THE SUMMIT HERPETOFAUNA OF AUYANTEPUI, VENEZUELA: REPORT FROM THE ROBERT G. GOELET AMERICAN MUSEUM–TERRAMAR EXPEDITION

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One of many waterfalls dropping from the inner escarpment of Auyantepui. This helicopter view is southerly, looking into the southern end of the mesa from the head of Cañón del Diablo (Devil's Canyon). Camp 1 of the AMNH–Terramar Expedition was situated upstream in the broad valley in upper left (see map 1 and fig. 3). From a transparency by C. W. Myers, February 20, 1994.

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ABSTRACT

Auyantepui is an immense sandstone table mountain in the Venezuelan Guayana. This mesa did not appear on aviation maps and was unknown to the literate world prior to the late 1930s. It was explored from the air by Jimmy Angel, a bush pilot and colorful soldier of fortune for whom the world's highest waterfall is named (Angel Falls at the northern end of Auyantepui). About the same time, in 1937, Captain Félix Cardona Puig and Gustavo Heny discovered an access crack in the sandstone, allowing ascent onto the southern end of the mesa. The first scientific exploration followed immediately—the 1937–1938 Phelps Venezuelan Expedition of the American Museum of Natural History made the first zoological and general botanical collections. Today, no tepui other than the ''Lost World'' of Cerro Roraima is better known to the general public.

The summit of Auyantepui has a known fauna of 24 species of amphibians and reptiles, including species added by the Robert G. Goelet American Museum–TERRAMAR Expedition in 1994. This expedition collected 16 species during a month of fieldwork in the dry season (February), in five camps at elevations of 1700–2100 m above sea level. All species known from the summit of Auyantepui are treated in this bulletin; illustrations where possible include tadpoles, bioacoustic spectrograms, and hemipenes.

Four new species are described—two frogs (*Hypsiboas angelicus*, n. sp., *Eleutherodactylus auricarens*, n. sp.), a lizard (*Arthrosaura montigena*, n. sp.), and a snake (*Atractus guerreroi*, n. sp.). *Arthrosaura montigena* possesses a hemipenial character not previously described—an orifice (*orificium*) of unknown function, situated in the lobular crotch between the two lobes. Attention is called to a probably undescribed snake (*Liophis* ''*miliaris*'' sensu lato) from the nearby Gran Sabana.

The herpetofauna of the Auyán summit comprises 12 families, 20 genera, and 24 species. This is compared with the known herpetofauna of the Chimantá massif, lying less than 50 km south-southeast of Auyantepui. Despite the proximity and similar dimensions, the summits of Auyantepui and Chimantá have in common only 11% of the combined number of species (4 of 36), 44% of the genera (11 of 25), and 62% of the families represented (8 of 13), showing that neighboring tepuis may have herpetofaunas very different from one another. Nonetheless, the adjacent mountains that constitute the more fragmented Chimantá massif are relatively close to one another and seem to have a unified herpetofauna.

RESUMEN

El Auyantepui es una inmensa mesa de piedra arenisca en la región de la Guayana Venezolana. Esta montaña no aparecía en mapas de la aviación y era desconocida en el mundo letrado antes hasta finales de los años 1930s. Fue explorado desde el aire por Jimmy Ángel, aventurero colorido y piloto para quien fue nombrada la cascada más alta del mundo (Salto Ángel en el norte del Auyantepui). Al mismo tiempo, en 1937, el capitán Félix Cardona Puig y Gustavo Heny descubrieron una grieta de acceso en la piedra arenisca que permitió subir la mesa. La primera exploración científica ocurrió inmediatamente—el 1937–1938 Phelps Venezuelan Expedition of the American Museum of Natural History hizo las primeras colecciones zoológicas y botánicas generales. En la actualidad, con la excepción del ''Mundo Perdido'' de Cerro Roraima, no hay ningún tepui mejor conocido al público que Auyantepui.

La cumbre del Auyantepui tiene una fauna conocida de 24 especies de anfibios y reptiles, incluyendo especies obtenidas por The Robert G. Goelet American Museum–TERRAMAR Expedition en 1994. En esta expedición se colectaron 16 especies durante un mes de trabajo de campo en la temporada seca (febrero), en cinco campamentos a alturas entre 1700 y 2100 m sobre el nivel del mar. En este boletín se incluye la totalidad de las especies conocidas en la cumbre del Auyantepui; en lo posible se incluyen también ilustraciones de renacuajos, espectrogramas bioacústicas, y hemipenes.

Se describen cuatro especies nuevas—dos ranas (*Hypsiboas angelicus*, n. sp., *Eleutherodactylus auricarens*, n. sp.), una lagartija (*Arthrosaura montigena*, n. sp.), y una serpiente (*Atractus*

guerreroi, n. sp.). *Arthrosaura montigena* presenta un carácter hemipenial no descrito previamente—un orificio (*orificium*) de función desconocida, situado entre los dos lóbulos. La atención se llama a una serpiente (*Liophis* ''*miliaris*'' sensu lato) probablemente nueva desde la Gran Sabana cercana.

La herpetofauna de la cumbre del Auyantepui incluye 12 familias, 20 géneros, y 24 especies. Se compara esta fauna con la del macizo fragmentado del Chimantá, localizado a menos de 50 km al sudsudeste de Auyantepui. A pesar de estar tan cerca y presentar dimensiones similares, las cumbres de Auyantepui y Chimantá comparten solamente el 11% de las especies (4 de 36 especies en total), el 44% de los géneros (11 de 25), y el 62% de las familias representadas (8 de 13), lo cual demuestra que tepuis vecinos pueden tener herpetofaunas muy diferentes. Sin embargo, las montañas adyacentes que conforman el macizo fragmentado del Chimantá son relativamente cercanas y parecen presentar una herpetofauna unificada.

INTRODUCTION

The sandstone table mountain is a characteristic landform of southern Venezuela, and every isolated mesa rising fortresslike and seemingly impregnable from the savanna is a veritable *mesa encantada* for the student of life forms and a challenge to the explorer. Roraima achieved fame as the "lost world"; Duida proved a rival attraction; but Auyantepui offers perhaps even more interesting possibilities.

So wrote the American Museum's veteran field man G.H.H. Tate in *Geographical Review*, in the first scientific report from an expedition to the "new lost world" of Auyantepui (Tate, 1938a: 452). At the time, every unexplored tepui, or sandstone table mountain, was a *mesa encantada*, an enchanted mesa. Indeed, the enchantment lingers, outliving the original explorers and still affecting those seeking an understanding of these wild highlands and their "highly peculiar" floras and faunas.

Much has been learned since the first British ascents of Mount Roraima in the 1890s (Im Thurn, 1885; Quelch, 1895) and since the American Museum's tripartite exploration of Roraima, Duida, and Auyantepui in 1927–1938 (summary in Myers, 2000: 154–160). Ensuing investigations by other workers and institutions in the following decades advanced knowledge on a variety of fronts, particularly in the fields of ornithology and botany.

Following their participation in the Auyantepui expedition, W. H. Phelps of Caracas and his son W. H. Phelps, Jr., supported their own ornithological expeditions to a few dozen Venezuelan tepuis, this work reaching maximum intensity during 1944–1954. The results of all but the latest Phelps expeditions were summarized by Mayr and Phelps (1967, 1971), who coined the biogeographically useful term "Pantepui" for the sandstone mesas (tepuis) and faunistically related granitic mountains of southern Venezuela and adjacent Brazil and Guyana.

Tate (1938a: 471) collected plants as well as animals and recognized that "The entire region of Venezuelan Guiana between Roraima, Duida, and Auyantepui above 1000 meters is a mine of unimagined phyto-

logical wealth". Within a few years, numerous botanical excursions were to start proving Tate's assertion, especially the many expeditions conducted by the late Julian Steyermark for the Field Museum of Natural History and (after 1958) for the Instituto Botánico in Caracas, and by the late Bassett Maguire and associates for the New York Botanical Garden. The physical geography, botanical exploration, and vegetation of Pantepui were well summarized by Huber (1995a, 1995b, 1995c) in the introductory volume to the *Flora of the Venezuelan Guayana*.

Apart from the birds, knowledge of the general zoology of Pantepui lags far behind that of the vegetation. A census of the amphibians and reptiles, for example, is only fractionally complete. Many tepui collections have been opportunistic, the result of a collector spending only a few daylight hours between helicopter flights to and from the summit. Partly because of this, only 1–3 species of amphibians and reptiles are known from 17 of the 39 tepuis subjected to some degree of herpetological collecting (summarized from McDiarmid and Donnelly, 1999: 517–540).

Species endemicity is high, and, although herpetofaunas on individual tepuis are relatively depauperate, some of the component species resist discovery by virtue of their being either rare or secretive (or both). For a faunal sample to be reasonably representative, amphibians and reptiles must be collected day and night over a period of days or weeks, and ideally during repeat visits in different seasons. Myers has been fortunate to collect samples meeting all but the last of these criteria on eight sandstone tepuis and one granitic mountain with a tepuilike fauna—in company with Donnelly on six of the nine mountains. Our samples include a dry-season collection made on the summit of Auyantepui in 1994.

The Robert G. Goelet American Museum– Terramar Expedition to Auyantepui in 1994 marked the museum's return to the mountain nearly 70 years after the first pioneering expedition—this time with the advantage of helicopter support and in fruitful collaboration with Fundación Terramar. The use of helicopters allowed establishment of five camps scattered over a large area of this immense tepui (map 1, fig. 1).
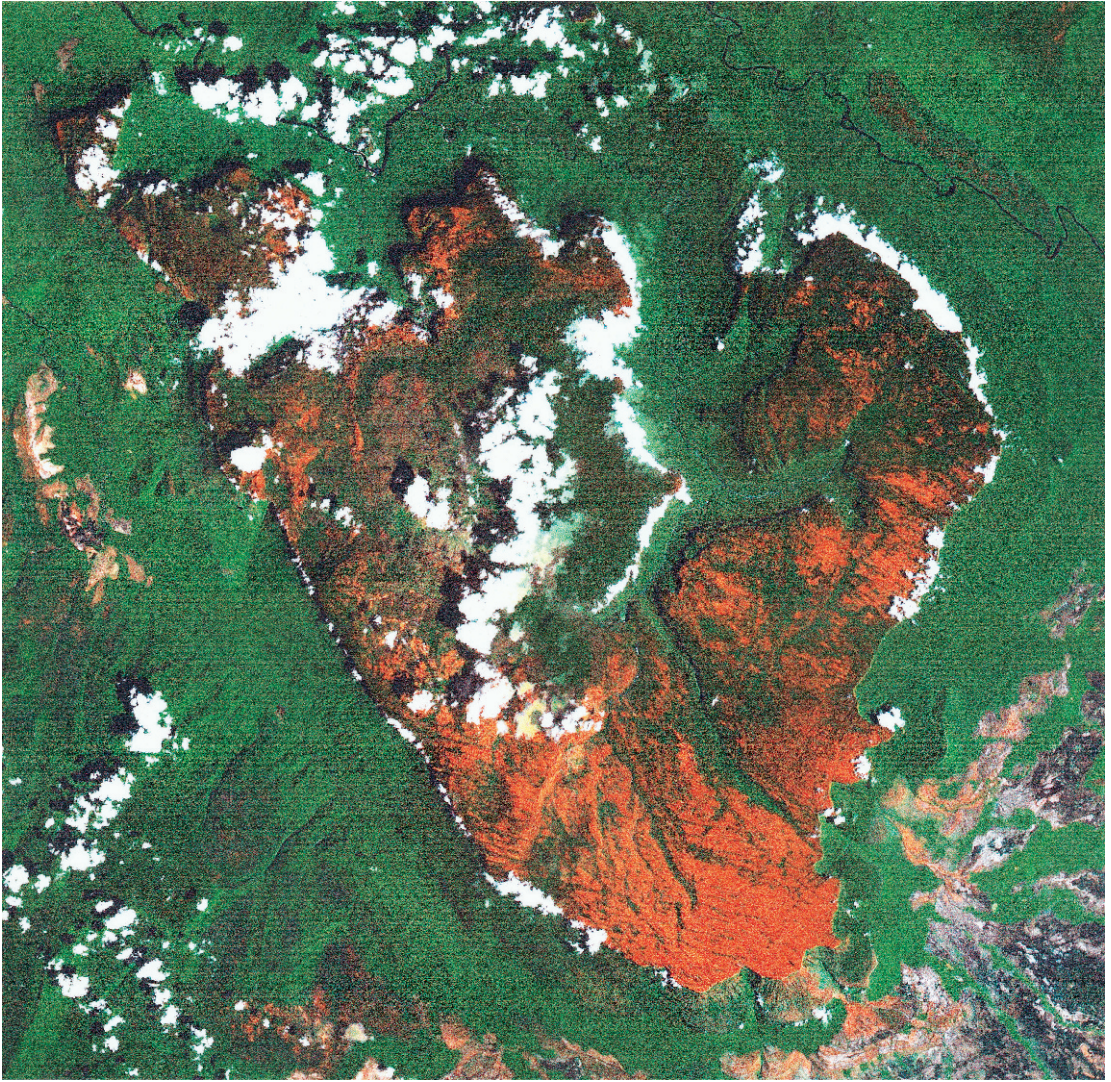
Fig. 1. Satellite image of Auyantepui (Google Earth Plus©). Compare with map 1.

We here present the herpetological results of the 1994 expedition, along with recognition of other published work contributing to knowledge of the summit herpetofauna of Auyantepui. First, a summary of what went before.

MODERN DISCOVERY AND EXPLORATION OF AUYANTEPUI

It is futile to ask who first "discovered" Auyantepui, which was known to Amerindians from time immemorial and was seen by early missionaries. According to F. Miche-

langeli Ayala (2000: 44; 2005: 155), Serro Auyan (Auyantepui) was shown by Friar Carlos de Barcelona, on a map appearing in 1772 under the title *Tierras pertenecientes a la conquista de los reverendos capuchinos catalanes de la Guayana, desde el río Orinoco hasta la Equinoccial*.

Certainly, however, Auyantepui was essentially unknown to the literate world prior to 1937. Since then, it has come to rank next to Roraima in reputation. Nowadays there is air service to Canaima, where excursions can be arranged to Auyantepui some 20 km to
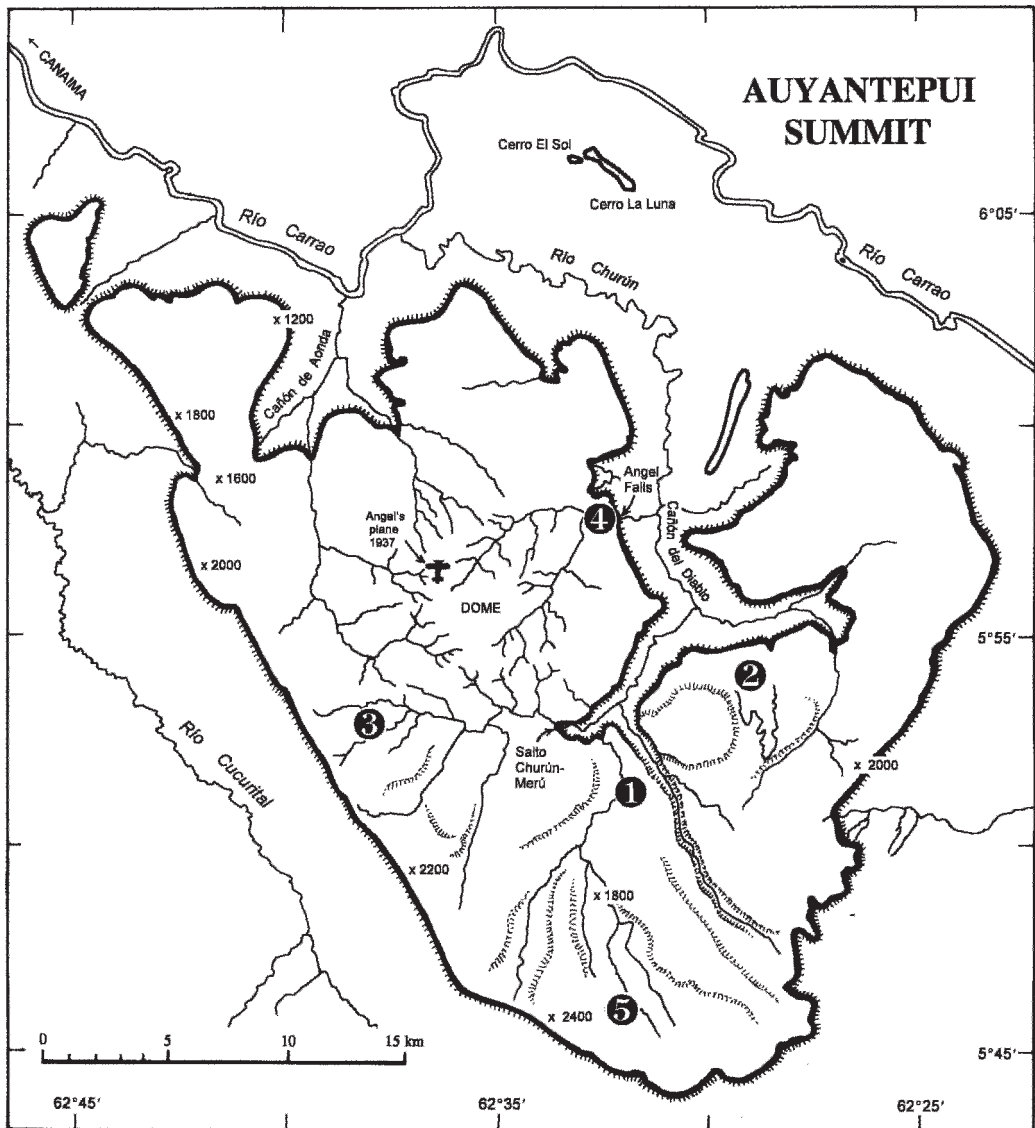
Map 1. Summit area of Auyantepui, showing locations of camps 1–5 established by the AMNH–TERRAMAR Expedition. The approximate site of Jimmy Angel's abandoned plane is taken from Dunsterville's (1965) map; Angel's plane was disassembled and removed by the Venezuelan Air Force in 1970. (Adapted from an unpublished map by Maraven S.A., 1987, original scale 1:100,000.)

the southeast. Tourists see the world's highest waterfall—Angel Falls—and are captivated by the legend of James "Jimmy" (or "Jimmie") Angel (1899–1956), the American pilot and soldier of fortune whose exploits first brought Auyantepui to public awareness.

Auyantepui lies in the direction taken by Sir Walter Raleigh in 1595, in his quest for *the great and Golden Citie … which the Spanyards call El Dorado* (see Nicholl, 1995). For centuries, the region has attracted prospectors for gold and diamonds. Those keeping their eyes open for possible riches in the 1920s and 1930s included Captain Félix Cardona, who explored and mapped the Auyantepui area, and Jimmy Angel, who sacrificed his plane to the high summit of Auyantepui while looking for gold.

Angel had flown combat in World War I, after which he traveled in Southeast Asia, purportedly flew for a warlord in North China, and prospected for gold in Tibet. He returned home to a varied life as a barnstormer, Hollywood stunt pilot, and pilot-for-hire to various companies and agencies. His diverse contract work and various business schemes had him flying in Mexico, Central America, and in South America as far south as Chile and Peru. A historic figure in Latin American aviation (Time-Life Books, 1984; Soto, 2003), Angel was inclined to exaggeration and outright fiction, but his charismatic personality made those embellishments convincingly real, especially to financial backers in his obsessive search for gold.

Angel claimed to have met a [John] McCracken, an "old mining engineer" in a bar in Panama, where McCracken hired Angel to fly him to Venezuela, thence in a roundabout way to the summit of Auyantepui. Angel said that they landed near a summit stream as directed by McCracken, where in three days they took from the gravel 75 pounds of gold (20 pounds in some later accounts). McCracken wanted to take Angel in as a partner for additional trips but died after returning home to the United States, leaving Angel free to return to Auyantepui on his own. This is the version of the story as told by Angel to L. R. Dennison on March 24, 1935, in the New York offices of Case, Pomeroy and Company (Dennison, 1942: 22–25). Dennison, a knowledgeable mining engineer, was skeptical but eventually came to believe Angel's story. American Museum ornithologist E. Thomas Gilliard (1940, 1941b) accepted the legend and repeated a more theatrical version of it (the prospector McCracken is called "Williamson" in Gilliard's accounts). This tale has been often retold.

It is not known with certainty when or how Angel learned of Auyantepui, a mountain that did not then appear on any map available to aviators. But find it he did. Auyantepui lies in the drainage of the Río Caroní, long known as a rich source of diamonds and gold (Dennison, 1943; Nicholl, 1995), and it would not have taken much imagination to suppose that the mountain was the source of some of the Caroní river gold. When he could afford it, Angel made repeated visits to overfly Auyantepui. He discovered an exceptionally high waterfall with an unbroken drop of nearly 1000 m. He more than once flew into Cañón del Diablo—Devil's Canyon—in the northern side of the mountain, sometimes to show a passenger (e.g., Dennison, 1942: 39) and to dip a wing in the plummeting stream of "his" waterfall.

Angel provisioned a camp on a savanna that served as a landing field at the mountain's southern base. Fortuitously, Félix Cardona had also been exploring the region on foot. Events unfolded as summarized by Tate (1938a: 452–453):

> Not very long ago Mr. Angel, accompanied by his wife and a friend, Gustavo Heny, flew to the mountain and set up a comfortable camp a few miles west of the Arecuna Indian village of Urullén. Cardona, arriving from the [Río] Paragua, found them there. While the Angels engaged in aerial exploration, Cardona and Heny contrived to reach the plateau by way of a joint crack in the sandstone. They spent a month exploring the adjoining parts of the mountaintop without finding gold, but they were barred from the northwestern part of the tableland by a huge rock wall a few miles from their point of ascent.
>
> The next move was carefully planned. The party left a portable radio at its base and carried another set in the plane. Cardona remained at the base to operate the field set while Mr. and Mrs. Angel, Heny, and a peon [Miguel Delgado from Caracas, hired by Heny], with ample supplies, flew to the top of the mountain and landed on a level area in the northwestern part. Unfortunately, in landing, the wheels of the plane sank into the waterlogged, peaty soil, from which it could not be extricated. Radio communication was established with Cardona, but transmission proved defective, so that the circumstances of their plight remained unknown. Heny and [Miguel Delgado], both of whom were excellent woodsmen, acted as guides to bring the Angels safely out of the intricate labyrinth of cliffs, fissures, and tangled brush. The journey, which would have required less than an hour by air, took ten days on foot and was accomplished only through the skill, good judgment, and knowledge of Heny and the pluck and fortitude of the party.
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> Mr. W. H. Phelps of Caracas, a keen ornithologist, heard the story. So deeply impressed was he by the photographs and descriptions of Cardona and Heny that he wrote Dr. F. M. Chapman of the American Museum of Natural History urging that a party be dispatched to study the region and at the same time offering to defray its expenses.

Time was not lost in mounting the Phelps Venezuelan Expedition of the American Museum of Natural History, which commenced in the same year that Angel and his party had escaped off the summit of Auyantepui. Cardona and Heny's discovery of the access crack in the side of Auyantepui made the mission feasible, although equipment and provisions were transported with great difficulty, as graphically related by Gilliard (1940: 270–271). Some years later, Dunsterville (1965: 169) succinctly described this passageway:

El Zanjón (Access Crack).—The steeply rising boulder-filled diagonal crack leading from Rest Point to the summit: no alpine skills are needed but at one point a short rope is of very great help. The final exit point at the top of Access Crack is a tricky double twist upwards between giant boulders, which must have given Cardona and Heny an anxious hour or two before they discovered it.[1]

The main geographical and zoological results of the 1937–1938 expedition were published by Chapman (1939) and by expedition members Tate (1938a, 1938b, 1938c, 1939) and Gilliard (1940, 1941a, 1941b).[2] Expedition member Phelps (1938) summarized the expedition in Caracas, with Félix Cardona's map of the Auyantepui region being published at the same time (Cardona Puig, 1938). Phelps also had Tate's (1938a) first report translated for the Venezuelan

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[1] The Cardona–Heny route at the southwestern end of Auyantepui, above Jimmy Angel's old camp, is still considered to be the only practical way to reach the summit on foot. In 1936, L. R. Dennison and a few men worked their way from the Río Cucurital and around the northern end of Auyantepui, passed Angel Falls, and purportedly made an ascent from within the great canyon, up ledges with dangerously unstable footing (Dennison, 1942: 190–202). Dennison was looking for a particular stream that Jimmy Angel had pointed out from the air as possibly the place where he had landed with the prospector McCracken (aka Williamson), but "there was no gravel in the stream and the geological formation was far from being auriferous" (Dennison, 1942: 203–205).
[2] G.H.H. Tate's abilities in organizing and carrying out complex expeditions were self-evident, but Gilliard's (1940, 1941b) popular accounts provided a rare glimpse of his personality and perseverance under difficult field conditions. Gilliard (1941b) admiringly exclaimed that "You couldn't call that three-initialed Englishman a sissy"!

scientific community (Tate, 1938c). Tate's plant specimens were studied by Gleason and Killip (1939).

The successful conclusion of the expedition led the president of Venezuela to commission a survey of the Auyantepui area and the Gran Sabana generally. Aerial photographs of Angel Falls were included in the thick, quickly assembled report, which was published late in 1938 (Aguerrevere et al., 1939).

It was an eminently successful expedition, but Jimmy Angel, who was in large part responsible, never did find his gold. He died after a plane accident in Panama in 1956. The legend of his finding a small fortune in gold after landing on a mesa with an old prospector was repeated in his obituary (New York Times, December 9, 1956: 87). In 1970, the Venezuelan Air Force disassembled the plane that Angel had abandoned in 1937 and removed it by helicopter from the summit of Auyantepui, where it had lain for over 30 years.

HERPETOLOGICAL HISTORY

The first herpetological specimens from Auyantepui were collected by the Museum's 1937–1938 Expedition. An expedition from the Universidad Central de Venezuela in 1956 resulted in additional specimens a few decades later (Lindorf, 2006). The reptiles from the American Museum and the Universidad Central expeditions were reported by Roze (1958a). Much of this material originated from lowland camps below 500 m, but Roze described a new lizard (Tropidurus bogerti) from the summit of Auyantepui, as well as a new lizard (Neusticurus racenisi) and a new snake (Liophis trebbaui) from the southern slope at about 1000–1100 m elevation (see fn. 27 and Liophis account for correction and explanation of locality). Although Phelps and Tate recorded full data for the American Museum specimens, Roze (1958a) did not cite the cataloged elevation for many specimens, leading to incorrect assumptions that the elevations are unknown (e.g., McDiarmid and Donnelly, 2005: 523).

Additional herpetological specimens were obtained in subsequent years by several collectors, including Roy W. McDiarmid

(specimens in USNM), Adrian N. Warren (specimens in BMNH), and Stefan Gorzula and José Ayarzagüena (specimens in MHNLS), with much of the MHNLS material reported on by Ayarzagüena, Gorzula, and Señaris (see References).

Gorzula's (1992) Auyantepui records are particularly pertinent, since they were given in a report on the herpetofauna of the Chimantá massif. Gorzula conducted fieldwork on Auyantepui in addition to his extensive work on Chimantá. Observations from the experience of a single collector were especially useful in making a preliminary comparison of the diverse herpetofaunas on these neighboring tepuis (Myers, 1997).

Thus, as summarized by Myers (1997), a general framework of the summit herpetofauna of Auyantepui had been established before the start of the 1994 expedition. The intent of the herpetological team on the AMNH–TERRAMAR expedition was to add to the baseline data by making a systematic exploration of summit habitats over an extended period (one month).

MATERIALS AND METHODS

DEPOSITION OF SPECIMENS: Contractual agreements with PROFAUNA and INPARQUES provided that one half of the collection, including all holotypes and half of the species represented by single specimens, would be cataloged in the collection of the Museo de la Estación Biológica de Rancho Grande (EBRG) in Maracay, with the other half going to the amphibian and reptile collections of the American Museum of Natural History (AMNH) in New York. In order to assure an equitable split, specimens were divided after identifications, sex, and maturity were determined at the American Museum; EBRG numbers were then assigned and cross-referenced to CWM field tags. We thank Francisco J. Bisbal, Director of the Rancho Grande Museum, for facilitating the cataloging process and for helping in other ways.

Most specimens were collected by a herpetology team comprised of the two of us and John Daly, but obliging colleagues of other disciplines also provided specimens. All of this material is cataloged as collected by

the 1994 AMNH–TERRAMAR Expedition— an abbreviation for the official name "The Robert G. Goelet American Museum of Natural History–TERRAMAR Expedition to Auyantepui".

Specimens collected by J. Celsa Señaris, a guest in two of our camps, were retained by her for the collection of the Museo de Historia Natural La Salle (MHNLS) in Caracas, with half of her specimens also going to EBRG. Except for *Oreophrynella* (fig. 12), this material adds no species and did not contribute to the present report.

MEASUREMENTS, WEBBING FORMULAE, TADPOLES: Measurements of less than 12 mm were taken with an ocular micrometer fitted in a Wild dissecting microscope; larger measurements were made with digital calipers read to the nearest 0.1 mm or with a ruler read to the nearest 1 mm. For anuran webbing formulae, we use the notational device of Savage and Heyer (1967) as modified for general use by Myers and Duellman (1982: 6). Tadpoles were staged according to Gosner (1960), which has been long accepted by many workers as a standard for taxonomic descriptions, and further championed in McDiarmid and Altig's (1999: 8–11) masterful *Tadpoles*. We use the larval terminology in chapter 3 (Altig and McDiarmid, 1999) of *Tadpoles*, although we are perplexed why the term "jaw sheath" was proposed as a replacement for the more familiar and visually descriptive "beak".[3]

VOCALIZATIONS: Tape recordings of frog calls were converted to electronic format through a Kay CSL 4500 16-bit analog-to-digital converter (sampling rate 22050 Hz) and stored on a computer hard drive and optical discs. Waveforms and sound spectrographs were analyzed and printed using the

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[3] Rationale for the term *jaw sheath* (Altig and McDiarmid, 1999: 35–36) is concisely summarized in the book's glossary (p. 343): "Used as a separate term from 'beak' because it is unlikely these structures are homologs of other structures termed beaks in birds and turtles". By that reasoning, one should not use the authors' expression *labial teeth* (vs."denticles" for example), inasmuch as tadpole teeth are not even homologous with adult teeth in the same animal. Lack of homology is not a significant source of confusion for common words such as "wings", "tails", "teeth", "beaks", "scales" etc.—technical jargon is a more-frequent hindrance to understanding.

CSL software (Kay Elemetrics Co.). Sound spectrographs are similar to older analog standards: **wideband**, with an effective band-width filter of 323.00 Hz, and/or **narrowband**, with an effective bandwidth filter of 63.09 Hz. It is important to note that time measurements of notes were made from wideband spectrograms and/or from the waveforms, whereas statements concerning frequency were derived from narrowband analysis. Failure to distinguish between time and frequency correlated aspects of changing bandwidth has caused ambiguity and confu-sion in the bioacoustical literature (Zweifel and Myers, 1989: 11).

We cannot improve on Zweifel's (1985: 272) concise definitions for the sometimes confused terms ''call'' and ''note'':

> A *call* is a discrete unit of vocalization composed of one or more separate bursts of sound and temporally distinct from units similarly uttered. A *note* is heard as a single unit of sound. A call may thus consist of a single note, or of a number of notes grouped into one call. *Pulses* are discrete units of sound energy resolvable [by waveform or wide-band analysis].

Notes may be nonpulsatile (single pulsed) or, depending on degree of amplitude mod-ulation of the waveform, weakly to strongly pulsed. Variation is tremendous (e.g., see Heyer et al., 1990: 387–404) and there are borderline cases of ambiguity between notes and pulses (e.g., Myers and Donnelly, 1997: 23).

SPECIES SYNONYMIES: In addition to senior and some junior synonyms, the synonymies may include references that mention Auyantepui specimens or that oth-erwise are pertinent to an understanding of the listed taxon. There is no intention of completeness. Additional references for the rapidly growing anuran literature can be found in Barrio Amorós (2004), Faivovich et al. (2005), Frost et al. (2006), Grant et al. (2006), and Señaris and Ayarzagüena (2005).

Taxonomic accounts of genera and species are arranged alphabetically within families. Lack of strict alphabetical order of listed frog families reflects recent taxonomic changes, which require corroboration as a matter of course.

CARTOGRAPHIC SOURCES
AND NOMENCLATURE

An unpublished map drafted by Maraven S.A. (1987, scale 1:100,000.) was used in the field and was particularly useful in giving an overview of drainage patterns and locations of some of the rock walls. Later attempts to add standard coordinates of latitude and longitude to this map led to puzzling results, until it was realized that the map's north-south axis was tilted slightly eastward. The map published herein (map 1) was drafted from this source after correction of the compass orientation. Camp locations were verified by use of the computer-display coordinate cursor on a satellite image (fig. 1) produced with the program Google Earth Plus©. Camp locations on map 1 are accurate within the errors necessitated by rounding off GPS readings.

Field coordinates had been determined by two hand-held Global Positioning System (GPS) satellite receivers. Readings were rounded to the nearest minute of latitude and longitude because point-position accura-cy of civilian GPS devices was limited (for military reasons) to about 100 m prior to May 2000. GPS was particularly untrustwor-thy for elevation, and camp elevations were recorded after cross-checking two or more altimeters, sometimes including that of the helicopter. The base comparison for eleva-tions was 380 m at Canaima.

We follow Tate (1938a, 1938b, 1938c), Cardona Puig (1938), Dunsterville (1965), Huber (1995a, 1995b, 1995c), and M. Michel-angeli Ayala (2005) in using the orthography **Auyantepui** for the Auyán massif. Other informed authors have used the alternative spellings Auyan-tepui or (more correctly) Auyán-tepui, and Auyantepuy or Auyán-tepuy. Earlier renditions of the name includ-ed Yauyan, Yauyang, and Auyang (Steyer-mark, 1967: 19)

THE NATURAL LANDSCAPE AND
COLLECTING SITES

Frontispiece, Map 1, Figures 1–11, 18

The cliff-walled table mountain or massif called Auyantepui is among the largest of the tepuis, with dimensions of nearly 50 km from

northwest to southeast and nearly 35 km across from east to west. The Auyantepui massif is for practical purposes a single large mountain, although a low ridge connects it with a few erosional remnants to the north and there is a small, herpetologically unexplored satellite mountain (Uaipán) to the south (Huber, 1995a: fig. 1–25).

At its southern end, Auyantepui rises about 1400 m above the savanna below (Tate, 1938a: fig. 2). Mayr and Phelps (1967: 279) estimated the summit area as 700 km^2 and the talus area as 200 km^2;[4] Huber (1995a: 60) gave 666.9 km^2 for the summit area, excluding the northern erosional remnants (Cerro La Luna and Cerro El Sol; map 1). The summit has an annual average temperature of about 13°C according to Huber (1976). Some general information on Auyantepui (which has its own mythological animal) and striking photographs are to be found in National Geographic (George, 1989), and in the books Inseln in der Zeit (George, 1988) and Tepuy (A. Michelangeli Ayala, 2005: 213–229).

Auyantepui is deeply eroded from the north, with the great Cañón del Diablo (Devil's Canyon) almost dividing the mesa into a large western branch and a smaller eastern one (map 1). Elevation is highest (2000–2450 m)[5] around the southern edge of the mesa, from where there is inward drainage to Cañón del Diablo of the Río Churún. Much of the mesa has the drainage inclined slightly inward from the encircling rim, but the southern part has a steeper northerly gradient down to the head of Cañón del Diablo. There is a smaller catch basin draining into Cañón de Aonda in the northwest part of Auyantepui.

The eastern branch and southern part of the Auyán plateau presents a varied but generally open landscape of bare rock, rocky ridges, cliffs, and "walls" formed by lines of gigantic sandstone blocks. There are chasms, deep crevices, and labyrinths arising from erosion of intricately jointed sandstone of the Roraima formation.

Vegetation[6] includes "a relatively homogeneous 1- to 3-m tall scrub [that] occurs between 1600 and 2400 m elevation" (Huber, 1995a: 134), as well as small patches of Bonnetia forest. Tate (1938a: 469) recognized only two kinds of forest above 2000 m on the southern end of Auyantepui: Shrubby Bonnetia roraimae forest on deep boggy humus, and tangled, semirecumbent Bonnetia crassa forest growing in a mixture of sand, rock, and humus and reaching optimal development in the larger jointing troughs. In a sheltered gully at 1850 m, Tate (1938a: 469) found "a type of forest … that in appearance approximates normal subtropical forest [with some tall straight trees] nearly two feet in diameter [and with] epiphytic arums and vines" (see also Dunsterville, 1965: 167; Steyermark, 1967: 22). Boggy tepui meadows occur in flat places along streams, but seem to be uncommon in eastern Auyantepui.

The outer western side of the mesa also is sandstone with scrub and small patches of forest, but inward toward Cañón del Diablo, the plateau has extensive tepui meadows and larger areas of forest growing over extensive diabase intrusions (Dunsterville, 1965; Steyermark, 1967: 14–15; Huber, 1995a: 15):

the eastern half of the north-west arm [of Auyantepui] provides a great change in topography and vegetation, and thus of scenery in general. Here the surface rock, exposed in many places from under a fairly thin covering of soil, is igneous in character, and the cliffs and chasms are replaced by rather featureless undulating country clothed in grass and scrub, small trees and shrubs, with frequent boggy

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[4] The "magnificent forest of the talus slopes" (Mayr and Phelps, 1967: pl. 18) was in places destroyed or highly modified by fire in the early 20th century. Speaking of the southern slope of Auyantepui, Gilliard (1940: 270) said that "Tate's trail led us onto a vast, burned incline. Gaunt, denuded forests of seared trunks attested to the severity of a fire which had ravaged this area ten or fifteen years before". Fire had reached the rocky summit also (Tate, 1938a: 469).

[5] A government-sponsored report gave a maximum elevation of 2425 m. (Anon., 1993: 7, table 1); Huber (1995a: 39–40) showed 2450 m at the southwest corner.

[6] The flora of Auyantepui has been relatively well explored, starting with Tate's original descriptions and study of his collections by Gleason and Killip 1939); the flora was monographed by Steyermark (1967). See Delascio Chitty (1997) for a recent summary. Rull (1991) provided preliminary historic perspective through pollen analysis from the summits of Auyantepui, Chimantá, and Guaiquinima.

Fig. 2. Helicopter view from above a forested dome-shaped hill—a conspicuous landmark on the western branch of Auyantepui (map 1). This presumptive igneous intrusion bears the largest area of forest on the mesa, the vegetation probably owing its relative luxuriance to underlying diabase-derived soil. Sections of forest appear destroyed, possibly by fire.

stretches of large extent and, all along the eastern margin, a covering of incredibly dense elfin forest …. (Dunsterville, 1965: 168)

A dome-shaped hill—certainly an erosion-resistant igneous intrusion—is conspicuous when flying over the western branch of Auyantepui (map 1). This dome is covered over with what seems to be the most extensive area of forest on the mountain, although fire (or disease?) appears to have made encroachments (fig. 2). The fauna of this forest deserves study; only a few herpetological specimens have come from the general area (e.g., Gorzula and Señaris, 1999: 254, locality H-007).

Rull (1991: xviii–xix) commented on data from sedimentary pollen analyses on the western branch of Auyantepui, noting that two sampling sites at a river margin "show local differences between about 4,400 and 2,400 BP [from which] date a shrinking of the forest was recorded, elapsing until ca. 1,000 BP". However, data were insufficient to determine whether vegetational oscillations were local phenomena controlled by changing hydrology or by climate change.

In the main canyon, waterfalls are numerous, sometimes falling close together (e.g., Steyermark et al., 1995: pl. 30) and sometimes emerging from the cliff walls, uncountable after heavy rains.

After the thunder, came the rains—rains that come down in such magnitude that Auyan-Tepui suddenly blossoms out with thousands of

waterfalls, and rivers are formed directly in one's path. (Dennison, 1942: 194)

Angel Falls, with an uninterrupted drop of nearly 1000 m is the best known of the permanent falls.

> Angel Falls, whose waters are derived from a small gathering area on the top of the massif, drops from the west wall of this gorge. All the walls … are of most impressive height, but at the particular point where Angel river takes its jump the scree slopes at the base of the cliff have been cut away adding an appreciable extension to the vertical rock face, making this fall the highest in the world. During heavy rains not only Angel Falls but literally dozens of other great falls adorn the walls of the Churún gorge and the outer bastions of the massif as a whole, but most of these dry again a few hours after the rains stop, and even Angel Falls itself comes close to drying up at times. (Dunsterville, 1965: 166)

Huber (1995a: 39) mentioned that Angel Falls (Salto Angel or Karepa-Kupai-merú) "is often called Churún-merú, a waterfall farther southwest in the Cañón del Diablo" (indeed, as of 2005, the names were shown as synonymous in the Geonames online database, but see map 1).

Large expanses of the eastern and southern parts of the mesa are virtually bare rock that is swept clean by sheets of water during torrential rains, the water then finding its way into shallow stream beds and into small rivers in gorges flanked by rock walls. "At times, where the sandstone bedding dips more steeply than the river bed itself, a river may disappear wholly or partly underground, to appear in full volume again lower down its course" (Dunsterville, 1965: 167).

Five AMNH–Terramar camps were opened in February 1994, numbered 1–5 as shown in map 1. The camp numbers match those in one ornithology report from the Expedition (Barrowclough et al., 1997), but a different sequence was given in a second report (Lentino et al., "1998" [1999]).

Camp 1, 1700 m (5°51′N, 62°32′W)

Map 1, Figures 3, 4, 18

Herpetology Camp 1 was established on a field of bare rock that slopes toward a gorge faced by a rocky bluff on the other side. A waterfall immediately below camp impeded downstream collecting. Upstream, however, a second, much larger field of bare rock slopes down to the open edge of the shallow, easily accessible river of a clear coffee color. At Camp 1, the drainage system runs from southeast to northwest. A helicopter overview of the area is shown in figure 3 (see frontispiece for a distant view from the edge of the canyon).

The broad rock flats had conspicuous clumps of carnivorous tube bromeliads (*Brocchinia reducta*) growing as volunteer vegetation in the slightest depressions where soil had accumulated (fig. 3, lower); other plants in these patches included *Epidendrum* and spiny-based *Orectanthe*, both with tall inflorescences. White-flowered *Maguireothamnus* was conspicuous in the dense shrubbery along the edges of the fields of bare rock, along with the peculiar *Xyris* with low, flat leaves, and sundews and flowering pitcher plants.

One could easily work along a scrubby forest on wet soggy ground, at the edge of the large sandstone flat beyond camp, but upland (away from river) progress was abruptly halted by a dangerously deep crevice at the far edge of the flat. There also was a system of crevices in exposed rock closer to camp (fig. 4, top); a shallow stream on the bottom of one crevice provided habitat for *Anomaloglossus* (see fig. 18).

The best forest near Camp 1 was found upriver and on the opposite side of camp, on a slope below a broken rocky ridge. It is a rather dense forest (fig. 4, bottom)—interrupted by sandstone bluffs and great boulders—growing on well-drained spongy ground that has a thin but uniform layer of leaf litter. There are few ferns and only occasional clumps of large bromeliads. Canopy height is 8–10 m; there are scattered palms and small sclerophyllous trees with straight trunks. There are no buttressed trees, but some nonpalms have stilt roots. The tree-trunk "moss" layer is mostly sparse except where it becomes heavy locally, especially on logs.

Camp 1 was established on February 1 and vacated on the afternoon of February 7, 1994. There was frequent rain, which was nearly continuous from the night of February 3 into the following night.

CAMP 2, 1750 M (5°54′N, 62°29′W)

Map 1, Figures 5 (top), 6–7

Herpetology Camp 2 was situated in the flood zone on an open sandstone flat near a shallow river. Vegetation, including small colonies of the ubiquitous tube bromeliads (*Brocchinia*), was similar to that of Camp 1, but the terrain at Camp 2 is flatter, with poorer drainage.

The valley upstream from Camp 2 is broad and flat, with extensive boggy meadows and very small patches of forest (fig. 6). The stream is on a rock bed and can be waded for some distance, but one had to be on the lookout for narrow crevices crossing the stream at a right angle, sometimes associated with a low fall (fig. 6, upper).

At camp, the stream dropped sharply into a short section difficult to work. However, low waterfalls were easily accessible a short distance downstream (fig. 7, upper); nonbreeding *Stefania* were easily found here at night. Erosional remnants of sandstone lay about on raised sandstone ledges near the falls (fig. 7, lower), where the only specimen of *Liophis* was found in a shallow pool on the rock surface.

Below the low falls is a steep waterfall, where the stream drops into a wild canyon of house-sized boulders and increasing gradient. Two specimens of *Oreophrynella* were found in this section. The stream apparently then goes underground before exiting the northern edge of the plateau (map 1).

A low wet patch of forest was accessible along the river upstream from camp, as was dense forest on a hill below camp, but night collecting yielded only some *Eleutherodactylus* and *Tepuihyla*.

Herpetology Camp 2 was occupied from the afternoon of February 7 and vacated on February 14, 1994. Rain fell during the nights of February 8 and 9, without flooding.

CAMP 3, 1850 M (5°53′N, 62°38′W)

Map 1, Figures 5 (bottom), 8

Herpetology Camp 3 was established in a broad, gently sloping basin in the western sector of Auyantepui (figs. 5 bottom, 8 top). It was easier to move around than at camps 1 and 2, owing to large expanses of bare rock and absence of dangerous crevices. Vegetated areas are dense and brushy, but one could push through these into open sandstone glades with an abundance of rocks to turn.

A dense *Bonnetia* forest (fig. 8 bottom) was found on well-drained ground upriver from Camp 3, but collecting in it was unproductive. No frogs were heard calling by day or night.

The most common elements of the Camp 3 herpetofauna were two frogs (*Leptodactylus* and *Tepuihyla*) and a lizard (*Tropidurus bogerti*). All three species were as common under rocks as anywhere else; both kinds of frog and the lizard were sometimes found under the same rock. In some places (e.g., Camp 1), *Tepuihyla* seemed to be nearly confined to the ubiquitous tube bromeliads, but at Camp 3 they were more often found under rocks or sitting completely exposed at night.

Camp 3 was occupied on February 14 and vacated on February 19. There was some mist during this period but no rain.

CAMP 4, 1600 M (5°58′N, 62°33′W)

Map 1, Figure 9

Herpetology Camp 4 was situated on a rocky stream a short distance above the head of Angel Falls. What looks like open fields from the air (fig. 9, top) are boggy meadows that are of difficult passage. The head of Angel Falls is formed from several streams of water flowing from deep channels at the edge of the mesa. The dry-season flow was nearly minimal during our time there (fig. 9, bottom), but can be impressive at other times (e.g., photos in George, 1988: 108–110; A. Michelangeli, 2005: 214–215). With an unbroken drop of 965 m, it is judged the world's highest waterfall.

Dense forest and a stream were accessible at Camp 4. This camp was lower and, owing to orographic mist and rain at the edge of the tepui, much wetter than any of the other camps. Camp 4 was occupied on February 19 and vacated on February 24, 1994.

CAMP 5, 2100 M (5°46′N, 62°32′W)

Map 1, Figures 10, 11

Herpetology Camp 5 was occupied from February 24 until March 1, 1994. At 2100 m

Fig. 3.   **Top:** Helicopter overview of Camp 1 area, looking upstream in a southeasterly direction (see frontispiece for a more distant perspective). Camp was situated on the smaller flat sandstone outcrop to left of center. Beyond that, a larger field of bare sandstone slopes down to the edge of a shallow river, which flows into the rocky gorge visible below (February 20, 1994). **Bottom:** The larger sandstone outcrop above river, with colonies of carnivorous tube bromeliads (*Brocchinia reducta*) growing in shallow soil-filled depressions (February 5, 1994).

Fig. 4.   **Top:** Deep crevices in sandstone near Camp 1; see also figure 18. **Bottom:** Interior of slope forest near (upriver from) Camp 1 (February 6, 1994).

Fig. 5.   Expedition camps 2 and 3 in the sweeping landscapes of Auyantepui. **Top:** AMNH–Terramar Camp 2 was established on the eastern arm of the mesa, on an open sandstone flat in the flood zone of a shallow river (shown in figs. 6–7) (February 11, 1994).

Fig. 5. Continued.   **Bottom:** AMNH–Terramar Camp 3 was situated in a broad, gently sloping basin on the western arm of the mesa. Expedition tents are visible scattered across the middle distance (February 17, 1994).

Fig. 6. **Top:** Rock-bottomed stream above Camp 2. The low fall marks the position of a crevice across the stream bottom. A small species of pitcher plant grew densely alongside the stream at the edge of the wet meadow. **Bottom:** Boggy meadow extending inland from above stream to a rocky ridge. Small patches of forest are established on ground that is slightly elevated above the meadow (February 11, 1994).

Fig. 7. **Top:** Waterfalls below Camp 2. Habitat of a nonbreeding colony of *Stefania*. **Bottom:** Erosional remnants lying on nearby sandstone ledge. A specimen of *Liophis* was found in one of the standing pools with *Tepuihyla* tadpoles (February 11, 1994).

Fig. 8. **Top:** Camp 3, 1850 m elevation. **Bottom:** Interior of *Bonnetia* forest near river upstream from Camp 3 (February 17, 1994).

Fig. 9. **Top:** Helicopter view of Camp 4 (indicated by arrow, right of center), on stream feeding Angel Falls (out of sight on left). The open areas are boggy marsh with rock outcroppings (February 20, 1994). **Bottom:** Head of Angel Falls in the dry season (late February 1994), the time of minimal water flow. From here, the falls plummet unbroken, nearly 1000 m to the canyon below.

Fig. 10.   Panoramic view looking northerly to the interior of Auyantepui from its southern end.

above sea level, this was the expedition's highest station. However, the dry season had arrived and the stream level near camp was dropping fast. Probably for that reason, nothing was added to the species list. The visible herpetofauna comprised a few species of lizards (*Neusticurus*, *Tropidurus*) and frogs (*Tepuihyla* adults and tadpoles, a juvenile *Stefania*, and *Hypsiboas jimenezi* tadpoles).

Camp 5 was situated in the general area of Tate's ''2200 m. camp'' of the 1937–1938 expedition (maps in Tate, 1938a; Gilliard, 1941a). The most prominent landmark is a large distinctly shaped block of the ''first wall'', as seen by ourselves and photographed by Tate and Gilliard 56 years earlier (compare figs. 10, 11). This is the general locality for the only amphibians and reptiles obtained on the summit of Auyantepui by the 1937–

1938 Expedition: *Tepuihyla edelcae*, *Anolis chrysolepis planiceps*, *Tropidurus bogerti*, and *Mastigodryas boddaerti*. According to the AMNH catalog, W. H. Phelps collected all the herpetological specimens, in December 1937–February 1938.

SPECIES ACCOUNTS
FROGS

FAMILY BUFONIDAE
Oreophrynella cryptica Señaris
Figure 12

Oreophrynella quelchii Boulenger: Gines, 1959: 135, 138 (mention of a specimen from Auyantepui, with drawings of whole body, lateral head, hand, and foot).

Oreophrynella cryptica Señaris, ''1993'' [1995]: 178, fig. 1 (hand and foot). Holotype EBRG 2956

Fig. 10. Continued. AMNH–TERRAMAR Camp 5 is marked by widely spaced tents (showing as pale dots to the right of center), in the general region of Tate's "2200-meter Camp" of the 1937–1938 Expedition (February 27, 1994).

from sector este, cima del Auyan-tepui, Estado Bolívar, Venezuela (5°53′36″N, 62°29′12″W), 1750 m, collected February 10, 1994, by "J. C. Señaris and Petia Alcócerez [sic]."

MATERIAL: Stream below Camp 2, <1750 m: EBRG 2956 (holotype), MHNLS 12916 (paratype). See Señaris ("1993" [1995]) for description.

REMARKS

Although the little tepui toads of this genus are sometimes conspicuously common, only a few collectors have encountered *Oreophrynella* on Auyantepui. The first Auyantepui record was that of Gines (1959: 135, 138), who mentioned and illustrated a specimen under the name *O. quelchii*, without

providing further details. On August 19, 1974, Adrian Warren collected five specimens for the British Museum of Natural History. Museum records for BMNH 1976.169–172 state that the specimens were "caught sitting in temp. pools on or under rocks, or among grass roots"—"close to bust of Liberator".[7] Warren's specimens

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[7] This refers to a bust of Simón Bolívar (photo in Steyermark, 1967: pl. 5M), which "was placed by a party from the Universidad Central. The immediate neighborhood is all rocks and chasms, elevation about 2400 m." (Dunsterville, 1965: 169). "*El Libertador*" is used as a place name and is shown on maps in Dunsterville (1965) and Steyermark (1967). It is close to the southern edge of the summit, at the 2400 m mark shown on map 1, above Cardona and Heny's Access Crack *El Zanjón* (footnote 1), west-southwest of AMNH–TERRAMAR Camp 5.
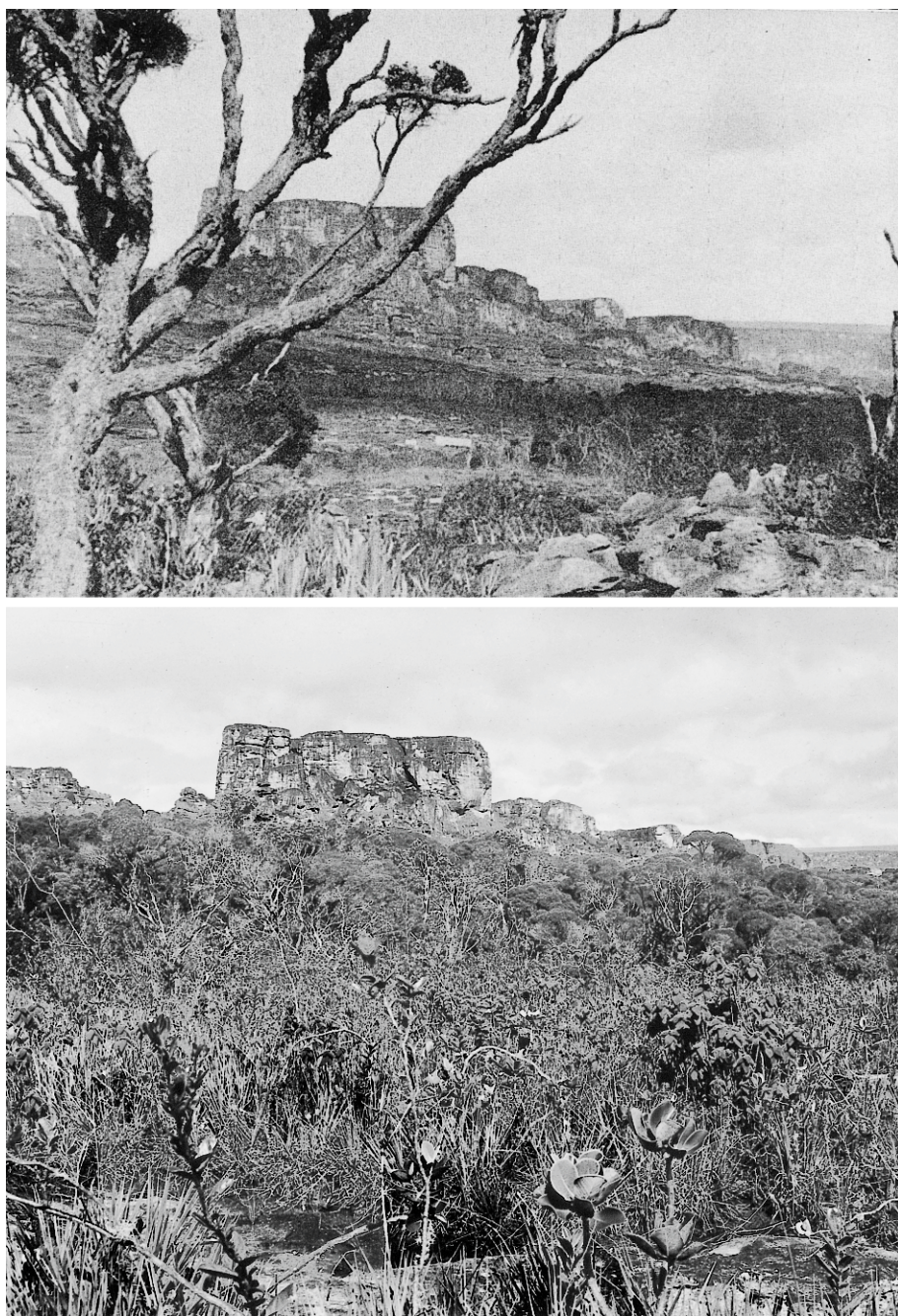
Fig. 11.   Two views from 1938 of a section of the "first wall"—"an irregular line of huge quartzite blocks"—which impeded pioneering exploration of Auyantepui during the Phelps Venezuelan Expedition of the American Museum of Natural History. **Top:** The 1937–1938 "Base camp for collecting parties stands in foreground, 2200 meters above sea level" (photograph reproduced from Tate, 1938b: 116). **Bottom:** Another view of the wall (a previously unpublished photograph by expedition member E. Thomas Gilliard), showing more clearly a huge block that helps place the relative position of the 1994 AMNH–TERRAMAR Camp 5 (compare figure 10).

Fig. 12. *Oreophrynella cryptica* Señaris. One of the two type specimens photographed at AMNH–TERRAMAR Camp 2.

probably were the basis for McDiarmid and Gorzula's (1989: 445) statement that an undescribed species of *Oreophrynella* occurs on Auyantepui.

