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A New Herpetofauna from Cerro Yaví, Venezuela: First Results of the Robert G. Goelet American Museum–TERRAMAR Expedition to the Northwestern Tepuis

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ABSTRACT

Cerro Yaví is a 2 km tall sandstone table mountain standing apart from other highlands near the northern edge of the Venezuelan State of Amazonas (5°43'N, 65°54'W). The small summit is divided by a few deep gorges. Mossy, upper montane evergreen forest is limited to steep slopes in the gorges, with the exposed summit terrain being a patchwork of jumbled sandstone blocks, rocky flats, small patches of scrub, and boggy meadows, one of which holds a small lake at an elevation of 2150 m above sea level.

The 1995 American Museum–TERRAMAR Expedition discovered a summit fauna of unnamed amphibians and reptiles during a five-day period in the dry season (February); additional species would be expected in the rainy season. The new fauna includes three frogs (*Eleutherodactylus cantitans*, n. sp., *E. pruinatus*, n. sp., *E. yaviensis*, n. sp.), two lizards (*Euspondylus goeleti*, n. sp., *Phenacosaurus bellipeniculus*, n. sp.), and one snake (*Thamnodynastes yavi*, n. sp.). A third lizard, suspected to be an undescribed species of *Arthrosaura*, was represented only by a tail from a stomach of the snake *Thamnodynastes yavi*. This snake also preys on eggs of the new lizard *Euspondylus goeleti*, which has communal nesting sites.

A snake from Cerro Duida is also described (*Thamnodynastes duida*, n. sp.), based on a spec-

imen collected by the American Museum's 1929 Duida Expedition. It more closely resembles the geographically distant *T. chimanta* (some 400 km to the northeast) than its near neighbor (250 km north) on Cerro Yaví. The type specimen of *Thamnodynastes duida* contained in its stomach a lizard, *Riolama* sp., a rare microteiid genus previously confirmed from Cerro Roraima and Cerro de la Neblina.

Known highland relatives of the reptiles of Cerro Yaví occur as widely scattered endemics at distances of 180–550 km in the eastern, east-central, west-central, and southern groups of tepuis. Two geographically closer relatives (*Eleutherodactylus*, *Euspondylus*) from the northwestern tepuis are under study from nearby Cerro Yutajé.

Amphibian and reptile species endemic to only one or a few tepuis outnumber widespread highland species. Some (not all) tepui amphibians and reptiles, including at least the summit reptiles of Cerro Yaví, may be remnants of a once widespread fauna now represented by sets of related, spottily distributed species. Factors complicating analysis include (1) very incomplete sampling and small size of the montane faunas, (2) habitat differences among tepuis, (3) extinction events, especially on the smaller tepuis, and (4) original, regional faunal differences within Pantepui.

RESUMEN

El Cerro Yaví es una meseta aislada, de piedra arenisca y de 2 km de alto, situado cerca al extremo norte del Estado Amazonas, Venezuela (5°43'N, 65°54'W). La pequeña cima está dividida por algunos cañones. El bosque es montano siempreverde y está limitado a las profundas pendientes de los cañones, siendo la expuesta cima un mosaico de roquedales de arenisca, sitios rocosos planos, pequeñas manchas de arbustos y herbales pantanosos, uno de los cuales contiene un lago pequeño a una elevación de 2150 m sobre el nivel del mar.

En la cumbre del Cerro Yaví, la expedición 1995 American Museum–TERRAMAR descubrió una fauna nueva de anfibios y reptiles durante cinco días de trabajo de campo en la temporada seca (febrero); es de esperar que en la temporada lluviosa se encuentren especies adicionales. La fauna nueva incluye tres ranas (*Eleutherodactylus cantitans*, n. sp., *E. pruinatus*, n. sp., *E. yaviensis*, n. sp.), dos lagartijas (*Euspondylus goeleti*, n. sp., *Phenacosaurus bellipeniculus*, n. sp.) y una serpiente (*Thamnodynastes yavi*, n. sp.). Además se sospecha que una tercera lagartija podría ser una especie nueva del género *Arthrosaura*, pero está represen-

tada únicamente por una cola encontrada en el estómago de un ejemplar de *Thamnodynastes yavi*. Esta serpiente también se alimenta de los huevos de la lagartija *Euspondylus goeleti*, que hace nidos comunales.

Se describe además una serpiente del Cerro Duida (*Thamnodynastes duida*, n. sp.), basándose en un ejemplar obtenido por la Expedición del American Museum al Duida en 1929. Esta se parece más a *T. chimanta*, geográficamente distante (a unos 400 km al noreste de Duida), que a su vecino más cercano del Cerro Yaví (250 km al norte). El espécimen tipo de *Thamnodynastes duida* tenía en su estómago una lagartija, *Riolama* sp., un género raro de microteíido previamente encontrado en el Cerro Roraima y en el Cerro de la Neblina.

Especies relacionadas a los reptiles del Cerro Yaví se encuentran en las altiplanicies como especies endémicas esparcidas extensamente a distancias de 180–550 km en los grupos de los tepuis orientales, centrales del este y del oeste, y los meridionales. Se están estudiando dos especies estrechamente relacionadas (géneros *Eleutherodactylus* y *Euspondylus*) del Cerro Yutajé, más cercano geográficamente.

El número de especies de anfibios y reptiles endémicas en uno o dos tepuis parecen ser mayor que el número de especies de amplia distribución en las cumbres de los tepuis. Algunos (pero no todos) los anfibios y reptiles de los tepuis, incluyendo los reptiles de la cima del Cerro Yaví, deben ser remanentes de una fauna una vez ampliamente distribuida en Pantepui pero ahora representada

por grupos relacionados de especies distribuidas esparcidamente. Los factores que complican el análisis incluyen (1) colecciones muy incompletas y diversidad limitada de las herpetofaunas tepuianas, (2) diferencias en los tipos de habitat entre tepuis, (3) eventos de extinción, especialmente en los tepuis más pequeños, y (4) diferencias regionales en la fauna original del Pantepui.

INTRODUCTION

The 1995 American Museum–TERRAMAR Expedition established helicopter-supported camps on several Venezuelan table mountains (*tepuis*) in headwater drainages of the Río Manapiare—some 100 km east of the upper Río Orinoco, 5–6° North Latitude. The highest of these was Cerro Yaví, with a summit over 2100 m above sea level, where we collected in late February.

The first expedition to the summit of Cerro Yaví was conducted in early 1947 by the late William H. Phelps, Jr., and his wife Kathleen D. de Phelps, in company with Charles B. Hitchcock of the American Geographical Society. Hitchcock (1947, 1948) published an itinerary and geographical account; Lasser and Maguire (1950) reported on the plants collected, and Phelps (1947) and Mayr and Phelps (1967) summarized the birds. Kathleen D. de Phelps published her account of the Phelps Expedition in 1987 (reprinted 1994), including diary excerpts and other documentary material.

Otto Huber also collected plants on Cerro Yaví (Huber, 1995b: 93) and has remarked on aspects of the summit vegetation and topography (1995a, 1995c). Visits to Cerro Yaví by other parties seem to have been few and brief, perhaps entirely by helicopter. We found no signs of disturbance except for a few stepping stones placed across a boggy area.

We are unaware of any reference to the herpetofauna of Cerro Yaví, except mention of a “small brown lizard” sighted on the summit (Hitchcock, 1947: 547). We here report on a collection of 63 specimens comprising seven species (3 frogs, 3 lizards, 1 snake) from the vicinity of our summit camp, which we occupied during the five-day period February 19–23.

Most extraordinarily, six of the seven species in this dry-season collection appear to

be undescribed. The seventh species, represented by a fragment of lizard tail, may also be nameless, but the only sure thing is that Cerro Yaví did not yield all of its secrets.

ACKNOWLEDGMENTS

The 1995 expedition was made possible by the generosity and commitment of Mr. Robert G. Goelet, former president and Chairman Emeritus of the Board of Trustees of the American Museum of Natural History.

The expedition could not have been successfully concluded or even started without the help and splendid collaboration of many Venezuelan friends and colleagues. No jungle trail is more labyrinthine than those leading through government ministries to the necessary permits and signed agreements in this new age of environmental concern. For critical help in those matters, we warmly thank Dr. Armando Michelangeli Ayala, President of Fundación TERRAMAR, General Francisco Loreto, then President of the Instituto Nacional de Parques (INPARQUES), Dr. José Luis Méndez Arocha, Director General of the Servicio Autónomo para la Protección, Restauración, Fomento y Racional Aprovechamiento de Fauna Silvestre y Acuática del País (PROFAUNA), and Mrs. Kathleen de Phelps, of the Colección Ornitológica Phelps.

The following companions shared our days and nights on Cerro Yaví and were largely responsible for the success of the expedition: George F. Barrowclough and Paul R. Sweet (AMNH Dept. Ornithology), John W. Daly (National Institutes of Health and AMNH Dept. Herpetology), Ricardo Guerrero (Instituto de Zoología Tropical, Univ. Central de Venezuela, and TERRAMAR), Expedition Leader Armando Michelangeli Ayala, Petia Alcócer, Adriana Sánchez H., and Fabián Ar-

mando Michelangeli H. (TERRAMAR). And thanks to Sergio Bermúdez Dugarte (PROFAUNA), who caught one of the few snakes at the Cerro Yaví camp after we left and carried it alive for us until we all assembled at base camp.

We look forward in a future paper to acknowledging other expedition members who contributed specimens and help in camps on other tepuis. But in our memories of every camp, we reserve a special place for our helicopter pilot Ricardo Trevisi and mechanic Juan Vasconcelos, who spent a sweltering month at the lowland base camp in order to give us unparalleled access to some very lonely places.

Dr. Luis Arturo Ayala, of TERRAMAR, importantly facilitated expedition planning by piloting his Piper Seneca in an initial aerial reconnaissance of the northwestern tepuis, in September 1994. We gratefully acknowledge the Venezuelan Air Force (FAV) for subsequent logistical support to and from the Yutajé base camp in early 1995.

We thank Drs. George F. Barrowclough, Darrel R. Frost, Ricardo Guerrero, John D. Lynch, Lily Rodríguez, Jay M. Savage, and Richard G. Zweifel for reading and commenting on sections of the manuscript and other advice, and Harold K. Voris and Alan Resetar, Field Museum of Natural History (FMNH) for lending the type specimen of *Thamnodynastes chimanta*. All drawings are from the pen of Patricia J. Wynne.

DEPOSITION OF SPECIMENS

Contractual agreements with PROFAUNA and INPARQUES provided that one-half of our 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. We thank Francisco J. Bisbal, Director of the EBRG Museum, for facilitating the cataloging process and for help in other ways.

Most specimens were collected by a herpetology team comprised of ourselves and John Daly, but, as was commonplace in the camps of this expedition, obliging colleagues

of every discipline lent a hand. For this reason we have not cited individual collectors in the lists of type specimens. All material is cataloged as having been collected by the 1995 AMNH-TERRAMAR Expedition—an abbreviation for the official name “The Robert G. Goelet American Museum-TERRAMAR Expedition to the Northwestern Tepuis.”

THE NATURAL LANDSCAPE

Cerro Yaví is a sandstone table mountain situated at 5°43'N, 65°54'W,³ in sight of and about 28 km northeast of the landing field at Yutajé (fig. 1). This tepui has a vertical relief of 2.1 km and stands apart from other highlands (fig. 2A), rising abruptly from forested hill country and lowlands at the edge of a savanna (about 200 m elev.) to approximately 2300 m at its highest point. The relatively small summit has been estimated at 14 km² by Mayr and Phelps (1967: 281) and at 5.62 km² by Huber (1995a: 61). The summit tableland is split into a small southern and a larger northern part (fig. 2) by an easterly draining valley that contains the headwater drainage of the Caño Platanal, whose waters eventually reach the Orinoco via the southerly flowing Caño Parucito, Río Manapiare, and Río Ventuari.

The northern summit of Cerro Yaví is itself divided into eastern and western sections by a wide gorge (fig. 3) draining from the north and emptying into the rift between the north and south summits. The Phelps Expedition came up the Caño Platanal valley and ascended the western side of this tributary gorge in late February 1947 and thus attained the western part of the north summit, whereas all our work, nearly a half century later, was confined to the eastern side. The eastern half of the north summit affords better helicopter landing and better water, there being a small lake (fig. 4) that was visible to the Phelps party but unreachable from their vantage on

³ Coordinates were determined by two hand-held Global Positioning System (GPS) satellite receivers at the small summit lake, site of the 1995 Expedition camp. More precise readings were not recorded inasmuch as accuracy of GPS devices may currently vary by as much as 100 m.



Fig. 1. Cerro Yaví on horizon, looking north-east from 180 m elevation at Yutajé airstrip, 5°37'N, 66°07'W (September 16, 1994).

the other side of the gorge (Hitchcock, 1947: 547):

The only water available had to be dipped from a tiny pool (57° F.) in the dry bed of a brook. Remarkably, a small pond not accessible because of an intervening valley and cliffs was being maintained on the east side of the northern summit area.

The eastern part of the north summit is an irregular floor of sandstone bearing mounds of huge, irregularly broken and eroded sandstone blocks (fig. 5). Below 1500 m elevation, along the bed of the Caño Platanal, the Phelps expedition found intrusive igneous rocks—diorite and granite, succeeded mainly by sandstones above (Hitchcock, 1947: 561–562):

At 4840 feet [1475 m] the stream profile flattens out and the granite is succeeded by great angular blocks of interbedded conglomerate and sandstone cut by narrow quartz veins . . . [From this contact] to the summit only sandstones and interbedded conglomerates were observed, and conglomerates were rare above 6000 feet [1800 m]. The sandstone ranges in texture from fine to coarse-grained, is pinkish to gray in color, and is locally highly silicified, breaking with difficulty. Cross-bedding is characteristic. Small current ripples were observed in only a few places . . . The interbedded conglomerates were locally found to lense out rapidly horizontally. The coarser material ranges from cobbles eight inches in diameter in the lowest horizons to small, rounded, and subangular material. The material is generally pinkish to gray quartzite; well-rounded quartz pebbles are common in some horizons.

The sandstones of the summit area of Yaví, the cliff-forming beds, are gently inclined to the south [and] are strongly jointed. . . . As a result of weathering and erosion along these joint systems, the summit area is cut by numerous deep crevasses and valleys, including the large valley trending east-west that carries the headwaters of the Caño Platanal. The total thick-

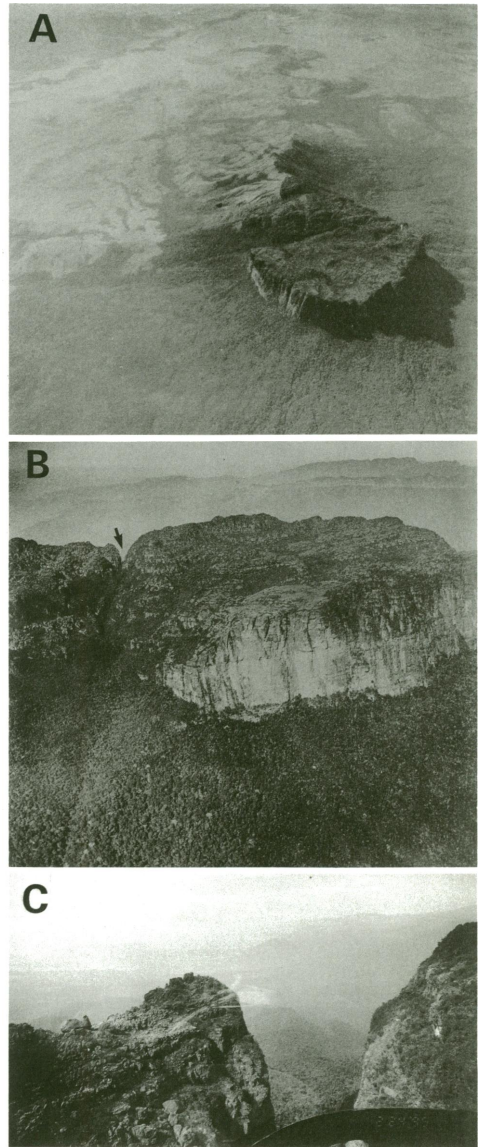


Fig. 2. A, B. Two early aerial views of Cerro Yaví (from Hitchcock, 1947: figs. 6, 26): A. Showing summit "cut by large valley at head of Caño Platanal. South from 5°34'N, 65°59'W [from] 20,000 feet. North and west slopes heavily wooded; grasslands rising on eastern and southern ridges from savanna lowland." B. Northern summit, showing partial separation (arrow) from southern summit on left. Looking westward, with eastern cliffs of Cerro Yutajé in middle distance. C. View from helicopter passing through gap (arrow in B) separating north and south summits, February 24, 1995.



Fig. 3. Views from vicinity of AMNH-TERRAMAR camp on eastern sector of the north summit of Cerro Yavi (February 23, 1995). **Upper.** Looking across gorge to the western sector, which was explored by the 1947 Phelps Expedition. The jagged western rim can also be seen in figure 2B. **Lower.** Looking across lower end of gorge as it drops into headwater valley of Cãno Platanal. Southern end of western sector in middle distance on right; south summit in far distance, across Cãno Platanal.



Fig. 4. Meadow habitats on eastern sector of north summit of Cerro Yaví, about 2150 m above sea level. **Upper.** Lake on deep boggy meadow near AMNH-TERRAMAR camp (February 18, 1995). **Lower.** A better drained meadow near eastern escarpment (February 22, 1995).

ness of sandstone above the granite is about 2750 feet [838 m].

We found only the gray to pink sandstone in the narrow elevational range worked on the eastern part of the north summit of Yaví (although presumably Hitchcock's conglomerate stratum of quartzite cobbles was

seen below 1700 m on adjacent Cerro Yutajé). Narrow crevasses were common on a few parts of the summit and were deep enough to require considerable caution in getting about.

