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## A Tepui Herpetofauna on a Granitic Mountain (Tamacuari) in the Borderland Between Venezuela and Brazil: Report from the Phipps Tapirapecó Expedition

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### ABSTRACT

Pico Tamacuari, the highest point (2340 m) in the Sierra Tapirapécó, dominates the skyline on the border between Brazil and Venezuela. It is a granitic dome that rises some 800 m above the wet montane forest below. This forest supports a depauperate herpetofauna reminiscent of a middle elevation forest fauna on a sandstone table mountain (tepui).

Eleven species of amphibians and reptiles were collected during a six-day period in the dry season (March), at 1160–1460 m above sea level. This sample includes six new frogs (*Hyalinobatrachium crurifasciatum*, n. sp., *Colostethus tamacuarensis*, n. sp., *Stefania tamacuarina*, n. sp., *Eleutherodactylus avius*, n. sp., *E. cavernibardus*, n. sp.).

At least some of these have counterparts that are endemic to tepuis.

Other species include a frog (*Hyla benitezi*) and two lizards (*Arthrosaura synaptolepis*, *Neusticurus racenisi*) endemic to the Pantepui Region, and a lizard (*Anolis chrysolepis*) and a snake (*Thamnodynastes pallidus*) widely distributed in Amazonia and Guayana. All five of these nonendemic Tamacuari species occur also on sandstone tepuis.

It seems not to matter to such species whether the underlying rock is sandstone or granite. The herpetofauna of Pantepui resembles the avifauna in not being completely restricted to habitats on sandstones of the Roraima Formation.

### RESUMEN

El Pico Tamacuari, el sitio más alto (2340 m) en la Sierra de Tapirapécó, domina el horizonte en la frontera entre Brasil y Venezuela. Es un domo de granito que se levanta unos 800 metros sobre el bosque húmedo montano. Este bosque tiene una herpetofauna de biodiversidad limitada que recuerda la fauna del bosque en la altura intermedia en un tepui de arenisca.

Se realizó una colección de 11 especies de anfibios y reptiles durante seis días en la temporada seca (marzo), a elevaciones de 1160 a 1460 m sobre el nivel del mar. Esta muestra incluye seis ranas nuevas (*Hyalinobatrachium crurifasciatum*, n. sp., *Colostethus tamacuarensis*, n. sp., *Stefania tamacuarina*, n. sp., *Eleutherodactylus avius*, n. sp., *E. cavernibardus*, n. sp.).

Algunas de estas especies tienen contrapartes que son endémicas en otros tepuis.

Además se colectaron una rana (*Hyla benitezi*) y dos lagartijas (*Arthrosaura synaptolepis*, *Neusticurus racenisi*) que son endémicas de la Región del Pantepui, y una lagartija (*Anolis chrysolepis*) y una serpiente (*Thamnodynastes pallidus*) que están ampliamente distribuidas en la Amazonia y en Guayana. Todas estas cinco especies no endémicas ocurren también en tepuis de arenisca.

Aparentemente no importa a tales especies si la roca fundamental es arenisca o granito. La herpetofauna del Pantepui se parece a la avifauna en que no se restringe a habitats de arenisca de la formación Roraima.

### INTRODUCTION

The 1988–1989 *Expedición a la Sierra de Tapirapécó* was a major multidisciplinary exploration of a wilderness in extreme south-

ern Venezuela—from the upper Río Mavaca south into the Sierra Tapirapécó on the Brazilian border—a rain forest sparsely peopled

only by the Yanomami. This was a Venezuelan venture, organized by Eugenio de Bellard-Pietri for the Caracas-based Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales (FUDECI). The total of 126 expedition members included 55 scientists and naturalists, mostly Venezuelans but including 18 foreigners (de Bellard-Pietri, "1993" [1996]: 183–187). The American Museum of Natural History (AMNH) was privileged to contribute personnel for the final month of this grand endeavor. The members of the *Phipps Tapirapecó Expedition* were the invited AMNH contingent of nine scientists, who helped close out the FUDECI expedition in early 1989.

The present report gives the herpetological results from one of the highland sites—a helicopter-supported montane camp below Pico Tamacuari in the Sierra de Tapirapecó. Tamacuari is a prominent peak rising up from undisturbed montane forest on the Brazilian border. Although Tamacuari is a granitic mountain, its small herpetofauna proved to be not unlike what might be expected in forest at equivalent elevation (1000–1500 m) on a sandstone table mountain (tepui) of the region.

#### ACKNOWLEDGMENTS

The American Museum part of the Tapirapecó Expedition was made possible by financing from the Howard Phipps Foundation, for which we are greatly indebted to AMNH trustee (now Chairman of the Board) Anne Sidamon-Eristoff and her brother Howard Phipps, Jr.

As AMNH coordinator of the Phipps Expedition, the first author acknowledges that the expedition would not have come off without additional vital aid and encouragement from the late Thomas D. Nicholson, Museum Director, and Robert G. Goellet, then president and now Chairman Emeritus of the Board of Trustees. Even though such administrative support is threaded throughout the Museum's expeditionary history, we do not take it for granted and are forever grateful for it.

The late Francisco Carrillo-Batalla, as President of FUDECI, issued the original invitation to the American Museum. The Tap-

irapecó Expedition was very capably organized by FUDECI Expedition Leader Eugenio de Bellard-Pietri and by Assistant Expedition Leader Pedro Pérez-Ramírez. Dr. de Bellard also arranged for all the various permits, including permission for importing firearms. Support from the Venezuelan Air Force (FAV) was crucial to this expedition.

Collecting was carried out under the authority of the Servicio Autónomo para la Protección, Restauración, Fomento y Racional Aprovechamiento de Fauna Silvestre y Acuática del País (PROFAUNA). We thank Dr. José Luis Méndez-Arocha, Director General of PROFAUNA, and his staff for many courtesies.

Dr. Antonio Machado-Allison, then Director of the Museo de Biología de la Universidad Central de Venezuela, also has been of particular help in many aspects of our work in Venezuela, including arrangements for the sharing of collections.

For lending critical specimens, we thank Dr. John E. Cadle and Mr. José Rosado, Museum of Comparative Zoology (MCZ), and Dr. William E. Duellman, University of Kansas Museum of Natural History (KU). For comments on various parts of the manuscript and other help, we are grateful to Mr. Taran Grant and Drs. Eugenio de Bellard-Pietri, William E. Duellman, Darrel R. Frost, John D. Lynch, Paulo E. Vanzolini, and Richard G. Zweifel. Figures 14 and 19 were drawn by Mr. Ted Kahn, figures 12, 28, and 39 by Ms. Patricia J. Wynne.

At the time of the expedition, the second author was an AMNH Boeschenstein Research Fellow (in Herpetology).

#### MATERIALS AND METHODS

**DEPOSITION OF SPECIMENS:** According to mutual agreement, herpetological materials from the Phipps Tapirapecó Expedition were, after completion of study, to be divided between the American Museum (AMNH) and the Museo de Biología de la Universidad Central de Venezuela (MBUCV) in Caracas. The entire collection was thus treated identically to one from Cerro Guaiquinima (see Donnelly and Myers, 1991: 3), with the collection being cataloged in the American Museum prior to division, to allow for perma-

nency of records and tracking. For purposes of this paper, Dr. Antonio Machado-Allison kindly arranged to provide MBUCV catalog numbers before specimens were returned to Caracas, and the MBUCV numbers are cited herein.

**METHODS:** Insofar as practical, we find it useful to follow Ruiz-Carrenza and Lynch's (1991a, 1991b et seq.) standardized format for definitions ("diagnoses") and descriptions of centrolenids, and Lynch's long-term format and methodology for eleutherodactyline leptodactylids (best summarized in Lynch and Duellman, 1980). For anuran webbing formulae, however, we use the notational device of Savage and Heyer (1967) as modified for general use by Myers and Duellman (1982: 6); see also Myers et al. (1991: 6) regarding the desirability of using this convention for dendrobatids. Tadpoles were staged according to Gosner (1960).

Measurements were read to the nearest 0.1 mm with digital calipers or (if  $< 12$  mm) with an ocular micrometer fitted in a Wild dissecting microscope. Sound spectrographs and waveforms were produced using a Kay 5500 DSP Sona-Graph.

#### PERSONNEL AND ITINERARY

On March 7, 1989, participants and supplies for the final month of the Tapirapecó Expedition were transported by a Venezuelan Air Force cargo plane from the Caracas international airport to Ocamo, a Yanomami mission on the upper Río Orinoco. From there, people were ferried by Air Force helicopters and heavy cargo moved by dugout, about 140 km by river south to the lowland base camp on the upper Río Mavaca (fig. 1).

Venezuelan scientists arriving with us at the FUDECI base camp included Ricardo

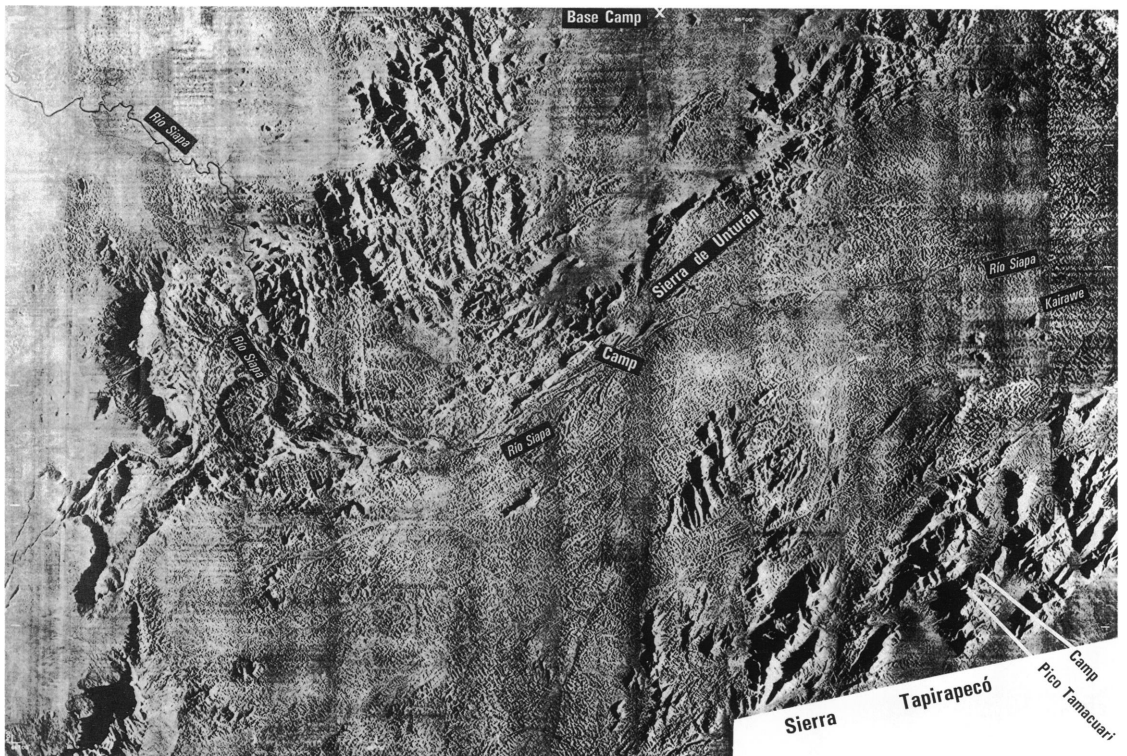


Fig. 1. Side-looking radar image of the upper Río Siapa drainage and the Sierra Tapirapecó on the Venezuelan-Brazilian frontier. Also included is the extreme upper Río Mavaca drainage (base camp), top center, north of Sierra de Unturán. The image slightly exceeds the area enclosed by parallels  $1^{\circ}$  to  $2^{\circ}$  North, and meridians  $64^{\circ}30'$  to  $66^{\circ}$  West. See also map of Pantepui Region (fig. 50 on page 66).



Guerrero, Omar E. Hernández P., and Johani Ojasti in mammalogy and parasitology, Antonio Machado-Allison and Ramiro Royero in ichthyology, and Raúl Walder and Octavio Manuel Suárez Freites in virology and epidemiology. American Museum representatives included George F. Barrowclough and Patricia Escalante-Pliego for ornithology, Carl J. Ferraris, Jr. for ichthyology, David A. Grimaldi for entomology, and a herpetological group composed of Charles J. Cole, John W. Daly, Carol R. Townsend, and ourselves.

Herpetological collections were made in the vicinity of base camp by all five herpetologists, in the upper Siapa valley by Ferraris in conjunction with ichthyological work, at a highland camp on the crest of the Sierra de Unturán by Cole and Townsend in company with Grimaldi, and at the Pico Tamacuari camp in the Sierra Tapirapecó. The present paper concerns itself only with the Pico Tamacuari collection, which was made by Daly, Donnelly, and Myers, in company with Barrowclough, Escalante, and an Indian assistant known to us only as Rafael.

On the afternoon of March 11, the six members of the Pico Tamacuari party were transported in two Air Force helicopters, from Mavaca base southeast to a mountain ridge near the Brazilian border—a distance of 100 km, with a flight time of 35 minutes at 110 knots. Camp was made at a helipad that some time previously had been hand-cleared by workers dropped by helicopter; to our knowledge, no trails have ever been cut up to the high reaches of the Sierra Tapirapecó, although the Yanomami have a trail crossing from Venezuela to Brazil over an adjacent, lower divide.

The two-way radio sent with our party failed, we were isolated for a few days longer than expected, and so we rationed food accordingly. Our helicopters arrived unannounced and unexpectedly early, shortly after first light on the morning of March 18, circling while we lowered tents and broke camp in about 10 minutes time. We learned that a period of bad weather north of the Sierra de Unturán had prevented their checking on us after failing to make radio contact. The extra days, however, had permitted additional collecting, especially at night (the last mornings

had been spent taking down tents and waiting for helicopters until late afternoon).

## THE NATURAL LANDSCAPE

The Sierra Tapirapecó<sup>3</sup> is part of the southern Venezuelan highlands that, as summarized by Huber (1995a: 34), “include a series of ill-defined and almost entirely unexplored uplands, ranging mainly between 600 and 1400 m elevation. Some isolated higher peaks [include] Cerro Tamacuari.” The Sierra Tapirapecó forms part of Venezuela’s southeastern border with Brazil, extending from southwest to northeast for a little over 100 km and having a width of about 20 km; Pico Tamacuari rises far above the rest of the chain, to an elevation of 2340 m (de Bellard-Pietri, 1989, “1993” [1996]).

Very little has been written about Sierra Tapirapecó. A Brazilian source summarizes the geomorphology as follows (Projeto Radambrasil, 1975: 155, translated by P. E. Vanzolini):

Serra Tapirapecó, Sheet NA.20-Y-A, is formed by an ensemble of ridges 600 to almost 2000 m above sea level, and a lower step at about 600 m, dissected in hills and entrenched valleys. These sets of reliefs demonstrate the intense structural control of the faults and fractures with main direction NE–SW. The ridges present pediments on their slopes; they are reshaped by a first-order drainage, and in some places they show distinct edges. Serra Tapirapecó is constituted of rocks of the Guianese Complex (Lower to Middle Precambrian) and runs from SW to NE for some 100 km. Its limits are the rivers Marauíá to the west and Jurupari to the east.

The NE–SW orientation of both the sierra and its parallel ridges can be seen in the lower right corner of figure 1, which shows somewhat over half its length. The lower areas intervening between the ridges, at a purported elevation of about 600 m (see above), are crossed by the divide that separates north-flowing Venezuelan waters (Río Siapa drainage) from south-flowing Brazilian streams.

The individual ridge from whence Pico Tamacuari rises can appropriately be called Cerro Tamacuari. But other ridges are not individually named and we find it more con-

<sup>3</sup> We follow cartographic convention in using the grand-sounding *Sierra* (*Serra* on Brazilian maps) for this small range, although a few recent authors have used *Serranía* instead (e.g., de Bellard-Pietri, “1993” [1996]). A few authors insert the preposition *de*, but most authors and cartographers do not use it.

venient to relate our collecting localities to the peak itself. "Pico Tamacuari" is a prominent if not often seen geographic feature that frequently appears on maps (e.g., foldout map in Mayr and Phelps, 1967; folded topographic map in Steyermark et al., 1995). The underlying and frequently exposed rock of the Sierra Tapirapécó evidently is mainly granitic, although the possibility of Roraima sandstones or quartzites occurring unconformably on the basement rock cannot be completely dismissed. A small area ( $< 1 \text{ km}^2$ ) attributed to the Roraima Group occurs in Brazil only some 30 km SW of Pico Tamacuari (Projeto RadamBrasil, 1975: mapa geológico 1:1,000,000). But the nearest large remnant of the Roraima Formation is vested in the Serranía de la Neblina to the west and southwest (Brewer-Carías, 1988).<sup>4</sup>

The Sierra Tapirapécó is blanketed primarily in evergreen lower montane and upper montane forest that is very poorly known botanically (see comments by Huber, 1995b: 130). The forest cover is broken by exposed rock faces and rocky stream beds and by shrubby areas with grass or bromeliads on narrow ridges and steep hill sides.

#### THE PICO TAMACUARI COLLECTING AREA

Pico Tamacuari dominates the skyline (figs. 2, 3). Our camp was situated on a short spur ridge to the north (NNE) of the peak, at the lower, more northerly of two helipads that had been hand-cleared for the expedition. Elevation of our campsite (i.e., the lower helipad) was 1270 m above sea level according to our altimeter. The same instrument gave 1460 m at the second helipad higher on the same ridge; this reading corresponds well to an earlier, rounded one of 5000 ft ( $\approx 1500 \text{ m}$ ) taken from a helicopter altimeter at the upper helipad. Coordinates for our camp and area of activity were recorded as  $1^{\circ}13'N$ ,  $64^{\circ}42'W$  (expedition files, courtesy Eugenio de Bellard-Pietri).

<sup>4</sup> But to further complicate matters, the Tapirapécó Expedition resulted in a still undocumented discovery on Sierra de Unturán of a purported new formation, said to comprise ancient, fine-grained, white sandstones (FUDCI, 1990: [8], [41]; de Bellard Pietri, "1993" [1996]: 173). Cerro de Unturán has been considered granitic (e.g., Huber, 1995a: 35, 49).

We collected at several places along the camp ridge, especially in dense, wet forest just south of the camp helipad. Working southwestward along this ridge, which delimits the western side of a small hanging valley, brought one to the western base of Pico Tamacuari (fig. 4).

Much of our collecting was at the northern base of Pico Tamacuari in the little hanging valley, which was situated southeastward from camp—upstream from the deep gorge due east of camp (fig. 5, upper). Our trail from camp (1270 m) first led easterly down to a narrow stream at 1200 m where we got our water (and collected a species of small catfish), then south over the crest of a little side ridge (1210 m) and down to a larger stream at 1160 m. This was about a 20 minute walk over a muddy trail; another 30 minutes up and across this stream took us to a wooded hillside at 1260 m, close to the north base of Pico Tamacuari.

The small, high valley below the north face of Pico Tamacuari is heavily forested for the most part. The main stream is subject to flash flooding, as immediately suggested by the scoured stream bed and adjacent expanses of clean-swept, bare bedrock. Shortly after a midday rainstorm, the normally wadable stream was a torrent about a minute after it started to rise, separating some members of our party from camp for several hours.

The Pico Tamacuari area was frequently windy and subject to violent storms during our brief stay. We experienced significant rainfall during three of our seven days and nights in the "dry season." The night of March 13 was especially remarkable. The wind changed from westerly to southerly, bringing from Brazil a nightlong series of thunderstorms with lightning and hard, driving rains. Winds were so fierce that a tent anchored on the helipad (one of the few flat places) would have been lost without the weight of its occupants and their gear. A journal note put it simply as "a wild night in a wild place."

#### THE DIVIDE BELOW

Some hours before that memorable storm, at 1:10 pm on March 13, Rafael called from the helipad that he had just seen a small airplane crash into the jungle below our ridge. Less than a minute later, others of us who had



Fig. 2. Approaching Pico Tamacuari (arrow) in the Sierra Tapirapecó, Venezuelan-Brazilian border. Viewed looking SSW from Venezuelan Air Force (FAV) helicopter, March 11, 1989.

Lower photograph shows location (x) of hand-cleared landing spot at 1270 m above sea level, on ridge crest north of Pico Tamacuari. Following photographs (figs. 3–6) were taken from this helipad on March 13–15.



Fig. 3. Pico Tamacuari, a granitic dome rising from evergreen montane forest to a purported elevation of 2340 m above sea level. Viewed looking SSW ( $210^\circ$ ) from camp helipad.

been working in camp could see a huge plume of oily smoke coming up through the forest canopy, hundreds of meters below and several km distant, at a compass bearing of  $303^\circ$ .

The plane had been heading toward Venezuela from Brazil when it went down on the international divide (fig. 6, lower). We were astonished to hear human shouts drifting up the mountainside within half an hour afterwards and continuing for two or three

hours—the kind of noises woodsmen make to penetrate forest while keeping in touch with one another. But Rafael said that a Yanomami trail crosses that divide from the upper Río Siapa to Brazil, so Indians presumably had been nearby. Our radio was inoperable and in our isolation we could only bear witness. A wisp of smoke was still rising from the crash site as night fell.

Three days later, on March 16, a small



Fig. 4. Head of drainage system between west base of Pico Tamacuari and three smaller peaks, as viewed looking SW ( $230^\circ$ ) from camp helipad. The great mass of Pico Tamacuari contributes to substantial runoff and flooding in the heavily forested drainage system along its northern base.

nonmilitary plane came from Brazil, flying low and making several passes back and forth across the divide below us. During the following afternoon, a small helicopter flew back and forth from Brazil, landing several times at or near the crash site—on one occasion lifting off with a cargo net containing what might have been a body bag (as viewed through binoculars). Our subsequent fly-over in a Venezuelan Air Force helicopter revealed that the smaller Brazilian craft had landed not in a stream bed, as surmised, but in the forest in a new clearing made with chain saw—which must have been packed in from Brazil. We saw no wreckage or other break in the forest canopy. It was odd that from our vantage we had been able to hear the calling of searchers but not the sounds of a plane crash or noisy chain saw. The use of this air corridor seemed unknown to Venezuelan authorities and we never learned who had been in the fallen plane.

Later in this paper we name *Eleuthero-*

*dactylus memorans*, a little frog that was common in the forest around our helipad. We suppose that it still voices its tinklike calls at the place where we were, and we leave it as our proxy—remembering and wondering about whoever it was that died on the divide, below our high ridge camp.

## SPECIES ACCOUNTS<sup>5</sup>

### FROGS

#### FAMILY CENTROLLENIDAE

#### *Hyalinobatrachium crurifasciatum*, new species

Figures 7–10

HOLOTYPE: AMNH 131329 (field no. CWM 18764), an adult male from forested

<sup>5</sup> An account is not included for *Bufo* sp. (Bufonidae), which was heard but not collected at Pico Tamacuari. The unmistakable trill of what was probably a small to medium-size species of *Bufo* was heard one night upstream from our water source east of camp. It was a solitary call not repeated.

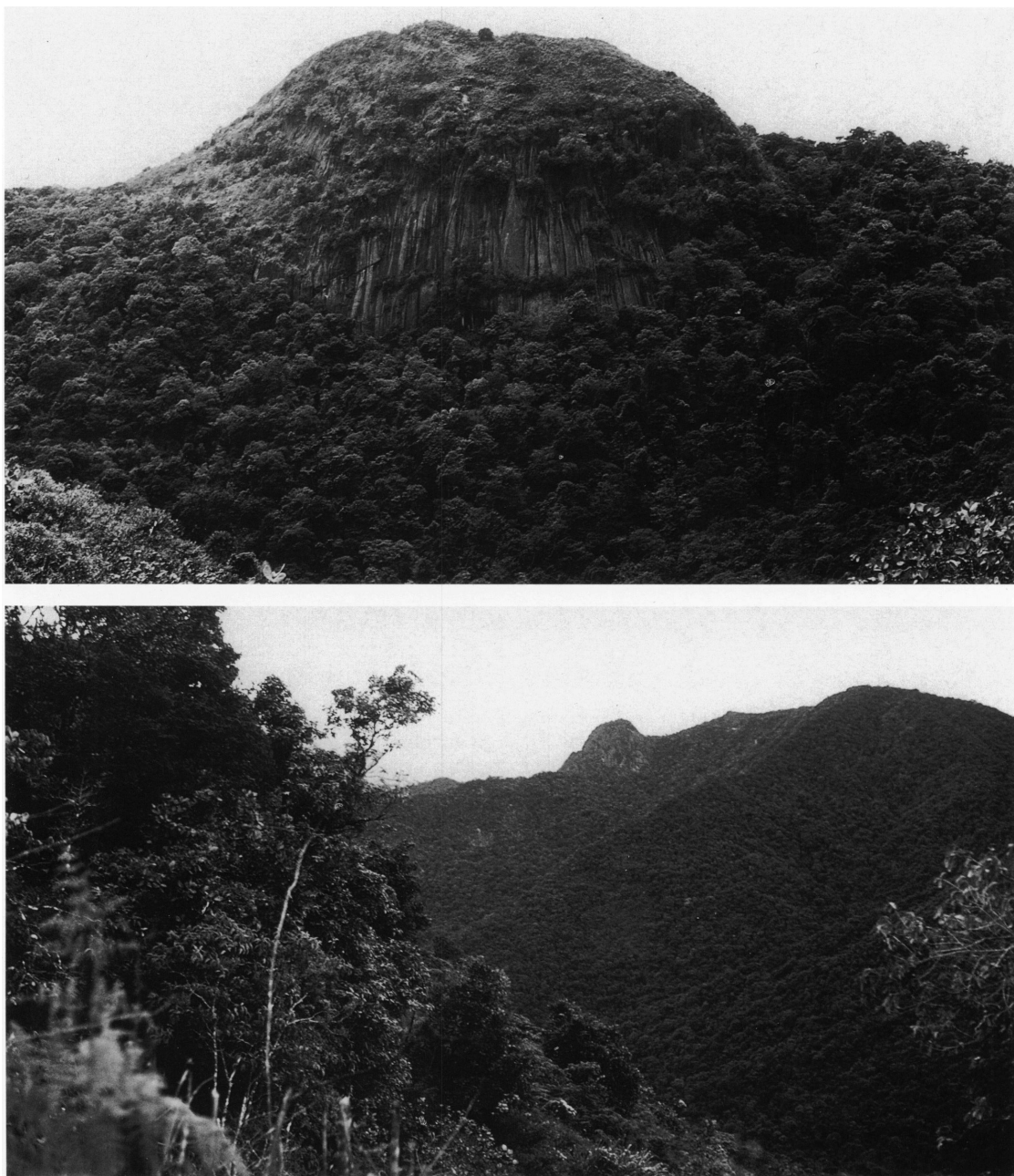


Fig. 5. Views east and west from camp helipad. **Upper.** East across gorge to a small, partly vegetated granitic dome. **Lower.** West into Brazilian part of the Sierra Tapirapécó.

stream at north base of Pico Tamacuari, 1160–1200 m elevation, Sierra Tapirapécó, Amazonas, Venezuela ( $1^{\circ}13'N$ ,  $64^{\circ}42'W$ ). Obtained in the period March 11–17, 1989; Myers, Donnelly, and Daly collection.

PARATOPOTYPES: AMNH 131331, MBUCV 6428, two adult males with same data as holotype.

ETYMOLOGY: The species name is an adjective in neuter gender, derived from the





Fig. 6. Views north-northeast and northwest from camp helipad. **Upper.** Looking NNE ( $25^{\circ}$ ) through the Sierra Tapirapécó to *Kairawe*, the far distant peak that rises in isolation in the valley of the upper Río Siapa. **Lower.** Looking NW ( $303^{\circ}$ ) to smoke from plane crash on forested divide between Brazil on the left and Venezuela on the right (1315 hours, March 13, 1989).

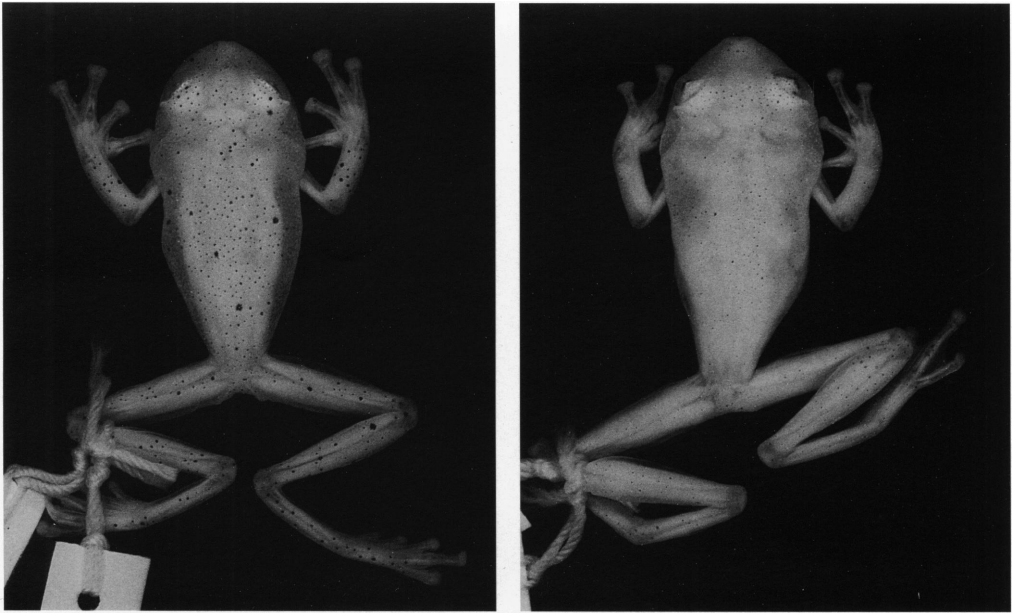


Fig. 7. *Hyalinobatrachium crurifasciatum*, new species. Holotype (AMNH 131329♂) left and paratype (MBUCV 6428♂) right,  $\times 2$ . In life, these frogs had yellow spots set in a green reticulum and the limbs were distinctively banded in dark and lighter green. Except for minor markings, the characteristic color pattern has disappeared in preservative, as often is the case with centrolenid frogs.

Latin *crus*, gen. *cruris* (leg) + connecting *-i* + *fasciatus* (banded), in allusion to the limbs, which are green crossbanded in life (markings disappear in preservative).

**DEFINITION AND DIAGNOSIS:** A *Hyalinobatrachium* (liver bulbous) belonging to the *fleischmanni* species group and characterized by the following combination of characters (in the format of Ruiz-Carranza and Lynch, 1991b): (1) Vomerine teeth absent; (2) bones white in life; (3) parietal peritoneum clear; liver, stomach and intestines, and part of pericardium silvery white; (4) in life, head and dorsum with yellow spots set in a light green reticulum dotted with melanophores, sides unpigmented; limbs banded dark and paler green; in preservative, spots and limb bands lost, dorsum becoming cream with purple melanophores; (5) webbing basal between inner fingers; webbing formula for outer fingers III 2–2 IV; (6) webbing formula for foot I 2–1 II 1–2 III 1–2 $\frac{1}{4}$  IV 2 $\frac{1}{2}$ –1 V; (7) snout truncate in dorsal and lateral views; (8) dorsal skin smooth in preservative; (9) weak ulnar and tarsal folds present; (10) male humeral spine absent; (11) tympanum covered by skin (visible through

skin); (12) size medium, males 22–24 mm SVL; (13) nuptial excrescences white, forming a type 1 pad (sensu Flores, 1985).

This species appears to differ from other named members of the *fleischmanni* group in having distinctly green-banded limbs in life. In addition, the dorsal color pattern and/or the presence of an ulnar fold differentiates *H. crurifasciatum* from its geographically nearest *fleischmanni*-group neighbors. See Remarks for further comparison.

**MEASUREMENTS OF HOLOTYPE** (in mm): The undissected holotype is an adult male as revealed by presence of vocal slits and partially distended, subgular vocal pouch. SVL 22.0, tibia length 12.0, foot length from proximal edge inner metatarsal tubercle to tip of longest toe 9.7, head width 9.0, head length on the diagonal from angle of jaw to tip of snout 7.0, upper eyelid width 1.4, interorbital distance 3.2, eye to posterior edge of nostril 1.9, eye length 2.3, tympanum 0.6.

#### DESCRIPTION

Adult males moderate-sized, 22.0–24.0 mm SVL ( $\bar{x}$  = 23.33, SD = 1.155,  $N$  = 3);



females not known. Liver bulbous (based on dissection of AMNH 131331). Head wider than body; head width 39.6–42.1 percent of SVL. Snout short, truncate in dorsal and lateral views; canthus rostralis indistinct; loreal region sloping to lip; lips not flared; nostrils terminal, protuberant, directed laterally; internarial region flat. Eyes large, directed anterolaterally, length greater than eye-nostril distance; eye length/eye-nostril distance 1.19–1.25. Upper eyelid width 36.7–43.8 percent of interorbital distance. Supratympanic fold absent; tympanum covered by skin but visible through skin (at least in preserved specimens). Vomerine teeth absent; choanae small, oval; tongue round, entire, barely free posteriorly. Vocal slits extending from lateral base of tongue toward angle of jaw; distensible subgular vocal pouch.