Stefan Gorzula did not collect it during eight trips to Auyantepui (Gorzula and Señaris (1999: 254–255). However, in May 1987, Gorzula obtained a sample of *Oreophrynella* on the tiny summit of Cerro El Sol, an apparent erosional remnant of Auyantepui north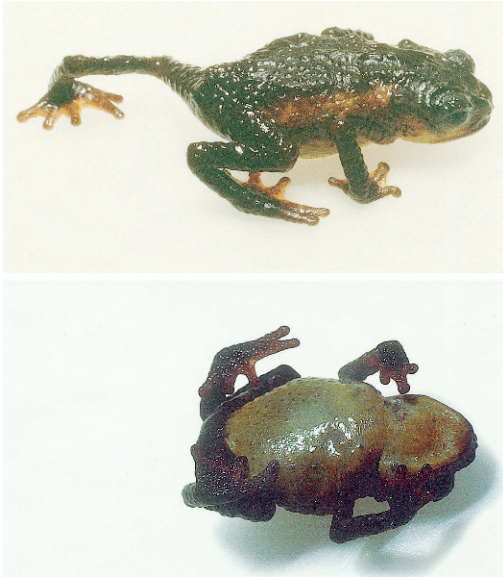-northeast of the main summit (see map 1). These were described as the new species *Oreophrynella huberi* by Diego-Aransay and Gorzula (''1987'' [1990]), who twice stated (pp. 234, 237) that the sample consisted of ''tres ejemplares'' (MHNLS 11147–11149), although Gorzula and Señaris (1999: 19, 255) said that five specimens were collected.

Only two specimens of *Oreophrynella* were found during the 1994 AMNH–TERRAMAR Expedition. One was caught by Petia Alcócer on February 9, the other by J. Celsa Señaris on February 10, 1994. The locality was in the gorge downstream from Camp 2, in an area of fractured sandstone and gigantic boulders.

The two specimens, said to be adult females, were named *Oreophrynella cryptica* by Señaris (''1993'' [1995]), who provided

drawings of the hand and foot in palmar and plantar view. They are about 21–22 mm SVL. Color in life was very dark reddish brown above, with a yellowish orange lateral stripe, and either yellow or yellowish orange below. An unlabeled color photograph of one specimen in mainly ventral view graces the cover of number 140 of the *Memoria de Sociedad de Ciencias Naturales La Salle*. One of the type specimens also is shown herein as figure 12.

Señaris noted that *Oreophrynella cryptica* resembles the neighboring *O. huberi* from Cerro El Sol in possessing large cranial crests. But *O. cryptica* differs in color (e.g., *huberi* was described as rufous-orange in life) and in having the skin tubercles smaller, flatter, and less dense. Morphological similarity and geography suggest the likelihood that they may be sister species.

FAMILY CENTROLENIDAE

Centrolenid frogs were neither seen nor heard during the AMNH–TERRAMAR Expedition. This was not surprising inasmuch as fieldwork was conducted in February, well before the start of the rainy season. On Auyantepui, centrolenids have been collected in June and August; only seven specimens have been reported from the summit, all collected by Ayarzagüena and Gorzula on the western arm of the mesa. These small, delicate arboreal frogs may be confined to the more extensively forested parts of the western summit. (If present in smaller patches of forest on the eastern side, they conceivably might spend drier parts of the year in deep, moist rock crevices, where they would be protected against desiccation.)

Venezuelan members of the family were monographed recently by Señaris and Ayarzagüena (2005), who recognized the following three taxa on Auyantepui. One species of *Centrolene* may be endemic to this tepui, whereas two *Hyalinobatrachium* are relatively widespread. All three occur in sympatry as stated by Señaris and Ayarzagüena (''1993'' [1994]: 124; 2005: 251).

Centrolene gorzulai (Ayarzagüena)

Centrolenella gorzulae Ayarzagüena, 1992: 19, fig. 3E (preserved holotype in dorsal view), fig. 4

(palmar view of hand). Holotype MHNLS 11221[♂] from Cerro Auyantepuy-Centro, Estado Bolívar, Venezuela (5°56′N, 62°34′W), 1850 m, collected August 26, 1983 by S. Gorzula.

Centrolene gorzulai (Ayarzagüena): Duellman, 1993: 35 (new combination and correction of incorrect original spelling).

Centrolenella auyantepuiana Señaris and Ayarzagüena, "1993" [1994]: 122, fig. 1 (hand and foot) + sound spectrogram. Holotype MHNLS 12482(♂) from sector centro oeste del Auyantepui, Estado Bolívar, Venezuela (5°54′N, 62°38′W), 1850 m, collected June 5, 1992 by J. Ayarzagüena.

Cochranella auyantepuiana: Myers and Donnelly, 1997: 16 (new combination).

Hyalinobatrachium auyantepuiana: Ayarzagüena and Señaris, "1996" [1997]: 12–13 (new combination).

Hyalinobatrachium auyantepuianaum: Myers and Donnelly, 1997: 71 (correction of spelling).

This species is known only from Auyantepui, based on a total of four specimens, one collected by Gorzula in August 1983 and three by Ayarzagüena in June 1992. See Señaris and Ayarzagüena (2005: 79–84, 299) for an account of this seemingly endemic species.

Hyalinobatrachium crurifasciatum Myers and Donnelly

Hyalinobatrachium crurifasciatum Myers and Donnelly, 1997: 9, figs. 7–10 (dorsal views of preserved holotype and paratopotype, drawings of hand and foot in palmar and plantar views, sound spectrographs and waveforms). Holotype AMNH A-131329 (ad. ♂) from forested stream at north base of Pico Tamacuari, 1160–1200 m, Sierra Tapirapecó, Amazonas, Venezuela (1°13′N, 64°42′W), obtained March 11–17, 1989 by C. W. Myers, M. A. Donnelly, and J. W. Daly. Myers and Donnelly, 2001: 20, fig. 13A (eye of holotype), 22, fig. 15 (replacement drawings of hand and foot of holotype).

C[entrolenella] sp. (cf. *orientalis*): Señaris and Ayarzagüena, "1993" [1994]: 124, from sector centro-oeste del Auyán-tepui (5°54′N, 62°38′W), 1850 m, June 1992 [two specimens fide Señaris and Ayarzagüena, 2005: 302].

Señaris and Ayarzagüena (2005) have shown that *Hyalinobatrachium crurifasciatum* is unexpectedly widespread in the Venezuelan Guayana, but that it has been repeatedly misidentified as *Centrolenella orientalis* or

Hyalinobatrachium orientale. For synonymy and a thorough species account, with an abundance of illustrations, see Señaris and Ayarzagüena (2005: 161–172, 274, 302).

The two specimens of *Hyalinobatrachium crurifasciatum* from Auyantepui were collected at 1850 m, in June 1992, in sympatry with *H. taylori* and *Centrolene gorzulai* according to Señaris and Ayarzagüena ("1993" [1994]: 124; 2005: 251). (However, slightly different coordinates are given for the three species on Auyantepui [Señaris and Ayarzagüena, 2005: 299, 302, 305).

Figure 110a in Señaris and Ayarzagüena (2005: 163) suggests the possible presence of a *bulla* in the webbing between fingers III and IV. We described this shallow bubblelike structure in *H. crurifasciatum* and the morphologically similar *H. eccentricum* (Myers and Donnelly, 2001: 22, figs. 12, 15), but the taxonomic distribution and significance of this easily overlooked structure remains to be determined.

Hyalinobatrachium taylori (Goin)

Centrolenella taylori Goin, 1968: 115, fig. 1 (drawings of holotype in dorsal view, side of head, hand and foot). Holotype BMNH 1939.1.1.65, from along New River, 750 ft elev., Guyana, collected by C. A. Hudson.

C[entrolenella] taylori: Señaris and Ayarzagüena, "1993" [1994]: 124, sector centro-oeste del Auyán-tepui (5°54′N, 62°38′W), 1850 m, June 1992 [one specimen fide Señaris and Ayarzagüena, 2005: 305].

Hyalinobatrachium taylori: Ruiz-Carranza and Lynch, 1991: 25 (new combination).

Hyalinobatrachium taylori is known from Auyantepui by a single specimen collected at 1850 m, in June 1992. It was found by Ayarzagüena in sympatry with *H. crurifasciatum* and *Centrolene gorzulai*. See Señaris and Ayarzagüena (2005: 221–232, 274, 305) for a full species account and illustrations.

SUPERFAMILY DENDROBATOIDEA
(FORMERLY FAMILY DENDROBATIDAE)
FAMILY AROMOBATIDAE
Anomaloglossus tepuyensis (La Marca)
Figures 13–19, 21

Colostethus, undescribed species from Auyantepui, Myers, 1997: 3; Myers and Donnelly, 1997: 24;

Grant et al., 1997: 8, 35, fig. 3B (photo of median lingual process).

Colostethus tepuyensis La Marca, ''1996'' [1998]: 49, fig. 11 (hand and foot). Holotype ULABG 2557 from a small stream ''entre Danto y Piñón, a casi una hora caminando desde Danto, en el trayecto desde Kamarata hasta las laderas del Auyantepui'', Estado Bolívar, Venezuela, 1650 m, collected May 28, 1988, by D. Lussner and H.-P. Reinthaler. Myers and Donnelly, 2001: 34 (allocation of previous references to this name).

Anomaloglossus tepuyensis (La Marca). Grant et al., 2006: 158 (new genus for species of *Colostethus* sensu lato with median lingual process).

This species was named in 1998 by La Marca on the basis of one specimen, an adult female from an elevation of 1650 m on the southeastern slope of Auyantepui. La Marca et al. (2002) subsequently mentioned the existence of several other specimens reported as a range extension of about 40 km to the NW (not ''NE'' as stated) of the type locality, at lower elevations of 390 and 445 m. in the Río Cucurital drainage near the northwestern base of Auyantepui (map 1).

Based on a sample of 33 specimens and several lots of tadpoles from the summit of Auyantepui, a fuller characterization of adult morphology and descriptions of the advertisement call and larva can now be given.

New Description

MATERIAL: 1.1 km NNE Camp 1, 1650 m: AMNH A-164834–164839 (larvae), EBRG 2649 (7 larvae). Camp 1, 1700 m: AMNH A-164817–164822, EBRG 2693–2699. Camp 3, 1850 m: AMNH A-164823, 164840–164843 (larvae), EBRG 2650 (8 larvae), 2700. Camp 4, 1600 m: AMNH A-164824–164833, 164844–164848 (larvae), EBRG 2651 (15 larvae), 2701–2709. All from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

DIAGNOSIS: A small frog (♂ about 21–24 mm, ♀ about 24–28 mm SVL) with an elongated median lingual process; no cloacal tubercles; fingers with keel-like lateral folds, broadest and best developed on fingers II and III; feet moderately webbed, toes with folded flaplike fringing; dorsal blotched pattern; an

incomplete oblique pale lateral line either present or absent. See Discussion and Other Comparisons.

MORPHOLOGY: Adult male *Anomaloglossus tepuyensis* about 21–24 mm SVL, adult females larger at about 24–28 mm SVL (table 1). Sexual maturity was judged by the presence of open vocal slits in males (open only on right in two specimens of 22 mm SVL), and by the presence of enlarged pigmented ova and convoluted oviducts in females.

Dorsal skin granular in life, becoming somewhat tuberculate on hind limbs (fig. 13), but skin much smoother in preservative; ventral skin virtually smooth in preservative, weakly granular on throats of some males. Dorsal skin forming a well-defined rounded, posteriorly projecting flap well above vent, which opens at upper level of thighs. Proximal thighs coarsely granular below vent, but no pronounced, symmetrically arranged tubercles in cloacal region.

Head slightly wider than long; greatest head width (between angles of jaws) 33%–39% of SVL. Snout sloping, rounded to bluntly pointed in profile, truncate to broadly rounded or bluntly pointed in dorsal and ventral view. Nares situated near tip of snout and directed slightly posterolaterally; nares visible from front, barely visible from above or below; posterior rim of naris bordered behind by a crescent-shaped, finely incised groove; posterior rim not raised but usually bearing a small tubercalike prominence posterodorsally to naris. Canthus rostralis slightly rounded; loreal region weakly concave, sloping slightly outward to lip. Interorbital region much wider than upper eyelid. Snout subequal to eye length; distance from center of naris to edge of eye/eye length = 0.55–0.74. Usually two low but inconspicuous postrictal tubercles. Tympanum usually inconspicuous, concealed posterodorsally by a diffuse supratympanic bulge; tympanum less than half of eye length.

Hand moderate, its length 24%–29% of SVL, 62%–82% of greatest head width. Relative lengths of appressed fingers III > IV > II > I; disc of finger I either failing to reach or else overlapping disc of finger II. Discs of all fingers moderately expanded; third finger disc in adults 1.4–2.0 times wider

TABLE 1
Size (in mm) and Proportions of *Anomaloglossus tepuyensis* La Marca, from the Summit of Auyantepui[a]

Character	N	Mean ± 1 SE	SD	CV (%)	Range
Snout-vent length (SVL)	7 ad.♂	22.47 ± 0.49	1.30	5.78	20.6–23.8
	6 ad.♀	25.58 ± 0.38	0.94	3.67	24.3–26.5[b]
	7 juv.♂	15.19 ± 1.24	3.27	21.56	12.0–20.7
	13 juv.♀	14.26 ± 0.59	2.12	14.90	11.5–18.8
Tibia length[c]/SVL	7 ad.♂	0.521 ± 0.008	0.022	4.20	0.49–0.55
	6 ad.♀	0.494 ± 0.009	0.021	4.29	0.47–0.51
	7 juv.♂	0.516 ± 0.004	0.012	2.27	0.50–0.53
	13 juv.♀	0.498 ± 0.006	0.021	4.21	0.46–0.55
Head width[d]/SVL	7 ad.♂	0.362 ± 0.004	0.011	3.10	0.35–0.37
	6 ad.♀	0.494 ± 0.005	0.011	3.37	0.33–0.35
	7 juv.♂	0.362 ± 0.007	0.018	4.94	0.34–0.39
	13 juv.♀	0.371 ± 0.003	0.011	3.00	0.36–0.39
Center naris to edge eye/eye length	7 ad.♂	0.658 ± 0.014	0.011	5.60	0.60–0.71
	6 ad.♀	0.650 ± 0.024	0.059	9.05	0.57–0.72
	7 juv.♂	0.679 ± 0.012	0.031	4.54	0.64–0.71
	13 juv.♀	0.659 ± 0.016	0.011	8.74	0.55–0.74
Hand length[e]/SVL	7 ad.♂	0.271 ± 0.004	0.011	4.03	0.25–0.29
	6 ad.♀	0.261 ± 0.005	0.012	4.53	0.25–0.28
	7 juv.♂	0.257 ± 0.004	0.011	4.24	0.25–0.28
	12 juv.♀	0.252 ± 0.002	0.008	3.01	0.24–0.26
Hand length/head width	7 ad.♂	0.747 ± 0.017	0.046	6.16	0.67–0.82
	6 ad.♀	0.772 ± 0.008	0.020	2.58	0.75–0.80
	7 juv.♂	0.710 ± 0.008	0.022	3.09	0.69–0.75
	12 juv.♀	0.677 ± 0.009	0.030	4.47	0.62–0.71
Width 3rd-finger disc/finger width below disc[f]	7 ad.♂	1.558 ± 0.056	0.138	8.87	1.40–1.75
	6 ad.♀	1.744 ± 0.070	0.172	9.87	1.50–2.00
	5 juv.♂	1.450 ± 0.079	0.177	12.22	1.25–1.67
	12 juv.♀	1.382 ± 0.044	0.153	11.05	1.25–1.75

[a] N = 33 specimens, pooled from AMNH–TERRAMAR camps 1, 3, and 4.

[b] The female holotype is larger, measuring 28.3 mm SVL fide La Marca (''1996'' [1997]).

[c] Tibia length is the shank measured from the heel to the convex surface of the knee (with limb segments flexed at right angles), roughly approximating length of the tibiofibula.

[d] Greatest head width as measured between jaw articulations.

[e] Hand length measured from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger.

[f] Digit width measured near distal end of penultimate phalanx.

than distal end of adjacent phalanx, average width greater in females. Third finger broadly keeled or fringed but not swollen. Keel-like lateral folds on fingers usually low and inconspicuous except on finger III and, to a lesser extent, finger II; these keel-like structures appear to be tightly folded ventromedially around the fingers—with the edge of the fold recurved in a groove along the ventral side of the finger, usually best developed on medial side of finger III (figs. 14, 21); no obvious sexual dimorphism in finger keeling, which is also detectable but inconspicuous in small juveniles.

Base of palm with large median metacarpal tubercle, generally distally flattened, but in some specimens slightly cordiform or rounded; smaller elliptical inner metacarpal tubercle on base of first finger; one or two low, rounded subarticular tubercles (one each on fingers I and II, two each on fingers III and IV, with distal tubercle tending to be inconspicuous on IV). A faint outer metacarpal fold extending from lateral side of

Fig. 14. *Anomaloglossus tepuyensis*. Right hand and right foot of AMNH A-164828 ♂, 22 mm SVL, showing maximal development of keel-like lateral folds on fingers (see also fig. 21), and folded flaplike fringes on toes. Scale line = 1 mm.

Fig. 13. *Anomaloglossus tepuyensis*, showing color variation in life. Above, an adult male from Camp 1 (AMNH A-164818, 21 mm SVL); below, an adult male from Camp 4 (AMNH A-164824, 24 mm SVL).

fourth finger to the large palmar tubercle, sometimes bearing a small tubercle. No ulnar tubercles or fold. Often a small tubercle situated below palmar tubercle toward lateral side of wrist (fig. 14). No fleshy supracarpal pad atop wrist.

Hind legs moderately long, with heel of adpressed limb reaching from between eye and snout to beyond snout; tibia 49%–55% of adult SVL, relatively shorter in females (table 1). Relative lengths of appressed toes IV > III ≥ V > II > I; first toe short, reaching or failing to reach base of subarticular tubercle of second toe. Toe discs moderately expanded (sometimes only weak-
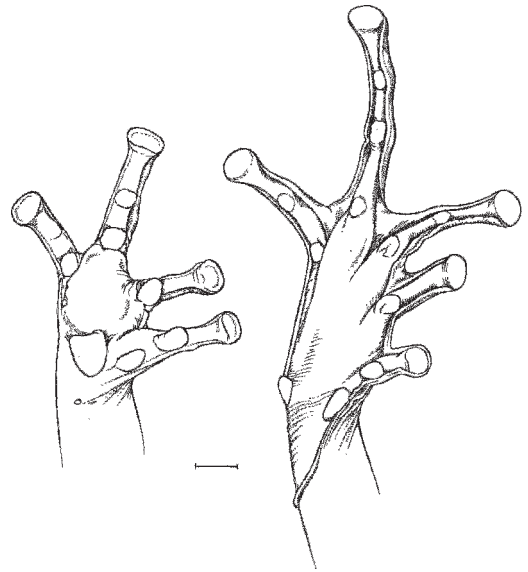
ly expanded on first toe), subequal or larger than finger discs. Feet moderately webbed, the webbing distally continuous with distinct lateral fringing on all toes; the lateral fringing is folded downward along sides of toes ("folded flaplike fringes", see Discussion and fig. 14). Modal webbing formula of adults: **I** 1½–2½ **II** 1½–3 **III** 2½–3½ **IV** 4–2½ **V**. One specimen has a short first toe with only the first phalanx (disc) free of web; otherwise there is slight variation only between the third to fifth toes: **III** (2–3)–(3½–4) **IV** (2–4)–(2–2½) **V**.

A small, usually elliptical inner metatarsal tubercle, and a small, usually round outer metatarsal tubercle subequal in size (either may be equal to or larger than the other). One to three nonprotuberant subarticular tubercles (one each on toes I, II, two each on III and V, three on IV). The fringe along outer edge of the fifth toe is continuous with a weak outer metatarsal fold that terminates at the outer metatarsal tubercle. Distinct fringe along free edge of first toe is continuous with an oblique tarsal fold extending proximolaterad on the distal half of the

tarsus (fig. 14); the nearly straight tarsal fold terminates abruptly in a curved tuberclelike structure (similar to condition shown in fig. 20A [*A. tamacuarensis*]).

Teeth present on maxillary arch. Tongue longer than wide; free posteriorly, with rounded margin; a usually prominent median lingual process is either pointed or distally rounded and is present in all specimens including juveniles. Vocal slits large, each extending from edge of tongue nearly to angle of jaw.

COLORATION: In life (fig. 13), the dorsal ground color of *Anomaloglossus tepuyensis* ranged from grayish brown to orangish brown and bronzy brown in adults, mostly orange-brown in subadults, and brown or gray-brown with conspicuous white flecking in small juveniles—all with irregularly pigmented dark brown or blackish brown markings (obscure or indefinite only in a few specimens) usually arranged in the following pattern (fig. 15): (1) a dark interorbital bar, often with a slightly concave (sometimes straight) anterior margin, with or without a posteriorly produced apex; (2) a V-shaped to cordiform (transversely straight in a few) median dark blotch between arms, sometimes connected with the following; (3) a transverse pair of smaller paravertebral blotches at midbody—these markings sometimes fused with the anterior blotch to form a vaguely X-shaped dorsal mark; (4) usually a single small median posterior blotch near end of body.

The dorsal dark markings listed above are formed from irregular distributions of melanophores and usually contain pale areas of brown ground color; the paired paravertebral blotches and posterior median blotch often are circular with pale centers (ocellus-like). The snout anterior to the interorbial marking is brown like the rest of the dorsum, often with one or a few small dark marks or blotches, but the top of the snout is unmarked in about 27% of the sample and is never darkened overall. The eyelids occasionally have a few unpigmented dots but are usually unicolor except where crossed by the interorbital bar.

An incomplete pale oblique lateral line (in life, pale brown to blue) present or absent; extending from groin and terminating dorso-

laterally behind arms when distinct, but often poorly defined and broken, or completely absent (frequently present on one side but absent on the other). A blackish stripe or face mask along side of snout passing through eye and widening above shoulder, tending to continue posteriad just below dorsum but changing along its lower edge on flanks to indefinite brown mottling or reticulum with irregular or ill-defined pale spots of bluish white, pale blue, or pale bronze, this area interrupted or not by a pale oblique lateral line of similar color. Pale spotted pattern of flanks extending to ventrolateral edge of venter (no hint of a pale ventrolateral stripe).

Black face stripe sometimes continuous around tip of snout, which otherwise varies from uniform brown to pale spotted. Upper lip pale to dark brownish, variously and indefinitely marked with small pale areas or spots (sometimes bluish white) or irregular dark blotching. Often a bronze (white to pale brownish in preservative) stripe extending obliquely from eye to forearm, just below the postocular widening of the black face mask; this pale postocular stripe distinct in some specimens, virtually absent in others in which it may lack contrast with a pale lip or else be interrupted and obscured by infusion of dark pigment.

Forearms and hind legs brown with distinct to vague dark bars or irregular spots, and with a tendency toward orange suffusion on the thighs. Often a dark brown stripe along anterior edge of upper arm, sometimes extending forward to corner of mouth, with a similar horizontal brown stripe varying from distinct to absent along anterior surface of thigh. Posterior thigh brown with indefinite pattern of pale flecks or small spots, only rarely with an ill-defined horizontal brown line or stripe on one or both sides (EBRG 2695, 2696, 2701). Some specimens have conspicuous pale spots or crossbands on the joints of the digits of hands and feet, but this pattern usually vague or digits uniformly pigmented. Digit tips noted as being ''white marked'' in life, but in preservative all digital scutes tending to be completely dark above, only occasionally with a pair of small inconspicuous pale spots.

Ventral color varies ontogenetically in life: (1) small juveniles are green or greenish gray, with silvery white flecking; (2) larger juveniles
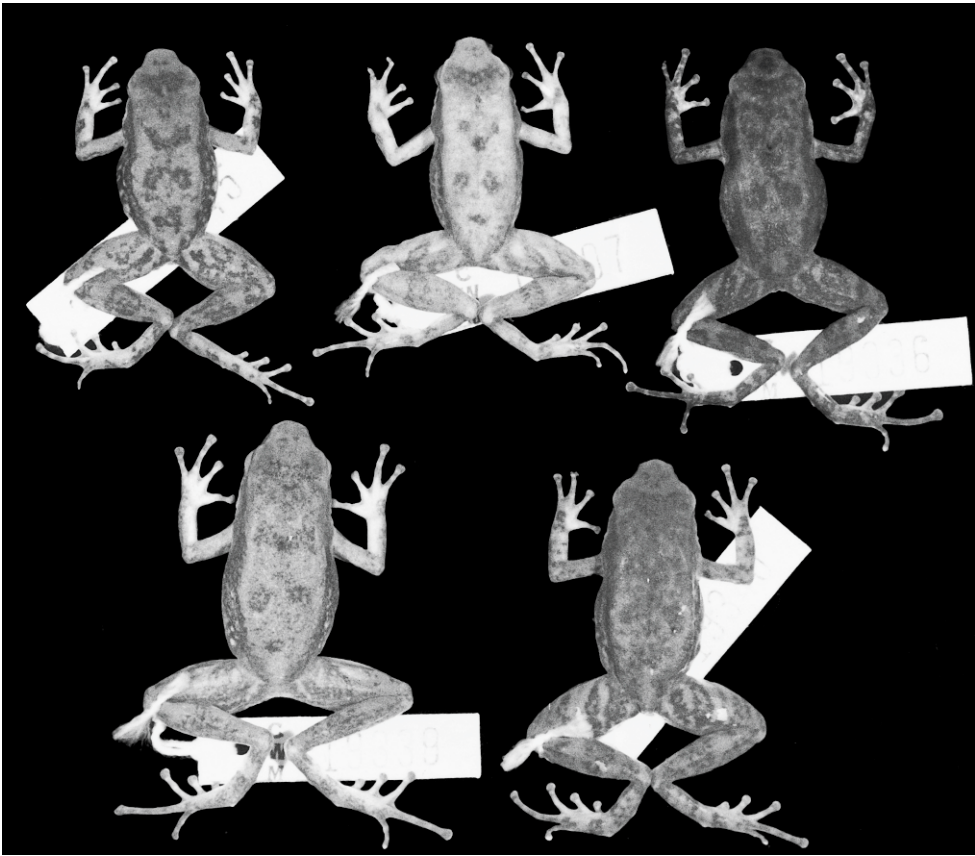
Fig. 15. *Anomaloglossus tepuyensis*, showing variation in dorsal color pattern. **Top, males:** Left to right: EBRG 2693, AMNH A-164823, 164824. **Bottom, females:** AMNH A-164827, EBRG 2701.

had all ventral surfaces orange except green-ish on underside of thigh and shank and gray on palms and soles; (3) a few adult males at camp 1 were greenish gray ventrally becoming yellowish green under the limbs, whereas an adult male at camp 3 had the throat and chest gray with conspicuous white flecking that continued along the sides of the belly, the belly and undersides of limbs otherwise bright greenish yellow; ventral color at camp 4 (including adult males and females) was mostly gray with white flecking on throat and/or chest, turning bright greenish yellow or even (in a few) golden yellow posteriorly and under limbs, but a few adults had even the throat and chest bright colored like the belly and undersides of limbs. (Some degree of sexual dimorphism in ventral coloring is probable, but specimens could not be reliably sexed in the field.)

In preservative, ventral surfaces (fig. 16) vary from pale tan with a weak suffusion of melanophores, most dense on throat, to overall darker brown owing to dense suffusion of melanophores, which sometimes form a reticulum around pale spots. The axillary region tends to be weakly pigmented or unpigmented (but not forming in life a flash mark differently colored from ventral surfaces), this area being continuous ventrally with a small unpigmented area proximal to the arm insertion, which stands out as a small distinct spot (except in specimens with the palest venters). Undersides of hands and feet dark brown.

Iris pale bronze or orange-bronze, darkened with black suffusion, sometimes paler below pupil than above; pale bronze or orange-bronze pupillary ring usually interrupted by a black tick mark below pupil.
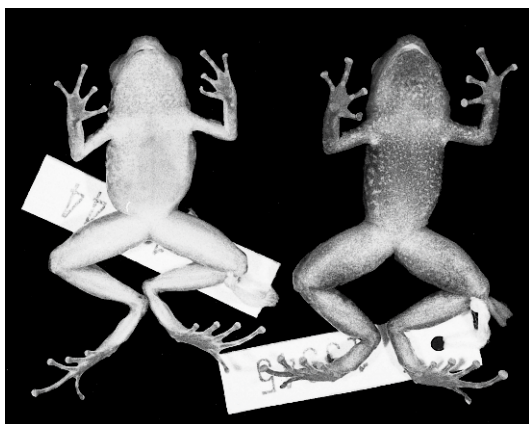
Fig. 16. *Anomaloglossus tepuyensis*, showing variation in ventral pigmentation. Left to right: AMNH A-164818♂, 164829♂.

Nictitating membrane translucent, with brown pigment along free edge.

TADPOLES

The following description is based on *Anomaloglossus tepuyensis* larvae in stage 36 (fig. 17), followed by notes on ontogenetic change. See table 2 for additional measure-ments. See Natural History and Vocalization for larval habitats.

HABITUS AND PROPORTIONS: Head and body elliptical and rounded at both ends in dorsal view; midbody width 70%–75% of head-body length. Head-body depressed (midbody depth 76%–80% of midbody width), somewhat flattened dorsally and ventrally. Snout rounded in dorsal and lateral view. Eyes dorsal, directed laterally; interorbital distance (between centers of pupils) 3.9 mm. Nares dorsal, directed laterally; internarial distance (between centers of nares) 2.6 mm. Nares approximately equidistant to tip of snout and anterior edge of eye. Spiracle sinistral, directed posterodorsally, positioned low on body, a tube (1.5–2.1 mm long) with the medial wall attached to the body; opening 6.9–7.6 mm from snout, at 55%–58% of head-body length. Vent tube dextral to caudal fin.

Lateral line system with a supraorbital and infraorbital branch originating from near upper labium and connecting behind eye. Angular branch originating ventral to the infraorbital branch near the upper lip and continuing posteriorly as the middle body branch; a branch connecting the angular
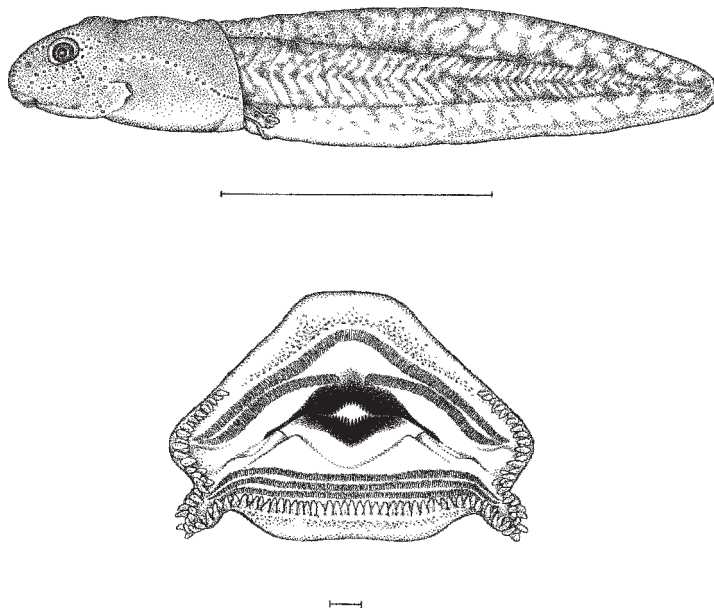

Fig. 17. *Anomaloglossus tepuyensis*. Stage-36 tadpole and mouthparts of same specimen (AMNH A-164837). Scale lines = 10 mm above and 1 mm below.

TABLE 2
Measurements (in mm) of *Anomaloglossus tepuyensis* Tadpoles
(Values are ranges, followed below by means ± 1 SD when N > 2)

Stage	N	Total length	Head–body length	Body width	Body depth	Tail depth	Oral disc width
25	29	13.0–25.9	4.4–9.9	2.5–6.6	1.8–5.4	2.3–5.8	1.4–2.7
		20.98 ± 2.80[a]	8.01 ± 1.22	5.16 ± 0.81	4.13 ± 0.70	4.09 ± 0.72[b]	2.25 ± 0.29
26	7	25.7–28.2	9.9–11.1	5.8–7.6	4.2–6.4	4.2–6.0	2.6–2.9
		26.88 ± 0.98[c]	10.37 ± 0.49	6.56 ± 0.69	5.17 ± 0.80	4.89 ± 0.66	2.73 ± 0.11
27	11	27.2–29.5[d]	9.4–11.6	5.5–7.4	4.2–6.1	4.3–6.0	2.6–3.1
		28.49 ± 0.72[d]	10.76 ± 0.67	6.79 ± 0.61	5.29 ± 0.61	5.29 ± 0.58[d]	2.91 ± 0.14
29	3	28.5–31.8	10.6–11.8	7.2–7.5	5.4–5.6	4.9–5.8	2.7–3.0
		30.27 ± 1.67	11.32 ± 0.63	7.3 ± 0.17	5.47 ± 0.12	5.47 ± 0.49	2.83 ± 0.15
30	1	37.8	12.5	8.2	6.6	7.2	2.9
31	1	36.1	12.6	8.7	6.0	6.9	3.0
32	3	29.3–31.1[e]	10.6–12.8	7.2–8.8	5.7–7.1	6.0–7.7	3.0–3.4
		–	11.62 ± 1.12	7.87 ± 0.83	6.37 ± 0.70	6.70 ± 0.89	3.17 ± 0.21
33	1	35.2	12.3	8.4	6.2	6.0	3.3
36	2	39.4–40.1	12.6–13.1	8.8–9.8	6.7–7.9	6.9–7.8	3.1–3.2
37	1	–[f]	12.5	9.6	7.3	7.8	3.2
40	1	–[f]	13.4	10.0	7.7	8.3	3.3

[a] N = 25 (four larvae with broken or incomplete tails).
[b] N = 28 (one larva with damaged tail).
[c] N = 6 (one with broken or incomplete tail).
[d] N = 10 (one with broken or incomplete tail).
[e] N = 2 (one with broken or incomplete tail).
[f] Tail broken or incomplete in only specimen.

branch to the infraorbital branch posterior to the eye, this branch continuing ventrally onto the ventral surface of the body anterior to the spiracle. Superior trunk branch continuing onto tail in the dorsal fin just above the musculature, for about 25% of tail length.

Tail 67%–68% of total length, with low fins, maximal height approximately equal to body depth; dorsal fin not extending onto body; dorsal fin higher than ventral fin; tail tip rounded, extending slightly past tip of musculature.

PIGMENTATION: In preservative, head-body brown dorsally and laterally; ventral body clear, flecked with melanophores and some light brown blotches; tail musculature tan with irregularly shaped dark brown blotches and flecks; ventral fin lacking pigment near body, with dark blotches and flecks posteriorly; dorsal fin dark near body, with flecks and blotches posteriorly.

MOUTH PARTS: Mouth ventral. Oral disc laterally emarginate. Labial teeth in 2/3 rows; anterior rows nearly equal in length, A2 row with median gap; posterior rows 2 and 3 equal in length, slightly longer than P1;

P3 not as heavily keratinized as P1 and P2. Upper jaw sheath a broad arch with slender lateral processes and blunt serrations; lower jaw sheath V-shaped with blunt serrations like those on upper jaw. Marginal papillae from lateral edges of upper labium in single row above emargination; in weak double row below emargination and then single across middle of lower labium; papillae on lower labium more pointed than those on upper labium.

ONTOGENETIC CHANGES: Changes in body size are summarized in table 2. The ratio of head-body length to total length decreases from 38% in stage-25 tadpoles to 31% in stage-36 specimens. Body width increases during development relative to oral disc width; the ratio of oral disc width to body width changes from 55% in stage-25 tadpoles to 42% in the single stage 40-specimen. The lateral line system is not visible in several stage-25 tadpoles, but is distinct by stage 29.

In several stage-25 tadpoles, labial tooth row P3 is lightly keratinized (this row commonly is the last to be keratinized in dendrobatoid larvae [e.g., Myers et al., 1978;

Fig. 18.   John Daly looking up from bottom of deep sandstone crevice near Camp 1 (see also fig. 4). *Anomaloglossus tepuyensis* was calling from a shallow stream running along the bottom of the crevice (February 6, 1994).

Donnelly et al., 1990; Myers and Donnelly, 1997]).

There is some variation in the marginal papillae on the lower labium (a single row or double rows), but we did not detect ontogenetic change in the character. (Ontogenetic change from one to two rows seems to be common among dendrobatoids.)

NATURAL HISTORY AND VOCALIZATION

As would be anticipated from the fringed toes and moderately webbed feet, *Anomaloglossus tepuyensis* is a riparian frog. At Camp 1, a few individuals were found in vegetation near the river's edge below camp, but they were most common in and along small shallow, sand-bottomed streams within deep sandstone crevices near camp (figs. 4, 18).

They would dive into shallow pools and attempt to hide on the bottom; they were calling infrequently but were difficult to approach and were not recorded at this locality. They were somewhat easier to find along a forest stream at Camp 4, either active or under rocks, and a recording was obtained.

Nurse frogs transporting tadpoles were not seen. Three lots of free-living larvae were dip-netted from pools near three camps. Tadpoles were not collected where frogs were found at Camp 1, but a series of larvae in stages 25–40 were taken from a pool in the river 1.1 km NNE of Camp 1. At Camp 3, larvae in stages 25–33 were taken from an isolated rocky sandstone pool, about 50 cm deep, next to a stream. At Camp 4, larvae in stages 25–32 were netted in the backwater of
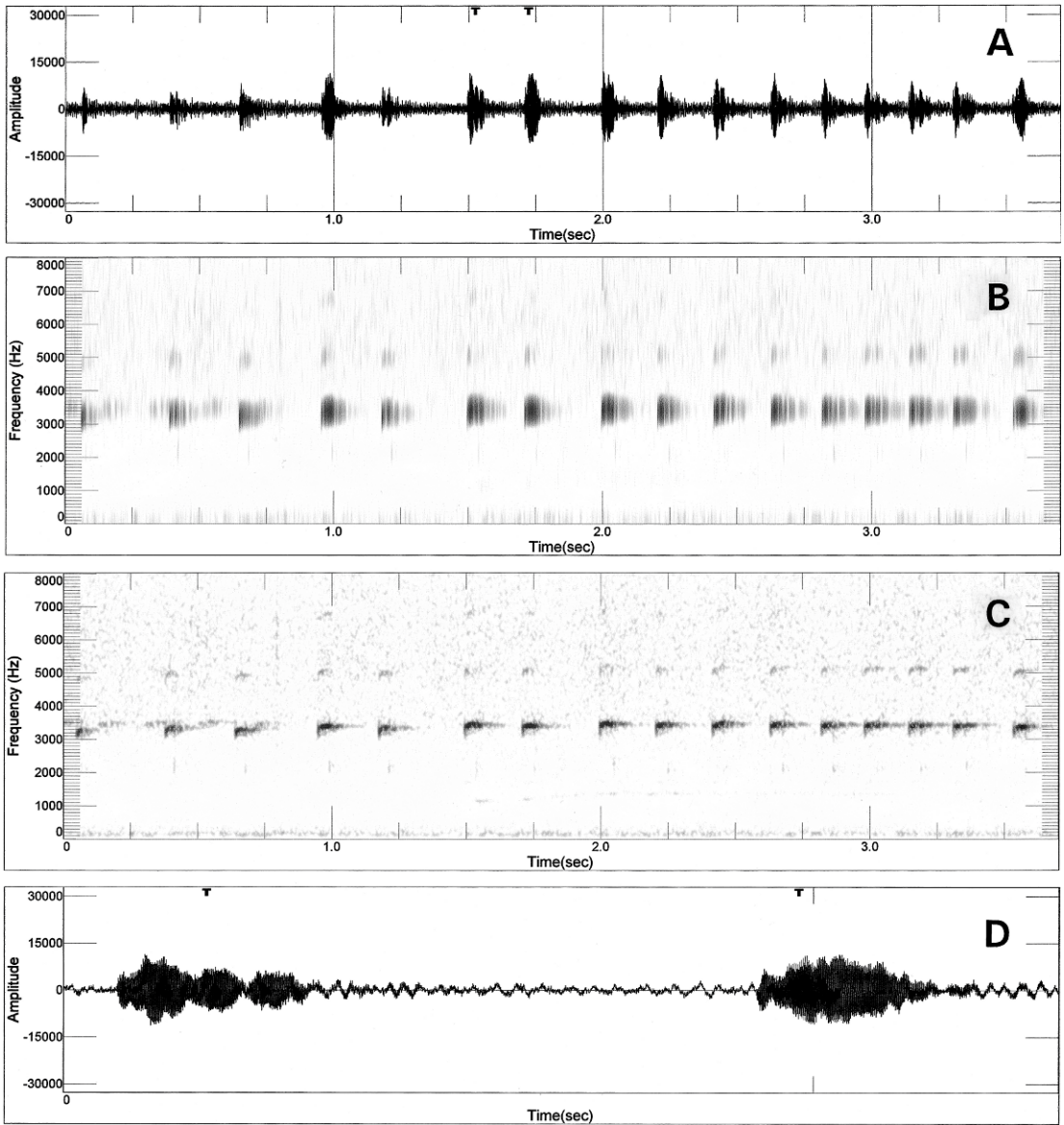
Fig. 19. Vocalization of *Anomaloglossus tepuyensis*. A complete call sequence of 16 notes, given in 3.7 sec. **A:** Waveforms (T = tagged notes, see below). **B:** Wideband (323 Hz) spectrogram. **C:** Narrowband (63 Hz) spectrogram. **D:** Expanded waveforms of two notes tagged (at sixth and seventh notes) in first panel; note durations = 0.63 and 0.73 sec; time between notes = 0.14 sec. (Unvouchered recording of specimen [associated with AMNH A-164824–164833, EBRG 2701–2708] calling from boggy area near Camp 4, February 21, 1994, 10:14 a.m.; air temperature 18.8°C. AMNH herpetology reel 263: 3.)

a river. Tadpoles of *Hypsiboas jimenezi* were in the same pools as *Anomaloglossus* near Camp 1 and at Camp 4.

A tape recording was made of two or more males calling at Camp 4. The advertisement call (fig. 19) is a short train of 14–22 notes ($\bar{x}$ = 16.0 notes, N = 8), which are heard as a series of rapid ''peeps'' given at a variable intracall rate of about 4–7 notes per sec. Calls begin slowly and then speed up. In the

illustrated call, the interval is 0.36 sec between the initial two notes and 0.07–0.13 sec between the last several notes. Note length varies from about 0.06 to 0.10 sec within the call.

Narrowband analysis shows a very slight rise in frequency at note initiation, after which the frequency is narrowly tuned and remains nearly flat, varying from about 3270 Hz to 3580 Hz. A few simultaneously calling males show nonoverlapping differences of about 300 Hz. Also, there is slight internote variation in frequency within a call. Waveforms and wideband spectrographic analyses show individual notes within single calls to vary from nonpulsatile to weakly pulsatile, with 2–4 distinct pulses per note.

COMPARISON WITH THE DESCRIPTION OF THE HOLOTYPE OF *ANOMALOGLOSSUS TEPUYENSIS* (LA MARCA)

We recognized in 1994 when collecting apparently the first specimens of a dendrobatoid from the summit of Auyantepui that we were sampling an unnamed species (Myers, 1997). La Marca (''1996'' [1998]) has independently provided the specific name *tepuyensis*, based on a specimen collected in 1988 at 1650 m elevation on the southern slopes of Auyantepui. It seems probable that only a single species is involved, although one aspect of the described color pattern of the holotype of *tepuyensis* does not agree with the observed variation in summit material. Some relevant points for comparison, from La Marca's (''1996'' [1998]: 52–53) description of the holotype (specimen not examined by us), include the following (free translation):

> Dorsum dark brown with irregularly distributed blackish marks. These are very small and inconspicuous, so the dorsum at a glance shows no evidence of color pattern. Abundant blackish and some dirty whitish marks on the upper part of the head, making the head seem darker than the rest of the dorsum. This pattern closes behind in a V-shape, from the posterior part of the eyelids with the apex on the occipital region. The eyelids show nearly circular marks that perhaps correspond in life

> with flat tubercles …. Arms and forearms lighter than the dorsum. The first with a dark brown band that extends to the posterior part of the lips, the second with dark brown marks not forming bracelets …. There is a dark longitudinal stripe on the posterior part of the thighs. Upper part of thighs and tibias the same as the dorsum; there is a dark spot on the middle of the tibia that does not form a [cross]band …. [In the recently preserved holotype]: Dorsal surfaces dark brown, the ventral surfaces yellowish, with intense yellow color on the posterior part of the venter and undersides of thighs, tibias and forearms. There is a yellowish cream band from the loreal and infratympanic regions to near the insertion of the front leg.

The posterior V-shape of the dark head of the holotype obviously corresponds to the posteriorly projecting rear edge of the interorbital bar in many of our specimens, but none of the 33 specimens from the summit collections has the overall head darker than the body; the interorbital bar, when present, is always distinct from any anterior blotching atop the snout (which is unmarked in over 25% of the sample). Except where crossed by the interorbital bar, the eyelids are unicolor brown except in occasional specimens having a few or several pale dots on each eyelid, possibly but not clearly equivalent to the *manchitas casi circulares* of the holotype. The dorsal markings in summit specimens are somewhat variable but nonetheless are arranged in a distinct pattern as described above and as shown in figure 15. However, a few summit specimens are virtually patternless (fig. 15, lower right) and in that regard may approach the condition of the holotype.

The holotype has a few dark marks atop the lower arms and on the tibia that do not form crossbands, and the thighs are pale above; the summit specimens tend to have the forearms and hind legs crossbanded, but it is a tendency only and the markings may be vague. Only three summit specimens were noted as having an ill-defined horizontal brown stripe on the rear of the thigh, and two of these had it on one limb only.

The recently preserved holotype had yellow ventral surfaces becoming intensely yellow posteriorly and on the undersides of

the limbs; such coloration occurred in a few summit specimens. The yellowish band from the loreal region to the forearms likewise occurs within the variation of the summit specimens, some of which have the labial and infratympanic region pale to the forearm, whereas others do not (fig. 13).

La Marca stressed the absence of a pale oblique lateral line as a diagnostic character of *tepuyensis* (he also mentioned its *presence* in the second paragraph of the diagnosis, but reaffirmed the absence in the detailed description following). An oblique lateral line is present in some summit specimens (fig. 13), but it is rarely sharply defined, being often vague or broken and it is frequently absent.

La Marca (''1996'' [1998]: 49, 50) described the tip of the snout as being broadly rounded (*ampliamente redondeada*) in dorsal view; however, he inconsistently described the snout tip as being laterally rounded (*redondeada en vista lateral*) in the diagnosis, but laterally protuberant (*protuberante en vista lateral*) in the description. In the summit sample, the sloping snout in profile varies from rounded to bluntly pointed, and in dorsal view from from truncate to broadly rounded or bluntly pointed.[8]

In summary, although the coloration and color pattern of the holotype of *Anomaloglossus tepuyensis* is not typical of summit specimens, most aspects of color and pattern seem to fit within observed variation in the 33 specimens from the summit of Auyantepui. Only the overall darker head of the holotype seems inconsistent in this regard. The female holotype was measured at 28.3 mm SVL, which at first glance seems well outside the range for six summit females (24.3–26.5 mm). However, leaving aside the confounding

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[8] Such variation in snout shape seems more or less normal at least in some sections of ''*Colostethus*'' sensu lato. La Marca used the conditions of ''truncado o casi truncado'' vs. ''no truncado'' in the second couplet of a key to eastern Venezuelan *Colostethus*, but the character is unreliable in these frogs. In addition to normal variation, snout shape is sometimes altered in preservation, as when old, poorly fixed specimens have been crowded in a container. Snout shape also can be subjectively variable depending on angle of view—whether viewed dorsally at a right angle to the long axis of the body (as in fig. 15), or dorsally at a right angle to the upwardly inclined head.

effects of slight differences in measuring technique between investigators (as well as normal measuring error), adding the holotype gives a total range of 4 mm for adult females, which does not seem excessive for frogs of this size.

Therefore, so far as we can judge at this time, our population samples of *Anomaloglossus* from the summit of Auyantepui are conspecific with the holotype of *A. tepuyensis*. If the additional specimens recently mentioned by La Marca et al. (2002) are indeed of this species, *Anomaloglossus tepuyensis* has a noteworthy elevational range of 390–1850 m in the Auyantepui area and is not strictly a ''tepui species''.

DISCUSSION AND OTHER COMPARISONS

The following comparisons and discussion of character states were written prior to publication of the systematic revision of dendrobatoid frogs by Grant et al. (2006). The only substantive changes made herein were to substitute new and revived generic names (*Anomaloglossus*, *Allobates*, and *Hyloxalus*) for the name *Colostethus* sensu lato wherever appropriate.

La Marca (''1996'' [1998]: 50) stated in the original diagnosis that *Anomaloglossus tepuyensis* differed from all other ''*Colostethus*'' in the Venezuelan Guayana except *Anomaloglossus shrevei* in having thick lateral keels (*quillas laterales gruesas*) on fingers II and III and folded flaplike fringes (*repliegues laterales*) on the toes—two characters evidently meant to be used in combination. In the same paper, La Marca noted that the curious *repliegues* on the toes also characterize *Anomaloglossus ayarzaguenai*, *A. guanayensis*, and *Allobates sanmartini* as well as *Anomaloglossus shrevei* and *Anomaloglossus tepuyensis*, but he overlooked their presence in *Anomaloglossus parkerae*; to this list should also be added *Anomaloglossus tamacuarensis*, which was not available to La Marca.

Standard outline drawings of the feet of all seven of these species have been published (Rivero et al., 1986, fig. 4; Meinhardt and Parmelee, 1996, fig. 3; Myers and Donnelly, 1997, fig. 12; La Marca, ''1996'' [1998], figs.
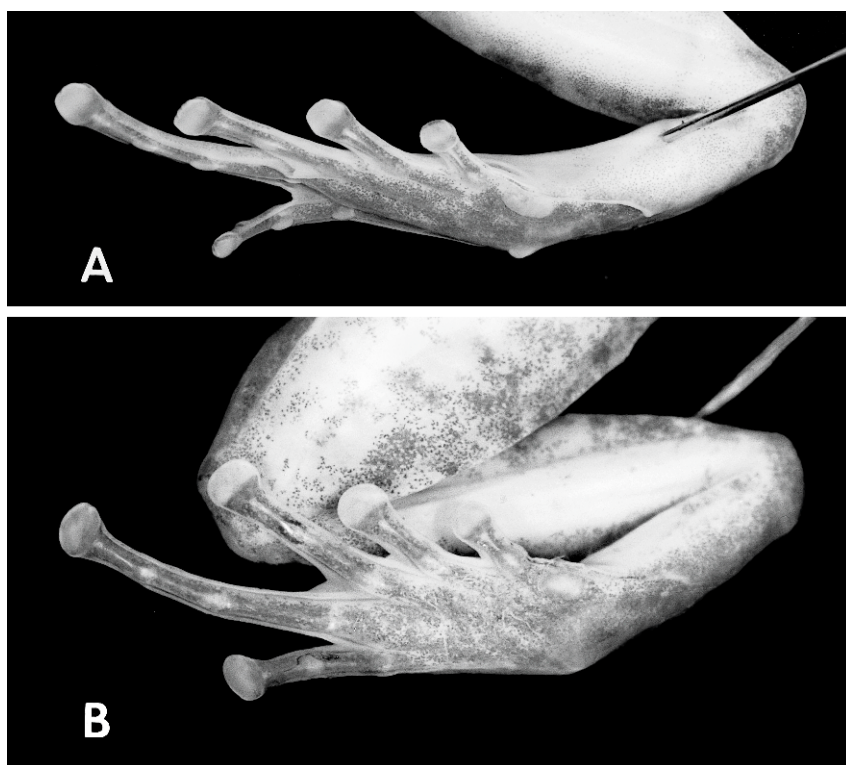
Fig. 20. Hind foot structure of two species of *Anomaloglossus* characterized by folded flaplike fringes on toes. **A.** *A. tamacuarensis*, with well-developed flaplike fringes (AMNH A-131342, paratopotype). **B.** *A. parkerae*, with relatively weak flaplike fringes (KU 167328, paratype). See also figure 14 (*A. tepuyensis*).

2, 4, 7, 10, 11)—but none of the diagrammatic drawings shows the folded nature of the toe fringes! The foldings (perhaps considered artifacts of preservation in some cases) were straightened out when the diagrammatic drawings were made. We here attempt to rectify the situation with new drawings (figs. 14, 21) and a few photographs (fig. 20). The following discussion deals first with the toe fringing and then with the finger fringing.

Enrique La Marca is to be credited for being the first worker to clearly define different states of toe fringing in dendrobatoids and to use the character for differentiating species. La Marca (1994: 6) defined the "terms keel, fringes and flaps [to] indicate whether the emarginations are very low, conspicuous but not folding around toes, and folding around toes, respectively". In a subsequent definition (La Marca,

"1996" [1998]: 7), "*rebordes membranosos* ('flaps')" were equated to the aforesaid "fringes" and "*repliegues* ('folds')" to his original "flaps".

The difference between low lateral keels and fringes can be subtle and influenced by desiccation in preserved material. In dendrobatoids, broad or otherwise well-defined lateral fringes or flaps seem always to be narrowed extensions of emarginate foot webbing, and some folding of webs necessarily follows when the toes are pressed together, but the folding, at least on the longest toes, seems to be a constant condition in certain dendrobatoids in the Venezuelan Guayana—although the actual taxonomic distribution of the character remains to be determined.[9] In any case, **folded flaplike fringes** (*repliegues*

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[9] The character does not seem to define a single monophyletic group of dendrobatoids. A folded

arropándolos) will be our preferred term for this character state, in which the folding seems constant in preserved specimens and presumably also in life.[10]

La Marca (see above) called attention to the presence of *quillas laterales gruesas* (thick lateral keels) on fingers II and III of *Anomaloglossus shrevei* and *A. tepuyensis*, and they also occur in *A. parkerae* and *A. tamacuarensis*. Thick keels occur on all the fingers in these species but tend to be broadest and most evident on the second and especially the third fingers. The inner (medial) edge of this structure on the ventral side of finger III often is especially well defined by a recurved edge in a deep groove—as though a much wider fringe had folded over and adhered to the ventrolateral edge of the finger (fig. 21). For this reason, we believe that the term **keel-like lateral fold** might prove useful (we previously used the term ''fleshy keel-like fringe'' [Myers and Donnelly, 1997: 19]). This is an interesting structure that needs both histological examination and a survey for taxonomic distribution; the character is easily overlooked when minimally developed.
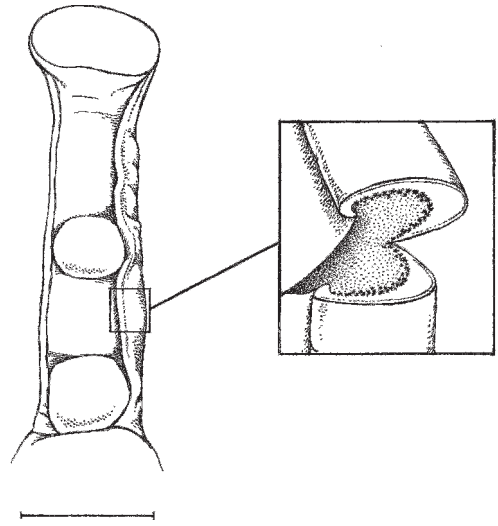

Fig. 21. *Anomaloglossus tepuyensis*. Finger III (right hand) enlarged from figure 14, showing keel-like lateral fold in greater detail, including diagrammatic section of a short transverse cut across fringe. An underlying layer of melanophores shows through the somewhat translucent lateral fold, giving it the appearance of being irregularly pigmented. Scale line = 1 mm.

We have not seen specimens of two species (*Anomaloglossus ayarzaguenai*, *A. guanayensis*) of the six named web-footed anomaloglossines in the Venezuela Guayana that are characterized by folded flaplike fringes on the toes.[11] However, at least the remaining four species (*Anomaloglossus parkerae*, *A. shrevei*, *A. tamacuarensis*, *A. tepuyensis*) share the

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fringe on the longest toe of trans-Andean *Hyloxalus chocoensis* sensu stricto was illustrated by Myers (1991: fig. 2) and confirmed by re-examination of the holotype, in which the fringes along the distal half of toe IV are abruptly folded, as are the fringes on the medial sides of toes II and III and the outer fringing along toes I and IV. The situation is somewhat similar in *Aromobates nocturnus* from the Venezuelan Andes, although the greater extent of webbing reduces the chance for folding on the medial sides of toes II and III; a few preserved specimens show unfolded fringes along the outer free edges of toes I and V, but these are abruptly folded in most.

La Marca (1994) noted the presence of folded flaplike fringes in some species of the dendrobatid genus *Mannophryne*. Well-folded fringes are present in AMNH specimens of *Mannophryne collaris* and *M. riveroi*, but the fringes are narrower and more keel-like in *M. herminae*, *M. neblina*, *M. olmonae*, and *M. trinitatis*, with only feeble (if any) indication of folding.

[10] The downward folding of the lateral fringes does not seem to be an artefact of preservation. The fringes on toe IV and the outer free edge of toe V are not evident (i.e., they are folded down) in photographs of living *Aromobates* (Myers et al., 1991: fig 1; confirmation provided by examination of original transparencies under magnification). Whether the flaps (especially on the longest toe) are unfolded during swimming remains to be seen.

[11] The character state of the toe fringing is unknown in two additional web-footed species from southern Venezuela—*Anomaloglossus triunfo* and *A. wothuja*—recently named by Barrio-Amorós et al. (2004). These authors stated simply that fringes are present in *wothuja* and vary from well developed to ill defined in *triunfo*. Finger fringes were said to be absent in *triunfo* and keel-like in *wothuja*.

Another Venezuelan species, *Colostethus sanmartini* Rivero, Langone, and Prigioni (1986), was recently transferred to the genus *Allobates* by Grant et al. (2006). La Marca (''1996'' [1998]: 42–43) commented on some ambiguities in the original description. We have seen the female holotype (MNHN 540) and female paratype (MNHN 549) borrowed by Taran Grant from the Museo Nacional de Historia Natural de Montevideo. There are pronounced folded flaplike fringes on the toes and similar fringes on finger II (unpublished drawing of hand and foot of holotype).

additional characters of keel-like lateral folds on the fingers and a median lingual process (Grant et al., 1997; Myers and Donnelly, 1997, 2001: 34). We suspect that the median lingual process—a synapomorphy of *Anomaloglossus* Grant et al.—will be found also in *ayarzaguenai* and *guanayensis* and would not be surprised if the unusual finger folds are also found to be more widespread. NOTE: Grant et al. (2006: 159) suggested that two additional La Marca species tentatively assigned to *Anomaloglossus*—*murisipanensis* and *parimae*—probably have a median lingual process. La Marca (''1996'' [1998]: 22, 24, 27, 28) characterized the finger fringing of *murisipanensis* as *quillas laterales poco nítidas* in the diagnosis, but as *quillas laterales gruesas* in the description; finger fringing was termed *quillas laterales* in *parimae*; the toe fringing of both *murisipanensis* and *parimae* was characterized as *rebordes membranosos laterales*.