Small meadows (figs. 4, 5), presumably occupying basins of various depth in the sand-



Fig. 5. Other summit habitats near camp at 2150 m elevation. **Upper.** Meadow backed by rocky terrain and one of the characteristic hills of sandstone blocks that dot the summit (February 23, 1995). **Lower.** A rocky flat, edged by a scrub of brush and low trees (February 22, 1995). The open rocky area was the site of several communal nests of *Euspondylus goeleti* (see fig. 16). *Phenacosaurus bellipeniculus* and one *Eleutherodactylus yaviensis* were found in the adjacent scrub.

stone, must be boggy most of the year, since the soil was still wet well into the dry season (February). These meadows support several kinds of low sedges (Lasser and Maguire, 1950:76–77; Huber, 1995c: 153) and have a ground-level covering of sphagnum and lichens overall, with scattered clumps of club moss. The meadows also have a sparse scattering of melastomes, a low, yellow-flowered composite, and what we take to be *Pleurostima celiae* (Velloziaceae),⁴ which grows also on rock substrates as mentioned by Huber (1995c: 153).

Huber (loc. cit.), incidentally, wrote that “There are no high-tepui meadows” on Cerro Yaví, in apparent contradiction to his fitting statement elsewhere (1995a: 43) that the summit of Yaví “presents a very broken, rocky terrain covered by open scrub and tepui meadows.” Huber (1995c: 153) perhaps left out a qualifier and may have intended to say that there are no *broad-leaved* or *Kunhardtia* (Rapateaceae) meadows, since he was making the interesting point that the “small summit plateau of Cerro Yaví is very peculiar” in lacking species of Rapateaceae. Owing to the gramineous morphology, the Cerro Yaví meadows fit Huber’s (1995c: 139) definition of “gramineous meadows or grasslands (*herbazales gramíneos*), dominated by grasses and/or sedges.”

One particularly wet meadow on Cerro Yaví is an exceptionally deep bog that holds the small lake (fig. 4) seen from afar by the Phelps party. We used this pristine lake only for drawing buckets of water, at one end where some earlier visitor had laid a few flat rocks for access. Because of the thick vegetation mat, one can walk on the bog nearly to water’s edge, but a 1½ m walking staff could be thrust down through the mat without striking bottom, which does not fit with a statement (Ber-

ry et al., 1995: 180) that Cerro Yaví is a dry tepui “with little or no peat formation” on its summit. Cores for radiocarbon measurements and palynological study could be usefully made at this site.

The boggy meadows are broken by sandstone flats and ledges and small hills of jumbled blocks—this terrain forming the habitat of a small terrestrial snake (*Thamnodynastes*) and its lizard prey (*Euspondylus* and ?*Arthrosaura*). Fringing these rocky places is a scrub of brush and low trees of several families, including Clusiaceae (*Clusia* spp.) and Melastomataceae. An arboreal lizard (*Phenacosaurus*) inhabits the patches of scrub but was more common in the ecotone between an open rocky area and the mossy forest below.

The only real forest readily accessible from our camp grows near the head and along the sides of the gorge that divides the east and west sides of the north summit. It is a dense, mossy, upper montane evergreen forest of precarious footing, with trees growing densely among great blocks of sandstone and tending to form a second floor of humus atop elevated, intertwined roots. Huber (1995c: 125) identified the dominant forest trees on the summit of Cerro Yaví as *Schefflera hitchcockii* (Araliaceae), *Clusia* (Clusiaceae), *Ilex retusa* (Aquifoliaceae), *Ternstroemia* (Theaceae), *Cyrilla racemiflora* (Cyrillaceae), and *Weinmannia* (Cunoniaceae). There were some small seepage areas on the steep slopes but no stream beds. This forest was the principal habitat of three species of *Eleutherodactylus*, which comprised the entire frog fauna of our dry-season sample.

SPECIES ACCOUNTS

FROGS

FAMILY LEPTODACTYLIDAE

As indicated above, frogs are represented in our collections solely by three species of forest-dwelling *Eleutherodactylus* (fig. 6). All three seem to be undescribed, although we cannot yet point to their closest relatives. On the basis of external characteristics, two of the species named herein (*cantitans* and *yaviensis*) belong to the large South American

⁴ Based on color plate 57 in Steyermark et al. (1995), although we do not recall seeing it in bloom during our stay. According to Berry et al. (1995: 180), *Pleurostima celiae* has a remarkable distribution, being known only from Cerro Yaví and from Serra Tepequém in northern Brazil. Both mountains are remnants of the Roraima Formation, but seem to share little else in common. The outlying, highly eroded Tepequém is little more than the stub of a tepui.

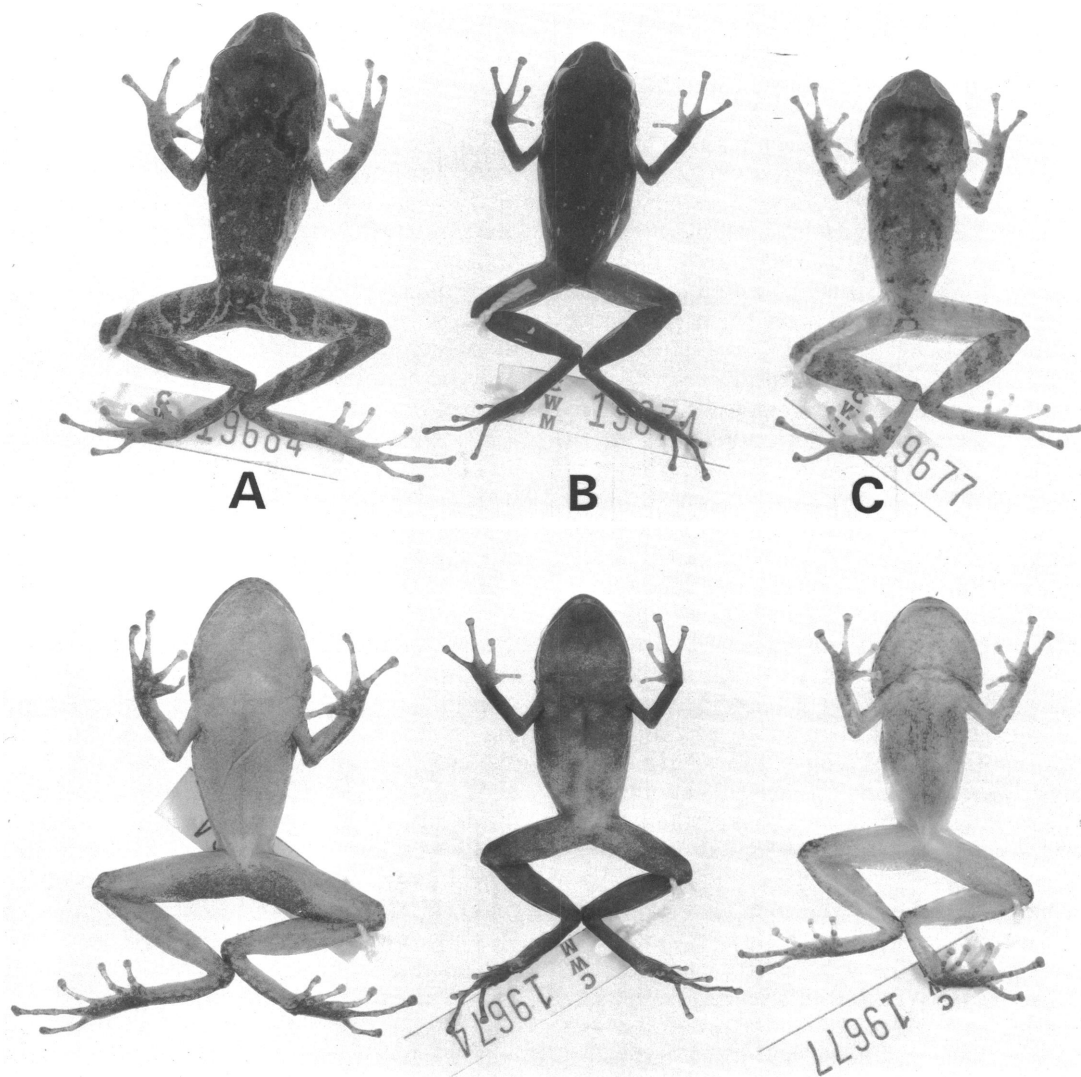


Fig. 6. Holotypes of three sympatric *Eleutherodactylus* spp. from Cerro Yaví. A. *E. cantitans* ♂, 35 mm SVL. B. *E. pruinatus* ♀, 27 mm SVL. C. *E. yaviensis* ♀, 29 mm SVL.

unistrigatus group sensu Lynch (1976, 1994), which approaches 200 species. The shared characters include areolate (coarsely granular) ventral skin, first finger shorter than second, and fifth toe much longer than third (tip of toe V reaching distal subarticular tubercle of IV, tip of III only reaching penultimate subarticular tubercle of IV; figs. 8, 14). We compare these two species as best we can with other *unistrigatus*-group species, especially

those known from Venezuela and eastern Colombia.

The third species named from Cerro Yaví, *Eleutherodactylus pruinatus*, is particularly enigmatic and we do not assign it to a species group. It shares with the other two species a short first finger and areolate ventral skin and would be placed in the *unistrigatus* group according to Lynch's early (1976) definition. But it disagrees with a recently discovered

toe-length character (Lynch, 1994) that appears useful in separating the *fitzingeri*, *conspicillatus*, and *unistrigatus* groups—the last group being characterized by an unusually long fifth toe (see above).

Eleutherodactylus pruinatus has a much shorter fifth toe (tip of toe V reaching midway between penultimate and ultimate subarticular tubercles on IV and being little longer than III, the tip of which extends slightly distad from the penultimate tubercle; fig. 10). These relative lengths of appressed toes III–V are more suggestive of the *conspicillatus* group than of the *unistrigatus* group (see Lynch, 1994: 187–188, 193), but members of the *conspicillatus* group have smooth or weakly granular ventral skin and the first finger is longer than the second (Lynch, 1976).

Eleutherodactylus pruinatus further differs from the two sympatric members of the *unistrigatus* group in having a relatively narrower head (fig. 6). According to Lynch (personal commun.), the chunky head shape of *E. cantitans* and *E. yaviensis*, as seen in figure 6, is characteristic of the *unistrigatus* group and probably plesiomorphic for South American *Eleutherodactylus*. The coloration of *E. pruinatus* also is unusual among South American *Eleutherodactylus*.

Dissections of one or two specimens each of *E. cantitans*, *E. pruinatus*, and *E. yaviensis* showed the mandibular ramus of the trigeminal nerve passing lateral to the *m. adductor mandibulae*, as is characteristic of most South American *Eleutherodactylus* (Lynch, 1986).

For measurements and diagnoses of *Eleutherodactylus*, we follow Lynch's methods and format (most completely described in Lynch and Duellman, 1980); we follow Lynch and Myers (1983: 489n) and Lynch's recent papers for definitions of the digital disc and its subdigital pad. Webbing formulae follow the Savage and Heyer (1967) notational device as modified by Myers and Duellman (1982: 6).

***Eleutherodactylus cantitans*, new species**

Figures 6A, 7, 8

HOLOTYPE: EBRG 3005 (field no. CWM 19684), an adult male from the summit of Cerro Yaví, 2150 m, Amazonas, Venezuela;

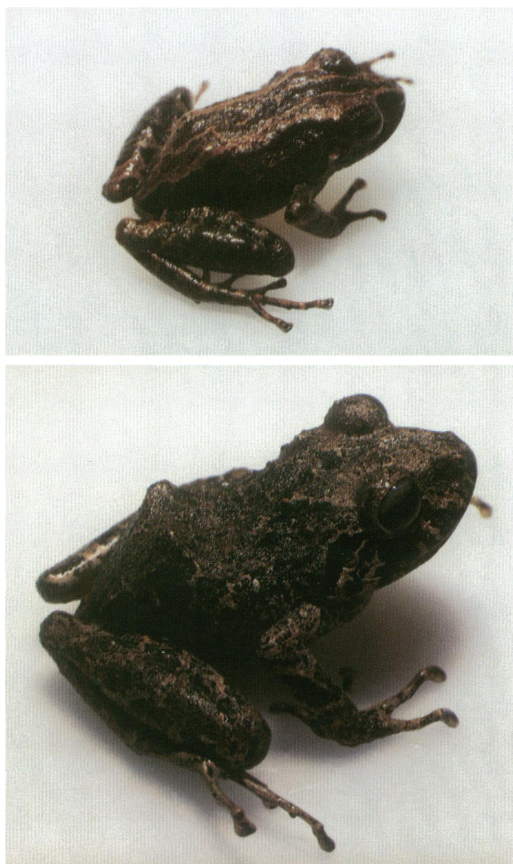


Fig. 7. *Eleutherodactylus cantitans*, new species, paratopotypes in life. Upper. AMNH 143360 ♂, 24 mm SVL. Lower. AMNH 143359 ♀, 44 mm SVL.

obtained on February 23, 1995 by the AMNH–TERRAMAR Expedition.

PARATOPOTYPES: Five specimens (2♂, 2♀, 1 juv.), AMNH 143359–143361, EBRG 3003–3004, collected February 20–22; other data same as holotype.

ETYMOLOGY: The species name is the present participle of the Latin *cantito* (to sing often), in allusion to the day-and-night calling behavior.

DEFINITION AND DIAGNOSIS: (1) Dorsal skin weakly granular and rugose, nearly smooth, ventral skin areolate; dorsolateral folds weakly developed or absent; (2) tympanum present, distinct anteriorly and ventrally; (3) snout rounded in dorsal and lateral view; canthus

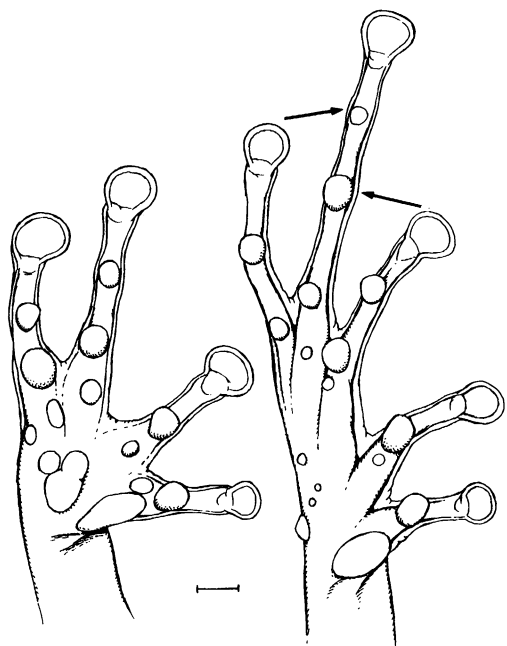


Fig. 8. *Eleutherodactylus cantitans*, new species. Right hand and right foot of holotype (EBRG 3005♂). Arrows indicate position of tips of third and fifth toes when these digits are straightened and appressed against the fourth toe. Scale = 1 mm.

rostralis concave, rounded; (4) upper eyelid with small warts; (5) vomerine odontophores triangular, obtuse, behind and between oval choanae; (6) males with vocal slits and weak nuptial pads; (7) finger I shorter than II, broad discs on fingers II–IV; (8) weak lateral keel on fingers; (9) ulnar tubercles absent; (10) small, low nonconical calcar tubercles; (11) two metatarsal tubercles, inner elongate, four times size of round outer; (12) toes with weak lateral fringes and basal webbing; toes with broad discs, as broad as or smaller than those on fingers; (13) gray (brown in life) with variable dorsal markings and with indication of pale (yellowish) diagonal markings; rear thigh dark with pale (yellowish) flecking; with banded limbs, lip bars, and rose wash ventrally and in groin and concealed part of shank; (14) males about 25–35 mm, females about 32–45 mm SVL.

Eleutherodactylus cantitans is unique among *Eleutherodactylus* species known from Venezuela and eastern Colombia in having

the posterior thigh surface blackish with yellow flecking, and with a rose wash in the groin, anterior thigh, and concealed portion of the shank.

MEASUREMENTS OF HOLOTYPE (in mm): The undissected holotype is an adult male as revealed by presence of large vocal slits. SVL 33, tibia length 17.8, foot length from proximal edge inner metatarsal tubercle to tip of toe IV 16.4, head width 13.3, head length on the diagonal from angle of jaw to tip of snout 11.5, upper eyelid width 3.5, interorbital distance also 3.5, eye to posterior edge of nostril distance 3.8, eye length 4.8, tympanum length estimated 1.9.

DESCRIPTION

Females larger than males (\bar{x} female SVL/ \bar{x} male SVL = 1.24). Three males 24.9–34.5 mm SVL (\bar{x} = 30.80 mm), two females 31.9, 44.7 mm SVL (\bar{x} = 38.30 mm). Head wider than body, wider than long; head width 38.0–42.2 percent of SVL in males, 40.9–42.3 of SVL in females. Snout rounded in dorsal and lateral view; eye-nostril distance 76.5–90.6 percent of eye length in males, 83.3–106.5 percent in females; nostrils protuberant, directed dorsolaterally; canthus rostralis slightly concave, edge rounded but distinct; loreal region concave. Upper eyelid with low tubercles; upper eyelid narrower than or equal to interorbital distance. Tympanum present, somewhat obscured posterodorsally but distinct anteriorly and ventrally; supratympanic fold weakly developed or absent. Postriatal tubercles 1–3. Choanae small, oval to round, not concealed by palatal shelf of maxillary arch; vomerine odontophores large; posterior and median to choanae; odontophores as wide or wider than choanae; triangular in outline, only faintly indicated in the juvenile paratype (EBRG 3004). Tongue longer than wide, posterior two-thirds free. Large vocal slits present in males, ventral to posterior edge of tongue.

Dorsal skin indistinctly granular and rugose, nearly smooth in preservative; mid-dorsal raphe present. Dorsolateral folds feebly developed or absent; throat smooth; venter areolate; triangular patch of glandular skin on posteroventral thigh surface distinct; discoidal fold anterior to groin; ulnar tubercles absent.

Relative length of appressed fingers III > IV > II > I; first finger reaching subdigital pad of second; weak lateral keels on fingers and weakly developed nuptial pad along posteroventral side of thumb in males. Finger discs broader than long, rounded apically, with subdigital pads wider than long; disc on thumb slightly expanded. Palmar tubercle large and cordiform or divided, when divided inner portion larger than outer portion; the nalar tubercle ovoid; supernumerary palmar tubercles distinct, round, protuberant, smaller than round subarticular tubercles.