Humeral spine absent; a low, white ulnar fold extending from elbow along ventrolateral edge of arm to disk on finger IV. Relative length of appressed fingers III > IV > I > II. Webbing basal between inner fingers; webbing formula for outer fingers III 2–2 IV. Finger discs truncate. Thenar tubercle elliptical, low; palmar tubercle small, round, low; supernumerary palmar tubercles small and round, subarticular tubercles small, low, round, entire. Hind limbs slender; tibia length 49.6–54.6 percent of SVL ( $\bar{x}$  = 52.7%). Low white ridge from heel to disk of toe V. Inner metatarsal tubercle elliptical, low; outer metatarsal tubercle absent; subarticular tubercles low, round, entire. Feet about three-quarters webbed; webbing formula for foot I 2–1 II 1–2 III 1–2 $\frac{1}{4}$  IV 2 $\frac{1}{2}$ –1 V. Toe discs rounded to truncate, smaller than those on fingers.

Skin overall smooth except areolate on belly and ventral thigh surfaces. Vent directed posteriorly at upper level of thighs; cloacal opening concealed by short anal flap; anal ornamentation consisting of folds and enlarged white tubercles.

**COLOR AND PATTERN:** In life, the head and dorsum of body had a pattern of pale yellow spots set in a light green reticulum, which was dotted with melanophores; the flanks lacked pigment. The limbs were banded above in dark and paler green. Parietal peritoneum clear; heart mostly visible, only part of pericardium being silvery white; intestinal

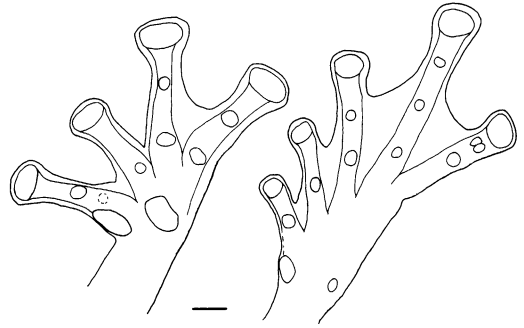


Fig. 8. *Hyalinobatrachium crurifasciatum*, new species. Left hand and left foot of male holotype. Scale line = 1 mm.

tract and liver silvery white. Bones white. Iris golden, with sparse dark dots.

In preservative, dorsal surfaces are cream; eyelids white; dorsal surfaces of body (including eyelids), lower arm, thigh, shank, tarsus, foot, and outer toes dotted with purple melanophores of varying size; a few small white spots scattered over all dorsal surfaces. Ventral surfaces uniform cream. Liver and digestive tract white.

#### TADPOLES

One lot of 18 larvae (AMNH 131339, MBUCV 6429) hatched from a clutch of eggs from the underside of a leaf (see below). The tadpoles are in early stage 25, with total lengths of 12.8–13.8 mm ( $\bar{x}$  = 13.33, SD = 0.316). The musculature of body and tail is tan, peppered with melanophores. The low fins are transparent. The eyes are dorsolateral; the vent tube opens medially to the ventral fin; the just-developed spiracle is sinistral and low on the body.

The mouthparts are poorly developed. There is no significant keratinization of beak or denticles, although at least two denticle ridges are discernible on the posterior labium, which is pendent; the anterior labium is not developed. The oral disc is not indented laterally. The anterior edge of the oral disc is nude, but its lateral and posterior edges are fringed with a single row of small papillae.

In Venezuela, centrolenid tadpoles have been reported for *Centrolene andinum* by Mijares-Urrutia (1990). In contrast to *H. crurifasciatum*, stage-25 *andinum* have the

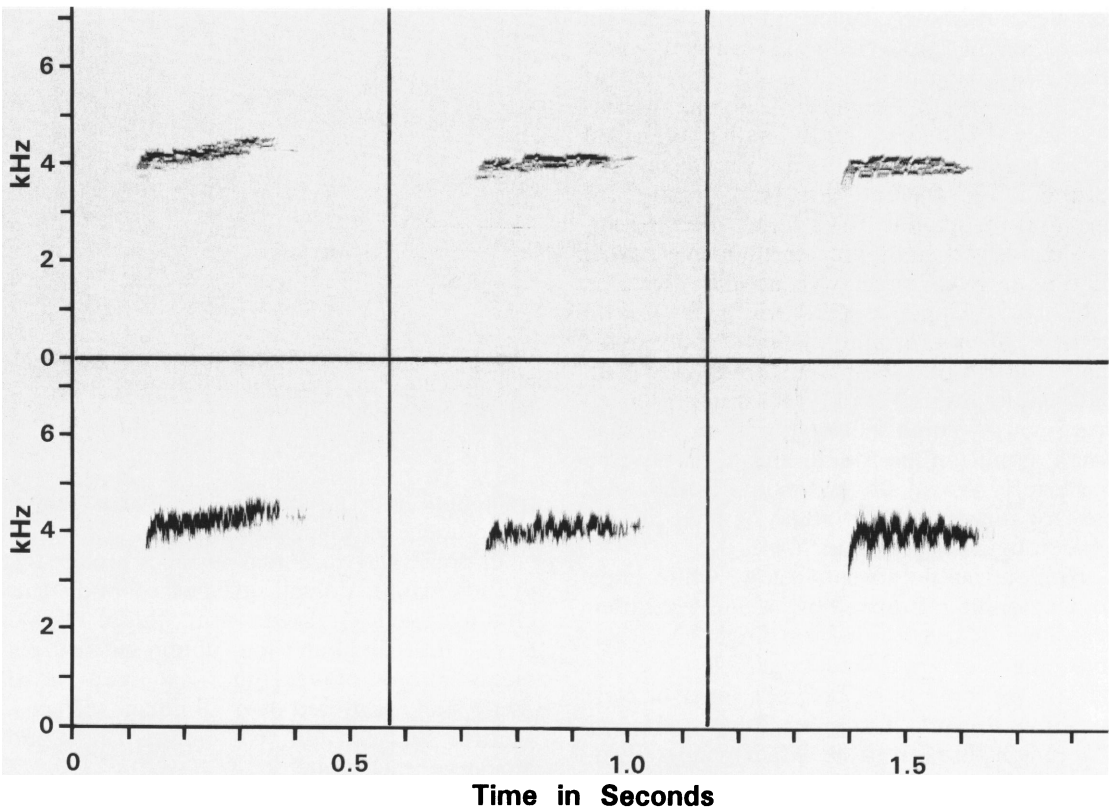


Fig. 9. Variability in frequency modulation and duration of the single-note call of *Hyalinobatrachium crurifasciatum*, new species. Three selected calls (= single notes) from a single frog, graphed with narrow-band (59 Hz) filter above and with wide-band (300 Hz) filter below. Recorded March 16, 1989, at air temperature of 17.4°C (AMNH herpetology reel 256: 6).

eyes barely visible but keratinization of the beak is extensive; the tooth row formula was stated as 2(2)/2(1), although not readily discernible from the figure. Subsequent development in *C. andinum* includes loss of keratin from the beak and denticles, with the denticles being replaced by papillae.

#### NATURAL HISTORY AND VOCALIZATION

The three type specimens were calling at night from undersides of leaves overhanging a rock cliff, about 2–4 m above a forest stream in the hanging valley. Females were not seen, but a clutch of eggs with pale green yolks was found nearby, plastered to the underside of a leaf. These were put in a plastic bag and produced 18 tadpoles (see above), whose yolk reserves showed pale green through the abdominal wall.

A sound recording was made from a fourth male that also was calling in an upside-down position, but it escaped capture. The recording consists of a series of well-spaced, single-note calls heard as drawn-out “peeps.” The single-note calls are 0.20–0.29 sec in duration ( $\bar{x}$  = 0.237 sec, SD = 1.974,  $N$  = 32), with intercall intervals of 1.8–6.3 sec ( $\bar{x}$  = 3.33 sec, SD = 1.20,  $N$  = 31). The call is seen to be weakly pulsed in the waveforms (fig. 10), with pulsation also suggested by the parallel traces in narrow-band spectrograms (fig. 9, upper).

These calls vary in quality, some being shorter and slightly louder than the others. All are initiated with a brief rise in frequency from  $\geq 3500$  Hz to 4000 Hz. Either kind of note may be maintained along a flat frequency of 4000 Hz or in a rise to  $\leq 4600$  Hz.

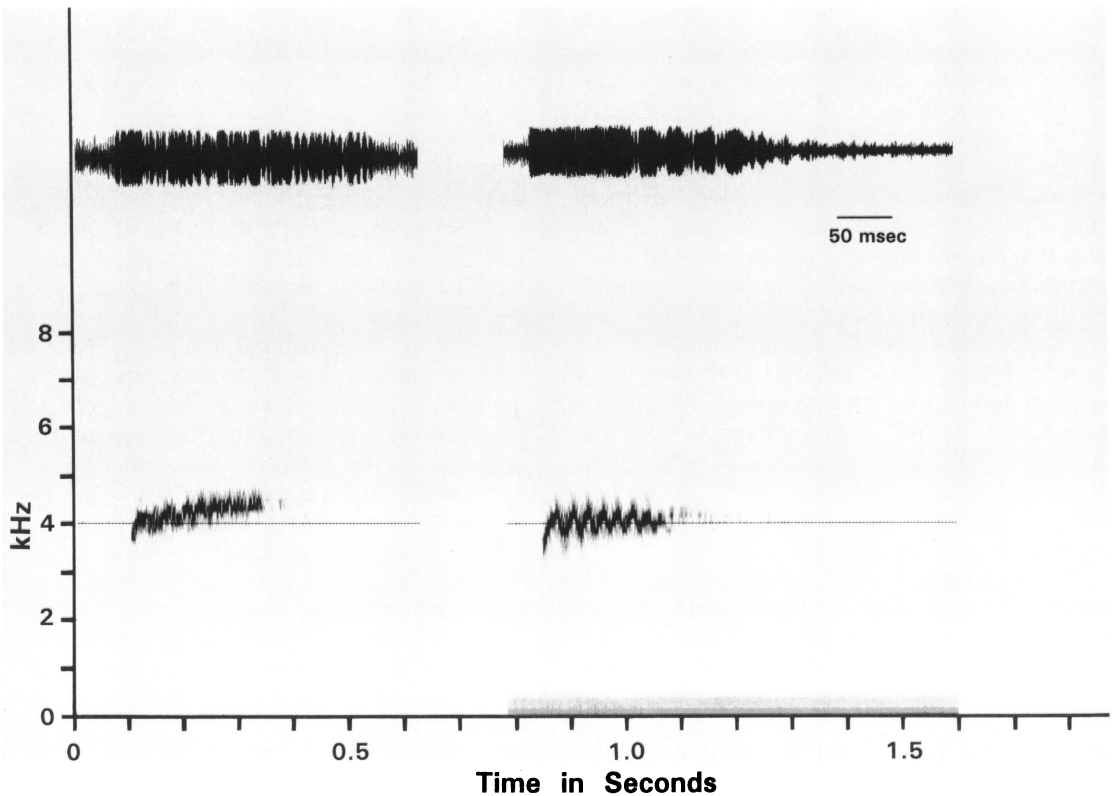


Fig. 10. Two calls (= single notes) of *Hyalinobatrachium crurifasciatum*, new species. Expanded waveforms above and wide-band (300 Hz) spectrograms below, with frequency cursor set at 4000 Hz. "Slurred" note on left (0.2484 sec duration) is given with a constantly rising frequency; internal modulation is obscure. Slightly louder and shorter note (0.2453 sec) on right shows pronounced modulation around a constant frequency. Other data same as for figure 9.

Spectrographically, the slightly shorter notes show more pronounced modulation above and below the base frequency, whereas the slightly longer notes have a slurred quality (figs. 9, 10). Where pulsation is evident, each pulse has a sharp rise and drop of frequency of about 800 Hz total; the same pattern of frequency modulation occurs in the apparently unpulsed, initial part of the right-side note in figure 10, but the waveform analysis is unsatisfactory because of stream noise in the close background.

The call variation described above seems to have been produced within a sequence of calls from a single frog and may possibly be an antipredator mechanism.

Four species of Venezuelan centrolenids have been reported to give single note calls (*Cochranella auyantepuiana*, *C. duidaeana*,

*H. iaspidiense*, and *H. orientale*), but a spectrograph has been published only for the first one. *Cochranella auyantepuiana* has a reported note duration of 0.17 s at a dominant frequency of 4000–4500 Hz at apparently constant frequency (Señaris and Ayarza-güena, "1993" [1994]: 125).

#### REMARKS

Twenty-two named species of centrolenids occurring in Venezuela are recognized in the literature, which is mostly the work of Juan A. Rivero. In 1961, Rivero was able to list only three species (*buckleyi*, *fleishmanni*, and one unnamed), all in the genus *Cochranella*. Goin (1963) then named *Centrolenella antis-thenesi* from Rancho Grande. Rivero (1968a) subsequently followed Goin in not recogniz-

ing *Cochranella* and described seven new Venezuelan taxa of *Centrolenella* (*altitudinalis*, *andina*, *estevesi*, *orientalis*, *orocostalis*, *pulidoi*, and [as a subspecies of *buckleyi*] *venezuelensis*—a name ignored by most authors). In a third major paper, Rivero (1985) listed 16 Venezuelan *Centrolenella* in total, including eight more new species (*duranti*, *fragilis*, *lentiginosa*, *loreocarinata*, *ostracodermoides*, *pallida*, *pleurolineata*, *revocata*<sup>6</sup>).

It has been suggested that two of Rivero's 1968 species (*estevesi* and *pulidoi*) may be hylids (Frost, 1985: 80, 84), and two other species have been synonymized. Cannatella and Lamar (1986) synonymized *orocostalis* Rivero, 1968, under *orientalis* Rivero, 1968. Ruiz-Carranza and Lynch (1995) placed *lentiginosa* Rivero 1985 as a junior synonym of *andina* Rivero 1968.

Ruiz-Carranza and Lynch (1991a) assessed the rich suite of centrolenid characters, synonymized the generic name *Centrolenella* Noble (under *Centrolene*), and proposed a new generic partitioning, using the names *Centrolene* Jiménez de la Espada, *Cochranella* Taylor, and *Hyalinobatrachium* Ruiz-Carranza and Lynch. These genera form an unresolved trichotomy and no evidence of monophyly could be provided for *Cochranella* (containing the *granulosa* and *ocellata* species groups), which may be relatively plesiomorphic. Ruiz-Carranza and Lynch redistributed most named species under these genera, changing the endings of species names as appropriate to the generic name (except neglecting to change *altitudinalis*).

Ayarzagüena (1992) reviewed species from the Venezuelan Guayana under the name *Centrolenella*. He named five new species (*duidaeana*, "*gorzulae*," *helenae*, *iaspidensis*, and *riveroi*), extended the range of *C. taylor* Goin<sup>7</sup> from Guyana into Venezuela (Edo. Bolívar), and provided new records for

*C. orientalis* Rivero. Ayarzagüena (1992: 7) seemingly accepted *Centrolenella pulidoi* Rivero as a valid species in the region but made no other comment—not even to compare it with *C. duidaiana* being described from the same locality (summit of Cerro Duida).

Duellman (1993) distributed Ayarzagüena's species among the genera *Centrolene*, *Cochranella*, and *Hyalinobatrachium* according to Ruiz-Carranza and Lynch's arrangement. In so doing, Duellman (1993: 44) inadvertently misspelled *duidaiana* as "*duidaensis*," but he correctly changed *gorzulae* (an incorrect original spelling) to *gorzulai* as required by the *International Code*.

Señaris and Ayarzagüena ("1993" [1994]) named *Centrolenella auyantepuiana* from Edo. Bolívar, saying that it would be a *Cochranella* following the Ruiz-Carranza and Lynch arrangement.

A list of the 22 currently recognized centrolenids in Venezuela, after the generic partitioning of Ruiz-Carranza and Lynch (1991a), follows:

#### **Centrolene** (neuter)

*Ce. altitudinale* (Rivero, 1968)

*Ce. andinum* (Rivero, 1968)

*Ce. gorzulai* (Ayarzagüena, 1992)

*Ce. venezuelense* (Rivero, 1968), new combination

#### **Cochranella** (feminine)

*Co. auyantepuiana* (Señaris and Ayarzagüena "1993" [1994]), new comb.

*Co. duidaiana* (Ayarzagüena, 1992)

*Co. helenae* (Ayarzagüena, 1992)

*Co. riveroi* (Ayarzagüena, 1992)

#### **Hyalinobatrachium** (neuter)

*fleischmanni* group

*H. crurifasciatum*, new species

*H. durante* (Rivero, 1985)

*H. fragile* (Rivero, 1985)

*H. iaspidiense* (Ayarzagüena, 1992)

*H. loreocarinatum* (Rivero, 1985)

*H. orientale* (Rivero, 1968)

*H. ostracodermoides* (Rivero, 1985)

*H. pallidum* (Rivero, 1985)

*H. pleurolineatum* (Rivero, 1985)

*H. revocatum* (Rivero, 1985)

*H. taylori* (Goin, 1968)

*pulverata* group

*H. antisthenesi* (Goin, 1963)

#### **Incertae Sedis**

*Centrolenella estevesi* Rivero, 1968

*Centrolenella pulidoi* Rivero, 1968

<sup>6</sup> Rivero (1985: 351) relegated his earlier Venezuelan records of *fleischmanni* to his new *Centrolenella revocata*. It should be noted that most of Goin's (1964: 7) Venezuelan specimens of purported *fleischmanni* were ones earlier reported by Rivero and the name *fleischmanni* therefore is dropped from the Venezuelan fauna.

<sup>7</sup> Goin (1968: 118) had suggested that a Venezuelan (Cerro Marahuaca) specimen discussed by Rivero (1961: 152–153, as *Cochranella* sp.) might be *taylori*, but the distribution seems unlikely.

As indicated in the diagnosis, *Hyalinobatrachium crurifasciatum* is a member of the *fleischmanni* species group, as suggested by the absence of vomerine teeth, white bones, and turning whitish in preservative. In life, the green-banded limbs seem to set it off from other named members of the group. Because of the banded limbs, *H. crurifasciatum* most closely resembles one or two unnamed Venezuelan species from Amazonas and Bolívar. Specimens of one of these populations, from the Escalera region, have been reported in the literature as *Centrolenella orientalis* (= *H. orientale*) by Cannatella and Lamar (1986). A color description is provided by Duellman (in press), who comments that Cannatella and Lamar, "apparently were unconcerned about the hiatus of more than 500 km between the localities in the [La Escalera region] and the [type locality]; this gap includes the intervening dry forests, savannas, and Río Orinoco."

The wide-ranging *Hyalinobatrachium orientale* sensu Cannatella and Lamar (1986) seems to be a complex of sibling species that are of nearly identical morphology but that are differentiated by color pattern in life and probably by average body size. These authors (p. 308) diagnosed *orientale* as being green "with profuse white to yellowish white spots," which (p. 312) are "uniformly distributed on all dorsal surfaces including limbs." But this characterization is based on Colombian specimens and hardly agrees with fieldnote descriptions cited by Cannatella and Lamar (pp. 312–313) for other populations—including Myers' notes and photograph (their fig. 1, bottom) for Isla Tobago, Duellman and Edward's notes for the Rancho Grande area, and Duellman's notes for the La Escalera region. Excluding the flecking and clumping of melanophores, the Isla Tobago frogs are spotless, the Rancho Grande area frogs have yellow flecks, and the La Escalera frogs have yellow spots like *H. crurifasciatum*. So far as we know, green limb bands occur only in populations of *Hyalinobatrachium* south of the Río Orinoco.

In addition to green-banded limbs, the head and body pattern (in life) of yellow spots in a light green dorsal reticulum distinguishes *H. crurifasciatum* from its other geographically closest *fleischmanni*-group

neighbors, as follows: *H. iaspidiense* has large irregular green spots, with indication of the pattern being retained in preservative (Ayarzagüena, 1992: fig. 3G). *H. taylori* evidently has small white spots over the dorsum, this pattern being retained in preservative on a lavender dorsum (Goin, 1968; Ayarzagüena, 1992: 32, fig. 3B).

The presence of an ulnar fold or ridge distinguishes *Hyalinobatrachium crurifasciatum* from *H. orientale* and from the unnamed *fleischmanni*-group species (color not described) mentioned by Ayarzagüena (1992: 33, 38), and also probably from *H. revocatum* (*fleischmanni* auctorum) of northern Venezuela. The last species also differs from *H. crurifasciatum* in being more uniformly green and in having the tympanum visible (Rivero, 1985: 352–353).

We discovered *Hyalinobatrachium crurifasciatum* late in our week at Tamacuari and failed to get photographs of the living frog before being air-lifted to the lowland base camp, where the frogs were soon preserved after showing evidence of heat stress. One of the two paratypes (AMNH 131331) had died in the jar and consequently is less well preserved than the holotype and paratype shown in figure 7.

#### FAMILY DENDROBATIDAE

##### *Colostethus tamacuarensis*, new species

Figures 11–16, 17C, D

**HOLOTYPE:** AMNH 131347 (field no. CWM 18745), an adult male, from forested stream at north base of Pico Tamacuari, 1160–1200 m elevation, Sierra Tapirapecó, Amazonas, Venezuela (1°13'N, 64°42'W). Obtained in the period March 11–17, 1989; Myers, Donnelly, and Daly collection.

**PARATOPOTYPES:** AMNH 131341–131342, 131345, MBUCV 6430–6433 (1♂, 2♀, 4 juv.), same data as holotype.

**ETYMOLOGY:** Derived from Tamacuari + the adjectival-forming suffix *-ensis* (belonging to a place).

**DIAGNOSIS:** A medium-sized *Colostethus* (to 25 mm SVL) with an elongated median lingual process, moderate foot webbing, cloacal tubercles, dorsal blotched pattern, and a variable, poorly defined, oblique pale lateral line.



Fig. 11. *Colostethus tamacuarensis*, new species, a female paratopotype in life (MBUCV 6430, 25 mm SVL).

*Colostethus tamacuarensis* is similar to *C. shrevei* from the Duida-Marahuaca massif. The two species differ in the shape of the median lingual process (a slender and distally tapering process in *tamacuarensis* vs. a short, round bump or blunt cone in *shrevei*), and in the shape of the inner tarsal fold (proximal end distinctly curved laterad in *tamacuarensis*, more or less straight in *shrevei*). See Remarks for elaboration and for comparison with *C. parkerae*.

**MEASUREMENTS OF HOLOTYPE** (in mm): The undissected holotype is an adult male as indicated by presence of large vocal slits. Length from snout to vent 22.4; tibia length between heel and outer surface of flexed knee 11.7; greatest width of body 9.9; head width between angles of jaws, and between outer edges upper eyelids, 8.0, 6.7, respectively; approximate width of interorbital area 2.5; head length from tip of snout to angle of jaw 6.3 (sagittal plane) or 7.7 (diagonal); snout length from tip to edge of eye (sagittal) 2.5; center of naris to anterior edge of eye 2.0; distance between centers of nares 3.2; eye length from anterior to posterior edge 3.3; horizontal diameter of tympanum > 1 (concealed posterodorsally); corner of mouth to lower edge of tympanic ring 0.2; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger

6.2; width of disc of third finger (and width of penultimate phalanx below disc) 1.0 (0.7); width of 3rd finger at base 0.9 left finger/1.0 right; width of discs (and penultimate phalanges below discs) of third and fourth toes identical at 1.0 (0.6).

#### DESCRIPTION

**MORPHOLOGY:** Dorsal skin granular in life, with enlarged granules or small tubercles occurring sparsely over dorsal and lateral surfaces of body and limbs (fig. 11), but skin becoming nearly smooth in preservative; ventral skin also nearly smooth in preservative but showing weak indication of granulation or rugosity (especially on throats of males), becoming smooth under thighs. Dorsal skin forming an unusually well-defined rounded, posteriorly projecting flap well above vent, which opens at upper level of thighs; a prominent tubercle (normally pigmented, not white) on each thigh lateral to and slightly above vent opening; small inconspicuous tubercles on thighs below vent.

Head little wider than long; greatest head width (between angles of jaws) 35–39 percent of SVL, averaging largest in juveniles (table 1). Snout sloping, rounded to bluntly pointed in profile, broadly rounded to nearly truncate in dorsal and ventral view. Nares situated near tip of snout and directed slightly posterolaterally; nares visible from front, barely or not visible from above or below; posterior rim of naris raised slightly and bearing a low, rounded tuberclelike prominence posterodorsally to naris. Canthus rostralis rounded; loreal region feebly concave (nearly flat), sloping slightly outward to lip. Interorbital region much wider than upper eyelid. Snout nearly equal (a little longer) to eye length (eye appears longer than snout in sagittal plane); center naris-edge eye/eye = 0.59–0.68. One or two low postrictal tubercles, either matching the ground color or whitish. Tympanum inconspicuous, a portion ( $\leq \frac{1}{2}$ ) concealed posterodorsally by diffuse supratympanic fold. Tympanum not measurable (without dissection) but seemingly more than a third and less than half of eye length; tympanum positioned close behind eye and low, nearly touching angle of jaws.

Hand moderate, its length 27–29 percent

TABLE 1  
Size and Proportions of the Type Series of *Colostethus tamacuarensis*  
(values are means  $\pm$  1 SD with range in parentheses)

Character	Males (N = 2)	Females (N = 2)	Juveniles (N = 4)
Snout-vent length (SVL) in mm	21.90 $\pm$ 0.71 (21.4–22.4)	24.90 $\pm$ 0.14 (24.8–25.0)	18.28 $\pm$ 1.29 (16.9–20.0)
Tibia length/SVL	0.516 $\pm$ 0.009 (0.51–0.52)	0.490 $\pm$ 0.003 (0.49–0.49)	0.540 $\pm$ 0.016 (0.53–0.56)
Head width/SVL	0.363 $\pm$ 0.008 (0.36–0.37)	0.353 $\pm$ 0.009 (0.35–0.36)	0.374 $\pm$ 0.011 (0.36–0.39)
Center naris-edge eye/eye length	0.613 $\pm$ 0.010 (0.61–0.62)	0.621 $\pm$ 0.021 (0.61–0.64)	0.648 $\pm$ 0.038 (0.59–0.68)
Hand length/SVL	0.277 <sup>a</sup>	0.275 $\pm$ 0.007 (0.27–0.28)	0.284 $\pm$ 0.005 (0.28–0.29)
Hand length/head width	0.775 <sup>a</sup>	0.778 $\pm$ 0.001 (0.78–0.78)	0.760 $\pm$ 0.010 (0.75–0.77)
Width 3rd finger disc/ finger width below disc	1.581 <sup>a</sup>	1.667 $\pm$ 0.236 (1.50–1.83)	1.563 $\pm$ 0.149 (1.40–1.75)

<sup>a</sup> N = 1.

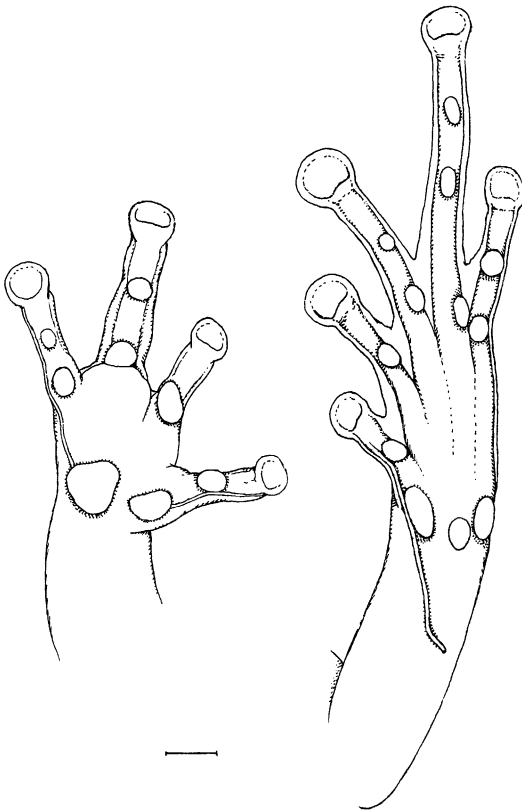


Fig. 12. *Colostethus tamacuarensis*, new species. Right hand and left foot of male holotype. Scale line = 1 mm.

of SVL, 75–78 percent of greatest head width. Relative lengths of appressed fingers III > IV > II > I; tip of first finger reaching disc of second. Discs of all fingers moderately expanded; third finger disc 1.4–1.8 times wider than distal end of adjacent phalanx. In the male holotype only, the base of the third finger is slightly swollen, being about as wide as the disc (fig. 12); the other adult male has deformed forelimbs. Base of palm with large median metacarpal tubercle, generally rounded except distal edge often flat; elliptical to rounded inner metacarpal tubercle on base of first finger; one or two sub-articular tubercles (one each on fingers 1, 2, two each on fingers 3, 4); all tubercles low, with rounded surfaces. A fleshy keel-like fringe along sides of fingers; fringe on median side of first finger extending as a weak keel or fold to inner metacarpal tubercle; fringe on lateral side of fourth finger continuous with a weak outer metacarpal fold extending to large palmar (outer metacarpal) tubercle (fig. 12). No ulnar tubercles or fold.

Hind limbs of moderate length, with heel of appressed limb reaching eye or anterior to eye; tibia 49–56 percent of SVL, averaging longest in juveniles (table 1). Relative lengths of appressed toes IV > III > V > II > I; first toe reaching to base, or distal edge,



Fig. 13. Color pattern variation in *Colostethus tamacuarensis*, new species, encompasses that of *Colostethus shrevei* (Rivero). Left to right: *C. tamacuarensis*, AMNH 131342♀, 131347♂ (holotype), 131345 subad. ♀; *C. shrevei*, MCZ 28567 subad. ♀ (holotype),  $\times 1.3$ .

of subarticular tubercle of second toe. Toe discs moderately expanded. Feet moderately webbed, the web distally continuous with a narrow fringe on toes 2–5. Webbing formula almost invariably<sup>8</sup> I 1–2 II 1–3 III 2–3 IV  $3\frac{1}{2}$ –2 V; a narrow fringe along outer free edges of toes 1 and 5. One to three nonprotuberant subarticular tubercles. Two to three metatarsal tubercles, including a small round outer metatarsal tubercle, a slightly larger elliptical inner metatarsal tubercle, and sometimes a median metatarsal tubercle; median metatarsal tubercle smaller than others and well developed only in AMNH 131345 and MBUCV 6430, being present but weak in holotype and virtually absent in some specimens. A strong tarsal fold or keel, on distal half of tarsus, continuous with the narrow fringe on free edge of first toe; no tubercle at proximal end of distinctly raised tarsal

keel, which in all specimens curves laterad (dorsad) along its proximal end.

Teeth present on maxillary arch. Tongue longer than wide; free posteriorly; median lingual process longer than wide, tapering distally to a point (fig. 17C, D). Vocal slits large, extending from near tongue insertion nearly to angle of jaw.

**COLOR AND PATTERN:** In life, the dorsal color was brown to yellowish brown with darker brown markings, as follows: (1) A dark interorbital bar, usually with slightly concave anterior margin and with or without posteriorly produced apex. (2) Usually a dark heart-shaped or triangular median blotch between the arms; one juvenile with several small irregular spots instead. (3) Usually a transverse pair of smaller paravertebral blotches at midbody. (4) A single small, median posterior blotch near end of body. The dark dorsal markings tend to be distinct except in the two adult males, in which vertebral and lateral extensions extend posteriorad from the first blotch—isolating a large pair of pale brown areas situated paravertebrally behind the arms. The dark dorsal markings, which appear pale-speckled in most specimens, are seen under magnification to be formed by an irregular clumping and vermiculation of dark brown pigment, with

<sup>8</sup> There is a degree of subjectivity in coding foot webbing because of distal fringing and slight variation in emargination of the web, with the holotype showing somewhat less web than the paratypes. This specimen may be perceived as differing from the above at II  $1\frac{1}{2}$ –3 III, with the left foot also differing at III  $2\frac{1}{2}$ –3 IV. As noted by Myers and Duellman (1982: 6): "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," as in this case.