Of the above species known to have both a median lingual process and folded flaplike fringes on the toes, the geographically nearest to *Anomaloglossus tepuyensis* is *A. parkerae*, which occurs at known elevations of 860–1150 m in the La Escalera region, some 100 km east of Auyantepui. *Anomaloglossus parkerae* is a smaller species (1 ♂ *parkerae* 19 mm SVL, 7 ♂ *tepuyensis* 21–24 mm; largest ♀ *parkerae* < 25 mm SVL, ♀ *tepuyensis* 24–28 mm.); there is some resemblance in coloration (compare Duellman's [1997: 10] color plate with fig. 13 herein), although *parkerae* seemingly has an indefinite or less well-defined dorsal pattern as viewed from above.[12] The keel-like lateral folds on the fingers and the folded flaplike fringes of the toes are only

weakly developed in *Anomaloglossus parkerae* (fig. 20B). A groove indicating recurved folding of the narrow lateral keel is evident distally on finger III; the toe fringes also are narrow, but do tend to be folded downward. The median lingual process of *Anomaloglossus parkerae* is relatively short and about as long as or little longer than wide, whereas that of *A. tepuyensis* is usually more tapered and longer than wide (Grant et al., 1997: fig. 3B).

The color pattern of *Anomaloglossus tepuyensis* closely resembles that of three other tepui species, *A. shrevei*, *A. tamacuarensis*, and *A. triunfo*. The normal dorsal pattern of *tepuyensis*, *shrevei*, and *tamacuarensis* is extraordinarily similar, as can be seen by comparison of figure 15 herein with figure 13 in Myers and Donnelly (1997: 20).

Anomaloglossus shrevei differs from the other two in tending to have a straight tarsal fold (versus proximal end curved laterad), and a very short median lingual process in the shape of a round bump or blunt cone (Myers and Donnelly, 1997: fig. 17A, B). The lingual process is longer and more slender in *Anomaloglossus tamacuarensis* (Myers and Donnelly, 1997: fig. 17C, D) and *A. tepuyensis* (Grant et al., 1997, fig. 3B).

Anomaloglossus tamacuarensis differs from *A. tepuyensis* in a somewhat greater extent of foot webbing and in the possession of cloacal tubercles (one on each thigh lateral to and slightly above vent opening). The advertisement calls differ. *Anomaloglossus tamacuarensis* produces a long (≥ 1 min) train of double notes or couplets, in which the individual notes are too closely spaced (20–30 msec) to be easily resolved by the human ear; the repetition rate is 3 couplets/sec given at a frequency of about 3800 Hz. The call of *Anomaloglossus tepuyensis* differs in being a much shorter train of single notes produced at a rate of about 4–7 notes/sec at a lower frequency (< 3600 Hz). The individual notes are variably pulsed in each species.

The normal dorsal color pattern of *Anomaloglossus tepuyensis* is also very similar if not identical to that of the recently described *A. triunfo* (see description and color photo of

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(Continued.) As originally described and illustrated, *Allobates sanmartini* has minimal webbing and a broken collarlike marking (now faded) on the base of the throat. The undulating dorsal pattern is remarkably similar to that of *Allobates undulatus* (Myers and Donnelly, 2001: fig. 19), which has very faint lateral keels on some digits, rather than pronounced fringing as in *A. sanmartini*.

[12] Our comments on *Anomaloglossus parkerae* are based on examination of three adult female paratypes (KU 167328–167330) and on published descriptions (Meinhardt and Parmelee, 1996; Duellman, 1997; La Marca, ''1996'' [1998]). Myers and Donnelly (1997: 23) described and gave measurements for the median lingual process of the three paratypes.

triunfo in Barrio-Amorós et al., 2004: 185, 190). The arrangement of dorsal dark markings is so similar that *A. triunfo* might be expected to share with *tepuyensis*, *shrevei*, and *tamacuarensis* the character of folded flaplike fringes on the toes, but that remains to be determined.

Anomaloglossus triunfo apparently differs from *A. tepuyensis* in having appressed finger I "distinctly" longer than finger II. Dorsal snout shape and presence or absence of an oblique lateral stripe also were said to distinguish *triunfo* and *tepuyensis*, but, as described herein, these characters vary in our sample of *tepuyensis* from Auyantepui and therefore are not diagnostic. Barrio-Amorós et al. (2004; 186) stated that the five type specimens of *Anomaloglossus triunfo* lack "keel-like fringes on fingers, except in EBRG 4758 [said to be an adult male], probably through the desiccation". Finger fringes in *tepuyensis* are tightly folded around the digits (fig. 14, 21) and might be overlooked in *triunfo* if present only as poorly developed homologs. Closer comparisons of finger and toe fringing seem warranted. Barrio-Amorós et al. (2004; 186) examined three of the 17 specimens of *tepuyensis* that we delivered to the Rancho Grande collection (the EBRG numbers cited include a juvenile from Camp 1 and two adult females from Camp 4), but it is not clear whether specimen-to-specimen comparisons were made with *triunfo*.

FAMILY HYLIDAE

Two genera occur on the summit of Auyantepui: *Hypsiboas* with three species and *Tepuihyla* with one species. A third summit genus, *Stefania*, has been transferred to another family (see following family).

Hypsiboas Wagler (1830: 200) recently was removed from the synonymy of *Hyla* Laurenti (1768) by Faivovich et al. (2005). The genus represents a clade mentioned in Duellman (2001: 860), for which the earlier name *Boana* Gray (1825) was resurrected by Wiens et al. (2005: 730). However, as had been pointed out by Faivovich et al. (2005: 85), the senior name *Boana* had been "coined as a synonym of *Hyla* and never subsequently validated as available under article 11.6.1

(ICZN, 1999)".[13] The *Hypsiboas benitezi* and *punctatus* species groups are represented on the Auyán summit, with one species (*angelicus*) in the former group and two species (*jimenezi*, *sibleszi*) in the latter.

Hypsiboas angelicus, new species
Figures 22–26

HOLOTYPE: EBRG 2733 (field no. CWM 19318), an adult male from summit of Auyantepui at 5°58′N, 62°33′W (AMNH–TERRAMAR Camp 4), 1600 m, Bolívar, Venezuela; collected February 19–21, 1994, AMNH–TERRAMAR Expedition. Figure 22.

ETYMOLOGY: The specific name is a Latin adjective pertaining to celestial angels, including, perhaps, legendary pilot Jimmy Angel of Auyantepui fame.

DIAGNOSIS: This species belongs to the former *Hyla geographica* group (as defined by Duellman, 1973), as indicated by the external characters of calcars, prepollical spines not projecting through the skin, basal webbing between fingers, and general habitus. Presence of a flat mental gland and close resemblance with *Hypsiboas roraima* places it in the *benitezi* group of *Hypsiboas* (Faivovich et al., 2005: 86–87).

It is further distinguished by the following suite of characters (in the format of Duellman and Hoogmoed, 1992): (1) body slender, with head distinct from body; (2) skin on dorsal surfaces including upper eyelids weakly granular (in life) or smooth (in preservative); head skin not co-ossified; (3) tympanum distinct; (4) fingers with basal webbing; (5) toes about half webbed; (6) fringes absent on limbs; a short conical calcar present; (7)

[13] "Boana *Gray*" was first published by John Edward Gray (1825: 214) but probably not invented by him. One did not purposely create new names to be published as synonyms. Names first published in synonymy usually (if not always) were manuscript or specimen-label names. The name *Boana* may have been attached to a BMNH specimen of "Rana Boans, *Lin.*" by Edward Whitaker Gray (1748–1806). J. E. Gray (1825: 93) mentioned his "late [great] uncle, who paid great attention to this department of zoology, and several of whose manuscript species still remain unpublished". E. W. Gray, Keeper of Natural Curiosities at the British Museum (Gunther, 1976), has been all but forgotten. He published at least one herpetological paper, an insightful critique of Linnaeus' class Amphibia (E. W. Gray, 1789).

Fig. 22.   *Hypsiboas angelicus*, new species. The adult male holotype in life (EBRG 2733, 38 mm SVL).

axillary membrane absent; (8) dorsum brown with pale lichenlike spots and irregular black spotting; broken black vertebral stripe present (at least in holotype); flanks grayish with small black spots; limbs brown with gray crossbanding; rear of thigh gray; venter pale (gray in life), unmarked; foot webbing brown like dorsum; upper half of palpebrum clear except for brown upper edge and brown flecking, lower half brown; (9) vomerine odontophores angular.

Hypsiboas angelicus is remarkably similar to *Hypsiboas roraima* (Duellman and Hoogmoed) from Cerro Roraima, differing most conspicuously in lacking pale reticulation on the palpebral membrane.

MORPHOLOGY: An adult male 38.4 mm SVL, with large vocal slits; a shallow subgular vocal sac, irregularly folded against posterior half of throat and chest. A thin, loosely organized mental gland on anterior half of gular region, with a convexly rounded posterior edge (fig. 25, ventral view). Body slender, head approximately as wide as long, prominent, much wider than body (head width/greatest body width = 1.25); snout slightly sloping, short, truncate in dorsal and lateral views, not projecting beyond margin of upper lip; canthus rostralis rounded; loreal region concave, inclined outward to rounded lip; nostrils protuberant laterally; internarial area slightly depressed; top of head flat; upper eyelid as wide as interorbital distance; eye length greater than its distance to naris (eye/naris-eye = 1.12), nearly as long as snout; tympanum distinct except for upper edge, circular, deflected dorsolaterally; separated from eye by a distance slightly greater than its length; supratympanic fold weak, but covering upper edge of tympanic annulus.

Axillary membrane absent; forearm slender, with row of large, ill-defined, closely spaced low ulnar tubercles situated along ventrolateral edge of arm; fingers slender, with rounded terminal discs; third finger disc subequal with length of tympanum; relative finger length III > IV > II > I; subarticular tubercles rounded, low, barely protuberant; supernumerary tubercles few, indistinct proximally; large palmar tubercle rounded, low and very indistinct; thenar tubercle elongate, not well defined, with median projection distally; basal webbing between fingers II–IV.

Hind limb long and slender; tibia 53.4% of SVL; heel bearing short conical tubercular
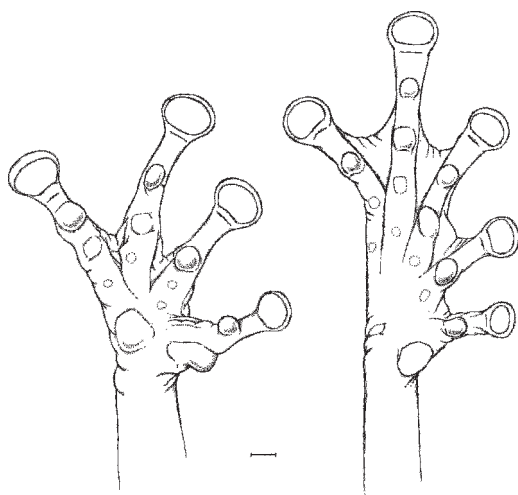
Fig. 23. *Hypsiboas angelicus*, new species. Right hand and right foot of the adult male holotype (EBRG 2733).
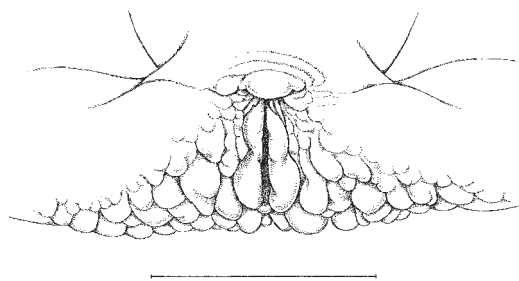

Fig. 24. *Hypsiboas angelicus*, new species. Cloacal region of the holotype in posterior view. The vent opening is concealed under the short cloacal flap at the upper level of the thighs, above the vertical channel that is flanked by large elongate tubercles.

calcar; toes with rounded terminal discs subequal in size to those on fingers; relative toe length IV > V > III > II > I; subarticular tubercles low, rounded, only slightly protuberant; supernumerary tubercles few, indistinct proximally; inner metatarsal tubercle oval; outer metatarsal tubercle small and indistinct; no tarsal fold; toes moderately webbed, with formula: **I** 2–2½ **II** 1½–2½ **III** 1½–2½ **IV** 2–1½ **V** (fig. 23).

Vomerine odontophores oblique, weakly arched, situated between large choanae and separated by a distinct medial gap, each with about a dozen teeth. Tongue large, covering floor of mouth, only lateral edges free, fully attached behind.

Skin on dorsal surfaces, including upper eyelids, weakly granular in life (fig. 22), becoming virtually smooth in preservative; skin on throat and under arms smooth in preservative, coarsely granular (areolate) on venter; proximal posteroventral surfaces of thighs crowded with smooth tubercles; ventral thigh surfaces covered with large, probably glandular tubercles, low and smooth in preservative. Supracloacal flap short, slightly overlapping vent opening, which is directed posteriorly at upper level of thighs; vent situated immediately above a smooth vertical channel situated between two large, vertically

elongate tubercles, which in turn are flanked by large, smoothly rounded tubercles that grade into those on proximal posteroventral surfaces of thighs (fig. 24).

MEASUREMENTS (in mm): Snout to vent 38.4; tibia 20.5; hand from proximal edge palmar tubercle to tip of longest finger 10.5; foot from proximal edge inner metatarsal tubercle to tip of longest toe 14.1; head length on the diagonal from tip of snout to angle of jaw 13.6; greatest head width (near angle of jaws) 13.8; width of upper eyelid 4.0; greatest body width 11.0; width of interorbital area 4.0; internarial distance 3.0; rear edge naris to anterior corner of eye 4.2; eye length from anterior to posterior corner 4.7; eye to tympanum 2.5; horizontal length of tympanum 2.2; width of third finger disc 2.1; width of fourth toe disc 1.9.

COLORATION: In life (fig. 22), grayish brown, with lichenlike spots of pale rose and irregular black spotting on dorsum; a narrow, broken black vertebral stripe from snout to midbody; flanks gray with small black spots; limbs brown with inconspicuous gray crossbanding; rear of thigh gray; foot webbing brown like limbs. Dull grayish yellow under chin, turning uniformly light gray over all remaining ventral surfaces, including palms and soles. Iris pale golden yellow, with very fine, scarcely noticeable, black venation. Upper half of palpebral membrane clear in life (except for brown upper edge and brown flecking, as noted in preservative), lower half brown.
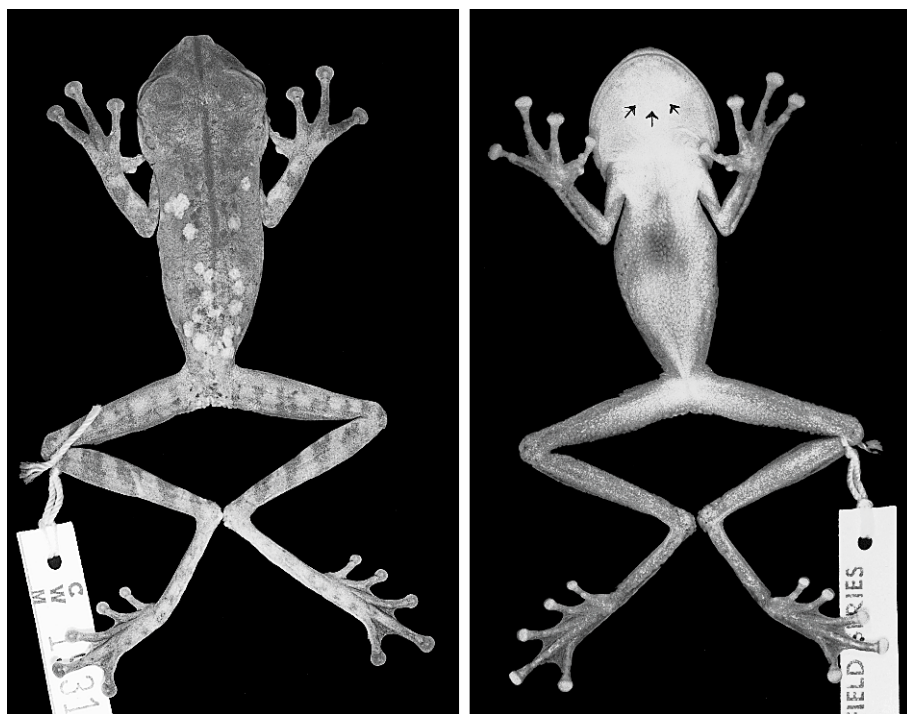
Fig. 25. *Hypsiboas angelicus*, new species. Dorsal and ventral views of the adult male holotype (EBRG 2733). Small arrows point to convex posterior edge of flat mental gland.

In preservative (fig. 25), pattern well retained, with rose coloring faded from lichenous dorsal spots, and with throat and venter turned pale yellowish and undersides of limbs pale brownish.

NATURAL HISTORY AND VOCALIZATION

A single specimen believed to be this species was recorded by Donnelly in dense vegetation next to the river at Camp 1 on February 4; this frog escaped capture. Identification was confirmed by capture of the holotype two weeks later in Camp 4, although further recordings were not obtained.

The advertisement call (fig. 26) was a long train of explosive, short "beeps" given continuously for over a minute, at a rate of 2.6 notes per second, with a mean internote interval of 0.35 sec (range 0.31–0.49 sec, N = 50). The note is weakly pulsatile or non-pulsatile, 0.03 sec long, and frequency modulated, starting at about 1800 Hz and rising to about 2400 Hz before a slight trail-off.

REMARKS

Faivovich et al. (2005: 86; 2006) postulated a "flat mental gland" as a synapomorphy of the *Hypsiboas benitezi* group; for additional comments on the composition of the group and illustration of the gland, see Faivovich et al. (2006: fig. 4A–C). This easily overlooked structure is a thin area of glandular tissue and is present in both *Hypsiboas roraima* and *H. angelicus* (fig. 25, ventral view). These two species are very similar, with the dorsal color pattern of *angelicus* seeming to fit comfortably with variation in *roraima* (compare figs. 25, 27). The presence of pale reticulation on the palpebral membrane is a diagnostic characteristic of various frogs, including *H. roraima* (Duellman and Hoogmoed, 1992: 6, 10; MacCulloch and Lathrop, 2005: 26–27), but is lacking in *H. angelicus*. To our knowledge, intraspecific variation has yet to be detected in this character, which is discernible in both living and preserved specimens (the
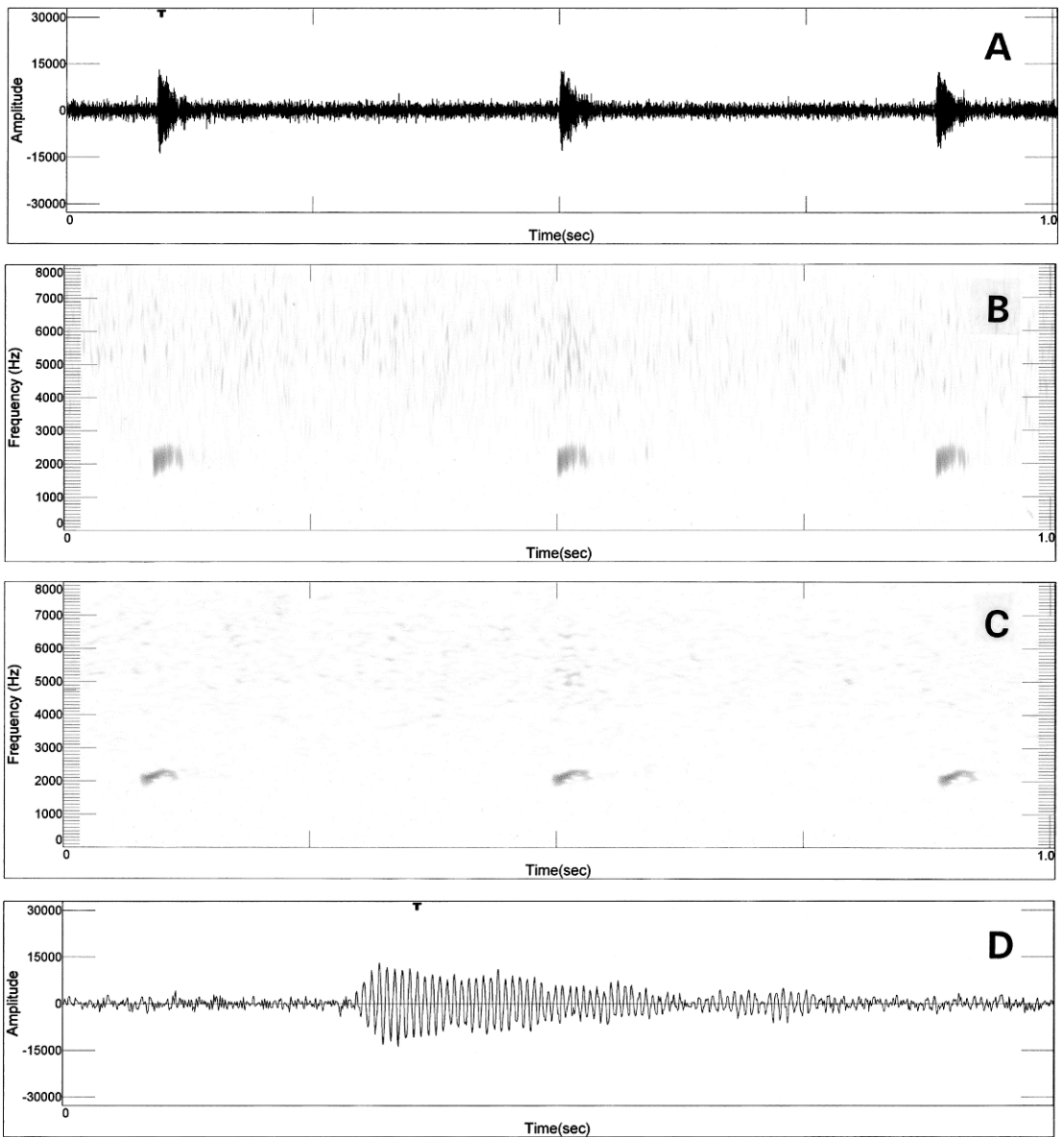
Fig. 26. Vocalization associated with *Hypsiboas angelicus*, new species. Three notes in 1 sec., from a long continuous call sequence. **A:** Waveforms (T = tagged note, see below). **B:** Wideband (323 Hz) spectrogram. **C:** Narrowband (63 Hz) spectrogram. **D:** Expanded waveform of note tagged in first panel; note duration = 0.03 sec. (Unvouchered recording of specimen calling at night from dense vegetation near river at Camp 1, February 4, 1994; air temperature 16.4°C. AMNH herpetology reel 263: 2.)

palpebral membrane of the *angelicus* holotype was examined in both states).

Hypsiboas roraima was indicated by Mac-Culloch and Lathrop (2005: table 2) as lacking all vestiges of finger webbing, but Duellman and Hoogmoed (1992: fig. 4) illustrated basal webbing between fingers III and IV that is similar to that of *H. angelicus* (fig. 23). Both species have a notably tuberculate cloacal area. The holotype of *H. angelicus* has a pair of conspicuously large, vertically elongate tubercles that flank a smooth

Fig. 27.   *Hypsiboas roraima* from Mount Ayanganna, Guyana (from left to right: ROM 39611, 39616, 39623, 39624). Note color-pattern similarity to *Hypsiboas angelicus* from Auyantepui (compare with figs. 22, 25).

vertical channel below the vent (fig. 24). Although the size and shape of these ridgelike tubercles conceivably might be diagnostic, they might also have resulted from intraspecifically variable fusion of the large round tubercles. The vocalization of *Hypsiboas roraima* seems to be unknown, but considering other close resemblances and seeming lack of sympatry, it would not be surprising if the two species had somewhat similar calls.

Hypsiboas species (*H. angelicus*?), TADPOLE
Fig. 28

MATERIAL: Camp 2, 1750 m: AMNH A-164998 (1 larva), from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

This curious little tadpole was found in a pool of water at the bottom of a deep (> 10 m) sandstone crevice, into which our colleague Petia Alcócer had descended by rope. Assuming that it does not represent a frog otherwise unknown from the Auyán summit, we tentatively associate it with *Hypsiboas angelicus*.

HABITUS AND PROPORTIONS: Head-body length 12.6 mm, body width 7.0 mm, body depth 6.0 mm, total length 35.7 mm. Body slightly depressed (body width/body depth = 1.17); snout acutely rounded in dorsal view, rounded in profile. Nares dorsolateral, directed laterally, 1.5 mm from tip of snout; distance between centers of nares 2.1 mm. Small eyes dorsal, directed laterally, diameter 0.4 mm; interocular plane 2.6 mm from tip of snout. Spiracle a 0.7 mm long tube adhered to body wall, sinistral. Large vent opening dextral to caudal fin; vent 1.5 mm long, with inner wall free of body.

Lateral line system (not illustrated) not pronounced, including: a pair of supraorbital lines diverging in straight lines from center of snout to top of eye; high and middle lateral lines on body; an angular branch with a short anteriorly extending loreal branch; a gular branch extending from the middle lateral line and ventrally converging toward the angular branch.

A single unpigmented bump (gland?), 0.4 mm in diameter, near end of body on each side.
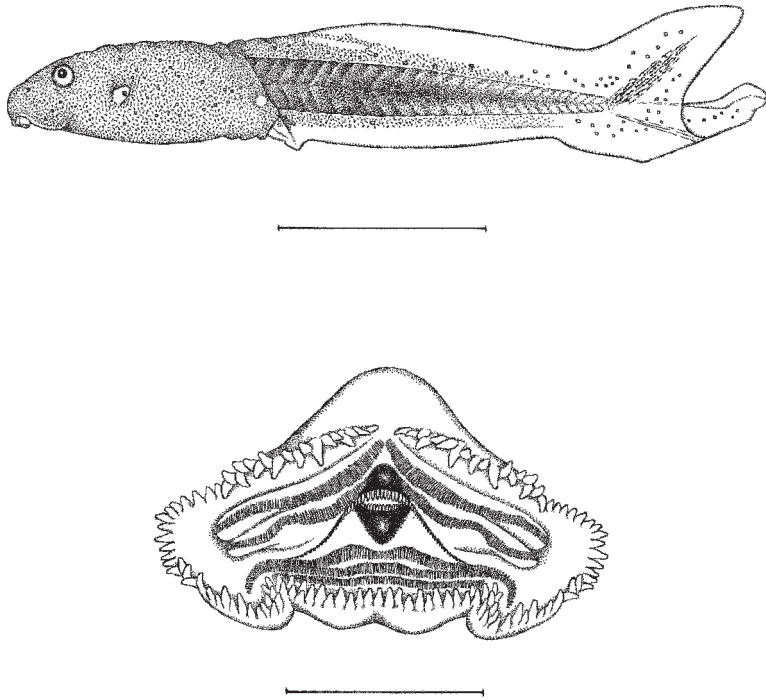
Fig. 28.   Larva assigned as *Hypsiboas* species (*H. angelicus*?). Stage-25 tadpole and mouthparts of same specimen (AMNH A-164998). This unidentified tadpole with an aberrantly forked tail is characterized by entirely rodular melanophores. Lateral line organs are not illustrated; the small scattered spots are yellowish chromatophores. Scale lines = 10 mm above and 1 mm below.

Tail length 64.7% of total length. Maximum tail height 16.8% of total length. Fins unequal in height; dorsal fin 1.8 mm and ventral fin 1.6 mm at maximum tail height. Tail distally forked.

PIGMENTATION: In preservative, head-body uniformly covered by rodular melanophores, brown in color. Brown rodular melanophores also overlying the pale yellowish brown tail musculature and extending proximally along both fins, becoming sparse and disappearing before the end of the tail. Well-defined pale yellow chromatophores are sparsely distributed, occurring mainly on the sides of the body and along the base of the upper tail fin.

MOUTHPARTS: Mouth ventral. Oral disc width 2.2 mm, not emarginate. Labial teeth in two anterior and three posterior rows, which are subequal in length except for last posterior row being shortest. Anterior tooth rows medially broken. Edges of upper and lower jaw sheaths with pointed serrations; laterally, the lower jaw sheath is only narrowly keratinized. Oral disc nearly surrounded by pointed marginal papillae, except for an anterior median break in the row. The marginal papillae are disposed in a single row (looking like a double row where folded posteriorly, fig. 28).

REMARKS

A uniform layer comprised solely of epidermal rod-shaped melanophores is a distinctive feature of this tadpole, which is identified only tentatively as *Hypsiboas angelicus*. Rodular melanophores occur widely in tadpoles of the tribe Cophomantini, but usually other shapes of melanophores are present as well (J. Faivovich, personal commun.). The bumplike structure on the rear of
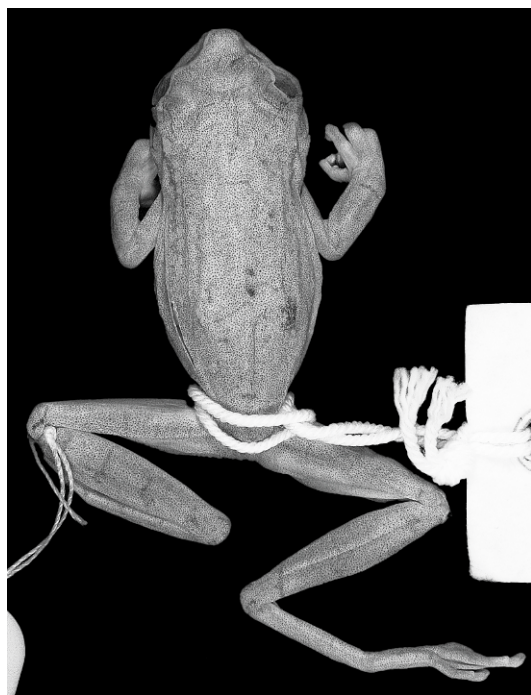
Fig. 29.   *Hypsiboas lemai*, ×1.5. This specimen (BMNH 1975.1356♀) is the basis for earlier inclusion of *H. lemai* in the Auyantepui fauna. However, it was obtained at the base of the tepui and is not a summit species.

the body is a usually overlooked character that also is widespread in the Cophomantini according to Faivovich.

Adult *Hypsiboas angelicus* appears to belong to the *benitezi* species group (sensu Faivovich et al., 2005: 86), for which tadpoles are virtually unknown. We earlier described a single tadpole from a flood-prone, granite-bottom stream on Cerro Tamacuari as possibly *Hypsiboas benitezi*, a common frog along that stream and the only adult hylid collected there (Myers and Donnelly, 1997: 28–29). Assuming that the present tadpole with 2/3 tooth rows is correctly associated with *Hypsiboas angelicus*, our earlier assignment of a tadpole with 5/8 tooth rows to *H. benitezi* sensu lato seems questionable. In any case, *Hypsiboas benitezi*, as currently recognized, is most likely a composite of two or more species (Myers and Donnelly, 1997: 30–33).

Hypsiboas lemai (Rivero)
[a nonsummit species]
Figure 29

Hyla lemai Rivero, "1971" [1972]: 183, fig. [1]C (dorsal view of holotype). Holotype UPR-M 3179 from "Paso del Danto, La Escalera, entre El Dorado y Sta. Elena de Uairén, Serranía de Lema, 1300–1400 m.", Estado Bolívar, Venezuela, collected March 22, 1968, by J. A. Rivero and J. Pulido. Hoogmoed, 1979a: 32 (mention of Auyantepui in range). Duellman, 1997: 10, 16 (color photo, description, and call analysis of specimens from general region of the type locality). MacCulloch and Lathrop, 2005: 25, figs. 5, 11 (description and illustrations of Guyana specimens, and map showing Auyantepui record).

MATERIAL: BMNH 1975.1356 from Auyantepui, 3200 ft. [975 m], collected by Adrian Warren (field no. 112).

REMARKS

As indicated above, *Hyla lemai* has been mentioned and mapped as occurring on Auyantepui. These references are based on BMNH 1975.1356, which was collected by A. Warren in 1974 and identified by M. S. Hoogmoed in 1977 according to BMNH records. The given elevation of 3200 ft. (≈ 975 m) indicates that it probably was collected near the old Guayaraca campsite on the footpath to Auyantepui—some 1400 m below the summit.

The specimen (fig. 29) is an adult female 40 mm SVL; it contains numerous large, unpigmented ova, the largest being about 2 mm in diameter. Coloration in alcohol is very faded, nearly without pattern. An ill-defined narrow black stripe (not evident in fig. 29) extends posteriad under the canthal ridge, across the outer edge of the upper eyelid, over the supratympanic fold, and ends about midbody. This dark line, very vague posteriorly, is emphasized along its upper edge by a barely discernible narrow, whitish stripe from snout to midbody. There is a thin black line across each wrist and another such line across the middle of the left forearm. The body and limbs otherwise are unicolor, densely punctated with melanophores over all dorsal surfaces (present but less dense in the pale dorsolateral line).

The black lines on the wrist and lower arms resemble markings on another Venezuelan specimen of *H. lemai* shown by Duellman (1997: fig. 10), and the positioning of the faint white dorsolateral stripe, from snout to midbody, is consistent with a more vividly marked Guyanese specimen shown in MacCulloch and Lathrop, 2005: fig. 5).

Hypsiboas jimenezi Señaris and Ayarzagüena
Figures 30–33

Hypsiboas jimenezi Señaris and Ayarzagüena, 2006: 309–319, figs. 1–2 (photo and hand and foot drawings of holotype), 3 (skull), 4 (sound spectrogram). Holotype: MHNLS 16070♂ from Quebrada Ataperé, headwater of Cucurital River (05°43′17.7″N, 62°34′21.1″W), 970 m, Canaima Natl. Park, Bolívar, Venezuela, collected November 8, 2002 by J. Celsa Señaris and Carlos Lasso.

Hypsiboas jimenezi was described by Señaris and Ayarzagüena on the basis of material from montane streams on the southern slope of Auyantepui (950–970 m), along with two specimens from the west-central summit (1850 m). We assign to this species three additional specimens from the western branch of the summit and also several collections of tadpoles from widespread summit camps.

MATERIAL: *TADPOLES.* 1.1 km NNE Camp 1, 1650 m: EBRG 2645. Camp 4, 1600 m: AMNH A-164852–164857, EBRG 2646–2647, 2731–2732. Camp 5, 2100 m: AMNH A-164858–164864, EBRG 2648. All larvae from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

FROGS. Auyantepui summit, 1700 m, 5°53′N, 62°35′W: AMNH A-169282, EBRG 3750, 3751, collected by Ricardo Guerrero, February 6–8, 1988.

The last three specimens are adult males 28.1–32.4 mm SVL ($\bar{x}$ = 30.70 mm, S.D. = 2.29 mm, N = 3); tibia length 52%–59% of SVL; head width 37%–39% of SVL, 95%–102% of diagonal head length; eye length greater than distance from its anterior edge to center of naris (EN/eye = 0.88–0.92); upper eyelid more than half the width of interorbital space (IOD/eyelid = 1.38–1.56); disc on finger III wider than discs on toes III–

Fig. 30. *Hypsiboas jimenezi.* Large, skin-covered prepollical spine; lacking an orifice in the prepollex, the spine is nonprotrusile (unless the skin is torn). Right hand of EBRG 3750, about ×12.

IV. Prepollical spine large, lacking an orifice (not protrusile, fig. 30).

COLORATION: Coloration is somewhat variable in preservative (originally fixed in 70% ethanol according to the collector), but all have a black canthal line and a variable dorsal pattern of small black spots (fig. 31). There are about 3–6 spots along the outer side of the lower arm, and conspicuous spotting on dorsal surfaces of the hind limbs, especially on the tibia and tarsus. Several black spots scattered over the dorsum are conspicuous in two specimens but reduced to a few black specks in another. One specimen (EBRG 3751) is dull brown dorsally owing to dispersal of pigment from the melanophores; the other two specimens are very pale
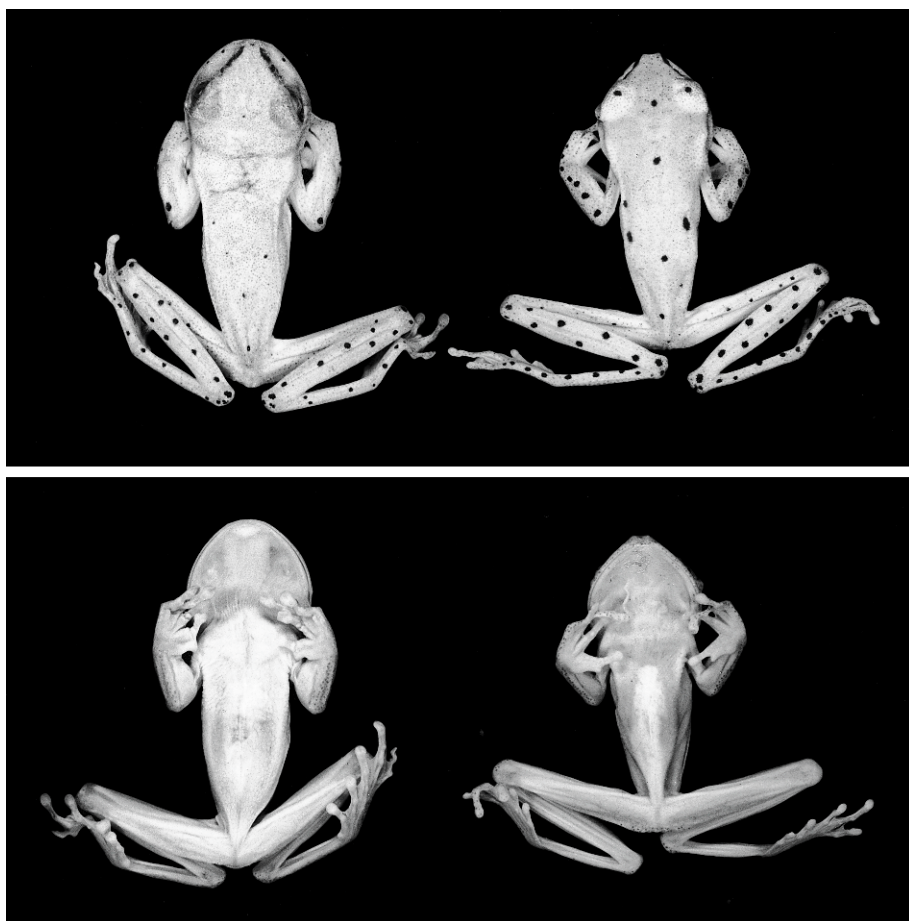
Fig. 31. *Hypsiboas jimenezi*. Dorsal and ventral views of two males from 1700 m elevation on the summit of Auyantepui, ×1.4. Left to right: EBRG 3750, 32 mm SVL; AMNH A-169282, 28 mm SVL. The scattered spots, especially on the limbs, and the dark canthal lines are diagnostic.

orangish or (in AMNH A-169282) pale orange over all dorsal surfaces, with minute melanophores visible under magnification. Rears of thighs are pale orangish; ventral surfaces, including palms and soles, are immaculate, the color varying from very pale orangish (nearly colorless) to pale orange. Two specimens have occasional silvery iridophores associated with the melanophores; the iridophores are relatively numerous in AMNH A-169282, appearing as silvery flecking under magnification.

Based on living specimens from the type locality on the southern slope of Auyantepui (970 m), *Hypsiboas jimenezi* has "a green dorsum with a dense matrix of [brown or reddish brown] chromatophores and with large spots on limbs and forelimbs"; white dorsolateral lines were present in topotypic specimens but absent in others (Señaris and Ayarzagüena, 2006: 310, fig. 1). In preservative, the green specimens faded either to cream or to reddish brown in specimens that had a very dense matrix of chromatophores. The bright yellow venter became cream in preservative (Señaris and Ayarzagüena, 2006: 312, 313).[14]

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[14] Although living frogs from lower elevations were green in life, the orange or brown coloring of the summit specimens described above suggests that they were not pure green when alive. Except for the lack of dorsolateral stripes, the orange coloring seems suggestive of the orange-suffused frogs from 2100 on the

TABLE 3
Measurements (in mm) of Tadpoles of *Hypsiboas jimenezi* Señaris and Ayarzagüena
(Values are ranges followed below by means $\pm$ 1 SD when N > 2)

Stage	N	Total length	Head–body length	Body width	Body depth	Tail depth	Oral disc width
25	4	24.22–41.23	8.7–13.8	4.9–7.0	5.9–8.8	5.3–9.0	2.0–3.5
		34.39 $\pm$ 8.98[a]	10.82 $\pm$ 2.41	5.65 $\pm$ 0.95	7.08 $\pm$ 1.39	6.63 $\pm$ 1.73	2.75 $\pm$ 0.71
27	4	38.2–47.3	11.5–13.8	5.9–7.0	7.4–8.7	7.7–8.9	3.4–3.7
		44.55 $\pm$ 4.30	13.08 $\pm$ 1.06	6.35 $\pm$ 0.51	7.98 $\pm$ 0.59	5.15 $\pm$ 0.54	3.55 $\pm$ 0.17
28	1	52.4	15.0	7.5	9.2	9.3	4.0
28/29	1	40.0	11.9	6.4	7.7	8.2	3.2
29	1	52.7	16.6	9.0	11.3	11.8	4.6
31	1	51.9	16.8	9.1	10.7	11.6	4.5
32	1	48.9	14.1	6.9	8.1	9.1	3.5
33	2	57.0[b]	16.5–17.4	7.9–8.7	9.9–11.2	10.7[b]	4.3–4.8
34	1	–[c]	16.8	9.0	11.5	11.4	4.4
37	4	53.1–57.2	15.0–17.8	7.2–9.0	9.2–11.3	9.5–10.3	3.9–4.3
		54.42 $\pm$ 2.38[a]	15.88 $\pm$ 1.27	7.70 $\pm$ 0.87	9.78 $\pm$ 1.02	10.76 $\pm$ 1.82	4.10 $\pm$ 0.18
40	3	50.9–52.0[d]	16.0–20.2	7.2–9.9	9.5–13.1	9.5–13.4	3.8–5.2
		–	17.51 $\pm$ 2.34	8.12 $\pm$ 1.42	10.77 $\pm$ 2.03	11.01 $\pm$ 2.52	4.3 $\pm$ 0.78

[a] N = 3 (one larva with broken or incomplete tail).

[b] N = 1 (one with broken or incomplete tail).

[c] Tail broken or incomplete in only specimen.

[d] N = 2 (one with broken or incomplete tail).

NOTES ON THE TADPOLES AND COMPARISONS
WITH *H. SIBLESZI*

We originally identified our tadpoles as *Hypsiboas sibleszi*, but several features do not agree with previous descriptions of larval *sibleszi* and they are assigned to *H. jimenezi* with reasonable confidence. Measurements of the larvae are summarized in table 3. There are both similarities and differences when this material is compared with Hoogmoed's (1979a: 27–29) and Duellman's (1997: 20) descriptions of *Hypsiboas sibleszi* larvae from the La Escalera region, about 110 km east of Auyantepui.

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neighboring Chimantá massif. A color photograph from Chimantá shows a head-on view of an orange-suffused brownish frog with orange stripes and small black spots on limbs. The stripes start on the snout tip above black canthal lines and extend over the eyes (interorbital bar lacking), apparently continuing posteriorly as weak dorsolateral lines (Gorzula, 1992: 269, color photo 153, as *Hyla sibleszi*; see also the photograph showing a greenish brown frog with orange stripes and spotted limbs in Gorzula and Señaris, 1999: color photo 25, as *Hyla sibleszi*). Señaris and Ayarzagüena (2006: 316, 319) have redetermined the available Chimantá specimens as *Hypsiboas* cf. *jimenezi*.

COLORATION: We noted in the field that some tadpoles had a noticeably *bright red* iris. The red color was explicitly noted for one large larva from Camp 4 (AMNH A-164853, stage 37), and for some (probably the larger ones) in one lot of 11 from Camp 5 (EBRG 2648, stages 25–33; AMNH A-164858–164864, stages 24–40). However, Duellman (1997: 20) described two small (stage-25) *Hypsiboas sibleszi* tadpoles as having a *pale bronze* iris. Although ontogenetic change or some other confounding factor cannot be ruled out at this time, red eye color seems diagnostic at least for larger larvae of the Auyantepui sample.

Hoogmoed (1979a: 29) said that *H. sibleszi* tadpoles in stages 42 and 43 have white interorbital and lateral lines, which are precursors of the pattern found in some but not all adults. None of our larvae show such markings. However, our largest tadpoles (stages 37 and 40) have conspicuous dark brown spots on the dorsum, which appear to be precursors of the adult spotted pattern of *Hypsiboas jimenezi* (compare figs. 31 and 33). Rodular melanophores are present among larger variably shaped melanophores.

MOUTHPARTS: We here compare Hoogmoed's (1979a: 27–29) description of the

mouth parts of *Hypsiboas sibleszi* larvae. Hoogmoed described *sibleszi* as having 2/4 labial tooth rows, with the P4 row poorly developed and consisting of several isolated patches of small denticles. In our sample of *Hypsiboas jimenezi*, some tadpoles in stages 25, 27, 28/29, and 32 have 2/4 tooth rows, but the most common formula is 3/5 rows (observed in stages 27, 28, 29, 31, 33, 37, and 40). A labial tooth-row formula of 2/5 is present in some tadpoles in stages 25, 27, and 40, and the formula 3/4 rows occurs in a single stage-33 larva.

The A3 and P5 rows, when present, are often obscured by the folds of the oral disc. The A1, A2, A3, P1, and P5 rows in our sample may have median gaps (in those tadpoles with 2/4 or 2/5 labial tooth rows, the A2 row has the median gap and the A1 lacks it; in tadpoles with 3/4 or 3/5 labial tooth rows, the A1 row has a very wide gap, A2 lacks one, and the A3 row has a narrow gap).

As shown by Hoogmoed (1979a: fig. 8d) for *Hypsiboas sibleszi* and in our figure 32 for *Hypsiboas jimenezi*, the oral disc is anteromedially emarginate on the upper labium and has a posterolateral fold or indentation on each side of the lower labium. *Hypsiboas jimenezi* additionally shows a median fold in the lower labium; the median fold varies from a weak median indentation (easily overlooked or considered artifactual) to a pronounced tuck (as in fig. 32) and would seem to be species specific.

The upper jaw sheath is a broad arch with blunt serrations and slender lateral processes; the lower jaw sheath is V-shaped with pointed serrations. Hoogmoed (1979a) illustrated and described a single row of marginal papillae around the oral disc in *Hypsiboas sibleszi*, but there are two rows in our sample of *Hypsiboas jimenezi*. As also shown by Hoogmoed (1979a: fig. 8d), the marginal papillae are broken by a median gap on the upper labium, at the point of anterior emargination (fig. 32). There are a few blunt submarginal papillae on the lower labium in some of our larvae (fig. 32).

Hoogmoed (1979a: 29) mentioned that there may be ''connections between the third and fourth lower denticle rows'' in *H. sibleszi* larvae, and we observed anomalies in various

tooth (denticle) rows in several tadpoles of *Hypsiboas jimenezi*. In one larva in stage 25 (EBRG 2646) and in another in stage 27 (AMNH A-164859), the A2 row curves upward to occupy a position normally occupied by A1 on the left. This results in a short A2 on the left and a short A1 on the right. In some cases, the tooth row consists of two or three ridges (short lateral segments and long medial segment), whereas in others there are short rows that are perpendicular to the tooth row (located near the submarginal papillae), and in one case there is a short lateral ridge between the P2 and P3 rows. The A3 and P5 rows in our samples are made up of several short ridges that are often adjacent to the marginal papillae.

LATERAL LINE SYSTEM: The infraorbital and supraorbital branches originate near the upper labium and join behind the eye to form a loop. There are scattered neuromasts inside the orbital loop. The middle trunk branch originates in the middle of the body slightly anterior to the spiracle, then curves ventrally posterior to the spiracle, to terminate at the level of the hind limb. There are two superior trunk branches, originating as parallel branches just posterior to the orbital loop; one branch curves medially and continues posteriorly in the dorsal tail fin, and the other branch curves ventrally and continues along the middle of the tail musculature. Hoogmoed's (1979a: fig. 8) drawing of *H. sibleszi* shows some resemblances to the above description.

There is an inconspicuous small unpigmented bump near the end of the body on each side (fig. 32).

NATURAL HISTORY

Tadpoles of *Hypsiboas jimenezi* were found near three of the expedition's five camps. Two larvae in stages 27 and 28/29 were taken from a pool in the river 1.1 km NNE of Camp 1. At Camp 4, larvae in stages 25–40 were taken from the backwater of a river and from isolated pools on sandstone. Larvae also in stages 25–40 were taken from a pool near Camp 5. Pools containing multiple developmental stages indicate a succession of breedings at those sites. Larvae were sympatric with those of *Anomaloglossus tepuyensis* at Camp 1 and at one of the
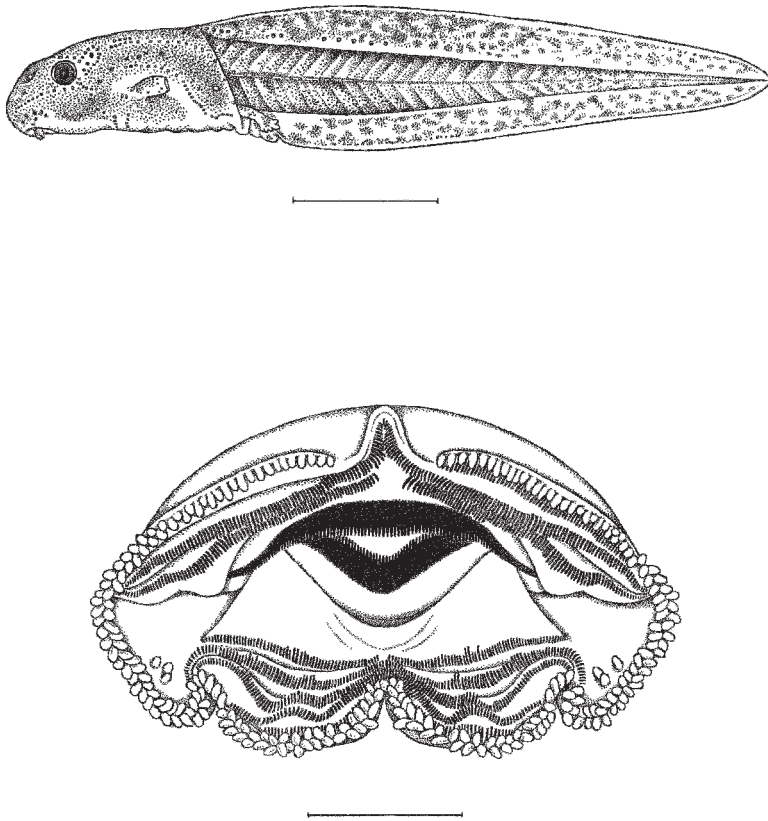
Fig. 32. *Hypsiboas jimenezi*. Stage-37 tadpole and mouthparts of same specimen (AMNH A-164856). There are 2/5 tooth rows, but note presence of an additional half row on right side of upper labium. Scale line = 10 mm (upper) and 1 mm (lower).

Camp-4 sites, and with *Leptodactylus rugosus* larvae at another Camp-4 site.

Señaris and Ayarzagüena (2006: 313, fig. 4, table 2) analyzed the vocalization based on recordings both from the type locality and the Auyán summit. Apparently, there were no significant differences in characteristics of calls between localities. The advertisement call was described as comprising three or occasionally four notes, all notes being "very similar [with] durations of 9.8–26 msec with regular intervals between them of 41–82 msec".

REMARKS

Tadpoles here assigned to *Hypsiboas jimenezi* only superficially resemble those of *H. sibleszi* as described by Hoogmoed (1979a). Based on present data, the characters appearing to distinguish *H. jimenezi*

larvae include a red iris, a median indentation in the lower labium (fig. 32), 2/4–3/5 tooth rows including a well-defined P4 row, a double row of marginal papillae around the oral disc, and appearance of black spots by about stage 37 (fig. 33).

The adult frogs are easily distinguished from *Hypsiboas sibleszi* by the presence of scattered dark spots (at least on the limbs) and a dark canthal line. According to Señaris and Ayarzagüena (2006: 310–311), *H. jimenezi* sometimes has dorsolateral white lines as also occurs in the variation of *H. sibleszi*, but, in *H. jimenezi*, the lines originate on the snout and there is no pale interorbital bar (dorsolateral lines in *sibleszi*, when present, originate above the eyes, often in marked association with an interorbital bar). Señaris and Ayarzagüena (2006: 310) also emphasized that the male prepollical spine is not
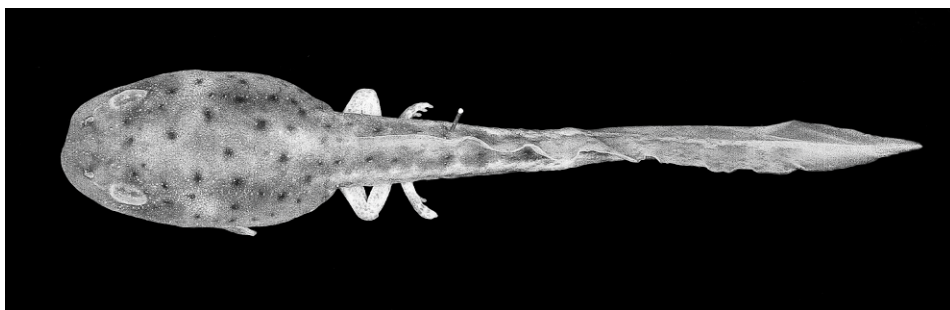
Fig. 33. Stage-40 tadpole (AMNH A-164857) of *Hypsiboas jimenezi*, ×2.3. The dark spots are precursors of the adult color pattern (cf. fig. 31).

protruding in *H. jimenezi*, whereas it is protrusible in *H. sibleszi*. Indeed, the summit specimens have relatively enormous prepollical spines that lack orifices (fig. 30), although a little pressure can cause them to tear through the skin. There also are obvious differences in head proportions as revealed, for example, by measurements of eye–naris/ eye (3 ♂ *jimenezi* 0.88–0.92; 5 ♂ *sibleszi* 1.06– 1.13) and eyelid/interorbital space (3 ♂ *jimenezi* 1.38–1.56; 5 ♂ *sibleszi* 2.00–2.50).

It is at least conceivable that summit specimens are not the same species as *Hypsiboas jimenezi* from lower elevations on the southern slope of Auyantepui. Since overlapping intrapopulational color variation has not been documented, similarly spotted sibling species differing in living coloration might be involved (see fn. 14). However, Señaris and Ayarzagüena (2006) noticed no differences in vocalizations recorded at the type locality and on the summit. Nonetheless, the significance of color similarities (orange coloring) possibly shared by *jimenezi*-like frogs from the Auyán summit and the neighboring Chimantá massif are worth noting.

In any case, there are at least two similarly spotted and perhaps closely related species of *Hypsiboas* in Venezuela. *Hypsiboas jimenezi* of Auyantepui (and Chimantá?) shares remarkable similarity in color pattern with a still undescribed frog from Cerro Duida, well over 400 km SW of Auyantepui, where two specimens were collected in amplexus by G.H.H. Tate in 1929 (fig. 34). The male of the Duida pair differs from *H. jimenezi* in having well-defined prepollical orifices for the protrusile spines.

Hypsiboas sibleszi (Rivero)
Figures 35–36

Hyla sibleszi Rivero, "1971" [1972]: 182–183, [pl. 1], figs. A–B (narrowband sound spectrogram and photo of preserved holotype). Holotype: Univ. Puerto Rico at Mayagüez 3177♂, from Paso del Danto, La Escalera, entre El Dorado y Sta. Elena de Uairén, 1300–1400 m, Serranía de Lema, Edo. Bolívar, Venezuela, collected March 22, 1968, by J. A. Rivero and J. Pulido.

Hyla sibleszi: Hoogmoed, 1979a: 23–33 (extensive redescription and diagnosis), figs. 7 (hand and foot), 8 (tadpole), pls. 3a (preserved spec.), 5 (sound spectrogram). Duellman, 1997: 19–20, fig. 11[B] (color photo of female).

Hypsiboas sibleszi (Rivero), Faivovich et al., 2005: 88, 162.

MATERIAL: Camp 4, 1600 m: AMNH A-164849–164851. All from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

These frogs were found only at Camp 4, where conditions were much wetter than at the other camps. Five adult males were collected. These males are 30.6–33.1 mm SVL ($\bar{x}$ = 31.46 mm, S.D. = 1.02 mm, N = 5); tibia length 53%–54% of SVL; head width 39%–41% of SVL, 84%–91% of diagonal head length; eye length slightly shorter than distance from its anterior edge to center of naris (EN/eye = 1.06–1.13); upper eyelid less than half the width of interorbital space (IOD/eyelid = 2.00–2.50); disc on finger III wider than discs on toes III– IV, which are subequal.

COLORATION: In life (fig. 35), the ground color of the five adult males varied either from light green to yellowish green, or

Fig. 34. An undescribed species of *Hypsiboas* from 1463 m elevation on Cerro Duida (Amazonas, Venezuela), ×1.3. AMNH A-23186♂, 29 mm SVL (left) and AMNH A-23185♀, 34 mm SVL (right), collected in amplexus by G.H.H. Tate in January 1929. The sparsely spotted limbs and dark canthal lines appear to relate these frogs to *Hypsiboas jimenezi* from Auyantepui (see fig. 31). Cerro Duida lies some 400 km SW of Auyantepui.

from pale to medium blue-green.[15] A variable number of small pale yellow dots sparsely scattered on dorsum, conspicuous or not; some specimens with dorsal surfaces also densely dotted with brown melanophores overall, this dotting inconspicuous or not evident in others (but conspicuously present in all specimens in preservative). Digits distally light orange above and below. Pale interorbital bars and dorsolateral stripes are lacking in this sample.

Vocal sac light yellow-green; rest of ventral surfaces light blue-green. Venter somewhat transparent, with heart, liver (including gall bladder), and intestinal tract tightly bound in white peritoneum; linea masculina visible.

Bones green. Iris pale bright yellow, with suffusion of light red-brown around pupil and with fine black venation.