Hind limbs relatively long; heels overlap when held at right angles to the sagittal plane; tibia 53–58 percent of SVL in males, 56–58 percent in females. Relative lengths of appressed toes IV > V > III > II > I; tip of toe V extends to base or distal edge of distal subarticular tubercle of IV, tip of III to the middle or distal edge of the penultimate subarticular tubercle of IV. Toe discs as wide as or slightly narrower than those on fingers, with wide subdigital pads. Toes with weak lateral fringes and basal webbing; webbing formula I 3–3 II 2–3½ III 3–4¼ IV 4½–3½ V. Inner metatarsal tubercle elongate, oval, about 4 times as long as round outer metatarsal tubercle; supernumerary plantar tubercles low and round; subarticular tubercles round or oval.

COLOR PATTERN: In life, the dorsal ground color of *E. cantitans* was brown (gray in preservative), usually with vague black markings that became somewhat better defined in preservative (compare fig. 6A with fig. 7, lower); the dark markings include an interorbital bar and a large X-shaped mark on the back. The holotype additionally had small yellow dots scattered over the dorsum. One specimen (fig. 7) had a light brown dorsum with well-defined, wavy longitudinal blackish brown markings, which formed three stripes between the eyes. This species seems to be characterized in life by indications of one or two pale yellow or greenish yellow diagonal lines on the flanks (not visible in fig. 7); the yellow fades in preservative and the lines are sometimes interconnected with other pale areas and are therefore less evident. Lips brown with darker bars, these markings poorly defined in the holotype.

The dark-banded thighs had pale yellow, greenish yellow, or light brown dorsal inter-

spaces; shank weakly barred. The posterior thigh surface was black with yellow flecking. Overall, the ventral surfaces were gray in life except in the juvenile (EBRG 3004), in which they were black with pale flecking; in preservative, the ventral surfaces of the two females are a much paler gray than in the juvenile and three males, which have a very faint median pale line on the throat that is not indicated in the females.

The groin, anterior thigh surface, and concealed part of the shank had a faint to a very prominent rose wash. The rose coloration persists in adults following fixation and preservation, being especially prominent and extensive in the holotype, which even shows a rose suffusion on the rear of the thighs. The iris was silvery gray (pale greenish bronze in a juvenile), with black venation and a reddish brown horizontal stripe.

NATURAL HISTORY

All specimens were collected at night on vegetation in the forest below camp except that the holotype was found calling from underneath a moss mat on sandstone. We first noticed *E. cantitans* because males called both during the day and night. They called from concealed sites in caves and from beneath thick moss mats growing over the sandstone (see under *Eleutherodactylus* Vocalizations).

REMARKS

During formalin fixation, all specimens of *E. cantitans* developed a temporary metallic sheen of blue-green over the hind limbs and on parts of the body. This transient coloration was useful as a sort of "field mark" in camp, when first sorting out the sympatric species of *Eleutherodactylus*.

Eleutherodactylus cantitans is a moderate-sized member of the *unistrigatus* species group that overlaps in SVL with nine other species from Venezuela (*briceni*, *colostictos*, *lancinii*, *mondolfi*, *paramerus*, *pulvinatus*, *reticulatus*, *tubernasus*, and *turumiquirensis*). Of these, only *E. mondolfi* has basal toe webbing (Rivero "1982" [1984]). The new species (first value in parentheses) differs from the Andean *E. mondolfi* in flank tubercles (absent vs. present), posterior thigh coloration (yellow flecking vs. light spots), groin coloration (di-



Fig. 9. *Eleutherodactylus pruinatus*, new species, the holotype in life (EBRG 3006♀, 27 mm SVL).

agonal yellowish markings vs. cream spots), and ventral coloration (gray vs. brown).

***Eleutherodactylus pruinatus*, new species**

Figures 6B, 9, 10

HOLOTYPE: EBRG 3006 (field no. CWM 19674), an adult female from the summit of Cerro Yaví, 2150 m, Amazonas, Venezuela; obtained on February 22, 1995, by the AMNH-TERRAMAR Expedition.

PARATOPOTYPES: AMNH 143362♂, 143363♀, collected February 20–23; other data same as holotype.

ETYMOLOGY: From the Latin *pruina* (frost) + *-atus* (pertaining to), in reference to the frosted appearance of the living frog.

DEFINITION AND DIAGNOSIS: (1) Skin of dorsum granular, ventral skin coarsely areolate; (2) tympanum small, ventral two-thirds visible; (3) snout rounded in dorsal and lateral view; canthus rostralis rounded; (4) small flat warts on upper eyelid; (5) vomerine odontophores triangular, obtuse, behind and between choanae; (6) males with vocal slits, lacking nuptial pads; (7) finger I shorter than finger II; broad discs on fingers II–IV; (8) no fringes or keels on fingers; (9) ulnar tubercles absent; (10) small, low nonconical calcar tubercles; (11) two metatarsal tubercles, inner oval, two times size of round outer; (12) toes lack lateral fringes, no toe webbing; toe discs as large or larger than finger discs; (13) body

uniformly blackish with a fine frosting of silver, which is lost in preservative; (14) one male 22 mm, two females about 27 mm SVL.

Eleutherodactylus pruinatus is unique among known species of *Eleutherodactylus* from Venezuela and eastern Colombia in having a frosted appearance in life, and it is further set apart by characteristics of head width and relative toe length (see prior discussion under Family Leptodactylidae).

MEASUREMENTS OF HOLOTYPE(in mm): An adult female as revealed by lateral incision high on the right side, showing a large oviduct and a small number of tightly packed, large ova about 2 mm in diameter. SVL 26.8, tibia length 12.9, foot length from proximal edge inner metatarsal tubercle to tip of toe IV 11.1, head width 10.3, head length on the diagonal from angle of jaw to tip of snout 11.1, upper eyelid width 2.2, interorbital distance 2.9, eye-nostril distance 2.7, eye length 3.1, tympanum length 1.1.

DESCRIPTION

Females larger than the one male (\bar{x} female SVL/male SVL = 1.21). One male 22.1 mm SVL, two females 26.6, 26.8 mm SVL (\bar{x} = 26.7 mm). Head slightly wider than body in a male and female, slightly narrower than body in female holotype (fig. 6B), longer than wide; head width 39 percent of SVL in the male, 40 percent of SVL in females. Snout rounded in dorsal and lateral view; eye-nostril distance 70 percent of eye length in the male, 87–91 percent in females; nostrils protuberant, directed dorsolaterally; canthus rostralis concave, edge rounded but distinct; loreal region concave, lips not flared. Upper eyelid with flat scattered tubercles; upper eyelid width 87 percent of interorbital distance in males, 67–76 percent in females. Tympanum present, distinct anteriorly and ventrally, its length 33 percent of eye length in the male, 33–35 percent in females. Postriatal tubercles 2–3. Choanae small, ovoid, not concealed by palatal shelf of maxillary arch; vomerine odontophores large, triangular in outline, median and posterior to choanae, odontophore width 1.3 times choanae width in the male, 2.0–2.5 times choanae width in females. Tongue longer than wide, emarginate, posterior two-thirds free. Small vocal slits

present in male, lateral to free end of tongue, somewhat closer to angle of jaws than to tongue.

Dorsal skin granular; middorsal raphe present; scattered low warts on flanks; throat smooth, venter areolate; triangular patch of glandular skin on posteroventral thighs distinct; discoidal fold anterior to groin. Ulnar tubercles absent.

Relative length of appressed fingers III > IV > II > I; first finger reaching between ultimate subarticular tubercle and subdigital pad of finger II; lacking lateral fringes. Finger discs broader than long, rounded apically, with subdigital pads wider than long; disc on thumb slightly expanded. Palmar tubercle large and cordiform or divided, when divided inner portion larger than outer portion; the nar tubercle large and elliptical; supernumerary palmar tubercles low and rounded, smaller than rounded subarticular tubercles.

Hind limbs relatively long; heels overlapping when held at right angles to sagittal plane; shank 50 percent of SVL in the male, 47–48 percent of SVL in females. Relative length of appressed toes IV > V > III > II > I; tip of toe V extends midway to proximal edge of ultimate subarticular tubercle on toe IV, tip of toe III slightly past penultimate subarticular tubercle of IV. Toe discs as wide as or wider than those on fingers, with wide subdigital pads. Toes lacking lateral fringes and webbing. Inner metatarsal tubercle oval, longer than wide, 2.0 times longer than rounded, protuberant, outer metatarsal tubercle; supernumerary plantar tubercles near toe IV larger than those on rest of sole; subarticular tubercles round.

COLOR PATTERN: In life, the body was uniformly blackish overall with dorsal surfaces finely speckled or frosted with whitish or silvery gray. Color transparencies of the holotype show that the elbows and heels were lighter (orange-brown) than the rest of the body. All ventral surfaces and anterior and posterior thigh surfaces were dark orange brown with only a sparse pale (gray) speckling on venter. Iris silvery gray with reddish brown horizontal stripe, one specimen with a black mark below pupil.

In preservative, the dorsal surfaces have become virtually uniform blackish gray, with the inguinal region and anterior and posterior

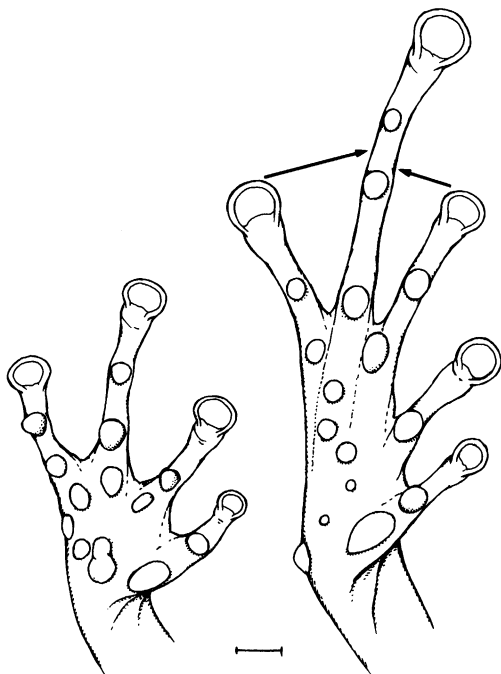


Fig. 10. *Eleutherodactylus pruinatus*, new species. Right hand and right foot of a paratotype (AMNH 143362♂). Arrows indicate position of tips of third and fifth toes when these digits are straightened and appressed against the fourth toe. Scale = 1 mm.

thigh surfaces faded to a lighter orangish brown than in life; ventral surfaces faded to a lighter brown, with indefinite yellowish white areas where pigment is thin on belly and under thighs.

NATURAL HISTORY

The female holotype and male paratype of *E. pruinatus* were collected at night on low vegetation in the forest below camp. The female paratype was collected at night from the inside wall of a small cave. Although we did not see a male calling, we suspect that one recorded call may belong to this species (see *Eleutherodactylus* Vocalizations).

REMARKS

Eleutherodactylus pruinatus is not assigned to a species group. It differs from sympatric congeners of the *unistrigatus* group in the narrower head and in relative toe length (see

TABLE 1
Analysis of *Eleutherodactylus* Vocalizations from Cerro Yaví^a

Date	Call type	Record- ing time (sec)	No. notes	Spectro- gram example	Ambi- ent temp, °C	Notes per sec ^b	Internote interval ^c	Note length ^c	Fundamental frequency (Hz) ^c
21 Feb.	I	21.8	8	Fig. 11A	17.8	0.32	3.13 ± 1.15 (2.3–4.9)	0.054 ± 0.007 (0.47–0.066)	1600 ± 43.82 (1520–1640)
21 Feb.	I	36.2	11	Fig. 11B	17.8	0.28	3.63 ± 0.83 (2.4–5.4)	0.053 ± 0.004 (0.050–0.063)	1630 ± 24.86 (1600–1680)
22 Feb.	I	23.4	5	Fig. 11C	15.2	0.17	5.88 ± 1.64 (3.8–7.8)	0.063 ± 0.011 (0.050–0.075)	1690 ± 20.00 (1680–1720)
21 Feb.	II	15.6	8	Fig. 12	13.6	0.45	2.23 ± 0.48 (1.5–2.9)	0.043 ± 0.010 (0.028–0.056)	2516 ± 47.89 (2440–2660)

^a Note length and frequency were measured using a Kay 5500 DSP Sona-Graph, which was used for production of sound spectrographs and waveforms. Note repetition rate and internote interval were measured after playing field recordings through a real-time Kay 7851 spectrograph and printing spectrograms/waveforms on continuous paper from a Honeywell LS-8 Linescan Recorder run at 10 mm/sec.
^b N-1 notes divided by recording time.
^c Mean ± 1 SD (range in parentheses).

prior discussion under Family Leptodactylidae). The frosted black body of living *E. pruinatus* seems to be unique. The dark, patternless body of preserved specimens also is unusual. Lynch (1992a) recently described *E. cacao* (*unistrigatus* group), a patternless brown species with rows of white flecks along edges of forearm, tarsus, canthus, supratympanic fold, and along edges of discs and digits. But *E. pruinatus* differs greatly from *E. cacao* in lacking cranial crests and toe fringes, in possessing a tympanum and vocal slits, and in smaller size (< 30 mm SVL in *pruinatus*, > 40 mm in *cacao*).

ELEUTHERODACTYLUS
VOCALIZATIONS

A soft, well-spaced, single-note call was heard day and night in the steep forest near camp, but the frogs called from concealed positions in shallow caves and under moss and were exceedingly difficult to locate. Unvouchered calls of different individuals were recorded on four occasions over a temperature range of 13.6–17.8°C. However, the holotype of *Eleutherodactylus cantitans* was observed calling from beneath a moss mat and, in the field, we were satisfied as to the identity of the usually unseen callers.

But in analyzing the calls spectrographi-

cally, we discovered two types of vocalizations (I and II) that sound similar to our ears but differ in frequency, note length, and internote interval (table 1). Both types of calls are weakly pulsatile, as shown by the waveforms (figs. 11, 12).
The type I call (fig. 11) is a single note given 2.3–7.8 sec apart, averaging 0.05–0.06 sec duration, with slight frequency modulation and with poor to good harmonic separation. The fundamental frequency averages 1640 Hz (1520–1720 Hz), with a harmonic segment at a frequency twice that of the fundamental. Either the fundamental or the first harmonic may be most emphasized or they may be essentially codominant, as shown in figure 11.
The type II call (fig. 12) is given 1.5–2.9 sec apart, the single note being of 0.03–0.06 sec duration, without frequency modulation and without clearcut harmonic separation. The fundamental or emphasized frequency is at about 2500 Hz (2440–2660 Hz); it is not certain whether the weak suggestion of an overtone (harmonic) in figure 12 indicates real harmonic structure or machine overloading. After comparing note repetition rates and internote intervals, and considering that the type II recording was made at the lowest temperature (table 1), it is probably safe to conclude that, at equivalent temperature, type

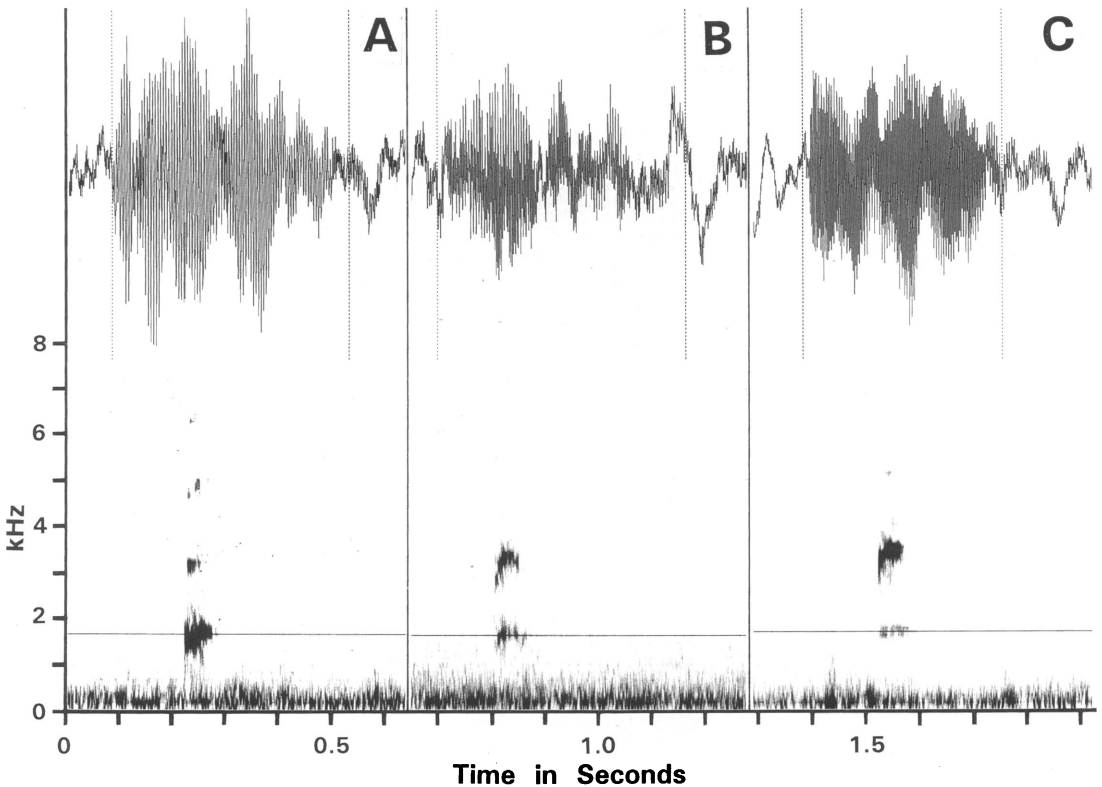


Fig. 11. *Eleutherodactylus* call-type I. Sound spectrograms of notes from three frogs, graphed with wide-band 300 Hz filter, with expanded waveforms of same notes above. Cursors through fundamental frequencies are set at 1640 Hz (A), 1600 Hz (B), and 1680 Hz (C); time between waveform cursors = 563 msec (A), 590 msec (B), and 469 msec (C). Recorded February 21–22, 1995, at air temperatures of 15.2–17.8°C (AMNH herpetology reel 265: segment 7 [2♂, A and B] at 17.8°C; segment 9 [C] at 15.2°C).

