p. 310 and pl. 22, fig. 1). In the absence of objective bioacoustical data, Duellman (p. 310) tentatively synonymized *H. lythrodes* because he could find only a single character that separated the type specimen from several large series of *H. rufioculis*. The character is that of tympanum size, also emphasized as a diagnostic character in Savage’s original description of *lythrodes*.

As determined by Duellman (1970, pp. 308, 310), the holotype of *H. lythrodes* has a ratio of horizontal diameter of tympanum/eye length = 0.555, whereas the ranges of this ratio in several samples of *H. rufioculis* were 0.302–0.356, 0.312–0.441, and 0.415–0.452. The three Panamanian specimens have relatively larger tympana than even the *lythrodes* holotype, with ratios of 0.571–0.625 (\bar{x} = 0.602). In addition to differences in tympanum size (>50% of eye in *lythrodes*, <50% in *rufioculis*), the two species may differ conspicuously in ventral coloration in life. Both have unpigmented vocal sacs and white venters in preservative, but in *H. rufioculis* the throat and venter are also white in life, whereas the Costa Rican holotype and three Panamanian specimens of *H. lythrodes* all had yellow undersurfaces.

NEW RECORD: AMNH 107263–107265, above Río Changuinola near Quebada El Guabo, 170 m. (16 km. airline W Almirante), Bocas del Toro, Panama.

Hyla palmeri Boulenger
Figure 19A, B

Hyla palmeri Boulenger, 1908, p. 515. Syntypes: British Mus. Nat. Hist. 1947.2.13.32, an adult male, and 1947.2.13.33, a juvenile, obtained by M. G. Palmer, at Jiménez [about 500 m., Depto. Valle del Cauca], Colombia.

Hyla albopunctulata: Cochran and Goin, 1970, p. 220 (part).

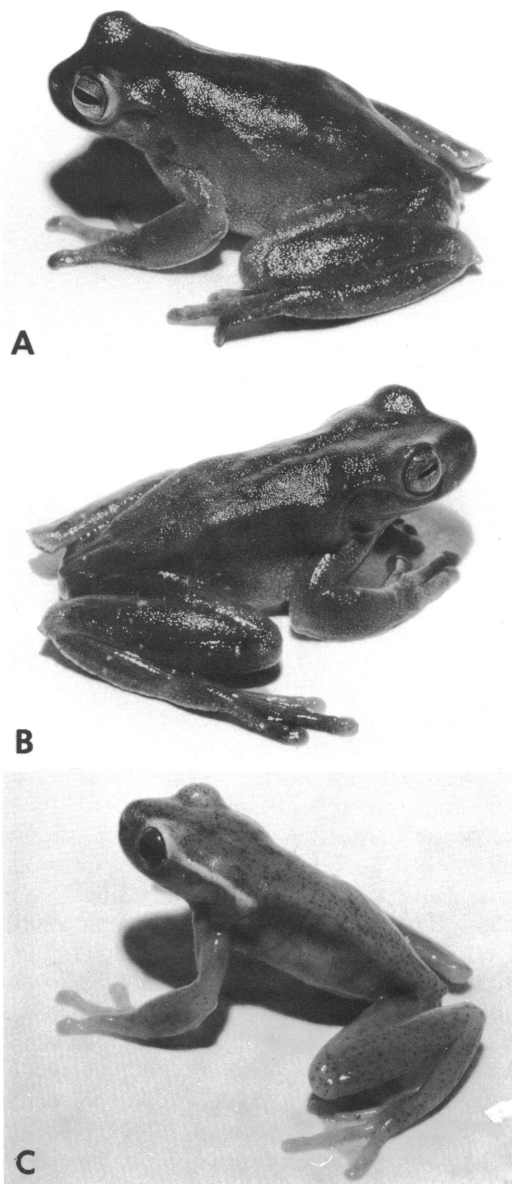


FIG. 19. Panamanian species of the *Hyla bogotensis* Group. A, B, *Hyla palmeri* as follows: A. Adult male (AMNH 88205) from Quebrada Guanguí, southwestern Colombia. B. Very similar specimen (AMNH 98366) from near continental divide N El Copé, 600 m., in west-central Panama. C. *Hyla colymba* (AMNH 98364), an adult male from same locality as B.