TABLE 2  
Measurements (mm) of *Colostethus tamacuarensis* Tadpoles  
(values are means, with 1 SD in parentheses when N > 1)

Stage	N	Body length	Body width	Body depth	Tail length	Total length	Tail length/total	Oral disc width
25 early	2	6.20 (0.00)	4.10 (0.14)	3.00 (0.14)	10.65 (0.35)	16.85 (0.35)	0.632 (0.01)	1.80 (0.14)
25	7	7.31 (0.48)	4.71 (0.30)	3.26 (0.18)	13.09 (1.26)	20.39 (1.68)	0.641 (0.01)	2.16 (0.15)
25 late	3	8.83 (0.42)	5.50 (0.20)	3.87 (0.15)	16.17 (1.33)	25.00 (1.73)	0.647 (0.01)	0.277 (0.12)
26	1	9.70	6.00	4.00	17.80	27.50	0.647	2.80
27	1	10.60	6.30	4.40	—	—	—	3.10
28	1	11.20	7.40	5.20	22.00	33.20	0.663	3.30
37	1	11.30	7.00	5.20	22.00	33.30	0.661	3.40
40	1	11.30	7.30	4.80	22.00	33.30	0.661	3.30
41	1	10.20	6.80	4.40	21.00	31.20	0.673	3.10
43	1	9.60	—	—	17.20	26.80	0.642	—
44	1	9.30	—	—	13.30	22.60	0.589	—

small areas of paler ground color in the interspaces.

A poorly defined pale oblique lateral line, tending to be complete from groin to eye—but faint overall or becoming especially faint toward eye, sometimes represented in the groin by a series of pale spots; in life, the pale oblique marking was yellow in groin, turning light brown anteriorly. An ill-defined blackish stripe around tip and along side of snout, passing through eye and over arm to groin, below the oblique line. Some specimens with very weak indication of white ventrolateral spots or broken stripe, not demarcated from ventral color.

Upper lip indefinitely marked, brownish, usually with sparse, small whitish spots or oblique streaks. An oblique pale brown (in life), ill-defined postocular stripe, starting at lower rear edge of eye and extending to arm.

Forearms and hind limbs light brown with distinct dark brown bars (which are indistinct or absent on left hind limb of MBUCV 6430 [fig. 11]); dark brown stripe on anterior side of upper arm and on anterior surface of thigh from groin to knee. Digital scutes tending to be whitish on fingers and toes I–III.

In life, males with gray throat, white-stippled chin, and pale dirty green or yellowish venter, with sheen from underlying parietal peritoneum. Females with pale gray or sil-

very white throats and silvery white venters. Entire ventral surfaces of hind limbs yellow in both sexes, with orange suffusion on posteroventral part of thigh. In preservative, ventral surfaces are pale tan in both sexes, with weak suffusion of gray under head and variably onto venter in all specimens, but darkest on adult males. Undersides of hands and feet dark brown.

Iris bronze, darkened with black flecking and with a small black mark set in a small area of pale gray immediately below pupil.

TADPOLES

One lot of 20 free-living larvae (AMNH 131348, MBUCV 6434) was netted from the forest-stream habitat of the adults on March 9, 1989. The lot includes tadpoles in Gosner stages 25–28, 37, 40, 41, 43, and 44 (measurements in table 2).

The following description is based on a single stage 40 tadpole, which has complete larval mouthparts and has undergone no external changes except for the development of hind limbs (fig. 14).

HABITUS AND PROPORTIONS: Body length 11.3 mm, body width 7.3 mm, body depth 4.4 mm, total length 33.3 mm. Body depressed (body width/body depth = 1.66). Snout rounded in dorsal and lateral view.

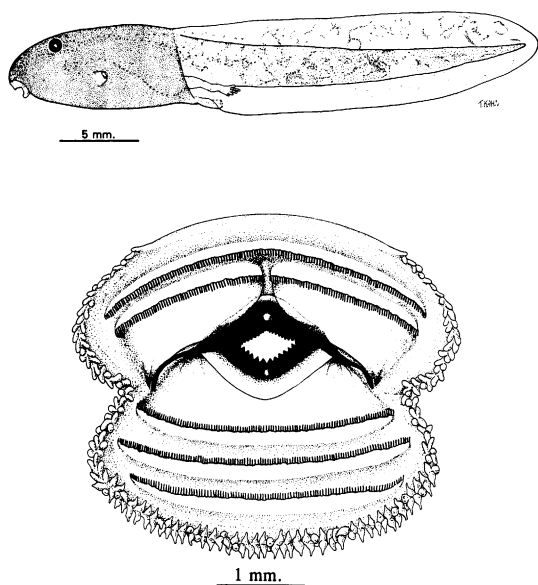


Fig. 14. *Colostethus tamacuarensis*, new species. Stage 40 tadpole (AMNH 131348) and mouthparts of same specimen.

Nares dorsal, directed laterally, 1.5 mm from tip of snout; internarial distance 2.4 mm. Eyes dorsal, directed laterally, 1.4 mm in diameter; interocular plane 3.6 mm behind snout; interorbital distance (between center of pupils) 3.5 mm. Spiracle low on body, sinistral, a posterodorsally projecting tube 1.3 mm long; opening 6.9 mm behind snout; opening 0.4 mm wide. Vent tube dextral to caudal fin.

Lateral line organ in four branches (following Escher, 1925). Supraorbital branch originating above anterior labium, extending posteriorly on top of snout to anterior corner of eye, with left and right branches slightly converging and then diverging between nares. Infraorbital branch originating above upper labium, extending posteriorly to below eye, terminating behind eye. Upper lateral and middle lateral branches originating as a single branch posterior to eye, diverging anterior to the tail. Upper lateral branch extending along dorsal fin; middle lateral branch in middle of tail musculature. Lower lateral branch originating on body above spiracle and curving ventrally to the caudal fin.

Caudal musculature moderately robust anteriorly, gradually tapering posteriorly, ter-

minating anterior to tail tip; height adjacent to body 2.7 mm. Tail length 66.1 percent of total length. Maximum tail height 18.0 percent of total length. Fins approximately equal in height; dorsal fin height at maximum tail height 1.6 mm, not extending onto body; ventral fin height 1.7 mm at greatest tail height. Tip of tail rounded.

**PIGMENTATION:** In preservative, dorsal body dark brown, lateral body lighter brown; ventral body tan, suffused with brown anteriorly. Caudal musculature tan; fins transparent. Anterior ventral fin without pigment; rest of tail with brown blotches; tail tip transparent. (But about half the larvae have a concentration of blackish brown pigment on the tail tip, either on the dorsal or the ventral fin edge or, less commonly, evenly across the tip in a distinctive bicolored pattern.)

**MOUTH PARTS:** Mouth ventral. Oral disc emarginate; oral disc width 3.3 mm. Labial teeth in 2/3 rows: Anterior rows equal in length, extending to near marginal papillae; second row interrupted narrowly above upper jaw sheath. First and third posterior rows subequal in length, second posterior row longest. Upper jaw sheath a moderately broad U-shaped arch with slender lateral processes; large blunt serrations. Lower jaw V-shaped, moderately robust; pointed serrations. Posterior labium bordered by two rows of large pointed marginal papillae. Marginal papillae extend to lateral margins of anterior labium.

**ONTOGENETIC CHANGES:** The mouthparts of early stage 25 tadpoles have one row of marginal papillae, and the third posterior row of labial teeth is lightly keratinized. In early stage 25 larvae, the tail musculature and posterior tail (except the tip) are brown with light spots, but the tail has a more mottled appearance in later stages.

#### NATURAL HISTORY AND VOCALIZATION

This diurnal frog was wary and hard to approach, possibly spending much of its time in concealment. We found it only at a rocky forest stream, in the small valley at the north base of Pico Tamacuari, and caught eight specimens (including four juveniles). As mentioned earlier, this stream is subject to flash-flooding and one assumes that adults and larvae both must have behavioral traits

that help to keep them from being washed away.

An unvouchered tape recording was made of a male *C. tamacuarensis* seen calling from beneath a large boulder. The call is a long train of double notes repeated generally at a rate of 3 pairs/sec and lasting 1 min or more. Narrow-band analysis shows the notes to be narrowly tuned, with frequency rising slightly to about 3840 Hz (fig. 15). For the six pairs, or couplets, of notes shown in figure 15, the duration is 0.13–0.15 sec per couplet, with intercouplet intervals of 0.17–0.24 sec (as measured from waveforms). Durations of the individual notes in figure 15 are 47–66 msec for the first note of a couplet and 47–59 msec for the second (by cursor scrolling of waveforms). The notes of a couplet are spaced so closely (about 20–30 msec, e.g., fig. 16) as to not be separable to our ears, which hear each couplet as a loud peep. The individual notes are variably pulsed as indicated in wide-band spectrograms (fig. 16) but better shown in the waveforms; there are generally 2–3 pulses per note.

#### REMARKS

*Colostethus tamacuarensis* needs to be compared for present purposes only with *C. parkerae* Meinhardt and Parmelee (1996) and *C. shrevei* (Rivero, 1961). These seem to be the only two named species from the Venezuelan Guayana that resemble *C. tamacuarensis* in having a median lingual process (Grant et al., 1997).

*Colostethus tamacuarensis* differs from *C. parkerae* of eastern Bolívar (La Escalera region) in having some indication of an oblique lateral stripe and in females having white throats in life (orange yellow in female *parkerae* fide Meinhardt and Parmelee, 1996: 74). *C. tamacuarensis* has the median lingual process noticeably longer than wide (fig. 17C, D), whereas the lingual process is about as wide as long in *C. parkerae*.<sup>9</sup>

<sup>9</sup> Three paratypes of *C. parkerae* (KU 167328–167330) were examined. The lingual process measures  $0.5 \times 0.5$  mm in two specimens and  $0.4 \times 0.5$  mm in the third (basal width  $\times$  total length). In the first two it is a blunt triangle, whereas it is bluntly pointed but relatively more slender in the third. By comparison, the lingual process shown in figure 17D measures  $0.4 \times 0.7$  mm.

Superficially, *Colostethus tamacuarensis* is most similar to *C. shrevei* (Rivero), of which we have examined the holotype (MCZ 28567♀) from Cerro Marahuaca, a paratype (now MCZ 27833♂) from Cerro Duida, and two additional specimens from Cerro Duida (AMNH 23196 juv., 23197♀). The color pattern of the holotype of *C. shrevei* fits within the variation of *C. tamacuarensis*, as seen in figure 13. The male paratype of *C. shrevei* appears mature at only 17.4 mm SVL (well-developed vocal slits and testes); the female holotype<sup>10</sup> is judged to be a subadult at 22.1 mm owing to the small ova (diameter  $\approx 0.2$ – $0.3$  mm) and unenlarged oviducts. The AMNH female is sexually mature at 27.5 mm SVL; Rivero (1961: 156) gave a maximum size of 36 mm for one female paratype of *shrevei*.

*Colostethus tamacuarensis* differs markedly from *C. shrevei* in the nature of the median lingual process. All specimens of *Colostethus tamacuarensis* have a slender process similar to that possessed by other *Colostethus* for which this unusual structure has been described (Grant et al., 1997). The four specimens of *Colostethus shrevei* have a lingual process that is a low bump or low cone little or no higher than wide (fig. 17A, B); this configuration corroborates Rivero's (1961) action in assigning the Marahuaca-Duida specimens to a single species.

*Colostethus tamacuarensis* also differs from *C. shrevei* in the alignment of the tarsal fold or keel. All specimens of *Colostethus tamacuarensis* have the proximal part of the tarsal keel smoothly curved laterad (fig. 12), whereas the keel is more or less straight in *C. shrevei*, which shows slight variation as follows: In the holotype of *C. shrevei*, the tarsal keel is straight with the mere hint of turning mediad at the very end. The tarsal keel seems similarly configured in the paratype of *C. shrevei*, which is poorly preserved; the keel on the left leg of the paratype is perfectly straight; a kink in the keel on the right tarsus seems to be a distortion artifact, but there is a faint mediad turning at

<sup>10</sup> Rivero (1961: 155) erred in calling the holotype a male, possibly having been misled by what could be taken as a vocal slit in the right side of the mouth. It appears to be a tear in the floor of the mouth as sometimes caused by careless handling of a specimen.

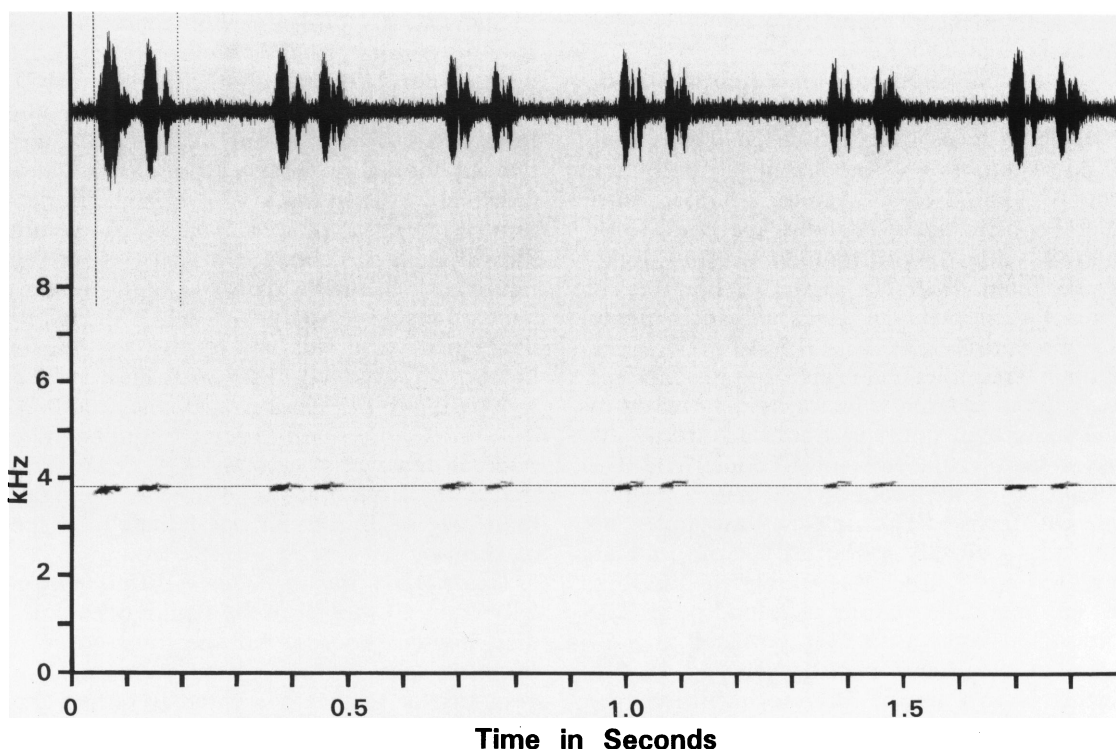


Fig. 15. Vocalization of *Colostethus tamacuarensis*, new species; 1.9 sec of a much longer train of note couplets given at 3 couplets/sec. Sound spectrogram graphed with narrow-band (59 Hz) filter, with cursor set at 3840 Hz. Matching waveforms show variation in pulsation; time between waveform cursors for first couplet = 0.153 sec. Recorded March 15, 1989, at air temperature of 20.2°C (AMNH herpetology reel 256:3).

the very end as in the holotype of *shrevei*. The tarsal keel is straight on both sides of AMNH 23196, a juvenile *shrevei*; it is also straight on the right tarsus of AMNH 23197, an adult female *shrevei*, but the keel on the left tarsus has a faint slant laterad at the proximal end (approaching but not equivalent to the condition in *C. tamacuarensis*).

*Colostethus shrevei* has more or less the same extent of foot webbing as *C. tamacuarensis*, seeming to be more variable in this regard. The modal webbing formula for the four specimens of *C. shrevei* is as follows (variation shown within parentheses): I 1–2(2–2½) II 1–2½(2½–3) III 2(1½–2)–3 IV 3(3–3½)–1½(1½–2) V.

Taran Grant's recent discovery (Grant et al., 1997) of the median lingual process in *Colostethus* s.l. is a remarkable event in dendrobatid biology. In the Venezuelan Guayana, the presence of the lingual process is

shared by *C. shrevei*, *C. parkerae*, *C. tamacuarensis*, and a few unnamed species currently under study—the undescribed ones being from localities as disparate as lowland forest at Cerro de la Neblina and the high summit of Cerro Auyantepui. The extent of relationship of these taxa with trans-Andean species possessing the lingual process remains to be elucidated, inasmuch as the lingual process is currently judged to be a dendrobatid plesiomorphy (Grant et al., 1997).

The premature suggestion by Myers et al. (1991: 18) that *Colostethus* s.s. might be defined by presence of a widened or swollen third finger in adult males was not formalized and was qualified as follows:

... use of this sexually dimorphic character is not without problems. The character is expressed more strongly in some species than in others and, in some species at least, it is not expressed in all adult males in a given sample. The intraspecific variability and a

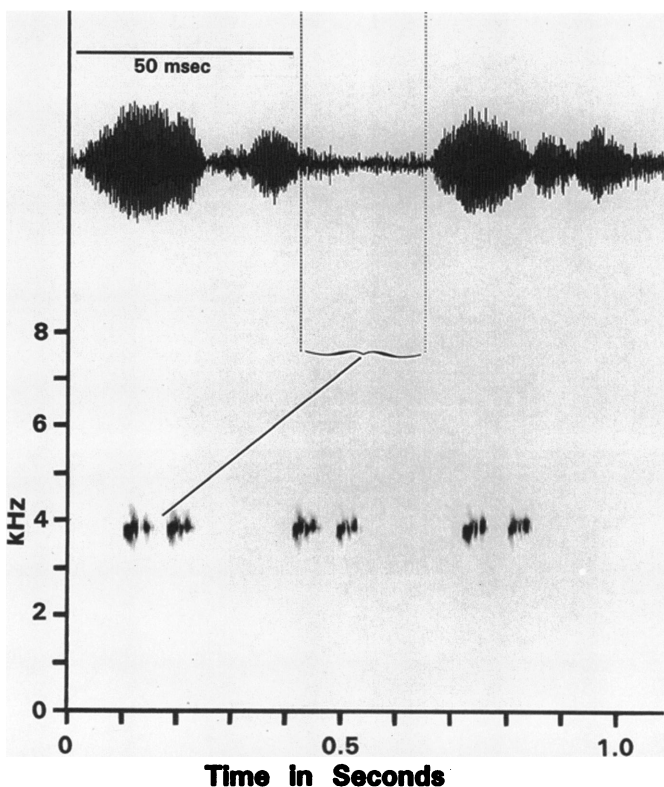


Fig. 16. Vocalization of *Colostethus tamacuarensis*, new species. Wide-band (300 Hz) spectrographic analysis of the second to fourth couplets of notes from figure 15. Expanded waveform of first couplet above, shows two pulses in first note and three pulses in second. Waveform cursors show an internote interval of 28.5 msec. Other data same as figure 15.

probable function in cephalic amplexus suggest that the character is under hormonal control.

The notion that the finger character might have imminent and unambiguous taxonomic usefulness was complicated almost immediately by Myers (1991: 14), who mentioned his lapsus in having forgotten that the character appears also in *Epipedobates*. The presence of a widened third finger in a male *Colostethus tamacuarensis* (fig. 12)—a species with a median lingual process—further suggests that the third finger character does not identify a well-defined, cohesive group. The swollen third finger may prove to be yet another plesiomorphic trait that (like the various pale stripes) is variably expressed in dendrobatids and should be viewed cautiously until we know more about it.

#### FAMILY HYLIDAE

#### *Hyla benitezi* Rivero

Figures 18–23

*Hyla benitezi* Rivero, 1961: 116–118, fig. 9. Holotype MCZ 28564 from Caño Wanadi, Mt. Marahuaca, Amazonas, Venezuela, collected by J. A. Rivero, May 20, 1950.

MATERIAL: AMNH 131374, 131377–131387, MBUCV 6435–6447 (21♂, 4♀), AMNH 131399 (tadpole tentatively assigned) from forested stream at north base Pico Tamacuari, 1160–1260 m.

#### DESCRIPTION OF PICO TAMACUARI SAMPLE

Females larger than males ( $\bar{x}$  female SVL/ $\bar{x}$  male SVL = 1.18). See table 3 for summary of SVL and proportions.

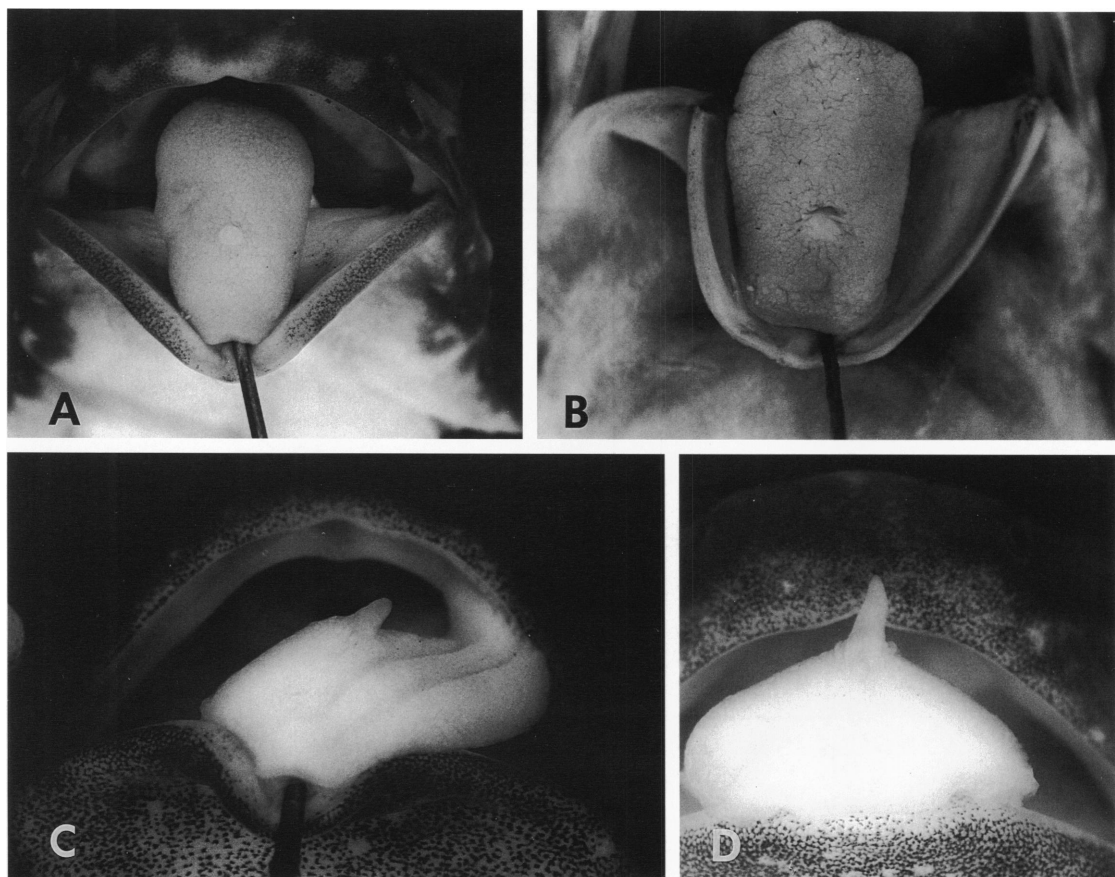


Fig. 17. Lingual processes of two Venezuelan highland species of *Colostethus*. **A, B.** *Colostethus shrevei* (Rivero) from Cerro Marahuaca and Cerro Duida. **A.** MCZ 28567 (holotype)  $\times 8.3$ . **B.** MCZ 27833 (paratype)  $\times 12.2$ . **C, D.** *Colostethus tamacuarensis*, new species, from Pico Tamacuari. **C.** AMNH 131347 (holotype), tongue twisted showing lingual process in profile,  $\times 12.5$ . **D.** MBUCV 6433  $\times 13.5$ .

Head about as wide as long; snout rounded to bluntly pointed in dorsal view, rounded in profile. Distance between eye and nostril more or less than eye length, more than twice the distance between tip of snout and nostril. Canthus rostralis rounded; loreal region slightly concave, gradually sloping to lip. Nostrils below canthus directed laterally and posterodorsally. Upper eyelid narrower than interorbital distance. Tympanum small, concealed under skin but visible in outline (obscured dorsally and sometimes posteriorly), 31–40 percent of eye length, separated from eye by distance greater than its diameter. Supratympanic fold low and ill-defined.

Choanae moderate, elliptical to kidney shaped, length about 50–85 percent of interchoanal distance. Vomerine odontophores

prominent, each with about 8–17 teeth ( $\bar{x}$  female = 14.4,  $\bar{x}$  male = 11.0 teeth per odontophore). Tongue circular, attached overall (narrowly free only around lateral and posterior margin), posterior edge entire or shallowly and irregularly notched.

Dorsal skin finely granular, becoming smoother in preservative; throat smooth in females, finely granular in males; skin of belly and ventral thigh surfaces coarsely granular. Anal opening at upper level of thighs, concealed by dorsal flap; ornamentation below anal opening consisting of two vertical ridges (usually smooth, sometimes tubercular) with lateral tubercles; tuberculate area usually pigmented like adjacent skin but sometimes white.

Thenar tubercle large, elliptical; smaller

TABLE 3  
Size and Proportions of *Hyla benitezi* Rivero from Cerro Tamacuari  
(values are means  $\pm$  1 SD with range in parentheses)

Character	Males (N = 21)	Females (N = 4)
Snout-vent length (SVL) in mm	41.34 $\pm$ 0.951 (38.4–43.5)	48.78 $\pm$ 2.846 (44.9–51.4)
Tibia length/SVL	0.504 $\pm$ 0.011 (0.49–0.52)	0.522 $\pm$ 0.023 (0.50–0.55)
Head width/SVL	0.361 $\pm$ 0.009 (0.34–0.38)	0.349 $\pm$ 0.011 (0.34–0.36)
Upper eyelid width/interorbital space	0.793 $\pm$ 0.112 (0.54–0.95)	0.670 $\pm$ 0.016 (0.65–0.69)
Tympanum/eye	0.343 $\pm$ 0.021 (0.31–0.40)	0.374 $\pm$ 0.020 (0.35–0.39)
Eye-naris/eye	0.887 $\pm$ 0.062 (0.79–1.05)	1.003 $\pm$ 0.087 (0.89–1.08)

palmar tubercle flat and inconspicuous; pollical swelling with concealed prepollical spine larger in males than in females; subarticular tubercles large, round, distinct, entire under fingers I and II in most specimens but distally bifid in a few; subarticular tubercles normally bifid under III and IV, rarely entire. Supernumerary tubercles on palm and proximal portions of digits low, round, and inconspicuous, not evident in all specimens. No webbing between first and second fingers; modal webbing formula for outer digits with variation in parentheses: **II** 2–3 **III** 2½(2–2½)–2(2–2½) **IV**. Finger discs round, third finger disc wider than tympanum. A row of ulnar tubercles from elbow to palm and a ridge, sometimes weakly developed, from palm to disc of fourth finger.

Inner metatarsal tubercle oval, low, flat, distinct. Outer metatarsal tubercle small, indistinct or absent. Subarticular tubercles round, prominent, entire. Small, low supernumerary tubercles rarely present on sole and proximal portions of toes. Toes extensively webbed; modal webbing formula with variation in parentheses: **I** 1½(1–1½)–1½(1–1½) **II** 1–2(1½–2) **III** 1–2(1½–2) **IV** 2–1 **V**. Discs on toes round, slightly smaller than finger discs. Heel feebly tuberculate; tarsus smooth or with a distinct lateral row of tubercles extending from heel onto lateral edge of fifth toe, sometimes becoming a ridge extending to fifth toe disc.

COLOR PATTERN: In life (fig. 18), the dorsal

ground color of 25 frogs varied from dark (most) to light brown, with a few individuals being yellow. Nearly all had narrow to wide transverse dark brown or black lines or irregular crossbands, except that one female (AMNH 131380) has several large blackish brown blotches and only a few transverse lines. Five individuals had white spots scattered on the dorsum and five individuals (including two with dorsal spots) had white canthal lines extending continuously over the eye and dorsolaterally to end at the middle or rear of the body. There sometimes is a tendency for the dorsolateral white line to be edged below by a blackish line broken at the eye; a few individuals lacking a white line show an indication of the lower dark edge, which was noted in life to form a conspicuous black canthal-dorsolateral line in one of the lighter males (AMNH 131378).

The limbs have variable dark banding, sometimes vague. The posterior thigh surface was orange to orange brown in life. The finger tips, toe tips, and webbing were orange; the digit tips become pale tan in preservative and the foot webbing is lightly to heavily peppered with brown. The anterior and posterior thigh surfaces vary in preservative from nearly pigmentless to brown, partly associated with the lightness or darkness of the ground color. In preservative as in life, the dorsal pattern is conspicuous on the light brown or yellowish individuals, but is less evident on the dark ones.



Fig. 18. *Hyla benitezi* Rivero, Pico Tamacuari specimens in life. **Upper.** AMNH 131374♀, 45 mm SVL. **Middle.** MBUCV 6435♀, 49 mm SVL. **Lower.** MBUCV 6436♂, 42 mm SVL.

In life, the throat was white with a pale to medium suffusion of gray. Except for a few individuals with white bellies, the venter and undersurfaces of the limbs were orange overall. In preservative, all ventral surfaces including palms and soles are pale tan, with variable brown suffusion; males tend to have the throat and occasionally all ventral surfaces suffused with brown, whereas females have brown mainly around the lip.

The iris of living frogs was light bronzy brown with fine black venation.

#### TADPOLE

One hyloid tadpole (AMNH 131399) was collected from the *Hyla benitezi* stream and we tentatively associate this single larva with the only adult *Hyla* collected.<sup>11</sup> The tadpole (fig. 19) is in stage 37 (Gosner, 1960), with complete larval mouthparts and small hind limbs.

**HABITUS AND PROPORTIONS:** Body length 15.7 mm, body width 9.6 mm, body depth 7.5 mm, total length 42.7 mm. Body depressed (body width/depth = 1.28); snout rounded in dorsal and lateral profiles. Nares dorsal, directed laterally, 2.2 mm from tip of snout, internarial distance 3.5 mm. Eyes dorsolateral, directed laterally, diameter 2.0 mm, interocular plane 4.5 mm from tip of snout, interorbital distance 6.0 mm. Spiracle sinistral, a tube 2.0 mm long, opening 11.2 mm behind snout. Vent tube dextral to caudal fin, 1.9 mm long.

Lateral line organ in five branches (Escher, 1925). Supraorbital branch originating above anterior labium, with right and left branches initially converging and then diverging between the nares, extending posteriorly to eye and forming a loop around eye with infraorbital branch. Postorbital line of hyoman-dibular branch originating laterally, curving posterodorsally, posterior to infraorbital branch. Upper and middle lateral branches originate on dorsal body posterior to eye, directed posteriorly, diverging anterior to tail; upper lateral branch above tail musculature, extending on tail for half of tail length; mid-

<sup>11</sup> One indication to the contrary, however, is the fact that the tadpole had patches of metallic green on its sides, a color not seen in the adult frogs.



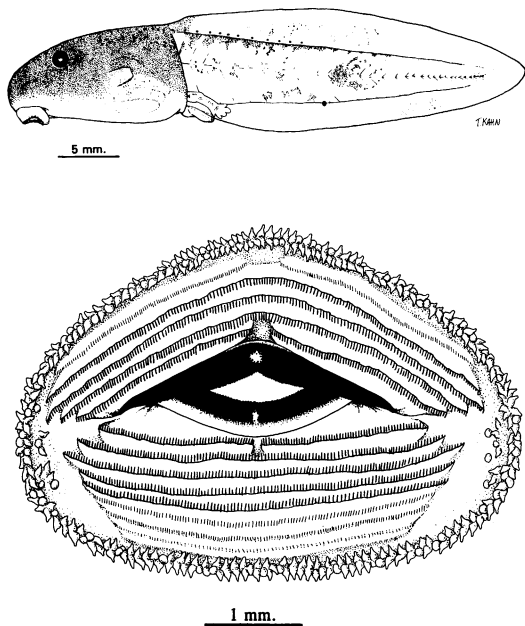


Fig. 19. Tadpole tentatively assigned to *Hyla benitezi* Rivero (AMNH 131399, stage 37).

dle lateral branch extending along middle of fin musculature, distinct near body.

Caudal musculature robust anteriorly, tapering posteriorly, extending to tail tip; height adjacent to body 5.1 mm. Tail length 63.2 percent of total length. Maximum tail height 23.7 percent of total length. Fins unequal in height; dorsal fin height at maximum tail height 3.4 mm, ventral fin height at maximum tail height 2.8 mm. Tail tip rounded.

**PIGMENTATION:** In life, the head and body were brown above with metallic green patches on the sides. In preservative, the dorsal body surface is uniform brown, the lateral body is brown dorsally and tan ventrally; the ventral body is tan with short brown streaks; gut visible through ventral skin. Tail musculature tan, transparent at tail tip; dark brown stripe on dorsal edge of musculature; ill-defined light spot at midtail; musculature with scattered flecks and spots. Fins transparent; dorsal fin with brown blotches on anterior three-fourths of fin; ventral fin with small brown flecks on posterior one-fourth of tail.