II calls are given at a faster rate than type I calls.

We think that these vocalizations are too different to have been produced by members of a single species in a small geographic area. Of the three sympatric species (assuming we caught them all), *E. yaviensis* lacks male vocal slits and both sexes lack ears, so *yaviensis* presumably does not call, leaving *E. cantitans* and *E. pruinatus* to consider. Both of these have visible tympana and vocal slits in males. Presence of male vocal slits and therefore a vocal sac (obvious or not) is good indication that there is a correlated vocalization, but lack of these structures, incidentally, does not necessarily preclude male vocalization (e.g., Myers, 1982: fig. 2)—lack of tympana (as determined by dissection) is a better indication of that.

If we had to guess, we would suggest associating the “common” type I call (3 of 4 recordings) with *E. cantitans* and the type II call with the arguably less common *E. pruinatus* (3 specimens vs. 6 of *cantitans*). The higher fundamental in the type II call might correlate with the smaller size of *E. pruinatus*. In any case, *E. cantitans* was witnessed giving a single-note call and it and a sympatric congener (presumably *E. pruinatus*) may well be tuned to frequency differences not detected by our ears.

Eleutherodactylus yaviensis, new species
Figures 6C, 13, 14

HOLOTYPE: EBRG 3017 (field no. CWM 19677), an adult female from the summit of Cerro Yavi, 2150 m, Amazonas, Venezuela;

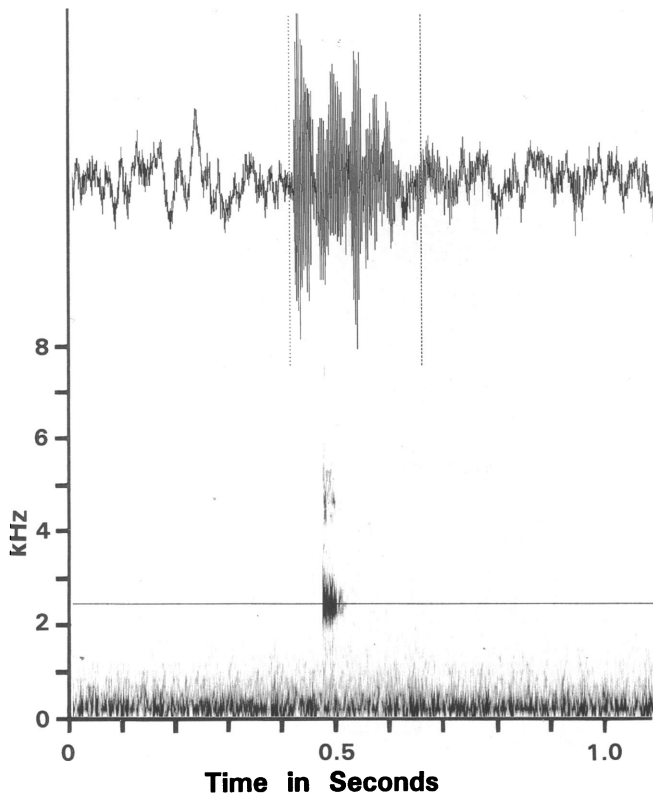


Fig. 12. *Eleutherodactylus* call-type II. Sound spectrogram of a single note graphed with wide-band, 300 Hz filter, with expanded waveform of same note above. Cursor through emphasized frequency is set at 2440 Hz (compare fig. 11); time between waveform cursors = 313 msec. Recorded February 21, 1995, at air temperature of 13.6°C (AMNH herpetology reel 265: segment 8).

obtained on February 22, 1995, by the AMNH-TERRAMAR Expedition.

PARATOPOTYPES: Total of 26 specimens (12♀, 9♂, 5 juv.), AMNH 143364–143376, EBRG 3007–3016, 3018–3020, collected February 20–23; other data same as holotype.

ETYMOLOGY: Yaví, with the last letter retained for euphony, + *-ensis* (belonging to).

DEFINITION AND DIAGNOSIS: (1) Dorsal skin finely granular to nearly smooth with scattered warts; ventral skin areolate; (2) tympanum absent; (3) snout rounded in dorsal view, rounded to truncate in profile; canthus rostralis concave, edge rounded; (4) small flat tubercles on upper eyelid; (5) vomerine odontophores triangular, round, elongate, or absent, between and behind choanae; (6) males with nuptial pads, vocal slits absent; (7) finger I shorter than finger II, broad discs on fingers

II–IV; (8) fingers lacking keels or fringes; (9) ulnar tubercles absent; (10) small, low non-conical calcar tubercles; (11) two metatarsal tubercles, inner one oval to elongate, two to three times size of round outer; (12) toes lacking lateral fringes or keels; basal webbing present; toes with broad discs, wider than those on fingers; (13) body color exceedingly variable, adults with orange on groin, anterior and posterior thigh, and concealed portion of shank in life; (14) males about 18–21 mm, females about 24–30 mm SVL.

Eleutherodactylus yaviensis is unique in the combination of earlessness, red flash marks, expanded digital discs, and absence of keels or fringes on fingers and toes.

MEASUREMENTS OF HOLOTYPE(in mm): Adult female as revealed through lateral incision high on right side, showing an enlarged

oviduct and tightly packed large ova about 2–2.5 mm in diameter. SVL 28.1, tibia length 14.4, foot length from proximal edge inner metatarsal tubercle to tip of toe IV 12.7, head width 12.0, head length on the diagonal from angle of jaw to tip of snout 12.1, upper eyelid width 2.8, interorbital distance 3.2, eye-nostril distance 3.2, eye length 3.2.

DESCRIPTION

Females larger than males (\bar{x} female SVL/ \bar{x} male SVL = 1.37). Males 17.9–21.4 mm SVL (\bar{x} = 20.00 mm, N = 9), females 24.1–29.7 mm SVL (\bar{x} = 27.48 mm, N = 12). Head wider than body, longer than wide; head width 37.3–40.0 percent of SVL in males, 38.2–43.0 percent of SVL in females. Snout rounded in dorsal view, truncate to round in profile; eye-to-nostril distance 70.0–90.5 percent of eye length in males, 81.5–111.1 percent in females; nostrils protuberant, directed dorso-laterally; canthus rostralis slightly concave, edge rounded but distinct; loreal region slightly concave. Upper eyelid with low tubercles; upper eyelid width 71.9–92.0 percent of interorbital distance in males, 71.1–87.5 percent in females. Tympanum absent (determined by dissection); glandular ridge extends from behind eye to axilla. Postriatal tubercles 1–3. Choanae small, oval to round, not concealed by palatal shelf of maxillary arch; vomerine odontophores large, triangular, round, or elongate, posterior and median to choanae, missing in some individuals; odontophores wider than choanae. Tongue longer than wide, notched posteriorly, posterior two-thirds free. Vocal slits absent in males.

Dorsal skin finely granular, becoming nearly smooth in preservative, with some scattered small warts; middorsal raphe distinct, feebly developed, or absent; throat smooth; venter areolate; triangular area of glandular skin present on posteroventral thigh surface; discoidal fold slightly anterior to groin; ulnar tubercles absent.

Relative length of appressed fingers III > IV > II > I; first finger barely reaching proximal edge of disc of finger II; white nuptial pad along posteroventral side of thumb in males; lacking lateral fringes. Finger discs broader than long, rounded apically, with



Fig. 13. *Eleutherodactylus yaviensis*, new species, paratopotypes in life. **Upper.** EBRG 3009 ♀, 27 mm SVL. **Middle.** EBRG 3008 ♀, 27 mm SVL. **Lower.** EBRG 3007 ♀, 29 mm SVL.

subdigital pads as wide as long or wider than long; disc on thumb slightly expanded; lacking lateral fringes. Palmar tubercle large and cordiform to nearly divided; thenar tubercle oval, large; subarticular tubercles round, conical; supernumerary palmar tubercles low and round, smaller than subarticular tubercles.

Hind limbs relatively long; heels overlap when held at right angles to the sagittal plane;

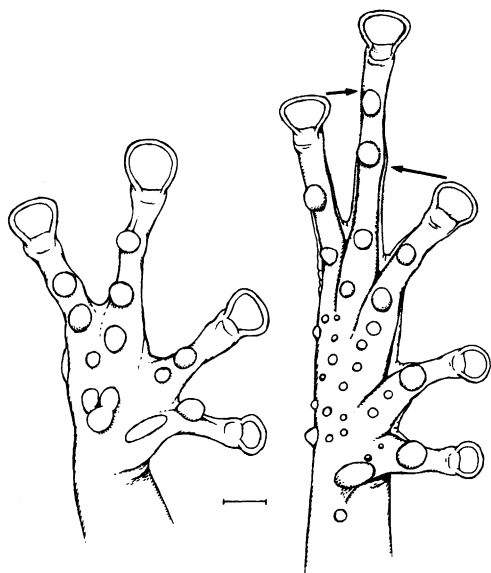


Fig. 14. *Eleutherodactylus yaviensis*, new species. Right hand and right foot of holotype (EBRG 30179). Arrows indicate position of tips of third and fifth toes when these digits are straightened and appressed against the fourth toe. Scale = 1 mm.

tibia 52.7–57.5 percent of SVL in males, 50.0–55.6 percent of SVL in females. Relative lengths of appressed toes $IV > V > III > II > I$; tip of toe V extending to distal edge of ultimate subarticular tubercle of toe IV, tip of III to middle of penultimate subarticular tubercle of toe IV. Toe discs broad, broader than those on fingers, with wide subdigital pads. Toes lacking lateral fringes; with basal webbing formula of $I\ 3-3\ II\ 2-3\frac{1}{2}\ III\ 3-4\frac{3}{4}\ IV\ 4\frac{1}{2}-3\frac{1}{2}\ V$. Inner metatarsal tubercle large, oval to elongate, 1.7–3.5 times as long in males and 1.7–2.3 times as long as round outer metatarsal tubercle in females; supernumerary plantar tubercles round and low to somewhat protuberant; subarticular tubercles round on toes I and II, protuberant on III, IV, and V; nonconical calcar tubercles present; small tarsal tubercles present.

COLOR PATTERN: In life, there was great variation in the dorsal color pattern including dark chevrons, longitudinal dark lines, or with middorsum sharply bicolor from sides; the

dorsal ground color was light or dark brown, grayish brown, or orangish brown. One female, AMNH 143364, had a small enamel white spot on the dorsal surface of each shank. The ventral surfaces were grayish or sometimes pale grayish yellow. Throat variably (weakly to strongly) mottled with small blotching or flecking of bronze. Bronze flecking also present on chest. Iris silvery to pale bronzy brown, sometimes slightly darker below than above pupil with reddish brown horizontal stripe. Orange-red flash marks in groin, on anterior and posterior thigh surfaces, and on concealed part of shank.

The color pattern variability is reflected in the preserved series as follows: There are four basic patterns that include: a uniform gray or brown dorsum with or without limb bars (AMNH 143364, 143368, 143370, EBRG 3008, 3011, 3015, 3016); one example (EBRG 3020) has a uniform gray dorsum with small dark scapula spots. Several individuals have a brown or gray ground color with darker dorsal markings (chevrons, spots, blotches) with vague to distinct dorsal limb bars (the holotype, AMNH 143365, 143369, 143371, and EBRG 3007, 3009, 3012, 3019). Some frogs have dark dorsolateral stripes (width of stripe variable) with vague to distinct limb bars (AMNH 143366–143367, 143372, 143374, EBRG 3010, 3013, 3018). Two frogs (AMNH 143375, 143376) have light dorsolateral stripes and vague limb bars, and two have dorsolateral stripes bordering either a vertebral stripe or paravertebral stripes (AMNH 143373, EBRG 3014).

In addition to these basic color patterns, most individuals have a distinct dark post-orbital stripe (from posterior corner of eye to insertion of arm), lip bars or spots are present in some (the holotype and AMNH 143367, 143373, EBRG 3010, 3013, 3015), and a few have weakly developed interorbital bars (the holotype and EBRG 3007, 3009, 3015).

In most individuals, the orange flash color persists only on the anterior thigh. It is distinct in the groin, anterior and posterior thigh, and concealed shank in one example (AMNH 143375), on both thigh surfaces (AMNH 143369, EBRG 3014), or on both surfaces of the thigh and the shank (AMNH 143374, EBRG 3017). The orange coloration is absent

in six of the smallest frogs (AMNH 143366, 143370, EBRG 3012, 3013, 3018, 3019).

NATURAL HISTORY

This is the common *Eleutherodactylus* on Cerro Yaví. Most specimens were collected on low vegetation at night in the forest below camp. However, one (EBRG 3016) was found on the summit in a more open, windy site—perched on a dry leaf about 1.5 m above ground, in a scrubby thicket near a sleeping *Phenacosaurus*.

REMARKS

Eleutherodactylus yaviensis is a member of the large *unistrigatus* species group (see prior discussion under Family Leptodactylidae). It can be compared with two types of frogs in this group, namely those with red or orange flash marks (Lynch 1980a, 1984, 1992b, 1992c) and those lacking ears (Lynch 1979, 1980b; Walker and Test, 1955). In the following comparisons, the first value in parentheses is for *E. yaviensis*.

Several species of *Eleutherodactylus* in the *unistrigatus* group have red or orange flash marks in the groin, anterior and posterior thigh, and on the concealed part of the shank. *Eleutherodactylus yaviensis* differs from *E. roseus* (Lynch, 1980a) in the condition of the tympanum (absent vs. hidden), fringes on the digits (absent vs. present), and toe webbing (present basally vs. absent).

Lynch (1984) suggested that seven species in the *unistrigatus* species group (*gladiator*, *leoni*, *myersi*, *ocreatus*, *pyrrhomerus*, *repens*, and *trepidotus*) form a monophyletic group, based on the synapomorphy of red or orange flash markings. *Eleutherodactylus yaviensis* differs from *myersi*, *ocreatus*, and *trepidotus* in having broad discs on the digits; it differs from the rest of the species in this group by lacking ears.

There are two species in the *unistrigatus* group (*erythropleura* and *bellona*) that have red flash marks present only in females. *Eleutherodactylus yaviensis* differs from *E. erythropleura* in lacking keels on the fingers (Lynch 1992b) and from *E. bellona* in lacking cranial co-ossification in females (Lynch, 1992c).

Eight other species in the *unistrigatus* group lack ears (*anotis*, *baryecuius*, *colodactylus*, *duellmani*, *pugnax*, *ruidus*, *sobetes*, and *surdus*). *Eleutherodactylus yaviensis* differs from *E. anotis* Walker and Test (1955) in female SVL (24–30 mm vs. 40–47 mm), posterior thigh color (orange vs. dark reddish brown), and dorsolateral folds (absent vs. present). The new species differs from *baryecuius*, *colodactylus*, *ruidus*, and *pugnax* in lacking fringes on the digits; it differs from *E. duellmani* in lacking finger fringes, in being less warty, and in posterior thigh color (orange vs. yellow to brown); from *E. surdus* in groin color (orange vs. variably brown and dirty white) and posterior thigh color (orange vs. brown with white spots); and from *E. sobetes* in posterior thigh color (orange vs. pale violet).

LIZARDS

FAMILY TEIIDAE

(Gymnophthalmidae, auctorum)

The genera treated in this paper are microteiids, recently placed in their own family, the Gymnophthalmidae, which we do not follow. Presch (1983), accorded family status explicitly because he thought that macroteiids and microteiids were not related and did not form a monophyletic group—a premise convincingly rebutted by Harris (1985) and by Estes et al. (1988). The last authors nonetheless continued the separate family arrangement for no obvious reason except that one of them (Estes) also had earlier recognized the Gymnophthalmidae—based on synapomorphies that “were for the most part variable characters” (Estes et al.: 217). The newer lists of putative synapomorphies (Estes et al.: 215–217) for the macroteiid and microteiid “families” are based on an unknown (unstated) number of genera and species and their extrapolated use requires perhaps more faith than should be necessary. Estes et al. (p. 256), viewed Teiidae and Gymnophthalmidae as a monophyletic group (which they named Teiioidea), and said that Gymnophthalmidae itself “appears to be monophyletic, although additional study of this taxon is needed.” We favor stability when the da-

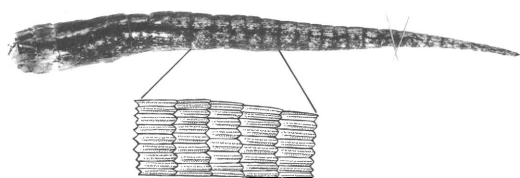


Fig. 15. Lizard tail (from a snake stomach), the only unidentified component in the herpetofaunal sample from Cerro Yaví. The pale basal stripes in combination with the caudal scutellation are probably diagnostic of this species, which is tentatively assigned to the microteiid genus *Arthrosaura*. Tail shown $\times 1.8$, enlarged inset $\times 3.9$.

tabase is inadequate and change is neither mandatory nor purposeful.

? *Arthrosaura* species

Figure 15

The sole "specimen" is the terminal 37 mm of a lizard tail that had been eaten by a snake (*Thamnodynastes yavi*, AMNH 141342) found on the open summit. The tail fragment is not obviously regenerated and may represent the original tail. It is roughly cylindrical, not noticeably compressed, with transverse rows or whorls of equal sized scales that are very elongate, about four times longer than wide. The "basal" dorsal and ventral scales are bluntly pointed, the ends becoming rounded over most of the fragment. Most of the scales are pentagonal, although many in the first several whorls have a hexagonal appearance. The hexagonal aspect arises when the pointed end of a scale falls in a longitudinal suture between scales in the adjacent whorl. Otherwise, each pointed or rounded free end overlaps the median base of the scale distal to it. The distal ends of the scales form a scalloped edge around the circumference of each whorl. Dorsally, the scales are strongly keeled to the end of the tail, ventrally they are weakly keeled, becoming smooth toward the end. Single apical pits are discernible on some scales. The tail fragment is heavily pigmented (brown in preservative) above and below, without definite pattern except for a pair of weakly defined pale dorsolateral and lateral stripes on the basal eight whorls (stripes evident on left side only, having been destroyed by digestion on the right).