The name *Hyla palmeri* is here removed from the synonymy of *Hyla albopunctulata* and is applied to a moderate-sized, green tree

TABLE 2
Measurements (in Millimeters) of Adult Male Specimens of *Hyla palmeri*^a

Character	AMNH 98366	AMNH 88205	BMNH 1947.2.13.32	KU 169548	KU 169549	KU 178800
Snout to vent	40.8	41.8	41.0	43.5	43.8	45.0
Tibia	20.8	21.0	21.5	23.3	22.5	22.2
Foot	18.0	18.3	17.4	20.4	20.2	20.8
Head length	12.0	12.1	13.9	14.5	14.5	14.6
Head width	13.5	14.0	13.9	14.9	15.2	15.2
Internarial	3.2	3.2	3.2	3.3	3.4	3.5
Naris to eye	2.7	2.8	3.2	3.0	3.2	3.3
Eye	4.6	4.5	4.6	4.7	4.8	4.4
Tympanum	1.4	1.4	2.0	1.6	1.5	1.6
Third finger disc	2.4	2.4	—	2.1	2.0	2.1

^a Measurements after Duellman (1970).

frog inhabiting low to moderate elevations along the western foot of the Andes in Colombia and northwestern Ecuador, and also known from one locality in the central cordillera of western Panama.

The single Panamanian specimen (AMNH 98366) was taken by Myers in October 1977, from low vegetation at the edge of a rocky forest stream at 600 m. above sea level. In life (fig. 19B), the dorsal surfaces of this frog were dark green with sparse and irregularly distributed grayish white flecking, a narrow yellowish white labial stripe, white supra-anal stripe, and tan tarsal fold extending to the calcar. The ventral surfaces were green with a yellowish suffusion on the mental gland and on the ventral surfaces of the limbs. The webbing on the feet was pale orange. The iris was light brown. The Panamanian frog is an adult male.

An adult male (fig. 19A) from toward the southern end of the range (AMNH 88205 from Quebrada Guanguí, southwestern Colombia) also was flecked with gray, but the supra-anal stripe was tan (vs. white) like the tarsal fold, and ventrally it changed from green to yellow on the median part of the chest and belly. The webbing on the feet was orange, and the iris was pale brown. (The webbing on the hands was pale green, and the bones were green; these features were not recorded for the Panamanian frog.) Two other adult males, from western Colombia (KU 169548–169549, Río Anchicayá drainage), were like the other specimens in dorsal col-

oration and in having orange webbing on the feet and a pale creamy white labial stripe. They differ in that the venter was predominately dull creamy yellow and the iris was somewhat paler (pinkish bronze) at night. A male from northwestern Ecuador (KU 178800, Las Palmas) is like the Panamanian and Colombian specimens in structure and generally similar in coloration: Its dorsum in life was dark olive-green with some indefinite pale olive-gray spots; the anal stripe was white and the stripe on the edge of the forearm was cream; the belly was yellowish medially and greenish olive laterally; the iris was brown with a bronze tint (John D. Lynch field catalogue, July 10, 1977); however, a color transparency revealed the hind-foot webbing to be pale olive-tan rather than orange.

In preservative the specimens are creamy white to creamy tan dorsally with a sprinkling of melanophores (most numerous on KU 169548–169549) and a few scattered white flecks (absent on AMNH 88205, BMNH 1947.2.13.32, and KU 178800). A suffusion of dark pigment persists on the plantar surfaces.

Two additional specimens (Los Angeles Co. Mus. 73000–73001, Camino de Yupe, northwestern Colombia) were questionably referred to *Hyla alytolylax* by Duellman (1972, p. 19). These two males having snout–vent lengths of 39.0 mm. certainly are conspecific with *Hyla palmeri*.

Five recently metamorphosed young from Colombia (AMNH 88809 from Quebrada

Guanguí, BMNH 1947.2.13.33 from Jiménez, and KU 148703–148704 and 170209 from the Río Anchicayá) have snout–vent lengths of 20.8, 22.2, 26.0, 22.6, and 21.7 mm., respectively. In preservative the dorsum of juveniles is creamy white with distinct small brown spots concentrated along the middle of the back. The identity of these juveniles is established by a series of tadpoles and metamorphosing young (KU 170210) from the Río Anchicayá.