**MOUTHPARTS:** Mouth (fig. 19) ventral. Oral disc not emarginate; oral disc width 5.2 mm.

Labial teeth in five anterior and eight posterior rows; tooth row formula: 5(1, 5)/8(1). Anterior rows much longer than posterior rows; first and fifth rows interrupted medially (A-5 gap = 0.3 mm); A-1 gap wide; A-1 row not keratinized as heavily as rows 2–5. The A-1 “gap” conceivably might be a developmental artifact and conceivably the A-5 gap might represent a break rather than a gap. First posterior row interrupted medially (P-1 gap = 0.1 mm), rows 6–8 not heavily keratinized. Upper jaw sheath a low broad arch with slender lateral processes; small pointed serrations. Lower sheath U-shaped with small, pointed serrations. Anterior labium massive, pendant, curves laterally to join posterior labium. Oral disc completely surrounded by two rows of pointed marginal papillae. A few pointed submarginal papillae.

#### NATURAL HISTORY AND VOCALIZATION

The 25 frogs in the Tamacuari sample of *Hyla benitezi* were collected at night from vegetation along the forested stream at the north base of Pico Tamacuari. The frogs were calling from, or perched on, low vegetation and on rocks near the stream. They were not elusive, being easily approached and easily caught.

As described earlier (The Pico Tamacuari Collecting Area), this stream lived up to its appearance and became torrential during the week in which these frogs were found breeding. Whether correctly identified or not, the single hylid tadpole associated with *H. benitezi* has a relatively deep tail fin that made it seem out of place in such a stream—but it had survived at least one flash flood before we netted it.

Advertisement calls of one individual were recorded. Calls on the tape comprise two notes ( $N = 17$  calls) or three notes ( $N = 7$ ), with a nearly imperceptible rise in frequency from the start of each note to 1880 Hz (figs. 20, 21). The first note usually has a duration of about 0.06–0.07 sec and in all calls is longer than the following notes(s), which are about 0.03–0.06 sec long. But the first note is twice as long as normal in several 2-note calls as shown in figure 20, in which the first note of the second call is 0.12 sec in duration (vs. 0.06 sec in the first call).

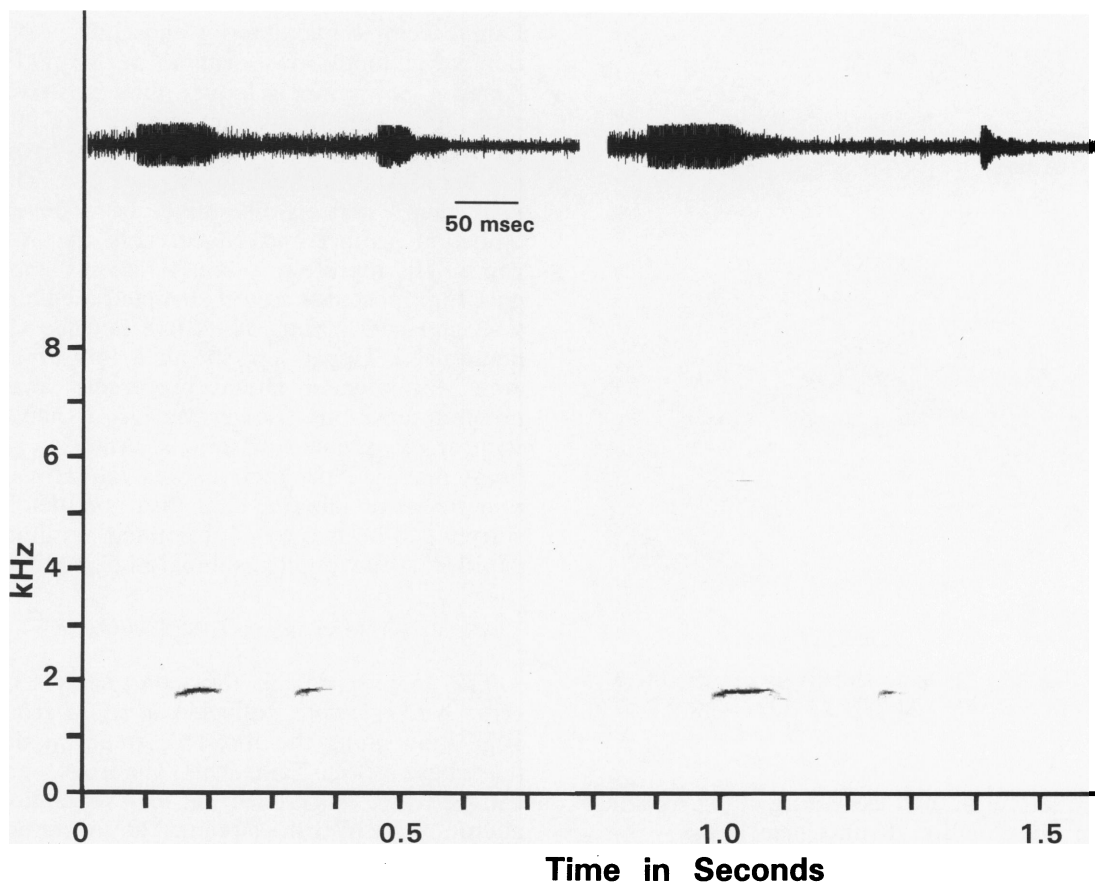


Fig. 20. Vocalization of *Hyla benitezi* from Pico Tamacuari. Two 2-note calls from the same frog, with total durations of 0.25 sec (left) and 0.33 sec; frequency slightly rising, mainly at 1880 Hz. The first note of the second call is twice as long as that of the first call. Graphed with 59 Hz narrow-band filter (AMNH 131377, recorded March 16, 1989, on leaf 1 m above stream at 17.4°C; AMNH herpetology reel 256:5).

#### REMARKS

*Hyla benitezi* is a Pantepui endemic that appears to have a fairly scattered highland distribution in the tepuis and along the Venezuelan-Brazilian border, although we suspect that at least two species may be involved. It originally was named from Cerro Marahuaca (Rivero, 1961: 116) and subsequently reported from the "Alto Orinoco" (Rivero, "1967" [1968]), Cerro Duida (Rivero, "1971" [1972]), Cerro Guaiquinima (Donnelly and Myers, 1991), and Sierra Pacaraima on the Brazilian border (Heyer, 1994).

There is significant size variation (fig. 23) among these populations but also a degree of

ambiguity owing to insufficient data for the Marahuaca-Duida population(s). The holotype and paratype of *benitezi* were males 36–37 mm SVL (Rivero, 1961). Adult specimens of *H. benitezi* from Cerro Guaiquinima and Sierra Pacaraima are in the size ranges of 31–37 mm ♂ SVL and 36–47 mm ♀ SVL.

The much larger frogs in the Pico Tamacuari population sample are 38–44 mm ♂ SVL and 45–51 mm ♀ SVL (table 3). These frogs average 7.51 (males) and 6.78 mm (females) larger in SVL than the Cerro Guaiquinima sample, with about a 2 mm gap in ranges for males and a 2 mm overlap for females. See figure 23 to visualize the size difference.

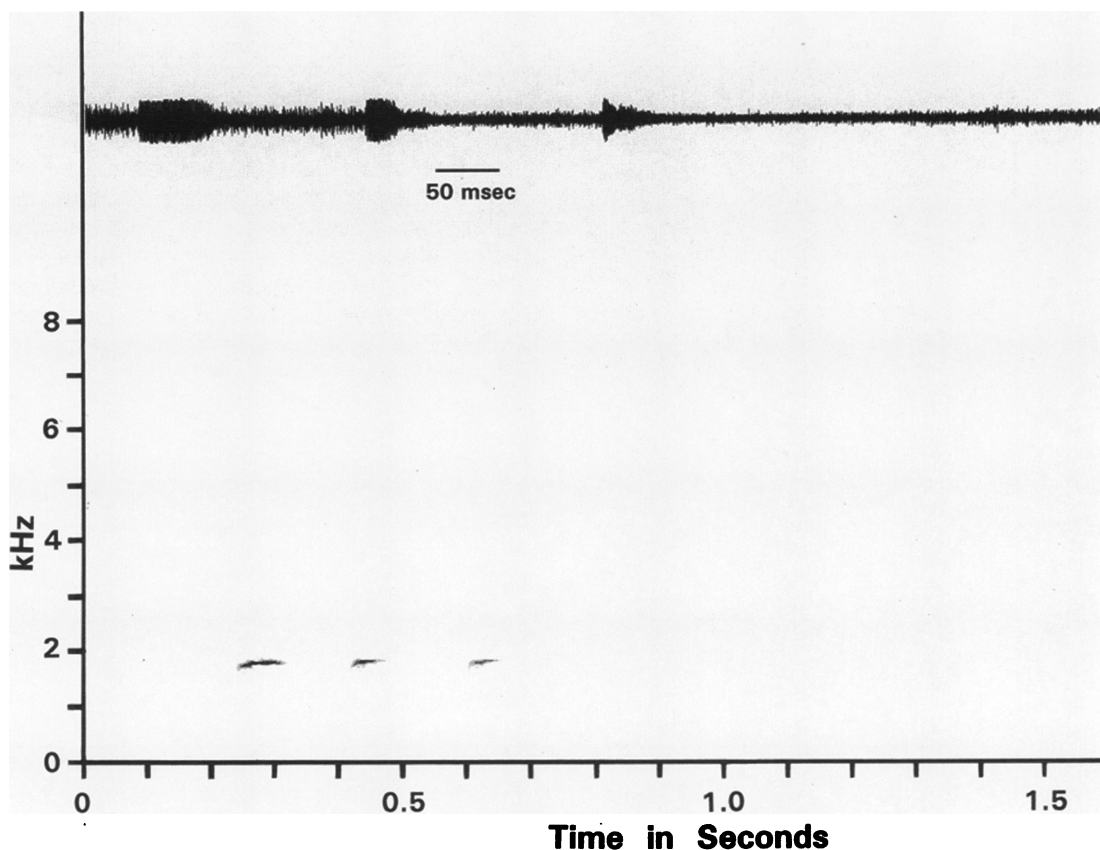


Fig. 21. Vocalization of *Hyla benitezi* from Pico Tamacuari. A 3-note call of 0.41 sec duration, mainly at 1880 Hz. Other data same as figure 20.

Differences of this magnitude suggest that the larger frogs from Pico Tamacuari might represent a species different from the smaller ones on Cerro Guaiquinima and Sierra Paracaima. However, Rivero ("1971" [1972]) reported on a sample of 23 *H. benitezi* from Cerro Duida, for which he unfortunately gave only the *maximum* size for males and females—42.5 and 47.0 mm respectively. Such a size for males fits only in the range for the large Pico Tamacuari specimens, whereas the female size fits either the upper end of the known range for Guaiquinima females or the lower end for Pico Tamacuari females.

The Pico Tamacuari frogs and the *benitezi* holotype can be separated from Cerro Guaiquinima specimens by the relative condition of the ventrolateral edge of the forearm—a ridge of discrete ulnar tubercles in the holo-

type and Tamacuari specimens vs. a virtually nontuberculate ulnar keel in the six Guaiquinima specimens still at the American Museum (half the series was transferred to MBUCV). This contradicts our earlier statement (Donnelly and Myers, 1991: 14) that "All [Guaiquinima] frogs have a ridge of low white tubercles on the ventrolateral surface of the arm that extends from the elbow to the disc on finger IV." Part of that statement was wrong because the second author's data sheets show that tubercles were not detected on several specimens. Actual counts of tubercles on left and right arms, however, were recorded for the other specimens—but today we can discern very faint indication of this tuberculation on only a few of these specimens, whereas the underlying ridge or keel is obvious on five of six specimens. We assume that there has been some progression

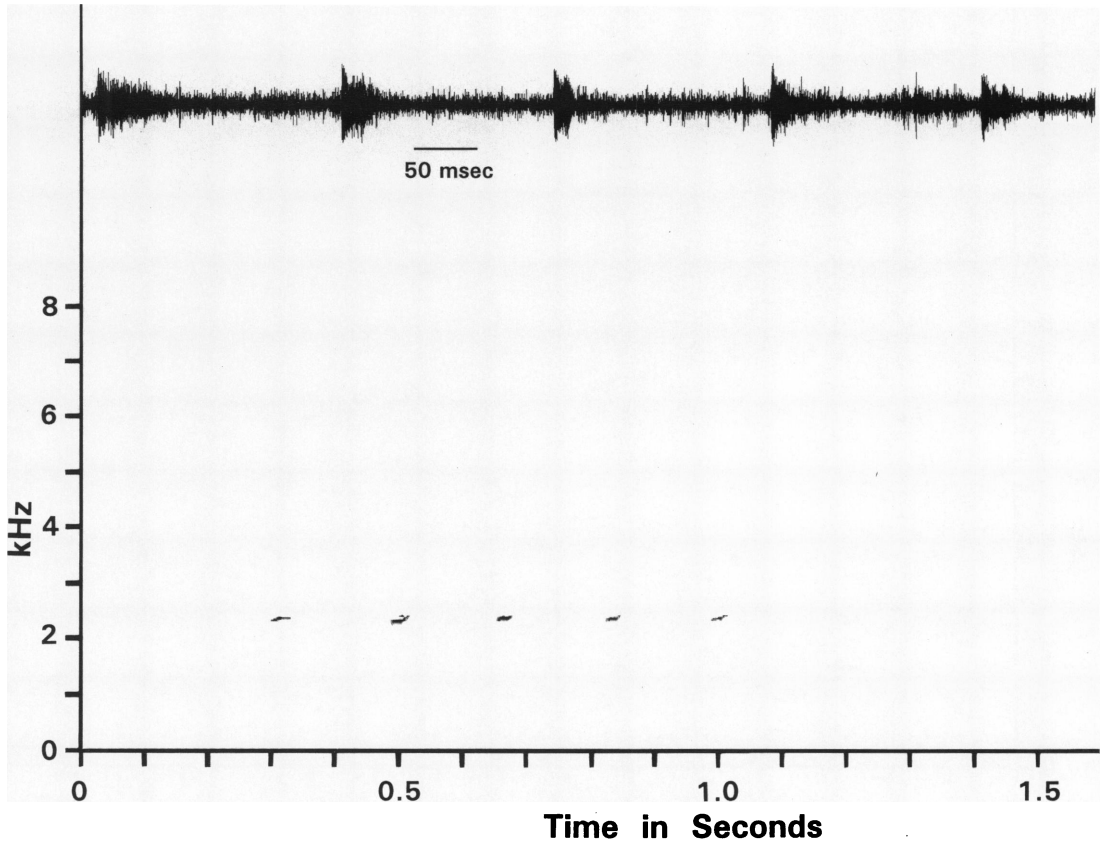


Fig. 22. Vocalization of *Hyla benitezi* from Cerro Guaiquinima. A 5-note call (range 2–6 notes) of 0.74 sec duration at 2360 Hz. Compare with figures 20–21 from Pico Tamacuari. (Recorded February 24, 1990, at 18.6°C; AMNH herpetology reel 257).

of loss in preservative and that tuberculation is probably inherently weaker in the smaller frogs. Extent of tuberculation conceivably is correlated with size.

The calls of *benitezi*-like frogs at Pico Tamacuari differ from those at Cerro Guaiquinima (Donnelly and Myers, 1991: 11, 14) and Sierra Pacaraima (Heyer, 1994) at least in dominant frequency and note duration. The dominant frequency is about 480 Hz lower for Pico Tamacuari (compare figs. 20–21 with fig. 22), but a frequency difference of this magnitude conceivably may be linked to larger body size. The Pico Tamacuari frogs have relatively longer notes (usually 0.03–0.07 sec, occasionally up to 0.12 sec, at 17.4°C) than the smaller Guaiquinima frogs (0.02–0.04 sec at 18.6°C), but note duration may be negatively correlated both with body size and with temperature.

Calls of a recorded Tamacuari frog comprised 2 or 3 notes, whereas Donnelly and Myers (1991: 11) and Heyer (1994) gave a range of 2–4 notes for individually calling specimens of the smaller frogs. All the tapes are of poor quality owing to the amount of background (stream) noise, but recent spectrographic video screening of the Guaiquinima tape also showed a few 5-note and 6-note calls that are not part of the longer “duets” mentioned by Donnelly and Myers (1991: 11 and fig. 10B); one of these longer calls is shown here as figure 22.

We hesitate to give taxonomic significance to any of the above differences without further study and conclude that the various populations are best assigned to a single taxon. As now construed, *Hyla benitezi* s.l. may be defined as either a medium-sized or small *Hyla*, with either a row of low ulnar tubercles

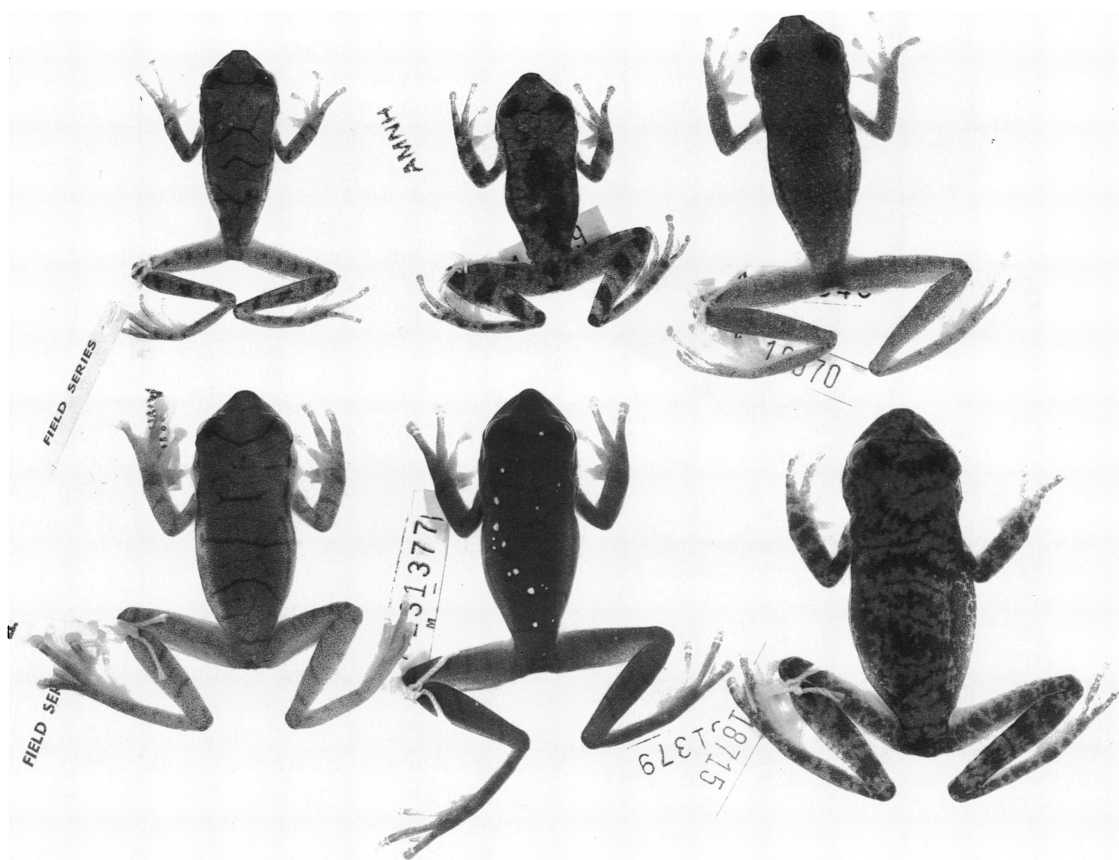


Fig. 23. Interpopulational and sexual size variation in adult specimens tentatively assigned to *Hyla benitezi* Rivero. **Top, Cerro Guaiquinima:** AMNH 133843♂, 133844♂, 133845♀. **Bottom, Pico Tamacuari:** AMNH 131378♂, 131377♂, 131379♀.  $\times 0.89$ .

or an ulnar keel from elbow to palm; hand with basal webbing between outer fingers; foot extensively webbed; various shades of brown in life with transverse darker lines, sometimes also with white spots or dorsolateral stripes; ventral limb surfaces and webbing orange.

*Hyla lemai* Rivero, from the Escalera region, also has dark transverse marks and might be confused with *Hyla benitezi* s.l. But Duellman's (in press) recent account shows *H. lemai* to have yellow coloring under the hind limbs (orange in *benitezi*) and a greenish gray iris (light bronzy brown or tan in *benitezi*), as well as a different call. *H. lemai* has much longer notes (short whistles of 0.45–0.66 sec) that are given at a higher fre-

quency ( $> 2.6$  kHz) than in the combined populations of *benitezi* (0.02–0.12 sec duration at 1.8–2.6 kHz).

#### *Stefania tamacuarina*, new species

Figures 24–26

**HOLOTYPE:** AMNH 131428 (field no. CWM 18746), a subadult female from camp on ridge N Pico Tamacuari, 1270 m elevation, Sierra Tapirapécó, Amazonas, Venezuela ( $1^{\circ}13'N$ ,  $64^{\circ}42'W$ ). Obtained in the period of March 11–17, 1989; Myers, Donnelly, and Daly collection.

**PARATYPE:** MBUCV 6448 (field no. CWM 18701), a subadult female from streamside forest at the north base of Pico Tamacuari,



Fig. 24. *Stefania tamacuarina*, new species, the paratype in life (MBUCV 6448 subad. ♀, 43 mm SVL).

1160–1200 m elevation. Other data as for holotype.

**ETYMOLOGY:** A geographical adjective from the mountain Tamacuari + the suffix *-inus* (belonging to), yielding *tamacuarina* in the feminine. It may bear pointing out that *Stefania*—a nominative generic commemorative honoring Mr. Luis Stefani—is unambiguously feminine owing to the form of the suffix (*-ius*, *-ia*, *-ium*). The only previous adjective (*marahuaquensis*) applied as a species name in *Stefania* is identical in masculine and feminine gender. Other names are patronyms except for *roraimae*, a geographic substantive in the feminine genitive.

**DIAGNOSIS:** A medium-sized or possibly large *Stefania* (known specimens are subadult females 43–50 mm SVL); head slightly wider than long; frontoparietal ridges absent; canthus rostralis distinct, angular, with one or more prominent knobs; tympanum more than half of eye length; first finger longer than second; discs well developed on all digits; toes basally webbed; dorsal skin weakly granular, with a bold color pattern—including a dark rectangular blotch on anterior dorsum, with anterior corners of blotch on upper eyelids, and one or two dorsal blotches posterior to first. The aforesaid color pattern distinguishes this species from all others.

Measurements of Holotype and Paratopotype (in mm): Both are females, judged to be subadult based on unenlarged oviducts and small ovarian ova (largest ova  $\approx 1.2$  mm in holotype, 0.7 mm in paratype). Following measurements are for the holotype first, paratype second: SVL 50, 43; tibia length 30.0, 26.5; foot length from proximal edge inner metatarsal tubercle to tip of fourth toe 22.2, 19.8; hand length from proximal edge palmar tubercle to tip of third finger 15.9, 13.9; head width 20.0, 17.5; head length on the diagonal from angle of jaw to tip of snout 19.7, 17.4; internarial distance 3.5, 3.4; upper eyelid width 5.0, 4.0; interorbital distance 5.5, 4.6; eye to posterior edge of nostril 6.0, 5.0; eye length 6.5, 6.0; tympanum 3.5, 3.3; width of third finger disc 2.9, 2.2; width of fourth toe disc 2.4, 1.8.

#### DESCRIPTION

**MORPHOLOGY:** Head slightly wider than long; depth more or less half of head length. Snout rounded in dorsal view and profile in holotype, nearly truncate in both views in paratopotype. Eye-nostril distance less than eye length, greater than three times distance between nostril and tip of snout; snout short in profile, roughly equal to eye length. Canthus rostralis distinct, angular, nearly straight or slightly wavy—each specimen with a prominent enlarged knob in middle of canthal ridge (holotype additionally has two smaller knobs on posterior half of left-side canthus, whereas paratopotype has a small knob at anterior end of each canthal ridge). Loreal region concave, sloping to lip. Nostrils protuberant, directed posterolaterally with a slight dorsal tilt; nasal swellings positioned laterally and slightly anteriorly to anterior ends of canthi rostrali. Distance between nostrils 64–74 percent of interorbital distance, 1.8–2.2 times distance between nostril and tip of snout; internarial region flat to slightly concave. Interorbital space flat, slightly wider than width of upper eyelid. Dermal frontoparietal ridges absent. Temporal region sloping. Tympanum distinct, large, round, 54–55 percent of eye length, separated from eye by distance half of its length. Supratympanic fold narrow, distinct, curved,

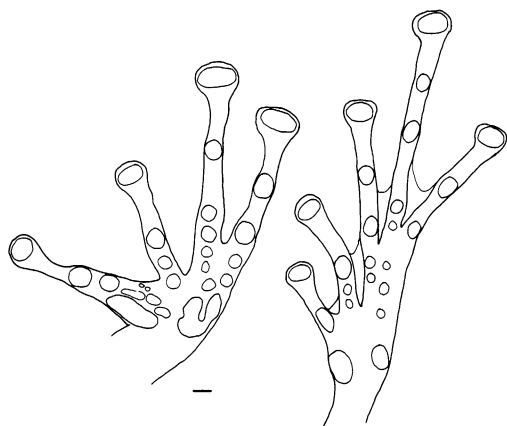


Fig. 25. *Stefania tamacuaria*, new species. Left hand and left foot of paratype (MBUCV 6448). Scale line = 1 mm.

extending over annulus from posterior corner of eye to above insertion of arm.

Choanae large, elliptical. Vomerine processes large, transverse, between choanae, bearing 5–8 teeth each; processes separated medially in the holotype, in contact in the paratype. Tongue large, round, posteriorly entire or feebly notched. Palpebral membrane not reticulated, with continuous brown pigmentation along upper rim and around lower margin.

Dorsal skin weakly granular with a few tiny tubercles sparsely scattered, becoming nearly smooth in preservative; granular on flanks and dorsal thigh surface, coarsely granular on posteroventral surface of thigh; venter granular. Eyelid with a few scattered tiny tubercles evident in life (fig. 24), and weak tuberculation at posterior end; posterior margin of eyelid feebly scalloped. Scattered tubercles in loreal region; skin around lower half of tympanum tuberculate, the posterior tubercles largest. Anal opening directed posteriorly at upper level of thighs.

Thenar tubercle large, distinct, oval; palmar tubercle large, distinct, distally bifid. Subarticular tubercles single, large, distinct, round. Supernumerary tubercles on palm and bases of fingers small, round; tending to fuse on base of first finger, lateral to thenar tubercle, forming an elongated raised or (in holotype) flattened tubercle. Relative finger length  $3 > 4 > 1 > 2$ ; appressed first finger

distinctly longer than second, with nonoverlapping discs. Fingers with ventrolateral keels, no webbing; third and fourth fingers fused at base. Finger discs large, truncate, wider than penultimate phalanx; smallest on first two fingers, largest on outer ones. Largest disc width greater than one-half tympanum length.

Inner metatarsal tubercle large, oval, distinct; outer metatarsal tubercle smaller, round (holotype) or oval, distinct. Subarticular tubercles large, single, round to oval, distinct. Supernumerary tubercles distinct, small, round, present mainly on proximal segments. Relative length of appressed toes  $4 > 5 > 3 > 2 > 1$ ; appressed fifth toe only slightly longer than third. Toes basally webbed, webs distally continuous with lateral keeling, which also is present on outer sides of first and fifth toes. Webbing formula: I  $2-(2\frac{1}{4}-2\frac{1}{2})$  II  $2-3$  III  $(2-2\frac{1}{4})-3\frac{1}{2}$  IV  $(3\frac{1}{4}-3\frac{1}{2})-2$  V. Toe discs oval, wider than penultimate phalanx, smaller than finger discs. Heels overlap when folded hind limbs are flexed at right angles to sagittal plane of body.

COLOR PATTERN: Ground color in life greenish brown (holotype) or brown with a bold darker brown pattern. Both specimens have a large, conspicuous, rectangular brown blotch anteriorly, with the corners of the anterior straight edge lying on the eyelids; this blotch tapers posteriorly, ending with a slightly concave transverse edge just behind the level of the arm insertions. A second dark brown blotch follows at midbody, being most conspicuous and anteriorly oval in the holotype and being fainter and rectangular in the paratype. The holotype has a small, irregularly shaped third dorsal blotch on the rear of the body. In both specimens, the interorbital edge of the first blotch is blackish brown and there is a sparse scattering of blackish spots in the dorsal brown blotches; in the paratype, the outline of the first dorsal blotch and anterior edge of the second are emphasized by pale (grayish tan in life) edging next to a vague blackish suffusion along the inner margins. Both specimens have a dorsolateral line of several blackish spots above vaguely brown mottled flanks. A scattering of granules along the flanks and at the rear of the body are unpigmented, standing out as pale (white in preservative) dots (fig. 24).



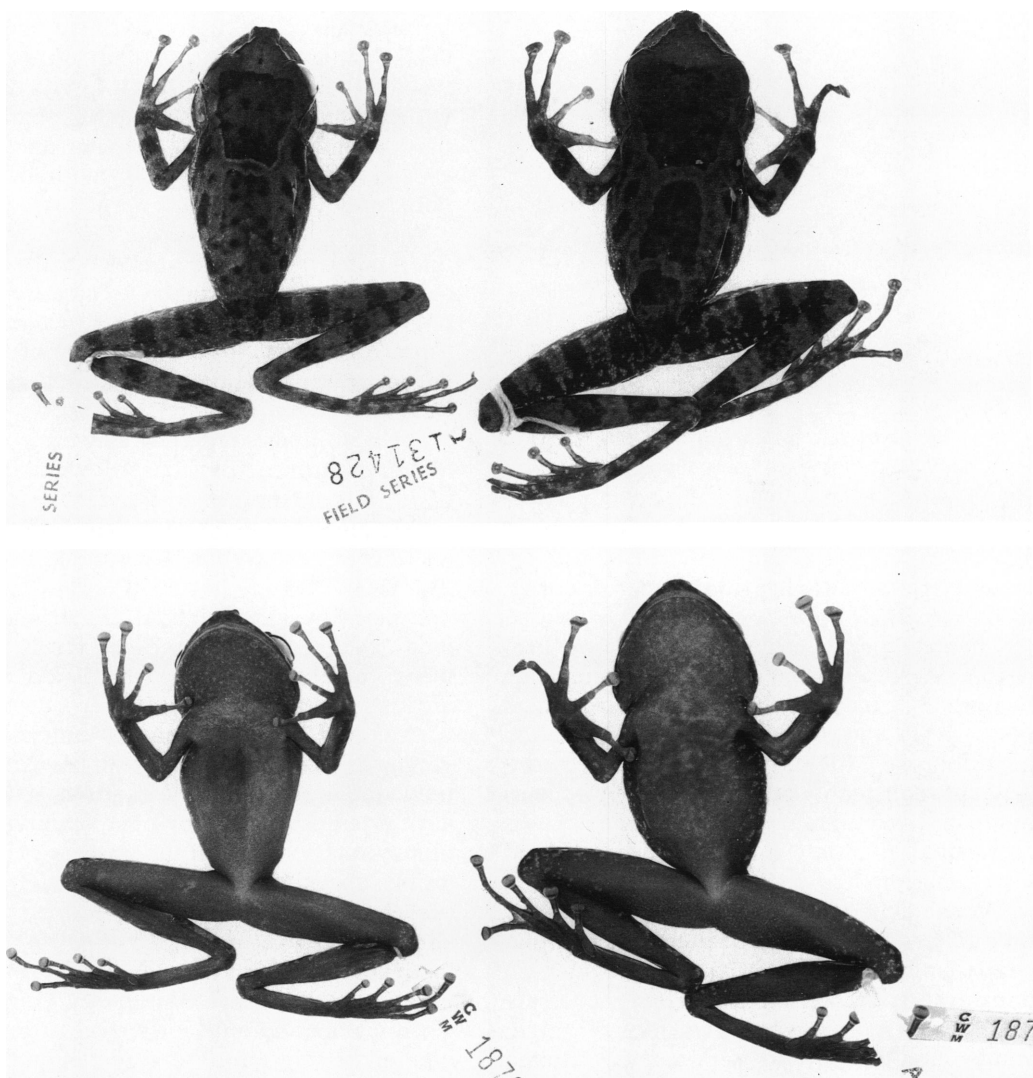


Fig. 26. *Stefania tamacuarina*, new species. **Left.** MBUCV 6448, subad. ♀ (paratype). **Right.** AMNH 131428, subad. ♀ (holotype).  $\times 0.94$ .

Ground color somewhat paler on sides of head and top of snout except for some dark suffusion along canthus rostralis; upper lip boldly marked with a few dark brown bars, including a short bar below loreal region and 1–3 bars below eye. The arms and legs were greenish brown or brown like the body with conspicuous dark brown banding. Rear of thigh dark brown, irregularly dotted or flecked with pale greenish brown (holotype) or pale brown.

Ventral surfaces of holotype in life overall

gray with small whitish patches on throat and chest; the smaller paratype also had gray undersurfaces except that the throat was brown with whitish speckling and there was a light silvery gray patch on the chest. In preservative, throat and venter pale brown, vaguely speckled or finely blotched with dirty white, becoming nearly uniform pale brown on ventral sides of limbs and in groin.