This tail differs conspicuously from that of sympatric *Euspondylus*, which has larger, more variable, and less elongate scales that are generally only about twice as long as wide and larger ventrally than dorsally; in *Euspondylus*, the scale ends are rounded on the basal part of the tail (vs. pointed) and more-or-less straight edged (vs. rounded) over the distal part, and the general shape of the caudal scales in *Euspondylus* is rectangular (vs. hexagonal to pentagonal).

A few other genera of microteiids known to inhabit tepui summits can be eliminated by quick comparison. Thus, the aquatic and semiaquatic species of *Neusticurus* have crested, laterally compressed tails with scales heterogeneous in size. *Riolama*⁵ has caudal scales mostly with rounded or straight ends, and, ventrally, the smooth scales are black with pale spots.

Several genera known from lowlands can also be eliminated: Caudal scalation is variable among species of *Bachia*, but these fossorial lizards have long, slightly tapering tails that are disproportionately thick to the end. *Gymnophthalmus* has smooth, broadly rounded scales. *Leposoma percarinatum* has both subcaudals and dorsals strongly keeled, each keel terminating in a long point continuous with the keel on the following scale. *Tretioscincus oriximinensis* has the dorsal and ventral caudals differently shaped, the dorsals being laterally flared distally and the subcaudals lanceolate.

The tail fragment seems most similar to *Arthrosaura*, species of which are distributed both on tepuis (*A. synaptolepis*, *A. tyleri*, *A. spp.*) and in adjacent lowlands (*A. reticulata*) fide Donnelly et al. (1992, and unpublished data). The caudal scales are as elongate in some *Arthrosaura*, in which, however, they tend to appear hexagonal nearly to the end of the tail. The present fragment, with a few hexagonal scales near the broken base, conceivably might fit the *Arthrosaura* pattern if it were the terminal 37 mm of a much longer tail. Such a tail would have pale stripes for a

⁵ *Riolama* spp. are tepui endemics definitely known from Cerro Roraima (Uzzell, 1973) and Cerro de la Neblina (McDiarmid and Paolillo, 1988). We here add Cerro Duida to this short list, based on a specimen (AMNH 141343) taken from the stomach of the snake *Thamnodynastes duidae* (q.v.).

considerable distance from the base, with the end of the tail bearing heavy, dark pigmentation ventrally as well as dorsally. We have not noticed such a combination of scalation and color pattern on the tail of any Venezuelan specimen. We therefore suspect that this tail tip is from an undescribed species.

Euspondylus goeleti, new species

Figures 16–20

HOLOTYPE: EBRG 3112 (field no. CWM 19639), an adult female from the summit of Cerro Yaví, 2150 m elevation, Amazonas, Venezuela; obtained February 19–20, 1995, by the AMNH–TERRAMAR Expedition.

PARATOPOTYPES: Five (1♂, 1♀, 3 juv.), AMNH 141329–141331, EBRG 3113–3114, with same data as holotype.

ETYMOLOGY: For Mr. Robert G. Goelet, who believes in the importance of natural history collections and expeditionary work.

DIAGNOSIS: One of the few *Euspondylus* having a lateral white stripe anteriorly passing below ear from upper lip to above insertion of forelimb. *Euspondylus goeleti* is most similar to another tepui species, *E. phelpsorum*,⁶ but is distinguished by a posteriorly expanded middorsal stripe (uniformly narrow for length of trunk in *E. phelpsorum*) and different ventral coloration in life (see Remarks).

DESCRIPTION

The type series comprises the adult female holotype (55 mm SVL), a second adult female (49 mm SVL), an adult male (50 mm SVL),

and three juveniles of 25–29 mm SVL. The male was judged sexually mature based on body size (relative to the females) and well developed hemipenes. The smallest adult female (opened on right side) has 1 mm ovarian ova and a well-developed oviduct 20 mm wide (recently spent?); the holotype has what appears to be a large collapsed (flattened) ovum 9 mm long in the right oviduct. The smallest juvenile is a male (everted hemipenes), another juvenile probably is a male (incipient femoral pores), and the third juvenile is unsexed. See table 2 for measurements, some scale counts, and relevant methodology.

Head length 23–26 percent of SVL, 1.2–1.5 times longer than wide, 1.3–1.5 times wider than high. Neck slightly narrower than head. Body wider than deep. Complete tail 2.4 times SVL in an adult female, 1.7 times SVL in a juvenile male; tail slightly flattened below but otherwise nearly cylindrical to tip. Limbs pentadactyl, all digits clawed. Forelimbs 31–36 percent of SVL, hind limbs 41–50 percent SVL; adpressed limbs overlapping. Tongue behind fork covered with imbricate scalelike papillae in oblique rows, which extend around onto ventrolateral sides of tongue; raised medioventral side of tongue smooth except for two or three chevron-shaped plicae behind fork; tips smooth. Anterior teeth short, becoming larger and tricuspid posteriorly.

Snout rounded. Rostral plate much wider than deep, laterally in contact with nasal and first supralabial, dorsally in contact with frontonasal. Frontonasal pentagonal, with anterior edge convexly curved and with apex (weak in holotype) on posterior edge. Paired prefrontals with a short median suture and a posterior apex, noticeably smaller than frontonasal. Frontal hexagonal, with pronounced anterior and small posterior apices, longer than wide. Paired hexagonal frontoparietals with a long median suture. Three large supraoculars, anteriormost largest. Interparietal longer than wide, heptagonal, with a straight posterior margin with small rounded or angled corners. Parietals wider than interparietal, hexagonal, with anterolateral edge in brief contact with upper postocular. Three occipitals (postparietals) followed by a transverse row of four postoccipitals, which are noticeably larger than dorsal neck scales.

⁶ Nomenclatural Note: *Euspondylus phelpsorum* is a required correction of the name *Euspondylus phelpsi* Lancini, 1968, as mandated in the 1961 edition of the *International Code of Zoological Nomenclature* then in effect and as reaffirmed in the 1985 edition of the *Code* (relevant articles 31a_{ii} regarding required use of *-i* and *-orum* terminations, and 32c, 32d regarding incorrect original spellings and correction thereof). The corrected name takes the author and date of the original spelling (art. 33b_{iii}).

The reason for this required change is that Lancini (1968: 3) dedicated his new species not to Phelps alone but explicitly to “Dr. William H. Phelps y su distinguida esposa Sra. Kathleen Phelps, quienes con su extraordinario entusiasmo y espíritu de organización hicieron posible el primer ascenso a la cumbre del macizo de Jaua por medio de helicópteros.”

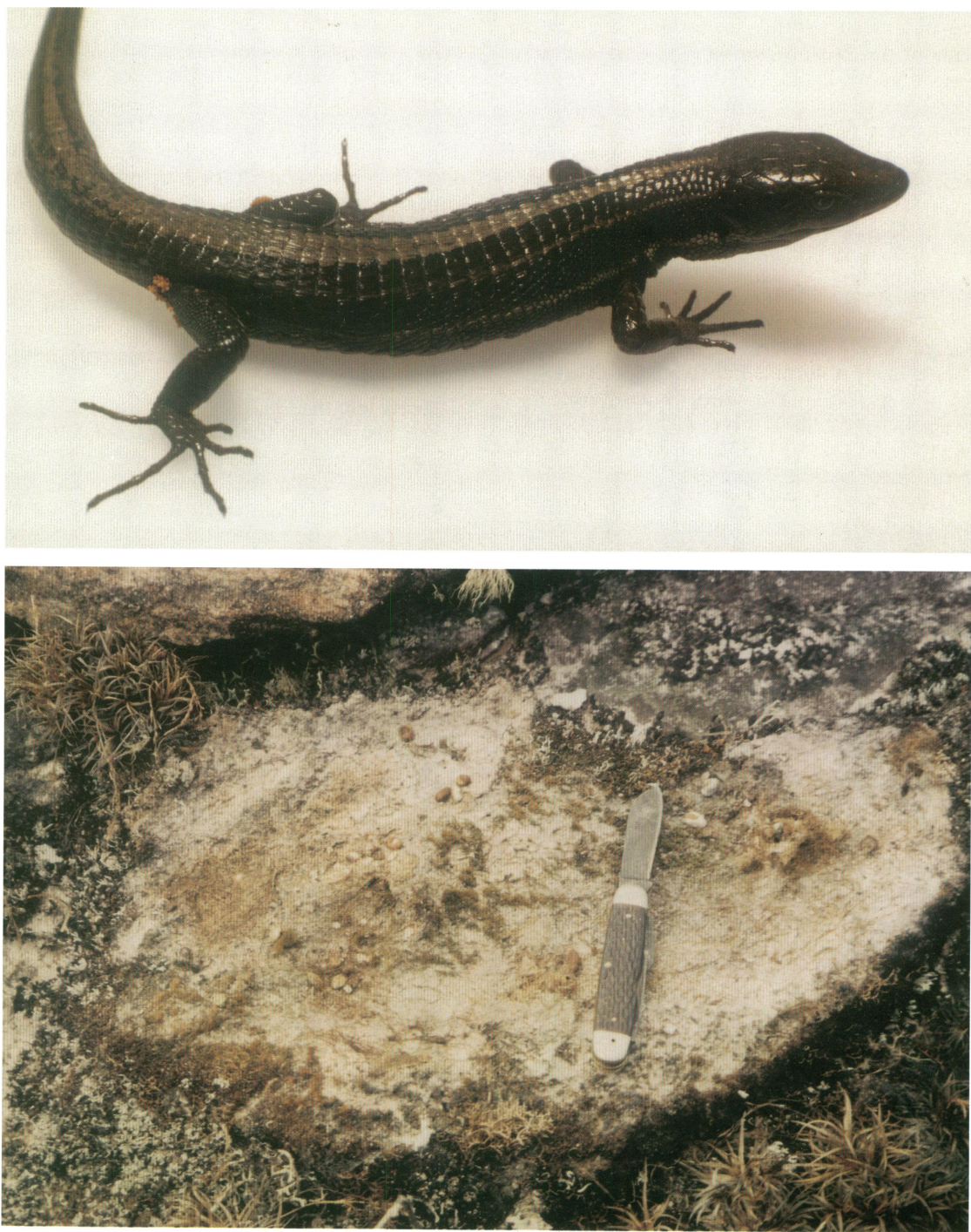


Fig. 16. *Euspondylus goeleti*, new species. **Upper.** The adult female holotype (EBRG 3112) in life. Note infestation of chiggers (*Parasecia* sp.) on rear legs. **Lower.** Communal nesting site of *Euspondylus goeleti*. An overlying rock has been turned, revealing a circular area of pale sand and fibrous plant material atop a flat section of sandstone. Careful search yielded 47 egg shells of varying age; some of the older (brown) shells had been engulfed by plant fibers (February 22, 1995).

TABLE 2
Measurements (in mm) and Scale Counts of Type Specimens of *Euspondylus goeleti*, new species

Specimen	AMNH 141329 ad.♂	EBRG 3112 ad.♀	AMNH 141330 ad.♀	AMNH 141331 juv.♂	EBRG 3113 juv.	EBRG 3114 juv.♂
Snout-vent length (SVL)	50	55	49	26	29	25
Tail length	76	70	116	46	17+	4+
Trunk (axilla to groin)	24	26	24	11	13	11
Forelimb length ^a	18	17	16	8	9	8
Hind limb length ^a	25	26	21	11	12	12
Head length (snout-ear)	12.8	13.2	11.3	6.0	7.0	6.5
Greatest head width	8.8	9.7	7.7	4.9	5.0	4.6
Greatest head depth	5.8	6.6	5.4	3.1	3.5	3.3
Subdigital lamellae finger IV	15/15	14/15	15/16	14/15	15/16	16/16
Subdigital lamellae toe IV	21/22	21/21	21/21	19/21	21/22	20/22
Middorsal scales ^b	35	38	33	33	35	36
Ventrals, longitudinal rows ^c	8	8	8	8	8	8
Ventrals, transverse rows ^d	20	21	21	21	22	21
Scales around midbody ^e	40	36	35	37	38	39
Supralabials	8/8	8/8	8/8	8/8	8/7	8/8
Infralabials	8/8	7/7	7/7	7/8	7/7	7/7

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

^b Middorsal scales counted from postoccipitals to level of posterior edge of thigh held at right angle to body.

^c Longitudinal ventral rows counted at midbody and including a small ventrolaterally positioned plate on each side.

^d Transverse rows of ventrals counted between collar and pair of anterior preanals; usually some irregularity in arrangement of scales designated first ventral row and sometimes in last row.

^e Scales around body counted at level of transverse ventral row 11.

Nostril slightly anterior of center in undivided nasal. Loreal higher than wide, with a posterior apex inserted partway between large presuperciliary above and large frenocular below. Three small preoculars around anterior edge of eye, as follow: (1) upper preocular in contact with suture between presuperciliary and first superciliary, (2) median preocular with anterior apex sometimes in contact with loreal (separating an otherwise narrow contact between presuperciliary and frenocular), (3) lower preocular in contact with first of three suboculars. Three elongate superciliaries posterior to large presuperciliary. A vertical row of three postoculars between last supraocular and last subocular; upper postocular usually in contact with last superciliary but sometimes separated from it by uppermost of several very small scales lying between eye and postoculars. Three (holotype) or usually four suboculars, all in contact with fourth supralabial. Eight or rarely seven supralabials, fourth largest.

Upper eyelid with two large median ciliaries and diminishingly smaller ones to either side. Half a dozen or more small lower cili-

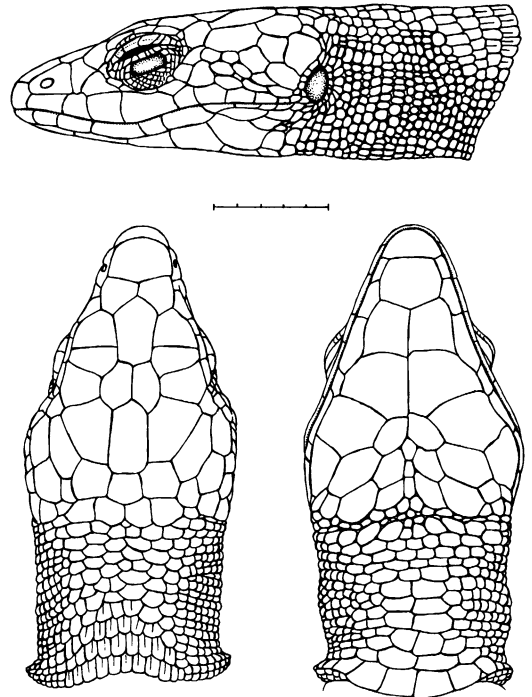


Fig. 17. *Euspondylus goeleti*, new species. Lateral, dorsal, and ventral views of head of holotype (EBRG 3112). Scale line = 5 mm.

aries of subequal size. Lower eyelid scaled, with a large opaque median window (palpebral disk), undivided or (in two specimens) with a vertical division setting off a posterior one-fourth or smaller section.

Temporal region between postoculars and ear opening with about 15–25 irregularly shaped, juxtaposed scales, of which the upper ones are large and the lower ones small to medium in relative size. Ear opening higher than wide and variably positioned, taking the form of a posterodorsally inclined or a vertical ovoid,⁷ sometimes with a nearly straight posterior edge. Ear edge with small, smooth scales all around, those on anterior edge tending to be raised posterolaterally. Auditory meatus varying from deep (in holotype) to shallow, tympanum always clearly visible.

Mental with a nearly straight posterior margin. Postmental large, slightly pentagonal, wider than long, laterally in contact with first two infralabials. Four pairs of genials, all in contact with infralabials, the first two pairs in broad contact medially; third and fourth pairs widely separated by intervening preular and other scales. Three preulars on each side, first two in lateral contact with genials 3 and 4; preulars on each side medially in contact with a line of 2–3 large scales that in turn are separated by a line or median cluster of small scales. Seven or eight infralabials, the third largest and the last two smallest.

There are 14–18 scales from the intergenial suture (2nd pair) to the free edge of the collar. This count includes 8–10 transverse rows of imbricate gulars between preulars and collar scales, the gulars increasing in size posteriorly and with a median pair of enlarged plates in the posteriormost five or six rows. Collar row with five (one juv.) or six enlarged scales ventrally, the collar scales to each side becoming gradually smaller. Posterior margin of collar conceals an irregular row of tiny scales. Side

of neck between ear and collar pebbled with subequal, rounded juxtaposed scales.

Elongated dorsal scales much larger than laterals, distinctly keeled, weakly imbricate, with posterior ends rounded to weakly pointed, in 33–38 transverse rows from postoccipitals to posterior margin of leg; enlarged dorsals roughly twice as long as wide, slightly pentagonal (appearing weakly hexagonal owing to imbrication), many with a pair of widely separated apical pores on posterior margin. About 12–15 longitudinal rows of enlarged dorsals at midbody, dorsolaterally grading to smaller juxtaposed scales, some feebly keeled. Small, smoothly rounded, juxtaposed lateral scales below lateral stripe, above arms, and in front of legs, becoming smaller and somewhat flattened around limb insertions. Transverse dorsal rows the width of 2–3 small lateral scales at midbody. Ventral scales smooth, imbricate with nearly straight posterior margins; ventrals mostly rectangular (to 1½ times wider than long) except male paratype has median two rows square; in eight longitudinal rows (including a small ventrolateral plate on each side) and 20–22 transverse rows between collar and pair of anterior preanals.

Two anterior preanal scales, tending to be wider than long, followed by two or four preanal scales anterior to vent (i.e., two wide preanal scales in males or four narrow anal scales in two adult females and an unsexed juvenile. Adult male with 11/13 femoral pores; pore scales swollen, in contact, forming an uninterrupted series on each leg. One juvenile (AMNH 141331, ♂?) with precocious pores set in nonswollen scales; femoral pores lacking in two adult females, a juvenile male (with partly everted hemipenes), and an unsexed juvenile.

Dorsal and lateral caudal scales rectangularly longer than wide, strongly to weakly keeled on base of tail and smooth distally; imbricate, with posterior edges slightly rounded on base of tail and tending to be straight-edged distally. Subcaudals smooth, same length as dorsals but wider (more or less square); imbricate, with slightly rounded to straight edges. Scales in transverse rows one-scale wide all around tail; about 100 rows in an adult female with complete tail, the first two rows being ventrally narrowed behind vent.