The following morphological description is based on six adult males (four from Colombia, including the adult syntype, one from Ecuador, and one from Panama). The snout is rounded in dorsal view, round to weakly truncate in profile; canthus rostralis indistinct and rounded; loreal region oblique and concave; interorbital region much broader than upper eyelid; tympanum barely evident; vocal sac subgular, moderately distensible; mental gland large, round, occupying all of the chin and extending about half the length of the throat; prevomerine dentigerous processes narrowly separated, positioned posteriorly behind choanae, each process bearing 7 to 9 teeth; dorsal skin weakly granular to nearly smooth in preservative; outer ulnar and outer tarsal folds present; calcar present; hands and feet moderately large with wide digits and moderately expanded discs; subarticular tubercles of hands and feet low, with rounded surfaces, single or bifid; outer fingers less than half-webbed; feet nearly fully webbed; hand-webbing formula, II 2–3 III 2 $\frac{2}{3}$ –2 IV; foot, I 1–1 II 1–1 III 1–1 $\frac{1}{2}$ IV 1 $\frac{1}{2}$ –1 V. Comparative measurements are given in table 2.

Cochran and Goin (1970, p. 220) did not make a convincing case for assigning the trans-Andean *Hyla palmeri* Boulenger (1908) to the synonymy of the cis-Andean *H. albopunctulata* (Boulenger, 1882, p. 385). The latter was described from Amazonian Ecuador as a reddish brown frog with a distinct canthus rostralis and with granular dorsal skin; the snout–vent length of a male syntype was given as 33 mm.

The presence of a mental gland distinguishes *Hyla palmeri* from all other species of the genus in Central America except *Hyla colymba*, which was collected in Panama at

the same locality as *H. palmeri*. *Hyla colymba* (fig. 19C) is readily differentiated by the presence in life of a short yellow stripe from the eye to the shoulder and by the absence of a projecting dermal flap or calcar on the heel. *Hyla colymba* also is a smaller species, with males attaining snout–vent lengths of about 37 mm. and females 43 mm. (Duellman, 1970, p. 328). Two Panamanian males (AMNH 98364–98365) obtained sympatrically with the male specimen of *Hyla palmeri* have snout–vent lengths of 32 and 33 mm. vs. 41 mm. for the latter.

NEW RECORDS: PANAMA: *Coclé:* AMNH 98366, near continental divide north of El Copé (80°36'W), 600 m. **COLOMBIA:** *Cauca:* AMNH 88205, 88809, Quebrada Guanguí, 0.5 km. above Río Patia (upper Saija drainage), 100–200 m. *Chocó:* LACM 73000–73001, Camino de Yupe, 420 m. *Valle del Cauca:* KU 148703–148704, 169548–169549, 170209, 170210 (tadpoles), Río Anchicayá, 8 km. W Danubio, 300 m. **ECUADOR:** *Pichincha:* KU 178800, Las Palmas, 920 m.; USNM (R. W. McDiarmid field nos. 11796, 11904), Centinella, 550 m., 14.1 km. ESE Patricia Pilar.

Agalychnis calcarifer Boulenger

Figures 20, 21

Although it is distributed from northern Costa Rica to Ecuador, this large and gaudy frog is known only from about six localities (Duellman, 1970, pp. 123–124). A small series from the middle Changuinola drainage doubles the number of available museum specimens and provides the first specimen-documented record of *Agalychnis calcarifer* in western Panama, although its occurrence in the Atlantic drainage has always been assumed.

The species was locally common in the forest canopy and understory above a headwater streamlet at 170 m. elevation, on a forested ridge (fig. 18). The frogs were seen at night on leaves and trunks of trees, at heights of 2–8 m. aboveground. Only a few were low enough to reach with poles; most were unattainable or had to be knocked from their perches with hurled sticks. It is a larger species than previously realized: The smallest male



FIG. 20. *Agalychnis calcarifer* (AMNH 107238), a large, vividly colored tree frog (upper surfaces green with pale blue spots; flanks yellow with vertical bars of grayish blue; undersides, and concealed parts of limbs, yellow to orange; iris golden yellow, with medial gray patch).

and smallest female in the present sample of 11 specimens are larger than the maximum sizes (δ 64.0 mm., ♀ 78.5 mm. SVL) recorded by Duellman (1970, p. 121) for the nine specimens then available from lower Central America. Snout-to-vent measurements for the Río Changuinola sample are: 8 males, 71.5–80.5 mm. (\bar{x} = 73.40 mm.); 3 females, 83.5–87.0 mm. (\bar{x} = 85.77 mm.).

The coloration of the Changuinola frogs is similar to specimens that we collected years ago near the Colombian border (for color, see Duellman, 1970, pp. 122–123, pl. 42), nearly 600 km. east of the new locality—with the notable exception that all the present specimens are conspicuously spotted with pale blue (fig. 20).