The iris was pale or light bronzy brown with fine black venation, a red-brown horizontal streak (noted only for holotype), and



an ill-defined black or gray vertical line below the pupil.

#### NATURAL HISTORY

*Stefania tamacuarina* is a montane forest frog insofar as known. The holotype was found at night after a rain, in the helipad clearing in ridgetop forest. The paratype also was found at night, in low vegetation near the forested stream in the drainage at the north base of Pico Tamacuari.

#### REMARKS

The genus *Stefania* is endemic to the Guayanian region of Venezuela and adjacent Guyana, with most species having restricted highland distributions. Rivero ("1966" [1968]) erected the genus for the frogs *Cryptobatrachus evansi* (Boulenger), *Hyla marahuaquensis* Rivero, and three new species (*ginesi*, *goini*, *woodleyi*). Rivero (1970) later described *S. scalae* and allocated the six named taxa to two species groups—the broad-headed *goini* group (*ginesi*, *goini*) and the narrower-headed *evansi* group (*evansi*, *marahuaquensis*, *scalae*, *woodleyi*). Duellman and Hoogmoed (1984) reviewed the genus, synonymizing *S. scalae* with *S. evansi* and adding two new species (*riae* and *roraimae* [*evansi* group]). These authors did not explicitly assign the seven recognized taxa to species groups in their taxonomic accounts, but they did use Rivero's group names in general discussion and summary (e.g., pp. 20, 34, 36).

The head of *Stefania tamacuarina* is barely longer than wide; head length/head width values (0.985 in holotype, 0.994 in paratype), are intermediate between values reported for members of the two species groups by Duellman and Hoogmoed (1984, table 1), but closer to the *evansi* group. The *goini* group members have prominent frontoparietal ridges, which are said to be absent, indistinct, or variably present in the *evansi* group and which are lacking in *Stefania tamacuarina*. *S. tamacuarina* is morphologically similar to *S. riae* from Cerro Sarisariñama, including the presence in both of one or more prominent knobs on the canthus rostralis. The holotype, but not the paratype, of *S. tamacuarina* has an ill-defined tu-

bercle on the posterior third of the upper eyelid. The tubercle on the left eyelid has a rounded, partially free lateral edge, suggesting possible homology with the very small triangular flap similarly positioned on the eyelid of *S. marahuaquensis*. Two rectangular dark dorsal blotches, which give *S. tamacuarina* a unique appearance, may represent a fragmentation of a pale-edged dark dorsum seen in such species as *S. roraimae* and *S. marahuaquensis* (illustrations in Duellman and Hoogmoed, 1984).

#### FAMILY LEPTODACTYLIDAE

Three species of forest-dwelling *Eleutherodactylus* were found at Pico Tamacuari and are described below. Our introductory remarks to three other new *Eleutherodactylus* recently described from Cerro Yaví (Myers and Donnelly, 1996: 9–11) could, with a change of names, be repeated almost but not quite verbatim here (close enough to give us a sense of *déjà vu*). Two of the new species named herein (*avius* and *memorans*) are placed in Lynch's large *unistrigatus* group for the same principal reasons given for two of the Cerro Yaví frogs (areolate ventral skin, first finger shorter than second, fifth toe much longer than third). However, the heads of the two new ones (especially *E. memorans*) seem less wide relative to body width than may be usual for *unistrigatus*-group species.

The *unistrigatus* group approaches 200 named species, with more coming even from the Venezuelan Guayana, which heretofore has contributed little to the known diversity. The two new species described in this paper may be related to one another and to species already named from Guayana, but there is no certainty about this.

The third species of Pico Tamacuari *Eleutherodactylus (cavernibardus)* has the same toe-length and head-shape characters that prevented us from assigning a Cerro Yaví species (*pruinatus*) to a named species group. These two species are, however, very different in other respects and we have no suggestions regarding the relationships of either one.



Fig. 27. *Eleutherodactylus avius*, new species, in life, with male and female shown at same scale. **Upper.** AMNH 131480 (paratopotype) ♂, 20 mm SVL. **Lower.** AMNH 131481 (holotype) ♀, 33 mm SVL. This pair was found in amplexus.

***Eleutherodactylus avius*, new species**

Figures 27–29

**HOLOTYPE:** AMNH 131481 (field no. CWM 18703), an adult female from forest at the north base of Pico Tamacuari, 1160–1200 m elevation, Sierra Tapirapecó, Amazonas, Venezuela (1°13'N, 64°42'W). Obtained in the period of March 11–17, 1989; Myers, Donnelly, and Daly collection.

**PARATOPOTYPES:** AMNH 131480, 131484, 131486, MBUCV 6456–6458 (1♀, 3♂, 2 juv.), same data as holotype. Additional Paratype: AMNH 131488 (juv.) from ridge N Pico Tamacuari, 1460 m.

**ETYMOLOGY:** The epithet *avius* is a Latin adjective meaning out of the way or remote, in reference to the type locality.

**DIAGNOSIS:** (1) dorsal skin tubercular, nearly smooth in preservative; ventral skin areolate; (2) tympanum distinct, 33–41 percent of eye length; (3) snout bluntly pointed or slightly rounded to truncate in dorsal view, rounded in profile; canthus rostralis straight

or slightly concave, rounded; (4) upper eyelid with a few small tubercles or not; (5) vomerine odontophores small, variably shaped, between and behind small, round choanae; (6) males with vocal slits (sometimes absent), a shallow subgular vocal pouch, and either two nuptial pads or one long one; (7) finger I shorter than II, broad discs on fingers II–IV; (8) no fringes on fingers, lateral keeling weak; (9) ulnar tubercles absent; (10) no pronounced calcar tubercle; (11) inner metatarsal tubercle oval, much larger than outer; (12) toes essentially webless; toes with broad discs, as broad as or smaller than finger discs; (13) dorsal color and pattern exceedingly variable; low scapular ridges, when present often black; rear of thigh brown, without definite pattern; ventral surfaces pale tan in preservative but with yellow or orange coloring in life; (14) three males 20–24 mm, two females 31–33 mm SVL.

*Eleutherodactylus avius* (*unistrigatus* group) is a small, highly variable frog that, like many of its congeners, might be hard to identify from a single specimen. It is morphologically similar to *E. cantitans*, which also has a striped morph (compare fig. 27 with fig. 7 in Myers and Donnelly, 1996: 11). *E. cantitans* is a larger species that is readily separated from *avius* in having the rear of the thigh black with yellowish flecking and in having a rose wash ventrally, in groin, and in concealed part of shank.

*Eleutherodactylus marmoratus* from Roraima and Marahuaca also has a striped morph, but it is a smaller species that differs from *avius* in having a small tympanum, a large vocal sac, and immaculate white or greenish white ventral surfaces<sup>12</sup> (Boulenger, 1900; Rivero, 1961). See Remarks for other comparisons.

*Eleutherodactylus avius* is the same size and similar in many respects to sympatric *E. memorans*, a less variable species that tends to have a dark W-shaped scapular mark and which, in life, has dark radiating lines below the pupil. Adult *E. avius* have some yellow or orange ventral coloring that is lacking in

<sup>12</sup> The ventral surfaces of the preserved holotype from Cerro Roraima were described as “grey-brown” (Boulenger, 1900: 56). One of the Cerro Marahuaca specimens was compared with the holotype by W. H. Parker (Rivero, 1961: 80).

*memorans*. See Remarks under *E. memorans* for further comparison.

**MEASUREMENTS OF HOLOTYPE** (in mm): The undissected holotype is an adult female that laid eggs in collecting bag. SVL 33.0, tibia length 17.9, foot length from proximal edge inner metatarsal tubercle to tip of fourth toe 14.4, head width 13.1, head length on the diagonal from angle of jaw to tip of snout 12.3, upper eyelid width 2.8, interorbital distance 4.2, internarial distance 2.9, eye to posterior edge of nostril 3.9, eye length 3.5, tympanum length 1.7; width third finger and fourth toe disc both 1.9.

#### DESCRIPTION

The type series comprises two adult females, three adult males, and three unsexed juveniles (sizes below). The females are clearly adult based on presence of large ova. The three males are also judged sexually mature although not all have vocal slits (see below); the smallest male was found in amplexus and all three have well-developed, white testes 1.5–2 mm long.

Females larger than males ( $\bar{x}$  female SVL/ $\bar{x}$  male SVL = 1.48). Three males 19.5, 21.5, 23.6 mm SVL ( $\bar{x}$  = 21.53 mm), two females 30.6, 33.0 mm SVL ( $\bar{x}$  = 31.80 mm), three juveniles 10.2–11.3 mm.

Head as wide as or wider than body (body wider than head only in one gravid ♀), wider than long; head width 37–38 percent of SVL in males, 40 percent in females, 38–39 percent in juveniles. Snout bluntly pointed or slightly rounded to truncate in dorsal view, rounded in profile; eye-nostril distance 67–77 percent of eye length in males, 90–111 percent in females, 59–65 percent in juveniles; nostrils slightly protuberant, directed posterolaterally; canthus rostralis straight or slightly concave, edge rounded; loreal region slightly concave, sloping outward to lip. Upper eyelid smooth or with a few small, low tubercles; upper eyelid width narrower than interorbital distance (eyelid/IOD = 0.75–0.96♂, 0.67–0.68♀, 0.65–0.79 juv.). Tympanum round or slightly oval, distinct except for being slightly obscured dorsally and posteriorly; tympanum length 29–49 percent of eye length (33–41%♂, 43–49%♀, 29–31% juv.); supratympanic fold originating at cor-

ner of eye and extending to shoulder, slightly arched. Small postrictal tubercles usually evident. Choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores small, bearing 1–6 teeth; posterior and medial to choanae; odontophores about as wide as choanae and variable in shape. Tongue broad, sometimes covering floor of mouth, about as long as wide, notched posteriorly, posterior half free. Short vocal slits lateral to tongue present or absent—vocal slit opened only on the right side in 19.5 mm male, not open on either side in 21.5 mm male, open on both sides in 23.6 mm male. Shallow, subgular vocal pouch at least in first and third specimens; pouch with a weak longitudinal expansion fold on each side of throat, seemingly not very distensible.

Dorsal skin tubercular (fig. 27), becoming nearly smooth in preservative; middorsal raphe faint in a few specimens, not evident in others. Several specimens (MBUCV 6456♀, 6457♂, 3 juv.) have a very low, sometimes interrupted scapular ridge extending from the eye to above the shoulder; these ridges are nearly straight except in MBUCV 6456♀, which has them crescent-shaped like a widely separated )(-mark. In a few specimens (especially MBUCV 6456♀, 6458 juv.) a narrow dorsolateral fold extends from the posterior end of the scapular ridge to the end of the body, but this structure is weak and easily overlooked. Throat smooth; venter coarsely granular (areolate); posteroventral thigh surface coarsely granular; weak discoidal fold anterior to groin; ulnar tubercles absent.

Relative length of appressed fingers III > IV > II > I; appressed first finger reaching or failing to reach proximal edge of subdigital pad of second; lateral keeling weak; males with two whitish nuptial pads, one adjacent to thenar tubercle and the other on posterodorsal side of thumb (one male with these pads contiguous, forming one long pad). Finger discs broader than long, slightly rounded to truncate; distal median edge usually straight but two males have a few finger discs with a slight concavity (weakly indented). Palmar tubercle large and cordiform; thenar tubercle large, ovoid; several small, rounded supernumerary tubercles present;

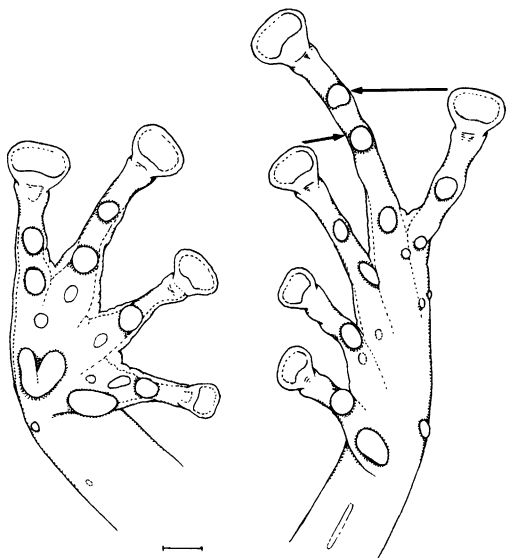


Fig. 28. *Eleutherodactylus avius*, new species. Right hand and left foot of paratopotype (MBUCV 6456♀). Arrows indicate position of tips of third and fifth toes when these digits are straightened and appressed against the fourth toe. Scale line = 1 mm.

subarticular tubercles protuberant, often conical.

Hind limbs relatively long; heels overlap when held at right angles to sagittal plane; tibia 54–58 percent of SVL in males, 54–56 percent in females, 51–54 percent in juveniles. Relative lengths of appressed toes IV > V > III > II > I; tip of toe V extends to distal edge of ultimate subarticular tubercle of IV, tip of III to the middle or distal edge of the penultimate subarticular tubercle of IV. Toe discs as wide or narrower than finger discs (adult 3rd finger disc/4th toe disc = 1.00–1.18), with wide subdigital pads. Toes with weak lateral keeling; basal webbing indistinct or absent. Inner metatarsal tubercle elongate, oval, much larger than small, rounded outer metatarsal tubercle; small supernumerary plantar tubercles low and round; subarticular tubercles protuberant, often conical. Calcar tubercle(s) small, low, scarcely elevated. Tarsal fold absent or indicated by an elongated low tubercle on distal half of tarsus; tarsal tubercle best developed (0.8–1.5 mm long) in the adult females.

COLOR PATTERN: The variably patterned

dorsal surfaces, faded in preservative to shades of gray and brown, were variably colored in life. Dorsal ground color varied from shades of orangish brown (1♀, 2♂) through brown (1♂, 2 juv.) or tan (1 juv.) to greenish brown (♀ holotype). There are several types of dorsal patterns. *Dark Stripes*: One male and all three juveniles had a median and two dorsolateral stripes of grayish brown or brown; these specimens are the only ones lacking a dark interorbital bar. *Pale Vertebral Line*: One male with a nearly uniform brown dorsum had a tan vertebral line, extending through the dark interorbital bar to the snout. *Dark Blotches*: The female holotype has several vague dorsal blotches not noted in life but evident in liquid—a transversely rectangular blotch between the arms, a large rounded one at midbody, and a small one in the sacral region. *Dorsal Chevrons*: A female has several well-defined chevrons. A male has a single, chevronlike mark in the shape of an inverted Y at midbody and a broken horizontal line between the arms. *Scapular Marks*: Segments of the scapular ridges are black in the juveniles and several adults; the ridges are continuously black in one female, but black pigmentation is lacking in the female holotype and one male that lack these ridges.

Flanks of all specimens were obliquely banded or mottled with grayish brown or brown on pale orangish brown, with limbs adorned with similarly colored cross-bands; in a few cases cross-bands are represented by spots or blotches on the dorsal thigh surfaces. A brown, sometimes ill-defined, postocular stripe across upper part of tympanum; this stripe, which usually does not touch the eye and fails to reach the shoulder, tends to be darkest along its upper edge on the supratympanic fold. All specimens have dark bars radiating from the eye to the upper lip.

The rear of the thigh was brown or light brown (2♂), dark brown with paler brown areas (♀ holotype), pale grayish brown with a distal suffusion of dark reddish brown (1♀), or greenish gray (1♂).

The ventral surfaces, faded in preservative to pale tan or dirty white, with variable brown or gray suffusion or mottling on the throats, differed in life by sex and age. *Males*: Ventrals of the three males were pale

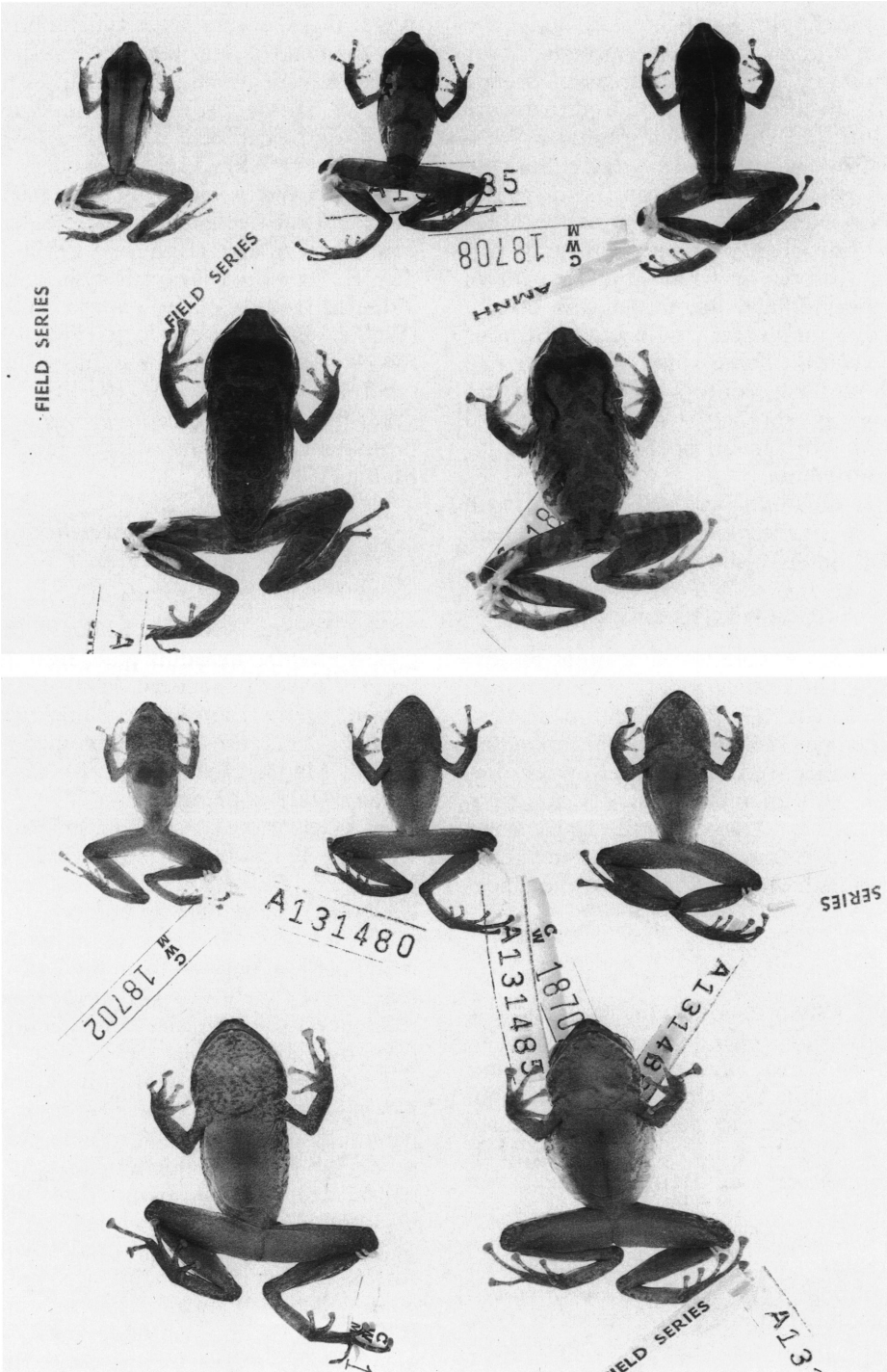


Fig. 29. *Eleutherodactylus avius*, new species, in dorsal and ventral view, showing color pattern variation and sexual dimorphism in size. **Top rows, males.** Left to right: AMNH 131480, MBUCV 6457, AMNH 131486. **Bottom rows, females.** AMNH 131481 (holotype), MBUCV 6456.  $\times 1.0$ .

bronzy orange with small areas of gray; the contrasting throats were either greenish gray (1 frog) or gray with small areas of orange (2 frogs). In preservative, the throats are heavily suffused with brown. *Females*: Ventrals of the two adult females were either pale yellowish with a bronzy sheen (holotype) or light bronzy yellow. The throat of the holotype was pale bronzy orange with gray vermiculation (brown on white in preservative); in the other female, the throat was bronzy yellow (like the venter), with inconspicuous spots. *Juveniles*: Three small specimens had greenish yellow venters and contrasting blackish gray throats. Undersides of the limbs were gray in all specimens, both juveniles and adults.

The iris of adults was pale bronze, with sparse, fine black venation and a reddish, horizontal butterfly-shaped stripe.

#### NATURAL HISTORY

All specimens were taken at night on low vegetation. The female holotype and a much smaller male (fig. 27) were found in amplexus, and she later laid 18 eggs in the collecting bag. The yolks were white (yellow in preservative). Yolk diameters 3.6–4.1 mm ( $\bar{x}$  = 3.93 mm, SD = 1.41); overall (jelly coat) diameters 4.5–5.0 mm ( $\bar{x}$  = 4.64 mm, SD = 0.176). No call was associated with this species.

#### REMARKS

Among *Eleutherodactylus* in southern Venezuela, *E. avius* seems most similar to *E. cantitans* of Cerro Yaví and *E. marmoratus* of Cerro Roraima and Cerro Marahuaca, but these species seem to be readily separated (see Diagnosis). It is also similar to sympatric *E. memorans* (see Remarks under that species).

The presence of low scapular ridges in some specimens of *avius* invites comparisons with additional species in the *unistrigatus* group that have similar structures. At least six species from northern Venezuela have scapular ridges or tubercles, but none seems close to the southern species: *E. ginesi* is a rotund páramo species with row of middorsal tubercles (Rivero, 1964; "1982a" [1984]: 27); the Andean *E. lentiginosus* has indented

finger discs, a very large tympanum, and the eye diameter is less than the eye-nostril distance (Rivero, "1982b" [1984]: 84); the Andean *E. melanoproctus* has indented finger discs and a black cloacal spot (Rivero, "1982b" [1984]: 75); the Andean *E. pleurostriatus* has a large but indistinct tympanum and the metatarsal tubercles are nearly equivalent in size (Rivero, "1982b" [1984]: 88); *E. reticulatus* from Rancho Grande has a distinctive reticulated pattern on the venter (Walker and Test, 1955; Rivero, 1961: 76); the Andean *E. tubernasus* has a distinctive tubercle on the snout (Rivero, "1982b" [1984]: 64); the Andean *E. vanadise*<sup>13</sup> has prominent ulnar and calcar tubercles (La Marca, 1984).

#### *Eleutherodactylus cavernibardus*, new species

Figures 30–36, 37A

**HOLOTYPE**: AMNH 131537 (field no. CWM 18770), an adult male from the north base of Pico Tamacuari, 1160–1200 m elevation, Sierra Tapirapécó, Amazonas, Venezuela (1°13'N, 64°42'W). Obtained in the period of March 11–17, 1989; Myers, Donnelly, and Daly collection.

**PARATOPOTYPES**: AMNH 131536, 131538–131541, 131548, 131550, MBUCV 6459–6466 (5♂, 5♀, 7 juv., 2 cleared and stained skeletons), same data as holotype.

**ETYMOLOGY**: The species name is a noun in apposition, derived from the Latin *caverna* (cave) + connective *-i* + *bardus* (singer), in reference to the diurnal sites commonly utilized by calling males.

**DIAGNOSIS**: (1) dorsal skin granular and weakly tuberculate, venter areolate; (2) tympanum distinct; (3) snout rounded to truncate in dorsal view, rounded in profile; canthus rostralis rounded but distinct; (4) upper eyelid granular, lacking tubercles; (5) vomerine odontophores absent; (6) males with vocal slits and a shallow subgular vocal sac; no nuptial pad; (7) finger I shorter than finger II, fingers bearing broad discs, medially notched above; (8) fingers lack fringes; (9) ulnar tubercles absent; (10) no pronounced

<sup>13</sup> The synonymous name *E. cerasoventris* Rivero was still in press when *vanadise* was published fide Rivero ("1982b" [1984]: 80).

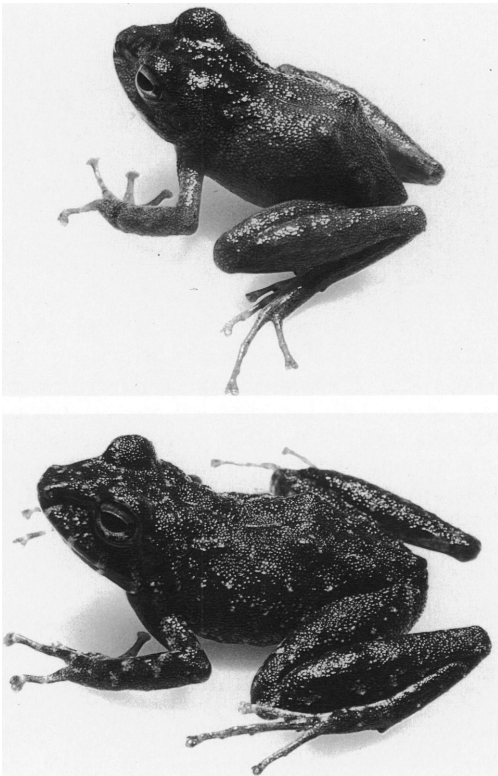


Fig. 30. *Eleutherodactylus cavernibardus*, new species, in life. **Upper.** AMNH 131537 (holotype) ♂, 29 mm SVL. **Lower.** AMNH 131536 (paratopotype) ♀, 32 mm SVL. Not to same scale.

calcar tubercle; (11) inner metatarsal tubercle oval, up to twice length of outer; (12) toes lack webbing and fringes (lateral keeling weak); toe discs broader than long, medially notched, smaller than finger discs; (13) dorsal color usually green (sometimes brown), often with a dark hourglass or X-marking; white median gular stripe and paired pectoral spots; (14) males about 27–31 mm SVL, females 30–32 mm.

*Eleutherodactylus cavernibardus* is distinguished from all other species of the genus by the combination of distinctly notched digit tips (fig. 37A), absence of vomerine odontophores, and color pattern including a pale gular stripe and pectoral spots (fig. 31). See Remarks for comparisons.

**MEASUREMENTS OF HOLOTYPE** (in mm): The undissected holotype is an adult male with well-developed vocal slits. SVL 28.8,

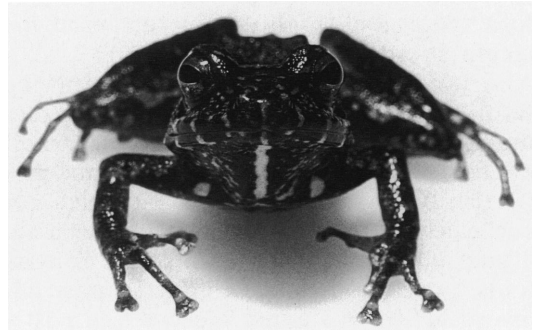


Fig. 31. Head-on view of *Eleutherodactylus cavernibardus*, new species, showing maximum development of pale gular stripe and pectoral spots (AMNH 131536).

tibia length 16.8, foot length from proximal edge inner metatarsal tubercle to tip of fourth toe 13.8, head width 10.9, head length on the diagonal from angle of jaw to tip of snout 10.8, upper eyelid width 2.8, interorbital distance 2.0, internarial distance 2.6, eye to posterior edge of nostril 2.9, eye length 4.2, tympanum length 1.7; width third finger disc 1.5, width fourth toe disc 1.2.

#### DESCRIPTION

Sexual size dimorphism not pronounced, females slightly larger than males ( $\bar{x}$  female SVL/ $\bar{x}$  male SVL = 1.08). Five males 26.7–31.2 mm SVL ( $\bar{x}$  = 28.84 mm), five females 29.9–31.8 mm SVL ( $\bar{x}$  = 31.02 mm), seven juveniles 10.7–21.9 mm.

Head as wide as body, slightly longer than wide; head width 37–41 percent of SVL in males, 38–39 percent in females, 35–39 percent in juveniles. Snout rounded to truncate in dorsal view, rounded in lateral view; eye-nostril distance 69–75 percent of eye length in males, 73–85 percent in females, 55–75 percent in juveniles; nostrils slightly protuberant, directed posterolaterally; canthus rostralis straight or slightly concave, edge rounded but distinct; loreal region slightly concave, sloping to lip. Upper eyelid granular like dorsum, lacking tubercles; upper eyelid narrower or wider than interorbital distance (eyelid/IOD = 0.96–1.40 ♂, 0.90–1.12 ♀, 1.00–1.45 juv.). Tympanum round or higher than wide, distinct, dorsal edge sometimes slightly obscured by supratympanic

fold; tympanum length 39–51 percent of eye length in adults (40–48% ♂, 39–51% ♀, 24–43% juv.); supratympanic fold low, varying from smooth and indistinct to sharply defined, extending from eye and ending short of arm. A few postrictal tubercles, sometimes whitish. Choanae round or tear-shaped, not concealed by palatal shelf of maxillary arch; vomerine odontophores absent. Tongue round or longer than wide, posterior edge entire (usually) or slightly nicked, free posteriorly. Vocal slits present in males, posterolateral to tongue; shallow subgular vocal sac.

Dorsal and flank skin granular and weakly tubercular (fig. 30), the granulation (tubercles to a lesser extent) well retained in preservative; middorsal raphe distinct. Throat smooth, venter coarsely granular; posteroventral thigh surface coarsely granular; distinct discoidal fold anterior to groin; no distinct ulnar tubercles.

Relative length of appressed fingers  $III > IV > II > I$ ; first finger usually reaching subdigital pad of second; lateral keeling weak; males lacking nuptial pads. Finger discs and subdigital pads wider than long; disc on thumb distinctly expanded but smaller than those on fingers II–IV; ungual flap deeply notched (fig. 37A) in either a V- or U-shape. Palmar tubercle large, cordiform; thenar tubercle oval; supernumerary palmar tubercles round or elongate, smaller and lower than subarticular tubercles, which have rounded surfaces.

Hind limbs relatively long; heels overlap when held at right angles to the sagittal plane; tibia 54–64 percent of SVL (56–64% ♂, 57–61% ♀, 54–63% juv.). Relative length of appressed toes  $IV > V \geq III > II > I$ ; tips of toes V and III extend just distal to the penultimate subarticular tubercle of toe IV. Toe discs and subdigital pads broad, but narrower than those on fingers; ungual flap notched. Lateral keeling faint, webbing absent. Inner metatarsal tubercle elongate, oval, longer than round to oval outer metatarsal tubercle; supernumerary plantar tubercles absent; subarticular tubercles low, with rounded surfaces. No pronounced calcar tubercles (any tubercles on heel are minute and inconspicuous). No tarsal fold or pronounced tarsal tubercle; some specimens have a row of about 4–5 well-spaced, small whitish tuber-

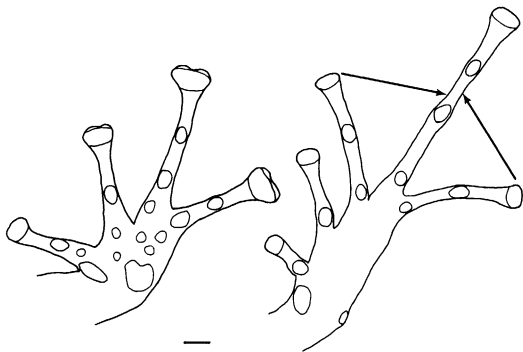


Fig. 32. *Eleutherodactylus cavernibardus*, new species. Left hand and left foot of male paratype (MBUCV 6463). Arrows indicate position of tips of third and fifth toes when these digits are straightened and appressed against the fourth digit. Scale line = 1 mm.

cles, this row (when present) starting proximal to outer metatarsal tubercle and extending nearly to heel.

**COLOR PATTERN:** In life (fig. 30), dorsal surfaces were variable but usually included the color green. Most were green with a dark brown pattern (vague hourglass or X); other individuals were unicolor green or else greenish black with bright green streaks and flecks. A few were noted to be brown or olive brown; two of the brown specimens had the head and shoulders darker brown.

The preserved frogs (fig. 33) appear more constant, varying from light to dark brown, with light dorsal streaks forming either the outline of a brown hourglass-shaped mark (sometimes darker than the flank color) or else the outer edges of a vague, thick X-shaped mark (with the dorsal ground being similar to the flanks). All frogs have a variably distinct pale interorbital line, which forms the anterior edge of any hourglass mark. There is a usually ill-defined dark canthal stripe extending from the eye through the nostril to the snout tip. Several variably distinct light lines (or spots) radiating from the eye and crossing the lips were yellowish or greenish in life; there also is a thin vertical line of the same color on the tip of the snout, in line with the white gular stripe below (fig. 31).