⁷ There appears to be an ontogenetic change, inasmuch as the ear opening is sharply inclined posterodorsally only in juveniles, one of which (AMNH 141331) has the opening much more rounded than do the others. The opening is vertical in the adult male and female holotype (fig. 17) but retains a slight posterodorsal tilt in the smaller female (AMNH 141330).

Dorsal surfaces of arm with large imbricate scales, weakly striated and obtusely pointed at least on upper arm, tending to have broadly rounded or straight edges on lower arm. Ventral side of upper arm with very small, smooth, round juxtaposed scales; ventral side of lower arm like dorsal side but scales smaller. Anterodorsal and ventral sides of hind limbs with large, mostly obtusely pointed imbricate scales that are weakly striated or keeled dorsally and smooth ventrally; scales becoming small on posterodorsal side of lower limb. Posterior and posterodorsal sides of thigh pebbled with small, round and raised juxtaposed scales.

Several large scales atop hands and feet; palms and soles with small, round, and slightly raised juxtaposed scales. Supradigital scales single; upper and lower ungual-sheath scales covering base of claws, leaving tips well exposed. Subdigital lamellae rounded, mostly divided, becoming single distally near claw. Longest (4th) finger with 14–16 subdigital lamellae; longest (4th) toe with 19–22 subdigital lamellae (table 2).

COLORATION: In life, the three adults had a beige median stripe on a dark brown mid-dorsum, with a pale brown dorsolateral line to either side. The median dorsal stripe originates on the nape, where it is about 2 scales wide; it is 2–3 scales wide between the arms, expanding to a width of about $3\frac{1}{2}$ –4 scales by midbody and to the equivalent width of 5 scales above the inguinal region, thence continuing well onto the tail (fig. 18). The dorsolateral line originates behind the eye, but is very faint until it reaches the trunk, thence fading on the base of the tail.

The sides were dark brown (of a slightly different hue than the dorsum) with a whitish or pale tan narrow lateral stripe anteriorly originating from a pale stripe on the upper lip, thence extending posteriad under the ear opening and over the arm insertion to the groin. The pale lateral stripe either extends straight back from the mouth or else dips slightly under the ear and is slightly undulating on the side of the neck. In the male, the lateral stripe was pale orange on the lips, turning white on the side of neck and pale tan on the body; in the females, the stripe was white on the lips, turning whitish to pale tan on the body. In addition, there is an short

anterior ventrolateral stripe extending from under the jaw to the arm insertion, being whitish in preservative (see below for ventral coloring in life).

Ventral coloration, like labial color, was sexually dimorphic in life. The adult male was orange over all the venter and undersides of head and tail, with heavy black markings under the head and throat especially; the undersides of the limbs were a contrasting greenish yellow, with black markings. The two adult females were either white or bluish white under the head and greenish white over other ventral surfaces, with a pale orangish tinge beneath the tails. The undersides of the limbs and tails were variably marked with black in all specimens albeit somewhat heaviest in the male. In preservative (fig. 18), the whitish (females) or orange ventral surfaces curiously have become mostly gray or blackish gray, apparently owing to expansion of melanophores that were not evident in life—except that the pale orangish (females) or orange ground color beneath the tails have faded to whitish as expected.

The iris was orangish brown. The anterior third of the tongue, including the fork, was black, the buccal cavity being otherwise unpigmented.

Three juveniles are colored similar to the adults although the pale brown middorsal stripe was of a slightly different hue in life and tends to contain a darker vertebral line (fig. 19). Also, the pale middorsal stripe is relatively narrower and its posterior widening is less pronounced in the juveniles than in adults (compare figs. 18, 19). In the juveniles, the middorsal stripe is the width of $2\frac{1}{2}$ scales between the arms, 3–4 scales wide at midbody, and only 4 scales wide (vs. 5 in adults) above the inguinal region. The undersides of the heads were white and the venters pale green in the juveniles.

HEMIPENIS: The genitalia of AMNH 141329 were field everted and the left organ subsequently was removed and inflated with red petroleum jelly for study and illustration (fig. 20). The hemipenis is 6 mm in overall length, including lobes 1 mm long. The short lobes are smooth and irregularly flattened and folded terminally. The shallow sulcus spermaticus is very wide, running a medial course to bifurcate just past a knob of tissue rising from

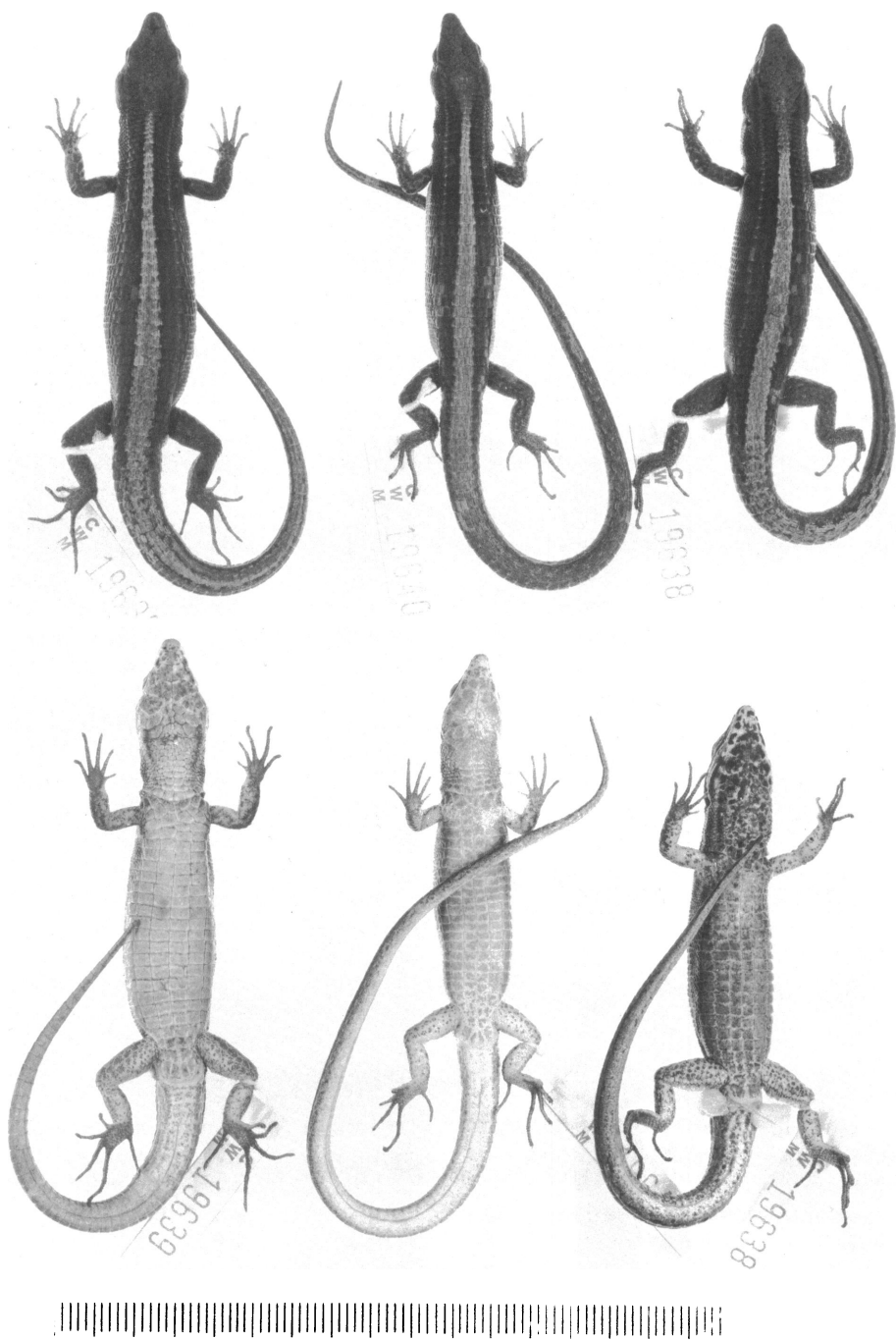


Fig. 18. *Euspondylus goeleti*, new species. Dorsal and ventral views of adults in type series. From left to right: EBRG 3112 (♀ holotype), AMNH 141330♀, 141329♂. Scale divisions in mm.



Fig. 19. *Euspondylus goeleti*, new species. Dorsal views of juvenile paratopotypes. From left to right: AMNH 141331 (CWM 19641), EBRG 3113, EBRG 3114. Scale divisions in mm.

the floor of the sulcus; the sulcus branches (concealed in fig. 20) extend centripetally, each branch terminating at the edge of a lobe without entering onto the broad apex. On the asulcate side of the organ, a basal set of dome-shaped plicae lies proximal to a median nude valley that extends up to the nude crotch between the lobes. This median asulcate depression separates to each side the short arms of 10–12 asymmetrical chevron-shaped plicae, which point proximally and occupy the sides of the organ; the long arms of these plicae terminate on the sulcate side at longitudinal ridges of tissue paralleling but well separated from the lips of the sulcus spermaticus. At magnifications exceeding 20 times, the plicae are seen to have very small, presumably calcified structures—but these minute spinules are embedded or feebly protruding at best.

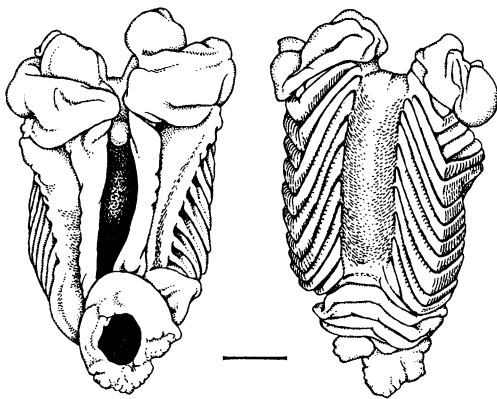


Fig. 20. Hemipenis of *Euspondylus goeleti*, new species. Everted left organ of AMNH 141329, in sulcate (left) and asulcate view. Scale line = 1 mm.

HABITAT AND NATURAL HISTORY

Euspondylus goeleti was found in open summit habitats (e.g., fig. 5, lower). Of our sample of six specimens, two were found under rocks and three were moving about on the ground by day; one adult female was clinging to a low vertical rock face at forest edge by night, but it is not known whether it had been sleeping there or (as seems likely) had been flushed from concealment under a rock. Several others seen on the ground by day escaped capture. We had the impression that this lizard is more active during periods of fog and overcast than during times of extended, intense sun, but it was too uncommon to be certain about this.

Adult and juvenile lizards were infested with chiggers, which were identified by Dr. Ricardo Guerrero (in litt.) as belonging to the genus *Parasecia* Loomis, 1966, Trombiculidae. These mites were clustered primarily around the limb insertions (fig. 16).

Euspondylus goeleti evidently uses communal nest sites under sandstone rocks—four such sites being found. The largest nest under one rock (fig. 16) contained about 50 shells scattered on a layer of fibrous plant material, including moss—this layer itself resting on flat, bare sandstone. Plant fibers had engulfed the older egg shells (brown vs. white). Two other nests with > 12 hatched eggs were found under nearby rocks, one on a similar fibrous mat and the other on a few cm of fine sand with little plant material. A fourth nest at a distant site contained about 15 shells atop a mixture of sand and fibrous plant material; several recent (white) eggs in this nest were shriveled but unhatched, probably having perished from desiccation during a dry period. All the nests were in very open rocky sites with sparse, low vegetation. A sample of 15 shells from the first nest measured 11.1–12.2 mm (\bar{x} = 12.24, S.D. = 0.436). Width measurements for the six best preserved shells were 5.6–7.7 mm (\bar{x} = 6.70).

The small snake *Thamnodynastes yavi* probably is an important predator on *Euspondylus*, inasmuch as one snake contained two freshly ingested eggs, which measured 11.2×6.2 and 11.6×5.7 mm, falling within the ranges for the hatched shells. These two eggs were slit open after measuring but did

not contain identifiable embryos. Identification therefore is based on the probability that the most commonly found terrestrial lizard is the source of the common eggs.

REMARKS

As presently comprised, *Euspondylus* is an Andean genus with a few outliers on the Venezuelan tepuis. A synopsis and key were provided by Uzzell (1973), with subsequent taxonomic changes being annotated by Vanzolini (1986: 9).

Among the named species currently assigned to *Euspondylus*, *E. goeleti* seems close only to *E. phelpsorum*, which was described by Lancini (1968: 2–3, figs. 1, 2, 7) on the basis of an adult female (containing two eggs) from 1917 m elevation on the summit of Cerro Jaua—a tepui about 180 km southeast of Cerro Yaví. The anterior positioning of the lateral white line is the same in *phelpsorum* (compare fig. 16 with Lancini's fig. 2) and *goeleti*. We would call the dorsal scales noticeably keeled in *goeleti* rather than weakly keeled (*débilmente aquilladas*) as described for *phelpsorum*. Possible differences in scutellation cannot now be investigated, but several scale counts given for the holotype of *phelpsorum* either fall within the ranges for the type series of *goeleti* or differ slightly. Thus, the holotype of *E. phelpsorum* had 38 scales around the middle of the body (35–40 in *goeleti*), 40 dorsal scales from the head to the base of the tail (33–38), 23 ventrals from the collar to the preanals (20–22 or 21–23 if the anterior pair of “preanals” are counted), and 15 scales from the genial suture to the border of the collar (14–17).

Differences in dorsal color pattern and ventral coloration in life are judged significant despite the small sample sizes. Lancini (1968: 3) described the vertebral marking of *E. phelpsorum* as being a yellowish brown line up to two scales in width, as documented or suggested also in his photographs of the anterior and whole body (his figs. 1 and 7 [specimen on right side]). The equivalent marking in *goeleti* is 2–3 scales wide anteriorly but posteriorly expands to a width of 5 scales (4 scales in juveniles).

Lancini was a member of the 1967 Phelps Expedition to Cerro Jaua and thus was able

to describe the coloration of the adult female holotype from life. He said (op. cit.: 3) that the color of the throat and venter was similar to the subcaudal region, which was gray with black markings (*gris plumizo salpicado de negro*). In contrast, the ventral surfaces of female *E. goeleti* were white or bluish white under the head, greenish white on the venter, and pale orangish under the tail (in preservative, the throats and venters have turned mostly gray whereas the underside of the tail is white with inconspicuous black punctations); a male specimen of *E. goeleti* was much brighter ventrally—overall orange except greenish yellow under the limbs.

FAMILY POLYCHROTIDAE
(FORMERLY
ANOLOID IGUANIDAE)

***Phenacosaurus bellipeniculus*, new species**

Figures 21–24

HOLOTYPE: EBRG 3120 (field no. CWM 19688), an adult male from the summit of Cerro Yaví, 2150 m elevation, Amazonas, Venezuela; obtained February 23, 1995, by the AMNH–TERRAMAR Expedition.

PARATOPOTYPES: A total of 15 (3♂, 3♀, 9 juv.) AMNH 141334–141341, EBRG 3116–3119, 3121–3123, collected February 21–23; other data same as holotype.

ETYMOLOGY: The specific epithet, a noun in apposition, is derived from the Latin *bellus* (pretty) + *peniculus* (a little penis), in reference to the unusual orange color of the everted hemipenes.

DIAGNOSIS: A *Phenacosaurus* with homogeneous flank scales, most closely resembling *P. neblininus* but differing in details of color in life. The skin of the dewlap is pale yellow in adult male *P. bellipeniculus*, with rows of light brown scales that show through strongly translucent skin from one side to the other. Adult *bellipeniculus* have a transient suffusion of bright greenish blue (turquoise) on the flanks and both adults and juveniles undergo color changes that may include ill-defined dark bands on the body. Adult male *P. neblininus* have the dewlap skin creamy or whitish, with bluish gray or bluish white to pink scales. Turquoise patches and dark bands on the body are lacking in the color repertoire

of *P. neblininus*. See Remarks for further differences, including comparison of female dewlaps.

DESCRIPTION⁸

SIZE AND MEASUREMENTS: The type series consists of 16 specimens, including nine unsexed juveniles 27–40 mm snout-to-vent (SVL), three adult females 58–59 mm SVL, two subadult males 47–55 mm SVL, and two adult males 68–70 mm SVL. The females are sexually mature as shown by presence of large ova; the two largest males are mature as judged from their large dewlaps and well-developed hemipenes.

Four measurements (in mm) are given for each specimen in the type series, in the following sequence: SVL + tail length (if complete), HL (head length from tip of snout to end of mandible by callipers), HW (greatest head width). *Females* (3): (1) 58.4 + 80, 17.3, 9.7; (2) 59.1 + 88, 18.4, 10.0; (3) 59.4 + 84, 18.2, 9.4. *Males* (2): (1) 68.0 + 102, 22.4, 11.4; (2) 70.2 + 98, 22.7, 11.5. *Subadult Males* (2): (1) 47.4 + 67, 15.9, 8.3; (2) 55.2 + 78, 16.9, 9.3. *Unsexed Juveniles* (9): (1) 27.6 + 34, 8.7, 5.0; (2) 27.8 + 37, 8.9, 5.3; (3) 27.9 + ?, 9.1, 5.1; (4) 28.2 + 37, 9.3, 5.6; (5) 31.1 + 42, 9.7, 5.9; (6) 33.0 + 46, 10.0, 5.9; (7) 34.5 + 35, 10.5, 6.2; (8) 39.2 + 56, 12.7, 7.0; (9) 39.5 + 56, 12.4, 7.1.

HEAD

Phenacosaurus bellipeniculus has a weak casque, which is formed by low supraorbital and circumparietal outgrowths. These are undeveloped in juveniles and feebly developed in females and subadult males, being best defined in adult males. There are also weak postocular outgrowths with an underlying bony structure on the side of the head.

Adult and subadult males have relatively larger heads than females as suggested by ratios of head length and head width/trunk length (trunk = SVL – HL), as follow:

⁸ The description mirrors that of Myers et al. (1993) for *Phenacosaurus neblininus*, based on standards and terminology set by Prof. E. E. Williams for anoline lizards.