NATURAL HISTORY AND VOCALIZATION

Specimens of *Hypsiboas sibleszi* were found on the night of February 23, calling on vegetation from a few cm to about 2 m above a stream at Camp 4. The recorded advertisement call is a single note of 0.06 sec duration, with a fundamental frequency at about 1125 Hz and with emphasized frequency in the range of 1750–2080 Hz. Internote interval is variable; seven calls of what seem to be the same individual are spaced 9.2–23.6 sec apart on a recording made at 18.8°C. (Hoogmoed [1979a: 29] reported more frequent calling at 10–11 notes per minute.)

The waveform and wideband spectrogram of *H. sibleszi* show the note to be strongly pulsatile albeit somewhat loosely organized,

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[15] Hoogmoed (1979a: 26) suggested that dorsal ground color was sexually dimorphic in *Hyla sibleszi*, with females dark bluish green and males light green. However, both colorations apply to our sample of adult males, and Duellman (1997: 11) published a photograph of a light green female.

Fig. 35. *Hypsiboas sibleszi*, showing color variation in life. Above, AMNH A-164849, 31 mm SVL; below, AMNH A-164850, 33 mm SVL. Both are adult males.

with the initial two pulses well separated from the others (fig. 36). Another waveform and wideband spectrogram from an unstated locality in Bolívar state shows at least one initial pulse to be well separated (Señaris and Ayarzagüena, 2006: fig. 6).

The notes have a quacklike sound on our February recording from the Auyán summit, which seems consistent with Duellman's (1997: 19) "wrack" for frogs calling in January in the La Escalera Region about 110 km E of Auyantepui (region of the type locality of *H. sibleszi*). However, Duellman contrasted that sound with "one or two soft *Phyllomedusa*-like clucks" given by frogs calling during the month of July, which suggests the possible existence of temporal complexity in vocalization. In another report from the La Escalera region, Hoogmoed (1979a: 39, pl. 5C) quite differently described the call as a short low-pitched "wraah", but

his sound spectrogram is uninformative, showing an overloaded note (probably narrowband) on a mislabeled time axis. Rivero ("1971" [1972]: 189, fig. A) showed two notes, about 1.7 sec apart, graphed with a narrowband filter.

REMARKS

Hypsiboas sibleszi is best known from Hoogmoed's (1979a) detailed redescription and analysis of distribution. It is an upland species appearing to have a moderately widespread distribution from Guyana (MacCulloch and Lathrop, 2005: 27, color fig. 2F) west into Bolívar, Venezuela, although the range is probably disjunct. It was thought to be one of the few amphibians and reptiles shared between Auyantepui and the neighboring Chimantá (Myers, 1997), but the Chimantá specimens prove to be a different species that is close to *H. jimenezi* (fn. 14; Señaris and Ayarzagüena, 2006: 316).

The westernmost-known station for *Hypsiboas sibleszi* is some 400 km W of Auyantepui, at Cerro Guanay, where the frogs are relatively large (see map in Señaris and Ayarzagüena, 2006: fig. 5). Gorzula and Señaris (1999: 36) mentioned four males collected by Gorzula that measured 39–42 mm SVL ($\bar{x} = 40.3$ mm). Our sample of 20 adult males from Cerro Guanay are in the range of 34.0–39.0 mm SVL ($\bar{x} = 35.75$ mm, SD 1.480 mm); the one adult female in our sample is 41.2 mm SVL. Even allowing for individual measuring error, there may be a size difference between the demes sampled by Gorzula and by us on Cerro Guanay. Some of the Guanay frogs have a pale interorbital bar and dorsolateral stripes but were otherwise similar in living color to our sample from Auyantepui. However, differences in vocalization (e.g., in note duration and pulse structure) may necessitate specific status for the *sibleszi*-like frogs on Cerro Guanay (unpublished data).

Tepuihyla edelcae
(Ayarzagüena, Señaris, and Gorzula)
Figures 37–40

Ololygon sp.: Gorzula, 1992: 269, color photos 152, 154 (observations on distribution and natural history).
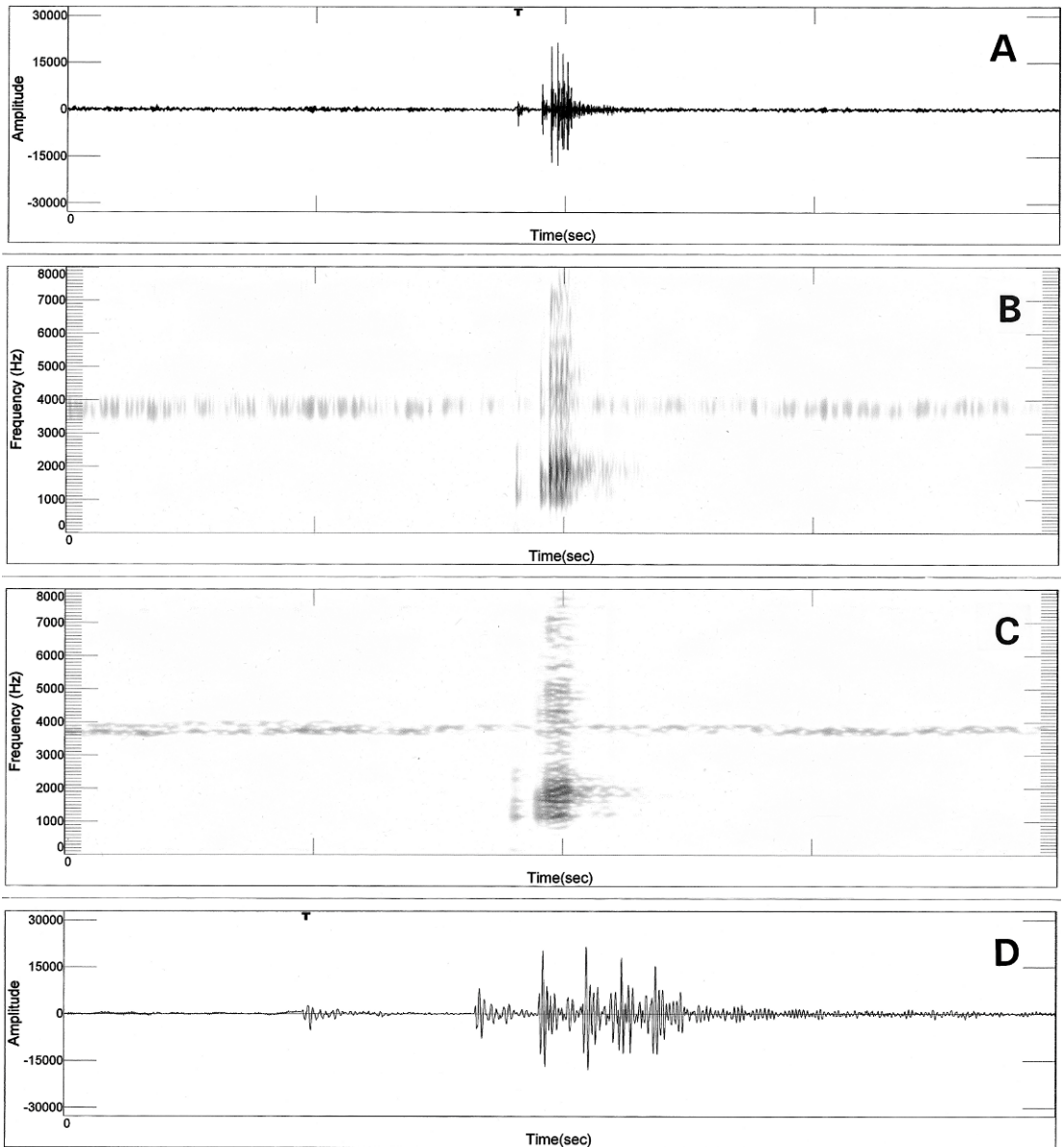
Fig. 36. Vocalization of *Hypsiboas sibleszi*. A strongly pulsatile, single-note call shown in a time frame of 1 sec. **A:** Waveform (T = first pulse). **B:** Wideband (323 Hz) spectrogram. **C:** Narrowband (63 Hz) spectrogram. **D:** Expanded waveform showing clear separation of pulses. First pulse (tagged T) is spaced 190 msec from second pulse; excluding terminal trail-off in signal, total duration of pulses 1–7 = 550 msec.

Sound across spectrograms at 3750 Hz is of calling orthopterans. (Unvouchered recording of specimen [associated with AMNH A-164849–164851 and EBRG 2731–2732] calling from above stream at Camp 4, February 23, 1994, 10:49 p.m., air temperature 18.8°C. AMNH herpetology reel 263: 4.)

Osteocephalus sp.: Duellman and Hoogmoed, 1992: 15 (undescribed species from Auyantepui).

Osteocephalus edelcae Ayarzagüena, Señaris, and Gorzula, 1992a: 122, fig. 4 (hand and foot). Holotype MHNLS 10626(♂) from Auyantepuy, 10.8 km al este del Salto Angel, Estado Bolívar, Venezuela (5°58′N, 62°29′W), 1970 m, collected May 25, 1984 by S. Gorzula.

Tepuihyla edelcae: Ayarzagüena, Señaris, and Gorzula, 1992b: 215.

MATERIAL: Camp 1, 1700 m: AMNH A-164865–164878, 164879–164880 (larvae), EBRG 2596–2609, 2628 (larvae). Camp 2, 1750 m: AMNH A-164881–164899, 164900–164909 (larvae), EBRG 2610–2619, 2629–2631 (larvae). Camp 3, 1850 m: AMNH A-164910–164917, 164918–164923 (larvae), EBRG 2620–2627, 2632–2634 (larvae). Camp 4, 1600 m: AMNH A-164924–164926, EBRG 2637–2639. Camp 5, 2100 m: AMNH A-164927–164931, 164932–164935 (larvae), EBRG 2640–2644, 2635–2636 (larvae). All from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

ADDITIONAL MATERIAL: Auyantepui Plateau, 2200 m (7218 ft): AMNH A-46033–46035, 146339 (larvae), from the 1937–1938 AMNH–Phelps Venezuelan Expedition.

Females are larger than males ($\bar{x}$ female SVL/$\bar{x}$ male SVL = 1.24) and there is little overlap in size between sexually mature males and females. The following measurements were obtained by combining all adult males and all adult females from the 1994 Expedition:

Adult ♂ (51), $\bar{x}$ = 36.53, SD 2.084, 32.0–41.5 mm SVL
Adult ♀ (23), $\bar{x}$ = 45.43, SD 2.858, 39.3–50.5 mm SVL

There is no obvious variation in size across sites (data not shown); analysis of variance for males from camps 1–5 shows no statistically significant difference between the mean SVL at the 95% confidence level (F = 2.30, P = 0.0731).

All adult males have a well-developed nuptial pad on the base of the thumb; the pad is a pale brown color owing to minute centers of cornification (visible with a dissecting microscope). The vocal slits of males are relatively small apertures situated near the corner of the mouth; it is difficult to find these openings on some specimens, and a few individuals of adult size with nuptial pads seem to lack them. There is a degree of sexual dimorphism in skin texture, with males well covered with small spicules and with females tending to have smoother or slightly pustulate skin, as seen in figure 38 (males above, female below); some adult females, however, do have sparse spicules (especially anteriorly) additional to smoother pustules. Adult males have enormous white testes that fill most of the body cavity; females in the sample have convoluted oviducts and numerous small pigmented ova.

COLORATION: Based on a large sample of 95 specimens, *Tepuihyla edelcae* was diagnosed as having a uniformly dark dorsal color (Ayarzagüena et al., 1992a: 122), with some limited variation being mentioned in the description (p. 126). However, in life this is a colorfully variable frog, at least on Auyantepui (figs. 37–38), with a basic dorsal color of brown, orange-brown, red-brown, or gray; a few specimens had the dorsolateral areas slightly lighter than the darker mid-dorsum and one individual (AMNH A-164916) has distinct pale dorsolateral stripes that are retained in preservative. Some frogs had orange or yellowish spots or blotches over the head and dorsum and also on the throat. Limbs colored like the dorsum, rarely with indication of dark crossbanding; rear of thigh orange-brown to gray, sometimes with small areas of silvery gray frosting. Upper lip white or variably suffused with dark pigment. Throat and venter dirty white, turning gray under the limbs. Bones white. The iris varies from light bronze to dark brown or gray, with variable black venation and a tendency for a dark horizontal stripe through the pupil.

In preservative the frogs are darker, but any light markings are well retained in our material. Two specimens were noted as having either faint or distinct dark crossbanding on the limbs (AMNH A-164869, 164916, respectively); the rear of the thigh is light to dark orange. Some specimens retain a distinct pale labial line in preservative; Ayarzagüena et al. (1992a: 126) seemed to suggest that this is a juvenile character retained in some adults. We see no ontogenetic linkage in the Auyantepui material,

Fig. 37. *Tepuihyla edelcae*. Color variants top to bottom from Camp 1 (EBRG 2596♂, 38 mm SVL), and Camp 2 (EBRG 2611♂, 35 mm SVL). (Not to scale with fig. 38.)

inasmuch as the upper lip is dark in some small specimens such as AMNH A-164872 (a metamorph 16 mm SVL), EBRG 2639 (20 mm), and EBRG 2641 (25 mm).

TADPOLES

The tadpole of *Tepuihyla edelcae* has not been described, although there was reference to its habitat and behavior in the original description (Ayarzagüena et al., 1992a). Ayarzagüena et al. (1992b: 216) cited a formula of 2/3 for the genus, without specifying which species were examined. *Tepuihyla edelcae* differs from that generic diagnosis in having 2/4 larval tooth rows as the most common condition in a variable formula including also 2/2 and 2/3.

Fig. 38. *Tepuihyla edelcae*, showing color variation at Camp 3. From top to bottom: AMNH A-164910♂, 33 mm SVL; EBRG 2621♂, 37 mm SVL. EBRG 2620♀, 51 mm SVL.

We netted tadpoles from shallow sandstone pools at four of our five camps. At camp 1, 11 tadpoles (stages 25–32) were taken from a surface pool near a clump of *Brocchinea*. Three collections were made at Camp 2, with one large sample containing only stages 24–25 (N = 64), and with two small samples containing a greater range of stages (27–42, N = 9, and 25–39, N = 12). At camp 3, two collections included only early stage-25 tadpoles (N = 36, 55), whereas a
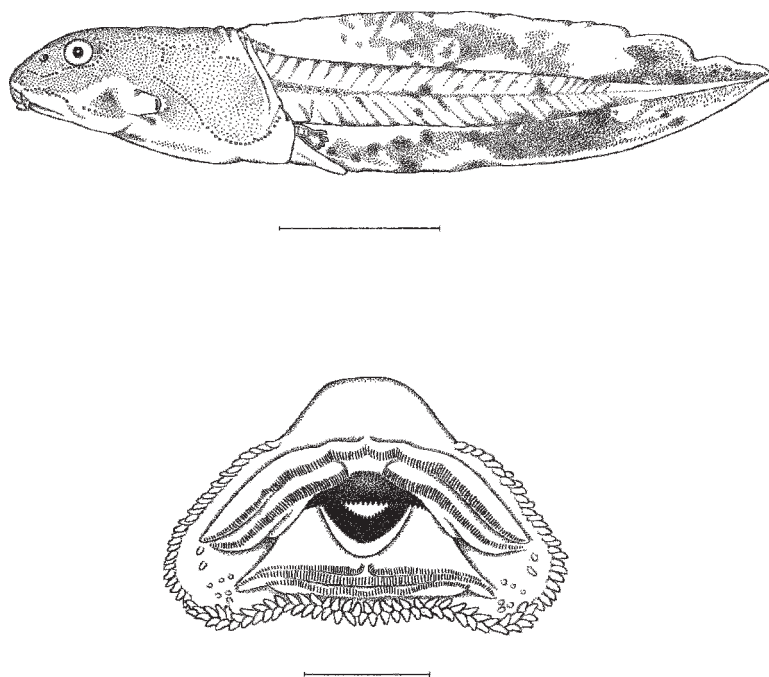
Fig. 39. *Tepuihyla edelcae*. Stage-37 tadpole and mouthparts of same specimen (AMNH A-164907). Larvae of this species have 2/2, 2/3 (shown here), or 2/4 tooth rows, with the last formula being most common; when present, row P4 (the last to appear) often is poorly developed. Scale lines = 10 mm above and 1 mm below.

third included stages 25–40 (N = 75). Two small collections of 13 larvae each from at Camp 5 consisted of stage-25 tadpoles and a single stage-36 tadpole.

We did not find tadpoles of other species in pools with *Tepuihyla*, although some other pools contained tadpoles of two species (*Hypsiboas jimenezi* and *Anomaloglossus tepuyensis*, or *H. jimenezi* and *Leptodactylus rugosus*).

The following description is based on one stage-33 larva (AMNH A-164902) and one in stage 37 (AMNH A-164907 [fig. 39]), followed by notes on ontogenetic change. See table 4 for additional measurements.

HABITUS AND PROPORTIONS: Head and body elliptical and rounded at both ends in dorsal view; maximum body width 53.8%–54.6% of head-body length. Body higher than wide (maximum body depth about 117.6%–118.2% of maximum body width); body flattened dorsally and somewhat wedge-shaped in profile, increasing in depth from anterior to posterior. Eyes dorsal, directed laterally, not visible from below. Nares dorsal, directed anterolaterally, approximately equidistant between tip of snout and eye. Spiracle sinistral, low on body, a short tube (1.4–2.2 mm long) directed posteriorly with medial wall attached to body; spiracle opening at 58.2%–59.5% of head-body length. Vent tube attached to ventral fin, opening dextral to fin.

Lateral line system somewhat indistinct. Supraorbital and infraorbital branches forming a loop around eye; superior and middle trunk branches originate behind eye; superior branch continues posteriorly in dorsal fin above musculature; middle trunk branch continues posteriorly in the middle of tail musculature; inferior body branch originates on body near spiracle and curves ventrally to the ventral body.

Tail 64.7%–66.5% of total length; maximum tail height approximately equal to body depth; dorsal fin not extending onto body, higher than ventral fin; musculature height greater than fin height; margins of dorsal fin slightly scalloped; tail tip rounded.

TABLE 4
Measurements (in mm) of *Tepuihyla edelcae* Tadpoles
(Values are ranges followed below by means $\pm$ 1 SD when N > 2)

Stage	N	Total length	Head–body length	Body width	Body depth	Tail depth	Oral disc width
24/25	3	12.0–12.6	4.0–4.3	2.1–2.3	2.3–2.5	2.5–2.6	0.80–0.85
		12.32 $\pm$ 0.32	4.11 $\pm$ 0.13	2.20 $\pm$ 0.10	2.42 $\pm$ 0.10	2.58 $\pm$ 0.03	0.83 $\pm$ 0.03
25E	11	15.36–17.28	5.2–7.4	2.6–3.8	3.3–4.7	3.0–4.3	1.2–2.0
		16.29 $\pm$ 0.73[a]	6.04 $\pm$ 0.75	3.29 $\pm$ 0.41	4.01 $\pm$ 0.50	3.61 $\pm$ 0.48	1.46 $\pm$ 0.31
25L	21	23.6–41.8	10.0–18.6	4.7–9.8	6.0–13.6	4.6–9.3	2.2–4.0
		34.22 $\pm$ 6.37[b]	13.85 $\pm$ 2.91	7.00 $\pm$ 1.62	8.66 $\pm$ 2.44	6.66 $\pm$ 1.62[c]	3.11 $\pm$ 0.60
26	1	29.3	10.6	5.5	6.4	5.8	2.3
27	2	35.2[d]	11.8–15.4	6.5–8.3	7.5–9.9	6.2–8.7	2.5–3.1
28	1	–[e]	12.8	6.5	7.7	6.4	3.0
31	1	42.1	14.1	6.7	8.0	6.0	2.9
32	1	39.2	13.4	7.2	8.5	7.0	3.0
33	1	34.4	13.3	6.7	8.0	6.0	2.9
36	2	38.9[d]	13.6–17.6	6.6–9.9	8.0–12.3	6.1[d]	3.1–3.5
37	2	42.1–44.7	14.1–15.8	7.7–8.5	9.1–10.0	6.9–9.3	2.5–3.4
39	1	–[e]	17.0	9.0	11.0	10.0	3.3
40	2	34.28[d]	12.6–15.7	6.4–7.8	8.3–10.2	6.0–7.9	2.6–2.9

[a] N = 9 (two larvae with broken or incomplete tails).
[b] N = 15 (six with broken or incomplete tails).
[c] N = 19 (two with damaged tails).
[d] N = 1 (one with damaged tail).
[e] Tail broken or incomplete in only specimen.

PIGMENTATION: In preservative, head-body brown dorsally and laterally; ventral skin clear, with underlying tissue having an iridescent blue sheen; tail musculature tan, flecked with melanophores, becoming vaguely blotched posteriorly. Dorsal and ventral fins brown (heavy melanophore deposition), paler at tail tip and adjacent to body on lower fin.

MOUTH PARTS: Mouth ventral. Oral disc not emarginate. Labial teeth in 2/3 (AMNH A-164907) or 2/4 rows (AMNH A-164902); A1 and A2 rows subequal in length, A2 row with distinct median gap; P1 slightly shorter than P2; P3 either shorter than P1 or equal to P2; P1 with or without a short gap in median curvature; P4 row (in AMNH A-164902) small and barely keratinized. Upper jaw sheath a broad arch bearing pointed serrations and with slender lateral processes, its surface with a minutely pebbled texture that is highly reflective under certain light conditions. Lower jaw sheath V-shaped with pointed serrations. Marginal papillae with a broad anteromedial gap on upper labium; one row of marginal papillae on upper labium and along lateral margins of disc; two rows of slightly blunter papillae on

lower labium; several pointed to blunt submarginal papillae laterally.

ONTOGENETIC CHANGES: In three available tadpoles of *Tepuihyla edelcae* in stage 24/25, maximal tail height exceeds body depth, and body depth and width are approximately equal. The body depth exceeds tail height and body width in all other stages. Changes in body size are summarized in table 4.

The three larvae in stage 24/25 have paired patches of raised, pigmented skin posterior and lateral to the oral disc. These raised patches may be adhesive glands; they are reduced to pigmented spots in early stage-25 larvae, with the spots disappearing by late stage 25.[16]

The stage 24/25 larvae have 2/2 tooth rows that are barely keratinized; jaw sheaths are keratinized in this stage and pointed serra-

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[16] According to Altig and McDiarmid (1999: 34), adhesive glands (when present) are transient structures usually visible between stages 18–25 and sometimes persisting as pigmented spots for several stages later. They serve "to provide stabilization prior to the further development of the oral disc and tail which afford more coordinated adhesion and locomotion for active tadpoles."

tions are present; marginal papillae are also present in these tadpoles but submarginal papillae are lacking. Early stage-25 tadpoles have 2/3 labial tooth rows; the P3 row is the smallest and lightly keratinized; these tadpoles also lack submarginal papillae. The posteriormost tooth row (P4) is the last to appear and it is often not well developed. The submarginal papillae also appear relatively late in development.

Variation in the tooth-row formula is as follows: The three available tadpoles in stage 24/25 have 2/2 tooth rows; some tadpoles in stages 25 (N = 6), 26 (1), 27 (2), 33 (1), and 37 (1) have 2/3 tooth rows; all others (stages 25–40) have 2/4 tooth rows.

Some unusual configurations of mouthparts are not associated with ontogeny and may be environmentally caused (see Natural History). In one stage-33 tadpole (AMNH A-164902), the P4 row is short, is situated to the right of the midline, and is positioned in the marginal row of papillae. In some cases, the tooth-row ridges are comprised of short and long sections (i.e., A1 in three sections—two short lateral and one long medial section; A1, A2, or P2 in two sections—one short and one long). In some tadpoles, the tooth-row ridges are unusually short (P1 and P2 missing on the left, A1 and A2 short on right, P3 short on right). In many tadpoles, the P4 row is small, difficult to discern, and mixed with the marginal papillae. In one late stage-25 larva, there are large pointed papillae between tooth rows), and in one there is a single papilla in the median gap on the upper labium.

DISTRIBUTION, NATURAL HISTORY
AND VOCALIZATION

Tepuihyla edelcae is the most common frog on Auyantepui and occurred at all five of our camps (although only tadpoles were found at Camp 5). It was the only amphibian taken from the summit by the 1937–1938 AMNH–Phelps Venezuelan Expedition (it was not found at the lower-elevation camps). The species was described from an abundance of specimens collected mostly by S. Gorzula on Auyantepui (the type locality) and various parts of the Chimantá massif (Ayarzagüena et al., 1992a). Señaris and MacCulloch (2005:

21) stated that *Tepuihyla edelcae* is ''Endemic to summits of Auyán-tepui and Macizo de Chimantá … 1630–2600 m'', but Gorzula and Señaris (1999: 49) had additionally reported a specimen from ''Altiplanicie S Terekyurén-tepui'' in the Los Testigos range to the east of Auyantepui. It occurs on Cerro La Luna (Gorzula and Señaris, 1999: 49), an erosional remnant standing north of Auyantepui (map 1), and might also be expected on the poorly known Uaipantepui, a satellite mountain south of Auyantepui (Huber, 1995a: fig. 1–25).

Tepuihyla edelcae is best known through the work of Stefan Gorzula, who studied it on the Chimanta massif and on Auyantepui. Gorzula noted its affinity for tube bromeliads, of which the species *Brocchinia hechtioides* and *B. reducta* occur on Auyantepui (Steyermark, 1967; Givnish et al., 1997). On Chimantá, Gorzula recounted that this frog

is a very easy species to locate, since the majority utilize *Brocchinia hechtioides* as hiding places during the day. It is enough to walk carefully through the *turberas* where this bromeliad abounds, in order to observe them in the upper part of the tube of the *Brocchinia*. They are frightened by a vibration or a slight shadow, hiding themselves in the water reserve in the base of the tube. Even if the *Brocchinia* provides an appropriate habitat for the refuge of adult specimens of this frog, the small reserve of water in the base of the tube has characteristics that are not favorable for spawning. This frog spawns in temporary puddles in the *turberas* or in shallow pools between rocks adjacent to colonies of *Brocchinia*. (translated from Gorzula [1992: 270], under *Ololygon* sp.)

Aside from the possibly unfavorable characteristics of the bromeliad water mentioned by Gorzula, the relatively large number of small ova contained by gravid female *Tepuihyla*, and the enormous size of the testes, suffice to show that it is not a bromeliad breeder—the small tube bromeliads could hold only a small fraction of the clutch. On Auyantepui, Gorzula found 12 *T. edelcae* in a transect of some 100 m × 10 m, representing one frog for every 30 *Brocchinia*; both *Brocchinia hechtioides* and (in our experience) *B. reducta* are utilized, or sometimes the tank bromeliad *B. acuminata*, usually with only a single frog in a bromeliad (Ayarzagüena et al., 1992a:

126–127). The claim (loc. cit.) that this species uses its head as a plug to prevent evaporative water loss needs confirmation, inasmuch as the skin is not co-ossified with the skull as in the case of other hylid genera exhibiting the behavior (Trueb, 1970).

We collected *Tepuihyla* at night at Camp 1, on low vegetation (< 0.5 m aboveground). The majority of frogs were on, or peering from within, tube bromeliads growing in patches on flat sandstone outcrops (fig. 3, bottom). One froglet peering out of a *Brocchinia* tube was a recent metamorph.

We had the impression at Camp 1 that *Tepuihyla edelcae* was indeed associated primarily with tube bromeliads, but our experience with them at Camp 3 suggested much greater behavioral plasticity. Although we avoided destroying bromeliads because the frogs are easily spotted in the beam of a headlight at night, *Tepuihyla* seemed less common in the tube bromeliads at Camp 3 than at Camp 1. Instead we found them in a greater diversity of situations, such as in the middle of the stream bed at night, on various kinds of low vegetation at night (usually < 1 m aboveground), and by day under rocks on open sandstone flats, sometimes in company with other concealed frogs (*Leptodactylus rugosus*) or lizards (*Tropidurus bogerti*).

Two groups of unusually large stage-25 tadpoles collected from drying pools near Camp 5 have a high incidence of damaged fins, suggesting that high tadpole density in a decreasing volume of water may have had led to tail damage from abrasion and/or cannibalistic events.

Some abnormalities of the larval tooth rows (see above) may have an environmental cause. Bresler (1954) experimentally found that tooth-row abnormalities in *Bufo* and *Rana* developed more frequently at high temperature. Temperature in small sandstone pools at high elevation fluctuates widely, as shown by Gorzula (1992: 270), who recorded a 15-hour temperature range of 12.2–27.0°C in a pool containing larvae of *Tepuihyla edelcae* (reported as *Ololygon* sp.), at an elevation of 2100 m on the neighboring Chimantá. Gorzula noted that the tadpoles of this species are inactive on the bottom during the colder hours of night.

At Camp 1, *Tepuihyla edelcae* was calling back and forth from bromeliads around a small pond at night. Two individuals recorded seemed to be responding to one another in a duet (fig. 40). One male (AMNH A-164873) gave single-note calls, his neighbor double-note calls. The note sounds like a soft chickenlike ''cluck''. Each well-spaced call note is 0.02 sec in duration and nearly nonpulsatile, with but slight indication of two poorly separated pulses. Narrowband analysis shows a fundamental frequency of about 1400 Hz, with poorly resolved harmonics at roughly 1400 and 2300 Hz.

REMARKS

The gender of *Tepuihyla* was stated to be masculine by its authors (Ayarzagüena et al., 1992b: 215), presumably because the Pemón Indian word *tepui* (or *tepuy*) is treated as masculine in Spanish. But gender must be based on the *last* component of a compound generic name ending in a Latin word (ICZN, 1985: art. 30a; 1999: art. 30.1.1). Although *Hyla* was derived from the name of the mythological boy Hylas (Laurenti, 1768: 32–33), the generic name itself is universally and correctly treated as feminine, as recently reaffirmed by Myers and Stothers (2006).

Required correction of the gender of *Tepuihyla* from masculine to feminine has no effect on the endings of the six specific names transferred to that genus by Ayarzagüena et al. (1992a: 215). Most are singular nouns in the genitive case (i.e., four are dedicatory names or ''patronymics'', including two, *aecii* and *edelcae*, derived from acronyms). A fifth name, *rimarum* (''of or belonging to cracks or crevices''), is a noun in the genitive plural.

As originally explained by Ayarzagüena et al. (1992b: 131), the sixth specific name seemed as if it should be a noun in apposition: ''*luteolabris*, derivado del latín *luteo* (amarillo) y *labris* (labio)''. However, *labris* is not the Latin substantive equivalent of Spanish *labio* (= lip, a noun). The name *luteolabris* is an adjective, derived from the stem of *luteus* + connecting *o* + *labris* (''lipped''). The last component is an adjective derived from the Latin noun *labrum* and
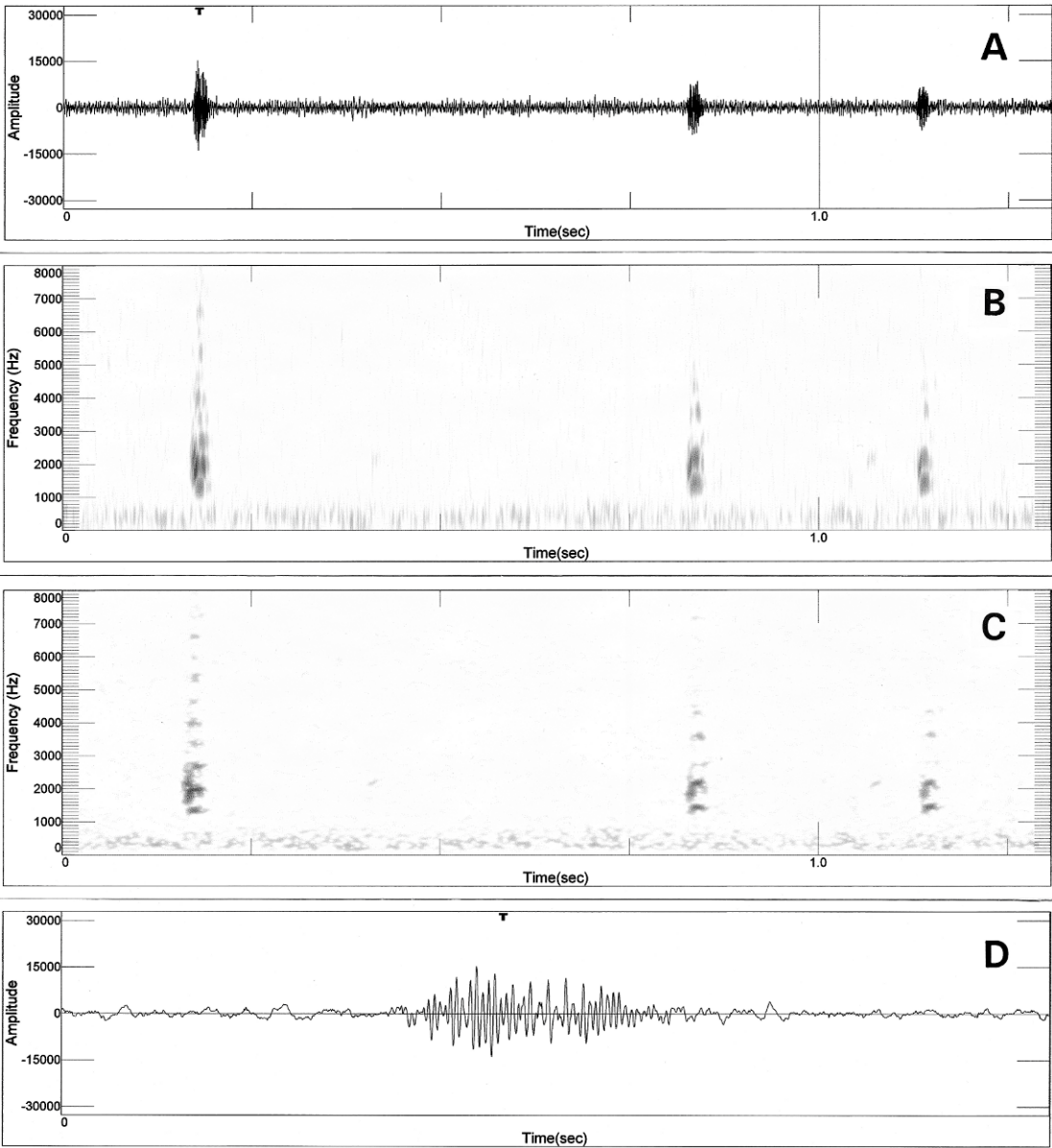
Fig. 40.   Vocalization of *Tepuihyla edelcae*. A single-note call (left) and a double-note call (right) from two duetting frogs; time shown = 1.3 sec. **A:** Waveforms. **B:** Wideband (323 Hz) spectrogram. **C:** Narrowband (63 Hz) spectrogram. **D:** Expanded waveform of single-note call tagged in first panel; note duration = 0.03 sec. (Single-note individual AMNH A-164873, other frog not captured, both calling from tube bromeliads at Camp 1, February 4, 1994, 9:20 p.m.; air temperature 15.4°C. AMNH herpetology reel 263: 1.)

suffix *-is*, thus *labris* (masculine and feminine) and *labre* (neuter)—the declension like that of *collis* (''necked''), from *collum* (Brown, 1956: 45). Compared with alternative adjectives and participles such as *labralis* (from *labrum*), *labialis*, and *labiatus* (the last two from *labium*), the shorter *labris* is a better choice for use in compound names, and it is

employed mainly (if not entirely) as a suffix in taxonomic compounds.

Words formed with adjectival suffixes like –is (with a short vowel) must not be confused with the dative and ablative plural cases (normally with long *i*) of the original nouns, because these *cannot* qualify as specific names. Although the ablative plural noun *labris* (''with lips'') might have been preempted for use as an adjective, the adjective properly derived from the stem of *labrum* is formed with -is—the adjective-forming suffix meaning ''with or having the nature of'' (Brown, 1956: 549).[17]

The Venezuelan frog *Hyla rodriguezi* Rivero (1968b) was transferred to the genus *Osteocephalus* by Duellman and Hoogmoed (1992: 16). Ayarzaqüena et al. (1992a) described five new species of *Osteocephalus* and established a *rodriguezi* species group. In the following issue of the same journal, Ayarzaqüena et al. (1992b) elevated the group to generic status under the name *Tepuihyla*. Unfortunately, no summary was given of species possessing the purported diagnostic characters, including various cranial features, 2/3 larval tooth rows, and sperm with two tail filaments.

Ayarzagüena et al. (1992b) said that, according to Fouquette and Delahoussaye (1977), *Ololygon* [now *Scinax*] and *Sphaenorhynchus* were the only other hylid genera with double-tailed sperm (although Fouquette and Delahoussaye also mentioned a species of *Hemiphractus*) and therefore paid particular attention to comparing *Tepuihyla* with *Scinax*. Duellman and Yoshpa (1996) commented that most morphological features mentioned by Ayarzagüena et al. ''are homoplastic in their appearance in diverse genera of hylids''. Duellman and Yoshpa said that if ''all species of *Tepuihyla* have a double-filamented sperm, this may be the only synapomorphy [if independently derived] for the genus'', or else a synapomorphy uniting *Tepuihyla*, *Scinax*, and *Sphaenorhynchus*. (*Tepuihyla* most recently has been allied with *Osteocephalus* and *Osteopilus* [Faivovich et al., 2005: fig. 12]).

However, there are two problems involving the sperm character in the above context. Although Fouquette and Delahoussaye (1977) did in effect use the character as a derived feature to define *Ololygon* [now *Scinax*], they also presented valid reasons for considering two or more sperm tails (as they understood the character) as the primitive condition among frogs—a plesiomorphic not a synapomorphic character. But this is now unimportant, because it seems that the two-tailed sperm character was a misinterpretation of morphology that is not well studied by standard light microscopy. After examination of ultrastructural data from transmission electron microscopy of the spermatozoan tail of *Scinax ranki* (as *Hyla ranki*), Taboga and Dolder (1993: 85) summarized:

> The flagellum contained a typical vertebrate type axoneme and an electron dense, F-PTA positive axial rod, in parallel association and interconnected by an undulating membrane. The parallel arrangement had previously and erroneously been interpreted as a separate structure, or double filaments, when examined by light microscopy. These results suggest that this structure is not a dependable taxonomic character.

Kuramoto (1998: 113) independently noted the presence of an axonemal fiber and axial rod in hylid sperm tails and, in reference to Fouquette and Delahoussaye's (1977) taxon-

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[17] The inclusion of etymological information for new names in zoology is customary nowadays and is recommended by the Code (International Commission, 1999: art. 25B, app. B5). But it has escaped the attention of many authors, reviewers, and editors (nor is it mentioned in the Code) that an important reason for so doing is to enable future workers to determine easily if a new generic combination will require changing the ending of a specific name for mandatory agreement in gender. The difference between adjectival specific names (adjectives and participles in the nominative singular), which *must* agree in gender with the generic name, and unchangeable nouns in the genitive case or in the nominative singular (standing in apposition to the generic name), is not always self-evident and sometimes impossible to determine by inspection. It would be helpful if authors were to explicitly give the part of speech of new names; if the author cannot do so and cannot find the name or its components in standard Latin or Greek dictionaries, a little research or a substitution might be in order prior to publication. It needs remembering, however, that Latin is a dead language. Many words, including adjectives formed by regular transformations of Latin nouns, may not be shown in Latin dictionaries unless they are established in the classical literature.

omy, suggested that "If a single tail fiber involves two flagellar components … it seems not essential to separate 'two-flagellated' from 'single-flagellated' species, until further studies reveal that each of the two 'flagellas' contains an axoneme". Sperm morphology appears to have potential for taxonomic insight, but comparative data from ultra-structural studies are needed for it to be useful. The recognition of *Scinax*, however, is not considered to be dependent on the dubious sperm character (Faivovich, 2002; Faivovich et al., 2005).

Although the monophyly of *Tepuihyla* remains to be rigorously tested (Faivovich et al., 2005: 110), Ayarzagüena et al. (1992a, 1992b) have usefully called attention to this interesting group of high-elevation frogs. *Tepuihyla*, like *Stefania* below, is a Guayana endemic comprised primarily of tepui species, but with representatives in nontepui habitats.

FAMILY HEMIPHRACTIDAE
(FAMILY CRYPTOBATRACHIDAE AUCTORUM)

One genus, *Stefania*, occurs on the summit. It is one of five genera of Neotropical "marsupial frogs" that formerly were grouped in the hylid subfamily Hemiphractinae. Consistent with growing evidence from other authors, the hemiphractines were formally removed from Hylidae by Faivovich et al. (2005: 49–50), who questioned the group's monophyly while tentatively placing it as a subfamily of paraphyletic Leptodactylidae. Subsequently, Frost et al. (2006) separated the group into three families—Hemiphractidae (*Hemiphractus*), Cryptobatrachidae (*Cryptobatrachus*, *Stefania*), and Amphignathodontidae (*Flectonotus*, *Gastrotheca*). However, Wiens et al. (2005, 2007) argue for recognition of a monophyletic family Hemiphractidae. Differences between these alternative classifications remain to be resolved.

Stefania schuberti Señaris, Ayarzagüena, and Gorzula
Figure 41

Stefania ginesi Rivero: Duellman and Hoogmoed, 1984: 17 (2 juvs. from Auyantepui).
Stefania sp.: Gorzula, 1992: 271. Myers, 1997: 3.

Stefania schuberti Señaris, Ayarzagüena, and Gorzula, "1996" [1997]: 39, figs. 13–14 (drawings of hands and feet and dorsum of skull). Holotype MHNLS 12917(♂) from sector este, cima del Auyan-tepui, Estado Bolívar, Venezuela (5°53′36″N, 62°29′12″W), 1750 m, collected February 10, 1994, by J. C. Señaris. [The holotype was collected near Camp 2 during the 1994 AMNH–TERRAMAR Expedition.] Gorzula and Señaris, 1999: 48, color photo 39.

MATERIAL: Camp 2, 1750 m: AMNH A-164992–164997, EBRG 2686–2691, all topotypes. Camp 5, 2100 m: EBRG 2692. All from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

COLORATION: In life (fig. 41), *Stefania schuberti* was olive to olive-brown over the dorsal surfaces, with ill-defined black spotting and limb bars. The rear thigh surfaces were grayish brown with small vague spots of yellow or olive. Ventral surfaces were gray, with vague white mottling that is most evident on the chest. Iris olive above, below dark bronze greatly darkened by black venation.

Juvenile frogs of about 21–23 mm SVL were similar to adults, with some color differences. They were gray above, with a suffusion of reddish brown in the blackish spots and limb bars. The rear of thigh was black with gray flecking. Ventral surfaces were gray with whitish flecking, especially on the throat and chest. Iris pale gray across the upper third, very dark brown on the lower two thirds, with slight black venation (which did not seem to contribute much to the darkening of the lower two thirds).

NATURAL HISTORY: Most specimens were found at night at a series of low waterfalls below Camp 2 (fig. 7 top), where they were discovered mostly by eyeshine while they were looking out of crevices around the falls or sitting on wet rock. One adult female (EBRG 2691) was found by day on a sandstone wall in the dark of a crevice cave that had a floor of water. Two juveniles (21–23 mm SVL) were found by day under rocks on a sandstone ledge well above the waterfalls below Camp 2 (fig. 7, bottom). Another juvenile (30 mm SVL) was found under a rock near the south rim of Auyantepui, near Camp 5.

Stefania appeared to be reproductively inactive during our work in February. Calling was not heard (although vocal slits

Fig. 41. *Stefania schuberti*. Two specimens from the type locality. Above, a subadult female (AMNH A-164992, 51 mm SVL); below, an adult female of maximum known size (AMNH A-164993, 85 mm SVL). Photographs at same scale, near life size.

are lacking in male *Stefania*, at least a few species are believed to call [see Duellman and Hoogmoed, 1984: 8]). The two females judged as sexually mature at 62 and 85 mm SVL have convoluted oviducts and maturing ova of about 1.3 to 1.5 mm in diameter. Three immature females of 50–52 mm SVL have nonconvoluted oviducts and largest ova

of about 0.6–0.8 mm. The two adult males are 72 and 74 mm SVL.

REMARKS

Duellman and Hoogmoed (1984: 17) assigned two juvenile frogs from 2400 m on Auyantepui to *Stefania ginesi*. Gorzula (1992:

271) subsequently collected additional specimens on several tepuis, including Auyantepui, and recognized that on the basis of inadequate material more than one undescribed species had been identified as *S. ginesi*, which he considered endemic to the Chimantá massif. The matter was clarified in a revision by Señaris et al. ("1996" [1997]), who named *Stefania schuberti* as the species endemic to the summit of Auyantepui.

Señaris collected the holotype (a male 76 mm SVL) and three paratypes of *Stefania schuberti* at our Camp 2, with another 13 paratypes having been collected by Gorzula at two other localities on the summit. Data presented by Señaris et al. ("1996" [1997]: 12, 40) showed a larger size for males (49–76 mm SVL, N = 7) than for females (62.8–63.5 mm. N = 2). However, the largest of our two sexually mature females is 85 mm SVL, suggesting that females attain the larger size as is usual for most frogs, including *Stefania*.

FAMILY BRACHYCEPHALIDAE

The only genus on the Auyán summit is *Eleutherodactylus*, which, in a major taxonomic rearrangement, was recently transferred from family Leptodactylidae to a greatly expanded Brachycephalidae (Frost et al., 2006). Corroboration is needed for the proposed association. In any case, much confusion revolves around the huge polyphyletic genus ''*Eleutherodactylus*'' and tepui species are assigned provisionally (but see Note Added in Proof, p. 147).

Eleutherodactylus auricarens, new species
Figures 42–45, 47B, 47C

Eleutherodactylus sp.: Myers, 1997: 3 (small forest species on Auyantepui).
Eleutherodactylus auricarens (nomen nudum): Sánchez H. and Bisbal E., "2002" [2004]: 17 (mention of type specimens in EBRG).

HOLOTYPE: EBRG 2725 (field no. CWM 19213), an adult female from summit of Auyantepui at 5°54′N, 62°29′W (AMNH–TERRAMAR Camp 2), 1750 m elevation, Bolívar, Venezuela, collected February 9–11, 1994, AMNH–TERRAMAR Expedition.

PARATOPOTYPES: AMNH A-164951–164953, EBRG 2724, 2726–2727, with same collection data as holotype.

Fig. 42. *Eleutherodactylus auricarens*, new species. From top to bottom: AMNH A-164936, juv. ♂, 14 mm SVL; AMNH A-164937, adult ♀, 23 mm SVL; amplectant pair (AMNH A-164951♂, 17 mm SVL, A-164952♀, 25 mm SVL).

OTHER PARATYPES: Camp 1, 1700 m: AMNH A-164936–164950, EBRG 2709–2723, collected 2–4 February, 1994. Camp 4, 1600 m: AMNH A-164954, EBRG 2728–2729, collected 23 February 1994. All from the 1994 AMNH–TERRAMAR Expedition.

ETYMOLOGY: The specific name *auricarens* ("lacking ears") is an adjective of common gender derived from the Latin *auris* ("ear") + *carens* (the present participle of *careo*, "to be without"), alluding to the absence of the tympanic apparatus.

DEFINITION AND DIAGNOSIS: A small *Eleutherodactylus* belonging to the *unistriga-*

tus species group and characterized by the following combination of characters (in the format of Lynch and Duellman, 1980, 1997): (1) dorsal skin tubercular, ventral skin areolate; (2) tympanic membrane and annulus absent (annulus possibly vestigial in a few specimens, see Remarks); (3) snout truncate to bluntly pointed in dorsal view, rounded in profile; canthus rostralis gently concave or nearly straight, rounded; (4) upper eyelid weakly tubercular (tubercles low, subequal); (5) vomerine odontophores small but distinct, with detectable teeth, oblique, well separated and situated between and behind choanae; (6) males lacking vocal slits/vocal sac; weak nuptial pads seemingly present; (7) finger I shorter than II; broad discs on fingers II–IV; (8) weak lateral keeling but no fringes on fingers; (9) ulnar tubercles absent or low and inconspicuous (not forming a distinct line); (10) no pronounced calcar tubercle; (11) inner metatarsal tubercle oval, much larger than small outer metatarsal tubercle; (12) toes weakly keeled, webless; toe discs broad, subequal with finger discs; fifth toe much longer than third; (13) varying shades of brown above, with interorbital bar and often a vague undulating longitudinal dark marking on dorsum; polymorphism limited, but occasionally with a pale postocular stripe posteriorly widening to cover flanks, or with a few oblique dark stripes extending posteroventrad from indefinitely patterned dorsum; (14) four males about 16–18 mm, nine females 20–25 mm SVL.

Eleutherodactylus auricarens is distinguished from sympatric *E. pulvinatus* by absence of a distinct tympanic apparatus, which is externally well defined in *E. pulvinatus* (see following species account for other differences).[18] The only other *Eleutherodactylus* known to lack the tympanic apparatus in eastern and southern Venezuela is *E. yaviensis* from the northwestern tepuis, although specimens in one population of

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[18] Occasional specimens of *auricarens* have small indistinct circular areas (≈0.05 mm, fig. 47B, arrows) under the postocular ("supratympanic") fold that are suggestive of concealed tympana, but if the surrounding skin is cut and reflected, the expected tympanic membrane and annulus are found lacking. The occurrence of possible vestiges of the annulus in a few specimens remains to be corroborated (see under Remarks).

yaviensis (Cerro Yutajé) have a vestigial annulus and membrane concealed under the skin (see Remarks). *E. yaviensis* is a larger species with a higher degree of pattern polymorphism, although it lacks the vague undulating middorsal marking that is present in many specimens of *auricarens* (see Remarks for further comparisons between *E. auricarens* and *E. yaviensis*).

MEASUREMENTS OF HOLOTYPE (in mm): The holotype (figs. 44, 45) is an adult female as revealed by presence of large ova and convoluted oviducts. SVL 23.6, tibia length 13.6, foot length from proximal edge inner metatarsal tubercle to tip of toe IV 11.2, head width 9.2, head length on the diagonal from tip of snout to angle of jaw 8.0, upper eyelid width 2.7, interorbital distance 3.2, internarial distance 2.3, center of nostril to eye 3.0, eye length 3.1, tympanum absent, width of third finger disc and width of fourth toe disc both 1.3.

DESCRIPTION

The type series of 40 frogs includes only 13 specimens (4♂, 9♀) judged to be sexually mature. Maturity of females was determined through dissection by presence of enlarged ova and markedly convoluted oviducts. Maturity of males was more difficult to determine because vocal slits are absent, nuptial pads are but faintly developed, and testes are not greatly enlarged. However, the largest males (16.2, 16.8, 17.1, and 17.8 mm SVL) are considered adults, inasmuch as weak nuptial pads seem to be present and the last two specimens amplexed mature females in their plastic collecting bag. Data on size and proportions for both juveniles and adults are summarized in table 5.

MORPHOLOGY: Females are larger than males ($\bar{x}$ female SVL/$\bar{x}$ male SVL = 1.33). Head little wider than long, usually wider than body (body as wide as head in a few froglets, wider than head in some gravid females); head width 36%–40% of SVL in adults, 34%–39% in juveniles. Snout truncate to bluntly pointed in dorsal view, rounded in profile; eye-nostril distance 74%–97% of eye length in adults, 72%–94% in juveniles; nostrils slightly protuberant, directed dorsolaterally; canthus rostralis gently concave or

TABLE 5
**Size (in mm) and Proportions of *Eleutherodactylus auricarens*, New Species,
from the Summit of Auyantepui[a]**

Character	N	Mean ± 1 SE	SD	CV (%)	Range[b]
Snout-vent length (SVL)	4 ad ♂	16.98 ± 0.33	0.67	3.92	16.2–17.8
	9 ad ♀	22.59 ± 0.52	1.55	6.85	20.2–24.7
	2 juv. ♂	14.55	1.06	–	13.8–15.3
	2 juv. ♀	18.25	0.92	–	17.6–18.9
	23 juv.	12.78 ± 0.26	1.25	9.76	10.3–15.7
Tibia length[c]/SVL	4 ad ♂	0.577 ± 0.010	0.021	3.57	0.55–0.60
	9 ad ♀	0.556 ± 0.010	0.029	5.17	0.51–0.59
	2 juv. ♂	0.553	0.006	–	0.55–0.56
	2 juv. ♀	0.567	0.001	–	0.57–0.57
	23 juv.	0.552 ± 0.006	0.027	4.82	0.50–0.59
Head width[d]/SVL	4 ad ♂	0.377 ± 0.007	0.014	3.69	0.36–0.39
	9 ad ♀	0.390 ± 0.003	0.008	2.01	0.37–0.40
	2 juv. ♂	0.371	0.002	–	0.37–0.37
	2 juv. ♀	0.383	0.004	–	0.38–0.39
	23 juv.	0.365 ± 0.002	0.012	3.28	0.34–0.39
Center naris to edge eye/eye length	4 ad ♂	0.834 ± 0.027	0.053	6.37	0.76–0.88
	9 ad ♀	0.874 ± 0.021	0.063	7.21	0.74–0.97
	2 juv. ♂	0.807	0.049	–	0.77–0.84
	2 juv. ♀	0.829	0.085	–	0.77–0.89
	23 juv.	0.848 ± 0.013	0.064	7.60	0.72–0.94
Upper eyelid/interorbital distance	4 ad ♂	0.910 ± 0.023	0.046	5.10	0.87–0.95
	9 ad ♀	0.862 ± 0.013	0.040	4.67	0.82–0.93
	2 juv. ♂	0.972	0.039	–	0.94–1.00
	2 juv. ♀	0.909	0.064	–	0.86–0.95
	23 juv.	0.864 ± 0.016	0.078	9.00	0.72–1.08

[a] The total sample (N = 40) includes 30 specimens from AMNH–Terramar Camp 1 (5 adult ♀, 2 ♂ + juveniles), 7 specimens from Camp 2 (3 adult ♀, 2 ♂ + juveniles), and 3 specimens from Camp 4 (1 adult ♀ + juveniles). Sexually immature specimens comprise 67% of the sample, with 23 juveniles being unsexed (i.e., not dissected).

[b] For proportions, ranges are rounded from 3 decimal places (after calculation of other statistics).

[c] Tibia length is the shank measured from the heel to the convex surface of the knee (with limb segments flexed at right angles), roughly approximating length of the tibiofibula.

[d] Greatest head width as measured between jaw articulations.

nearly straight, edge rounded; loreal region concave, sloping outward to lip. Upper eyelid bearing low, more-or-less subequal small tubercles; upper eyelid width usually narrower than interorbital distance (82%–95% of interorbital distance in adults, 72%–108% in juveniles). Tympanic apparatus absent (as judged from dissection of all adults and selected juveniles, but see Remarks); a usually pronounced glandular ridge (''supratympanic'' fold) sloping from eye nearly to forearm, the skin below this fold varying from rugose to nearly smooth (see fn. 18 and Remarks). Two or three sometimes inconspicuous postrictal tubercles between corner of mouth and forearm. Choanae small to moderate, oval to round, not concealed by palatal shelf of maxillary arch; vomerine odontophores distinct, rounded to slightly elongate and slanted posteromedially, distinctly separated medially, situated posterior and median to choanae, each bearing several teeth. Tongue longer than wide, posterior edge varying from straight to rounded, with or without a slight notch, posterior half free. Adult males lacking vocal slits (hence there is no vocal sac); adult males appearing to have a weakly developed, unpigmented, nuptial pad along edge of thenar tubercle.

Dorsal skin finely granular in life (fig. 42) and weakly tuberculate, somewhat more strongly tuberculate on limbs; middorsal

raphe present, although only anterior portion visible in some juveniles; throat smooth, venter areolate; a broad triangular area of glandular skin present on posteroventral thigh surfaces; discoidal fold (inconspicuous on most specimens) situated anterior to groin; no ulnar ridge or defined line of tubercles.

Relative lengths of appressed fingers III > IV > II > I; tip of first finger sometimes reaching disc of second; males seeming to have a weakly developed unpigmented nuptial pad along edge of thenar tubercle; fingers with lateral keeling absent or weak, but downward, tightly folded flaplike fringing developed in some adults on medial sides of fingers II–III and lateral side of V (e.g., AMNH A-164938♀, 164954♀). Finger discs broader than long, slightly rounded to nearly truncate, with subdigital pads much wider than long; disc on thumb slightly expanded. Palmar tubercle large, cordiform; thenar tubercle oval, large; subarticular tubercles low to somewhat protuberant, either rounded or conical; several supernumerary palmar tubercles (fig. 43), either low or slightly protuberant, sometimes nearly as large as subarticular tubercles.

Hind limbs relatively long; heels overlap when held at right angles to sagittal plane; tibia 50%–60% of SVL (table 5). Relative lengths of appressed toes IV > V > III > II > I; tip of toe I not reaching disc of toe II; tip of toe V normally extending to the distal edge of, or well past, the ultimate subarticular tubercle of toe IV; tip of toe III extending to or slightly past the penultimate subarticular tubercle of toe IV.[19] Toe discs broad, usually as broad or slightly broader than those on fingers. Toes with lateral keeling weak or absent, but downward, tightly folded flaplike fringing developed in some adults on medial sides of toes III–IV and lateral side of toe V (e.g., AMNH A-164938♀, 164954♀). Basal webbing essentially absent.[20] Inner metatar-

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[19] Toe V is normally much longer than toe III, but in a few small juveniles (e.g., AMNH A-164941) the tip of toe V barely reaches the ultimate subarticular tubercle of toe IV and is only slightly longer than the third.