The arms, colored like the dorsum, sometimes show light and dark crossbanding; all



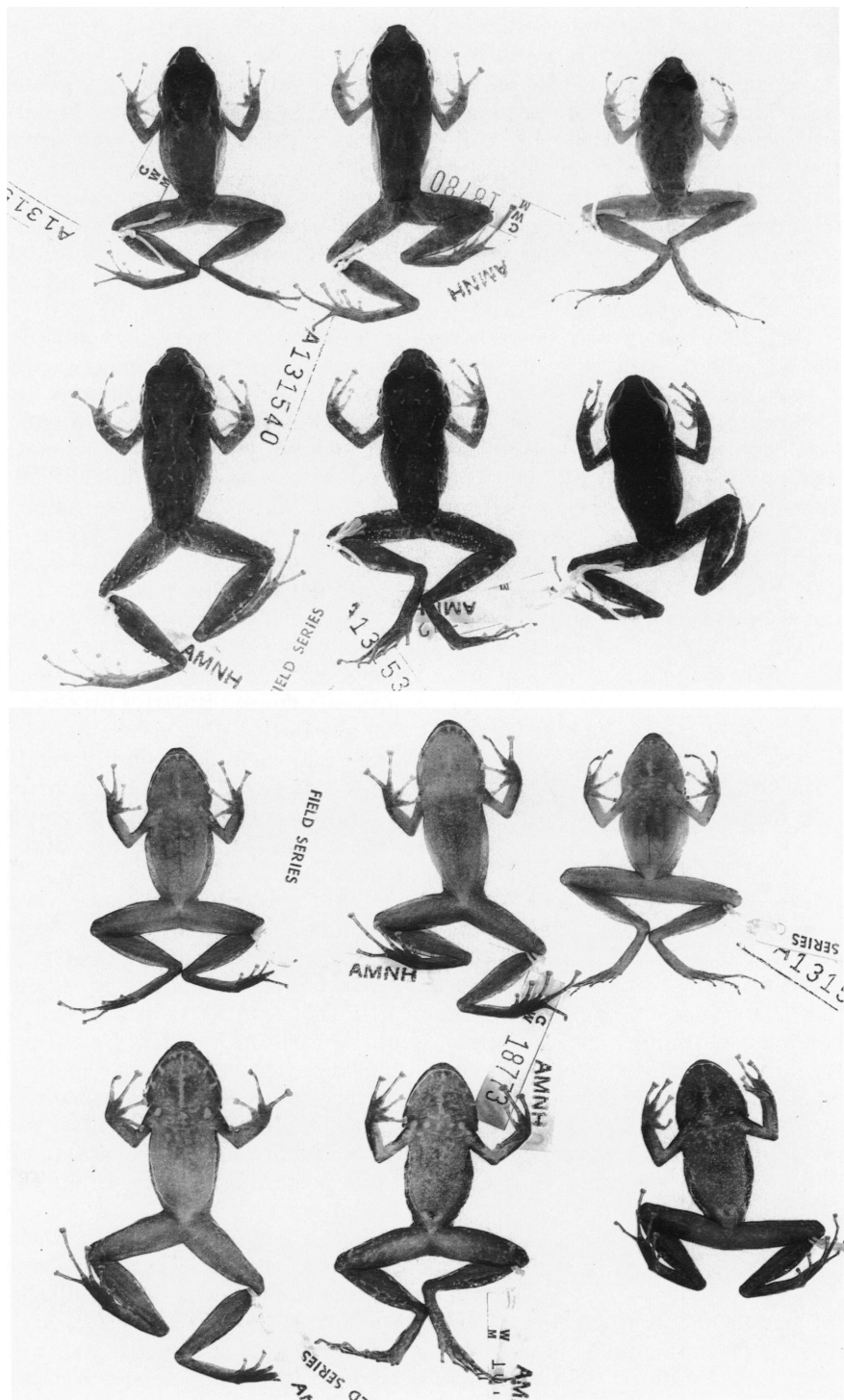


Fig. 33. *Eleutherodactylus cavernibardus*, new species, in dorsal and ventral view. **Top rows, males.** Left to right: AMNH 131537, 131540, MBUCV 6464. **Bottom rows, females.** AMNH 131536, 131538, 131539.  $\times 0.82$ .

have dark wrist bands. The anterior thigh surfaces and sometimes the groin are brown in preservative. Pale spots or flecks on the upper limb surfaces sometimes are arranged as vague cross-banding. Two pale lines diverge ventrally from the vent, enclosing a usually distinct dark seat patch. The posterior thighs were brown to blackish gray in life (brown in preservative), usually with indistinct gray flecks.

The ventral surfaces were overall blackish gray in life (faded to brown or pale brown in preservative), with a scattering of white dots on the venter, a white gular stripe, and paired white pectoral spots—one or two small spots on each side at the arm insertions (visible in life in head-on view, fig. 31). The yellowish lines (white in preservative) from the upper lip extend onto the underside of the lower lip. Two of the preserved specimens (AMNH 131540, MBUCV 6461) have very pale tan ventral surfaces, but the aforementioned pale markings are discernible; the throat is darker than the venter in several preserved specimens.

The iris was bright bronzy orange with a reddish brown horizontal stripe and, especially on the lower part, with slight black suffusions or inconspicuous black flecking (vs. venation).

**JUVENILE COLOR PATTERN:** Very small juveniles between 10 and 16 mm SVL ( $N = 5$ ) looked very much like the adults. The body of five froglets varied from entirely brown to entirely green, or brown dorsally and green dorsolaterally and over the limbs. The pale streaks outlining the hourglass marking appeared in life as green or tan )-(shaped markings. The ventral surfaces were gray with the same white gular stripe and pectoral spots as in adults, except that the white markings were indistinct in one of the smallest juveniles.

#### OSTEOLOGY

Two adult female paratopotypes (AMNH 131550, MBUCV 6466), about 31 and 33 mm SVL, were skinned in the field and later cleared and double-stained. The following notes are from the still-articulated preparations.

Skull little wider than long. Frontoparie-

tals moderately ossified, narrowly separated along entire length in smaller specimen, closely sutured along the posterior three-quarters in larger specimen. Nasals moderate, not in medial contact, well separated from frontoparietals by sphenethmoid. Occipital condyles on short stalks, widely separated.

Premaxillae with alary processes directed posterodorsally; maxilla with deep facial lobe; pedicellate teeth on premaxillae and maxillae. Squamosal markedly triradiate, with anteriorly directed zygomatic ramus not approaching maxilla; relative length of squamosal branches: ventral ramus  $>$  otic ramus  $>$  zygomatic ramus. Vomers widely separated, lacking dentigerous processes. Parasphenoid with a jagged anterior edge level with anterior edge of orbits; parasphenoid alae approaching but not overlapping the median rami of pterygoids. Anterior ramus of pterygoid not reaching palatine.

Hyoid plate completely cartilaginous, about as wide as long. Each posterodorsally curving hyale bearing a long, slender anterior process; the two anterior processes of the hyalae anteriorly curve medially toward one another and each has a small lateral hook. Alary processes of hyoid plate directed anterolaterally, not expanded; posterolateral processes shorter. Posteromedial processes ossified except for distal cartilaginous tips.

Eight procoelous presacral vertebrae, with nonimbricate neural arches. Transverse processes of vertebra II relatively short, longest on vertebra III, shorter and subequal on IV–VIII (but transverse processes more robust on IV than on V–VIII). Sacral processes directed posterolaterally, barely dilated distally. Sacral-coccygeal articulation bicondylar. Urostyle slightly shorter than vertebral column, lacking lateral processes, strong dorsal ridge present anteriorly. Ilium with a strong dorsal crest.

Pectoral girdle arciferal; no discrete epicoracoidal horns. Sternum a large cartilaginous plate (slightly mineralized in larger specimen), posteriorly bifurcated. Omosternum large, cartilaginous, anteriorly expanded. Clavicles long and slender, barely curved, laterally fused with scapulae. Tarsal elements not fused. Phalangeal formula of hands 2-2-3-3, of feet 2-2-3-4-3. Terminal phalanges of all digits T-shaped.

## NATURAL HISTORY AND VOCALIZATION

*Eleutherodactylus cavernibardus* is known only from montane forest at the north base of Pico Tamacuari. It appears to be diurnal but it is not easily caught by day. We were first attracted by its calls, which usually emitted from small caves under granite boulders. A few males called from aroid roots on the tops of boulders, but the vast majority were calling from small caves in the rocks, into which one crawled or slithered with flashlight in hand.

It is an incredibly wary and secretive frog. Males would cease calling when approached or when a light was directed toward them. Males and females were seen together in caves during the day; when one female was captured, her companion male gave a different sounding call that was not recorded. Juveniles were taken during the day on leaf litter; when approached, they would jump a considerable distance to escape. In contrast with their diurnal wariness and speleological proclivity, we easily caught several frogs at night that were perched (sleeping?) on leaves in the forest about 1 m aboveground.

The call is a 1.6–11.2 sec train of loud notes given at a rate of 4–5 notes per sec; note duration is 0.08–0.12 sec ( $\bar{x}$  = 0.102,  $N$  = 48); the notes are distinctly pulsed (at about 55–67/sec) as evident from waveforms and wide-band spectrograms (figs. 34, 35). As evident from narrow-band spectrograms, the notes are narrowly tuned at a fundamental frequency of about 1500 Hz (1480–1520 Hz), with a pronounced harmonic at twice the fundamental. Frequency is not modulated except at the beginning of two calls, in which the first note drops rapidly from 2400 Hz to nearly 1400 Hz, with the second note initiated at the lower frequency before rising to a fundamental frequency of 1520 Hz for the remainder of the call (fig. 36). Otherwise the notes are rather constant and evenly spaced, except that the first one or two are sometimes hesitating and may be shorter and softer than those following.

Note-repetition rate may be correlated positively with temperature: two 1.6–2.4 sec calls of one frog recorded at an air temperature of 17.4°C (ground 16.3°C) were given at 3.9–4.3 notes/sec. At an air temperature of

21.6°C (ground 19.5°C), 13 1.6–11.2 sec calls of two frogs were given at rates of 4.2–5.3 notes/sec ( $\bar{x}$  = 4.71  $\pm$  0.093, SD = 0.339). Pulse rate varies somewhat in a progression of same-call notes and was not examined for possible temperature influence.

Call length is individually variable, as shown by the two frogs recorded at the higher temperature: Call length was 1.6–4.3 sec ( $\bar{x}$  = 2.94 sec,  $N$  = 7 calls) for the frog in the foreground versus 2.7–11.2 ( $\bar{x}$  = 7.45 sec,  $N$  = 6 calls) for one in the near background. In four of six cases, the background caller initiated vocalization in the beginning of the shorter calls. Several times we heard *E. cavernibardus* form choruses after one had initiated calling. Based on the frequency of calling, *E. cavernibardus* seems to be one of the most common frogs in the area.

## REMARKS

As previously stated (under Family Lepidodactylidae), *Eleutherodactylus cavernibardus* is not assigned to a species group. It has a short first finger and coarsely granular (areolate) ventral skin in common with members of the large *unistrigatus* group, but it differs in having a relatively narrower head and a relatively short fifth toe (toe V  $\geq$  III). In all these respects, *E. cavernibardus* is reminiscent of *E. pruinatus* from Cerro Yaví (Myers and Donnelly, 1996: 14), but the two differ in nearly all other respects: *E. pruinatus* is uniformly dark except for pale speckling (frosting) above and unlike *cavernibardus* it has flat warts on the eyelids and supernumerary tubercles on the hind feet.

*E. cavernibardus* further differs not only from *pruinatus* but apparently from all other *Eleutherodactylus* in its combination of distinctly notched digit tips (fig. 37A), absence of vomerine odontophores, and color pattern including a pale gular stripe and pectoral spots (fig. 31). White throat stripes are widespread in *Eleutherodactylus*, but, in the Guayana region, the gular and pectoral pattern of *E. cavernibardus* seems to be approached only in *E. gutturalis*, which was originally described in the *fitzingeri* group (Hoogmoed et al., 1977: pl. 1). *E. cavernibardus* is immediately distinguished from *E. gutturalis* by coarsely granular ventral skin (smooth in

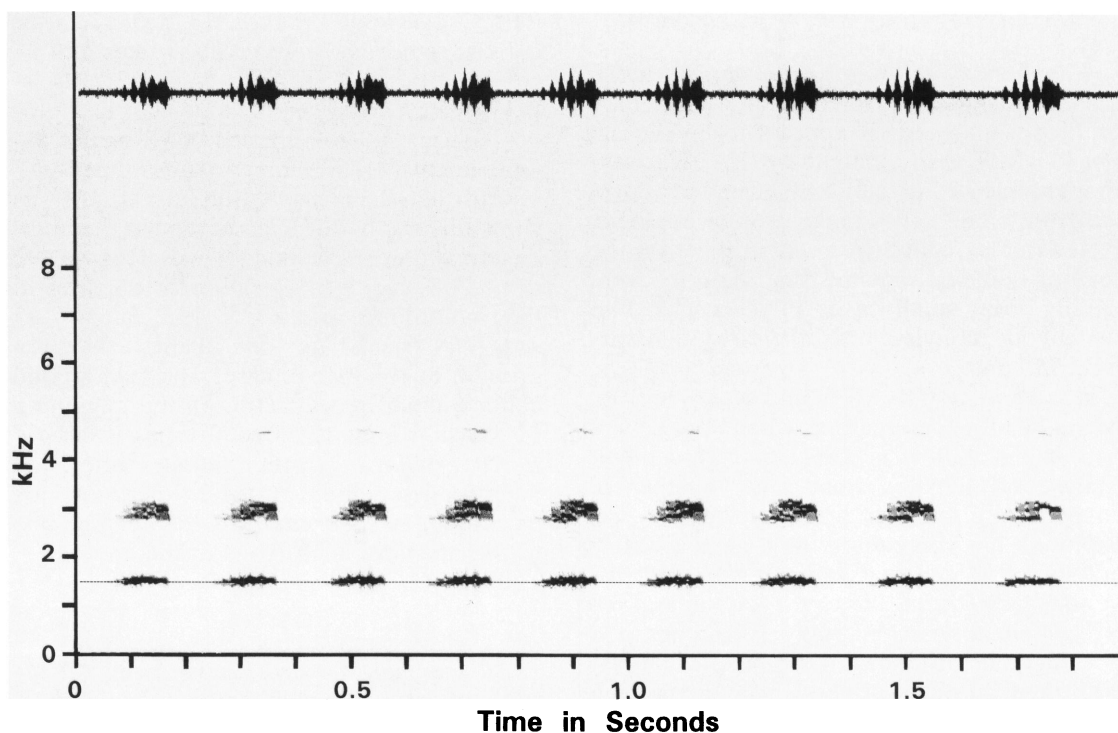


Fig. 34. Vocalization of *Eleutherodactylus cavernibardus*, new species. Waveforms and narrow-band (59-Hz filter) sound spectrogram of last 9 (of 13) notes in a 2.68 sec call; cursor line through fundamental frequency set at 1480 Hz. Recorded March 13, 1989; ground temperature 19.5°C, air 21.6°C at calling site (AMNH herpetology reel 256:1).

*gutturalis*) and in having finger I shorter than II ( $I > II$  in *gutturalis*).

The deeply notched disc of *E. cavernibardus* differs fundamentally from that of *Dischidodactylus duidensis* from Cerro Duida (Rivero, 1968c; Lynch, 1979). In *D. duidensis*, the unguis flap is indented and then longitudinally divided to a proximal transverse groove—leaving the digit tip distally divided on its dorsal side (fig. 37B).

Distinctly notched<sup>14</sup> digits are less com-

mon in *Eleutherodactylus* than indented ones (having broader or more shallow concavities), and these in turn are less common than uninterrupted rounded or truncate digits. Other than *E. cavernibardus*, we are unaware of any species of *Eleutherodactylus* with notched or indented discs that also lacks odontophores; we suspect that the combination is uncommon. Added to these traits, the diurnal behavior, distinctive call, green and black dorsal coloring, and pale gular stripe with pectoral spots all combine to set off *E. cavernibardus* as a very distinctive species whose relationships are still to be sought.

*Eleutherodactylus memorans*,  
new species  
Figures 38–43

HOLOTYPE: AMNH 131466 (field no. CWM 18748), an adult female from camp on ridge N Pico Tamacuari, 1270 m elevation,

<sup>14</sup> The word *notched* is unambiguous when referenced to figure 37A. It is one of the meanings of *emarginate* (literally, “deprived of a margin”), both words also having been used interchangeably with *indented* and *bifurcated* for a range of configurations. Savage (1987: dorsal outlines in fig. 4) differentiated “indented” and “notched” conditions on rounded digital discs and “emarginate” on a truncate disc—the last for what might be described as a broad notch. We use “notched” and “indented” in the present paper for two conditions on wide (truncate) digital discs, with “indented” implying a relatively broad and shallow concavity.

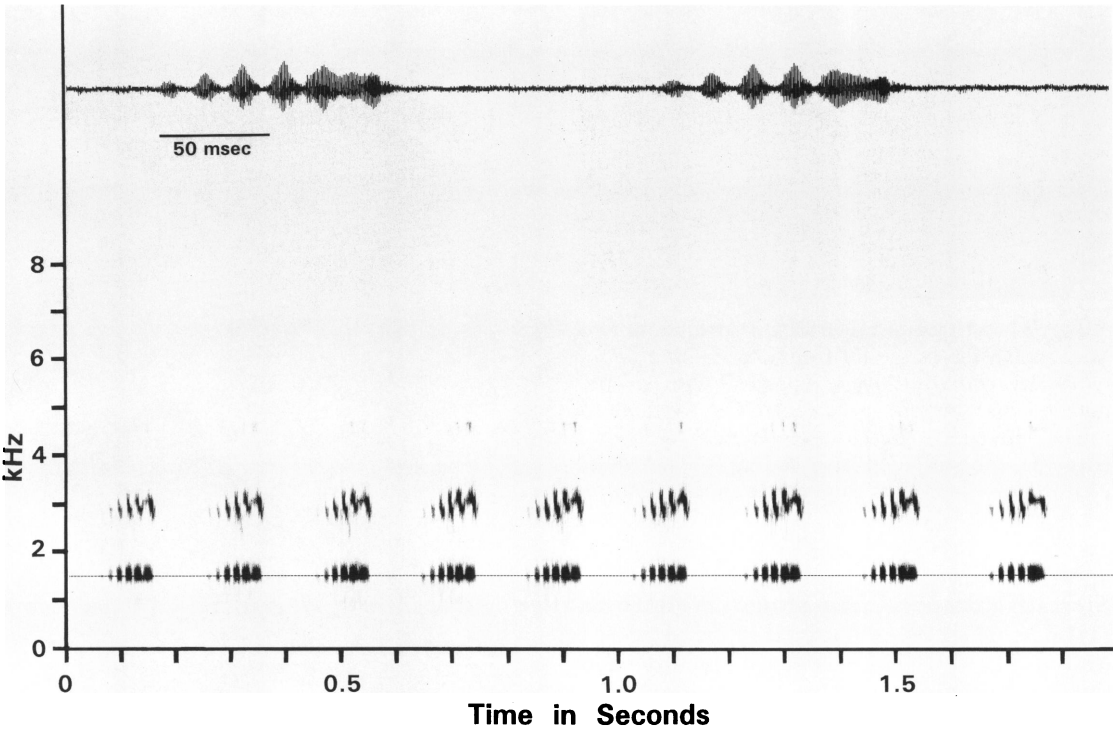


Fig. 35. *Eleutherodactylus cavernibardus*—same call notes as in figure 34, but waveforms of last two notes are expanded and sound spectrogram is wide-band (300-Hz filter).

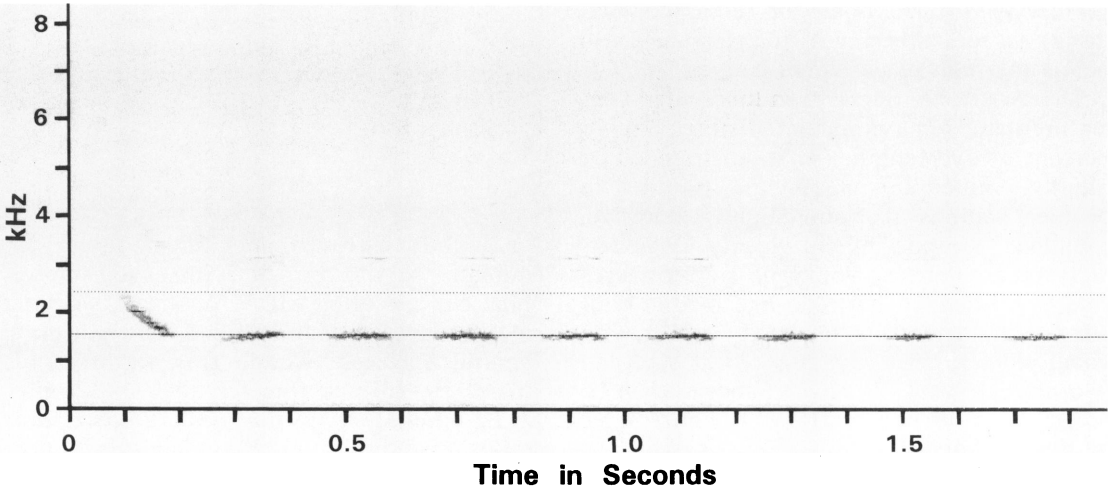


Fig. 36. *Eleutherodactylus cavernibardus*. A call variant in which frequency is strongly modulated in the first note; frequency cursors are set at 1520 and 2440 Hz. Narrow-band (59 Hz) spectrogram of first 9 notes (of 13) in a 2.65 sec call. Other data as for figure 34 (specimen calling in background of that recording).

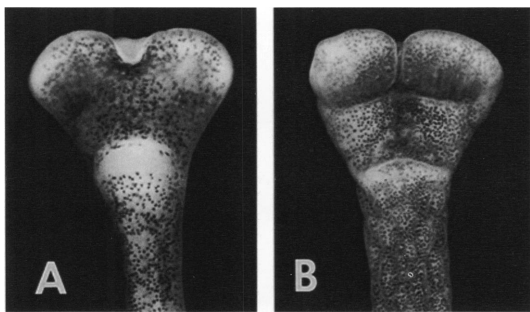


Fig. 37. Unusual finger disc structures in two Venezuelan leptodactylid frogs. **A.** *Eleutherodactylus cavernibardus*, new species, with deeply notched disc margin,  $\times 14$  (MBUCV 6462, third finger, left hand). **B.** *Dischidodactylus duidensis* (Rivero), with divided disc cover,  $\times 13$  (AMNH 23190, holotype, third finger, right hand).

Sierra Tapirapécó, Amazonas, Venezuela ( $1^{\circ}13'N$ ,  $64^{\circ}42'W$ ). Obtained in the period of March 11–17, 1989; Myers, Donnelly, and Daly collection.

PARATYPES: AMNH 131465, 131467–131472, MBUCV 6449–6453 (2♀, 8♂, 2 juv.), same data as holotype. MBUCV 6454, 6455 (1♀, 1♂) from streamside forest at the north base of Pico Tamacuari, 1160–1200 m elevation. Other data same as for holotype.

ETYMOLOGY: The name given to this frequent vocalizer is the present participle of the Latin *memoro* (to relate or recount something)—a remembering of the airplane crash below the high place where it lives.

DIAGNOSIS: (1) dorsal skin tubercular, venter areolate; (2) tympanum distinct, 26–43 percent of eye length; (3) snout rounded or bluntly pointed in dorsal view, rounded in profile; canthus rostralis slightly concave, rounded; (4) upper eyelid weakly to moderately tubercular; (5) vomerine odontophores small but distinct, between and behind choanae, with detectable teeth; (6) males with vocal slits, a large subgular vocal sac, and two nuptial pads; (7) finger I shorter than II; broad discs on fingers II–IV; (8) no fringes on fingers, lateral keeling absent or weak; (9) ulnar tubercles low and weak; (10) no pronounced calcar tubercle; (11) inner metatarsal tubercle oval, much larger than small outer; (12) toes lacking distinct lateral keeling and basal webbing; toe discs broad, as large



Fig. 38. *Eleutherodactylus memorans*, new species, in life, with male and female shown at same scale. **Upper.** AMNH 131465 (paratopotype) ♂, 23 mm SVL. **Lower.** AMNH 131466 (holotype) ♀, 32 mm SVL.

or slightly narrower than finger discs; (13) dorsum variably brown, with vague interorbital bar and often with a W-shaped scapular mark; rear of thigh unmarked brown or gray; ventral surfaces overall gray in life; (14) males 19–23 mm, four females 31–32 mm.

*Eleutherodactylus memorans* (*unistrigatus* group) is similar to *E. pulvinatus* Rivero from the Escalera region, Edo. Bolívar. The color patterns are similar but more constant and more vivid in *E. pulvinatus* (compare fig. 44 with fig. 41), which also has a more tuberculate upper eyelid. At least the males of

*E. pulvinatus* are larger than those of *E. memorans*. See Remarks for further comparison.

*E. memorans* is the same size as the sympatric and morphologically similar *E. avius*, but *memorans* is distinguished by the W-shaped scapular mark and other subtleties of coloration and proportions (see Remarks).

MEASUREMENTS OF HOLOTYPE (in mm): The undissected specimen is an adult female based on size and large ova visible through body wall. SVL 31.5, tibia length 17.8, foot length from proximal edge inner metatarsal tubercle to tip of fourth toe 14.0, head width 12.5, head length on the diagonal from angle of jaw to tip of snout 12.1, upper eyelid width 2.8, interorbital distance 3.9, internarial distance 2.5, eye to posterior edge of nostril 3.6, eye length 4.0, tympanum length 1.7; width third finger disc 1.9; width fourth toe disc 1.8.

#### DESCRIPTION

The type series includes nine adult males, all with vocal slits and large vocal sacs, four adult females with large ova visible through the abdominal wall, and two juvenile females with undeveloped ovaries (ova about 0.2–0.3 mm).

Females larger than males ( $\bar{x}$  female SVL/ $\bar{x}$  male SVL = 1.47). Nine males 18.9–22.7 mm SVL ( $\bar{x}$  = 21.40 mm), four females 31.2–31.7 ( $\bar{x}$  = 31.45 mm), two juvenile females 17.9, 22.2 mm SVL. Head distinctly narrower than body in females, slightly narrower than body in males, longer than wide; head width 39–42 percent of SVL in males, 39–41 percent in females (also 39–41 percent in juveniles). Snout rounded to bluntly pointed in dorsal view, rounded in profile; eye-nostril distance 78–97 percent of eye length in males, 76–90 percent in females, 78–81 percent in juveniles; nostrils slightly protuberant, directed posterolaterally with a slight tilt dorsad; canthus rostralis slightly concave, edge rounded; loreal region slightly concave, sloping outward to lip. Upper eyelid weakly to moderately tubercular, the tubercles being low and mostly rounded and

inconspicuous, but there may be a few prominent ones especially posteriorly and on the edge of the lid (fig. 38); upper eyelid narrower than interorbital distance (eyelid/IOD = 0.76–0.96♂, 0.72–0.88♀, 0.75–0.86 juv.♀). Tympanum oval, higher than wide, distinct except tending to be slightly obscure posterodorsally; tympanum length 26–43 percent of eye length (26–41%♂, 36–43%♀, 30–38% juv.♀); supratympanic fold low and weak, extending from eye and ending short of arm. Small postrictal tubercles, one or more often prominent. Choanae small, variably shaped, not concealed by palatal shelf of maxillary arch; vomerine odontophores distinct, subequal in size to choanae, positioned posterior and median to choanae; odontophores variable in shape, bearing 1–6 teeth. Tongue longer than wide, posterior two-thirds free, notched posteriorly. Males with well-developed vocal slits lateral to posterior half of tongue; subgular vocal sac large, distensible, its expansion fold forming a semicircle behind chin.

Dorsal skin tubercular in life (fig. 38), becoming smoother in preservative; dorsolateral folds absent; dorsal tuberculation includes, in all specimens, two or three or more small to moderate-size tubercles arranged linearly and slightly converging from behind each eye to the scapular region—these tubercles marking the course of the arms of a W-shaped dark marking whenever that marking is present. Middorsal raphe present in all specimens. Throat smooth, venter coarsely granular; posteroventral thigh surface coarsely granular; distinct discoidal fold anterior to groin; ulnar tubercles low and weak, often unpigmented.

Relative length of appressed fingers III > IV > II > I; first finger reaching or failing to reach proximal margin of subdigital pad of second; lateral keeling absent or weak. Males with two whitish nuptial pads—the first on base of thumb, contiguous with the large thenar tubercle, and the second slightly distad (not touching) on the posterodorsal side of thumb (fig. 40). Finger discs and subdigital pads wider than long, disc on thumb slightly expanded; distal median edge usually straight, sometimes feebly indented. Palmar tubercle large and bifid or divided, when divided inner part larger than outer; thenar tu-



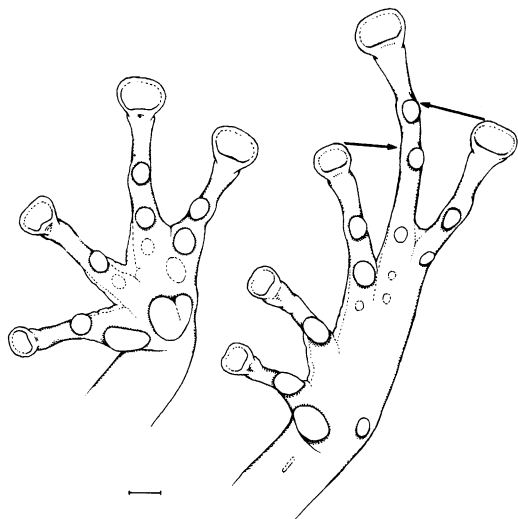


Fig. 39. *Eleutherodactylus memorans*, new species. Left hand and left foot of a paratopotype (AMNH 131466♀). Arrows indicate position of tips of third and fifth toes when these digits are straightened and appressed against the fourth toe. Scale line = 1 mm.



Fig. 40. *Eleutherodactylus memorans*, new species. Left hand of an adult male (AMNH 131470), showing two nuptial pads on the thumb,  $\times 13.6$ .

bercle ovoid; subarticular tubercles rounded, protuberant; supernumerary tubercles low, round.

Hind limbs relatively long; heels overlap when held at right angles to the sagittal plane; tibia 59–62 percent of SVL in males, 56–59 percent of SVL in females (juvenile females same range as adult males). Relative lengths of appressed toes  $IV > V > III > II > I$ ; tip of toe V extends to the distal edge or beyond the ultimate subarticular tubercle of toe IV; tip of toe III extends to proximal or distal edge of penultimate subarticular tubercle of toe IV. Toe discs as wide or slightly narrower than finger discs (adult 3rd finger disc/4th toe disc = 1.00–1.12), with wide subdigital pads. Lateral keeling and basal webbing absent or indistinct. Inner metatarsal tubercle elongate, oval, much larger than small rounded outer metatarsal tubercle; supernumerary tubercles small and low; subarticular tubercles moderately protuberant. Calcaneal tubercles absent or low and indistinct. Tarsal fold lacking; a small tarsal tubercle usually distinguishable on distal part of tarsus near inner metatarsal tubercle.

COLOR PATTERN: In life, dorsal ground col-

or was usually brown, but a few were reddish or orangish brown and one male was dark greenish brown. All had vague black markings, including an interorbital bar, and one or two individuals of each sex had a sparse scattering of small, pale yellow spots.