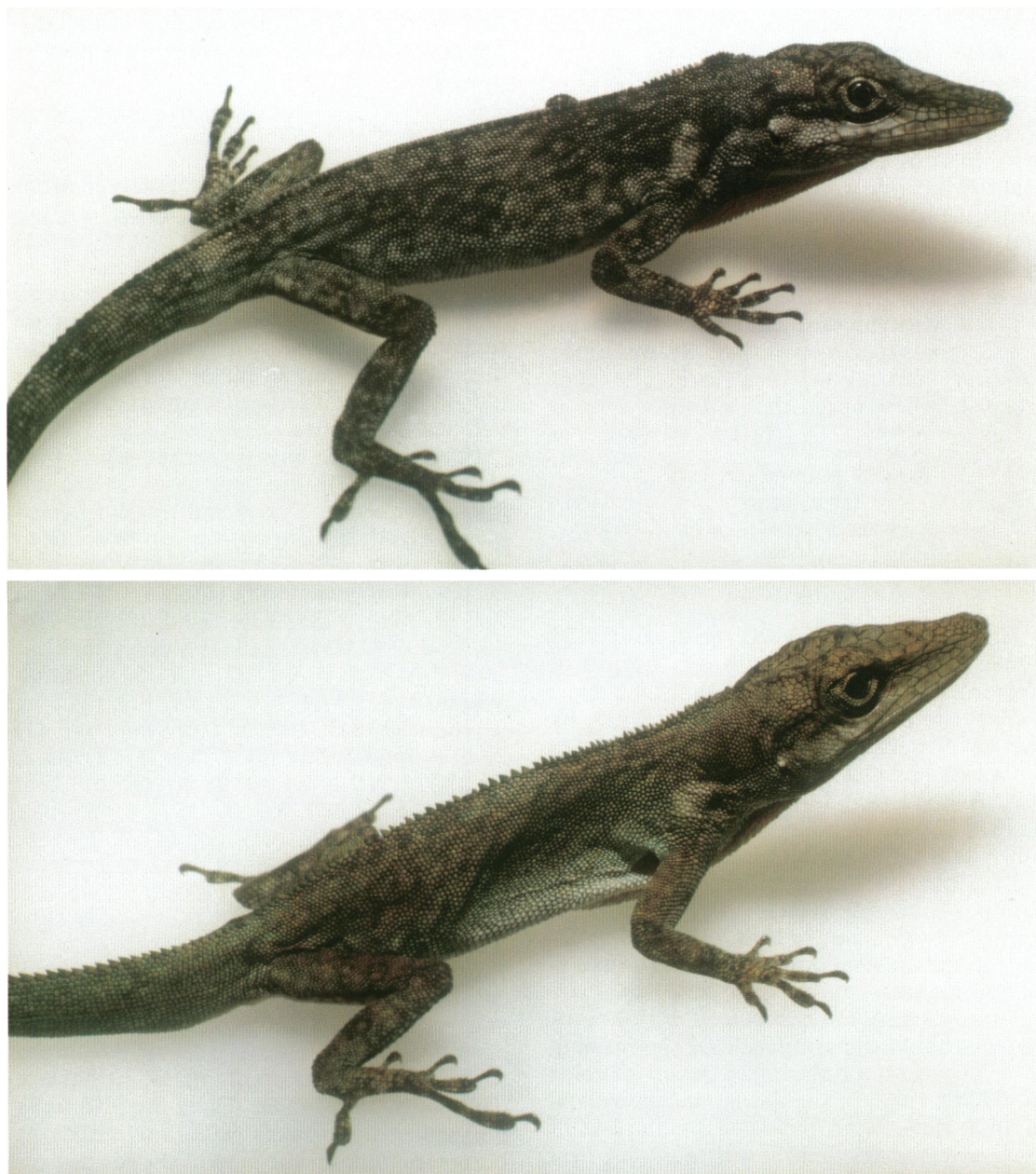


Fig. 21. *Phenacosaurus bellipeniculus*, new species. Adult males in life. **Upper.** EBRG 3116♂, paratopotype. **Lower.** EBRG 3120♂, holotype. Note trace of greenish blue on lower flanks, a transient coloring that changes from bright turquoise to nearly absent in the color repertoire of individual adults.

HL/Trunk = 0.43–0.45 (\bar{x} = 0.438, 3♀), 0.44–0.51 (\bar{x} = 0.479, 4♂). HW/Trunk = 0.23–0.25 (\bar{x} = 0.237, 3♀), 0.24–0.26 (\bar{x} = 0.250, 4♂).

Nine unsexed juveniles are on average intermediate between adult males and females

in proportional head length, but their heads are proportionately wider than adult females and most males: HL/Trunk = 0.44–0.49 (\bar{x} = 0.463). HW/Trunk = 0.26–0.30 (\bar{x} = 0.270).

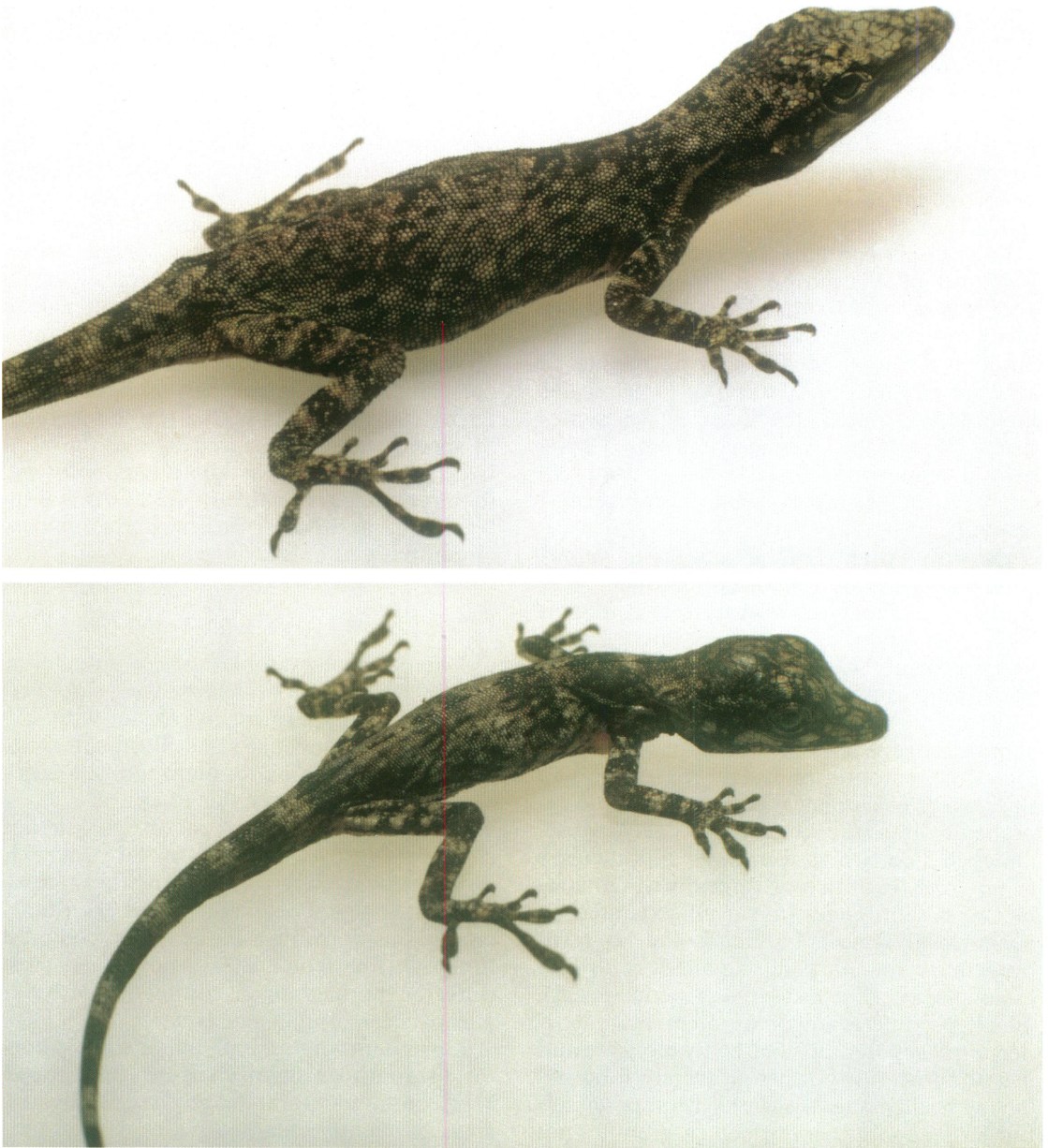


Fig. 22. *Phenacosaurus bellipeniculus*, new species. Adult female and juvenile in life. **Upper.** AMNH 141336♀. Note the suggestion of oblique dark body bands, a juvenile trait that appears only vestigially in adults. **Lower.** AMNH 141337 juv. Note the vertical dark bands, which usually are more obliquely aligned when appearing in the color repertoire of juveniles; there is, however, a suggestion of obliqueness in melanophore deposition on this specimen in preservative (see text).

Dorsal Head Scales and Crests

ANTORBITAL AREA: Scales moderate to small, smooth to lightly rugose. Four to eight

postrostrals, always including circumnasals. Circumnasal slightly encroached on or not by a postrostral (which therefore is also an anterior nasal), or by a supranasal. Circumnasal

always in at least narrow contact with rostral at rostral-first supralabial sulcus (broad contact when rostral is fused with first labial). Three to six scales between the circumnasals dorsally. Supranasals present or not. Frontal depression moderately deep, a central scale largest or not, nearly all scales in depression larger or much larger than those at tip of snout.

Four to six canthals on each side (5/5 in 62%), usually the third or sometimes the second largest, one to three smaller scales between anteriormost canthal and circumnasal. Small variable-sized scales lying medial to anterior canthals and lateral to larger scales in middle of snout, the larger scales sometimes forming two vague longitudinal rows behind postrostrals. Five or six scales (4 in one juv.) across snout between the second canthals.

ORBITAL AREA: Lateral margin of supraorbital semicircles in adults overlying a bony supraorbital crest that is anteriorly confluent with hard, sharp canthus rostralis and posteriorly confluent with circumparietal and postorbital crests (see below); crest not evident in small juveniles, which lack a sharp canthal ridge. Scales of supraorbital semicircles large, smooth, or lightly rugose, two to three pairs in contact medially. Scales of supraocular area smooth or very weakly rugose. On each side two to four large supraoculars in one row, with two or three always in contact with semicircles (never all separated by subgranular scales). Lateral to the large supraoculars are markedly smaller scales (occasionally one or two as large as medial scales), which become granular at superciliary border. First superciliary markedly elongate and usually posteriorly tapering (rarely followed by one small elongate scale), with superciliary border posteriorly continued by granules not distinguishable from adjacent granules of supraocular region.

PARIETAL AREA: Circumparietal crest externally comprising lateral ridges curving gradually medially and connecting posteriorly across occiput; posterior part of this crest usually broadly transverse (but nearly V-shaped in holotype, fig. 23), lowered but lacking a definite median notch. Circumparietal crest externally absent to weak in ju-

veniles and subadult males, weak in adult females and strongest in adult males. Scales on circumparietal crest lacking distinct pustulations or rugosities, not noticeably larger than adjacent supratemporal or nape scales. The interparietal and scales lateral to it distinctly larger than other scales in parietal area, smaller or subequal to large scales in frontal depression, but weakly to strongly rugose or pustulate. Small parietal eye visible. Interparietal distinctly longer than wide, variable in shape (oval, quadrangular, hexagonal, or pentagonal, often anteriorly pointed and posteriorly either pointed or squared off). Interparietal distinctly larger than ear opening; interparietal in contact with a semicircle (38% of specimens) or separated by one (56%) or two scales (1 juv., 6%). About two (holotype) to seven scales, variable in size, between interparietal and posterior (transverse) part of circumparietal crest.

Lateral Head Scales, Crests, and Ear

Two or usually a maximum of three loreal rows, with total of 7–15 loreals per side. Preoculars 2–3, uppermost in contact with second canthal. Suboculars 3–4. Postoculars not well defined, grading into temporals. Supralabials 6–9 to below center of eye.

A vertically aligned, parenthesis-shaped ridge behind eye, followed by short, weakly differentiated, horizontal (slightly arched) temporal ridge. Postocular ridges essentially contiguous, forming a)— or —(shaped crest (left/right) on side of head; postocular crest dorsally approaching or contiguous with circumparietal-supraocular crest.

Lower temporals small, flat or slightly convex, smooth or slightly rugose, juxtaposed. Horizontal temporal ridge covered by two rows of slightly enlarged scales, largest next to postoculars thence grading posteriad to scales not distinguishable from nape scales. Upper temporals above temporal crest small, flat or slightly convex, smooth or slightly rugose, subequal, becoming somewhat larger adjacent to circumparietal crest.

Ear opening obliquely ovoid, varying in size but always smaller and usually much smaller than interparietal, almost surrounded by subgranular scales but one to three scales

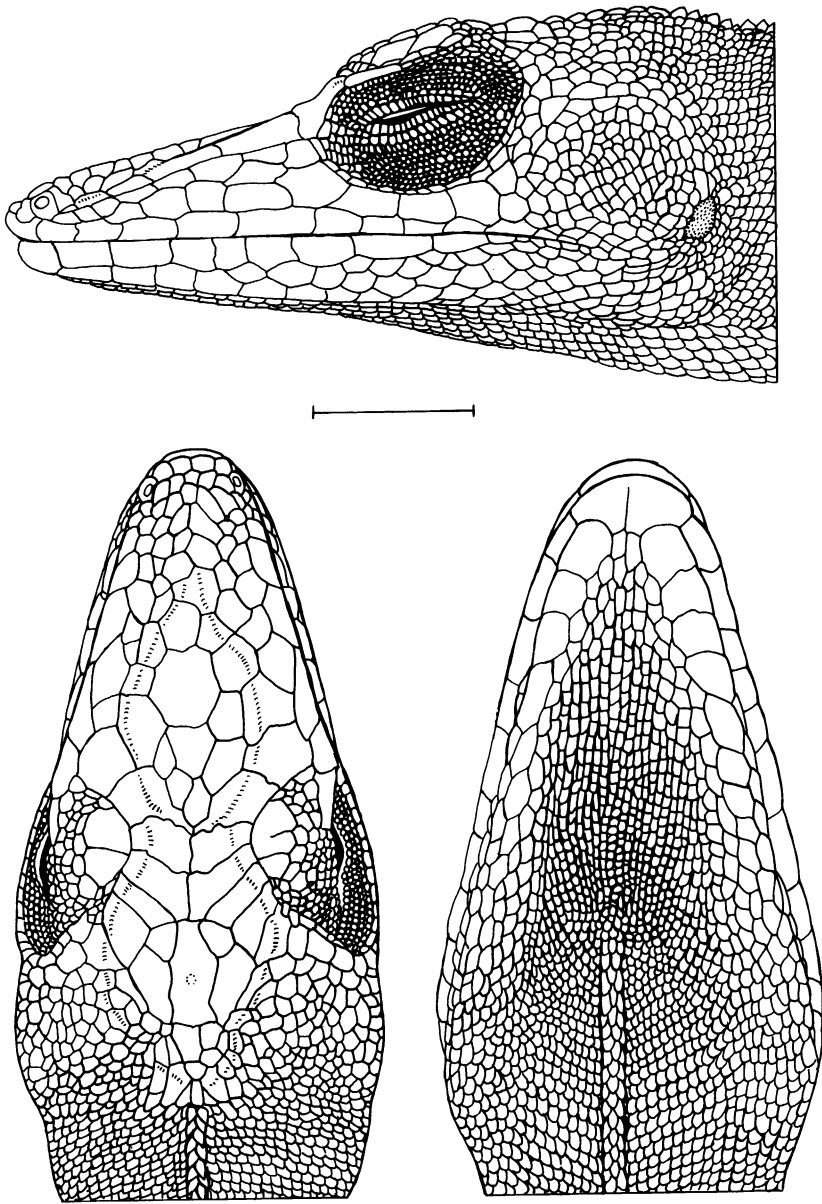


Fig. 23. *Phenacosaurus bellipeniculus*, new species. Lateral, dorsal, and ventral views of head of adult male holotype (EBRG 3120). Scale line = 5 mm.

at upper anterior margin noticeably larger, the largest of which tends to project laterally.

Ventral Head Scales

Mental almost completely divided, indented medioposteriorly, in contact with 4–

6 postmentals (normally 4) between infralabials, including very well-developed first sublabials on each side that are much larger than medial (postmental) gulars. A total of 3–5 sublabials (2–4 additional to first) on each side in contact with infralabials. Central gulars small, smooth, slightly swollen, becom-

ing somewhat larger and more or less polygonal toward sublabials.

TRUNK

MIDDORSAL SCALE CREST: A low vertebral crest, starting close behind circumparietal crest and continuing onto tail, this crest developing ontogenetically and sexually dimorphic, becoming weakly developed on females and strongest on adult males (subadult males with crest as strong or stronger than on larger females).

Crest indicated even in the smallest juveniles by a single line of vertebral scales about twice the size of adjacent dorsals, the incipient crest scales being elongated or not, flat or slightly swollen, usually smooth but sometimes keeled; the crest line may be continuous or interrupted by dorsals. Larger juveniles of about 39 mm SVL have posterodorsally projecting points on many of the scales and the still faint crest has become visible in profile.

The crest is very low and broken in three adult females (58–59 mm SVL), in which some to many of the crest scales have become laterally compressed and triangularly raised along the length of the dorsum; these modified scales are subequal for the length of the body, not higher on the nape than on rear of body.

One subadult male (47 mm SVL) has the crest as in adult females, but a larger subadult male (55 mm SVL) has enlarged triangular crest scales with a height about twice the diameter of adjacent dorsals; the crest of this immature male is already better developed than in larger adult females. Two adult males (68–70 mm SVL) have triangular crest scales for the length of the dorsum, these scales being subequal among themselves and elevated as much as three times the width of paravertebrals.