[20] There is very minimal fleshy "webbing" between the toes, but no thin, clear webbing. The determination of basal webbing as minimal or absent is therefore somewhat subjective.
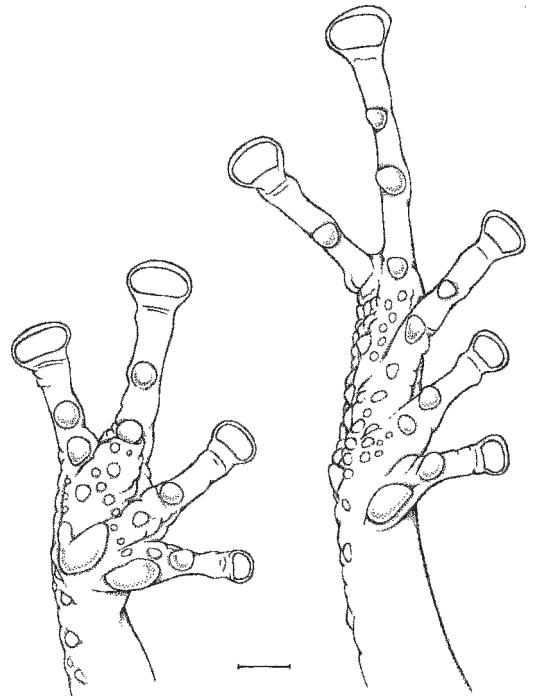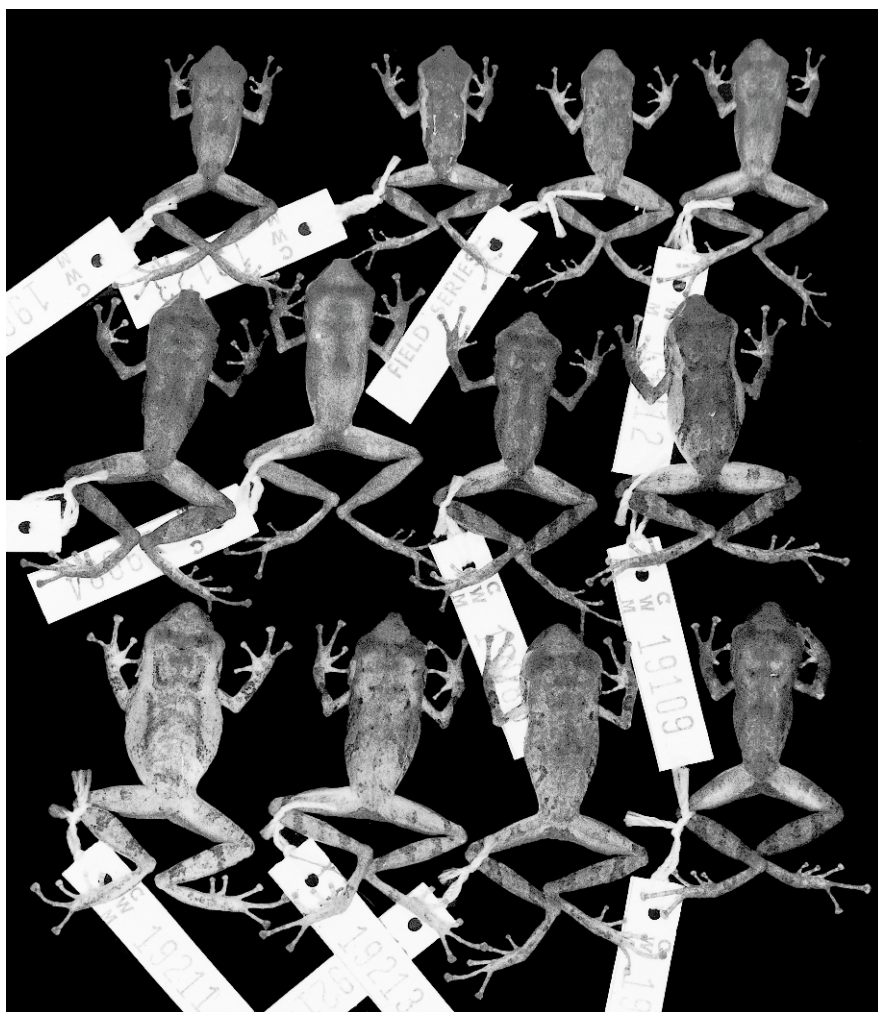

Fig. 43. *Eleutherodactylus auricarens*, new species. Right hand and right foot of a female paratype (AMNH A-164940) showing maximum tuberosity of palmar and plantar surfaces. Scale = 1 mm.

sal tubercle large, an elongated ovoid, much larger than small round outer metatarsal tubercle; several or many small to moderate supernumerary plantar tubercles (fig. 43), low or protuberant; subarticular tubercles larger, moderately protuberant, rounded to nearly conical. Calcar tubercles low and indistinct, none prominent. Tarsus somewhat tuberculate, lacking a tarsal fold or constantly positioned tarsal tubercle (a small tubercle sometimes distinguishable on distal part of tarsus near inner metatarsal tubercle).

COLORATION: In life (fig. 42), dorsal coloration some shade of brown—gray-brown, brown, blackish brown, greenish brown, orange-brown—with darker interorbital bar and often with a vague, ill-defined, middorsal longitudinal dark marking that usually has a few transverse or sometimes chevronlike lateral extensions or undulations (fig. 44). The longitudinal dorsal mark is lacking in some specimens, including the following: one male and two females each have a dark dorsum and a contrasting pale (orange or

Fig. 44. *Eleutherodactylus auricarens*, new species. Dorsal view of adults from the type series, ×1.1. **Top row, males:** Left to right: AMNH A-164939 and EBRG 2723 from Camp 1, AMNH A-164951 and EBRG 2724 from Camp 2. **Middle row, females:** AMNH A-164937, 164938, EBRG 2710, AMNH A-164940, all from Camp 1. **Bottom row, females:** AMNH A-164952, EBRG 2725 (holotype), and AMNH A-164953 from Camp 2, and AMNH A-164954 from Camp 3.

gray in life) postocular stripe that extends ventrolaterally and expands on the flank; and a few females have indefinite dark dorsal coloration, from which a few dark stripes extend obliquely (posteroventrally) onto the flank.

Some specimens with an ill-defined dark stripe below the canthus rostralis from eye to snout, often broken or incomplete, with only the anterior half remaining as a longitudinal dark blotch enclosing the nostril, absent in some. Often a brown postocular stripe with or without conspicuously darkened upper and lower edges, sometimes represented only by its upper edge—a narrow black line superimposed on the postocular ("supratympanic") fold. Frequently, one to several dark bars radiating from eye to lip, with pigmented but slightly lighter interspaces, but lip sometimes moderately pigmented without obvious pattern.
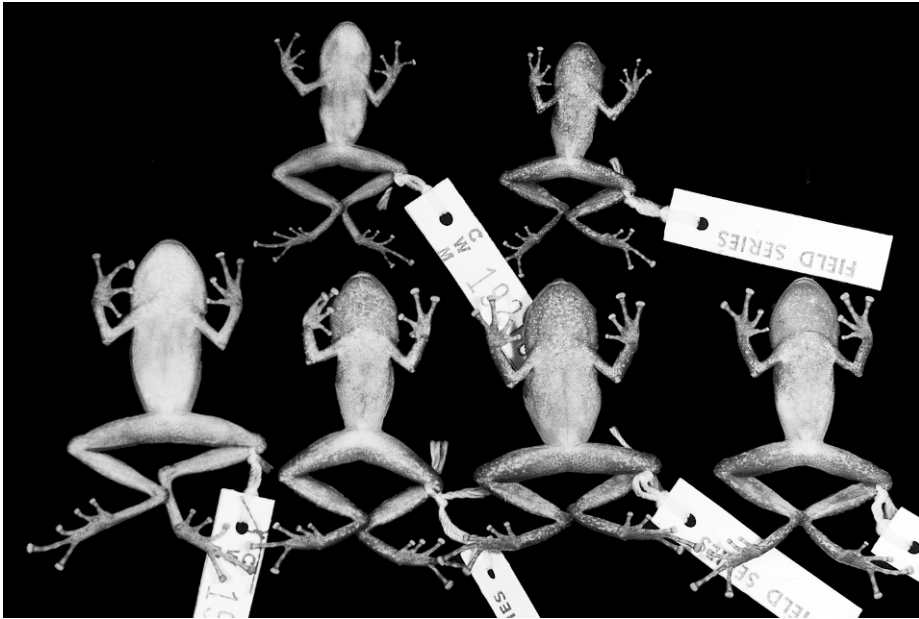
Fig. 45. *Eleutherodactylus auricarens*, new species. Ventral view of selected adults from the type series, showing approximate extent of variation in dark pigmentation of preserved specimens (ventral surfaces were darker in life), ×1.1. **Top row, males:** Left to right: AMNH A-164951, EBRG 2723. **Bottom row, females:** EBRG 2725 (holotype), AMNH A-164954, 164940, 164938.

Dark crossbanding on limbs sometimes indistinct, but forearms usually with one distinct band, thighs usually with two, shanks usually with three. Groin suffused with orange, which color often occurs also on concealed part of shank, anterior side of thigh and/or top and rear of thigh. In other specimens, the posterior thigh and concealed part of the shank is uniformly gray or brown in life, uniform or with pale dots.

There is some ontogenetic change in ventral coloration. In life, the ventral surfaces are nearly black in the smallest juveniles, then becoming gray or greenish gray in larger specimens. Ventral coloration tends to be darkest (blackish) under the head, where an occasional specimen has a weakly developed pale midgular line (which is usually absent, see fig. 45); there may be patches or dots of bronze on the gray chest and sometimes on the throat as well. Some sexual dimorphism was suggested by two amplectant males, whose ventral surfaces and posterior thighs (as well as dorsal surfaces, see fig. 42) were much darker than in their respective females, but in preservative there are males and

females showing a range of ventral pigmentation from pale to dark. In preservative, the ventral surfaces are pale yellowish, sparsely to densely punctuated with brown, the throat usually being somewhat darker to much darker than the belly (fig. 45). Palms and soles lightly pigmented, palmar and plantar tubercles tending to be somewhat darker, some subarticular tubercles on feet also may be pigmented.

There is individual variation in the living color of the iris, which may be light to dark bronze, golden bronze, or greenish bronze, tending to be paler above than below pupil, and with a red or reddish brown horizontal stripe (which may be ill-defined) through pupil.

NATURAL HISTORY

Eleutherodactylus auricarens was found in patches of forest at camps 1, 2, and 4. It is evidently nocturnal, having been found at night on leaf litter and perched on leaves up to about 1 m aboveground; many were found in leaf litter by day. Two males (AMNH A-

164951, EBRG 2724) amplexed adult females (AMNH A-164952 and EBRG 2725, respectively) in the collecting bag; the females are, respectively, 7.6 and 5.7 mm larger (SVL) than the smaller males (e.g., fig. 42 bottom).

REMARKS

The phylogenetically nearest relative of *Eleutherodactylus auricarens* may be *E. yaviensis*, a frog of the northwestern tepuis, which are situated several hundred km west of Auyantepui. The two species are similar in lacking vocal slits and in loss (or near loss, see below) of the tympanic apparatus, as well as in most other morphological detail, including hand and foot structure. Although we indicated the presence of basal webbing on the feet of *yaviensis* (Myers and Donnelly, 1996: 21), the determination of *minimal* basal webbing is subjective (see fn. 20); direct comparison of the two species shows that, although somewhat translucent, the skin (''webbing'') between the bases of the digits is fleshy and that webbing could as well be coded as absent in both taxa.

Eleutherodactylus yaviensis is a larger species than *E. auricarens*, with little size overlap (*auricarens* ♂ about 16–18 mm, ♀ 20–25 mm SVL, versus about 18–21 and 24–30 mm in *yaviensis*). In life, both species (especially adults) tend to have orangish coloration in the groin, on the anterior and posterior thigh surfaces, and on the concealed part of the shank, although this color is more conspicuous and forms orange-red ''flash marks'' in *yaviensis*, whereas it is more variable and best described as a ''suffusion of orange'' in *auricarens*. Ventral surfaces are pigmented brownish or grayish, sometimes with a yellowish (*yaviensis*) or greenish (*auricarens*) cast, with patches or flecking of bronze on the throat and chest of *yaviensis* and some specimens of *auricarens*. Each has a reddish horizontal stripe through the pupil, but the rest of the iris color is somewhat variable in both species.

Although *Eleutherodactylus yaviensis* is more variable in color pattern (Myers and Donnelly, 1996; 20, fig. 13; 2001: 40, figs. 26, 27), it lacks the vague undulating middorsal marking that is present in many specimens of *E. auricarens* (compare figs. 44 and 46).

However, some specimens of *E. yaviensis* have, just posterior to the interorbital bar, an indefinite dark blotch that resembles the anterior end of the longitudinal blotch of *E. auricarens*. This vague anterior blotch is present in some specimens of *E. yaviensis* from both Cerro Yaví (fig. 46) and Cerro Yutajé (e.g., AMNH A-159162); the anterior blotch may be more evident in preserved specimens of *E. yaviensis* than in life (in Myers and Donnelly [2001: 40–41], compare their fig. 26, bottom, with same specimen in their fig. 27). Although some frogs in both species have an indefinite dorsal pattern, most of the distinctive pattern morphs of *E. yaviensis* seem to be lacking in *E. auricarens*, except for one morph characterized by a conspicuous pale lateral stripe.

We recently called attention to an unusual case of intrapopulational variation in presence or absence of the tympanic annulus and membrane in *E. yaviensis*, in which the tympanic apparatus, when present, is a feebly developed structure that is concealed beneath the skin (see Myers and Donnelly, 2001: 42–43, fig. 28).

Because of the variation in *E. yaviensis*, we dissected (on one side) all 13 adult specimens and five selected juveniles of *E. auricarens*. We found no compelling or clear-cut evidence of a concealed or vestigial annulus or tympanic membrane in most specimens. However, in a few specimens (e.g., AMNH A-164937, left side; A-164938, right side), there is the faintest suggestion of what might be a small tympanic annulus tipped under the anterior edge of the m. depressor mandibulae (fig. 47C). As already stated (fn. 18), some other specimens of *auricarens* externally have small indistinct circular areas situated under the postocular (''supratympanic'') fold. Although corresponding tympanic structures could not be found, these areas, measuring about 0.05 mm across, are externally suggestive of concealed tympana (fig. 47B).

Thus, we suspect that there are external and/or possibly internal vestiges *in some specimens* of a tympanic structure that otherwise has virtually disappeared in *Eleutherodactylus auricarens*. However, the situation is not as clear-cut as in *E. yaviensis*, in which vestigial tympana are clearly present in some specimens (Myers and Donnelly, 2001: fig. 28).

Fig. 46. Color pattern polymorphism in the earless tepui frog *Eleutherodactylus yaviensis* at the type locality. Left to right, top to bottom: AMNH A-143364, 143367, 143371, 143373, 143374, 143376, all paratopotypes, ×1.2. Compare with *Eleutherodactylus auricarens* (fig. 44).

In *Eleutherodactylus auricarens*, the anterior part of the m. depressor mandibulae either (1) overlaps and appears to originate in part from the epimysium of the m. adductor mandibulae, or (2) the anterior edge of the depressor mandibulae is sharply defined, with its fibers more clearly originating from a thin, white tendinous edge. Somewhat similar variation was noted in earless specimens of *Eleutherodactylus yaviensis*. In four specimens of *E. yaviensis* having concealed tympana, a small portion of the m. depressor mandibulae was seen to originate from the posteroventral part of the tympanic annulus in three cases, but not in a fourth specimen in which the tympanic structure seemed particularly vestigial and possibly too weak for even partial anchorage of the depressor mandibulae (Myers and Donnelly, 2001: 42–43). Such variation in the jaw musculature seems likely to be correlated with ongoing loss of the last internal remnants of the tympanic structure in *E. yaviensis*, and at least the last external remnants in *E. auricarens*.

Eleutherodactylus pulvinatus Rivero
Figures 47A, 48

Eleutherodactylus pulvinatus Rivero, 1968a: 4. Holotype MCZ 64741, an adult male from Paso del Danto, Región de la Escalera "around 1400 m above San Isidro", road from El Dorado to Sta. Elena de Uairén, Estado Bolívar, Venezuela. Duellman, 1997: 11 (color photograph), 23 (new diagnosis based on
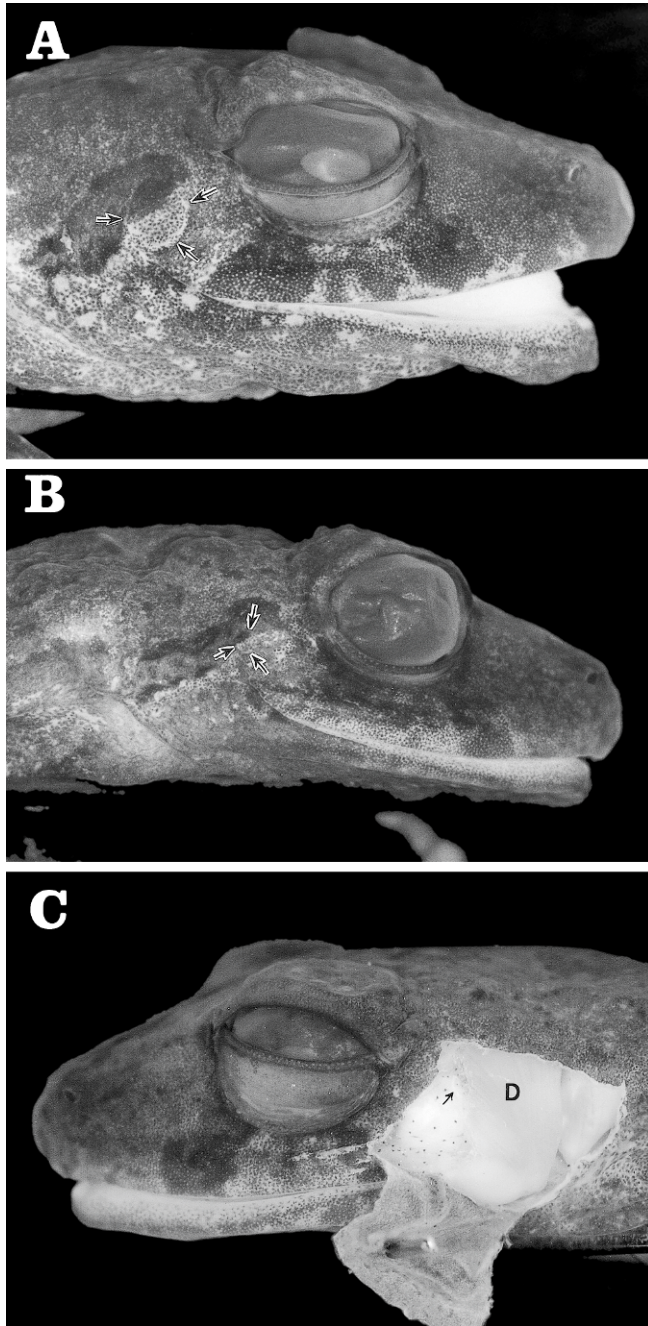
Fig. 47. Heads in profile of two species of *Eleutherodactylus* occurring in sympatry on the summit of Auyantepui, about ×6.8–7.5. **A.** *Eleutherodactylus pulvinatus* Rivero (EBRG 2730♂, 23 mm SVL). Note externally distinct tympanum (arrows). **B, C.** *Eleutherodactylus auricarens*, new species (B = EBRG 2709, 21 mm SVL; C = AMNH A-164937, 23 mm SVL). Occasional specimens of this earless species show a small circular area having the appearance of a tiny tympanum (arrows in **B**). Dissection of these and most other specimens fails to reveal an underlying tympanic apparatus. A few specimens, however, have a possily vestigial tympanic annulus (arrow in **C**) tipped under the edge of the m. depressor mandibulae (D); the dissected specimen in **C** lacks the external, circular tympaniclike area shown in **B**.

sample from La Escalera region). Myers and Donnelly, 1997: 56–57 (photograph and measurements of the holotype).

MATERIAL: Camp 1, 1700 m: AMNH A-164955, juv. ♀, collected 2–4 February, 1994. Camp 4, 1600 m: AMNH A-164956♂, EBRG 2730♂, collected 19–22 February 1994. All from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

Eleutherodactylus pulvinatus is readily distinguished from sympatric *E. auricarens* by presence of an externally distinct, relatively large tympanum (fig. 47A). The two adult males in our collection measured 22.8 and 23.0 mm SVL, with the following proportions: tibia/SVL = 0.583 in both; head width/SVL = 0.387–0.399; eye-naris/eye length = 0.765–0.906; tympanum/eye = 0.313–0.324; eyelid/IOD = 0.852–0.920. The juvenile female is 13.4 mm; tibia/SVL =0.575; head width/SVL = 0.373; eye-naris/eye length = 0.850 tympanum/eye = 0.350; eyelid/IOD = 1.063. The males have two slightly whitish nuptial pads, one along edge of thenar tubercle and the other on posterodorsal side of thumb; these are best developed in AMNH A-164956, the second pad only weakly indicated in EBRG 2730. Vomerine odontophores are small but easily seen, situated between and slightly posterior to the choanae.

COLORATION: In life, gray-brown over the dorsal surfaces, with obscure darker markings and crossbanding on the limbs; a poorly defined dark interorbital bar and what seem to be remnants of a dark W-shaped scapular mark are perhaps somewhat more evident in preservative (fig. 48) than in life; the thighs appeared virtually uniform gray in life (pale orangish brown in preservative, with or without pale flecking). EBRG 2750 has several pale oblique bars crossing the flanks, but these markings are lacking in AMNH A-164956. A dark brown stripe below the canthus rostralis, from eye to nostril, is evident in one (EBRG 2750) of the adult males but vague in the other. Both have an oblique postocular brown stripe with a blackish upper edge, and several dark bars radiating from eye to lip (most distinct in EBRG 2750, obscure in the other).

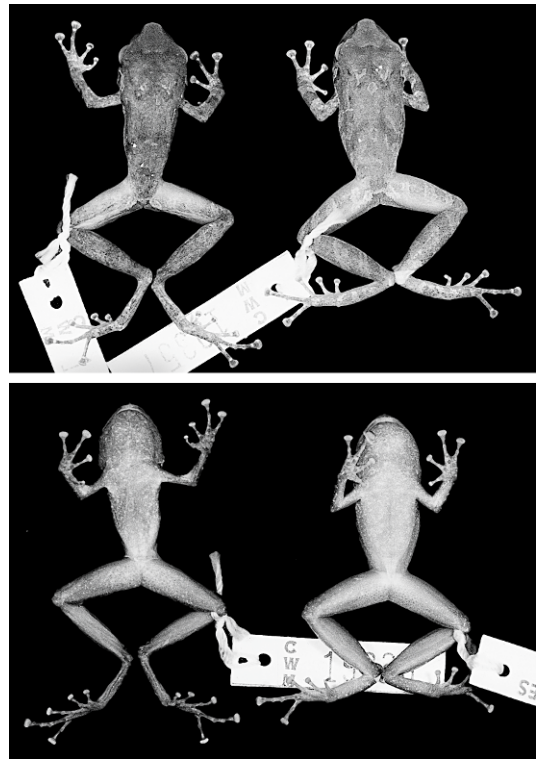The ventral surfaces were medium gray overall, with inconspicuous pale gray flecking

Fig. 48. *Eleutherodactylus pulvinatus* Rivero, adult males in dorsal and ventral view, ×1.05. Left to right: AMNH A-164956, EBRG 2730.

on throat and venter (pale brown in preservative, with unpigmented flecks and small spots). There was a horizontal red-brown stripe through the pupil; the iris was bright bronze above the pupil, with minimal black venation, whereas below the pupil it was darkened by black venation in a more-or-less vertically aligned pattern.

The juvenile female (AMNH A-164955) lacks a distinct dorsal pattern, lacks oblique pale bars on the flanks, and lacks the brown canthal stripe, although the dorsally black-edged postocular stripe is present; the upper lip has dark bars along its length. The rear of thigh is brown with pale flecking, and the ventral surfaces are like those of the adults except a darker brown.

REMARKS

Only three specimens assigned to this species were obtained. *Eleutherodactylus pulvinatus* was not distinguished in the field from

the more abundant *E. auricarens*. A juvenile female was taken in forest at Camp 1 with a series of *auricarens*, and two adult males were found along with *auricarens* at Camp 4.

Except for the relatively obscure dorsal pattern (fig. 48), the Auyantepui specimens agree very well with the recent diagnosis of *E. pulvinatus* provided by Duellman (1997: 23). The specimens have been compared directly with the holotype of *E. pulvinatus* (MCZ 64741), which differs in having a more vivid pattern (see photographs in Myers and Donnelly, 1997: 57) and in being a few mm longer and more robust. The greatest body width (10.5 mm at midbody) of the male holotype is marginally greater than head width (10.4 mm), whereas midbody width in the two Auyantepui males is noticeably less than head width (midbody width = 73%–92% of head width in two males from Auyantepui versus 1.01% in the male holotype (and 99% in the juvenile female from Auyantepui). At 22.8–23.0 mm SVL, the two Auyantepui specimens are at the low end of the size range reported for sexually mature male *pulvinatus* (22.8–26.1 mm SVL, combined from Rivero [1968a] and Duellman [1997]).

Eleutherodactylus pulvinatus Rivero probably may be related to *E. avius* and *E. memorans*, which occur in sympatry on Cerro Tamacuarí, some 500 km southwest of Auyantepui (Myers and Donnelly, 1997). All three species have paired nuptial pads in males (sometimes fused into one long pad in *avius*). *E. pulvinatus* is most similar to *E. memorans*, as discussed in Myers and Donnelly (1997: 56–57). Iris coloration is another point of resemblance. *E. memorans* was described as having the iris "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" (Myers and Donnelly, 1997: 54); this is similar to the iris of our Auyantepui *pulvinatus*, which had a bronze iris with a red-brown stripe and more or less vertically aligned black venation below the pupil. Duellman's (1997: 11, 23) photograph of a specimen from near the type locality of *pulvinatus* shows the bronze iris and a reddish brown horizontal stripe; the lower part of the iris is barely visible but there seem to be at least a few vertically aligned black lines.

FAMILY LEPTODACTYLIDAE

Frost et al. (2006) attempted to correct problems rising from the long-recognized non-monophyly of the Leptodactylidae, which is greatly reduced as a result (e.g., see Brachycephalidae above). However, their sample size was small compared with the great number of species and morphological diversity, for which reason further refinements are certain to follow. Only the type genus occurs on the Auyán summit.

Leptodactylus rugosus Noble
Figures 49–52

Leptodactylus rugosus Noble, 1923: 297–299. Holotype AMNH A-1169, an "adult male" [actually an immature male fide Donnelly and Myers, 1991: 23], from near Kaieteur Falls, British Guiana [Guyana], collected August 13, 1911 by F. E. Lutz. Heyer, 1995 (latest revision, including mention of a tadpole from Auyantepui). Heyer and Thompson, 2000 (synopsis).

Leptodactylus rugosus, Part: Heatwole et al., 1965: 360 (includes a specimen of *L. lithonaetes*); Heyer, 1979: 32 (includes the later recognized sibling species *L. lithonaetes* and *L. myersi*); Gorzula and Señaris, 1999: 65 (includes *L. lithonaetes* from Cerro Guanay).

MATERIAL: Camp 1, 1700 m: AMNH A-164957–164963, EBRG 2653–2659. Camp 3, 1850 m: AMNH A-164964–164985, EBRG 2660–2680. 4 km NE Camp 3, 1430 m: EBRG 2681. Camp 4, 1600 m: AMNH A-164986–164989, A-164854–164857 (4 larvae), EBRG 2652 (larva), 2682–2685. All from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

Color and pattern are somewhat variable (figs. 49–50), as is size. Combining all adult males and all adult females gives the following measurements:

Adult ♂ (21), $\bar{x}$ = 54.75, SD 3.752, 48.5–63.2 mm SVL
Adult ♀ (10), $\bar{x}$ = 58.16, SD 2.952, 54.6–63.7 mm SVL

Size overlap between the sexes is considerable, but females are significantly larger than males (t = −2.7482, P = 0.0117). Sexual maturity in males on Auyantepui seems to be attained between about 48 and 54 mm SVL[21];

[21] Donnelly and Myers (1991: 23) found that maturity in males "seems to be approached starting at about 41 mm" on Cerro Guaiquinima, about 80 km west of Auyantepui. They also reported a smaller maximum of 55 mm SVL for the Guaiquinima sample of 11 adult males; the one adult female was 56 mm SVL.

Fig. 49.   *Leptodactylus rugosus* Noble, from camps 1 and 3 on the summit of Auyantepui (not to same scale). **Top:** From Camp 1 (AMNH A-164957, subadult ♂, 54 mm SVL). **Middle:** Camp 3 (AMNH A-164985, adult ♂, 52 mm SVL). **Bottom:** Camp 3 (EBRG 2680, adult ♀, 61 mm SVL).

Fig. 50. *Leptodactylus rugosus*, showing approximate extent of variation in ventral pigmentation of males from two summit populations, ×0.78. **Top:** Camp 1, left to right, EBRG 2653, EBRG 2656. **Bottom:** Camp 3, EBRG 2665, EBRG 2670.

four subadults in the range 49–54 mm SVL had unopened vocal slits, unpigmented or pale gray vocal sacs, and small and/or noncornified thumb spines; two males, coded as adult at 52 mm SVL, each had only one open vocal slit; the vocal sacs were dark and the thumb spine weakly cornified in one of these specimens, but the other had pale vocal sacs and a noncornified thumb spine.

Most adult males have a single, externally evident thumb spine (fig. 51) in various stages of cornification, but a specimen each from camps 1 and 3 have two thumb spines. Less than half the adult males have 1–2 small spines on each side of the chest. Some have several minute spinules clustered around the spines, and one specimen (AMNH A-164979) from Camp 3 has a band of small spinules or tubercles extending across the chest (fig. 51). Adult male *rugosus* are characterized by paired chest spines but not by such a "distinctive band of black tubercles across the chest in larger males", which is a property of *Leptodactylus lithonaetes* (Heyer, 1995: 699, 701, 708). A

Fig. 51.   *Leptodactylus rugosus* (AMNH A-164979). A male showing cornified spines, including single, large thumb spines, paired chest spines, and a transverse band of minute spinules extending between the arms. In *L. rugosus*, the tiny spinules, when present, usually are clustered around the larger spines; this is the only specimen from Auyantepui in which the spinules were noted to extend completely across, ×4.1.

patch of black skin tubercles on the anterior throat is diagnostic of *L. lithonaetes* (Heyer, 1955: 708) but absent in *L. rugosus*, including all specimens from Auyantepui.

COLOR IN LIFE: See figures 49–50 and table 6, which summarizes color and pattern by locality.

TADPOLES

Three tadpoles were netted in isolated pools on sandstone near the river at Camp 4; larvae of *Hypsiboas siblezsi* were found in the same pools. The *Leptodactylus* larvae are in stages 39/40 and 40. These are long, slender tadpoles about 41–50 mm total length, tail 71%–74% of total, with protuberant eyes, dorsoventrally compressed bodies, median vent tube, and very low, inconspicuous tail fins; the posterior sides of the body are wrinkled or ridged in a longitudinal pattern (fig. 52).

The vent tube has a large opening and is strictly medial in all three larvae; the proximal end is attached dorsally to the anterior end of the low tail fin.[22] One larva in stage 39/40 (EBRG 2652) has a rather large, pointed flap extending ventrad from between the legs and the proximal end of the vent tube. It is a double-walled flap of the same translucent tissue that comprises the vent tube. Although it conceivably corresponds with the "vent flaps" found in several genera with suctorial larvae (Altig and McDiarmid, 1999: 34), the flap is present only in one of the three larvae.

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[22] Heatwole et al. (1965: 361) also reported the larva of *Leptodactylus rugosus* as having a median vent tube, whereas Duellman (1997: 25) described one as having the vent tube "attached dextrally for its entire length to ventral fin, with diagonal opening". Heyer (1995: 711) described a tadpole of the very similar *L. lithonaetes* as having a median vent.

TABLE 6
Leptodactylus rugosus Noble. Color and Pattern Variation (in Life)
in Three Populations on the Summit of Auyantepui

Body region	Camp 1	Camp 3	Camp 4
Dorsum	Brown to reddish brown; a variable pattern of pale tan to bluish white lines, including transverse interorbital line and 2–3 long lines on body that are sometimes cross-connected. (fig. 49 top)	Most very dark brown or blackish brown. Nearly patternless, but a pale gray or tan interorbital line present; and usually a hint of grayish to reddish dorsolateral lines, and often a median blotch of the same color (gray to reddish) high on back. (fig. 49 middle and bottom)	Blackish or dark brown, sometimes nearly uniformly so. But usually with a gray interorbital line and dorsolateral lines, and sometimes a median spot of same color. Median spot and dorsolateral lines may be suffused with red.
Limbs, rear thigh	Limbs banded dark and lighter brown, with the lighter interspaces being greenish yellow on rear thigh, this color sometimes forming the hint of a horizontal line low on thigh.	(Limbs not noted.) Rear thigh mottled black and greenish yellow (or orangish in juveniles).	Same as Camp 3.
Ventral surfaces	Venters white, with brown to grayish mottling on chest and throat (fig. 50 top). Pale yellowish white under hind limbs, or orange suffused in juveniles.	White with variable amount of gray mottling on chest and throat (fig. 50 bottom). Hind limbs tending to be pale greenish yellow in adults, but orange in juveniles.	White. Throat and chest either suffused with gray or else mottled gray and white. (Limbs not noted); juvenile orange under thigh.
Groin	Weak suffusion of greenish yellow in groin (and also in concealed part of shank [not mentioned in other samples]).	(Not noted.)	Tending toward a yellow tinge.
Iris	Basically pale bronze overall or else turning pale gray below pupil. Overall darkened by dense black venation, with dark brown on each side of pupil in an ill-defined butterfly mark.	Upper part of iris bronze; lower median sector white with brown suffusion to each side. These sections not sharply defined (no butterfly mark). Dense black venation overall.[a]	Similar to Camp 3.

[a] This iridial color pattern matches that described for *Leptodactylus rugosus* on Cerro Guaiquinima, about 80 km west of Auyantepui (Donnelly and Myers, 1991: 22). However, some other aspects of color and pattern are different. For example, the elongated glands situated near the groin and posteroventrally along the lower thigh were not distinctively colored on Auyantepui, whereas these glands were suffused with orange, sometimes brightly so, in specimens from Cerro Guaiquinima.

Descriptions or partial descriptions of tadpoles of this species were given by Heatwole et al. (1965: 361), Heyer (1995: 701), and Duellman (1997: 25–26, fig. 21). Heyer noted the "series of glandular ridges on the body above the abdominal cavity", which appear to be characteristic for *L. rugosus* and also for the very similar *L. lithonaetes*. The tadpole of *L. rugosus* corresponds closely with that of *L. lithonaetes* (compare fig. 52 with the virtually identical illustration in Heyer, 1995: 711, fig. 5); however, another published illustration for larval *L. rugosus* does not show the posterior ridging on the body and the mouthparts are configured somewhat differently (see Heyer and Thompson, 2000: fig. 2).

Gorzula and Señaris (1999: 66, color photos 53–56) observed that *rugosus* tadpoles can wriggle out of the water completely "to
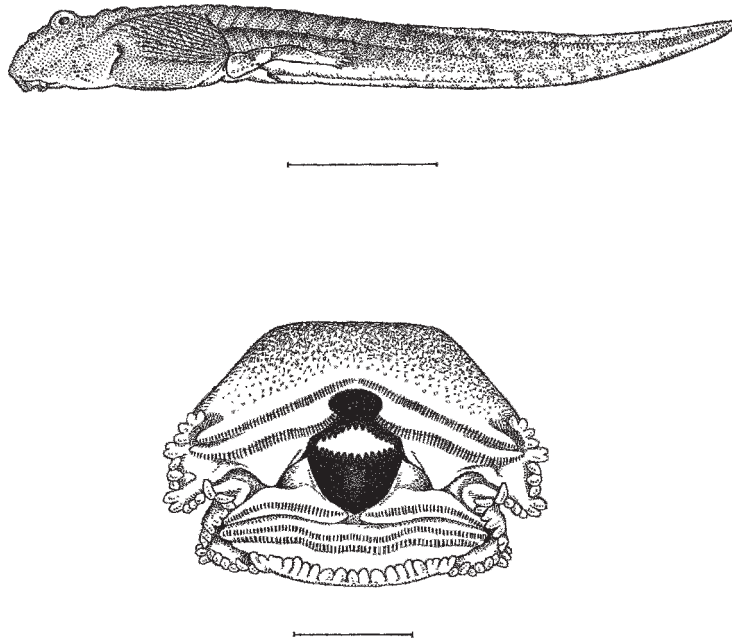
Fig. 52.   *Leptodactylus rugosus*. Stage-40 tadpole and mouthparts of same specimen (AMNH A-164857). Scale lines = 10 mm above and 1 mm below.

graze on damp rock surfaces several centimeters away from any water in which they could have taken refuge''.

NATURAL HISTORY

Leptodactylus rugosus is not confined to areas of granitic bedrock as formerly believed (Heyer, 1979: 34); it is now known to also occur abundantly on some sandstone outcrops and tepuis. The species was collected in an elevational range of 1430–1850 m, near three of our five camps on Auyantepui. It was common in the vicinity of Camp 1 (14 specimens collected), where it was found by night along the river below camp, sitting in and out of shallow flowing water; it also was found at night sitting on bare sandstone flats in and around camp, well above the river (fig. 3). The species was even more abundant at Camp 3 (44 specimens taken), where some were found at night on bare sandstone in and along the river (fig. 5 bottom). However, the majority of Camp-3 specimens were found by day, hiding under rocks in open areas of sandstone, sometimes under the same rocks with hylid frogs (*Tepuihyla edelcae*) or lizards (*Tropidurus bogerti*). Only eight specimens were taken at Camp 4, but these were found in the open by night and day in a diversity of habitats—on sandstone near the river and on the ground in both forest and marshy places.

The call was not heard and there was no other evidence of current breeding activity; females coded as sexually mature in our February sample had enlarging ova of about 1.5–2 mm in diameter. Heyer (1979: 34–35), Duellman (1997: 26), and Heyer and Thompson (2000) described and illustrated calls from Venezuelan localities.

REMARKS

Sibling species in the *Leptodactylus rugosus* group have been difficult to demonstrate, but, as shown by Heyer (1995), *L. rugosus* as now recognized occurs in eastern Venezuela and Guayana, replaced to the south and east by *L. myersi* and to the west by *L. lithonaetes*.[23] Subtle differences perceived in

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[23] The questioned westernmost locality in Heyer and Thompson's (2000) range map of *Leptodactylus rugosus* was based on juvenile specimens from Cerro Guanay in the northwestern tepuis. Adult males from Cerro Guanay are assignable to *Leptodactylus lithonaetes* (unpublished data).

the field had us wondering whether frogs collected at Camp 1 on Auyantepui really represented the same species as the frogs at camps 3 and 4. After comparing the specimens, we tentatively assign all to *L. rugosus*, which, however, shows more interpopulational variation on Auyantepui than might be expected.

As suggested by table 6, there are subtle differences between Camp-1 frogs and those from camps 3 and 4, at least in dorsal pattern, ventral pattern, and iris coloration. At Camp 1, longitudinal and transverse whitish lines (partly separating irregular dark blotches) tended to be conspicuous (fig. 49 top). Both juveniles and adults from Camp 1 tend to have paler ventral surfaces than those at camps 3 and 4. Specimens from Camp 1 have the throat and chest less heavily mottled with brown or gray, and the bellies are paler on average (fig. 50). Iris coloration at Camp 1 differed from that at camps 3 and 4—the last two agreeing with Donnelly and Myers' (1991: 22) description for *L. rugosus* on Cerro Guaiquinima, about 80 km to the west (table 6).

Of 66 specimens collected, 30 (21♂, 10♀) were sexually mature. Males from Camp 3 average smaller than those from the other camps:

Camp 3 (N = 15), $\bar{x}$ = 53.75, SD 3.246, 48.5–60.3 mm SVL
Camp 1 (N = 4), $\bar{x}$ = 57.05, SD 2.517, 55.4–60.8 mm SVL
Camp 4 (N = 2), $\bar{x}$ = 57.60, SD 7.920, 52.0–63.2 mm SVL

Assuming that the more than 3 to 1 difference between the largest and smallest standard deviations is due merely to sampling inadequacy at Camp 4 (where N = 2), analysis of variance shows no statistically significant difference among mean snout-vent lengths at the 95% confidence level (F = 2.05, P = 0.1573). None of the four adult males from Camp 1 has chest spines, compared with their presence in 6 of 10 adult males (excluding 5 skinned carcasses) from Camp 3; we do not know whether these small spines are permanently present or correlated with breeding condition (collections at Camp 3 started nine days after the last *rugosus* was taken at Camp 1).

Considering that *Leptodactylus rugosus* occurred both along open flowing rivers and also on bare rock well away from streams, we were puzzled in the field as to why we failed to find this conspicuous frog in apparently suitable habitats around Camp 2 (1750 m elev.; figs. 5 top, 7). Neither was it found at the higher elevation of Camp 5 (2100 m, fig. 10). Our only conclusion is that *L. rugosus* has a spotty distribution on the summit of Auyantepui. Perhaps isolation or colonization from different source areas has led to the interpopulational variation mentioned above. The possibility that two sibling species of "*rugosus*" exist on Auyantepui seems unlikely but cannot be dismissed out of hand. These frogs, conspicuous and often abundant where they occur, would be suitable subjects for finer-grain comparisons of possible genetic differences on Auyantepui.

LIZARDS

FAMILY GYMNOPHTHALMIDAE

The three species of teiioid lizards occurring on the summit of Auyantepui are all "microteiids", family Gymnophthalmidae. We previously argued against recognition of family status for microteiids as premature and misleading, since there was no convincing evidence for monophyly. Macroteiids and microteiids seemed monophyletic (Harris, 1985), but acceptance of Gymnophthalmidae was based on undocumented characters, incomplete data, and, especially, on authoritarianism (Myers and Donnelly, 2001: 48–49). That is no longer true.

In a major re-classification of microteiids based on mitochondrial and nuclear DNA from 50 species in 26 genera, Pellegrino et al. (2001) provided reasonably strong support for microteiid monophyly. Castoe et al. (2004) added taxa and re-evaluated the classification, making changes and corrections, but they did not disturb the support for monophyly.

Anadia species

Anadia species b: Gorzula and Señaris (1999: 115–117), description of specimens from Auyantepui.

Gorzula (1992: 276) discovered an unnamed species of *Anadia* on Auyantepui in

1984. According to Gorzula and Señaris (1999: 115–117) the species is known only from a single collection of seven specimens obtained "6 miles E Angel Falls" in May and June. The specimens were found mostly in concealment by day, in association with the frogs *Stefania schuberti* and *Tepuihyla edelcae* and the lizard *Tropidurus bogerti*. One "was observed basking on the edge of a vegetation mat … [and on] being approached it dove into a small pool that was about 6 cm deep, and hid in the detritus on the bottom".

Gorzula and Señaris (1999: 115) were unable to ascertain the present whereabouts of the specimens and therefore refrained from formally describing the species. They did, however, describe the individual lizard that was to have been designated the holotype and indicated variation in the potential paratypes. The color in life "was dark olive with irregularly distributed black flecks … ventral color of females was white with irregular black spots … [male ventral color] similar to that of the females except … tinged with red". Illustrations were unavailable.

Anadia is a primarily Andean genus that also extends north and west into lower Central America, and east across extreme northern Venezuela to the Península de Paria (Rivas et al., 1999), thence southeastward to the tepuis in Estado Bolívar. There are in the last region at least three still-unnamed species according to Gorzula (1992: 276), who mentioned one species from the Chimantá massif and two species from Auyantepui and the La Escalera region, although only the Chimantá and Auyantepui species were listed in the later work by Gorzula and Señaris (1999: 114–117). Gorzula (1992: 310) provided color photographs of the undescribed species from the Chimantá massif (see also photo 88 in Gorzula and Señaris, 1999).[24]

Aside from the above mentioned description of the Auyantepui species and Gorzula's photographs of the one on neighboring Chimantá, nothing has been published on the unnamed species of *Anadia* in the Venezuelan Guayana. We have noted that *Anadia*

> differs most conspicuously from other tepui microteiids in having a tight covering of nonmucronate (and usually smooth) dorsal scales that are juxtaposed or only subimbricate, as well in having a very long tail and a relatively attenuated, flat-topped snout that give it a distinctive aspect. *Anadia* evidently differs from *Adercosaurus* in hemipenial morphology (comblike rows of spinules in *Anadia*) and in the dorsal surface of the tongue (scalelike papillae anteriorly), but summary data for *Anadia* have not been published. *Anadia*, however, has been characterized as having (in 9 species) 6–10 swollen infralingual plicae (Harris, 1985) …. (Myers and Donnelly, 2001: 52)

Although *Anadia* is normally characterized by smooth dorsal scales, the species on Auyantepui has smooth dorsals on the neck and then "dorsal scales progressively keeled and less rounded" (Gorzula and Señaris, 1999: 116). The hemipenis of *Anadia metallica* (= *A. ocellata*), a Central American species, had been incorrectly described as a smooth, unbifurcated bulbous structure, but fully everted organs of that species are seen to be bilobed and to bear comblike rows of spinules, which are characteristic of many albeit not all microteiids (Myers and Donnelly, 2001: 49). The extent of variation in the hemipenis and other internal structures of *Anadia* is unknown. Despite the monographic treatment by Oftedal (1974), *Anadia* remains poorly characterized and additional study is sorely needed.

Added in press: The Auyán species was rediscovered recently according to Gilson Rivas and Renaud Boistel (GR personal commun., October 10, 2007), who kindly sent a photograph (taken by J.-C. de Massary) that shows a brown lizard with irregular black markings and apparently keeled dorsal scales. Confirmation as *Anadia* awaits closer examination, but it clearly differs from the species on the Chimantá massif.

Arthrosaura montigena, new species
Figures 53–57

Arthrosaura montigena (nomen nudum): Sánchez H. and Bisbal E., "2002" [2004]: 13 (mention of holotype in EBRG).

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[24] For the Chimantá species, Gorzula (1992) used the manuscript name "*Anadia breweri*", which is a nomen nudum as pointed out by Gorzula and Señaris (1999: 114).

Fig. 53. *Arthrosaura montigena*, new species. The adult male paratype (AMNH R-140230) shown approximately five times life size.

HOLOTYPE: EBRG 2905 (field no. CWM 19354), an adult female from summit of Auyantepui at 5°58′N, 62°33′W (AMNH–TERRAMAR Camp 4), 1600 m elevation, Bolívar, Venezuela, collected February 22, 1994, AMNH–TERRAMAR Expedition.

PARATYPE: AMNH R-140230 (CWM 19165), a male from summit of Auyantepui at 5°51′N, 62°32′W (AMNH–TERRAMAR Camp 1), 1700 m, Bolívar, Venezuela, collected February 7, 1994, AMNH–TERRAMAR Expedition. Figure 53.

ETYMOLOGY: The specific name *montigena* is an adjective meaning "mountain born". It is derived from the Latin noun *mons* ("mountain") + the adjective-forming suffix *-genus* ("born or produced in a certain place").

DIAGNOSIS: A small highland species of *Arthrosaura* readily distinguished from its nearest geographic neighbor (*A. testigensis*, Los Testigos range, east of Auyantepui) in having three (vs. four) supraoculars and in having a pale dorsolateral line on each side and an unmarked venter (vs. four narrow yellowish stripes on dorsum and brown spots on venter). A presumably unnamed species from the Chimantá massif (southeast of Auyantepui) evidently differs from *A. montigena* in having a dark brown middorsal stripe (Gorzula and Señaris, 1999: photo 89).

Arthrosaura montigena shares many characteristics of *A. versteegii* (French Guiana to extreme eastern Venezuela[25]) but differs in having a more complete pale dorsolateral line and in not having the ventral or ventrolateral scales sharply demarcated by a zone of small scales. A key to the named species of *Arthrosaura* is provided at the end of this section.

DESCRIPTION

The undissected male paratype is considered sexually mature because of its well-developed hemipenes with hardened spines; the undissected female holotype is significantly larger than the male and is judged to be an adult on that basis.

The following description mirrors as closely as practical that of Hoogmoed and Ávila-Pires (1992: 470–477) for *Arthrosaura versteegii*, with identical phrasing where appropriate (but with a few additional characters added). Possibly significant differences from *A. versteegii* are italicized (with the comparative data for *versteegii* sometimes quoted

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[25] As redefined by Hoogmoed and Ávila-Pires (1992: 470–477), *Arthrosaura versteegii* has a suspiciously broad geographic and elevational range—occurring as low as 100 m above sea level in Suriname and as high as 1400 m in Venezuela, without intervening records from Guyana. With this in mind, the two Venezuelan specimens reported by Hoogmoed and Ávila-Pires eventually need direct comparison with *A. montigena*, and, particularly, with Guyanese highland specimens when such become available.

TABLE 7
**Measurements (in mm) and Other Data
for *Arthrosaura montigena*, new species**

Character	AMNH R-140230 ♂ paratype	EBRG 2905 ♀ holotype
Snout-vent length (SVL)	40	48
Tail length	47+	82 (21 + 61)
Trunk (axilla to groin)	19	25
Forelimb length[a]	10.6	11.9
Hind limb length[a]	17.7	19.0
Head length (to anterior edge ear)	7.7	8.7
Greatest head width	5.8	6.0
Greatest head depth	4.0	5.0
Supralabials	6/6	6/9
Infralabials	7/7	7/8
Temporals	20/19	17/20
Transverse rows dorsal scales[b]	31	31
Scales around midbody[c]	35	35
Ventrals, longitudinal rows[d]	6	6
Ventrals, transverse rows[e]	18	18
Subdigital lamellae finger IV	11/11	11/12
Subdigital lamellae toe IV	15/15	−/15
Preanal pores	2	0
Femoral pores	4/4	0

[a] Limb length measured from axilla or from groin to tip of claw of longest digit.

[b] Transverse rows of dorsal scales counted from interparietal to level of posterior edge of thigh held at right angle to body.

[c] Scales around body (including ventrals) counted at transverse ventral row 11.

[d] Longitudinal ventral rows counted at midbody.

[e] Transverse rows of ventrals counted between collar and triangular preanal.

within parentheses). Some characteristics of the type specimens of *Arthrosaura montigena* are summarized in table 7.

A small microteiid; one adult male 40 mm SVL, one adult female 48 mm SVL. Head length/SVL = 0.18–0.19; head length/head width = 1.33–1.45; head width/head depth = 1.20–1.45. Temporal region in male *not* swollen (''in males distinctly swollen''). Snout blunt, rising gently posteriad. Neck approximately as wide as head and anterior body. Body depressed, noticeably wider than high; midbody width/height = 1.29 ♂, 1.37 ♀. Tail/ SVL = 1.71 in female (incomplete in male); tail approximately as high as wide at base, tapering to tip. Limbs well developed,

relatively short, forelimb/SVL = 0.25–0.27, hind limb/SVL = 0.40–0.44. Distance between forelimbs and hind limbs (trunk length)/forelimb length = *1.8–2.1* (''2.3– 2.6'').

Tongue of holotype lanceolate, anterior half gray. A central area of scalelike papillae behind fork interrupting half a dozen oblique, anteriorly aligned plicae, which extend around onto ventrolateral side of tongue as distinct folds; several partial plicae also indicated anterolaterally on base of fork. Posterior few plicae subdivided into smaller segments, with only the posteriormost line medially convergent behind the anterior scalelike plicae; remainder of visible tongue covered completely with scalelike papillae (base of tongue not accessible without undue damage to specimen). Raised midventral side of tongue with a median groove extending anteriorly through three pairs of thin (non-swollen), oblique, anteriorly converging (chevronlike) infralingual plicae immediately behind fork; first pair of infralingual papillae largest, third smallest. Anterior maxillary and dentary teeth short, becoming bicuspid and then primarily tricuspid posteriorly.

Rostral rectangular, 2.4–2.6 times as wide as high, visible from above, in broad contact with frontonasal. Frontonasal single, weakly pentagonal with small posterior apex, laterally in contact with nasal and in *broad* contact with loreal *and also in contact with anterior point of first supraocular.* Prefrontals *relatively small, quadrangular* (''irregularly pentagonal''), with a *very* short medial suture (''short to relatively long''), laterally in contact only with first supraocular. Frontal hexagonal, 1.6–1.7 times longer than wide, about as wide anteriorly as posteriorly, laterally weakly or markedly concave; frontal with a relatively *broad* border (''usually a short border'') with first supraocular, in contact nearly with entire length of second supraocular, and frontal either narrowly separated from third supraocular, or, on right side in male, with point contact. Frontoparietals pentagonal, little longer than wide, with relatively broad medial suture; each frontoparietal in contact with frontal, in point contact with second supraocular except on right side in male, and in broad contact with third supraocular, one parietal, and

interparietal. Interparietal 1.6–1.7 times longer than wide, pentagonal with straight sides slightly converging posteriad, as long or slightly shorter than parietals, *as wide as greatest width of parietals* (''distinctly narrower than the parietals''). Parietals and interparietal form a relatively straight posterior margin, anteriorly each is obtusely angulate. Occipitals—the scales posteriorly touching interparietal and parietals—forming a row of five variably shaped scales in female, but reduced by fusion to three wide scales in male. Three supraoculars, first smallest, second and third subequal. Four superciliaries, first much larger than the others, median two shorter than fourth.

Nasal *semidivided* (''undivided''), the division running posterodorsally from naris in male and on left side of female (fig. 54), but running ventrad from naris to supralabial on right side of female; naris in center or slightly below center of nasal plate, directed slightly posterolaterally. Loreal an anteriorly inclined rectangle or, on left side of female, an irregular pentagon (fig. 54), in contact with nasal and frenocular, in narrow contact with or narrowly separated from a small preocular, and in contact with first superciliary, first supraocular, and the frontonasal; *loreal dorsally excluded from prefrontal by frontonasal-supraocular contact*, ventrally well separated from supralabials by frenocular. Two preocular scales, very small, between first superciliary and first subocular. Frenocular longer than wide, weakly pentagonal, about as large as loreal, followed by 3–5 suboculars (4/4 in male, 5/3 in female). Three postoculars of varying size, lowermost continuing from the subocular series, uppermost in anterior contact with last superciliary. Supralabials usually six, with either the fourth plate or the suture between third and fourth below middle of eye; suture between second and third supralabials situated either under posterior edge of frenocular or slightly posteriad; nine supralabials on right side of female owing to divisions in first and fifth plates.

Upper eyelid with eight or nine ciliaries, none exceptionally enlarged. Ocular recess with a short median row of 2–3 scales separating median ciliaries from superciliaries. Lower eyelid with 8–10 ciliaries, subequal or with one elongated. Lower eyelid
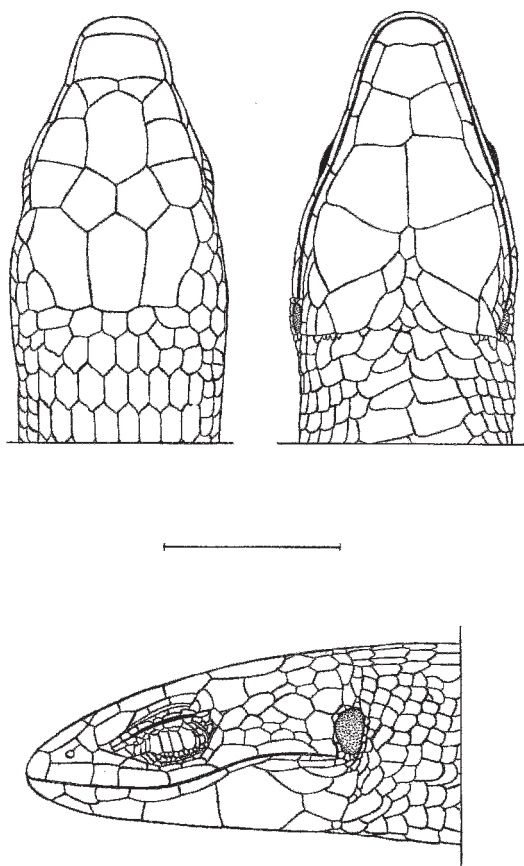

Fig. 54. *Arthrosaura montigena*, new species. Dorsal, ventral, and lateral views of head of holotype (EBRG 2905). Scale line = 5 mm.

scaled, with a large opaque window (palpebral disc) of three or, on left side of female, four vertical panes. Palpebral disc separated from lower eyelid ciliaries by a single row of small scales; several rows of smaller scales ventral to disc.

Temporal region between postoculars and ear with approximately 17–20 relatively large, irregularly shaped, juxtaposed smooth scales; one large anterior plate situated behind upper postocular and below suture between third supraocular and parietal; temporals otherwise increasing in size posteriorly, with two markedly enlarged scales bordering upper part of ear. Ear opening vertically oval, edged with small, smooth, somewhat swollen scales. Auditory meatus shallow, tympanum clear, not pigmented.

Posterior edge of mental nearly straight or slightly undulating. Postmental large, slightly pentagonal, laterally in contact either with first infralabial only or also with anterior end of second infralabial. Three large pairs of genials, in lateral contact with infralabials; a fourth pair of smaller ''genials'' or pregulars (fide Donnelly et al., 1992: fn. 2) separated from supralabials by 2–3 scales. First two pairs of genials in broad medial contact, with medial suture of second pair being much longer than that of first pair. Third pair of genials and pair of large pregulars medially separated by a wedge of smaller pregulars, of which 1–2 scales separate the third pair of genials and 2–4 scales separate the fourth pair of ''genials'' (or large pregulars). Only a hint of an incomplete gular crease, marked by line of granular scales from below each ear to about posterolateral edges of fourth pair of ''genials''. Gulars imbricate, smooth, with straight to rounded margins, in six transverse rows between posterior margins of last pair of ''genials'' and collar scales; first few gular rows somewhat irregular in the female; each succeeding row comprised of larger scales than the preceding, except scales in last (sixth) row smaller than in fourth and fifth rows; two middle scales in rows 4–5 forming double row of enlarged paramedian gulars. *Guttural fold indistinct* (''gular fold distinct''), indicated by small scales in weak fold on side of neck, ending ventrad at posterior end of fifth transverse gular row. Collar row with 7–8 scales, forming a lobed posterior margin; median four scales largest, scales decreasing in size laterad; incomplete collar fold indicated only on sides of neck behind collar, not crossing throat.

Head scales with numerous minute scale organs (pits), especially concentrated on anterior dorsal, lateral, and ventral head scales, becoming mainly distributed on margins of frontal and posterior head plates, and on posterolateral edges of body scales.