The dark pattern was vague in life (fig. 38) and best seen on preserved specimens immersed in liquid (fig. 41), where the markings show as brown on a lighter brown ground color. All have a poorly defined (nearly indistinct in a few) interorbital bar that varies from narrow to wide. All but one have a dark, variably distinct vertebral hairline superimposed on the middorsal raphe. Half a dozen specimens have a distinct W-shaped mark behind the head and traces of this mark are detectable on all but a few of the others. A few have a small chevron that represents the median part of the W-mark. A larger but vague chevron occurs

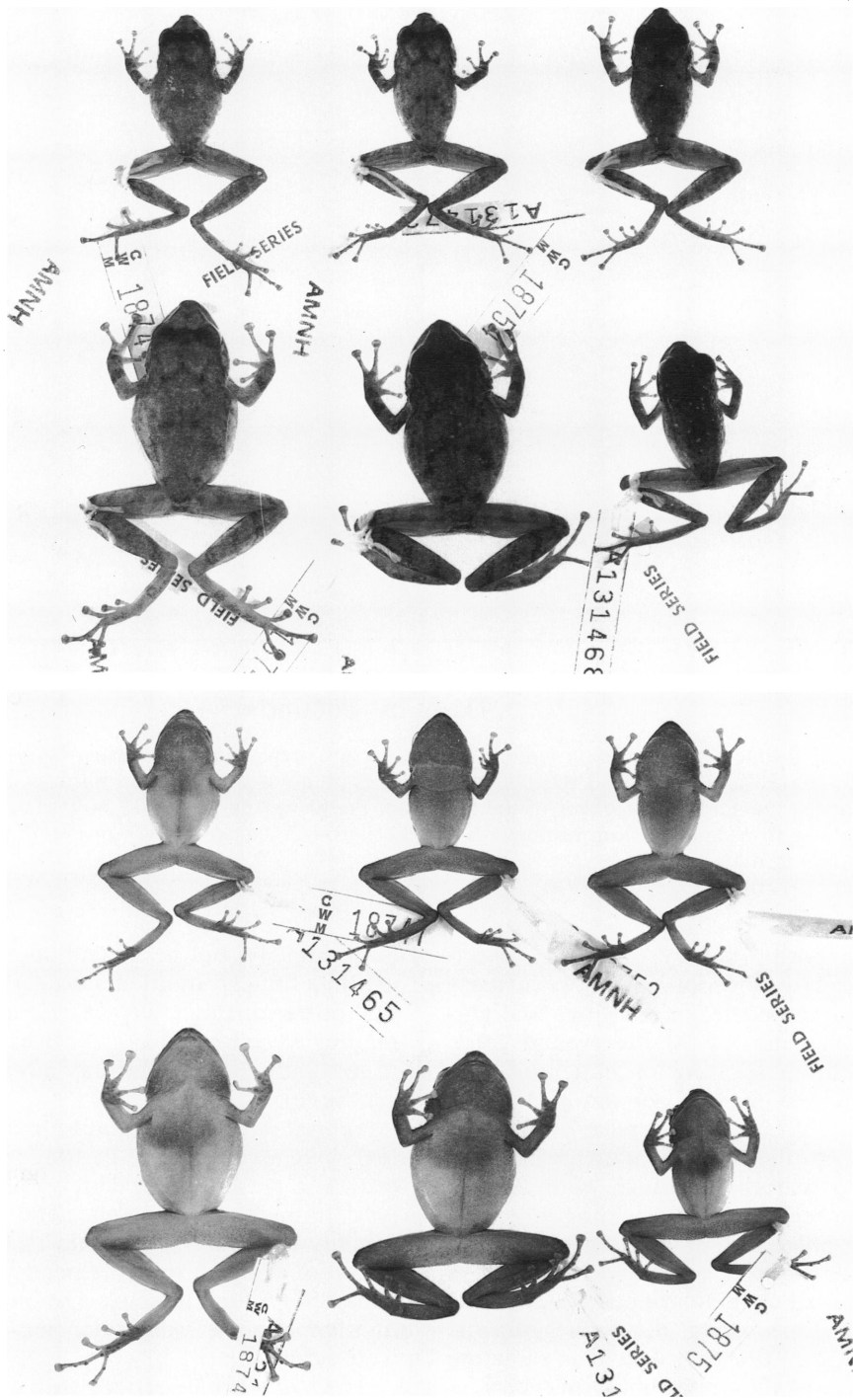


Fig. 41. *Eleutherodactylus memorans*, new species, in dorsal and ventral view. **Top rows, males.** Left to right: AMNH 131465, 131470, 131472. **Bottom rows, females.** AMNH 131466, 131467, 131468 (juvenile).  $\times 0.89$ .

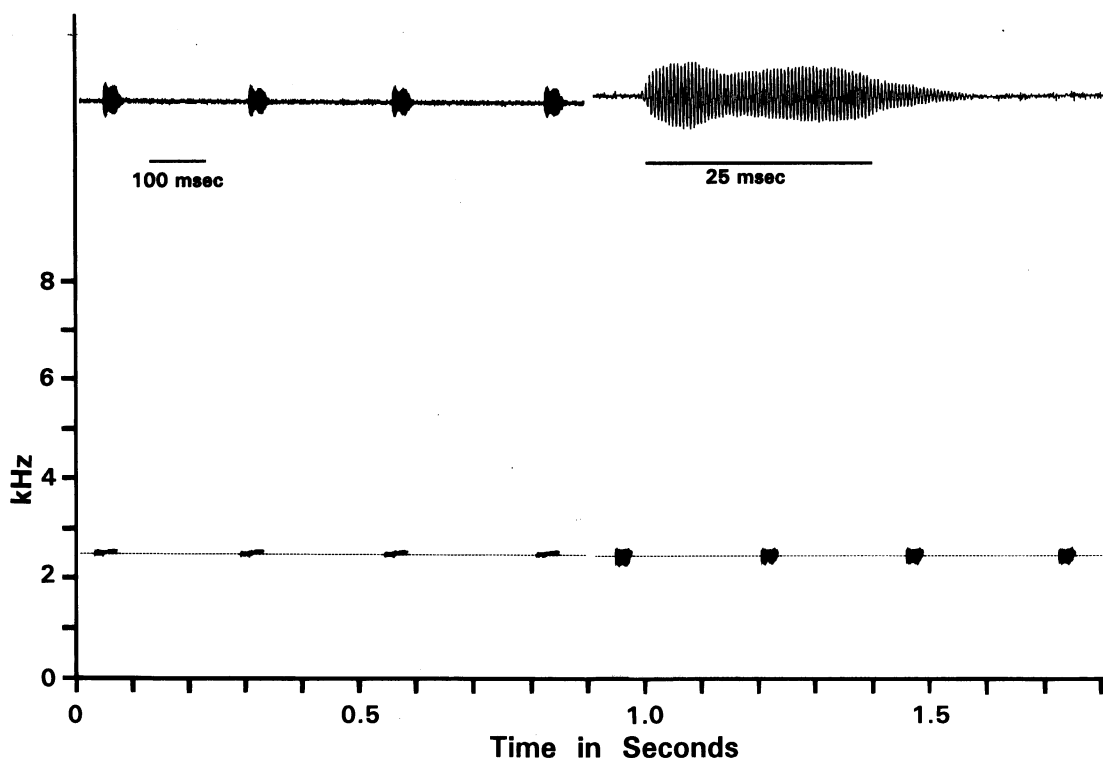


Fig. 42. A 4-note call of *Eleutherodactylus memorans*, new species. Narrow-band spectrogram (59-Hz filter) on left and wide-band spectrogram (300 Hz filter) of same call on right, with waveforms above. Expanded waveform on right is of the first note. Frequency cursor set at 2480 Hz (compare fig. 43). Frog calling from low-growing bromeliads at night; ground temperature 16.6°, air 18.0°C (AMNH herpetology reel 256:4).

posteriorly, past midbody, on many specimens; on a few, the dorsum between these two anterior and posterior markings is slightly darker than the rest of the ground color. Small indefinite spotting or blotching may occur anywhere on the dorsum and upper sides. The flanks are otherwise nearly unmarked except that some specimens have the hint of two widely separated, oblique dark bars, the posterior bar representing an extension of the posterior chevron.

There are at least weak indications of a dark eye-nostril canthal stripe and an oblique postocular stripe along the supratympanic fold. There are often 2–3 dark bars radiating from the eye to the upper lip, with intervening light spots, but the labial pattern tends to be obscure.

The lower arms have two dorsal cross-bars. The hind limbs usually are barred at

least vaguely, but in several specimens they are indefinitely mottled or nearly uniform. The posterior thigh surfaces were unmarked, ranging from brown to gray, usually uniform (a few show brown and gray mottling in preservative).

Ventral surfaces (including palms and soles) were overall gray in life, pale to light brown in preservative, with or without small pale (unpigmented) spots. The throat, especially in males, tends to have a heavier suffusion of pigment than the nearly translucent venter. One female and a few males have a thin, unpigmented, midgular line, but it is not well defined.

The iris was pale bronze with a brown horizontal stripe and vague black lines radiating from the lower edge of the pupil to the bottom of the eye; the radiating lines were obscure in a few small specimens.

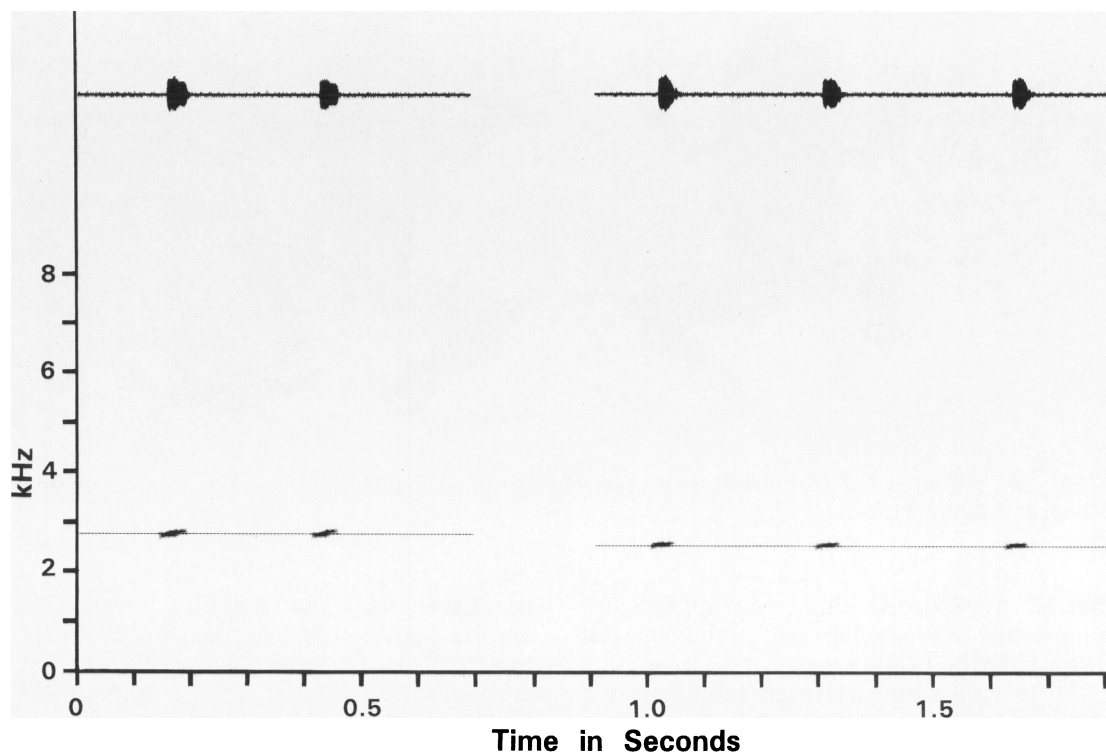


Fig. 43. A 2-note and a 3-note call of *Eleutherodactylus memorans*, new species. Waveforms and narrow-band (59-Hz filter) spectrograms, with frequency cursors set at 2760 Hz (left) and 2520 Hz (right). Other data as for figure 42.

#### NATURAL HISTORY AND VOCALIZATION

Judged from its day and night calling activity, *Eleutherodactylus memorans* was abundant although not easily located in the dense ridgetop forest around our camp. Calling was less frequent in the adjacent stream-side forest in the small hanging valley, where two were found on low vegetation at night.

The call is 1–4 loud “tinks” (figs. 42, 43). One-note ( $N = 2$ ), two-note ( $N = 5$ ), three-note ( $N = 8$ ), and four-note ( $N = 4$ ) calls were recorded. The “tink” notes are spaced 0.20–0.29 sec apart, with an individual note duration of about 0.04 sec (0.038–0.047,  $\bar{x} = 0.0415$ ,  $SD = 0.0024$ ,  $N = 13$  notes in 4 calls). Waveforms show the call to be weakly pulsatile, each note with two poorly defined pulses. Frequency is constant in a given call but variable in a series of calls by a single frog, from an observed low of 2480 Hz to a high of 2760 Hz (figs. 42, 43).

Males called sporadically, seemingly at

any time of day or night. Calling occurs from low vegetation at the forest floor to perhaps 1 m aboveground. Low bromeliads are frequent, but by no means exclusive, calling sites. During calling, neighboring males seemed to exchange similar calls; for example, two-note calls seemed to be answered by two-note calls. The intercall variation in frequency conceivably might be a predator avoidance mechanism, as suggested for certain vocalization characteristics of other *Eleutherodactylus* (Lynch and Myers, 1983: frontisp. + 556–557).

#### REMARKS

There are about 30 *unistrigatus* group species reported from Venezuela (Rivero, “1982a” [1984], “1982b” [1984]; Frost, 1985; Myers and Donnelly, 1996), and only several more from the vast area between Venezuela and the lower Amazon (Lynch and Hoogmoed, 1977: 424). With one excep-

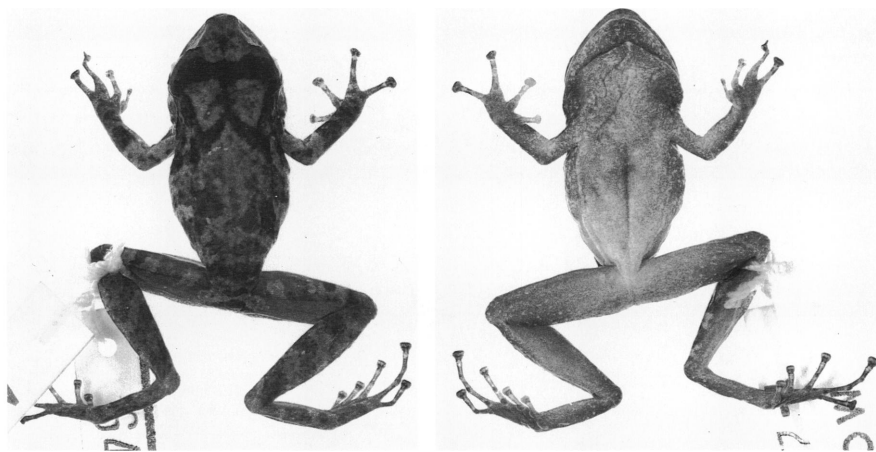


Fig. 44. Holotype of *Eleutherodactylus pulvinatus* Rivero (MCZ 64741),  $\times 1.5$ . Compare with *E. memorans*, figure 41.

tion (*E. lacrimosus*), the group appears unrepresented in the eastern half of the Amazon Basin (Lynch, 1980).

Of the 30-odd eastern members of the group, only a few Venezuelan species are known to have a dark W-shaped mark on the dorsum: *E. anotis* (Rancho Grande) is distinguished from *E. memorans* by larger female size (40–47 mm SVL), tympanum lacking (hidden?), and a brown and white mottled venter (Walker and Test, 1955). *E. orocostalis* (El Junquito, D. F.) has a large eyelid tubercle, a large calcar tubercle, and a marbled venter (Rivero, 1961: 68). *E. rozei* (Rancho Grande area) has one small, flat eyelid tubercle (Rivero, 1961: 73), a distinct canthus rostralis, and a finely granular venter. *E. vanadise* (Andean) has a prominent calcar tubercle, yellow spots in the groin, and reddish color on the posterior ventral surfaces (La Marca, 1984). None of the preceding species (all from northern Venezuela) seems to warrant particular comparison with *Eleutherodactylus memorans*.

Two species (one with a W-shaped mark) from southeastern Venezuela deserve closer comparison with *E. memorans*, namely *E. pulvinatus* and *E. avius*, which is sympatric with *memorans*. These three species share the presence of paired nuptial pads in adult males (fig. 40), a character first discovered by Rivero (1968b: 1) in *E. pulvinatus* and not subsequently reported in any other species to

our knowledge. The character, however, occurs in some other mainland *Eleutherodactylus* (fide J. D. Lynch, personal commun.) and we cannot suggest it as a synapomorphy for the species under consideration.

*E. pulvinatus* was based on a series of seven males described by Rivero (1968b) from 1400 m elevation in the Escalera region (Edo. Bolívar)—about 610 km NE of Pico Tamacuari. Duellman (in press) reported on an additional 13 specimens from the same area and provided a standardized diagnosis. The following comparison of *pulvinatus* with *memorans* is based on Rivero (1968b) and Duellman (in press) and on direct comparison with the holotype of *pulvinatus*, for which the following measurements (in mm) were taken for comparison with *E. memorans*: SVL 25.5, tibia length 13.8, head width 10.4, greatest body width 10.5, upper eyelid width 2.9, interorbital distance 2.8, eye to posterior edge of nostril 3.0, eye length 3.9, tympanum length 1.5; width third finger and fourth toe discs both 1.2. It is an adult male with well-developed vocal slits and paired nuptial pads as described by Rivero.

At least the males of *Eleutherodactylus pulvinatus* are larger than those of *E. memorans*, for which nine adult males average 21.40 mm SVL (18.9–22.7 mm), compared with published ranges for *pulvinatus* males of 23–26.1 mm ( $N = 6$ ; Rivero) and 22.8–25.0 mm (Duellman). The holotype of *E.*

*pulvinatus* is 12 percent longer (2.8 mm) than the largest male *memorans*. The *pulvinatus* holotype has a relatively shorter tibia (tibia/SVL = 0.541 vs. 0.591–0.617 in *memorans* [ $\bar{x}$  = 0.598  $\pm$  0.004, SD = 0.011,  $N$  = 9]). And the *pulvinatus* holotype has the upper eyelid slightly wider than the interorbital distance (eyelid/IOD = 1.04 vs. 0.759–0.960 in *memorans* [ $\bar{x}$  = 0.861  $\pm$  0.024, SD = 0.072,  $N$  = 9]).

There appear also to be differences in tuberculation, but these are hard to quantify. *E. memorans* has the upper eyelid weakly to moderately tubercular in life (fig. 38), but eyelid skin overall may be smoother than in *pulvinatus*, which is much more rugose in the preserved holotype than in either living or preserved *memorans*. Duellman's (in press) diagnostic section for *pulvinatus* stated "upperlid bearing many small tubercles," which is not applicable to *memorans*. *E. memorans* has two to several inconspicuous scapular tubercles marking the course of the arms of the W-shaped dark marking, although they are often small and insignificant; the small and indefinite tubercles in this area do not seem aligned in *pulvinatus*.

The dorsal color pattern of the holotype of *E. pulvinatus* is very similar to that of *E. memorans* except that the pattern is much more vivid in *pulvinatus* (compare figs. 41, 44). The pattern tends to be ill-defined in *memorans*, in which some specimens lack a discrete W-shaped scapular marking. But the W-shaped mark was present in all seven of the *pulvinatus* types (Rivero, 1968b: 5) and in 12 of 13 additional specimens reported by Duellman (in press); all the *pulvinatus* paratypes had variably distinct oblique lateral bars (well defined in the holotype), which are either lacking or extremely vague in *memorans*. *E. memorans* has an ill-defined dark stripe below the canthus rostralis, from eye to nostril, which is lacking at least in the holotype of *pulvinatus*.

There are apparent differences in living color and vocalization. Duellman (in press) described *E. pulvinatus* as having the W-shaped scapular mark orange-red (black in *memorans*) and in having a horizontal red streak across the bronze iris (a brown stripe in *memorans*). Duellman (in press) said that for *pulvinatus* "the call consists of a single

peep emitted infrequently." In contrast, the tinklike call of *E. memorans* usually is given as a series of 2–4 notes.

The above differences in total satisfy us that *memorans* is distinct from *pulvinatus*. Nonetheless, overall resemblances are striking and the two species may be closely related. Rivero (1968b: 5) commented that in *E. pulvinatus* the vomerine odontoids "cannot always be seen, but they can be felt with a needle . . . and in some specimens seem to be almost totally absent." The *pulvinatus* holotype has the small odontoids easily visible, as in most specimens of *memorans*; but the odontoids are not readily found in a few specimens of *memorans* (e.g., AMNH 131471, MBUCV 6449). Another resemblance worth noting is that the head of males is slightly narrower than the body in the males of both species (distinctly narrower in female *memorans*)—although their heads are not exactly narrow, *E. memorans* and *E. pulvinatus* lack the chunky head shape that is "characteristic of the *unistrigatus* group and probably plesiomorphic for South American *Eleutherodactylus*" (fide J. D. Lynch in Myers and Donnelly, 1996: 11).

Finally, *Eleutherodactylus memorans* needs comparing with sympatric *E. avius*, which is described earlier in this paper but whose call was not identified. Anyone casually comparing figures 29 (*avius*) and 41 (*memorans*) might well wonder whether *memorans* is nothing more than another pattern morph of the variable *avius*. Such suspicion would be reinforced by comparison of adult sizes and hand-and-foot morphology, all of which are virtually identical: Male snout-vent length is not statistically different at available sample sizes ( $t$  = 0.1318, 10 df,  $P$  = 0.898); hands and feet are essentially the same (figs. 28, 39); the males of both species have similarly positioned, paired nuptial pads (as in fig. 40).

But comparison of the descriptions and figures 29 and 41 do show that *E. avius* has a proportionately wider head relative to body width. *E. avius* has the head as wide as or slightly wider than the body (except for one gravid female); in *E. memorans*, the head is slightly narrower than the body in males and distinctly narrower in females. The differences in head width are also reflected in the

proportion HW/SVL for males<sup>15</sup> ( $t = -3.9663$ , 10 df,  $P = 0.002$ ). *E. avius* also has relatively shorter legs, as suggested by the proportion tibia length/SVL (for males,  $t = -3.0621$ , 10 df,  $P = 0.012$ ). There are subtle differences in tuberculation, with *E. memorans*, for example, having the upper eyelid more tubercular than in *E. avius*, but these differences are most evident in life (compare figs. 27 and 38) and are hard to quantify in any case.

One of the most clear-cut morphological differences is the subgular vocal sac, which in *E. memorans* is large and remains well distended in preservative, with the expansion fold usually forming a semicircle behind the chin. The vocal sac of *E. avius* is shallow and not distended in preserved specimens, which have only a weak longitudinal expansion fold on each side of the throat. Although a call was not identified with *avius*, sexual activity was indicated by the smallest male (fig. 27, upper), which was found in amplexus.

*Eleutherodactylus avius* and *E. memorans* were more easily separated in life than in preservative. Field marks included iris pattern and ventral coloration. *E. memorans* had a brown horizontal stripe through the pupil and vague black lines radiating from the lower edge of the pupil to the bottom of the eye; *E. avius* had a reddish butterfly-shaped stripe and fine black venation without a definite pattern. *E. avius* had bronzy orange or yellowish color on the venters (see description), whereas the ventral surfaces of *E. memorans* were overall gray in life. We would not want to work with small samples of such species without having seen them in life.

## LIZARDS

FAMILY POLYCHROTIDAE (FORMERLY  
ANOLOID IGUANIDAE)

*Anolis chrysolepis planiceps* Troschel

Figure 45

?*Draconura nitens* Wagler (1830: 149). Type locality, "America." Nomen dubium.

*Anolis planiceps* Troschel, 1848: 649–650. Type locality, "Caracas."

MATERIAL: MBUCV 7044, ridge N Pico Tamacuari, 1270 m.

This lizard, an adult female (74 mm SVL), was on the forest floor by day. It has 6/6 keeled loreals; 2 rows of keeled suboculars; 6/7 canthals; 12/12 supralabials (7/8 to center of eye); 13/11 infralabials; 14/14 expanded subdigital lamellae and 8/8 terminal subdigital lamellae under finger IV; 24/22 expanded subdigital lamellae and 7/8 terminal subdigital lamellae under toe IV; 44 ventral rows (from anterior margin of arm to mid thigh); 146 scales around midbody.

COLOR IN LIFE: Dorsum brown with a dark brown interorbital bar and scalloped middorsal stripe that was partly edged in tan. Ventral surfaces light, slightly metallic yellow. Small female dewlap light dull rose with yellow scales. Iris black with a bronzy rim around pupil. Corners of mouth pale blue; tongue light orange; throat unpigmented.

REMARKS: Although this widespread lizard tends to be most common in lowland forest, it has a wide elevational range and is frequently found on tepuis, where population densities appear to be relatively low. It is only an assumption that we are dealing with a single taxon in the Venezuelan Guayana, since there has been no critical study of material from this region; Vanzolini and Williams (1970: 22) had access only to about a dozen Venezuelan specimens from the region south and east of the Río Orinoco.

There has been a recent trend by a few authors (Savage and Guyer, 1991; Avila-Pires, 1995) to revive the older name *Draconura nitens* Wagler for the polytypic *Anolis chrysolepis* Duméril and Bibron. But no one has bothered to explain how Wagler's *nitens* can positively, or even *reasonably*, be associated with a known species (let alone subspecies!) of *Anolis*, especially since the type locality and holotype are unknown. Although we can see a hint of *chrysolepis* s.l. (in the thigh and sacral pattern) in Wagler's inadequate description,<sup>16</sup> we also see serious con-

<sup>15</sup> Collection sizes are small and only the samples of adult males seem adequate for statistical comparisons. Excluding immature specimens, male:female ratios are 3:2 for *E. avius* and 9:4 for *E. memorans*.

<sup>16</sup> Wagler's (1830: 149) full description, including generic diagnosis for the monotypic *Draconura*, follows: *Draconura*. "Vertex et nares Dactyloae; gula plica longitudinali subinflabili; digiti prope articulationes sub-





Fig. 45. *Anolis chrysolepis planiceps* Troschel from Pico Tamacuari (MBUCV 7044♀, 74 mm SVL).

traditions, particularly in the green or greenish dorsal coloring (*Virescens supra*<sup>17</sup>). *Anolis chrysolepis* is a basically brown lizard (e.g., see color photographs in Avila-Pires, 1995: figs. 224–231). A survey of preserved

*A. chrysolepis* in the American Museum collection revealed a few poorly preserved Ecuadorian specimens that were pale bluish gray in part, but this was due to underlying decomposition and the specimens otherwise still showed areas of the original brown.

Green coloring usually is lost quickly in lizards or snakes that are fixed in formalin prior to being stored in alcohol (a modern method of preservation). One might wonder whether the color green persisted longer in some of the spirits used for field preservation in Wagler's time, or whether he knew that green often turns blue and was extrapolating from that color, or whether he had a color description from the collector. In any case, there is more than one way for an anole to be green and not all species change to blue in preservative (e.g., Myers, 1971: 11), which renders speculation rather pointless.

Therefore we cannot explain away the green coloring claimed in Wagler's description and must regard *nitens* as a validly published and available name that nonetheless is a nomen dubium—a name not certainly applicable to any known species of lizard. This was essentially the common sense conclusion of Vanzolini and Williams (1970: 84), who, unfortunately, did not deign to specify the problems that they saw in Wagler's description.

If a reasonable argument for *nitens* = *chrysolepis* cannot be made, there is no reason why it should pose a continued threat to stability. The critical question is not whether *nitens* is a validly published name (yes) or an available name (yes) or a very important name in zoology (no), but whether it is a *recognizable* name based on the original description. If it is a nomen dubium without a holotype then it cannot serve as a senior synonym except by legalistic maneuver.

There is no mandate to pursue nomina dubia to the end of time, but when stability is truly an issue, the *International Code* (International Commission, 1985) allows a solution through neotype designation (Recommendation 75E), subject to the rather strict provisions set forth in article 75b, 75c, and 75d. We do not think that such action is warranted. If the name *nitens* was based on a green (or blue) lizard, it seems silly to force

←  
incrassati; cauda teres, basi incrassata, teretiuscula. (America.)

"Species: *Draconura nitens*. Virescens supra, nitore cupreo-aureo, subtus albo-virens, argenteo-splendens; cauda tota aureo-viridi, maculis supra os sacrum duabus arcuatis obscuris; femoribus digitisque obsolete fasciatis."

<sup>17</sup> *Virescens* is a present participle and the phrase "becoming green above" is open to interpretation as to the extent or degree of that color. Stearn (1983: 248) noted that, "Green is termed *viridis* without more critical definition, its synonyms, more or less accurate, being *virens*, *viridans*, *virescens*, *viridescens*, *viridulus*."

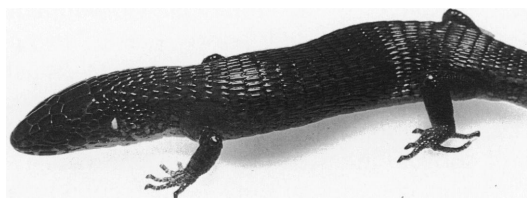


Fig. 46. *Arthrosaura synaptolepis* Donnelly, McDiarmid, and Myers, in life. Paratype (AMNH 131495♀, 46 mm SVL) from Pico Tamacuari.

it onto a brown one and pedantic to do so by fiat.

#### FAMILY TEIIDAE

### *Arthrosaura synaptolepis* Donnelly, McDiarmid, and Myers Figure 46

*Arthrosaura synaptolepis* Donnelly, McDiarmid, and Myers, 1992: 822. Holotype USNM 317882, from Camp VI, about 6.2 km NNE Pico da Neblina, 1400–1450 m, Cerro de la Neblina, Amazonas, Venezuela (00°51'45"N, 65°58'52"W), collected February 27, 1985, by Alfred L. Gardner.

**MATERIAL:** AMNH 134195 (paratype), north base Pico Tamacuari, 1160–1200 m. (A paratype from Cerro de la Neblina has been deposited in the MBUCV collection.)

This small, long-tailed lizard (46 mm SVL + 91 mm tail) was found on the ground by day, on a forested slope above a rocky stream. It was brown above, with the ventral surfaces entirely orange.

**REMARKS:** There are only two other specimens of *Arthrosaura synaptolepis*, both from Cerro de la Neblina, in the Venezuelan-Brazilian frontier about 150 km southwestward of Pico Tamacuari. The elevation range at the combined localities is 1200–1450 m.

*Arthrosaura synaptolepis* differs from its congeners in lacking prefrontals and in having two rather than three pairs of genials.<sup>18</sup> The species has been compared with *A. tyleri*, another montane species reported from localities at about 1750–2200 m on Cerro

Duida and Meseta de Jaua, a few hundred kilometers north of the highlands occupied by *synaptolepis*. These two microteiids resemble one another in having large smooth scales in the temporal region and also in having fewer midbody scale rows and subdigital lamellae than other named *Arthrosaura*. Furthermore, variation in the genials of *tyleri* seems to help explain the origin of the autapomorphic configuration of these plates in *synaptolepis*. The recent description of *Arthrosaura synaptolepis* postulated that it is the sister species of *A. tyleri*.

### *Neusticurus racenisi* Roze

Figure 47

*Neusticurus racenisi* Roze, 1958: 252–257, figs. 5–8. Holotype AMNH 61008 from base Auyantepui, 400 m, Estado Bolívar, Venezuela, collected by W. H. Phelps.

**MATERIAL:** AMNH 134196♂ from north base Pico Tamacuari, 1160–1200 m.

The specimen is an adult male (SVL 106 mm, tail length 207 mm), which was shot at night from vegetation overhanging a rock wall, about 4 m above water, downstream from a small waterfall. Another was seen sleeping on a branch about 1.5 m above water, but it dropped into the stream when approached. A third was seen on a rock at the edge of the same forested stream by day, but it dove into the stream before it could be shot. We found this species to be as wary and as difficult to approach here as on Cerro Guaiquinima (Donnelly and Myers, 1991: 35).

**COLOR PATTERN:** In life, dorsum greenish brown with darker brown square blotching extending onto tail; sides of body red-brown with pale greenish areas. Vivid pale blue preocular and postocular markings, the last a vertical stripe. Temporal region, loreolabial region, and infralabials dark blue, turning paler blue on chin shields and light yellow under throat. Venter and underside of tail light blue, turning black on distal half of tail. Iris dark (color not discernible). Tongue, including fork, gray-black anteriorly, pink posteriorly. (Color notes by headlight at night, prior to preservation.)

In preservative, the dorsum has lost its greenish aspect and turned dark brown; the

<sup>18</sup> Or three rather than four pairs of genials, depending on how these ventral head scales are defined (discussion and illustration in Donnelly et al., 1992).



Fig. 47. *Neusticurus racenisi* Roze from Pico Tamacuari (AMNH 134196♂, 106 mm SVL).

interspaces between the dark squarish blotches stand out conspicuously as dorsolateral series of pale brown squarish spots (fig. 47); reddish flanks now brown with three rows of small, bluish white spots, higher than wide. Limbs brown; dorsal thigh with a few indistinct light spots, posterior thigh with several large light spots. Preocular and postocular blue markings faded to white; postocular mark a vertical stripe, extending from supralabials to top of head, with a posterior dark edge. Former blue color of temporal region and labials faded to blackish gray, side of snout light brown. Chin shields white with large gray blotches, throat white; venter and undersides of hind limbs and proximal part

of tail remain bluish but with conspicuous white scale margins; underside of upper arm white, lower arm brown; palms and soles brown.

REMARKS: We recently (1991) redescribed *Neusticurus racenisi* on the basis of three new specimens from Cerro Guaiquinima, the holotype from nearby Auyantepui, and published data (Van Devender, 1969) for specimens from the Cerro Duida-Cerro Marahuaca area. The adult male from Pico Tamacuari differed from a Guaiquinima male in having the temporal region and labials blue (vs. brown temporal area and orangish brown supralabials), but the characteristic pale (blue in life) preocular and postocular markings are much alike (see fig. 23 in Donnelly and Myers, 1991). The Tamacuari specimen differs in few other ways from data compiled for the more northern specimens in the aforesaid redescription. It has fewer femoral pores (28/30 vs. 33–38) and minor differences in a few scale counts, but too few specimens of *racenisi*-like lizards are available to assess intrapopulational and/or geographic variation in such features.

Donnelly and Myers (1991: 1, 50) mentioned *Neusticurus racenisi* as a “predominantly tepui” or “highland” species because of its occurrence at Cerro Auyantepui (400 m), the Cerro Duida-Marahuaca area (100–1215 m), and Cerro Guaiquinima (1030 m). The new Pico Tamacuari specimen is from about 1200 m, but Cole and Myers also found two specimens in lowland rain forest near the Río Mavaca base camp (unpublished data). The species may prove to be fairly widespread in southern Venezuela in an elevational range of about 100–1200 m. We were unable to find it above the type locality (400 m) at the base of Cerro Auyantepui, where only *Neusticurus rudis* seems to occur on the high summit (1700–2100 m). We now suspect that *N. racenisi* is a “lowland invader” of mountain slopes and lower summits and that it is not a highland species of disjunct distribution.