Duellman (*loc. cit.*) observed that no biologist seems to have heard the mating call, so it is of interest that two kinds of vocalizations were heard at the Río Changuinola from specimens confined in plastic bags. Sounds emitted by the confined frogs included a low “whonk” and a “chuckle.” These calls were

taped in camp late at night, but, unfortunately, at such a low record-level (in order to exclude noise from an ongoing party) that spectrograms are difficult to obtain. The best print (fig. 21) shows a “whonk” call of 0.1 sec. duration, with maximum energy output at about 800 Hz and a calculated pulse rate of about 140/sec. The longer “chuckle” (possibly a release call) seems to be given at a similarly low frequency, but spectrograms were not obtained. Calling was not heard under field conditions, presumably because most of the frogs were high in the trees, and the vocalizations are soft, with little carrying power.

NEW RECORD: AMNH 107238–107248, above Río Changuinola near Quebrada El Guabo, 170 m. (16 km. airline W Almirante), Bocas del Toro, Panama.

Smilisca sordida (W. Peters)

Figure 22

Several specimens from the middle Río Changuinola confirm the existence of this

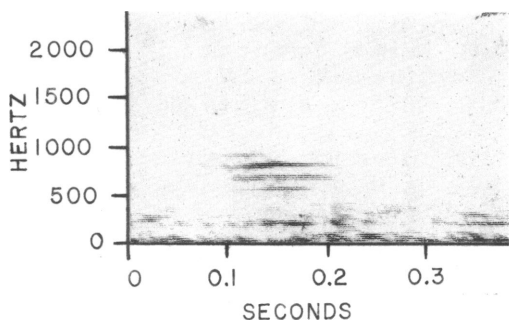


FIG. 21. Call of *Agalychnis calcarifer*, at air temperature of 26.0°C., April 21, 1980 (narrow-band sound spectrogram, 45-Hz filter, from AMNH reel 226 [see text for details of recording]; specimen one of AMNH 107238–107248).

species in the Atlantic drainage of north-western Panama, where it was expected to occur because of its proximity in the adjacent part of Costa Rica (Duellman and Trueb, 1966, pp. 328–329; Savage and Heyer, 1969, p. 60; Duellman, 1970, p. 618). The two syntypes of the species are presumably, but not certainly, from the Pacific side of western Panama (“Veragua,” Peters, 1863). In any case, in 1965 we confirmed that *sordida* does occur in the Pacific drainage of western lowland Panama (locality mapped in Duellman, *loc. cit.*); the single specimen obtained from the Pacific lowlands was calling at the edge of a gravel bar in the dry season (late February). Although *sordida* doubtless is less abundant and/or less widespread in western Panama than either *S. phaeota* or *S. sila*, the paucity of Panamanian specimens also reflects the minimal effort that has been put into dry-season collecting along the lowland streams in that part of the country.

The recent specimens of *Smilisca sordida*, from the Atlantic side of Panama, were collected during a dry period in early April 1980, at night on a rocky beach at river’s edge—the normal breeding habitat of this frog (Duellman and Trueb, 1966, p. 327). *Smilisca phaeota* was much more abundant in the general area, breeding in virtually any small body of water, especially in shallow depressions atop igneous boulders at the forested edge of the river bank, but not one *phaeota* was found in the gravel-bar habitat of *S. sordida*.



FIG. 22. *Smilisca sordida* (AMNH 107273), an adult female from Río Changuinola near Quebrada El Guabo, 40 m., Bocas del Toro.

NEW RECORD: AMNH 107273–107275, Río Changuinola near Quebrada El Guabo, 40 m. (16 km. airline W Almirante), Bocas del Toro, Panama.

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ADDED IN PROOF:
NEW OBSERVATIONS ON *HYLA GRACEAE*

After the present paper had gone to page proof, one of the authors (Myers) found *Hyla graceae* in cloud forest at 1120 m. elevation near the low continental divide north of the highland valley of the Río Chiriquí (see pp. 12–13). The new locality is some 50 km. northwest of the type locality at Cerro Colorado, and about 5 km. northeast of the Chiriquí Valley record included herein (p. 10) on the basis of a photograph. The locality lies at the extreme eastern end of the Cordillera de Talamanca as arbitrarily defined herein (p. 12).

Hyla graceae was abundant in the area, although the sample obtained was relatively small owing to the pressure of other work. Nineteen adult males have snout–vent lengths of 32.3–36.8 mm. ($\bar{x} = 34.81 \pm 0.25$), slightly smaller than in the type series (33.5–38.7 mm. SVL in 7 males, $\bar{x} = 35.80 \pm 0.66$); two adult females are 39.5–41.4 mm. SVL (40.5 mm. in a female paratype, see p. 6).