Scales on nape posterior to the row of postparietals (occipitals, see above) longer than wide, imbricate, in transverse rows, anteriorly smooth, the posterior ends rounded to bluntly pointed; grading posteriorly into dorsal body scales. Sides of neck with distinctly smaller, mostly oval, juxtaposed scales, not in well-defined rows, becoming granular near limb insertion. Dorsals hexag-

onal, elongate, strongly keeled, mucronate, in 31 transverse rows (including row of occipitals) between interparietal and posterior level of hind limbs. A zone of granular scales from anterior side of forelimb insertion extending above arm and becoming wider in axilla, followed posteriorly by a few vertical rows of small scales intercalated between the transverse rows of laterals; lateral scales becoming small toward groin, grading into granular scales just in front of hind limb insertion. Otherwise, the transverse scale rows are essentially uninterrupted on middle 70% of trunk; the upper lateral scales in these rows are similar to dorsals, with lower lateral scales becoming wider, less strongly keeled, and nonmucronate; keels lost on lowermost row of laterals. Lateral scales slanted posterodorsally, tending to be aligned more posteriorly in lowermost few rows.

Below the laterals, two rows of *ventrolateral scales*[26] (''ventrals''), which are aligned either posteriorly or slanted posteroventrally—in a more or less abrupt change of alignment from the lateral body scales (fig. 55). Ventrolaterals (''ventrals'') *not or but indistinctly demarcated from laterals* by an interrupted row of widely spaced small scales (''ventrals and laterals sharply demarcated by a zone of small scales''). At most, in the space of 10 transverse rows along midsection of body, the female has an interrupted line of about half a dozen small scales inserted between lowermost lateral and upper ventrolateral rows; these inconspicuous scales are short and therefore widely spaced from one another, giving the impression of being remnants of a lost scale row (fig. 55). The equivalent midsection of the male has only a single, similarly placed small scale on each side.

Ventrals imbricate, longer than wide, with rear margins progressively becoming more

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[26] These ''ventrolateral scales'' are usually counted in *Arthrosaura* spp. as longitudinal rows of ventrals that do not form continuous rows between the pectoral area and preanal plate. But it is difficult to make ventrals of them in *A. montigena* because of the shape change and especially because they face laterally (with only a slight ventral inclination). The situation is possibly paralleled in young *A. kockii*, a species with normally 10 longitudinal ventral rows except ''in the smallest specimens only the medial six rows are distinguished as ventrals'' (Ávila-Pires, 1995: 332).
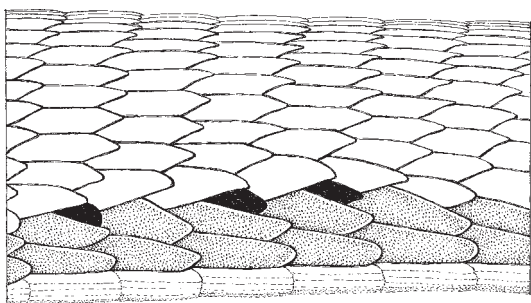
Fig. 55. *Arthrosaura montigena*, new species. Lateral view of an 8 mm section of midbody of holotype (keels omitted from scales). The scales shaded gray, herein termed "ventrolaterals" are more ventrally situated in most *Arthrosaura* spp. and therefore are included in midbody counts of the ventral rows. But in this species the "ventrolaterals" face laterad, with only a slight inclination ventrad; note their change of alignment relative to the lateral and dorsal scales. Small, widely separated azygous scales (emphasized in black) are irregularly distributed between the laterals and ventrolaterals; these little scales, shown here in maximum concentration, are even fewer in number in the male paratype.

rounded posteriorly, aligned in both transverse and longitudinal rows. Both specimens with 18 transverse rows between collar and preanal. Both specimens have six continuous longitudinal rows, with outermost row on each side separated by only 1–2 scales from collar scales. Hence, *six distinct ventrals in a transverse row at midbody* ("ten ventrals"), or 10 ventrals if ventrolateral scales are included in this count. Scales around midbody 35 in both specimens. Preanal plate consisting of four scales, including two large laterals, and two medial triangular scales in point contact, the anterior being larger than the posterior. Male with two preanal pores in same line as four femoral pores on each side, the pores separated by 1–2 scales.

Scales on tail in transverse rows dorsally and laterally, hexagonal and otherwise similar to body scales but shorter. Unpigmented subcaudals smooth, with rounded ends, in both transverse and longitudinal rows; transverse rows forming whorls with dorsals; six longitudinal rows basally.

Dorsal surfaces of upper and lower arms, and ventral side of lower arm with large,

imbricate, variably polygonal scales, mostly smooth (a few weakly keeled on male), becoming much smaller on inner side of lower arm; ventral surface of upper arm with small, rounded or somewhat swollen, imbricate, smooth scales. Thigh with 1–2 rows of large smooth scales on anterior face, bordered ventrally by 1–2 rows of somewhat smaller smooth scales reaching the line of femoral pores or equivalent area in females; large anterior scales bordered dorsally by a row of small smooth to keeled scales, grading into juxtaposed small scales and granules on posterodorsal and posterior side of thigh. Lower leg with small smooth to slightly keeled imbricate scales, becoming smaller and juxtaposed posteriorly; ventral side of lower leg with large smooth scales.

Tops of hands, feet, and digits with smooth imbricate scales; palms and soles covered with small, mostly elongate juxtaposed scales that are not thickened or raised. Two enlarged thenar scales on inner margin of palm below pollex, each with a black, produced inner edge. Similar black oblique keels present on basal sides of toes III and IV, each with several keels; each keel situated on the inner of a pair of basal subdigital lamellae. Subdigital lamellae divided basally, single on distal halves of some digits.

Subdigital lamellae as follow (Roman numbers indicate digits, Arabic numbers indicate paired or single lamellae on left/right feet); separate counts given first for male paratype, second for female holotype: forefoot **I** 4/4, 3/3 **II** 6/6, 6/7 **III** 9/9, 10/10 **IV** 11/11, 11/12 **V** 6/6, 7/6; hind foot **I** 3/3, 4/4 **II** 7/7, 7/7 **III** 12/11, 11/12 **IV** 15/15, -/15 **V** 11/10, 10/11. (A few counts are approximations owing to variation in scales at bases of digits; the divided lower ungual sheath scale is omitted from the counts.)

COLORATION: In life (fig. 53), dorsum brown with variably distinct tan dorsolateral lines; flanks blackish brown, with some small pale spots. Palms and soles black; other ventral surfaces either sexually dimorphic or individually variable as follows: Male—all ventral surfaces except palms and soles uniformly bright orange. Female—underside of head creamy white, turning light yellow under throat and over venter and base of tail,

Fig. 56. *Arthrosaura montigena*, new species. Dorsal view of the type specimens. Left, female holotype (EBRG 2905, 48 mm SVL); right, male paratype (AMNH R-140230, 40 mm SVL).

becoming orange under distal three fourths of tail. Iris orange. Tongue black.

COLOR AND PATTERN IN PRESERVATIVE: More detailed examination of the preserved specimens (fig. 56) shows the female to have a distinct pale dorsolateral line extending from the postorbitals onto the base of the tail. The male has this line extending weakly from the eye and along the outer edge of the parietal, then becoming distinct on the neck, present but poorly defined on the body, and then again distinct from above the groin onto the base of the tail; the dorsolateral line is continued posteriorly from the proximal part of the tail as a series of pale brown spots that disappear before the end of the tail in the female (tail incomplete in male). A parallel row of white spots on lower side of tail, also disappearing before the end of tail.

The hexagonal body scales—inconspicuously speckled with brown on a lighter brown ground and with a slight darkening along the keels—are sharply bicolored, with the free ends grayish brown. The grayish distal ends overlap irregular dark brown pigmentation across the bases of the scales in each succeeding row, forming a series of dark transverse lines across the dorsum and flanks, but there is an increase in the amount of dark brown pigmentation on the flanks of both specimens, and some of the scale tips of the lateral scales are white in the male, accounting for its pale-spotted blackish sides in life (fig. 53). The pattern of dark transverse lines extends only onto base of the tail, which becomes marked with small irregular dark spots and darker keels.

Top and sides of head brown, with some slightly darker brown pigmentation but no definite patterning. Supralabials appear either brown with white spots in the male, or white with brown bars in the female. Several elongated whitish spots with darker borders on side of neck. Ventral surfaces and ventrolateral scales on lower flanks white, with some light to dark brown pigmentation on the ventrolaterals and lateral row of ventrals; no pigment on genials, but some irregular dark brown markings at base of forelimb insertion and an occasional very small dark mark in preanal area or elsewhere; ventral surfaces otherwise immaculate.

HEMIPENIS

METHOD: The genitalia of the paratype of *Arthrosaura montigena* were everted in the field, and the left organ was later removed and inflated with carmine-dyed petroleum jelly. Because of a puzzling, well-defined aperture between the lobes of the organ and because the apices of the lobes seemed not to fully evert, the jelly was squeezed out and the organ soaked overnight in a solution of 3% KOH (also injected into the lumen) before being reinflated. The right organ was then removed, injected with 3% KOH and soaked in the KOH solution for about 10 hours before being inflated. Results were comparable, however, and the two organs are essentially identical. The tips of the lobes could not be completely extended manually,
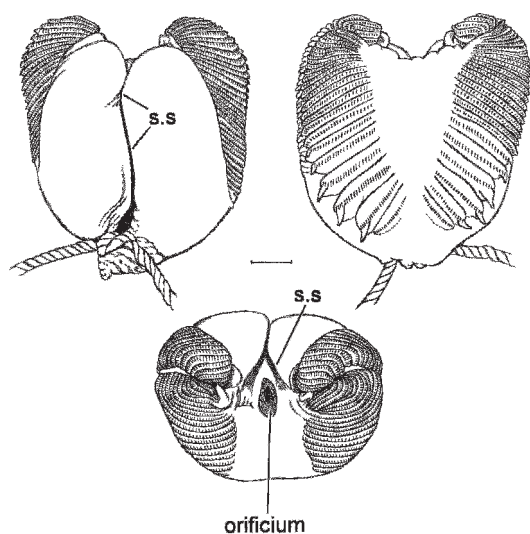
Fig. 57. Hemipenis of *Arthrosaura montigena*, new species. Everted left organ of paratype (AMNH R-140230), in sulcate, asulcate, and apical view. The "orificium"—an aperture in the hemipenial crotch between the branches of the sulcus spermaticus (s.s)—opens into a tunnel of unknown function. Scale line = 1 mm.

even by internal probing with the round head of a no. 000 insect pin. The following description and illustrations are of the left organ, showing maximally attained inflation.

DESCRIPTION: The inflated hemipenis (fig. 57) is 5.5 mm wide by about 7 mm in overall length; it is bilobed for about 30% of total length. The broad middle part of the sulcate side of the organ is nude, with the sulcus spermaticus being a deep, well-defined groove running a medial course to the crotch; the sulcus bifurcates as it enters the crotch, with the branches extending centripetally probably to the apices of the lobes. There is a well defined aperture (the "orificium") about 0.2 mm wide between the sulcate branches in the middle of the nude crotch, opening into a tunnel extending proximally into the hemipenis to a depth of perhaps 1 mm (which would = 14% of hemipenial length).

The median part of the asulcate side of the organ is nude from the base to the crotch. Plicae arise on either side of the nude midline in a weak chevron pattern; the basal six rows of plicae terminate laterally on each side, at a nude area on the lower side of the hemipenis; a

small spine rises at the lateral terminus of rows 2–5. Starting with row 7, the asulcate plicae meet a matching set of plicae on the sides of the lobes. At magnifications exceeding 20 times, the edges of all the plicae are lined with minute, presumably mineralized spinules.

COMMENTS: The puzzling orifice (here termed **orificium**) in the hemipenial crotch opens into a relatively deep tunnel of unknown function. The possibility was considered that the orificium might open into the lumen of a long, uneverted process. However, the opening and the shaft are equally well defined in both left and right hemipenes and there is no visible indication that the structure might be eversible. Although the apical tips of the lobes resisted complete eversion, the hemipenes overall were maximally inflated without apparent deformation of their distal, proximally extending tunnels. The orificium is a heretofore unknown hemipenial structure.

The hemipenis of *Arthrosaura montigena* is somewhat similar to that of *Arthrosaura synaptolepis* (fig. 3 in Donnelly et al., 1992), which differs most notably in having the hemipenial lobes terminally flattened and in having a bumplike "pronounced elevation of tissue" instead of an orificium. Clearly, there is considerable taxonomic potential in the hemipenial morphology of *Arthrosaura*.

REMARKS

The male paratype of *Arthrosaura montigena* was found active during the morning, on the forest floor (fig. 4 bottom) near Camp 1. The female holotype was under a rock near a forest stream at Camp 4.

Small brown lizards are hard to see and harder to catch in dense montane vegetation, and upland species of *Arthrosaura* are therefore poorly represented in collections. Seldom is more than a specimen or two taken at a given locality. Distributions at least have the appearance of being generally limited, and additional species must be waiting discovery in the Guayana highlands.

The key below is a practical guide to the currently recognized taxa of *Arthrosaura*, updating the species revised by Hoogmoed and Ávila-Pires (1992) with subsequent additions by Donnelly et al. (1992), Gorzula

and Señaris (1999: 117–124), MacCulloch and Lathrop (2001), and the present paper. We have not seen specimens of *A. versteegii*, *A. testigensis*, or *A. guianensis*, but have relied for data on the descriptions in Hoogmoed and Ávila-Pires (1992), Gorzula and Señaris (1999), and MacCulloch and Lathrop (2001), respectively.

Asterisks (*) in the key mark the four species named from Venezuelan tepuis. Additional to these, an unnamed species on the Chimantá massif may be distinguishable by the combination of a broad dark brown middorsal stripe and pale dorsolateral lines (see Gorzula and Señaris, 1999: photo 89—anterior half of body in dorsal view). Another probably unnamed species of *Arthrosaura*, from Cerro Yaví in the northwestern tepuis, is known only from a tail that had been ingested by a snake (Myers and Donnelly, 1996: 22, fig. 15).

KEY TO THE NAMED SPECIES OF *ARTHROSAURA*

1. Mainly lowland species occurring in Amazonia and/or in eastern Guayana region (French Guiana to Guyana) 2
– Upland and highland species in Venezuela and Guyana 4
2. Supraoculars four; a broad pale middorsal stripe from snout to end of tail; north and south of lower Amazon, from Suriname to Brazil; possibly disjunct in upper Amazon . . . . *A. kockii*
– Supraoculars three; no broad pale middorsal stripe 3
3. Seven supralabials; flanks usually conspicuously pale spotted; no pale dorsolateral line; to about 70 mm SVL; throughout Amazonian Basin and north to Guyana . . . *A. reticulata*
– Six supralabials; flanks not conspicuously pale spotted; a pale dorsolateral line at least anteriorly; < 50 mm SVL; scattered localities of 100–630 m elevation in northern French Guiana and Suriname, and one site at 1400 m in extreme eastern Venezuela . . *A. versteegii*
4. Supraoculars four; 2–4 pale lines on body . . 5
– Supraoculars three; dorsum with or without pale dorsolateral lines 6
5. Dorsum with four pale narrow lines; parietals and interparietal with 1–2 longitudinal keels; temporals small; Los Testigos massif, Bolívar. . . . . *A. testigensis* *
– Dorsum with pale dorsolateral lines and a lateral line of pale spots; head scales smooth; temporals large; Mt. Ayanganna, Guyana . . . . *A. guianensis*

6. Prefrontals present; three pairs of large genials, all in contact with infralabials. . . 7
– Prefrontals lacking; only two pairs of large genials, both in contact with infralabials; extreme southern Venezuela near Brazilian border at Cerro de la Neblina and in Sierra Tapirapecó . . . . *A. synaptolepis* *
7. Venter and gular region virtually immaculate 8
– Venter and gular region with conspicuous dark spots; southern Venezuela on Cerro Duida and Cerro Jaua . . . . *A. tyleri* *
8. Lateral body scales sharply demarcated from ventrolaterals by zone of small scales; pale dorsolateral line from eye to above arm, reappearing in sacral region; disjunct record at 1400 m in extreme eastern Venezuela (otherwise French Guiana and Suriname (couplet 3 above) . . . . *A. versteegii*
– Lateral body scales not demarcated from ventrolaterals, or very indistinctly demarcated by a row of well-separated small scales (Auyantepui); pale dorsolateral line complete on each side . . *A. montigena*, new species *

Neusticurus rudis Boulenger
Figures 58–59

Neusticurus rudis Boulenger, 1900: 53–54, pl. 5, fig. 1. Holotype BMNH 1946.8.31.64 from base of Mount Roraima, about 3500 ft, Guyana, collected by F. V. McConnell and J. J. Quelch. Roze, 1958: 251–252 (Auyantepui specimens). Gorzula and Señaris, 1999: 128 (Auyantepui specimen).

MATERIAL: 1.1 km NNE Camp 1, 1650 m: AMNH R-140200–140201, EBRG 2906. Camp 2, 1750 m: AMNH R-140202–140205, EBRG 2907–2909. Camp 3, 1850 m: AMNH R-140206–140208, EBRG 2910–2918. 4 km NE Camp 3, 1430 m: AMNH R-140209–140210. Camp 4, 1600 m: AMNH R-140211–140212, EBRG 2919. Camp 5, 2100 m: AMNH R-140213, EBRG 2920. All from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

COLORATION IN LIFE: A juvenile (AMNH R-140201, 38 mm SVL) was bicolored, with a brown dorsum and black sides (fig. 58 top); ventral surfaces whitish. Color becomes variable in larger specimens.

One subadult (EBRG 2906, 61 mm SVL) had a dark greenish brown dorsum; the throat and venter were pale yellow with suffusions of orange-brown beneath neck and orange-brown spotting ventrolaterally, becoming pale greenish beneath limbs and tail.

Fig. 58. *Neusticurus rudis* from the summit of Auyantepui, not to same scale. **Top:** Juvenile with black sides, 38 mm SVL (AMNH R-140201). **Bottom:** Adult female, 87 mm SVL (AMNH R-140200).

Another subadult (AMNH R-140202, 60 mm SVL) had a black-checkered, dark olive-brown dorsum; ventral and ventrolateral surfaces as in specimen above; iris brown around pupil, with dense gray suffusion toward periphery.

An adult female (AMNH R-140200, 87 mm SVL) was dorsally brown when photographed (fig. 58 bottom), but, at time of preservation, it was dorsally olive, with paler areas and some blackish scales; ventral surfaces pale yellowish; iris olive green turning gray toward periphery. A large male (AMNH R-140206, 85 mm SVL) was black above with conspicuously yellow-speckled sides.

HEMIPENIS: The hemipenes of AMNH R-140208 (73 mm SVL) were everted in the field. Both organs were later removed, immersed for 1 hr in 3% KOH solution, and inflated with carmine-dyed petroleum jelly. Attempts to obtain maximum inflation (usually a desirable thing) caused an apparent overinflation and swollen distortion of one lobe of each organ, but all structures are completely everted. The following description and illustration (fig. 59) are based primarily on the left hemipenis, with some interpretation provided by comparison with the right organ; the apparent distortion of
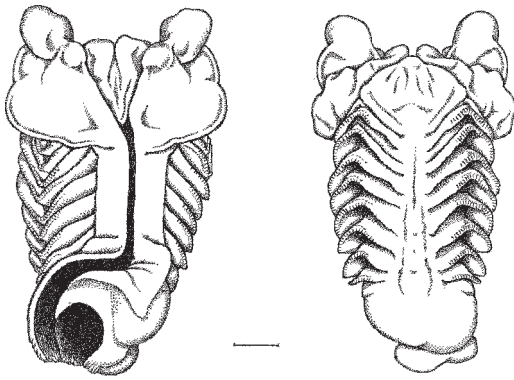
Fig. 59.   Everted hemipenis of *Neusticurus rudis* (AMNH R-140208, left organ) in sulcate and asulcate view. Owing to slight distortion in the midsection, the sulcate depiction also shows the angulation of tissue ridges on the left side of the organ. The chevron-shaped ridges point proximally in lateral view and distally in asulcate view. Scale line = 1 mm.

the swollen lobe is not illustrated, being replaced by a mirror-image drawing of the opposite lobe.

The everted hemipenis is robust, measuring 5.5 mm long and 4.2 mm across the midsection. The organ is very weakly bilobed, with the lobes strongly inclined to the sulcate side (fig. 59). The nude sulcate faces of the lobes are nearly flattened and are confluent with a pair of pronounced knobs (2 mm long, 1.5 mm wide) extending distally. There are four additional, much smaller protuberances, including a small round knob situated at the sulcate-side base of each large knob and a pair of protuberances in the lobular crotch. The sulcus spermaticus curves mediad from the base of the organ (coming from the left in the left organ [fig. 59], from the right in the right organ); the sulcus then extends centrolineally to bifurcate just beyond the base of the lobular area, with each branch extending between a large knob and the adjacent medial protuberance. The midsection of the hemipenis is nearly encircled by eight angulate tissue ridges that are interrupted by the sulcus spermaticus on one side and a narrow median nude space on the other. On the asulcate side the ridges are chevron-shaped and pointed distally, whereas the chevrons point proximally on the sides of

the hemipenis. Comblike rows of minute, presumably mineralized spinules are embedded in the tissue folds; there are no other spines. The base of the organ is nude.

NATURAL HISTORY

Neusticurus rudis has strong aquatic tendencies and nearly all our 29 specimens were found in rivers and streams, where they would try to escape by swimming under water or by hiding in a crack on the rocky bottom of a stream. They probably are mainly diurnal; a few individuals found in the water at night might have been startled and displaced from streamside places of concealment. One was found by day near Camp 2, in the dark of a sandstone crevice cave with water covering the floor; the lizard was in a crack in the rock wall above the water line; a frog (*Stefania schuberti*) was on the wall of the same cave.

REMARKS

Neusticurus rudis is sympatric with *Neusticurus racenisi* Roze on the southern slope of Auyantepui at about 1000–1100 m elevation, where W. H. Phelps collected the holotype of *N. racenisi* and a specimen of *N. rudis* (AMNH R-61025). However, *N. racenisi* has not been found on the Auyán summit.[27]

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[27] CORRECTION OF TYPE LOCALITY: Roze (1958a: 252) incorrectly gave ''400 m. de altura'' for both the holotype (AMNH R-61008) and the single paratype (AMNH R-61040) of *Neusticurus racenisi*. The paratype is catalogued as 1509 ft (460 m) and the holotype as 3909 ft (1100 m), which correspond to the 460 m (Urullén) and 1100 m (Guayaraca) camps of the 1937–1938 AMNH–Phelps Venezuelan Expedition. The 460 m camp was the expedition base in an area of savanna and forest. The higher camp was the site of Jimmy Angel's base camp on savanna bordered by dense forest. The elevation of the latter ''1100 meter'' or Guayaraca camp was corrected to ''1038 meters'' in Tate (1938a: 474) and cited as ''nearly 1,000 metres'' by Dunsterville (1965: 168). Both the 460 m and 1100 m camps are shown on maps in Tate (1938a) and Gilliard (1941a).

The collector, W. H. Phelps, doubtless ranged widely about the camps while hunting birds, and the type locality of *N. racenisi* may reasonably be corrected to: ''south slope Auyantepui, Guayaraca area, about 1000–1100 m''.

Myers and Donnelly (1997: 61) suggested that, rather than a highland species of disjunct distribution, *Neusticurus racenisi* "may prove to be fairly widespread in southern Venezuela in an elevational range of about 100–1200 m" and that it is a "lowland invader" of tepui habitats. However, there are few records and Gorzula did not take *N. racenisi* during his extensive collecting in the Venezuelan Guayana (Gorzula and Señaris, 1999: 157). *Neusticurus rudis*, on the other hand, "appears to be an upland and highland species in Venezuela", although known from lower elevations elsewhere (Gorzula and Señaris, 1999: 128).

FAMILY POLYCHRIDAE

Anolis chrysolepis planiceps Troschel
Figures 60–62

Anolis chrysolepis Duméril and Bibron, 1837: 94. Type locality, Mana, French Guiana, based on MHNP 2436, lectotype designated by Vanzolini and Williams (1970: 85).

Anolis planiceps Troschel, 1848: 649–650. Type locality, "Caracas" (erroneously given as "British Guiana" by Peters and Donoso-Barros, 1970: 51).

Anolis nitens: Roze, 1958a: 246 (Auyantepui). McDiarmid and Donnelly, 2005: 505, 515 (Guayana highlands).

Anolis eewi Roze, 1958b: 311–312. Holotype FMNH 74040, from Cumbre de Torono Tepui, Chimantá Tepui, Estado Bolívar, Venezuela, collected February 28, 1955, by J. A. Steyermark and J. Wurdack. Gorzula and Señaris, 1999: 145, color photos 93, 94 (name resurrected for Venezuelan upland and highland localities).

Anolis chrysolepis planiceps: Vanzolini and Williams, 1970: 83–86. Donnelly and Myers, 1991: 23–24 (Cerro Guaiquinima). Myers and Donnelly, 1997: 58–60 (Cerro Tamacuari).

Anolis chrysolepis eewi: Gorzula, 1992: 275.

Anolis nitens nitens: Gorzula and Señaris, 1999: 145–146 (Venezuelan lowland localities).

MATERIAL: Camp 1, 1700 m: AMNH R-140214–140217, EBRG 2902–2903. Camp 2, 1750 m: EBRG 2904. From the 1994 AMNH–TERRAMAR Expedition to Auyantepui. ADDITIONAL MATERIAL: Auyantepui plateau, 2200 m (7218 ft.): AMNH R-61013, from the 1937–1938 AMNH–Phelps Venezuelan Expedition.

COLORATION: Dorsal color and pattern variable in life, but pattern usually including a dark brown interorbital bar, pale diagonal line on shank, and a pair of brown sacral markings. Two juvenile females had tan middorsal stripes on brown (fig. 60 middle) or greenish gray dorsa; another juvenile was frosted gray over a complex darker pattern (fig. 60 top). Adults were gray or slightly greenish gray with indefinite darker gray markings, especially on the flanks (fig. 60 bottom). Ventral surfaces dirty white, grayish white, or chin white with venter pale yellow. Pale labial stripe and stripe through ear pure white, grayish white, or pale greenish gray (this marking tending to become obscure in preservative).

Dewlap of two males orange, with white or grayish white scales in basal rows, scales darker gray or blackish gray in distal rows. One adult female with a smaller but similarly colored dewlap. The small juvenile dewlaps seemed more variable based on four specimens from Camp 1: One juvenile (♂) had a red dewlap with yellow scales basally and dark gray scales peripherally; two others had either a red (♂) or orange (♀) dewlap with a mixture of pale and dark scales; a fourth juvenile (♀) had a large bluish black basal spot on the dewlap, which had a bright orange periphery and mostly white scales (only a few dark scales).

Iris of adults dark bronze heavily suffused with black and with a pale blue pupillary ring; iris of two juveniles appeared dark brown with a bluish white area above the pupil. Tongue pale yellowish or orangish; mouth lining pale grayish, throat lining not pigmented.

NATURAL HISTORY: Six of our seven specimens were collected in the forest (fig. 4 bottom) near Camp 1; one was sleeping on a leaf 1 m aboveground at night and the others were on the forest floor by day. An additional specimen was found by day in a patch of forest near Camp 2.

DISCUSSION

Venezuelan anoles of this complex are generally considered part of a single variable and geographically widespread species, which occurs throughout Amazonia, and south into Brazil to the northern half of the state of São Paulo, and northward through eastern Vene-

Fig. 60. *Anolis chrysolepis* from the summit of Auyantepui. **Top:** Juvenile male, 30 mm SVL (AMNH R-140214). **Middle:** Juvenile female, 34 mm SVL (AMNH R-140215). **Bottom:** Adult male, 66 mm SVL (AMNH R-140216).

zuela and west along much of its northern coast. The pioneering study was that of Vanzolini and Williams (1970), who detected four peripherally situated, extra-Amazonian "core areas".

> The core areas are defined as areas of maximum overlap of distinctive distributions of a number of characters. All 12 characters studied play a part in the definition of the cores, but 4 of them are relevant in all cases: dewlap color, fourth toe lamellae, scales across snout and tail length.
>
> In the cases where the boundaries of the core areas are not very far apart, one finds either sharp breaks in character values or smooth intergradations. In the Amazonian region, central for all four core areas, however, the patterns of transition are complex. (Vanzolini and Williams, 1970: 90)

Vanzolini and Williams' study (1970) was contemporaneous with the ornithological investigations of Haffer (1969). These two studies were important in advancing the theory that Quaternary climatic cycles induced contractions and expansions of tropical forest, leading to infraspecific differentiation and speciation of plants and animals in forest refugia. Subsequently, some authors enthusiastically managed to see refuges everywhere and anywhere there were a few shared species ranges. Nonetheless, virtually everybody was forced to abandon the myth of ancient, uniformly stable tropical forest unaffected by the vagaries of time. As noted by Vanzolini and Williams (1970: 108), the myth "was at base a naive extrapolation from annual constancy in climate to eons-long stability".

Although the establishment of formal subspecies of *Anolis chrysolepis* was not a principal objective (they considered "the issue of subspecies recognition an unimportant one"), Vanzolini and Williams (1970: 86) did propose a classification of four subspecific taxa associated with the four core areas. Vanzolini and Williams (1970: 12–13) realized that there are multiple levels of differentiation "that might be multiplied indefinitely by further collection and investigation", but believed that the levels of differentiation recognized nomenclaturally were "closest to species difference, and indicative, perhaps, of past and future

potential species formation". (Indeed, preliminary analysis indicates presence of substantial molecular divergence in the *chrysolepis* complex; see Glor et al., 2001.)

Vanzolini and Williams also resurrected a name (*Anolis bombiceps* Cope) for a closely allied species found in sympatry with *chrysolepis*. Excluding the core areas, the geographic ranges of the four *chrysolepis* subspecies were not explicitly mapped, and, owing to the discordance and overlap of most characters, the recognized subspecies seem most easily distinguished on the basis of different dewlap colorations.

A quarter of a century later, the *Anolis chrysolepis* complex was revisited by Ávila-Pires (1995: 67–88) in her monographic *Lizards of Brazilian Amazonia*. Using the name *Anolis nitens* in preference to *A. chrysolepis* (see below), Ávila-Pires provided a standarized description for each taxon recognized by Vanzolini and Williams and described an additional subspecies in the Amazon Basin; she identified to subspecies all specimens available to her. Ávila-Pires noted that additional material, including color descriptions from life, is still needed for a better understanding of this remarkably widespread lizard.

Unfortunately, the nomenclature of the *Anolis chrysolepis* complex has become more confused than it should be. Two problems needing attention are the status of the names *Anolis nitens* (Wagler) and *Anolis eewi* Roze, as discussed below.

Status of *Anolis nitens (Wagler)*

Draconura nitens Wagler (1830) was named with a brief four-line description in Latin (see below for the original description and translation). The type locality "America" is uninformative, and no other author seems to have examined the lost type specimen. Only seven years after its description, Duméril and Bibron appeared unable to diagnose the species for inclusion in the *Erpétologie générale*—the great herpetological synthesis of the time. Duméril and Bibron (1837: 91) placed *Draconura nitens* with a question mark in the synonymy of their new *Anolis refulgens* (type locality, "Surinam"), a Schlegel label name. The new *Anolis chryso-*

lepis was named a few pages later (Duméril and Bibron, 1837: 94–95).

A. A. Berthold, at the Zoological Museum in Göttingen, unsuccessfully tried to make some sense of the taxonomy under the subheading "Ueber das Genus Draconura Wagl". (Berthold, 1840: 899; 1842: 17–21; "1843" [1842?]: 61–65).[28] In recognizing *Draconura*, Berthold accepted *refulgens* over *nitens*, without concern for priority (not an established concept in those days), and added two additional species, *chrysolepis* and his new *12-striata*, the last of which is now recognized as a synonym of *Anolis* or *Norops auratus* (a species which Wagler had placed in the monotypic genus *Norops* immediately following the description of *Draconura*).

Several other 19th-century authors simply overlooked or ignored Duméril and Bibron's "?" in the *Erpétologie générale* and accepted *nitens* (Wagler) without question and with little or no discussion as the senior synonym of *refulgens* (Wiegmann, 1834: 16; Gray, 1840: 114; 1845: 207; Fitzinger, 1843: 69; Peters, 1863: 142; Bocourt, 1874: pl. 16, fig. 25; Boulenger, 1885: 91–92).

Use of either *nitens* or *refulgens* as a valid specific name in most of the secondary 19th-century references above are simple listings of little taxonomic importance, although Bocourt (1874) added head and digit drawings of the Paris Museum holotype of *refulgens*. During all this time, *Anolis chrysolepis* Duméril and Bibron (1837: 94–95) also was recognized as a valid species by most of these and other authors.

In the *Catalogue of the Lizards in the British Museum*, Boulenger (1885: 89–90) identified 15 specimens as *Anolis chrysolepis* but none as *A. nitens*. Boulenger's account for *A. nitens* (pp. 91–92) appears to have been paraphrased from Duméril and Bibron's (1837: 91–94) original description of *A. refulgens*. (Boulenger correctly translated the symbols ′′ and ′′′ used by Duméril and Bibron for cm and mm, but comparison of head, body, and tail measurements show that Boulenger's "108" mm total length is a misprint for 180 mm.) Boulenger's *Catalogue* provided the starting point for several 20th-century authors who were to deal with actual specimens from Venezuela and British Guiana (now Guyana).

In the early 20th century, Fowler (1913: 171–172) described as a Venezuelan subspecies *Anolis nitens bondi*.[29] Lidth de Jeude (1917: 46) mentioned *Anolis nitens* in Suriname, and Barbour (1934: 143) followed Boulenger in listing it as a senior name over *refulgens*. Finally, field experience with living animals was provided by Beebe (1944), who recognized both *Anolis chrysolepis* and *Anolis nitens* as the most abundant anoles at Kartabo, British Guiana, and Caripito, Venezuela. *Anolis chrysolepis* was considered an usually striped species with "infinite variation", whereas *A. nitens* was characterized mainly by "a series of posteriorly pointed V-shaped markings on the back from shoulder to beyond the base of the tail".

Shreve (1947: 524) saw through the extensive color variation and synonymized *Anolis chrysolepis* under *Anolis nitens*, closing the argument with field notes for two Venezuelan specimens "taken in copulation, the female having the light vertebral streak [a common female color morph of some anoles] of *chrysolepis*, the male presenting the *nitens* pattern of chevrons, their apices directed posteriorly". But Shreve also is the first author to question the adequacy of Wagler's (1830) description of *nitens*:

> As the original description of *nitens* is not very diagnostic, there appears to be some doubt about the applicability of the name. If it cannot be used, then *chrysolepis*, which was much better diagnosed, can be employed. (Shreve, 1947: 524)

Subsequent use of *nitens* as the valid name for Venezuelan specimens (Roze, 1958a: 246; Test et al., 1966: 13–14; Donoso-Barros, 1968: 112) derived from Shreve's action, but *chrysolepis*

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[28] The first Berthold citation is only a brief synopsis, given for completeness; the remaining two citations are differently paged preprint and journal versions of the same paper. See Myers and Böhme (1996) for a summary and bibliography of the herpetological part of "Berthold's rich and varied scientific career".

[29] Fowler's *bondi* was "described from a very poorly preserved type that displays no discernibly distinctive characters" according to Vanzolini and Williams (1970: 85), who corrected the type locality and synonymized it under *A. c. planiceps* based on better preserved specimens from a nearby locality.

was not universally discarded and both it and *nitens* were continued as valid species in the *Catalogue of the Neotropical Squamata* (Peters and Donoso-Barros, 1970: 51, 61).

Thus the stage was set for Vanzolini and Williams to make order out of 140 years of confusion. In formulating their concept of *Anolis chrysolepis* (Duméril and Bibron, 1837) as a polytypic species, Vanzolini and Williams (1970: 83–86) considered the 13 specific names that were available (only four of which are mentioned above). The oldest name is *Draconura nitens* Wagler, 1830, which they concluded "is probably, but hardly with certainty, applicable to some member of the *chrysolepis* group".

> The type is lost, the type locality ("America") insufficiently defined, and the usage of the name extremely confused, having been used primarily for one of the color morphs possible to *chrysolepis* group animals in Surinam (Boulenger, 1885) or British Guiana (Beebe, 1944) or Venezuela (Shreve, 1947). Such a name could be employed only arbitrarily, and we therefore set it aside. (Vanzolini and Williams, 1970: 84)

Draconura nitens was viewed by Vanzolini and Williams (1970: 84) not as a verifiable senior synonym of *chrysolepis* but as a name of "uncertain application" (i.e., a nomen dubium). By this time, the 1837 name *Anolis refulgens* had become a nomen oblitum (a "forgotten name", rejected under Article 23b of the Code edition then in force; see also ICZN, 1999: 111 and art. 23.12). Because of that and as first revisers, Vanzolini and Williams (1970: 85) selected *Anolis chrysolepis* Duméril and Bibron (1837) as "the earliest satisfactory name for any member of the group", noting that it fortuitously was also the "most familiar name in the complex".

Hoogmoed (1973, 1979b) followed the nomenclature of Vanzolini and Williams, but thought that none of the reasons given

> is sufficient to discard this name [*nitens*], for the original description is completely valid and the name has been in use until recently, alongside the now accepted name *A. chrysolepis* Duméril and Bibron *which was more widely used* [emphasis added]. The only means of discarding *nitens* Wagler and ensuring nomenclatural stability is to ask the International Commission on Zoological Nomenclature to use its plenary powers to suppress *nitens* Wagler. A suggestion

to this end has been made by me to Vanzolini and Williams. (Hoogmoed, 1973: 124)

Savage and Guyer (1989: 111–112) listed *chrysolepis* as a valid species of anole but considered *nitens* as a species "of uncertain generic assignment and questionably valid", seemingly in agreement with Vanzolini and Williams (1970: 84). However, two years later Savage and Guyer (1991: 366) decided that

> *nitens* had over 125 years of continuous [albeit not prevailing] usage for this species prior to 1970" and that Vanzolini and Williams' action in setting aside *nitens* was not only contrary to the Code in effect at that time (and currently), but required destabilization of a long-accepted name. (Savage and Guyer, 1991: 366)

Hoogmoed (1973) and Savage and Guyer (1991) believed that the synonymy of *nitens* and *chrysolepis* had been established by usage and that, under the Code then (and now) in effect, "the valid name of a taxon is the oldest available name applied to it" unless a junior name is preserved by the Commission. There is arguable merit in this interpretation. Literal reading of Article 23 in earlier editions (1961, 1985) of the Code might be interpreted to mean that, once applied, even an unidentifiable or erroneously applied subjective senior synonym not in prevailing usage must be maintained as valid under the Principle of Priority. But it seems questionable that such a consequence was originally intended by the Commission, which subsequently clarified the issue.

As a first underlying principle, the Code (ICZN, 1985, p. xiii; 1999, p. xix) "refrains from infringing on taxonomic judgment, which must not be made subject to regulation or restraint", and the Commission elucidated this issue in the current edition (Article 23.3.6), whereby a junior synonym "may be used as the valid name of a taxon by an author who considers the synonymy to be erroneous".

Except for continuing to use *Anolis* over *Norops*, Ávila-Pires (1995) accepted Savage and Guyer's suggestion that *Anolis nitens* corresponded to *A. chrysolepis planiceps* of Vanzolini and Williams. She stated that

> Considering the argumentation by [Savage and Guyer], and the fact that up to the present no application was made to the International

Commission on Zoological Nomenclature to suppress *nitens*, I think there is no reason not to adhere to the well-established rule of priority. Even considering that the type of *nitens* is lost, the name has been consistently linked to one taxon by *several* [emphasis added] authors, with no discrepancy between the taxon and the original description. Although some specimens from ''Suriname'' were identified as *A. chrysolepis planiceps* (see Hoogmoed, 1973) and *A. nitens* by some authors, generally the name *nitens* was associated with specimens from Guyana and Venezuela. This area corresponds to the distribution area of *A. c. planiceps* as used by Vanzolini & Williams (1970). Thus, in agreement with former usage and with the proposal of Savage & Guyer (1991), I consider the taxon occurring in Guyana and Venezuela as the nominal subspecies of *Anolis nitens*. (Ávila-Pires, 1995: 88)

However, problems are created in arbitrarily assigning the name *nitens* to a particular geographic area for purposes of fixing the nominotypical subspecies. The name *nitens* was used by 19th century authors for at least two species from ''Surinamia [and] Brasilia'' (Fitzinger, 1843), from ''Surinam'' (e.g., Gray, 1845; Bocourt, 1874; Boulenger, 1885), and from Pebas on the upper Amazon (O'Shaughnessy, 1875: 277). Not until the 20th century was the name applied to specimens *explicitly* from Venezuela and Guyana (e.g., Fowler, 1913; Beebe, 1944). Selection of any area without neotype designation is equivalent to the unsanctioned concept of ''restriction of type locality''—the inventing or hypothesizing (versus justifiable correction) of a type locality that is not binding nomenclaturally and therefore without practical value (Myers and Böhme, 1996: 18).

Somewhat amazingly, only a few authors (Shreve, 1947; Vanzolini and Williams, 1970; Myers and Donnelly, 1997) appear to have been explicitly aware of the inadequacy of the original description of *nitens*. To illustrate this point, Wagler's (1830: 149) complete description is given below, followed by an English translation.

DRACONURA. Drachenschweif.

Vertex et nares Dactyloae; gula plica longitudinali subinflabili; digiti prope articulationes subincrassati; 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.

DRACONURA. Dragon's Tail.

Crown and nostrils of *Dactyloa* [the preceding genus]; with somewhat inflated longitudinal throat fold; digits somewhat thickened near articulations; tail smooth, thickened and a little rounded at the base. (America.)

Species: Draconura nitens. Green [see fn. 32] above, with a coppery gold sheen; below, whitish green with a silvery brilliance; tail totally golden green, with two bowlike dark spots above the sacral bone; thighs and digits weakly banded.

Without a specific type locality and without a known holotype, *Anolis nitens* can be identified only by the original description above. Furthermore, as stated by Vanzolini and Williams (1970: 84), *nitens* ''could be assigned, if at all, only on the basis of color characters''; the generalized morphology might exclude some taxa but does not provide species-specific characters. Therefore, Wagler's portrayal of a brightly colored lizard must be assumed accurate—there is nothing else to go on and there are no objective grounds for concluding that some taxonomically critical item of coloration was omitted.

CHARACTERS CONSISTENT WITH *A. CHRYSOLEPIS*: A conspicuous sheen is emphasized in the original description of *nitens* and in the name,[30] suggestive of the metallic sheen seen in some anoles, including occasional specimens of *chrysolepis* (see below). The pair of dark sacral spots seems to be the *only* character really suggestive of the *chrysolepis* complex, but their presence is variable and they are not confined to *A. chrysolepis*. The indistinct thigh pattern seems relatively uninformative.

CHARACTERS INCONSISTENT WITH *A. CHRYSOLEPIS*: The fact that Wagler took the trouble to mention the sacral markings and the *obsolete*[31] thigh banding indicates that the animal was otherwise patternless. If

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[30] The specific name *nitens* is the present participle of Latin *niteo* and means ''shining'', ''glittering'', or ''glossy''.

[31] This is a Latin adverb derived from *obsoletus*, meaning ''rudimentary'', ''hard-to-see'', or ''scarcely apparent''.

so, the absence of all head markings, tail banding, vertebral stripe or dorsal chevrons or rhomboids, lateral marbling, or other such pattern elements is inconsistent with what is known of the normal variation of *Anolis chrysolepis*. (An occasional old, poorly preserved and faded specimen of *chrysolepis* might conceivably lack describable pattern, but neither should such a specimen show the bright colors attributed to *nitens*.)

As previously stated (Myers and Donnelly, 1997: 59), the *green* dorsal coloring ascribed to *nitens* is inconsistent with *Anolis chrysolepis*, which is a variably patterned, basically brown or gray lizard. This requires additional elaboration.

"GREEN" IN THE COLOR VARIATION OF *ANOLIS CHRYSOLEPIS*: Beebe (1944) indicated the great range of colors and color patterns of his composite *A. chrysolepis/A. nitens* at study sites in Venezuela and Guyana, including a specimen of *chrysolepis* having a general ground color of "olive with a strong greenish yellow tinge" and another one "grayish olive". A search of Myers' field catalog reveals a few specimens having a *slight* greenish cast in the basic ground colors in life, including a "greenish gray" juvenile (EBRG 2902) and a "greenish gray" adult (AMNH R-140217) from Auyantepui and a "pale greenish brown" adult female from Cerro Guanay.

Such pale greenish casts, washes, or suffusions are not rare in the normal variation of brown or gray-colored reptiles and amphibians, but they disappear more quickly than normal greens in preservative and often are photographically elusive as well (e.g., Lynch and Myers, 1983: 522, 540). Nonetheless, under certain light, a pale bluish gray or pale greenish gray ground color can be seen on the lower sides or venters of some preserved Auyantepui specimens (AMNH R-140214–140217), although, in life, a greenish gray color was evident in only one of these (AMNH R-140217).

However, it is difficult imagining that anyone would describe such subtle hues as "green" without qualification.[32] We earlier puzzled over the green in Wagler's description:

> 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 …. (Myers and Donnelly, 1997: 59)

A slight metallic bronzy or golden sheen sometimes is evident in living *A. chrysolepis* (fig. 229 in Ávila-Pires [1995] seems to show this) and especially in preserved specimens. However, reasons for presence of a sheen, sometimes in association with a greenish hue, are not evident to us. Duméril and Bibron (1837: 91, 93–94) described the holotype of *Anolis refulgens* as having a ground color of "gris verdâtre doré [golden greenish gray, or 'greyish…with metallic gloss' as rendered by Boulenger, 1885: 92]" above and "blanche, glacée de verdâtre [white with a greenish glaze]" below, with dark head marbling, oblique bars, and crossbands on limbs and tail. Perusal of AMNH material revealed a specimen of *A. chrysolepis scypheus* (AMNH R-97359) having a tan ground color replaced by irregular areas of pale metallic blue-green on the posterior dorsum and left side, but oblique blackish brown lateral bars are well developed even in the blue-green area. The metallic shine in these few specimens is reminiscent of Wagler's description of *nitens*, which, however, seems to have had a patternless body and tail.

SUMMARY COMMENTS ON *ANOLIS NITENS*: No author has argued that Wagler's (1830) description of *nitens* demonstrably applies to *chrysolepis*, only that the name has priority and has been applied to that species. However, despite perceived shortcomings of Wagler's description, his portrayal of color is so vivid that the name *nitens* probably could be assigned if a virtually

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[32] Both English and Latin are rich in terms for shades of olive and greenish gray (e.g., *olivaceous, olivaceo-niger, olivaceo-griseus, viridi-olivaceous, viridi-griseus*). The present participle *virescens*, used by Wagler for *Draconura nitens*, is one of several "more or less accurate" synonyms of *viridis* (green) fide Stearn (1983: 248).

patternless, green lizard were found matching the description—but would the hypothetical animal prove to be a rare color-pattern variant of a known species (e.g., *A. chryso-lepis*) or a representative of a rare or geographically restricted species not currently recognized (i.e., *A. nitens* sensu stricto)?

The name *nitens* is a nomen dubium that cannot unambiguously be assigned to any known lizard. Article 23.3.6 allows authors who reject the synonymy to use the junior name *chrysolepis* as valid. However, although never in prevailing usage historically, *nitens* remains in competing use with *chrysolepis* because of prior (and arguable) interpreta-tion of Article 23.

Until Ávila-Pires (1995), the body of work comprising the continuous usage of *nitens* was not impressive, inasmuch as the name had been mentioned mostly in lists and had been applied in print only to a few dozen specimens by 1970, compared with 761 specimens later assigned by Vanzolini and Williams (1970: 13) to the better known name *chrysolepis*. Studies using the name *nitens* subsequent to Ávila-Pires (1995) include Gorzula and Señaris (1999), Glor et al. (2001), and McDiarmid and Donnelly (2005).

Because of the confusion that has been engendered, we now agree with Hoogmoed (1973) that stability will best be served by petitioning the International Commission on Zoological Nomenclature to suppress *nitens*. A proposal for suppression was submitted by the first author in December 2007. Mean-while we use the name *Anolis chrysolepis* as allowed by Article 23.3.6 (ICZN, 1999).

Status of *Anolis eewi Roze*

This nominal taxon was described by Roze (1958b) on the basis of a specimen (fig. 61) from the Chimantá massif. The specific name *eewi* is a noun in the genitive case derived from the initial letters of Ernest E. Williams, late authority on anoline lizards. Roze compared the specimen only with *Anolis fuscoauratus*, but Vanzolini and Williams (1970: 85) examined the holotype of *eewi* and effectively synonymized the name by stating that the specimen "falls within the variation of [*Anolis chrysolepis*] *planiceps*".
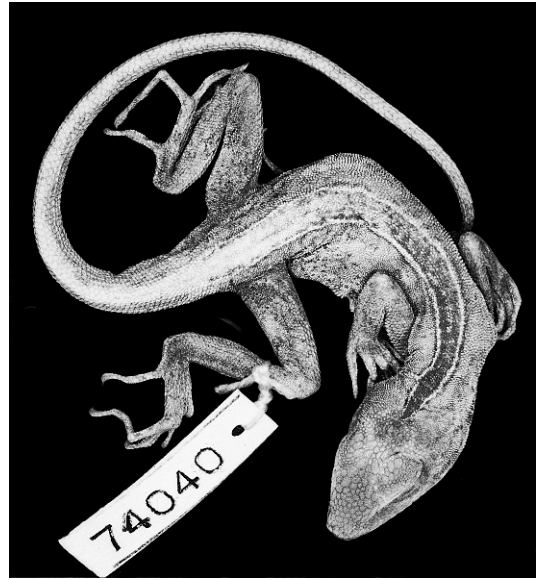
Fig. 61. *Anolis eewi* Roze (=*A. chrysolepis*). The holotype (FMNH 74040) from the Chimantá massif.

Gorzula (1992: 275) worked extensively on Chimanta and revived *eewi* as a subspecies of *Anolis chrysolepis*. More recently, Gorzula and Señaris (1999: 144–145) resurrected *Anolis eewi* as a valid species for upland and highland populations in the Venezuelan Guayana, restricting *A. chrysolepis planiceps* (as *A. n. nitens*) to lowland localities. According to these authors, although *Anolis eewi* shares many general characteristics with *A. c. planiceps*,

> *A. eewi* can be readily distinguished by its shorter legs. A regression was made for tibia length against SVL … using data from seven specimens …. The sample included males and females (SVL from 33.6 to 69.4 mm). The value for a tibia length of 16.1 mm at 65 mm body length is well below the ranges given by Vanzolini and Williams (1970) for male (17.8 to 23.3 mm) and female (17.6 to 21.1 mm) *A. nitens* [*chryso-lepis*]. (Gorzula and Señaris, 1999: 144–145)

Their regression analysis combined seven males and females from several localities (regression statistics are not given); there was no mention of comparison with any nearby lowland population. Our own small samples support Gorzula and Señaris' (1999) claim that tepui specimens have relatively short tibias. However, this is not inconsistent
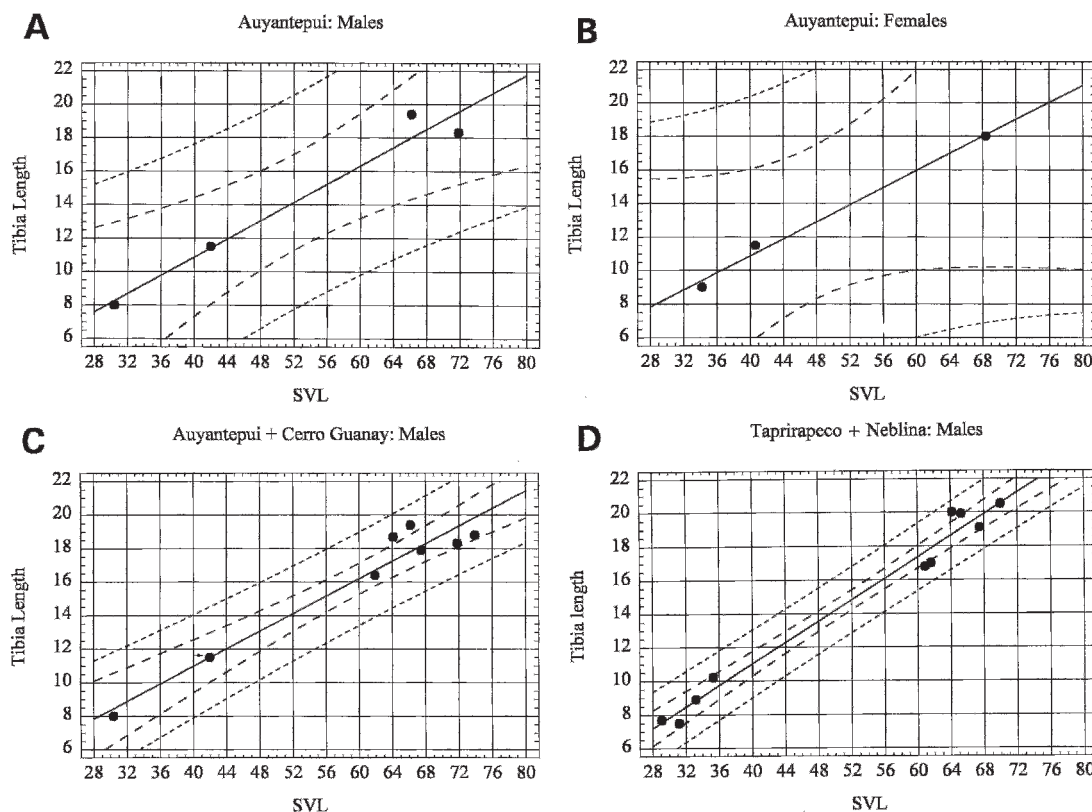
Fig. 62. Regression of tibia length on snout-vent length in Venezuelan samples of *Anolis chrysolepis* from south of the Río Orinoco. See table 8 for regression statistics. The inner dashed lines show 95% confidence limits for mean tibia length of many observations at given values of SVL; the outer dashed lines show 95% prediction limits for new observations. **A, B:** Males and females from 1700–1750 m on the summit of Auyantepui. **C:** Males from Auyantepui combined with males from 1150–1400 m on Cerro Guanay. **D:** Combined lowland (90–150 m) sample of males from region of base camps of Tapirapecó (Río Mavaca) and Neblina expeditions. (Localities mapped in Myers and Donnelly, 1997: figs. 1, 50.)

with a pattern of discordant geographic variation in tibia length as analyzed by Vanzolini and Williams (1970) for *Anolis chrysolepis* throughout its range.

Regressions of tibia length on SVL for four males and three females from the summit of Auyantepui are shown in figure 62A, B. The slopes of the regressions (0.27 ♂, 0.25 ♀) for the Auyantepui data are within the lower ends of the ranges given by Vanzolini and Williams (1979: tables 119, 121) for geographic samples of male and female *Anolis chrysolepis*; estimated tibia lengths at 65 mm SVL (17.5 mm ♂, 16.9 mm ♀) are only slightly lower (by 0.3 and 0.7 mm) than the ranges given by Vanzolini and Williams (1970: tables 120,

122) for these estimates. Gorzula and Señaris' (1999: 145) estimation of 16.1 mm of tibia length, for a hypothetical ♂/♀ lizard of 65 mm SVL, falls close to the regression lines for either males or females from Auyantepui, as does the female holotype of *Anolis eewi* (52 mm SVL, 14.5 mm tibia).

To enlarge sample size, the four males from Auyantepui were combined with four males from Cerro Guanay, a locality that also contributed specimens to the sample used by Gorzula and Señaris. Our Auyantepui + Cerro Guanay sample yielded a regression (fig. 62C) similar to that for Auyantepui alone. Gorzula and Señaris' estimated 16.1 mm of tibia length for 65 mm SVL would fall slightly outside the

95% confidence limits, but well within the 95% prediction limits for new observations.

Unfortunately, no series was available from lowlands adjacent to these tepuis. A juvenile male (AMNH R-103759) collected by Myers at a lowland site about 60 km south of the Río Orinoco and 200 km north of Auyantepui fits the tepui data marginally better than it does the northern coastal data; the measurements are 40.6 mm SVL, 11.6 mm tibia length. The estimating equation for figure 62C predicts a tibia length of 11.0 mm, compared with 12.3–12.5 mm for a 40.6 mm male lizard from northern coastal Venezuela. A single specimen naturally can fit any number of slopes and provides little information in a statistical sense, but this one example suggests that lowland specimens from south of the Río Orinoco might not be unambiguously distinguished from tepui specimens on the basis of tibia length.

Figure 62D shows a regression for males from a lowland region far to the south of Auyantepui and Cerro Guanay. The sample (AMNH specimens) comes from collections made at and near the lowland base camps of the Tapirapecó (Río Mavaca) and Cerro Neblina expeditions. This is a steeper slope than obtained from the tepuis, but the reason may reflect geographic distance rather than elevation. A single specimen (MBUVC 7044♀) caught at 1270 m elevation on Cerro Tamacuari—100 km SE of the Tapirapecó base camp (Myers and Donnelly, 1997: 4–5)—has a tibial length of 20.8 mm at 74 mm SVL. This large female (Myers and Donnelly, 1997: fig. 45) would fit well if the regression for lowland males in figure 62D could be accurately extrapolated past the last data point, but its much larger size precludes proper comparison.

Vanzolini and Williams (1970: 22) had access only to about a dozen Venezuelan specimens from the region south of the Río Orinoco. Although more individual specimens now reside in collections, there remains a lack of good samples for regression analysis. Nonetheless, the tepui data do show lizards of shorter legs when compared with Vanzolini and Williams' (1970: 16 [map B], 27) major samples designated as Falcón and Northeastern Venezuela—comprised of localities paralleling the Caribbean coast well

north of the Río Orinoco. Excluding sexual dimorphism, *Anolis chrysolepis* from this northern region seems relatively homogeneous in tibia length (regression coefficients = 0.33–0.34 ♂, 0.28–29 ♀; estimated tibia lengths at 65 mm SVL = 20.5–20.7 mm ♂, 19.4–19.5 mm ♀).