Except for one diurnal sighting, our specimens have been found by night at their sleeping spots on vegetation above forest streams. Dixon and Lamar (1981) similarly collected the Colombian *N. medemi* at night,



Fig. 48. *Thamnodynastes pallidus* (Linnaeus). MBUCV 7045 ♀ from Pico Tamacuari.

on vegetation over small creeks in primary forest.

## SNAKES

### FAMILY COLUBRIDAE

#### *Thamnodynastes pallidus* (Linnaeus)

Figures 48–49

*Coluber pallidus* Linnaeus, 1758: 221. Type locality, "Indiis."

**MATERIAL:** MBUCV 7045, camp on ridge N Pico Tamacuari, 1270 m.

This rear-fanged snake was found by night in ridgetop forest, where it was crawling in a tangle of vegetation about 1 m aboveground. It is a female 492 mm total length, 140 mm tail length (tail/total = 0.285); 17-17-13 dorsal scale rows; 144 ventrals; divided anal plate; 84 paired subcaudals; single loreal; 1/2 preoculars; 2/2 postoculars; 8/8 supralabials (4–5 in orbit); 9/9 infralabials; temporals basically 2 + 2 (excluding tiny azygous scales); left maxilla with 19 + 2 teeth.

**COLOR PATTERN:** In life, light olive brown middorsally, with a much broken dorsolateral

black line above paler brown, and a black-edged medium brown lateral stripe broken by faint, pale lines on rows 1 and 2. Skin between spread scales pale orange with a repeated black pattern, most evident on loose skin of neck; some dorsal scales partly black-margined, especially on anterior body.

Brown head cap with a thin black margin above eye. Supralabials and snout grading from olive brown to light yellowish brown. An oblique dark postocular stripe with thin black margins is set off from the head cap by a wedge of light brown ground color extending anteriorly from the neck to the rear edge of eye.

Underside of head and neck light yellow, grading posteriorly to light orangish tan over rest of ventral surfaces to the tail tip. A ventrolateral brown stripe on each side containing a median line of orangish tan; a midventral dark line faintly indicated anteriorly. Labials and ventral surfaces lightly flecked with black.

Iris light orangish brown with an extremely faint smudge of gray anterior and posterior to the elliptical pupil. Tongue, including fork,



Fig. 49. Dorsal and ventral views of *Thamnodynastes pallidus* (MBUCV 7045 ♀),  $\times 0.9$ .

pale grayish brown above with blackish gray lateral margins; pale gray ventrally.

REMARKS: Until recently, the occurrence of *Thamnodynastes pallidus* in Venezuela has been assumed rather than proven. The scalation of our specimen generally agrees with the account of *Thamnodynastes pallidus* provided by Roze (1966: 228–229), except that the specimen differs in having 17–17–13 dorsal scale rows (vs. 17–15). Roze’s description was obviously based on non-Venezuelan material, as he was unable to find a specimen that had been

reported from Puerto Ayacucho by Marcuzzi (1950: 14), under the name *Dryophylax pallidus*. However, as indicated by Roze (loc. cit.), Marcuzzi seemed to confuse this species with the very different *T. strigillis* and the record therefore is not reliable.

Lancini et al. (1989: 237) based their Venezuelan account of *T. pallidus* on Roze’s description, without mentioning specimens. Gorzula (1992: 278), however, mentioned in passing that *T. pallidus* has been found on Cerro Guaiquinima, and Gorzula and Ayarzagüena (“1995” [1996]: 5) cited the Guaiquinima specimen as being MHNLS 11020 from an elevation of 1370 m.

Our several photographs (figs. 48–49) of the Tamacuari specimen, in conjunction with the scale data, should facilitate comparisons. The genus *Thamnodynastes* is poorly known taxonomically, but the present specimen seems to represent the widespread lowland *T. pallidus*. It can not be confused with the several endemic highland species of *Thamnodynastes* in the Venezuelan Guayana (Gorzula and Ayarzagüena, “1995” [1996]<sup>19</sup>; Myers and Donnelly, 1996).

## DISCUSSION

Our objective here is to place the small herpetofauna of Pico Tamacuari within the broader context of Pantepui and the Pantepui Region, for which some preliminary explanation is needed.

First of all, the granitic Pico Tamacuari and the neighboring lower mountain ridges that constitute the Sierra de Tapirapecó are not “tepui”—the name given to the isolated sandstone table mountains of the Venezuelan Guayana and adjacent areas. Although the ancient (Precambrian) rock of Tapirapecó was probably overlain by Roraima sandstones and quartzites—the stuff of tepui—

<sup>19</sup> This paper first appeared about a year after its printed date (“Junio 1995”) and is not cited in Myers and Donnelly (1996). Gorzula and Ayarzagüena named *Thamnodynastes corocoroensis* (from Cerro Corocoro) and *T. marahuacuensis* (Cerro Marahuaca), which appear closest to Myers and Donnelly’s descriptions of *T. yavi* (Cerro Yaví) and *T. duida* (Cerro Duida), respectively. A species overlooked in Gorzula and Ayarzagüena’s key to the genus is *T. gambotensis* Pérez-Santos and Moreno (1989), described from the Caribbean lowlands of extreme northern Colombia.

these have been largely eroded away in the immediate area (see The Natural Landscape).

The word *Pantepui* was coined by Mayr and Phelps (1967: 275) as a convenient way of referring to,

the sandstone tabletop mountains in the Venezuelan Territorio Amazonas and Estado Bolívar and in the adjacent border regions of Brazil and Guyana.

But they recognized that other mountains in the region were "Faunistically to be included" even though differing geologically. In redefining Pantepui as a biogeographical province, Huber (1995a: 36) similarly included certain "high granitic ranges such as the Sierra de Maigualida and part of the Sipapo Massif" and listed the Sierra Tapirapecó in a table of tepuis and other areas. This listing proves to have been appropriate, although elevations in the Sierra Tapirapecó are lower than required by Huber's (loc. cit.) redefinition of Pantepui as,

a biogeographical province comprising all high-tepui ecosystems that are restricted to the Guayana Shield between 1500 and 3000 m elevation, but are best developed between 1800 and 2700 m.

Pico Tamacuari—the highest peak in the Sierra Tapirapecó—rises to 2340 m above sea level, but it is mostly bare rock (fig. 3). Surrounding vegetated areas may not exceed 1500 m and virtually all our collecting was done in the elevational range of 1160–1460 m—well below the summit elevations of some (not all) tepuis. But a major portion (29 of 39 species) of the birds collected is representative of the "approximately 100 upper elevation pantepui species of birds" (Barrowclough et al., 1995: 212) and Pico Tamacuari clearly falls within Mayr and Phelps' (1967) ornithological-based concept of Pantepui.

Sweeping statements cannot safely be made about the Pantepui herpetofauna, although tepui endemics do appear to outnumber widespread highland species and the endemics seem to have widely scattered counterparts.<sup>20</sup> Myers and Donnelly (1996: 54) suggested probable reasons to explain "the

present-day spotty occurrence of the faunal remnants" of a once widespread tepui fauna.

It bears pointing out that there are few endemic highland genera of Pantepui amphibians and reptiles and that some endemic species have congeners in nearby lowlands. After excluding lowland invaders, one can think of the Pantepui herpetofauna as an autochthonous unit when dealing with such taxa as *Oreophrynella*, *Riolama*, the *Phenacosaurus neblininus* complex, the dwarf species of *Thamnodynastes*, etc. But the addition of genera having both highland and lowland endemic counterparts (e.g., see *Colostethus* and *Stefania* below) starts to cloud the distinction. With that reservation and without trying to specify elevational limits, we shall continue to use *Pantepui* after Mayr and Phelps (for the highland fauna generally) and also in the sense of Huber (for the high-tepui ecosystems). The term *Pantepui Region* or *Pantepui Area* (fig. 50) is used in the broader sense to include the lowlands and high savannas.

#### THE PICO TAMACUARI HERPETOFAUNA

The summits of all the tepuis and faunistically related mountains probably have depauperate herpetofaunas, with faunal size being positively correlated with area and negatively correlated with elevation. The total of 12 species from 1160–1460 m on Pico Tamacuari compares favorably with our faunal samples of 15 species from 1030–1150 m on Cerro Guaiquinima (Donnelly and Myers, 1991), and 8 species from 2150 m on Cerro Yaví (Myers and Donnelly, 1996).<sup>21</sup>

The few endemic genera thought to be confined to higher-elevation tepui habitats

<sup>21</sup> These three samples are reasonably comparable in terms of collecting effort and actual area sampled. Collections made over a longer period in a greater area will increase the species count, especially on the larger tepuis.

The few available examples of increased sampling effort are: 15 species from 1800–2600 m on Chimantá Tepui (Gorzula, 1992), 20 species from 1600–2100 m on Auyantepui (Myers, in press), and 25 species from 770–2400 m on Cerro de la Neblina (McDiarmid and Paolillo, 1988).

Cerro de la Neblina is the best known of all the tepuis, as the result of coordinated work by eight herpetologists and other scientists during several segments of the 1984–1985 Neblina Expedition (brief summary in Myers et al., 1993: 2).

<sup>20</sup> We use the purposely vague term *counterparts* for congeneric species that we judge to be phenotypically and ecologically similar (Myers and Donnelly, 1996: 53). Phylogenetic closeness seems probable but degree of relatedness simply is unknown.

are not represented in the lower-elevation montane forest fauna of Pico Tamacuari.

After excluding the unseen *Bufo* (fn. 5), the Pico Tamacuari species may be summarized in context of the Pantepui Region as follows:

#### LOWLAND-HIGHLAND SPECIES

Rare Invaders from the Lowlands (1 sp.): The only snake found at Pico Tamacuari was *Thamnodynastes pallidus*—a widespread species of the Amazonian lowlands that has been reported from one tepui, Cerro Guaiquinima (Gorzula, 1992: 278).<sup>22</sup>

Frequent Tepui Invaders (2 spp.): The polytypic *Anolis chrysolepis* is widespread in the Amazonian and Guayanian lowlands and occurs seemingly in lower density on the summits of some tepuis, to elevations of at least 1750 m on Auyantepui and over 2000 m on Chimantá Tepui.

*Neusticurus racenisi* is endemic to the Pantepui Region and, on the basis of the few available records, was thought by Donnelly and Myers (1991: 1) to be a predominantly tepui species. We now know that it occurs also in lowland tropical rain forest away from tepuis and suspect that it invades suitable habitat of any adjacent highland. The type locality of *N. racenisi* is on the base of Auyantepui at 400 m, but only the highland *N. rudis* was found at summit elevations of 1700–2100 m.<sup>23</sup> At about 1200 m, the present Pico Tamacuari record is near the known elevation limit for *N. racenisi*.

#### TEPUI SPECIES

“Widespread” Species (2): As presently recognized, *Hyla benitezi* is a Pantepui endemic known from the Duida-Marahuaca massif, Cerro Guaiquinima, Sierra Pacaraima, and Pico Tamacuari; it evidently requires forested streams for breeding.

*Arthrosaura synaptolepis* is known from Cerro de la Neblina and Pico Tamacuari; its

sister species may be *A. tyleri* from the sandstone tepuis Duida and Jaua.

Tamacuari Endemics (6): The genus *Steфанia* is endemic to Pantepui, with most species occurring on sandstone tepuis. Exceptions include *S. evansi*, which also occurs in lowlands, and an undescribed species from lowland rain forest at the base of Cerro de la Neblina. *S. tamacuarina* is the first species from a granitic mountain.

*Colostethus tamacuaensis* is considered a tepui species based on its close resemblance to *C. shrevei* from the Duida-Marahuaca massif and to an undescribed species from Auyantepui. These share an unusual character—the median lingual process—which may be an ancient plesiomorphy rather than a synapomorphy within *Colostethus*. In any case, the character is known in *Colostethus* only in the Pantepui Region and in the trans-Andean region. Not all the species in the Pantepui Region are tepui endemics, however, since *C. parkerae* occurs in the Escalera region and an undescribed species occurs at the base of Cerro de la Neblina.

Little can be said at this point about four additional new frogs known only from Pico Tamacuari. If banded limbs are indicative of relationship, then the centrolenid *Hyalinobatrachium crurifasciatum* may be related to a species in the Escalera region and to a tepui species currently under study. *Eleutherodactylus avius* and *E. memorans* are morphologically similar species that are somewhat reminiscent of species on Cerro Yaví and in the Escalera region, respectively. *Eleutherodactylus cavernibardus*, on the other hand, resembles no other species known to us.

#### CONCLUSIONS

Like the avifauna, the herpetofauna of the granitic Pico Tamacuari is faunistically related to Pantepui. Only the lizard *Anolis chrysolepis* (a frequent tepui invader) and the snake *Thamnodynastes pallidus* (a rare invader) have the main body of their geographic ranges lying outside the Pantepui Region. The other nine Tamacuari species are endemic to this region—including six frogs known only from Pico Tamacuari and one frog and two lizards known also from sandstone tepuis.

All the non-endemic Tamacuari species of

<sup>22</sup> The Amazonian lowland snake *Imantodes lentiferus* was also found on Cerro Guaiquinima, which has a few endemic species in a predominantly lowland fauna (Donnelly and Myers, 1991: 40).

<sup>23</sup> Unpublished results of the 1994 Robert G. Goelet American Museum–TERRAMAR Expedition to Auyantepui.





amphibians and reptiles (5 of 11 spp.) occur also on sandstone tepuis, and some Tamacuari endemics have endemic counterparts on tepuis. So it seems not to matter to such species whether their habitat is based on sand-

stone or on granite. This realization seems to lessen the importance of the underlying geology when assessing the Pantepui herpetofauna, which is something more than a set of sandstone isolates.

## REFERENCES

- Avila-Pires, Teresa Cristina Sauer  
1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zool. Verh. (Leiden) 299: [viii] + 706 pp.
- Ayarzagüena, José  
1992. Los centrolenidos de la Guayana venezolana. Publ. Asoc. Amigos de Doñana 1: 48 pp.
- Barrowclough, George F., Patricia Escalante-Pliego, Ramón Aveledo-Hostos, and Luis A. Pérez-Chinchilla  
1995. An annotated list of the birds of the Cerro Tamacuarí region, Serranía de Tapirapecó, Federal Territory of Amazonas, Venezuela. Bull. Br. Ornithol. Club 115(4): 211–219.
- Boulenger, George Albert  
1900. Reptiles and Batrachians. In E. R. Lankester, Report on a collection made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana. Reptiles. Trans. Linn. Soc. London, Zool., ser. 2, 8(2): 53–56 + pl. 5.
- Brewer-Carías, Charles (ed.)  
1988. Cerro de la Neblina. Resultados de la expedición 1983–1987. Caracas: Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales, viii + 924 pp.
- Cannatella, David C., and William W. Lamar  
1986. Synonymy and distribution of *Centrolenella orientalis* with notes on its life history (Anura: Centrolenidae). J. Herpetol. 20(3): 307–317.
- de Bellard-Pietri, Eugenio  
[1989.] Venezuela tierra mágica. Tapirapecó: la gran aventura del sur. Caracas: Corpoven, S.A., 16 pp.
- “1993” [1996]. Expediciones científicas de FUDECI a la Serranía de Tapirapecó del Estado Amazonas. Bol. Acad. Cienc. Fis. Mat. Nat. 53(171–172): 149–188 + foldout map.
- Dixon James R., and William W. Lamar  
1981. A new species of microteiid lizard (Genus *Neusticurus*) from Colombia. J. Herpetol. 15: 309–314.
- Donnelly, Maureen A., and Charles W. Myers  
1991. Herpetological results of the 1990 Venezuelan expedition to the summit of Cerro Guaquinima, with new tepui reptiles. Am. Mus. Novitates 3017: 54 pp.
- Donnelly, Maureen A., Roy W. McDiarmid, and Charles W. Myers  
1992. A new lizard of the genus *Arthrosaura* (Teiidae) from southern Venezuela. Proc. Biol. Soc. Washington, 105 (4): 821–833.
- Duellman, William E.  
1993. Amphibian species of the world: additions and corrections. Univ. Kansas Mus. Nat. Hist. Spec. Publ. 21: iv + 372 pp.
- In press. Amphibians of La Escalera region, southeastern Venezuela: taxonomy, ecology, and biogeography. Univ. Kansas Mus. Nat. Hist. Sci. Papers.
- Duellman, William E., and Marinus S. Hoogmoed  
1984. The taxonomy and phylogenetic relationships of the hylid frog genus *Stefania*. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 75: 1–39.
- Escher, Konrad  
1925. Das Verhalten der Seitenorgane der Wirbeltiere und ihrer Nerven beim

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Fig. 50. The Pantepui Region (from Mayr and Phelps, 1967), with arrows showing localities mentioned in Discussion.

This 30-year-old map was prepared under the direction of geographer Charles B. Hitchcock—a veteran tepui explorer starting with the American Museum’s 1928–1929 Expedition to Cerro Duida (Tate and Hitchcock, 1930) and extending through some of the Phelps’ ornithological expeditions, including one to Cerro Yaví (Hitchcock, 1947, 1948). This elegant map remains useful as a general locator because of its bare-bones simplicity. (For more detailed 1:2,000,000 maps, see the topographic and vegetation maps compiled by Huber and Berry in Steyermark et al., 1995.)

- Übergang zum Landleben. *Acta Zool. (Stockholm)* 6: 308–414.
- Flores, Glenn  
1985. A new *Centrolenella* (Anura) from Ecuador, with comments on nuptial pads and prepollical spines in *Centrolenella*. *J. Herpetol.* 19(3): 313–320.
- Frost, Darrel R. (ed.)  
1985. Amphibian species of the world. Lawrence, KS: Allen Press and Assoc. Syst. Coll., vii + 732 pp.
- FUDECI  
1990. Memoria [de la] Fundación para el Desarrollo de las Ciencias, Físicas, Matemáticas y Naturales. Caracas: FUDECI, 48 unnumbered pp.
- Goin, Coleman J.  
1963. A new centrolenid frog from Venezuela. *Acta Biol. Venez.* 3(18): 283–286.  
1964. Distribution and synonymy of *Centrolenella fleischmanni* in northern South America. *Herpetologica* 20(1): 1–8.  
1968. A new centrolenid frog from Guyana. *Q. J. Florida Acad. Sci.* 30(2): 115–118.
- Gorzula, Stefan  
1992. La herpetofauna del macizo del Chimantá. In O. Huber (ed.), *El macizo del Chimantá*, pp. 267–280 + 304–310 (= photographs 152–171). Caracas: Oscar Todtmann Editores.
- Gorzula, Stefan, and José Ayarzagüena  
“1995” [1996]. Dos nuevas especies del género *Thamnodynastes* (Serpentes; Colubridae) de los tepuyes de la Guayana venezolana. *Publ. Asoc. Amigos de Doñana* 6: 17 pp.
- Gosner, Kenneth L.  
1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16(3): 183–190.
- Grant, Taran, Elaine C. Humphrey, and Charles W. Myers  
1997. The median lingual process of frogs: a bizarre character of Old World ranoids discovered in South American dendrobatids. *Am. Mus. Novitates* 3212: 40 pp.
- Heyer, W. Ronald  
1994. *Hyla benitezi* (Amphibia: Anura: Hylidae): first record for Brazil and its biogeographical significance. *J. Herpetol.* 28(4): 497–499.
- Hitchcock, Charles B.  
1947. The Orinoco-Ventuari region, Venezuela. *Geogr. Rev.* 37(4): 525–566 + foldout map.
1948. La región Orinoco-Ventuari, Venezuela. *Bol. Soc. Venez. Cienc. Nat.* 11(72): 131–179 + foldout map (translation of 1947 paper).
- Hoogmoed, Marinus S., John D. Lynch, and Jean Lescure  
1977. A new species of *Eleutherodactylus* from Guiana (Leptodactylidae, Anura). *Zool. Meded. (Leiden)* 51(3): 33–41 + pl. 1.
- Huber, Otto  
1995a. Geographical and physical features. In J. A. Steyermark, P. E. Berry, and B. K. Holst (general eds.), *Flora of the Venezuelan Guayana*, vol. 1: 1–61. St. Louis: Missouri Bot. Garden.  
1995b. Vegetation. In J. A. Steyermark et al., op. cit., vol. 1, pp. 97–160.
- International Commission on Zoological Nomenclature  
1985. International code of zoological nomenclature, 3rd ed. London: Internatl. Trust Zool. Nomencl., xx + 338 pp.
- La Marca, Enrique  
1984. *Eleutherodactylus vanadise* sp. nov. (Anura, Leptodactylidae): first cloud forest *Eleutherodactylus* from the Venezuelan Andes. *Herpetologica* 40(1): 31–37.
- Lancini V., Abdem R., and Paul M. Kornacker  
1989. *Die Schlangen von Venezuela*. Caracas: Verlag Armitano Editores C.A., 381 pp.
- Linnaeus, Carolus  
1758. *Systema Naturae*. 10th ed. Stockholm, vol. 1: [iv] + 824 pp.
- Lynch, John D.  
1979. A new genus for *Elosia duidensis* Rivero (Amphibia, Leptodactylidae) from southern Venezuela. *Am. Mus. Novitates* 2680: 8 pp.  
1980. A taxonomic and distributional synopsis of the Amazonian frogs of the genus *Eleutherodactylus*. *Ibid.* 2696: 24 pp.
- Lynch, John D., and William E. Duellman  
1980. The *Eleutherodactylus* of the Amazonian slopes of the Ecuadorian Andes (Anura: Leptodactylidae). *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 69: 86 pp.
- Lynch, John D., and Marinus S. Hoogmoed  
1977. Two new species of *Eleutherodactylus* (Amphibia: Leptodactylidae) from northeastern South America. *Proc. Biol. Soc. Washington* 90(2): 424–439.
- Lynch, John D., and Charles W. Myers  
1983. Frogs of the *fitzingeri* group of *Eleutherodactylus* in eastern Panama and Chocoan South America (Leptodactyl-

- idae). Bull. Am. Mus. Nat. Hist. 175(5): 481–568.
- Marcuzzi, Giorgio  
1950. Ofidios existentes en las colecciones de los museos de Caracas (Venezuela). Novedades Cient., Contrib. Ocas. Mus. Hist. Nat. La Salle (Caracas), Ser. Zool. 3: 20 pp.
- Mayr, Ernst, and William H. Phelps, Jr.  
1967. The origin of the bird fauna of the South Venezuelan highlands. Bull. Am. Mus. Nat. Hist. 136(5): 269–327 + pls. 14–21 + foldout map.
- McDiarmid, Roy W., and Alfredo Paolillo O.  
1988. Herpetological collections—Cerro de la Neblina, updated January 1988. In C. Brewer-Carías (ed.), Cerro de la Neblina. Resultados de la expedición 1983–1987, pp. 667–670. Caracas: Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales.
- Meinhardt, Daniel J., and Jeffrey R. Parmelee  
1996. A new species of *Colostethus* (Anura: Dendrobatidae) from Venezuela. Herpetologica 52(1): 70–77.
- Mijares-Urrutia, Abraham  
1990. The tadpole of *Centrolenella andina* (Anura: Centrolenidae). J. Herpetol. 24(4): 410–412.
- Myers, Charles W.  
1971. A new species of green anole (Reptilia, Sauria) from the north coast of Veraguas, Panama. Am. Mus. Novitates 2470: 14 pp.  
1991. Distribution of the dendrobatid frog *Colostethus chocoensis* and description of a related species occurring macro-sympatrically. Ibid. 3010: 15 pp.  
In press. Preliminary remarks on the summit herpetofauna of Auyantepui, eastern Venezuela. Acta Terramaris.
- Myers, Charles W., and Maureen A. Donnelly  
1996. A new herpetofauna from Cerro Yaví, Venezuela: first results of the Robert G. Golet American Museum-Terramar Expedition to the Northwestern Tepuis. Am. Mus. Novitates 3171: 56 pp.
- Myers, Charles W., and William E. Duellman  
1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. Am. Mus. Novitates 2752: 32 pp.
- Myers, Charles W., Alfredo Paolillo O., and John W. Daly  
1991. Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: phylogenetic significance of a new genus and species from the Venezuelan Andes. Am. Mus. Novitates 3002: 33 pp.
- Myers, Charles W., Ernest E. Williams, and Roy W. McDiarmid  
1993. A new anoline lizard (*Phenacosaurus*) from the highland of Cerro de la Neblina, southern Venezuela. Am. Mus. Novitates 3070: 15 pp.
- Pérez-Santos, Carlos, and Ana G. Moreno  
1989. Una nueva especie de *Thamnodynastes* (Serpentes: Colubridae) en el norte de Colombia. Boll. Mus. Reg. Sci. Nat. Torino, 7(1): 1–9.
- Projeto Radambrasil  
1975. Folha NA.20 Boa Vista e parte das folhas NA.21 Tumucumaque, NB.20 Roraima e NB.21; geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Rio de Janeiro: Departamento Nacional da Produção Mineral (Levantamentos de Recursos Naturais 8): 428 pp. + color pls. + 6 maps.
- Rivero, Juan A.  
1961. Salientia of Venezuela. Bull. Mus. Comp. Zool. 126(1): 1–207 + 1 pl.  
1964. Salientios (Amphibia) en la colección de la Sociedad de Ciencias Naturales La Salle de Venezuela. Caribb. J. Sci. 4(1): 297–305.  
“1966” [1968]. Notes on the genus *Cryptobatrachus* (Amphibia, Salientia) with the description of a new race and four new species of a new genus of hyliid frogs. Ibid. 6(3–4): 137–149.  
“1967” [1968]. Anfibios coleccionados por la Expedición Franco-Venezolana al Alto Orinoco 1951–1952. Ibid. 7(3–4): 145–154.  
1968a. Los centrolenidos de Venezuela (Amphibia, Salientia). Mem. Soc. Cienc. Nat. La Salle 28(81): 301–334.  
1968b. A new species of *Eleutherodactylus* (Amphibia, Salientia) from the Guayana region, Edo. Bolívar, Venezuela. Breviora 306: 11 pp.  
1968c. A new species of *Elosia* (Amphibia, Salientia) from Mt. Duida, Venezuela. Am. Mus. Novitates 2334: 9 pp.  
1970. On the origin, endemism and distribution of the genus *Stefania* Rivero (Amphibia, Salientia) with a description of a new species from southeastern Venezuela. Bol. Soc. Venez. Cienc. Nat. 28(117/118): 456–481.  
“1971” [1972]. Notas sobre los anfibios de Venezuela I. Sobre los hilidos de la Guayana Venezolana. Caribb. J. Sci. 11(3–4): 181–193.

- "1982a"[1984]. Los *Eleutherodactylus* (Amphibia, Leptodactylidae) de los Andes Venezolanos I. Especies del páramo. Mem. Soc. Cienc. Nat. La Salle 42(118): 17–56.
- "1982b"[1984]. Los *Eleutherodactylus* (Amphibia, Salientia) de los Andes Venezolanos II. Especies subparámicas. Ibid.: 57–132.
1985. Nuevos centrolenidos de Colombia y Venezuela. Brenesia. 23: 335–373.
- Roze, Janis A.
1958. Los reptiles del Auyantepui, Venezuela, basándose en las colecciones de las expediciones de Phelps-Tate, del American Museum of Natural History, 1937–1938, y de la Universidad Central de Venezuela, 1956. Acta Biol. Venez. 2(22): 243–270.
1966. La taxonomía y zoogeografía de los ofidios en Venezuela. Caracas: Univ. Central Venezuela, 362 pp.
- Ruiz-Carranza, Pedro M., and John D. Lynch
- 1991a. Ranas Centrolenidae de Colombia I. Propuesta de una nueva clasificación genérica. Lozania 57: 30 pp.
- 1991b. [Same title] II. Nuevas especies de *Centrolene* de la Cordillera Oriental y Sierra Nevada de Santa Marta. Ibid. 58: 26 pp.
1995. [Same title] VII. Redescrición de *Centrolene andinum* (Rivero 1968). Ibid. 64: 12 pp.
- Savage, Jay M.
1987. Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group. Fieldiana Zool., n. ser. 33: iv + 57 pp.
- Savage, Jay M., and Craig Guyer
1991. Nomenclatural notes on anoles (Sauria: Polychridae): stability over priority. J. Herpetol. 25(3): 365–366.
- Savage, Jay M., and W. Ronald Heyer
1967. Variation and distribution in the treefrog genus *Phyllomedusa* in Costa Rica, Central America. Beitr. Neotrop. Fauna 5(2): 111–131.
- Señaris, Josefa Celsa, and José Ayarzagüena
- "1993" [1994]. Una nueva especie de *Centrolenella* (Anura: Centrolenidae) del Auyantepui, Edo. Bolívar, Venezuela. Mem. Soc. Cienc. Nat. La Salle 53(139): 121–126.
- Stearn, William T.
1983. Botanical Latin, 3rd ed. Newton Abbot, Great Britain: David & Charles, xiv + 566 pp.
- Steyermark, Julian A., Paul E. Berry, and Bruce K. Holst (general eds.)
1995. Flora of the Venezuelan Guayana. St. Louis: Missouri Bot. Garden, vol. 1, xxii + 320 pp. + 84 color pls. + 2 accompanying maps (topographic and vegetation).
- Tate, George H. H., and Charles B. Hitchcock
1930. The Cerro Duida Region of Venezuela. Geogr. Rev. 20(1): pp. 31–52.
- Troschel, F. H.
1848. Amphibien. In R. Schomburgk, Reisen in Britisch-Guiana in den Jahren 1840–1844, Theil 3, Versuch einer Fauna und Flora von Britisch-Guiana, pp. 645–661. Leipzig: Verlagsbuchhandlung von J. J. Weber.
- Van Devender, Robert Wayne
1969. Resurrection of *Neusticurus racenisi* (Sauria, Teiidae). J. Herpetol. 3(1–2): 105–107.
- Vanzolini, P. E., and Ernest E. Williams
1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arq. Zool. (São Paulo) 19: 1–298.
- Wagler, Joh. [Johann Georg]
1830. Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel. Munich, Stuttgart and Tübingen, J. G. Cotta, vi + 354 pp. + 9 folio pls. (1–7 + 2 unnumbered).
- Walker, Charles F., and Frederick H. Test
1955. New Venezuelan frogs of the genus *Eleutherodactylus*. Occas. Pap. Mus. Zool. Univ. Michigan 561: 10 pp.

## NOTE ADDED IN PROOF

Two recent papers add to knowledge of Venezuelan frogs.

CENTROLENIDAE: Ayarzagüena and Señaris ("1996" [1997]) named *Cochranella castroviejoi* and *Cochranella vozmedianoï*, both patronymics applied to nontepui species from the Paria Peninsula. These names should be added to our list of Venezuelan centrolenids on page 16. Ayarzagüena and Señaris continued use of the names *Centrolene buckleyi* and *Centrolene lentiginosum* for Venezuelan taxa. The last name has been synonymized (with *C. andinum*) as mentioned herein, and it seems highly unlikely that *buckleyi* (type locality in Ecuador) reaches Venezuela; we have elevated an available subspecific name (*venezuelense*) for Venezuelan "*buckleyi*."

One tepui species should be repositioned in our list. Ayarzagüena and Señaris ("1996" [1997]: 12) used the new combination "*Hyalinobatrachium* (= *Centrolenella*) *ayantepuiana*," believing that this frog is not allied with *Cochranella* as they had first suggested. However, for the transfer to *Hyalinobatrachium*, the species name, an adjective, requires a neuter ending (i.e., *ayantepuianum*). Ayarzagüena and Señaris (loc. cit.) also rendered several other centrolenid names with incorrect endings.

HYLIDAE: Señaris et al. ("1996" [1997]) presented a new synopsis of *Stefania*, including descriptions of five new species, one (*S. schuberti*) being based partly on material collected by Señaris on the 1994 Robert G. Goelet American Museum-TERRAMAR Expedition to Auyantepui.

Although color patterns are not illustrated, none of the five new *Stefania* seem to approach the distinctive pattern thought to be diagnostic for *Stefania tamacuarina* (named herein), and all five differ from *S. tamacuarina* in presence of well-developed frontoparietal crests.

## NEW REFERENCES

Ayarzagüena, José, and J. Celsa Señaris

"1996" [1997]. Dos nuevas especies de *Cochranella* (Anura; Centrolenidae) para Venezuela. Publ. Asoc. Amigos de Doñana 8: 16 pp.

Señaris, J. Celsa, José Ayarzagüena, and Stefan Gorzula

"1996" [1997]. Revisión taxonómica del género *Stefania* (Anura; Hylidae) en Venezuela con la descripción de cinco nuevas especies. Publ. Asoc. Amigos de Doñana 7: 56 pp.

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