In life (fig. 23), the new specimens varied from light yellowish brown to dark bronzy brown dorsally, and the dorsolateral stripes ranged from bright yellow (in most) to light brown (in four) and light gray (one female). The ventral surfaces were uniformly light yellow, except that one male had the throat white rather than yellow. There is a dusting of melanophores on the underside of the head and on the palms and soles; two individuals have some scattered dark specks on the venter, which is immaculate in 19 others. The iris was strikingly variable: some had uniformly dark bronzy brown eyes, but most had the upper and lower parts of the iris bright blue-green, with an intervening narrow to wide horizontal stripe of bronzy brown.

The new series of *Hyla graceae* was taken on the nights of July 2 and 4, 1982, at several small standing pools that were formed by seepage water on a gentle slope, at the edge of a new clearing in cloud forest (fig. 24). These pools, connected by weak surface flow during periods of rain, were about 10–15 cm. in maximum depth and from less than 0.5 m. to about 1 m. in diameter; up to six males were calling at a single pool. Frogs also were seen calling on a rainy night at a slow-flow-

ing headwater rivulet under the canopy of dense cloud forest, and in isolated muddy tracks made by heavy machinery along a new road through the forest. Males called from the water's edge and, where available, on low perches above the water. Some calling was heard by day (see p. 9) but the greatest activity was at night.

The call is somewhat variable but generally consists of single or double "quacks" or "honks." There can be audible differences even between notes in a single call group, and this is well reflected in structural variation on sound spectrograms (fig. 25A–B). The notes tend to be about 0.10–0.15 sec. in duration, although the second note of a pair may be longer (0.16–0.37 sec.), in which case it is especially likely to break into two segments. Pulse rate varies from about 125–164 pulses/sec. Maximum energy is concentrated in the region between 800 and 1400 Hz, with sections (not figured) usually showing weak co-dominant peaks at about 800–1000 Hz and 1300–1400 Hz. The interval between paired notes varies greatly, from about 0.12 to 0.55 sec. in prepared spectrograms.

Either the single or double notes described above are sometimes followed by a longer growl or groanlike note, of roughly 0.4 sec. duration; this seems to begin as a normal note



FIG. 23. *Hyla graceae* (AMNH 114456), an adult male from cloud forest near Quebrada de Arena, 1120 m. elev. in the upper drainage of the Río Chiriquí.



FIG. 24. Habitat of *Hyla granceae*. *Top*: Upper end of highland valley of the Río Chiriquí, looking northeast across base of Cerro Las Lajas (mountain on right) toward low continental divide hidden in clouds (left of center). *Hyla granceae* occurs in the valley (see p. 10) but seems to be more common in cloud forest near the continental divide. *Bottom*: Clearing for new roadway through cloud forest near continental divide (1120 m. elev. on southern slopes Quebrada de Arena), upper Río Chiriquí drainage. *Hyla granceae* was breeding in small standing pools and in headwater rivulets at the edge of the clearing as well as under the dense canopy. (Both photographs by C. W. Myers, July 5, 1982. Upper scene, with glimpses of the Río Chiriquí, is from 1150 m. elev. looking across mouth of Río Hornito [not visible] and over La Sierpe, an old clearing soon to be flooded by the Fortuna Hydroelectric Project.)