Tibia lengths in our small tepui samples from Auyantepui and Cerro Guanay are most similar to those in Vanzolini and Williams' (1970: tables 119–122) major geographic samples designated as "Tapirapés", some 2400 km southeast of Auyantepui in northeastern Mato Grosso, and "Villavicencio", at the eastern foot of the Andes roughly 1300 km southeastward from Auyantepui. These two widely separated major samples of *chrysolepis* have regression coefficients (0.23–0.27 ♂, 0.24–0.26 ♀) very similar to those shown in table 8 for the tepui samples; estimated tibia lengths at 65 mm SVL (17.8–18.4 mm ♂, 17.6–18.0 mm ♀) are not appreciably different from the tepui estimates in table 8. Vanzolini and Williams (1970: 31–33, 58, 237–238 [graphs 32, 34]) included four Venezuelan males from Cerro Duida (a tepui) and nearby Esmeralda in their subsamples designated as the Colombo-Guianan transect and the Venezuelo-Brasilian transect, and concluded that "it is clear that the low Duida values are due to the influence of Villavicencio … not of Tapirapés".

It appears from the analysis by Vanzolini and Williams, and from data herein, that populations of relatively short-legged *Anolis chrysolepis* occur from the Andes eastward well into eastern Bolívar State. It would be interesting to know whether there are elevational correlates in tibia length, but, in any case, variation in tibia length is discordant with dewlap coloration—the key character for the pragmatic subspecies arrangement of Vanzolini and Williams (1970) and Ávila-Pires (1995). Dewlaps of male and female lizards in Venezuela south of the Río Orinoco show some intrapopulational variation but are basically red to orange with some dark and light scales, thus agreeing with *Anolis chrysolepis planiceps*. Ávila-Pires (1995: 70) listed eight scale characteristics of this subspecies (under the name *A. n. nitens*). Our tepui material generally agrees in these characters, with occasional exceptions of

TABLE 8
Regression Statistics for Tibia Length on Snout-Vent Length[a]
in Venezuelan Samples of *Anolis chrysolepis*

Geographic sample	N	Slope ß ± SE	Intercept α ± SE	R^2	Tibia length at 65 mm SVL
Northern Coastal[b]					
Falcón	21♂	.33 ± .014	−1.10 ± .74	.97	20.5 mm
	13♀	.28 ± .020	1.21 ± 1.00	.95	19.5 mm
NE Venezuela	17♂	.34 ± .023	−1.30 ± 1.23	.93	20.7 mm
	18♀	.29 ± .017	.32 ± .80	.95	19.4 mm
South and east of Río Orinoco (fig. 60)					
A. Auyantepui	4♂	.27 ± .039	−.03 ± 2.16	.96	17.5 mm
B. Auyantepui	3♀	.25 ± .024	.69 ± 1.22	.99	16.9 mm
C. Auyantepui + Cerro Guanay	8♂	.26 ± .027	.49 ± 1.63	.94	17.4 mm
D. Neblina + Tapirapecó	10♂	.32 ± .016	−1.70 ± .86	.98	19.1 mm

[a] Simple linear regression of the form $Y = α + ß*X$.
[b] Northern coastal data from Vanzolini and Williams (1970: tables 119, 120).

individual variation, most commonly in the "double row of slightly enlarged vertebrals distinct from nape to base of tail"; a transition between this double row and adjacent dorsals often obscures the distinction at midbody, and several specimens lack a distinct double row even on the nape.

Anolis chrysolepis as recognized is a polytypic species of great geographic range and considerable variational complexity. It would be difficult to segregate the Venezuelan Guayana portion as a separate species without some such evidence as sympatry or convincing molecular data. Unless such evidence becomes available, the name *Anolis eewi* Roze should remain in the synonymy of *Anolis chrysolepis planiceps*. Although this widespread lizard tends to be most common in lowland forest, it has a wide elevational range and is one of the most frequent lowland invaders of tepuis, where populational densities generally appear to be relatively low.

FAMILY TROPIDURIDAE

Tropidurus bogerti Roze
Figures 63–66

Tropidurus bogerti Roze, 1958a: 247–250, figs. 1–4. Holotype AMNH R-61011 from Auyantepui, [1100 m?; see Remarks], Estado Bolívar, Venezuela, collected by W. H. Phelps in January 1938. Myers, 1997: 4, fig. 1. Gorzula and Señaris, 1999: 155, photos 103–104.

MATERIAL: Camp 1, 1700 m: AMNH R-140218. Camp 2, 1750 m: AMNH R-140219, EBRG 2921–2924. Camp 3, 1850 m: AMNH R-140220–140227, 140228 (eggs), EBRG 2925–2928, 2929 (eggs). Camp 5, 2100 m: AMNH R-140229, EBRG 2930–2932. All from the 1994 AMNH–TERRAMAR Expedition to Auyantepui. ADDITIONAL MATERIAL: Auyantepui, 1100 m (3609 ft.) [elevation may be in error, see Remarks], AMNH R-61011 (holotype). Auyantepui Plateau, 2200 m (7218 ft.): AMNH R-61012, 61014–61015, 61017 (paratypes). Type specimens from the 1937–1938 AMNH–Phelps Venezuelan Expedition. (Another paratype, AMNH R-61016, was exchanged to the MCZ in 1958; four additional paratypes = MBUCV 3053–3056 fide Roze, 1958a).

Based on dissection only of the AMNH share of specimens (N = 11) from the 1994 expedition, females are appreciably smaller than the males. Five females, all reproductively active (see Natural History below), average 70.2 mm (67–75 mm) SVL, whereas four adult males average 88.3 mm (80–92 mm) SVL. Two additional specimens are immature males of 56 mm and 74 SVL; the last individual (AMNH R-140218) has faint indications of black patches starting to appear under the thighs and in the cloacal area.

COLORATION: In life (fig. 63), overall black above, with light orange spots that are formed from small clusters of orange granular
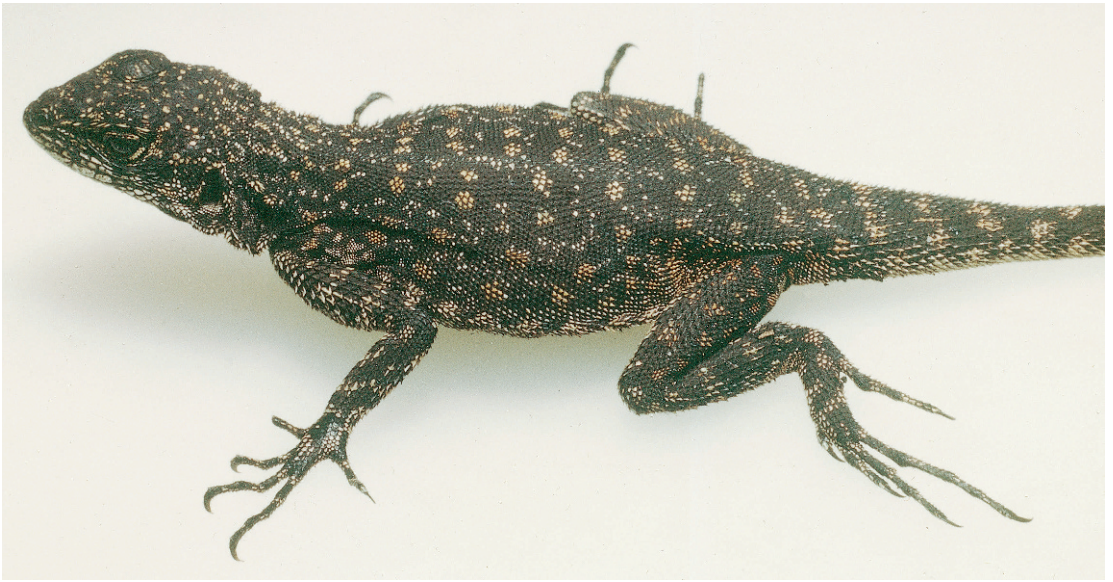
Fig. 63.   *Tropidurus bogerti* from the summit of Auyantepui (AMNH R-140219, 80 mm SVL). This distinctive lizard—black with orange spots—is endemic to Auyantepui.

scales; white or tan scales are interspersed among the orange spots in smaller clusters of scales or as individual scales. Ventral surfaces spotted or mottled bluish white or pale blue on black (ventral pattern in fig. 64). Venter in juveniles bronzy white with vague black reticulum. Adult males have a large black patch under each thigh and smaller pre- and postcloacal patches. Tongue pinkish gray or whitish, with gray tip. Iris turquoise blue, except noted as green in one adult male.

HEMIPENIS: The hemipenes are tiny (≤ 6.5 mm long) relative to the size of the males. The organ lacks spines of any size and is divided for nearly half its length (fig. 65). The basal stalk of the hemipenis is nude, without ornamentation; there is a pronounced swelling below the crotch, on the distal third of the asulcate side of the stalk. The hemipenial lobes are calyculate, with the calyces being confined to the separate lobes and not confluent across the hemipenial crotch. The sulcus spermaticus bifurcates proximal to the crotch; the sulcus branches extend in centrolineal orientation onto the apices of the lobes. Each sulcus branch terminates as a nude channel between dense lines of columnar papillae, which rise above the calyces on the tips of the hemipenial lobes (fig. 65C).

NATURAL HISTORY

Tropidurus bogerti is mostly found in open, rocky scrub, where the lizards are frequently seen moving about over bare rock, especially during sunny weather. They are exceedingly shy and hard to approach. Some were taken by use of a revolver with .22-caliber dustshot, but most were collected by turning sandstone rocks, where the specimens occasionally were found in association with frogs (*Leptodactylus rugosus* or *Tepuihyla edelcae*).

Males of this species prove to be considerably larger than females (see measurements above and fig. 64). Adult males are recognized by presence of large black patches under the thighs and around the cloaca. Scales in the black precloacal patch are irregularly covered with small tubercular scale organs (fig. 66) that seem absent in the postcloacal and thigh patches; see Harvey and Gutberlet (2000) for illustrations of other kinds of scale organs in *Tropidurus*.

Five mature females 67–75 mm SVL were reproductively active as shown by presence of large oviductal eggs and/or wide spent oviducts. Four females have a single large egg in either the right or left oviduct, and smaller ova in the other oviduct. The largest
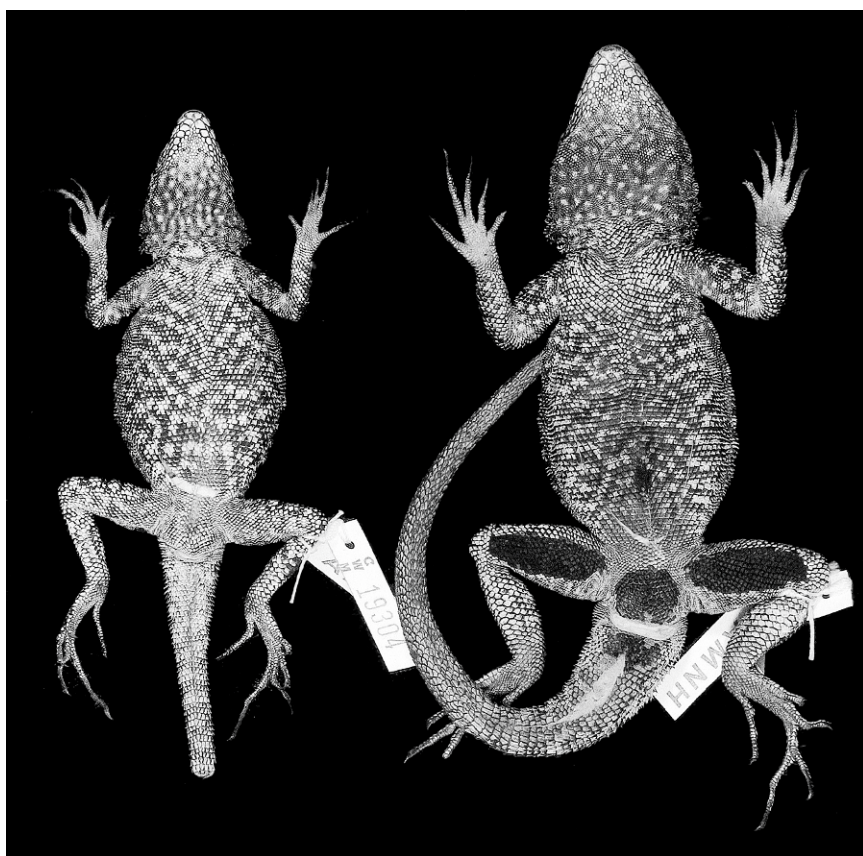
Fig. 64. *Tropidurus bogerti* showing sexual dimorphism in size and ventral color pattern, ×0.86. **Left:** An adult female (AMNH R-140225, 71 mm SVL) that contains a ready-to-lay shelled egg measuring more a third of the lizard's snout-to-vent length. The egg in the left oviduct is about 25 × 10 mm; the largest ovum on the right side is 5 × 3.5 mm. **Right:** A male (AMNH R-140221, 92 mm SVL) with black thigh and cloacal patches that characterize sexual maturity.

ovum in two individuals is round and about 8 mm or 12 mm in diameter; two other individuals each have a much larger and elongate egg in one oviduct. In one of these (fig. 64 left), the egg in the left oviduct is shelled and measures about 25 × 10 mm, whereas the largest ovum on the right side is 5 × 3.5 mm (eggs measured in situ). Such eggs that are nearly ready to be laid are very large relative to the size of the mother. It seems evident from this small sample that maturation of ova alternates between ovaries and that only one egg is laid at a time.

It follows that nests of multiple eggs must represent either repeat laying by the same female or communal nests. Two sets of three eggs each were found under sandstone rocks at Camp 3, one set already hatched and one set live. The three fresh eggs measure 25–27 mm by 12.5–13.5 mm in preservative. Gorzula found 35 eggs under a single rock slab in May—certainly a communal nest site—the eggs ranging from fresh ones with embryos to old empty shells (Gorzula and Señaris, 1999: 155, 254).

REMARKS

Tropidurus bogerti is endemic to Auyante-pui, where it may be confined to the rocky summit as assumed by Myers (1997: 1) and Gorzula and Señaris (1999: 155). However, although Roze (1958a) did not note an elevation for the holotype, it is listed as only
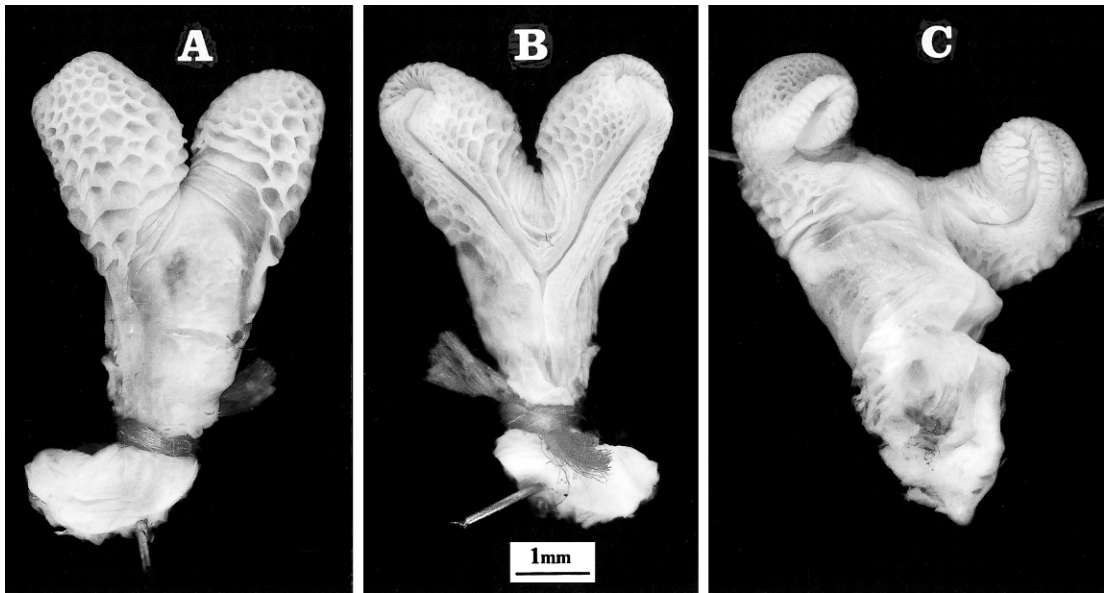
Fig. 65.   Hemipenes of *Tropidurus bogerti*, field eversions ×9.9. **A, B:** Asulcate and sulcate views showing general habitus of an organ preserved in straight position (AMNH R-140221, right organ); the apices of the calyculate lobes are not fully everted. **C:** An organ contorted but having fully everted apices, showing thick, columnar papillae flanking the termini of the sulcus spermaticus. This hemipenis was fully everted and tied off at time of preservation, with twisting and contortion caused by retraction of the internal muscle (AMNH R-140219, left organ).

1100 meters in the AMNH catalog. No other specimen of *T. bogerti* was obtained at the 1100 m camp (Guayaraca) of the 1937–1938 expedition, nor have subsequent workers reported it from that low an elevation. Ditto marks were used in the AMNH catalog to repeat the 1100 m elevation from preceding lines for *Ameiva ameiva* and *Tropidurus hispidus*, and a simple recording error is suspected.

The key to Venezuelan tropidurid lizards in Myers and Donnelly (2001: 75) followed the generic arrangement of Frost (1992), who had synonymized *Plica* and *Uracentron* under *Tropidurus*. Subsequently, Frost et al. (2001) reversed this action. Current names of the Venezuelan tropidurid species are:

Plica lumaria Donnelly and Myers
Plica pansticta (Myers and Donnelly), new combination
Plica plica (Linnaeus)
Plica umbra (Linnaeus)
Tropidurus bogerti Roze
Tropidurus hispidus (Spix)

Uracentron azureum (Linnaeus)
Uranoscodon superciliosus (Linnaeus)

Tropidurus bogerti is easily distinguished from *T. hispidus* by its orange-spotted color pattern and presence of tufts of spiny scales on the neck. However, three species of *Plica* (*lumaria*, *plica*, and *pansticta*) also are characterized by projecting tufts of elongate, spiny scales on the neck. *Tropidurus bogerti* is quickly distinguished from these by lack of a middorsal crest of enlarged scales and the orange-spotted color pattern.

Donnelly and Myers (1991: 32) thought that the neighboring *Plica lumaria* (Cerro Guaiquinima) and *Tropidurus bogerti* shared a color pattern of "vague pale cross-lines on a dark ground", although any perceived cross-lining in *T. bogerti* (based on variable arrangement of the pale spots) is much less evident than in *P. lumaria*. Nonetheless, we agree with Gorzula and Señaris (1998: 155) that "The general aspect [of *T. bogerti*] is very similar to *Plica lumaria*". Both are tepui rock
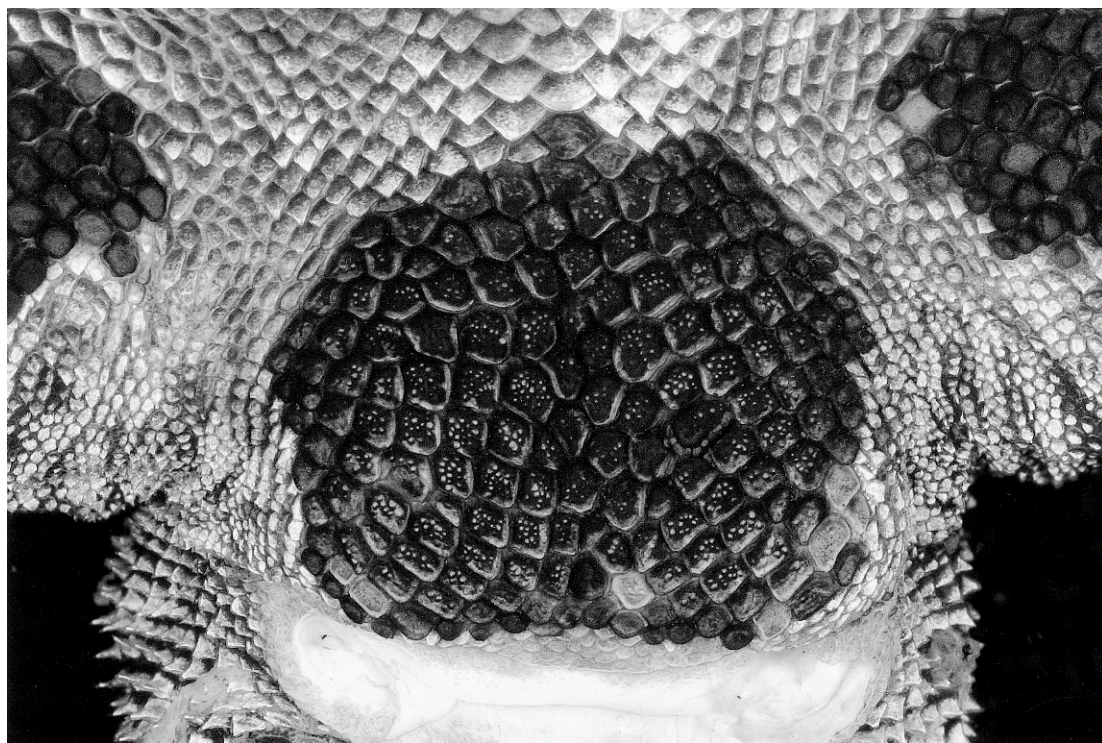
Fig. 66. *Tropidurus bogerti*, showing enlarged view of black precloacal patch of an adult male (AMNH R-140221), ×8. Scales in the patch are adorned with minute tuberculate scale organs. Scales in the black thigh patches (partly visible in upper left and right) and postcloacal patch lack these organs.

dwellers and resemblances may reflect common adaptations.

Frost et al. (2001: 362) maintained *Tropidurus bogerti* in its own species group based on morphology (lateral gular scales imbricating posteriorly rather than laterally, and moderately depressed habitus) and color pattern (pale dots on a black ground). Combined morphology and molecular data appear to ally *T. bogerti* with the *Tropidurus spinulosus* group, whose several species occur far south of the Amazon, suggesting that *T. bogerti* has been long isolated in southern Venezuela (Frost et al., 2001: 359, fig. 6).

SNAKES

FAMILY COLUBRIDAE
Atractus guerreroi, new species
Figures 67–69, 72

HOLOTYPE: EBRG 3403, an adult male from summit of Auyantepui at 5°46′N, 62°32′W, 2100 m elevation, Bolívar, Venezuela; collected by Ricardo Guerrero, February 6–8, 1988. (The type locality is the same as the later-established Camp 5 of the 1994 AMNH-Terramar Expedition; see map 1.) Figure 67.

ETYMOLOGY: This snake is named for our colleague and field companion Dr. Ricardo Guerrero, who collected the only known specimen several years before the AMNH–TERRAMAR Expedition.

DIAGNOSIS: An *Atractus* of small adult size (1 ♂ 250 mm total length), 17 dorsal scale rows, with a dark vertebral stripe and ill-defined lateral stripes; a prominent midventral line of large black spots; supralabials 7, with labials 2–3 touching short loreal and 3–4 touching eye; maxillary teeth 6; hemipenis noncapitate, feebly bilobed, completely spiny, with a long basal naked pocket on asulcate side.

Atractus guerreroi most closely resembles its geographic neighbor *Atractus steyermarki*
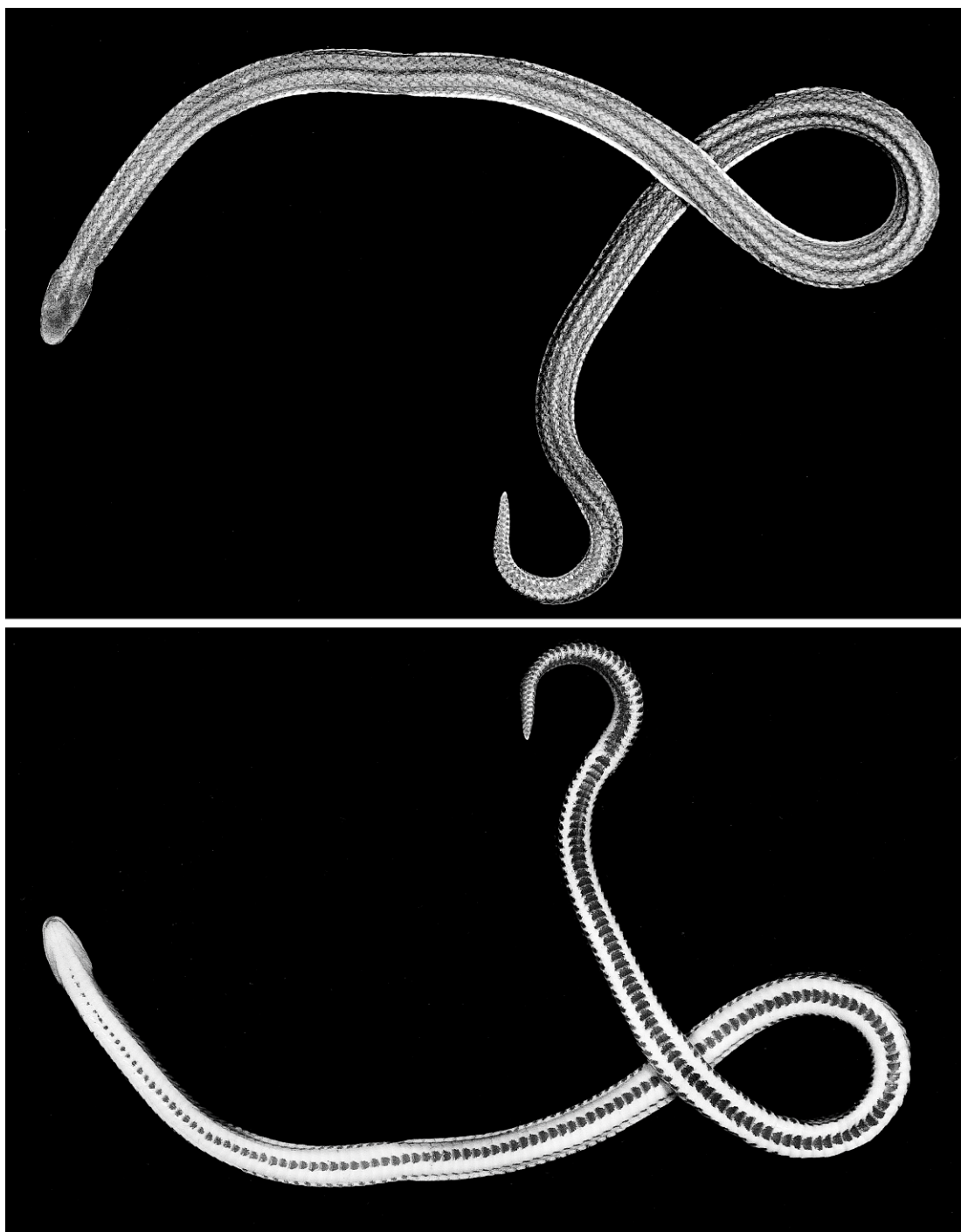
Fig. 67. *Atractus guerreroi*, new species. The holotype (EBRG 3403♂) in dorsal and ventral view, ×1.28.

Roze (Chimantá massif), which is relatively melanistic in color (dark stripes not evident or inconspicuous in life) and which has more conspicuous scale organs on some cephalic plates. *Atractus guerreroi* has a smaller head and shorter snout than *A. steyermarki*, with disproportionately smaller frontal, internasal, and loreal plates but with comparable sized parietals and prefrontals (as shown in fig. 72). See Remarks and Comparisons.

DESCRIPTION OF HOLOTYPE

The specimen is a male, undissected except for the tail; it is judged sexually mature because the hemipenial spines are well mineralized. It is slightly desiccated but otherwise in good condition; the stratum corneum is intact. See table 9 for detailed measurements.

PROPORTIONS AND SCUTELLATION: Total length 250 mm, tail length 35 mm (14.0% of total). A small slender snake, with body slightly wider than high, rounded ventrolaterally; greatest head width 70% of head length from snout to end of parietals and 63% of length from snout to end of mandible; greatest body width 2.7% of SVL. Dorsal scales smooth, lacking apical pits, in 17-17-17 rows; anal ridges present. Ventrals 166, anal plate undivided, subcaudals in 41 pairs.

Head slightly wider than neck; snout bluntly rounded in dorsal view, rounded in profile; rostral wider than high, visible from above; internasals small, slightly wider than long, half (50%) the length of prefrontal suture; prefrontals large, longer than wide (greatest prefrontal width 80% of greatest length); prefrontal suture asymmetrical (dextral) to the internasal suture; prefrontal suture 89% length of frontal plate; supraoculars longer than wide; frontal wider than long, pentagonal; interparietal suture much longer than prefrontal suture and longer than frontal plate (interparietal suture 1.28 × frontal length). See figure 68 for cephalic scutellation.

Eye moderate, longer than loreal, contained 2.0 times in snout length (sagittal); eye length 1.4 times longer than its distance to lip; eye protuberant to level of lip and visible from below. Pupil subcircular (sensu Myers, 1984). Nasal divided above and below naris,

TABLE 9
Measurements[a] (in mm) of Holotypes of *Atractus guerreroi*, new species, and *Atractus steyermarki* Roze

	A. guerreroi EBRG 3403 ad.♂	*A. steyermarki* FMNH 69920 ad.♂
Total length	250	257
Snout-vent length	215	219
Tail length	35	38
Tail/total length × 100	14.0%	14.8%
Head length snout to ends of parietals	6.9	7.8
Head length snout to end of mandible	7.6[b]	9.2[b]
Head, greatest width	4.8	4.9
Body, greatest width	6[c]	5.5[c]
Body, greatest height	6[c]	5.5[c]
Eye to snout tip (sagittal)	2.2	2.5
Eye length	1.1	1.2
Lower edge eye to lip	0.8	0.7
Nasal length	1.4	1.5
Loreal length	0.8	1.1
Loreal, maximum height	0.5	0.6
Internasal, greatest length	0.8	0.9
Internasal, greatest width	1.0	1.1
Internasal suture length	0.4	0.8
Prefrontal, greatest length	2.1	1.8
Prefrontal, greatest width	1.7	1.8
Prefrontal suture length	1.6	1.5
Frontal length	1.8	2.5
Frontal width (anterior)	2.2	2.6
Supraocular length	1.2	1.4
Supraocular, greatest width	0.8	1.6
Parietal, greatest length	3.6	3.9
Interparietal suture length	2.3	2.3
Genial length	2.4	2.3
Genial width	0.9	1.0

[a] Most measurements were made by ocular micrometer in a dissecting microscope (Wild M7S), with the main objective displaced coaxially to the left beam path, to eliminate problems of parallax. Other measurements were taken with dial calipers or by stretching the specimens along a metric ruler.

[b] Measurement made with calipers.

[c] Measurement a rounded estimate, made with calipers; slight desiccation and contortion of specimens precluded precision.

its greatest length 2 times loreal length; loreal short (73% of eye length), 1.6 times longer than its greatest height, broadly separated from internasal, entering eye; no preoculars; supralabials 7, 2nd–3rd touching loreal, 3rd–4th touching eye; postoculars 2, the upper 1.5 times larger than lower; temporals 1 + 2, the
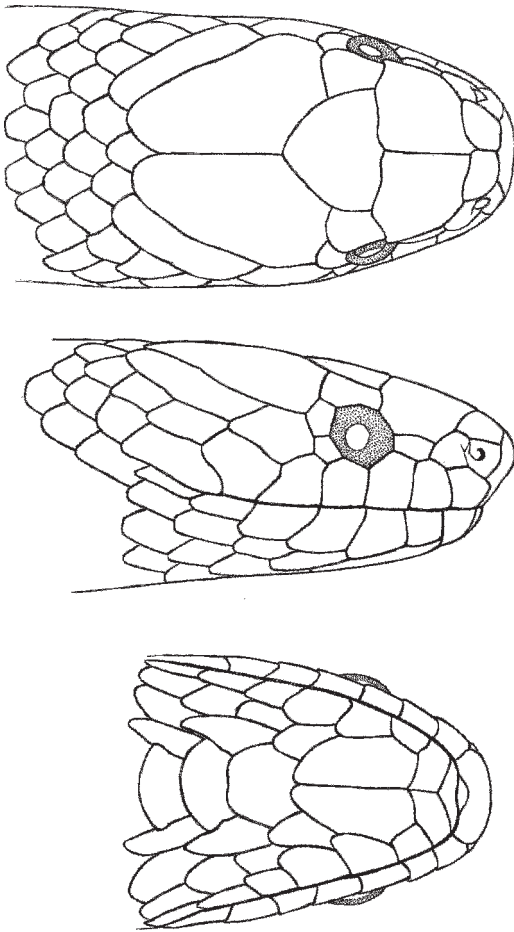
Fig. 68. Head scutellation of *Atractus guerreroi*, new species (holotype). Scale line = 1 mm.

upper one in row 2 very elongated, reaching past end of parietal.

Infralabials 7, first pair in contact behind mental, first three in contact with genials; single pair of genials, each genial 2.7 times longer than wide; four large median gulars (including two preventrals) between genials and first ventral. Head-plate tubercles tiny, inconspicuous, most concentrated on snout and chin, otherwise sparse. Some larger tubercles are discernible in a few places, particularly along the posterior edges of the prefrontals and anterolateral edges of the frontal.

COLOR PATTERN: The specimen is medium brown, with a generally poorly defined pattern of narrow brown stripes and a low lateral pale stripe (fig. 67). There is most prominently a middorsal stripe (vertebral scale row and adjacent edges of paravertebrals) extending from the parietal plates to the tail tip. And there are indications of several ill-defined lateral stripes—on scale-row 6, on the adjacent edges of rows 3–4, and on the adjacent edges of rows 2–3. The lower 1½ scale rows are white in preservative, forming a low lateral pale stripe. The lateral brown striping and the low pale stripe are anteriorly vague, becoming somewhat more pronounced posteriorly.

The white ventral surface bears a median line of prominent blackish brown markings, starting anteriorly as a small spot on the first ventral and gradually enlarging posteriorly as close-set half-moon markings that fuse to a solid stripe under the tail. The lateral edges of the ventral plates are brown (paler than the blackish midventral markings), setting off the pale lower lateral stripe.

The head is brown, with a pale area on the outer edge of each parietal anteriorly and a poorly defined pair of large pale spots posteriorly on the ends of the parietals. The brown pigmentation extends onto the upper edges of the supralabials, which otherwise are immaculate white. The anterior face of the rostral plate is dark brown, with a white lower edge. There is a pair of brown spots on the chin, each spot occupying a first infralabial and part of the adjacent genial; underside of head and neck otherwise white. A dorsad extension of white extending onto side of neck behind mouth.

MAXILLARY TEETH: Examined in situ on right side. There are six well-spaced, recurved teeth, the first three large and subequal, the last three smaller and decreasing in size, with the ultimate tooth being very small. The teeth are firmly ankylosed and there are no empty sockets.

HEMIPENIS: The noncapitate, noncalyculate hemipenis is spinose over all except the spinulate basal section. Weak bilobation, most evident in the uneverted organ, is discernible but inconspicuous after eversion. The right retracted organ was 10.5 mm long from base to the ends of very short lobes. Bilobation started at the level of subcaudal 14. The lobes were 0.3 mm long; the two slips
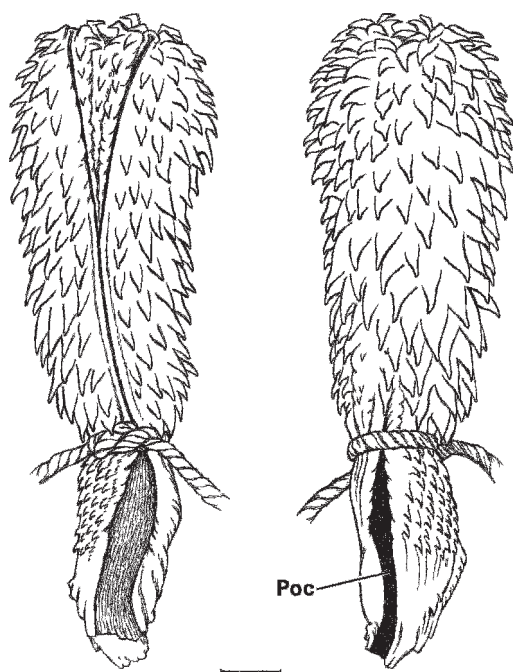
Fig. 69. Everted hemipenis of *Atractus guerreroi*, new species. Right organ of holotype (EBRG 3403) in sulcate and asulcate view. Poc = basal naked pocket on asulcate side. (Laboratory preparation from preserved retracted hemipenis, fully everted but probably incompletely expanded.) Scale line = 1 mm.

of retractor muscle merged 1.2 mm posterior to insertion, with the major retractor originating at the level of subcaudal 27. This organ was removed, soaked in a solution of 3% KOH for 10 hours and manually everted.

The everted hemipenis (fig. 69) is 11 mm long. The sulcus spermaticus forks more than halfway (64%) from the base, the two branches extending in centrolineal orientation to the tips of the lobes; bilobation is negligible (< 3% total length of organ). The distal 73% of the organ is densely covered with spines all around, mostly medium-sized but smaller near the sulcus spermaticus; the space between the sulcate branches is sparsely covered in small spines.

The basal 27% of the hemipenis is spinulate. There is a long basal naked pocket on the asulcate side, extending distad nearly halfway (45%) from the base, well into the zone of spines.

REMARKS AND COMPARISONS

Atractus is the largest genus of snakes in South America, with the montane species tending to have restricted ranges. Species from other parts of Venezuela (e.g., Roze, 1966) and other parts of Guayana (Hoogmoed, 1980; Ávila-Pires, 2005) seem not to have penetrated the uplands and highlands of the Venezuelan Guayana. A few *Atractus* are endemic to this region, where the genus is known primarily through the work of Janis Roze (1958b, 1961). Roze named four species—*A. insipidus* from Río Uraricapará on the Venezuelan-Brazilian frontier, *A. steyermarki* from the Chimantá massif, and *A. duidensis* and *A. riveroi* from Cerro Duida. *Atractus insipidus* is a spotted snake with 15 dorsal scale rows. The holotypes of the other three species, characterized by 17 scale rows, have been compared directly with the type specimen of *Atractus guerreroi*. *Atractus riveroi* is a much larger snake (486 mm total length) with transverse rows of pale spots and a dark checkered venter. *Atractus duidensis* is a larger brown snake (346 mm total length) without markings dorsally; ventral surfaces are dark, with suffusions of brown extending transversely across the ventral plates. Only *Atractus steyermarki* bears resemblance to *A. guerreroi*.

NOTES ON *ATRACTUS STEYERMARKI*: Roze (1958b) named *Atractus steyermarki* based on two specimens from elevations of 1430 m and 2160 on Chimantá-tepui. Later, Roze (1961: 116; 1966: 87) mentioned that the species had been rediscovered by Steyermark "en la región de El Dorado". The lowland town of El Dorado, about 150 km NE Chimantá, lies at an elevation of 130 m, but elevations above 1200 m occur well to the south along the "El Dorado–Santa Elena de Uairén road" (see the regional description in Duellman, 1997). Roze took the locality at face value and assumed a broad distribution "en la Gran Sabana en general", but he provided no descriptive data for the specimen. The El Dorado snake, cited by Roze (1966: 87) as an unnumbered MBUCV specimen (Museo de Biología de la Universidad Central de Venezuela, Caracas), apparently has not been seen by other Venezuelan

workers (e.g., Lancini and Kornacker, 1989; Gorzula and Señaris, 1999).

Gorzula (1992: 272) reported an additional specimen of *Atractus steyermarki* from Chimantá Camp VIII (= 2600 m fide Huber, 1992: 31). Gorzula and Señaris (1999: 161–162) also provided data for this specimen and mentioned the El Dorado record as unverified, concluding that "the available evidence indicates that this species is endemic to the highland summits of the Chimantá Massif". The known elevation range for *Atractus steyermarki* on Chimantá is 1430–2600 m.

The holotype of *Atractus steyermarki* (figs. 70, 71) has been examined; see table 9 for detailed measurements. The specimen is in fair condition and pliable, although somewhat desiccated; it evidently has faded sufficiently in preservative to reveal a basic striped pattern (see below). There are six maxillary teeth, which appear much as described for *A. guerreroi* above, and the hemipenis also is similar to that of *A. guerreroi*. Unfortunately, both hemipenes are damaged and can not be easily illustrated. The left organ had been opened irregularly from the medial side and is torn. The proximal section of the right organ is mutilated, although the distal part (opened midventrally) is in good condition; the right organ extends to subcaudal 13. The hemipenes are spinose and very feebly bilobed; the attachment slips of retractor muscle are correspondingly very short.

The male holotype ("270" [257] mm total length) and female paratype (420 mm) of *Atractus steyermarki* were described by Roze (1958b) as patternless dark gray, turning paler on the lower 1–2 scale rows. The midventral dark spots in the male cover most of the ventrals in the larger, more melanistic female. Gorzula (1992: 272) described the living colors of his intermediate-sized specimen (a male, 373 mm total length) as dark brown above, yellow below, with dark brown pigment midventrally.

The aforesaid descriptions document *Atractus steyermarki* as having melanistic tendencies that evidently cause the dorsum to appear essentially unicolor in life. Nonetheless, after a half century of preservation, the holotype has faded sufficiently for a striped pattern to appear (especially when immersed in alcohol, see fig. 70). Three
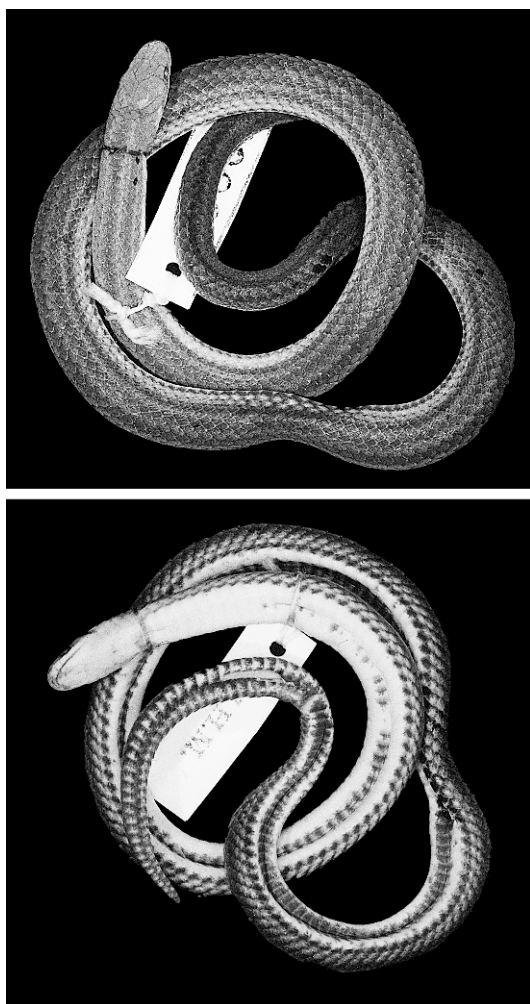
Fig. 70.   *Atractus steyermarki* Roze. The holotype (FMNH 69920♂) from the Chimantá massif, in dorsal and ventral view, ×1.3.

prominent dark brown stripes are now visible—a middorsal stripe confined to the scales of the vertebral row, a high lateral stripe centered on row 6 and overlapping onto adjacent edges of rows 5 and 7, and a lateral stripe on row 3 and adjacent edge of row 2. Scales in rows 1 and 2 are mostly pale gray (with brown pigment at the scale base), appearing as a low pale lateral stripe set off by the brown stripe above and black ventral tips below. The midventral marking starts as small spots on ventral 13, enlarging posteriorly as black half-moons that nearly fuse to form a median stripe.

COMPARISON OF *ATRACTUS STEYERMARKI* AND *A. GUERREROI*: As mentioned above, the maxillary teeth and hemipenes of *Atractus steyermarki* appear to be essentially the same as in *A. guerreroi*. The midventral dark pattern also is essentially the same in *Atractus guerreroi* and *A. steyermarki*. The dark dorsal stripes and ill-defined pale "stripe" on the first two scale rows of *A. guerreroi* are similar to the above-described pattern on the faded holotype of *A. steyermarki*, but there are differences.

The middorsal stripe of *A. guerreroi* is microscopically less dense and overlaps onto the paravertebral rows. Both have a stripe on row 6, but in *steyermarki* it is better defined and wider, overlapping onto the adjacent rows. *Atractus guerreroi* lacks the vivid lateral dark stripe (row 3 and edge of row 2) of *steyermarki*, having instead two very ill-defined lateral stripes or dark suffusions along the adjacent edges of rows 3–4 and rows 2–3. These differences in lateral stripes might be diagnostic, but, at this time, there is no way of assessing variation within populations. In *A. steyermarki*, the conspicuous stripes on the faded holotype seem likely to reflect a juvenile pattern that becomes ontogenetically obscured by melanism.

The holotypes of both *Atractus guerreroi* and *A. steyermarki* have the very minute, inconspicuous cephalic sensory tubercles that are widespread among colubrids. Both also have a larger kind of tubercle, which, in *A. guerreroi*, is discernible especially along the posterior edges of the prefrontals and anterolateral edges of the frontal. These organs are blackish and more numerous—or at least much more conspicuous—in *A. steyermarki*, where they cause the snake to look as if some of its head plates had been "riveted on".[33] in

[33] We borrow this apt phrase from unpublished notes by Frances J. Irish, who observed the presence of these usually overlooked structures in the types of *Atractus steyermarki* and in various species thought to be allied with *A. collaris*. Irish judged the structures as possibly homologous with apical pits on the body scales of some species; they seem to vary in appearance from pitlike to tuberclelike. They are easily seen under the dissecting microscope in *Atractus steyermarki* because of associated black pigmentation. They can be difficult to see in other species unless scale surfaces are blotted dry and the angle of light carefully adjusted.
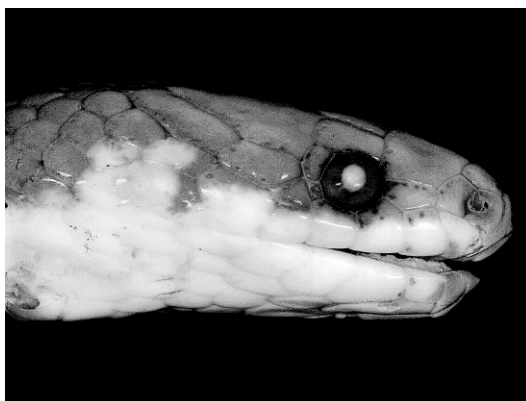

Fig. 71. *Atractus steyermarki*, showing enlarged lateral view of head of holotype (FMNH 69920♂) from the Chimantá massif, about ×7.5. The dark spots along edges of some scales anterior and posterior to eye are pigmented scale organs, which also are conspicuous along the edges of some plates on top the head.

A. steyermarki, the structures are prominent along the posterior edges of the rostral, internasals, and prefrontals, somewhat less prominent along the lateral edges of the frontal, and conspicuously present laterally on the top edge of the loreal, posterodorsal edge of the nasal, and on the upper parts of supralabials 2–3 (fig. 71).

The male holotypes of *Atractus steyermarki* and *A. guerreroi* are of comparable size, the former only 4 mm longer in SVL (3 mm longer in tail length), but *A. guerreroi* appears to have a disproportionately smaller head, as shown by measurements (table 9) and as readily visualized in side-by-side comparison (fig. 72). The parietals and prefrontals appear to be of comparable size in *A. guerreroi* and *A. steyermarki*, but the internasals and frontal are disproportionately smaller in *A. guerreroi*. *Atractus guerreroi* has a relatively shorter snout, as also reflected in a shorter loreal, which is 64% of eye length in *guerreroi* vs. 92% in *steyermarki*. Both have 7 supralabials, but there is a slight difference in the configuration. In *A. guerreroi*, the first supralabial is far enough removed from the loreal that contact might seem unlikely in intraspecific variation, whereas in *A. steyermarki* the first supralabial is in point contact with the loreal on the left side and nearly in contact on the right side.
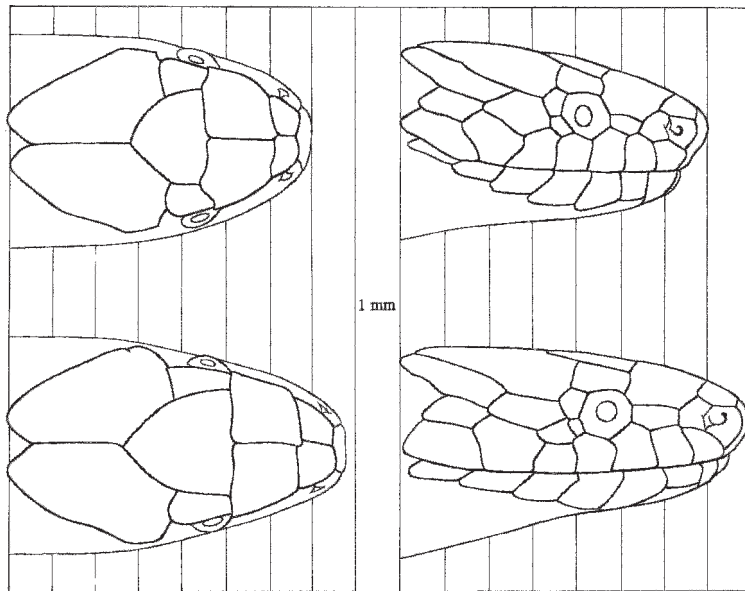
Fig. 72. **Upper:** *Atractus guerreroi*, new species from Auyantepui (holotype, 215 mm SVL). **Lower:** *A. steyermarki* from Chimantá (holotype, 219 mm SVL). Heads of holotypes shown at same scale. The noticeably smaller head and shorter snout of *A. guerreroi* is not explainable by the slight differences in snout-vent length; it has disproportionately smaller frontal, internasal, and loreal plates, although prefrontals and parietals are comparable to those of *A. steyermarki*.

In summary, *Atractus guerreroi* most closely resembles *A. steyermarki*. The limited data suggest to us that the evolutionary course of *A. steyermarki* has been toward melanism and that of *A. guerreroi* toward reduced head size—hypotheses needing larger sample sizes.

Chironius fuscus (Linnaeus)
Figure 73

Coluber fuscus Linnaeus, 1758: 222–223. "*Habitat in Asia*" in error.

Chironius fuscus: Roze, 1966: 97. Peters and Orejas-Miranda, 1970: 60. Dixon et al., 1993: 113, 261 (generic revision; BMNH specimen listed from "south side Auyantepui, 2283 m [in error for 6850 ft. = 2088 m]").

MATERIAL: Southern side of Auyantepui ("below final cliff face"), 6850 ft. [2088 m]: BMNH 1976.235, collected by Adrian Warren, August 17, 1974. Camp 3, 1850 m: AMNH R-155717 (fragment of shed skin, tentatively identified), from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

The one whole summit specimen (fig. 73) is a female, probably subadult, 937 mm total length, 279 mm tail length (29.8% of total length). Dorsal scales completely smooth except for a few weak anal ridges laterally above cloacal region, in 10-10-10 rows; apical pits absent. Ventrals 158, subcaudals 103, paired; anal plate entire. Supralabials 9/8, 2nd–3rd touching loreal, 4th–6th in eye; infralabials 8, first five touching anterior genials. Preoculars 1, postoculars 2. Temporals 1 + 1. About 41 maxillary teeth on right. Color in preservative indistinctly marked with dark gray transverse bands; the bands are separated by white middorsal scales anteriorly on the body and by whitish transverse lines posteriorly. These markings along with black scale edges and small spots give an overall mottled appearance of gray, black, and white (fig. 73 top).[34] Supralabials mostly yellowish white, with labials 2–3 having dark posterior edges. An ill-defined

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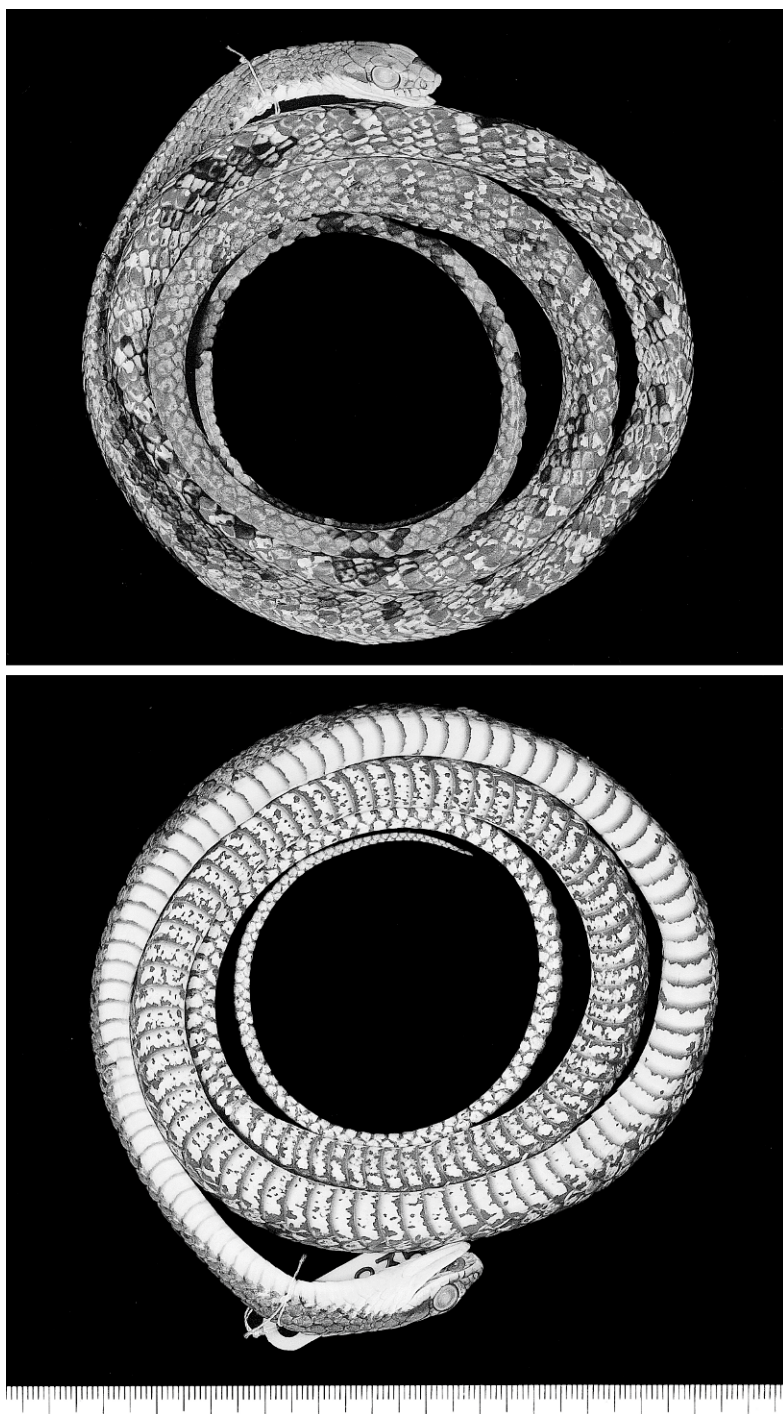[34] Some remaining patches of stratum corneum suggest that the living coloration is in shades of brown.

Fig. 73. *Chironius fuscus* (Linnaeus), ×0.7; the species is broadly distributed in the lowlands of northern South America. This specimen (BMNH 1976.235, subadult ♀) was caught on the summit of Auyantepui in August 1974; a shed skin found in 1994 indicates a possibly persistent presence of this racer on the Auyán summit.

black postocular stripe extending from eye across lower part of primary temporal and upper part of ultimate supralabial. Underside of head immaculate yellowish white; black transverse lines across bases of anterior ventrals, these lines becoming heavier, with intervening black spots posteriorly (fig. 73 bottom).

The fragment of shed skin is from a small snake of juvenile size. The scales are relatively large, in 10 rows anteriorly, eight rows posteriorly; no keeled scales are discernible; apical pits absent over most of body, but relatively large pits are present on some scales posteriorly on the neck, with paired pits being more common than single ones. The eyes are relatively large; there are two postoculars and 1 + 2 temporals; both postocular scales are in contact with the primary temporal. Anal plate torn.

REMARKS

The shed skin from Camp 3 is fragmentary but identifiable to genus and may also represent *Chironius fuscus*, although the possibility of a second congener on the Auyán summit cannot be excluded. Most other *Chironius* species in southern Venezuela (*carinatus*, *exoletus*, and *multiventris*) are differentiated from the material at hand by presence of 12 rows of dorsal scales anteriorly and at midbody. *Chironius scurrulus* has 10 midbody rows of smooth (unkeeled) scales, as do the whole specimen and skin fragment from Auyantepui; these materials, in fact, key out to *scurrulus* in Dixon et al. (1993: 57). However, immature *fuscus* may lack completely the key character of keeling (Dixon et al., 1993: 116); the whole specimen (fig. 73) has a color pattern consistent with *fuscus* and this identity was confirmed by Dixon et al. (1993: 261) in their Specimens Examined section.

Roze (1958a: 266; 1966: 95) listed three Auyantepui specimens of *Chironius carinatus* from the 1937–1938 AMNH–Phelps Venezuelan Expedition. The AMNH catalog shows that all were collected well below the summit. Two specimens (AMNH R-61020, 61024) were collected by W. H. Phelps at 1100 m (3609 ft.). The third specimen (AMNH R-61036) was obtained by Phelps

near the base of Auyantepui, at 460 m (1509 ft.). The last is a specimen of *Chironius exoletus* according to Dixon et al. (1993: 258 in Specimens Examined).

Leptodeira annulata ashmeadii (Hallowell)

Coluber ashmeadii Hallowell, 1845: 244, 247. Lectotype (by Duellman, 1958: 44): ANSP 10093, from "the Republic of Columbia [sic], within two hundred miles of Caracas", collected by Samuel Ashmead.

Leptodeira annulata ashmeadi: Duellman, 1958: 43 (new combination; emended name with single -*i* termination now considered an "incorrect subsequent spelling").

Leptodeira annulata ashmeadii: Roze, 1966: 168.

Roze (1958a: 265) recorded *Leptodeira annulata* from 400 m at the base of Auyantepui, but the only specimen from the summit is one collected by S. Gorzula on the northwestern sector of Auyantepui at 1630 m (06°02′N, 62°37′W) in November 1984 (Gorzula and Señaris, 1999: 167, 254). Various lowland species find their way onto most if not all tepuis in an irregular, unpredictable manner, although few species seem to be able to maintain populations on the highest summits. However, Gorzula (1992: 273) obtained seven of these snakes at elevations of 1920 to 2150 m on the neighboring Chimantá massif; two snakes were found at each of three camps and one specimen at a fourth camp. It therefore would seem that *Leptodeira* is permanently established at least in the highlands of Chimantá, where Gorzula found one specimen coiled inside a *Brocchinia* and the others under rocks.

Liophis trebbaui Roze
Figures 74–77

Liophis trebbaui Roze, 1958a: 262–264, fig. 11. Holotype AMNH R-61019 [lost, see Remarks] from [south slope] Auyantepui, [1100 m/3609 ft fide AMNH catalog = Guayaraca area, about 1000–1100 m], Venezuela, collected by W. H. Phelps on "2 de abril, 1938" [= February 4, 1938 fide AMNH catalog]. Donnelly and Myers, 1991: 46 (resurrection of *L. ingeri* and *L. trebbaui*).

Liophis cobella trebbaui: Dixon, 1983a: 159 (includes *L. ingeri*).

Liophis cobellus trebbaui: Dixon, 1989: 10 (incorrect subsequent spelling of *cobella*).

Fig. 74. *Liophis trebbaui* Roze (AMNH R-140231). This juvenile female documents occurrence of the species on the summit of Auyantepui; the type locality is on the southern slope at about 1100 m elevation.

MATERIAL: Camp 2, 1750 m: AMNH R-140231, from the 1994 AMNH–TERRA-MAR Expedition to Auyantepui. Cabanayén, 1230 m, (about 70 km SE Auyantepui): AMNH R-104803, collected by S. Gorzula in 1975. Marco de Fronteira BV8, Roraima, Brazil: MZUSP 9235–9236, collected by C. M. Carvalho in 1986.

The single specimen (figs. 74–76) from our expedition to Autantepui is a juvenile female, 221 mm total length, 35 mm tail length (15.8% of total length); dorsal scales lacking apical pits, smooth, in 17-17-15 rows, with reduction occurring by fusion of rows 3 + 4 at ventrals 107 on left side/104 on right. Ventrals 174, subcaudals 54, paired; anal plate divided. Supralabials 8, 2nd–3rd touching loreal, 4th–5th in eye; infralabials 8, first four touching anterior genials. Maxillary teeth 16 + 2 on right side.

COLORATION: In life (fig. 74), AMNH R-140231 was black with a thin, yellow nuchal bar followed by 40 ringlike yellow markings on body—the first 16 of these narrow crossbands being mostly unbroken above, the posterior ones broken dorsally, often with the two halves in alternating sequence. The ringlike crossbands are greenish yellow laterally and a deeper golden yellow dorsally. These markings are narrow, mostly about one-scale wide dorsally; they become wider on the lower sides, most conspicuously on the anterior body where they are about two-scales wide; markings are indistinct atop tail. Ventral and subcaudal surfaces

transversely black-banded and checkered on pale greenish white. Some areas of the pale ventral color are transversely continuous with the much narrower yellow crossbands above, but the overall aspect is not of a "ringed" pattern (fig. 75).

Head black, with dull olive-yellow small spots on parietals and adjacent temporal region and with olive suffusions on snout. Supralabials heavily edged in black on light yellow (fig. 76); infralabials pale greenish yellow with black edging; genial plates and gular region white. Iris brown with a small, ill-defined patch of bronze above pupil. Tongue, including tips, black.

DISTRIBUTION AND NATURAL HISTORY

VENEZUELAN SPECIMENS: Some previous assignments of specimens to this taxon are in error (see under Comparisons below). As documented herein, we know of *Liophis trebbaui* from six specimens—four from Venezuela and two from northern Brazil. The Venezuelan material includes our one specimen taken on the summit of Auyantepui at 1750 m, and the two type specimens collected on its south slope at about 1000–1100 m (see Comments on Type Specimens and Type Locality). A fourth Venezuelan specimen (AMNH R-104803) comes from Cabanayén, 1230 m elevation, about 70 km southeastward from Auyantepui (5°36′N, 61°44′W, fide Gorzula and Señaris, 1999:
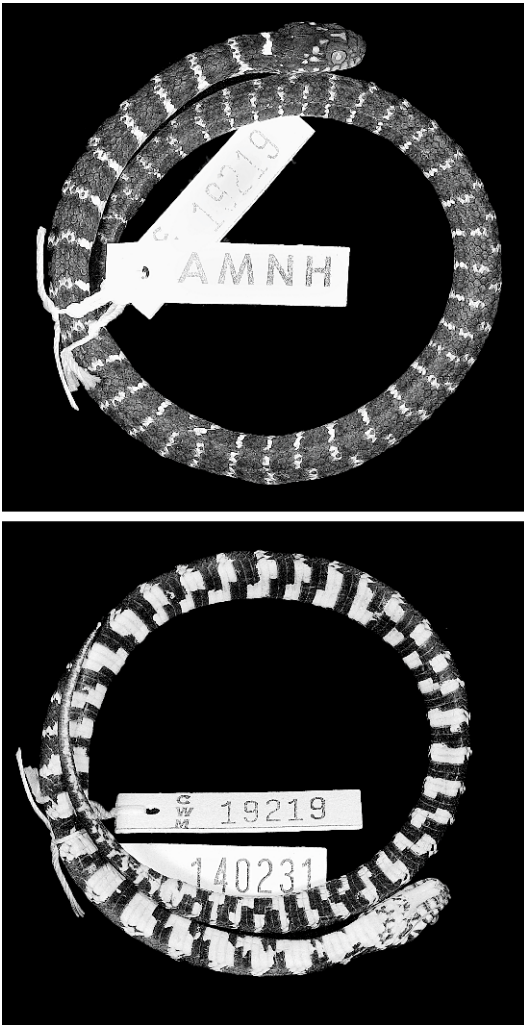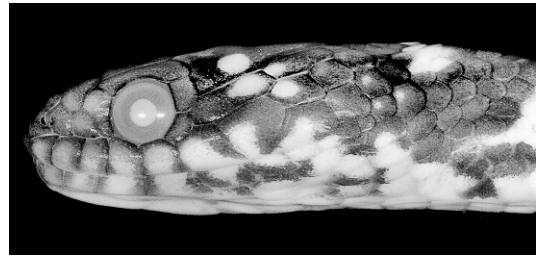
Fig. 76.   *Liophis trebbaui*, showing color pattern of head in lateral view (AMNH R-140231), ×5.1.

anterior genials. Maxillary teeth 17 + 2 on right side. There is a narrow nuchal ring (a shorter nuchal bar in the Auyán specimen) and 40 pale ringlike markings anterior to the tail (as in the Auyán specimen). Many of the pale markings are medially broken, with the two halves sometimes offset; they are noticeably wider on the lower sides (fig. 77). The labials and parts of the genials are edged with black; pale ventral surfaces are banded and checkered with black (but less heavily marked than in the Auyán specimen).

This specimen was one of a small collection donated to the American Museum by Gorzula in 1977, for collaborative study with then Research Associate Janis Roze. The

Fig. 75.   *Liophis trebbaui*, showing details of color pattern of the summit specimen (AMNH R-140231), ×1.2.
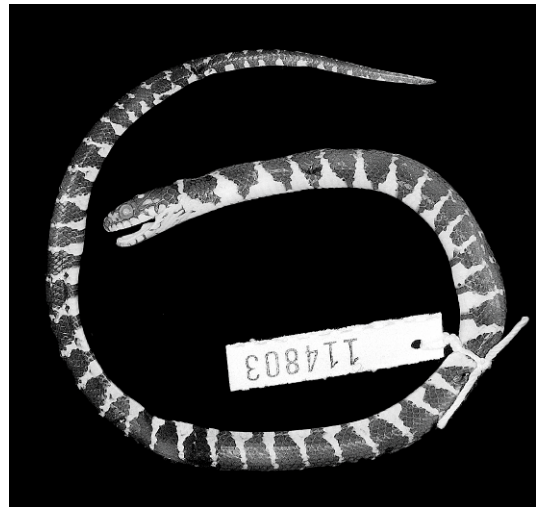
Fig. 77.   *Liophis trebbaui*, ×1.0. A juvenile female (AMNH R-104803) from Cabanayén, 1230 m, on the Gran Sabana about 70 km SE Auyantepui. The species is not endemic to Auyantepui as previously suspected.

246). According to the AMNH catalog, this specimen was collected at Cabanayén by Stefan Gorzula in 1975.

The specimen AMNH R-104803 (fig. 77) is a juvenile female that compares well with the one from the Auyán summit (compare figs. 74 and 76 with fig. 77). It is 200 mm total length, 35 mm tail length (17.5% of total length); dorsal scales lacking apical pits, smooth, in 17-17-15 rows. Ventrals 170, subcaudals 52, paired; anal plate divided. Supralabials 8, 2nd–3rd touching loreal, 4th–5th in eye; infralabials 10, first five touching

unidentified specimen was assigned a catalog number and tagged, but it was held aside until Roze's research materials were dispersed into the main collection in the late 1990s. The specimen is listed as *Liophis* sp. by Gorzula and Señaris (1999: 172, 250), who, however, gave the locality as "Parupa, CVG Agricultural Station", 1220 m at 5°41′N, 61°31′W. The locality "Parupa" is shown as "Campo Parupa" on Huber and Berry's topographic map of the Venezuelan Guayana (issued in Steyermark et al., 1995), about 20 km NE Kavanayén. We assume Cabanayén (=Kavanayén) to be correct, since this name was provided for AMNH cataloging, although it makes little difference for present purposes. Cabanayén and Campo Parupa are in reasonable proximity on the Gran Sabana, roughly 70–90 km SE–ESE of Auyantepui (some AMNH specimens collected by Gorzula are catalogued as "Parupa, nr. Cabanayen"). Gorzula and Señaris (1999: 246, 250) described Cabanayén as being in a "mixture of open savannas, scrub, and partially burned forest" and Parupa as "open savanna [and] riverine forest".

BRAZILIAN SPECIMENS: Two specimens were collected by Dr. Celso Morato de Carvalho in February 1986, in Roraima, near Vila Pacaraima, border marker BV (Brazil-Venezuela) 8, about 4°29′N, 61°09′W. Myers visited the locality in June 1993, in company with Drs. Carvalho and W. R. Heyer. The site is a rocky stream east of town, at about 830 m elevation in a very dense and humid evergreen forest. The locality is some 200 km SE Auyantepui, suggesting that *Liophis trebbaui* may be distributed fairly extensively in the uplands east of the Río Caroní.

Both specimens are juvenile males. Following data are for MZUSP 9235 and 9236, respectively: Total length (tail length) 203 (35) and 222 (42) mm; tail length 17.2% and 18.9% of total length. Smooth dorsal scales lacking pits in 17-17-15 rows. Ventrals (subcaudals) 169 (53) and 173 (57); anal plate divided. Supralabials 8, 2nd–3rd touching loreal, 4th–5th in eye; infralabials 10/10 and 11/10, 1st–5th touching anterior genials. Maxillary teeth on right side 17 + 2 and 18 + 2. A narrow nuchal ring (as in fig. 77, not a dorsal bar as in fig. 75); 39 and 38 pale ringlike markings anterior to tail, the rings relatively complete in

MZUSP 9236, more extensively broken in MZUSP 9235; some rings medially broken with the two halves slightly offset; all rings except first (nuchal ring) noticeably wider on lower sides. Pale markings in temporal region and on frontal plate similar to specimen in figure 77. The supralabials, infralabials, and genials are dark edged, relatively lightly so in MZUSP 9235, blacker in MZUSP 9236. Venter with transverse black bars (narrower than in fig. 75), many broken and offset to give a checkered appearance.

NATURAL HISTORY: Our specimen of *Liophis trebbaui* seems to be the first one from the Auyán summit. It is a juvenile found during the afternoon, in a shallow, rock-bottom pool containing *Tepuihyla* tadpoles (fig. 7 bottom). The diet of the similar *Liophis torrenicola* includes fish at 1000 m on neighboring Cerro Guaiquinima, but fish are absent from the higher summit of Auyantepui (although doubtless present on the lower slopes), where anurans and their tadpoles are the likely food source. No other specimens were seen despite intensive search.

COMMENTS ON TYPE SPECIMENS AND TYPE LOCALITY

The holotype (AMNH R-61019) of *Liophis trebbaui* is lost. Roze (1958a: 262; 1966: 182) published a photograph of what is inferred to be the adult female holotype. The catalog tag unfortunately appears to have been removed before the specimen was photographed. The specimen was not in the collection of primary type specimens when Myers joined the American Museum staff a decade after its publication, and it has not been found in the main collection. A search of the herpetology archives shows it as an unidentified snake (AMNH R-61019) on a 1957 invoice, along with specimens later designated as types of *Anilius scytale phelpsorum* Roze and *Neusticurus racenisi* Roze, but the *Liophis* holotype alone was not marked as having been returned, an unfortunate omission that went unnoticed.

Roze (1958a) only gave Auyantepui as type locality, but the AMNH catalog records the holotype as having been collected by W. H. Phelps on February 4, 1938, at an elevation of 1100 m. The 1100 m camp (= Guayaraca) of the 1937–1938 expedition is

the same locality given for the single MBUCV paratype of *L. trebbaui*, which was collected in 1956 by Pedro Trebbau at 1020 m; Tate (1938a: 474) corrected the elevation to 1038 m and Dunsterville (1965: 168) gave "nearly 1,000 metres" for Guayaraca. The type locality of *Liophis trebbaui* is essentially the same as that of *Neusticurus racenisi* (footnote 27) and may reasonably be corrected to: "south slope Auyantepui, Guayaraca area, about 1000–1100 m".

The single paratype (MBUCV 3049) of *Liophis trebbaui* was said to be a juvenile (size not stated), with a juvenile coloration of transverse bands of black and white (preserved color). The adult female holotype was uniformly olive gray above; total length was given as 570 mm, but the originally stated "13 mm" of tail length (Roze, 1958a) clearly is an error, being much too short (2.3% of total length) for the number of subcaudals (59) given. However, Roze's (1966: 182) subsequent correction to "130 mm" (= 22.8% of total length) possibly errs in the other direction. Other data provided by Roze (1958a) for the type specimens of *L. trebbaui*—including ventral and supralabial color patterns, scale counts, method of scale-row reduction, and dentition—seem consistent with the new specimens shown in figures 74–77.

COMPARISONS

The black-edged or dark-suffused supralabials with pale centers separates *Liophis trebbaui* at a glance from its geographic neighbors *L. ingeri*, in which the lips are not well differentiated from the greenish head color (Gorzula, 1992: photo 161; also Gorzula and Señaris, 1999: photo 114), and *L. torrenicola*, which has a conspicuously pale upper lip (Donnelly and Myers, 1991: fig. 28A; Mägdefrau et al., 1991: 23).[35] Other differences seem to pertain, but specimens are too few to

satisfactorily delimit ontogenetic and intra-populational variation of any one character.

The ventrolateral widening of the pale crossbars in juvenile *Liophis trebbaui* (figs. 74, 77) resembles the triangular widening of the lateral bars in juvenile *L. torrenicola* (Donnelly and Myers, 1991: fig. 28A)—a resemblance suggestive of possible affinities with Brazilian *L. longiventris* and *L. frenatus* from well south of the Amazon (Dixon, 1983a, 1989). However, there seems to be no question of possible conspecificity. Two juvenile specimens of *L. longiventris* (AMNH R-114263–114264) differ from the Venezuelan material in having numerous, very thin, pale dorsal crosslines, with only every other line confluent with the triangular or rounded top of a pale ventrolateral area (similar to fig. 1B in Dixon, 1983a). We have not seen adult *longiventris*, but an adult male *L. frenatus* (MZUSP 10160) is slender and remarkably attenuated—body width only 7–8 mm by 560 mm total length—quite unlike the habitus of *torrenicola*, *trebbaui*, and most other *Liophis*.

As previously discussed (Donnelly and Myers, 1991), there is no real evidence that any tepui *Liophis* is conspecific with *Liophis cobella*.[36] Dixon (1983a) had submerged *L. trebbaui* and *L. ingeri* together as the subspecies *Liophis cobella trebbaui*, which was said to have the following distribution: "Known only from the Chimantá and Auyán Tepuís, and km marker 144 of the El Dorado–Santa Elena [de Uairén] Highway, Bolivar, Venezuela" (Dixon, 1983a: 159; 1989: 10). The references to Chimantá and Auyán tepuis refer to *Liophis ingeri* and *L. trebbaui*, respectively, whereas the last locality is based on a third species, *Liophis miliaris* (sensu lato).

NOTES ON *LIOPHIS MILIARIS* IN VENEZUELA

GRAN SABANA SPECIMENS (*L. MILIARIS* SENSU LATO): The "km marker 144" local-

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[35] Kornacker (1999: 109, photo 40) included both *Liophis torrenicola* and *L. trebbaui* in a checklist, but the color photograph labelled "*Liophis trebbaui*" is misidentified. The photograph (credited to H. Mägdefrau on p. 270) shows a very small specimen of the pale-lipped *L. torrenicola* from Cerro Guaiquinima, apparently the same juvenile earlier illustrated in Mägdefrau et al. (1991: 23) under the name "*Liophis* cf. *longiventris*" (an illustration subsequently identified as *L. torrenicola* in Donnelly and Myers, 1991: 51).

[36] In a useful checklist of *Liophis*, Dixon (1989) incorrectly changed the name *cobella* to "*cobellus*", evidently under the assumption that the specific name is a normally declined adjective. However, it is a noun (possibly an Amerindian vernacular name). Linnaeus (1758: 218) named *Coluber Cobella* in his customary way of capitalizing initial letters of specific names used as nouns in apposition.
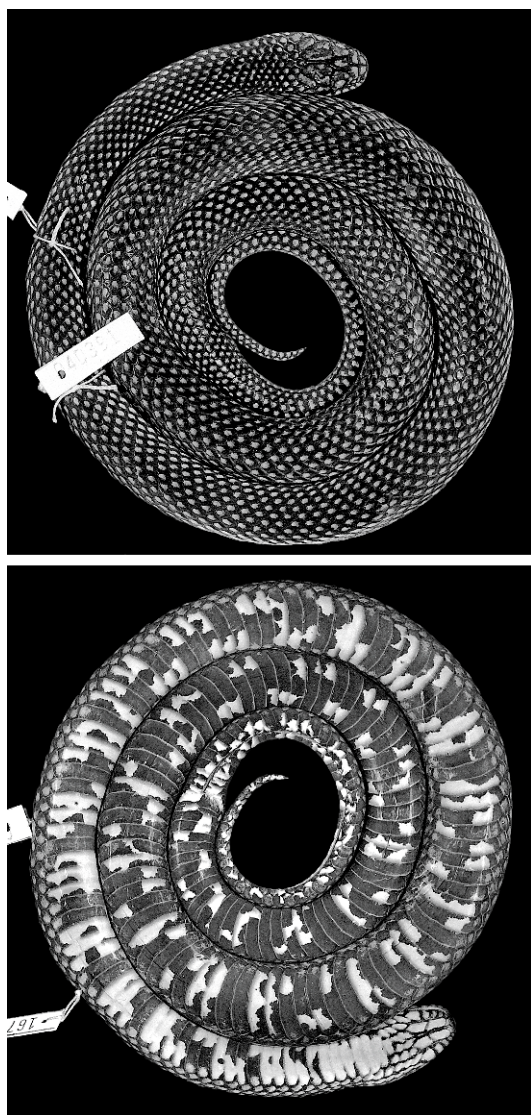
Fig. 78. *Liophis miliaris* sensu lato, ×0.6. Dorsal and ventral views of KU 167584, from 1210 m elevation at km marker 144 on road from El Dorado to Santa Elena de Uairén, Bolivar, Venezuela. This specimen has been cited in the literature as "*Liophis trebbaui*", a smaller, non-spotted snake (figs. 74–77).

ity cited above for "*Liophis cobella trebbaui*" was referenced by Dixon (1983a: 164) to KU 167584, a snake collected by W. E. Duellman in 1974, at an elevation of 1210 m. Although the specimen (fig. 78) is here assigned to *Liophis miliaris* sensu lato, it may represent

an unnamed species. It is a female 695 mm in total length, including 122 mm tail length (17.6% of total); dorsal scales lacking scale pits, smooth, in 17-17-15 rows; ventrals 176; paired subcaudals 55; anal plate divided; supralabials 8, 2nd–3rd touch loreal, 4th–5th in eye; infralabials 10/9, first five touching anterior genials; maxillary teeth 16 + 2 on right side. In life (Duellman's fieldnotes and transparency), the dorsum was black with a greenish yellow spot on each scale; venter cream with black markings; iris dark reddish brown; tongue black. The top of the head is black, with dense pale spotting; the supralabials, infralabials, and genials have heavy black margins (fig. 78).

A second, larger *miliaris*-like snake with a color pattern and scutellation virtually identical to the above is AMNH R-114801, collected by Gorzula in 1975 at Cabanayén (elevation 1230 m fide Gorzula and Señaris, 1999: 246). It is a female 860 mm in total length, 143 mm tail length (16.6% of total); ventrals 178, subcaudals 52. Head scales as above, except 10 infralabials on both sides; 15 + 2 maxillary teeth. A juvenile specimen of *Liophis trebbaui* (fig. 77) was collected at the same locality.

With total lengths of 695 and 860 mm, the aforesaid specimens (KU 167584, AMNH R-114801) here assigned to *Liophis miliaris* sensu lato are appreciably larger and more muscular than the adult holotypes of *Liophis torrenicola* (457 mm), *L. trebbaui* (570 mm), and *L. ingeri* (630 mm).

Liophis miliaris had not been explicitly recorded from Venezuela when Dixon (1983b) revised the species, although KU 167584 was the source for Hoogmoed's (1979b: 276) indication of the maximum elevation (1210 m) attained by *L. miliaris* and its placement in "Western Guiana" (M. S. Hoogmoed, personal commun.).[37] Dixon's (1983a) mistaken assignment of that specimen (KU 167584) to "*L. cobella trebbaui*"

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[37] An explicit Venezuelan record of *Liophis miliaris* was provided by Kornacker et al. (2002), who reported a specimen (MHNLS 1634) from km 67 on the El Dorado–Santa Elena de Uairén road in southeastern Bolívar state. These authors also corrected an earlier photographic record (Kornacker, 1995) of a living specimen of *L. miliaris* that had been misidentified as *L. reginae zweifeli*.

presumably was based on meristic data, similarity in head color pattern, and knowledge that a pale-spotted color pattern occurs in several nominal species of *Liophis*. However, *L. trebbaui* does not have a spotted pattern—Dixon (1983a: 157) seems to have extrapolated this from Roze's (1958b: 304) description of *L. ingeri*, which Dixon regarded as a synonym of *L. trebbaui*. Roze mentioned *una apariencia reticulada* produced by pale areas on the head plates and dorsal scales on the anterior body of *L. ingeri*. This weakly spotted anterior pattern may prove diagnostic of *L. ingeri*, but it is not the vivid "salt and pepper" pattern that characterizes the larger Venezuelan specimens here assigned to *L. miliaris* (e.g., compare fig. 78 with photos of *L. ingeri* in Donnelly and Myers [1991: fig. 30] and especially in Gorzula and Señaris [1999: photo 114]).

The two specimens of *Liophis miliaris* s.l. mentioned above come from the northern part of Venezuela's Gran Sabana (southeastward of Auyantepui). They do not match descriptions of any of the seven subspecies recognized by Dixon (1983b, 1989). *Liophis miliaris chrysostomus*, of lowland Amazonia, is similar in having a heavily checkered black venter but, unlike the present specimens, the underside of the tail tends to be unmarked (see Dixon, 1983b: fig. 3C). Furthermore the black ventral checkering in *chrysostomus* is mostly straight-edged with sharp corners (as is commonplace among snakes with such patterns), whereas in the present specimens the heavy markings have mostly nonlinear edges giving a different aspect from normal checkering (compare fig. 78 with fig. 3C in Dixon, 1983b).

OTHER SPECIMENS (*L. M. MILIARIS*): We are aware of two additional Venezuelan specimens of *Liophis miliaris*. (1) AMNH R-114755 comes from Santa Elena de Uairén (Estado Bolívar), near the Brazilian border (some 130 km SE of the Cabanayén locality mentioned above). It is a female (preserved in a hardened state and not accurately measurable) that resembles the two Gran Sabana specimens in having dark-edged labials and genials, and a spotted (salt-and-pepper) color pattern, but which differs from them as follows: a lower number of ventrals (ventrals

159, subcaudals 51); head dark brown without pale spots; pale venter inconspicuously marked with thin, pale gray streaks across the ventral plates; subcaudal surfaces unmarked; pale spots on scales of the first dorsal row enlarged to cover most of the scales. The last character causes the pale color of the first-row scales to nearly fuse with the pale venter. In these aspects of color pattern, AMNH R-114755 resembles photographs of the Linnaean holotype of *Liophis miliaris* (Gans, 1964, fig. 23 [a composite of 5 photos]). Thus, the AMNH specimen from Santa Elena (misidentified as *L. cobella* in Gorzula and Señaris, 1999: 170) fits Dixon's concept of *Liophis miliaris miliaris*, which occurs nearby in northern Guyana (Dixon, 1983b: fig. 1).

(2) The second specimen is MHNLS 1634 from km 67 on the El Dorado–Santa Elena de Uairén road (Estado Bolívar); Kornacker et al. (2002: 32) give the coordinates as 06°18′N, 61°18′W. The locality is some 180 km (airline) N of Santa Elena de Uairén, roughly 130 km ENE of Auyantepui, and nearly 100 km NNE of Cabanayén. It was identified as *Liophis miliaris miliaris* by Kornacker et al. (2002), who provided a photograph in dorsal view and scale data including 156 ventrals and 52 subcaudals (sex not stated). The numbers of ventrals and subcaudals of MHNLS 1634 from km 67 are close to the 159 and 51 counts given above for AMNH R-114755 from Santa Elena de Uairén. These two specimens resemble Gran Sabana specimens (e.g., fig. 78) in the spotted salt-and-pepper dorsal pattern, but head and ventral patterns are quite different.

The above specimens of *L. m. miliaris* resemble each other in lacking conspicuous pale spotting atop the head and in ventral pattern. Gilson Rivas Fuenmayor kindly provided a photograph of MHNLS 1634 in preservative that shows an orange-tinged venter with markings virtually the same as those of AMNH R-114755—the venters are marked inconspicuously with thin gray streaks across some ventral plates, the subcaudal surfaces are immaculate, and pale spots on scales of the first dorsal row are enlarged and nearly fused with the ventral color.

TWO KINDS OF *LIOPHIS* "*MILIARIS*" IN VENEZUELA: Gans (1964) surveyed the

variation and synonymy of *Liophis miliaris* (Linnaeus) in southeastern South America; he suggested that it is a polytypic species but did not formally recognize subspecies. Dixon (1983b) enlarged the study to include northern populations of other *miliaris*-like snakes. Dixon associated pre-existing names to seven subspecies, of which the two northernmost ones (*miliaris* and *chrysostomus*) appear to be widely allopatric (map in Dixon, 1983b: fig. 1); see Giraudo et al. (2006) for comments on southern populations. Dixon's (1983b: 796, 799) conclusion that the type specimen of Linnaeus' *miliaris* came from Suriname is particularly noteworthy, since it defined the nominotypical subspecies—*L. m. miliaris*—as the allopatric population in northern Guyana, Suriname, and French Guiana. The nominotypical form is now known in southeastern Venezuela from Santa Elena de Uairén (AMNH R-114755) and from km 67, about 180 km to the north (MHNLS 1634)—at elevations apparently well below 1000 m.

Liophis miliaris miliaris seems to be replaced at higher elevations (> 1000 m) in the Gran Sabana by an unnamed *miliaris*-like snake of very different aspect (KU 167584, AMNH R-114801). This form seems to differ from lower-elevation *L. m. miliaris* in having a higher ventral count, in having a conspicuously spotted head and, especially, in having a distinctively patterned ventral surface (fig. 78). The photograph of a living specimen from ''Kavac, Gran Sabana'' probably belongs to this population, judged from its vividly patterned head (Kornacker, 1995 [as *L. r. zweifeli*]; Kornacker et al., 2002: fig. 2).

ON *LIOPHIS ZWEIFELI*:   As demonstrated by Kornacker (1995) and Kornacker et al. (2002), specimens of Venezuelan *Liophis* ''*miliaris*'' can easily be confused with *Liophis zweifeli* (Roze) (=*Liophis reginae zweifeli* sensu Dixon, 1983c), a snake with a similar salt-and-pepper dorsal pattern (Roze, 1966: fig. 39); the similarity is real and collections should be checked with that in mind. The taxon *zweifeli* can be distinguished from Venezuelan ''*miliaris*'' in having apical pits on the dorsal scales (although these may be few and hard to find), in a lower number of ventrals (140–148 fide Roze [1966: 165], 132–148 fide Dixon [1983c: 115]), and in a longer tail with higher number of subcaudals (78–86

fide Roze [1966: 165], 69–88 fide Dixon [1983c: 127]).

Also, *Liophis reginae zweifeli* sensu Dixon possibly differs from Venezuelan *L.* ''*miliaris*'' in lacking black markings on the underside of head and lower part of the supralabials. The ventral color pattern seems to be variable in *zweifeli*; the holotype was described as having ventral scales heavily mottled with black on the posterior two thirds of the body (Roze, 1959: 5), but in an available paratype (AMNH R-59430) the venter is mostly pale, with minimal black edging laterally over most of the venter (subcaudals immaculate). A concise description of the taxon *Liophis reginae zweifeli* and re-evaluation of its relationships are needed. The extraordinarily variable and wide-ranging *Liophis reginae* (see map in Dixon, 1983c: 118) is likely a composite species; one species (*Liophis oligolepis* Boulenger) already has been resurrected from its synonymy, as summarized by Cunha and Nascimento (1993: 73–74).

Mastigodryas boddaerti (Sentzen)
Figure 79

Coluber boddaerti Sentzen, 1796: 59. Holotype and type locality unknown.

Eudryas b. boddaertii: Stuart, 1933: 2 (the double -*ii* termination used by various authors is an incorrect subsequent spelling).

Dryadophis boddaerti: Stuart, 1941: 66 (in generic revision).

Dryadophis boddaertii: Roze, 1958a: 264; 1966: 120 (Auyantepui specimens).

Mastigodryas boddaerti: Peters and Orejas-Miranda, 1970: 192 (new generic combination).

MATERIAL: Auyantepui Plateau, 2200 m (7218 ft.): AMNH R-61018, from the 1937–1938 AMNH–Phelps Venezuelan Expedition. Camp 2, 1750 m: AMNH R-155716 (shed skin), from the 1994 AMNH–TERRAMAR Expedition to Auyantepui.

The one whole summit specimen (fig. 79) examined is an adult male 1036 mm total length, 286 mm tail length (27.6% of total length); dorsal scales with paired apical pits, smooth, in 17-17-15 rows. Ventrals 183, subcaudals 105, paired; anal plate divided. Supralabials 9, 2nd–3rd touching loreal, 4th–6th in eye; infralabials 10, first five touching anterior genials. Temporals 2/1 + 2. Maxil-
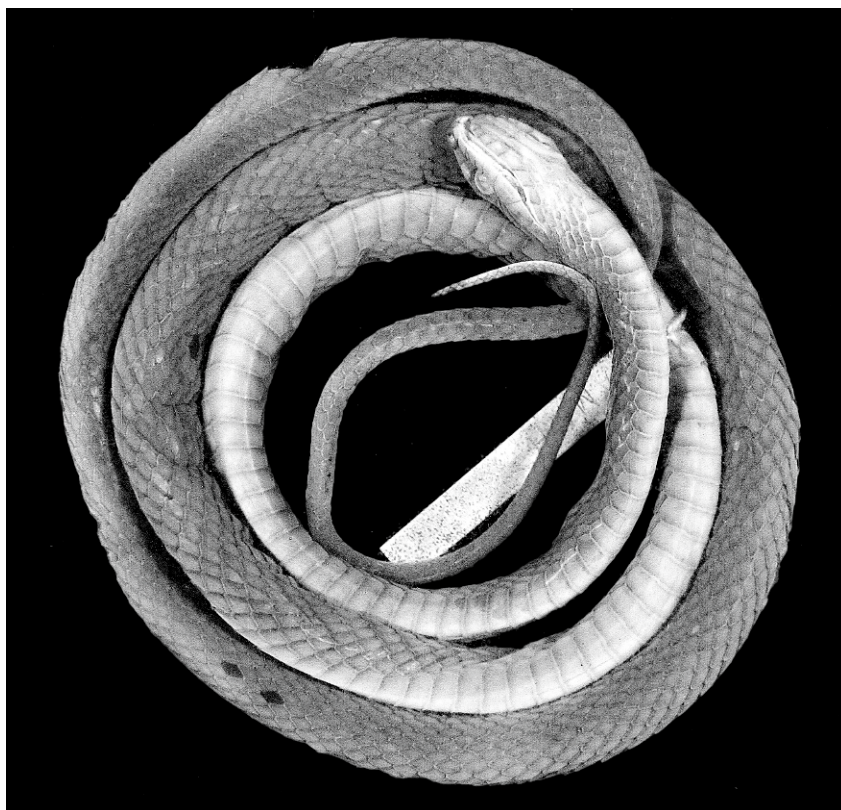
Fig. 79. *Mastigodryas boddaerti*, ×0.87. The first specimen (AMNH R-61018) collected on the summit of Auyantepui, by the 1937–1938 AMNH–Phelps Venezuelan Expedition. This snake, an invader from the lowlands, appears to have maintained a persistent presence on the Auyán summit for many years.

lary teeth 17 + 2 on right. Color gray, presumably brown in life, with a faint remnant of a pale lateral stripe on scale row 4. (The juvenile pattern of *M. boddaerti* is very different, consisting of squarish dorsal blotches alternating with lateral ones.)

The shed skin from Camp 2 is fragmentary but identifiable. It has smooth scales with paired apical pits, in 17 dorsal scale rows anteriorly. Shapes of the dorsal head plates correspond to those of the whole summit specimen and another specimen (AMNH R-61035) from the base of Auyantepui, and the configuration of 2/1 + 2 temporals (on both sides of the head) is identical in all three.

REMARKS

NOMENCLATURAL COMMENT: The available name *boddaerti* Sentzen (1796) is affixed to this species with complete arbitrariness—under a philosophy "often at a considerable stretch of the imagination … to use as many old names as possible" (Stuart, 1933: 1). The name is practically a nomen dubium and could well have been discarded as such. The fate of the original specimen is unknown, the type locality is unknown (the type locality cited in Kornacker [1999: 115] is that of a presumed synonym), and the original "description" could apply to many snakes (some of which are listed in the long synonymy in Boulenger, 1894: 11–12). The only data provided by Sentzen (1796: 59) were a count of ventrals and caudals ("Scut. 181 – 108 = 289") and total length and tail measurements in old German feet ("Ganze Länge 2 Fuss, 8 Zoll; Schwanzlänge 7 Zoll, 7 Lin."), for which there was more than one system.

Stuart (1941: 66) restricted the name to this species simply because Merrem (1820: facing pages 110) had early used *Boddaertische* and *Boddaerti* for a second specimen whose habitat was "*vorzüglich* [especially] Surinam", which, in Stuart's imagination, suggested "Dutch Guiana as the type locality". In its present sense, the specific name *boddaerti* has become well established through the influence especially of Stuart (1933, 1941), Roze (1966), and Peters and Orejas-Miranda (1970). A neotype should not be designated until there is actual need for defining the taxon more objectively.

AUYANTEPUI RECORDS: The snake known as *Mastigodryas boddaerti* has a broad geographic range and appears to be an invader from the lowlands with an established presence on the Auyán plateau. Records are few, but they span many years.

Roze (1958a: 265; 1966: 122) reported four specimens from Auyantepui, including AMNH R-61018 described above, and AMNH R-61035. The AMNH catalog shows the first as collected by W. H. Phelps on the summit at 2200 m elevation, in December 1937 or January 1938; the second was taken at at 460 m (base of Auyantepui) in February 1938. A third specimen (MBUCV 3073) was taken by P. Trebbau at 1020 m (Guayaraca) on the southern slope in April 1956. Two additional localities were given by Roze with identical catalog numbers (MBUCV 3072) and identical data except for one listed as "Auyantepui" and one as "El Oso, Auyantepui", both said to have been collected at 1800 m by P. Trebbau on April 24, 1956. Presumably these two entries are a duplication and apply to a single specimen. Aside from being on the southern end of Auyantepui, the location of Trebbau's 1800 m "El Oso" locality is uncertain. Dunsterville (1965: 170, foldout map) mapped a "Bosque del Oso" but gave an elevation of about 2050 m and equated it roughly with the "2200-meter camp" of the 1937–1938 expedition.

In May 1989, Fabián Michelangeli photographed a *cazadora* identifiable as *Mastigodryas boddaerti* on the northern end of the western branch of Auyantepui (inaccurately cited as "Sima Aonda" in A. Michelangeli, 2005: 135, fig. 7 [F. Michelangeli, personal commun.]). During the 1994 expedition, we found only the shed skin at Camp 2, on the eastern branch of the Auyán plateau.

The above records, from 1937 to 1994, suggest that *Mastigodryas boddaerti* maintains a permanent presence on the summit of Auyantepui.

FAMILY CROTALIDAE
Bothrops atrox (Linnaeus)
Figure 80

Coluber atrox Linnaeus, 1758: 222. "*Habitat in Asia*" in error.

MATERIAL: West side of Auyantepui summit, 5197 ft. [1584 m], at 5°55′56.9″N, 62°39′32.2″W fide R. Guerrero (personal communication). Specimen not preserved, photographed March 22, 2006 by José Miguel Pérez G. (see fig. 80).

The photograph provides the only record of a fer-de-lance from the summit of any tepui.

SUMMARY DISCUSSION
AND CONCLUSIONS

Much knowledge has accrued since Hoogmoed (1979b) provided a substantive review of the 408 species of amphibians and reptiles then known from the Guayana (or Guiana) Shield. Among later studies, Duellman (1999: appendix 5.1) increased the known amphibian fauna, and Gorzula and Señaris (1999) reported on the herpetofauna of the Venezuelan Guayana. Recent checklists tabulated 564 species of amphibians and reptiles for the Guayana Shield (Señaris and MacCulloch, 2005; Ávila-Pires, 2005). See McDiarmid and Donnelly (2005) for a review of the highland herpetofauna of Guayana, with specific emphasis on the tepuis.

Myers (2005) mentioned that over 100 species of frogs, lizards, and snakes have been found on sandstone tepuis and certain neighboring granitic mountains. McDiarmid and Donnelly (2005: 159) more specifically enumerated 159 species from these mountains, with a conservative prediction that further exploration will increase the number to over 200 species. Our own attempts at collecting representative samples (see p. 7; also Myers and Donnelly, 2001: 79) from a number of summits reinforce several general

Fig. 80. *Bothrops atrox*—the only venomous snake recorded from the Auyán plateau, where it may have a restricted distribution or temporary presence. This, the only known specimen, was found in March 2006 on the western branch of the summit, at an elevation of nearly 1600 m. (Photograph courtesy of Karel Bentata and José Miguel Pérez).

conclusions about the composition of tepui herpetofaunas:

> (1) Tepuis have relatively depauperate herpetofaunas; (2) neighboring tepuis are likely to have significantly different faunas; (3) tepui endemics outnumber widespread highland species; (4) some endemic species have widespread counterparts, the remnants perhaps of a once widespread tepui fauna; and (5) lowland species find their way onto tepuis in an irregular, unpredictable manner. (Myers and Donnelly, 2001: 79)

Consideration of the Auyán summit fauna allows some elaboration and clarification of these points.

1. Although summit herpetofaunas are depauperate relative to lowland faunas in general, they also are impoverished relative to one another according to a complex of factors that include elevation, area, and habitat. Generally, species diversity is negatively correlated with increasing elevation and positively correlated with increasing area and habitat diversity. The fewest species are to be expected on high (> 2000 m), cold summits that are covered mainly by bare rock and pioneer vegetation (e.g., Cerro Roraima, 34 km² with four or five species). Increased habitat diversity can increase faunal size even on high summits of small area (e.g., Cerro Yaví, < 6 km² with seven known species), whereas large summits with varying elevation and diverse habitats harbor the largest herpetofaunas (especially Cerro de la Neblina, 235 km² with 26 known species).

Auyantepui falls in the last category, with a summit area of 667 km² and 24 known species.[38] This fauna is relatively large (for a tepui) owing in part to intensity of collecting on the enormous, habitat-rich summit. We document 24 species on the summit—13 anurans, 5 lizards, and 6 snakes—of which 16 species were collected during the 1994 AMNH–Terramar Expedition. Although that dry-season expedition obtained only 67% of the presently known fauna, it contributed perhaps five or six species that to our knowledge had not been previously collected on the Auyán summit.

2. Myers and Donnelly (2001: 79–80) perceived an emerging generalization that neighboring tepuis may have significantly different faunas, which, although complicated by habitat differences, seemed evident in comparing the faunas of the northwestern tepuis (Yaví, Yutajé-Corocoro, Guanay). Myers (1997) had earlier commented on the striking difference between the herpetofauna of Auyantepui and that of the Chimantá massif. This deserves further comment, inasmuch as the Chimantá massif is highly dissected but nonetheless has a relatively unified fauna.

Auyantepui and Chimantá are massifs of comparable size and similar origin—remnants of the possibly Cretaceous "Auyán-tepui planation surface" (Briceño et al., 1990). They are less than 50 km apart at the 2000 m contour and are continuous at the 1000 m contour. The Auyantepui massif is for practical purposes a single large mountain (see p. 14). The Chimantá massif, on the other hand, is so highly eroded that its components comprise 10 adjacent tepuis (11 according to Briceño et al., 1990), whose combined summit area (615 km²) is smaller

than that of Auyantepui proper (667 km²) according to data provided by Huber (1995a: 60, table 1–3).

A total of 16 species are known from nine of the 10 or 11 adjacent mountains in the Chimantá massif. The endemic *Thamnodynastes chimantá* and *Stefania ginesi* are found on 6–7 of the Chimantá tepuis, which do appear to share a similar herpetofauna that can be treated as a unit, as was done originally by Gorzula (1992) and subsequently by Myers (1997).[39] The high headwater and other valleys separating some of the Chimantá tepuis are perhaps not deep enough in some cases, or not old enough in others, to have created significant vicariance within the general herpetofauna. Huber (1992: 26) observed that "A pesar de su complejidad fisiográfica, el macizo del Chimantá se presenta como un conjunto montañoso bastante homogéneo. [Despite its physiographic complexity, the Chimantá massif is a mountainous ensemble that is quite homogeneous]".

Treated as a unit, the herpetofauna of the Chimantá massif also appears homogeneous and very different from that of Auyantepui,

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[38] Additional to Cerro de la Neblina and Auyantepui, the only other tepui with a known summit fauna exceeding 20 species is Cerro Guaiquinima (1096 km² with 22 species at last count [McDiarmid and Donnelly, 1999: 533]). However, Cerro Guaiquinima is not quite comparable. Although there is a peak at about 1680 m, this is an exceptionally low tepui in average height. It is inclined downward from escarpments of about 1300 m elevation to 700 m on the southern side. There are a few highland endemics, but not surprisingly, the herpetofauna of Cerro Guaiquinima consists predominantly of lowland species that comprise well over 50% of the total.

[39] Gorzula (1992) listed his specimens as coming from Chimantá camps I–XIX, which were established in the period 1983–1986, as described and mapped by Huber (1992: 31–33, fig. 1–3), who gave an elevational range of 1800–2600 m for the 19 camps. Gorzula and Señaris (1999: 255–256) provided a few summary details and some individual tepui names in a gazetteer, and added Chimantá Camp XXII (2100 m) from 1988. But a bit of confusion was introduced in that coordinates and some elevations for camps I–IV do not quite match the data in Huber (1992); coordinates for Camp I are the same as given for Camp XIV.

McDiarmid and Donnelly (2005) perpetuated some of this confusion. Following the above duplication in Gorzula and Señaris, coordinates (5°16′N, 62°09′W) belonging to Camp XIV were assigned also to "Chimantá proper" (Camp I); Huber (1992) had described and mapped Camp XIV as situated at 2100 m in a broad valley between the northeast sector of Toronó-tepui and the southeast sector of Chimantá (herein shown as Chi/To in table 10). Coordinates (5°22′N, 62°08′W) belonging to Camp XIX also were assigned by McDiarmid and Donnelly (2005: 527) to Chimantá-tepui, but, in another place (pp. 526–527), correctly noted as lying between Apacará-tepui and Murey-tepui (herein shown as Ap/Mu in table 10).

Mainly because of locality mix-up, McDiarmid and Donnelly (2005: 527) listed 11 species for Chimantá-tepui proper, whereas only six are documented ("Chi" in table 10).

TABLE 10
Comparisons of the Herpetofaunas of Auyantepui and Chimantá Massif
(* = endemic species)

Family and Species Counts (Auyantepui/Chimantá) AUYANTEPUI	CHIMANTÁ MASSIF[a]
Aromobatidae 1/1 (0 shared)	
*Anomaloglossus tepuyensis	*Allobates rufulus[Am,Mu,Tir]
Brachycephalidae 2/1 (0 shared)	
*Eleutherodactylus auricarens	Eleutherodactylus sp.[Mu]
Eleutherodactylus pulvinatus	–
Bufonidae 1/0	
*Oreophrynella cryptica	–
Centrolenidae 3/0	
*Centrolene gorzulai	–
Hyalinobatrachium crurifasciatum	–
Hyalinobatrachium taylori	–
Hemiphractidae 1/1 (0 shared)	
*Stefania schuberti	*Stefania ginesi[Ab,Ac,Am,Chi,Chu,Mu,Tir]
Hylidae 4/2 (1 shared)	
*Hypsiboas angelicus	–
*Hypsiboas jimenezi	*Hypsiboas sp. cf. H. jimenezi[Chi/To]
Hypsiboas sibleszi	–
Tepuihyla edelcae	Tepuihyla edelcae[Ab,Ac, Am,Ap,Ap/Mu,Chu,Mu,Tir]
Leptodactylidae 1/0	
Leptodactylus rugosus	–
Microhylidae 0/1	
–	Otophryne steyermarki[Ac,Ap]
Gymnophthalmidae 3/3 (1 shared)	
*Anadia (sp. b)	*Anadia (sp. A)[Ab,Am,Mu]
*Arthrosaura montigena	*Arthrosaura (sp. A)[Ab,Ac,Am,Chi,Chu]
Neusticurus rudis	Neusticurus rudis[Ac,Am,Chi]
Polychridae 1/2 (1 shared)	
Anolis chrysolepis planiceps	Anolis chrysolepis planiceps[Ab,Ap,Ap/Mu,Chi/To,To]
–	*Phenacosaurus carlostoddi[Ab]
Tropiduridae 1/0	
*Tropidurus bogerti	–
Colubridae 5/4 (1 shared)	
*Atractus guerreroi	*Atractus steyermarki[Chi,Chu]
Chironius fuscus	–
Leptodeira annulata	Leptodeira annulata[Ac,Am,Ap]
Liophis trebbaui	*Liophis ingeri[Chi,Chi/To]
Mastigodryas boddaertii	*Thamnodynastes chimanta[Ac,Am,Ap,Chi/To,Chu,Mu]
Crotalidae 1/1 (0 shared)	
Bothrops atrox	Bothriopsis taeniata[Chi]

[a] Subdivisions of the Chimantá Massif (see diagram in Huber, 1995a: fig. 1–27): *Ab*, Abacapá-tepui; *Ac*, Acopán-tepui; *Am*, Amurí-tepui; *Ap*, Apacará-tepui; *Chi*, Chimantá-tepui; *Chu*, Churi-tepui; *Mu*, Murey-tepui; *Tir*, Tirepón-tepui; *To*, Toronó-tepui.

less than 50 km to the north-northwest. Comparisons are shown in table 10, in which the taxonomy and intramassif distribution of Chimantá taxa are updated from the basic accounts in Roze (1958b), Barreat et al. (1986), Gorzula (1992), and Gorzula and Señaris (1999). McDiarmid and Donnelly (2005) added several taxa to the faunas of Murey-tepui and especially Tirepón-tepui (which were visited by McDiarmid and Brewer-Carias in 1978).

There are 36 species in the combined faunas of Auyantepui (24 spp.) and the Chimantá massif (16 spp.), of which only

four (11%) wide-ranging species are known to be shared. Auyantepui has 11 endemic species (including endemics not confined to the summit, see below); the Chimantá massif has at least nine endemic species.[40] There are 25 genera in total, of which 11 (44%) are shared, usually by different species. Eight (62%) of 13 families are shared. Differences in shared families and genera probably could be somewhat diminished by increased collecting on Chimantá (it is difficult to believe that there are no centrolenid frogs there). Nonetheless, the family Tropiduridae (usually conspicuous lizards) is perhaps absent from Chimantá, and the microhylid genus *Otophryne* (with distinctive call and tadpoles) seems unlikely to have escaped detection on the summit of Auyantepui.

3.   Our generalization that endemics in a tepui fauna will outnumber widespread highland species applies to Auyantepui, which has nine species possibly endemic to the summit, three species endemic to the immediate area, and five more broadly distributed highland species, of which only one is a "tepui species". Excluding eight "invaders" from lower elevations (see point 5 below), the Auyán summit harbors a mainly highland fauna, whose species may be grouped as follows:

"WIDESPREAD" GUAYANA HIGHLAND ENDEMICS: *Hyalinobatrachium crurifasciatum*, *Hypsiboas sibleszi*, *Eleutherodactylus pulvinatus*, *Tepuihyla edelcae*, *Liophis trebbaui*. The first three frogs are upland species found occasionally on tepuis, but *Tepuihyla edelcae* is known only from tepuis. The snake *Liophis trebbaui*, once thought to be endemic to Auyantepui, appears to be widely distributed in uplands east of the Río Caroní, from Auyantepui to the Brazilian frontier.

ENDEMIC TO AUYANTEPUI REGION: *Anomaloglossus tepuyensis*, *Hypsiboas jimenezi*. These occur on the Auyán slopes and in adjacent lowlands as well as on the summit.

POSSIBLE AUYÁN SUMMIT ENDEMICS: *Oreophrynella cryptica*, *Centrolene gorzulai*, *Hypsiboas angelicus*, *Stefania schuberti*, *Eleutherodactylus auricarens*, *Anadia* sp., *Arthrosaura montigena*, *Tropidurus bogerti*, *Atractus guerreroi*. These nine species are known at present only from the Auyán summit, but some (e.g., *C. gorzulai*, *E. auricarens*) seem likely to inhabit forest at lower elevations and might prove to be endemic to the Auyán massif broadly.[41]

4.   Various authors have noted that a few genera of amphibians and reptiles are represented by obviously related species on different tepuis, a fact of obvious biogeographic significance. However, biogeographic scenarios for the highland herpetofauna are uncomfortably speculative, given the virtual lack of testable phylogenetic hypotheses and absence of molecular studies. Myers and Donnelly (2001: 80) simply observed that "tepui endemics are likely to have counterparts" on other tepuis—defining "counterparts" as a purposely vague term used for congeneric species judged to be phenotypically and ecologically similar, with phylogenetic closeness being probable.

With one notable exception, the Auyán endemics do have endemic congeneric counterparts on other tepuis (or, in the case of *Centrolene*, at least in other parts of the Guayana highlands), although degree of relatedness is unknown. The exception is the common lizard *Tropidurus bogerti*, whose phylogenetically closest relatives may occur south of the Amazon. Interestingly, *T. bogerti* does have a phenotypically and ecologically similar "counterpart" in the form of *Plica lumaria* on Cerro Guaiquinima.

Among the Auyán summit taxa, at least *Oreophrynella* (and perhaps *Stefania* and *Tepuihyla*) may represent part of a relatively old and widespread highland fauna in Pantepui. Certain other elements postulated as part

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[40] Omitted from these considerations are skins of a colubrid snake from Auyantepui and of a gymnophthalmid lizard from Tirepón-tepui in the Chimantá massif. These were included in the species counts in McDiarmid and Donnelly (2005: 511, 523, 529, table 18A.1), but there was no claim that the skins do not represent one of the five colubrids or three gymnophthalmids already scored from Auyantepui and the Chimantá massif, respectively.

[41] There may be an overemphasis here and elsewhere on summit endemics, especially for those species that seem disposed to forest habitats. Lower tepui slopes are extensive (for estimated areas, see Huber, 1995a: table 1–3), and are sometimes forested and well watered. But the terrain tends to be difficult and has not often been collected except by botanists and ornithologists (most serious herpetological collecting commenced after the advent of helicopters).

of this fauna are absent from Auyantepui. The missing taxa include the genus *Riolama*, species of the *Phenacosaurus neblininus* complex, and species of the dwarf *Thamnodynastes* complex, although members of the last two groups occur in the neighboring Chimantá massif. Such speculation assumes (1) that the involved species comprise monophyletic highland groups rather than separate invasions from lower elevations, and (2) that spotty distribution patterns are the result of random extinction events as well incomplete collecting.

5. Lowland species of amphibians and reptiles "doubtless invade all tepuis, although they may not necessarily reach the highest summits … or, if they do, they may not establish permanent populations there [and although] lowland invaders are expected they can seldom be successfully predicted" (Myers and Donnelly, 2001: 81). The summit of Auyantepui has been invaded by at least the following eight species from lower elevations: *Hyalinobatrachium taylori*, *Leptodactylus rugosus*, *Neusticurus rudis*, *Anolis chrysolepis planiceps*, *Chironius fuscus*, *Leptodeira annulata ashmeadii*, *Mastigodryas boddaerti*, *Bothrops atrox*.

Of these only the *Anolis* seems to be a regular invader of tepuis, although there are tepui records for a few of the other genera and species as well (for records, see McDiarmid and Donnelly, 2005; Señaris and Ayarzagüena, 2005: 230, for *H. taylori*).

Venomous snakes have rarely been found on tepuis. The present report of *Bothrops atrox* is only the second record of a viper from a tepui summit, the other being the holotype of *Bothrops lichenosa* (= *Bothriopsis taeniata*) collected in 1955 on the summit of Chimantá Tepui. Coral snakes occur as rarely; Myers (2005) pictured a specimen of *Micrurus psyches* from the lower part (1400 m) of the summit of Cerro Guanay.

Whether lowland invaders can maintain permanency on tepui summits is information hard to come by. However, documentation provided herein for *Mastigodryas boddaerti* indicates that this lowland racer has maintained a presence on the Auyán summit for nearly 60 years at least. And, judged from the number of records, the lowland snake *Leptodeira annulata* may be a permanent resident of the Chimantá massif, although only a single specimen is known from Auyantepui.

CONCLUDING STATEMENT

Auyantepui has had an interesting history of exploration and is among the best known of the Guayana table mountains, with a summit herpetofauna matched in size only on a few other tepuis having large summit areas. Although every tepui appears to have a distinctive herpetofauna not precisely matched on any other, some generalities have emerged concerning faunal composition. Tepuis even in the same region may have *very* different herpetofaunas. An exception is provided by the fragmented Chimantá massif, whose adjacent and incompletely isolated tepuis at least appear to share a common herpetofauna. However, although the Chimantá massif and Auyantepui are less than 50 km apart and of the same geological origin, they share only four (11%) of a combined total of 36 species.

On a given tepui, endemic species are expected to outnumber widespread highland species and, except on the very highest tepuis, a part of the fauna will consist of an unpredictable variety of invaders from lower elevations. Some lowland species may attain relative permanency, as in the case of the snake *Mastigodryas boddaerti*, which has been known on Auyantepui for nearly 60 years.

Some elements of the hypothesized old Pantepui herpetofauna can probably be identified. However, biogeographic scenarios lack corroboration, which eventually might be provided by revisionary studies with explicit phylogenies based on morphological and, in the best of possible worlds, molecular data. More collecting on more tepuis, with routine tissue sampling, will be necessary before the herpetofauna can be treated to the kind of analyses being provided for botanical taxa in Pantepui (e.g., see Givnish et al., 1997, 2000).

ACKNOWLEDGMENTS

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[42] Caption for figure 25 of plate 16 (drawings of dorsal head scutellation and digit of the Paris Museum holotype of *Anolis refulgens*—a Schlegel label name published by Duméril and Bibron, 1837: 91).

[43] See Vanzolini (1977: 115–116) for commentary on attribution of authorship and dates of the 17 livraisons of this monumental work, which considers species from South America and the Antilles as well as Middle America.

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NOTE ADDED IN PROOF

Based solely on DNA sequence data, Heinicke et al. (2007) identified three major divisions of eleutherodactyline frogs and resurrected *Pristimantis* Jiménez de la Espada (1870: 61) for a large clade of South American species. Means and Savage (2007) followed and transferred the names of most nominal tepui species to that genus. Such nomenclatural changes reflect advances in knowledge of evolutionary histories. However, in absence of DNA sampling and/or corroborated morphological criteria, generic assignments for tepui taxa will be based on a mix of guesswork and faith. With that reservation and to maintain some semblance of consistency with Means and Savage (2007), the name ''*Eleutherodactylus*'' as used herein should be read as *Pristimantis*.

There are many unnamed species of ''*Eleutherodactylus*'' in the Guayana highlands, as suggested by the list of unidentified/unnamed taxa compiled by McDiarmid and Donnelly (2005: 514). We are aware of the following named species that have been found on (or near) summits of sandstone tepuis and granitic mountains in the Venezuelan Guayana:

Pristimantis aracamuni (Barrio-Amorós and Molina, 2006), new combination

P. auricarens (Myers and Donnelly, 2008), new comb.

P. avius (Myers and Donnelly, 1997)

P. cantitans (Myers and Donnelly, 1996)

P. cavernibardus (Myers and Donnelly, 1997)

P. guaiquinimensis Schlüter and Rödder), new comb.

P. marahuaka (Fuentes and Barrio-Amorós, 2004)

P. marmoratus (Boulenger)

P. memorans (Myers and Donnelly, 1997)

P. pruinatus (Myers and Donnelly, 1996)

P. pulvinatus (Rivero)

P. stegolepis Schlüter and Rödder), new comb.

P. tepuiensis Schlüter and Rödder), new comb.

P. yaviensis (Myers and Donnelly, 1996)

All the species familiar to us were found in various-sized patches of forest. They are of slight or moderate build and show no evident adaptation to terrestrial existence in open treeless habitats. Consequently, even if most species prove to be endemic to particular mountains, all seem likely to occur in suitable forest below the summits (see fn. 41, p. 136).

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