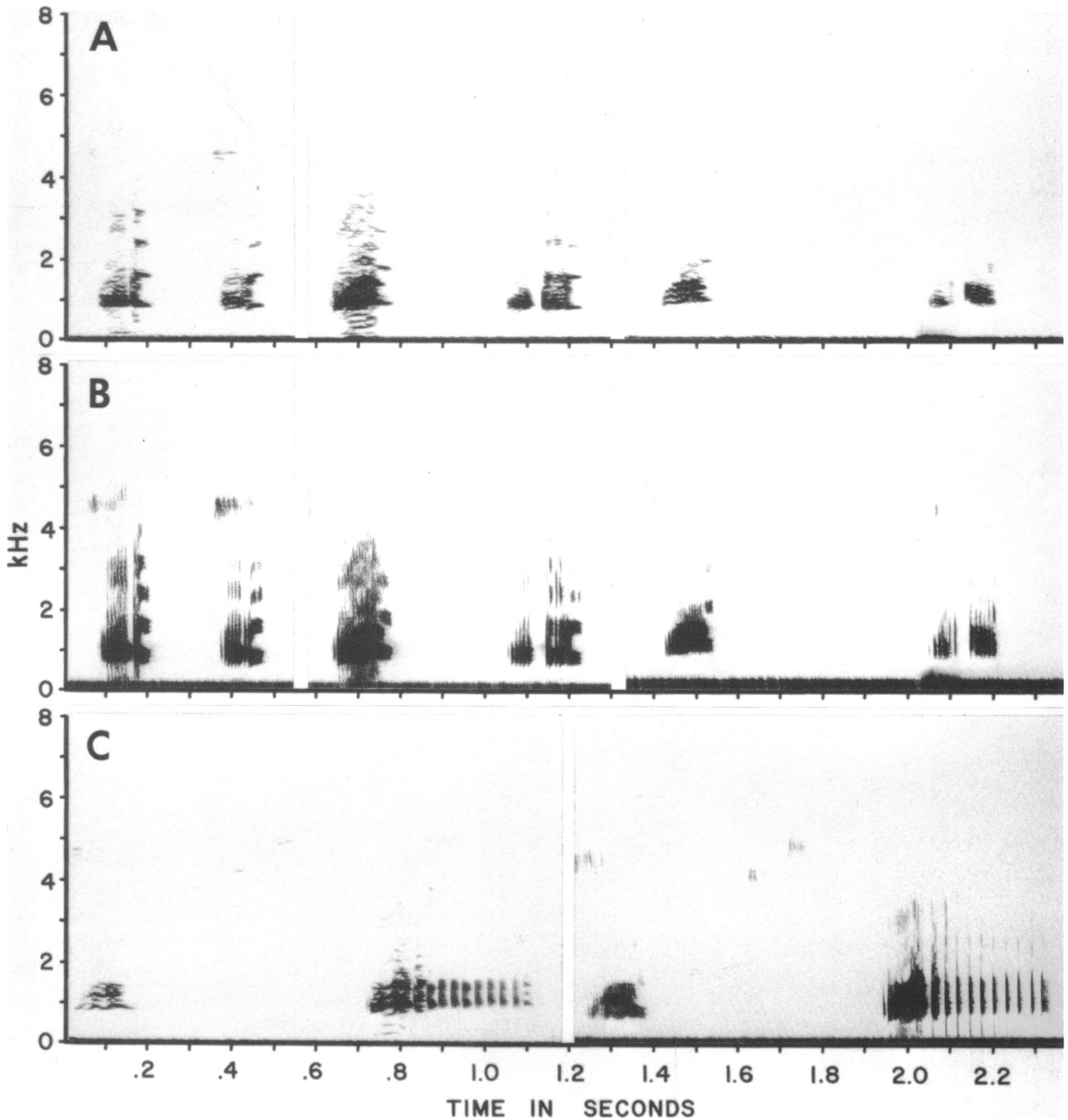


FIG. 25. Variability in calls of *Hyla graceae*. A. Three call groups of paired notes graphed with narrow band (45 Hz) filter, showing intragroup differences in note structure and varying intervals between notes. B. Same call groups as above graphed with wide band (300 Hz) filter. C. Single note followed by a "growl"; narrow band on left side, wide band on right. All recorded July 1982, at 19.0°C. at calling sites (AMNH reel 234); specimens are AMNH 114456 (last call group on right in A and B) and AMNH 114473 (all others).

but ends with a marked slowing of the pulse rate (fig. 25C). Based on very limited observation, the "growl" seemed to be produced most often when two or more males were calling in close proximity.

Excluding the growl-like sounds, the notes

of *Hyla graceae* show some similarity with those of its apparent relatives, *H. pseudopuma* and *H. angustilineata* (audiospectrograms in Duellman, 1970, pl. 20). But *graceae* seems normally to have a shorter note (~0.1 sec.) than that of *pseudopuma* (~0.3

sec. [accidentally rendered as "0.03" sec. in Duellman, *op. cit.*, pp. 65, 267]), and the note is lower pitched (maximum energy <1400 Hz) than that of *angustilineata* (>1600 Hz). The new observations reinforce previous indications (pp. 9–10) that the breeding habitat of *Hyla graceae* is ecologically similar to

that of *H. angustilineata* and *H. pseudopuma*.

NEW RECORD: AMNH 114456–114476, 114477 (tadpoles), south slope Quebrada de Arena, 1120 m. (about 0.6 km. SW continental divide, upper Río Chiriquí drainage, 82°12'43"W, 8°46'32"N), Chiriquí, Panama.