Although the nape scales are not noticeably higher than posterior crest scales in either sex, there is differentiation in that adult males (females to a lesser degree) tend to have a thicker clustering of anterior crest scales owing to a doubling of the vertebral row for nearly the length of the neck (fig. 21, upper). This doubling is not evident in juveniles, being first noticeable in subadult males and weakly or not developing in adult females.

DORSAL SCALES: Paravertebral and flank

scales subequal, slightly swollen, tending to form transverse rows. Juxtaposed or, on lower flanks, some partly separated by naked skin.

VENTRAL SCALES: Ventrals smooth, markedly larger than dorsals, subquadrate, in transverse rows; imbricate, subimbricate or, especially anteriorly, partly separated by naked skin.

LIMBS

No pocket in axilla, which is sparsely scaled. Upper arm scales subimbricate or juxtaposed to slightly separated, smooth to weakly rugose or sparsely keeled dorsally; larger and mostly smooth anteriorly; subequal to smaller and smooth posteriorly; ventrally smallest, smooth, slightly separated. Lower arm scales dorsally imbricate, smooth or weakly keeled, becoming larger and more distinctly keeled distally; larger and smoother anteriorly; smaller, smooth, juxtaposed or subimbricate posteriorly and ventrally.

Thigh scales anteriorly large, keeled (not rugose), imbricate; dorsally and posteriorly granular, juxtaposed or slightly separated; ventrally smooth, separated. Some tibial scales imbricate and keeled anteriorly and posteriorly; dorsally smaller, smooth or weakly keeled, juxtaposed or subimbricate; posteriorly and ventrally smooth and subimbricate to slightly separated.

Distal phalanx narrower than, and inserting above, the greatly dilated pads of the second and third phalanges. Supradigitals smooth to weakly uncarinate and bicarinate. Lamellae under phalanges ii and iii of fourth toe 18 to 23.

TAIL

Nonprehensile tail 1.0–1.5 times longer than SVL when complete (1.0–1.4 in eight juveniles, 1.4–1.5 in six adults). Tail laterally compressed (least evident in juveniles). Median crest indicated in juveniles by keeled, nonraised scales. Crest continuing onto tail weakly and inconspicuously in females, but higher and distinctly dentate in males, in which it continues nearly to tip). Crest on base of tail is higher than on posterior body in both sexes.

Lateral caudal scales smooth to weakly keeled near base of tail, small, quadrate, be-

coming larger and distinctly keeled posteriorly. Scales behind vent smooth, becoming keeled well posteriorly. A pair of postanals in one subadult and two adult males and in five small juveniles (sex not confirmed); enlarged postanals absent in one subadult male and in adult females.

DEWLAP INCLUDING COLOR

In males reaching onto anterior third of belly; in females extending only to just behind insertion of forelimbs. Dewlap scales nearly as large or larger than ventrals in males, much smaller than ventrals in females.

The skin of the male dewlap seemed remarkably translucent in a subadult male and two adult males, when color notes were being taken in daylight. The backsides of the scales on the opposing side were clearly visible through the skin.

In the three adult females, the small dewlaps were pale blue along the base, then pale grayish brown over the greater part, with rows of white or pale bluish scales.

Dewlaps of two subadult males, 47 and 55 mm SVL, differed as follows: The smaller subadult had the dewlap proximally gray, then light brown over the greater part, with rows of white scales. The larger subadult had the dewlap grayish brown anteroproximally, then pale yellow over the greater part, with pale grayish scales turning pale yellow (same hue as skin) in the distal rows. Thus, the smaller subadult had brown dewlap skin as in females, whereas the larger one had yellow skin as in the adult males below—suggestive of ontogenetic change in male dewlap color.

The two adult males had identically colored dewlaps, which were light brown along the base and then pale yellow over the greater part, with rows of light brown scales.

COLORATION EXCLUDING DEWLAP

JUVENILES: Sleeping juveniles appeared white in the light of a headlamp. By day, some individuals were seen to change pattern and ground color—from black body and limb banding on white, to yellow spots on either light green or light gray. The dark banding, when present, included a transverse scapular band and two or three diagonal lateral ones. One small juvenile differed in having a more

constant pattern of vertically aligned black bands that did not fade away when this individual was handled and photographed (fig. 22, lower). Ventrals were noted as whitish in life. Iris bronzy brown, lighter above pupil. Tongues yellowish.

None has retained a definite banded appearance in preservative, although elements of both the banded and pale spotted patterns are variously retained among the nine juveniles 27–40 mm SVL: Pale spots on some individuals are seen to be set in a vague light brown reticulum. Diagonally arranged and interrupted patches of black pigmentation seem to be largely superimposed on parts of the brownish reticulum, representing remnants of the dark bands. The individual with vertical dark bands in life also has suggestions of a few diagonal accumulations of melanophores within the former areas of vertical bands. Dark bands on limbs and tail, which were evident at some stage, also are retained to various degrees in preservative. The labial region is usually whitish with vertically aligned dark markings but in a few is nearly uniformly pale or nearly uniformly dark grayish. Ventral surfaces whitish, with ends of the blackish lateral bands encroaching laterally onto the venter, and often with a dense scattering of small grayish spots. Lower lips white, usually with conspicuous black markings along each side of mouth.

ADULTS: Sleeping adults were a rather uniform light brownish by headlight (never white like juveniles). By day, the color and pattern was changeable from a uniform light brown or uniform grayish green to development of a vague dark reticulum (fig. 21, upper) and vague diagonal banding (fig. 22, upper). The developing dark reticulum or ill-defined diagonal bands could come to enclose small spots of pale green or yellow. Dark limb and tail banding varied from vague to distinct. Adults and a subadult male had patches or suffusions of bright greenish blue (turquoise) in and behind the axilla on the anterior flanks and sometimes all along the lower flanks, and one male also had a light suffusion of this color on the chest. The turquoise coloring was transient, usually disappearing when specimens were handled for photography, but a faint trace remains visible in figure 21.

The normal juvenile condition of conspicuously dark bars on the pale supralabials is

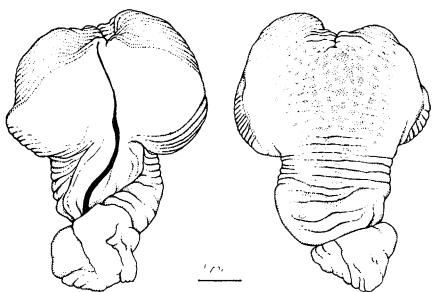


Fig. 24. Hemipenis of *Phenacosaurus bellipeniculus*, new species. Everted left organ of AMNH 141339, in sulcate (left) and asulcate view. Scale line = 1 mm.

retained in a subadult male and an adult female, but other males and adult females have lost the dark bars (vestigial remnants variously retained as brown smudges) giving the appearance of a pale labial stripe that in life was white, gray, or pale yellow—posteriorly nearly confluent with a vague pale stripe extending to the arm insertion.

Ventral surfaces white or (one male) pale bluish white, with turquoise suffusion on chest of one (see above) and with variable dotting or small spots of gray or black, especially on throat and ventrolaterally. Comparison of the preserved specimens shows that a subadult male, two adult males, and an adult female have relatively unpigmented venters, whereas another subadult male and two adult females have small brown spots (about the size of 1–2 ventral scales) rather densely scattered over the venters. Only a subadult male and one female retain the normal juvenile condition of blackish spots along the lower lips.

Iris pale brown or tan, turning darker brown around pupil and in some specimens darker on lower part of iris. Tongue light orangish yellow to (usually) light orange in life. Dissections show the peritoneum to be black.

HEMIPENIS

The hemipenes of the two adult males were pale orange when everted at time of preservation. The left organ of AMNH 141339 was inflated with petroleum jelly and removed for detailed study and illustration (fig. 24). It is about 7 mm long by 5 mm across the widest (distal) part. The distal half of the aspinose

hemipenis is bulbous and very shallowly bilobed. The sulcus spermaticus is single, running medially and distinctly between broad, circular nude faces of the broadly attached lobes; the sulcus spermaticus terminates at the high crotch, where the sulcus lips fuse distally around the end of the groove. The asulcate side of the organ is indistinctly crossed with transverse folds or plicae which are occasionally connected longitudinally. The cross-connections between these barely perceptible folds distally become more frequent and closer together around the circumference of the asulcate nude lobular faces, to form weak (very shallow) elongated small “calyces.”

HABITAT AND NATURAL HISTORY

Like many other anoline lizards, *Phenacosaurus bellipeniculus* is most easily found when it is sleeping at night. Only two specimens were taken by day—a juvenile in a ground bromeliad and a subadult male that had hitched a ride on a trouser leg of the first author, who had walked through a dense brushy area. The other 14 specimens were sleeping on vegetation 1–2.5 m aboveground at night. Juveniles were clinging head-up or horizontally on slender twigs, whereas adults were head-up on plant stems except for two females that were on broad leaves of small trees. Sleeping adults were rather uniform light brownish, whereas juveniles appeared ghostly white whether the night was clear or foggy.

Juveniles especially were found in isolated small patches of scrub and in brush along one side of the summit lake, but most adults were in the brushy ecotone between open rocky country and the mossy forest. It seems to be an edge species.

Adults and even the smallest juveniles gave an open-mouth display of the orange tongue and tried to bite, and males would also partly extend the dewlap in a threat pose. Predation on this lizard may be relatively light judged solely by lack of regenerated tails, which were complete and apparently original in 14 of 16 specimens.

REMARKS

The similar orange coloration of the tongue and hemipenis of this lizard is remarkable,

although there is no reason to suspect adaptive tongue-genital mimicry as suggested by one reviewer. But it is very curious, we admit that.

Phenacosaurus bellipeniculus differs from other phenacosaurus and other anolines in the same ways that *P. neblininus* differs (see Diagnosis in Myers et al., 1993: 3) and *bellipeniculus* therefore needs only be compared with *neblininus* at this time. *Phenacosaurus neblininus* is believed endemic to the highlands (> 1600 m) of the enormous Cerro de la Neblina, on the Venezuelan-Brazilian frontier some 500 km south of Cerro Yavi.

HEMIPENIS: Despite the concentrated effort spent in the faunal survey of Cerro de la Neblina, only six specimens of *P. neblininus* are known. Two of those specimens were preserved and closely examined by the senior author, but both were females and so he cannot state with *absolute* assurance that *neblininus* lacks pigmented hemipenes. However, adult male *neblininus* had been field-noted by professional herpetologists, who would have recognized the novelty of such a character when they were trying to evert the hemipenes during specimen preservation. Orange hemipenes are therefore hypothesized to be an apomorphy of *P. bellipeniculus*. We are unaware of previous reports of brightly pigmented hemipenes for any lizard or snake and the trait is at least highly unusual.⁹

Further comments on the hemipenes of these two species are given in a following section, Notes on Phenacosaur Hemipenes.

GROUND COLOR AND PATTERN: Coloration in life has been recorded in equal detail for both adult *P. neblininus* (Myers et al., 1993: 8) and *P. bellipeniculus*. Adults of both have individually changeable ground colors by day—light gray to light brown in *neblininus*, gray or grayish green to light brown in *bellipeniculus*. These changes are similar except that individuals of *P. bellipeniculus* were

sometimes virtually unicolor and sometimes had a definite green cast. The basic pattern in both consists of a dark reticulum containing diagonally arranged lateral spots of paler ground color. Within this pattern, however, transient diagonal dark bands and a transverse scapular band were seen only in *bellipeniculus*, being most pronounced in juveniles but also appearing in adults. One juvenile *bellipeniculus* (AMNH 141337) had more vertically arranged dark bands which were constant and not transient in life (fig. 22, lower).

The adults of both species tend to have a pale labial stripe posteriorly confluent (*neblininus*) or nearly confluent (*bellipeniculus*) with a posterior stripe ending at the arm. Despite variation in each species, this stripe is much stronger in *P. neblininus* than in *P. bellipeniculus* (compare fig. 21 with Myers et al., 1993: fig. 4).

BRIGHT COLORATION: The lateral and sometimes ventral turquoise coloring, although transient, seems diagnostic for *P. bellipeniculus*. In contrast, a male *neblininus* had a pale yellowish wash behind the forelimbs and another had a suffusion of orangish pink ventrally, neither situation being seen in the larger *bellipeniculus* sample. The turquoise color tended to disappear when specimens of *bellipeniculus* were being photographed, but a trace is visible in figure 21.

DEWLAPS: The strong translucency in life of the dewlap of male *P. bellipeniculus* was noteworthy, but it is not known if *P. neblininus* is comparable (the dewlap is equally translucent in preserved specimens, but in preserved anolines it is commonly translucent after loss of pigmentation).

Dewlap color, however, seems diagnostic. Two male *neblininus* had yellowish cream or bluish white dewlap skin, each with a mottling or blotching of bluish gray or greenish gray proximally; scales were bluish white or else bluish gray turning pink at the ends of rows. This contrasts with the proximally brown, distally pale yellow dewlap skin with light brown scales in two adult male *bellipeniculus*.

The smaller female dewlaps in *neblininus* were either pale gray with vague black spots (two specimens) or light and dark blue gray, all with rows of whitish scales. Adult female

⁹ Snake and lizard hemipenes rarely have blackish pigmentation (e.g., McDowell, 1979: 45), presumably owing to melanophore deposition. It seems likely that the orange hemipenial color in *Phenacosaurus bellipeniculus* may result from a heavy deposition of carotenoids, a class of pigments known to be accumulated in skin, muscle, liver, and intestines of certain lizards (Czeczuga, 1980).

TABLE 3
Comparison of Phenacosaurus from Cerro Yaví and Cerro de la Neblina

<i>Phenacosaurus bellipeniculus</i> N = 16	<i>Phenacosaurus neblininus</i> N = 6
Adult hemipenis orange; at least ♂ dewlap strongly translucent in life	?
♂ dewlap pale yellow (proximally brown) with light brown scales	♂ dewlap creamy or whitish (proximally bluish to greenish gray), with bluish white to bluish gray and pink scales
♀ dewlap light brown (proximally pale blue) with pale scales	♀ dewlap pale gray with black spots or light & dark blue gray, with pale scales
Ground color gray or grayish green to light brown, with basic dark reticulum containing diagonally arranged pale lateral spots	Light gray to light brown, with similar reticulated pattern
Transient blackish bands in pattern repertoire of juveniles and adults to lesser degree	Definite bands not developed
Transient suffusion of turquoise on flanks of adults	Turquoise lacking, yellowish wash sometimes present
Pale labial stripe to arm poorly developed in adults	Pale stripe sometimes strongly developed
Circumnasals in contact with rostral	Sometimes separated from rostral
2–3 supraoculars always in complete contact with semicircles	2 supraoculars in contact with semicircles or all separated from semicircles by subgranular scales
Suboculars 3–4	Suboculars 4–5
Body crest scales subequal, not highest on nape	Crest highest on nape in both sexes

dewlaps of *bellipeniculus* differed in being pale blue proximally and light brown over the greater part (with pale scales as in *neblininus* females).

SCALATION: Scale differences are seemingly minor and most could be due to sampling error (e.g., 4–6 canthals in *bellipeniculus* vs. 5–6 in *neblininus*)—but a few differences are summarized in table 3.

GENERAL COMPARISON: One might expect *Phenacosaurus bellipeniculus*, from a small tepui summit, to be less variable than *P. neblininus*, which occurs on a very large tepui on which gene flow among summit populations must be reduced because of the deeply dissected topography (map in Myers et al., 1993: 12). Considering the larger sample size of *P. bellipeniculus*, this species does seem less variable in dewlap color and in scalation features involving the circumnasal-rostral contact and supraocular-semicircle contact.

Based on study by Ernest E. Williams (in progress), *Phenacosaurus neblininus* and a still-unnamed species¹⁰ from Chimantá Te-

pui were tentatively placed in the *orcei* species group (Myers et al., 1993), to which *P. bellipeniculus* is also assigned. The three known tepui species may form a relatively compact cluster within *Phenacosaurus*.

NOTES ON PHENACOSAUR
HEMIPENES

Myers et al. (1993: 11, fig. 7) compared a partially everted hemipenis of *Phenacosaurus neblininus* with a fully everted organ of *P. nicefori*. New comparison of the *neblininus* organ (AMNH 136763) with the fully everted hemipenis of *P. bellipeniculus* (fig. 24) permits better interpretation of the incompletely everted *neblininus* hemipenis: The sulcate-side “crotch knob” previously described for *neblininus* has no counterpart in *bellipeniculus* and is “an artifact of partial eversion” as originally suspected (Myers et al., 1993: 12). More importantly, the “asulcate flap” shown in the original drawing of the *neblininus* organ also is an artifact—it is a serendipitous flaplike structure remaining at the base of a lobe after interruption of the eversion process. The very shallow and elongated calyces on the base of

¹⁰ The manuscript name published by Gorzula (1992: 275, 307) is a nomen nudum.

an uneverted lobe are like the calyces described herein for *P. bellipeniculus*, and the hemipenes of these two species are probably similar.

In contrast, the "asulcate-side crotch flap" of *Phenacosaurus nicefori* is a definite structure that is present also on partially everted hemipenes from *P. heterodermus* (AMNH 91752). Thus, the asulcate crotch flap is now known to characterize two members of the *heterodermus* species group (*P. heterodermus*, *P. nicefori*) and known to be absent in two members tentatively assigned to the *orcesi* group (*P. bellipeniculus*, *P. neblininus*).

Another difference of note involves the terminus of the sulcus spermaticus. In *P. heterodermus* and *P. nicefori*, the sulcus opens up distally and becomes confluent on each side with a broad, circular (*nicefori*) or elongate (*heterodermus*, partially everted) nude area on the sulcate side of each lobe; in *P. heterodermus*, the sulcus lips are greatly elevated proximal to bilobation of the organ and expansion of the sulcus. The hemipenial lobes of *P. bellipeniculus* (and presumably *P. neblininus*) have rounded nude faces (fig. 24) somewhat like the circular faces in *P. nicefori* (fig. 7B in Myers et al., 1993), but the sulcus spermaticus is entrenched between them and terminates abruptly when the sulcus lips meet in the crotch.

SNAKES

FAMILY COLUBRIDAE

Thamnodynastes yavi, new species

Figures 25–28

HOLOTYPE: EBRG 3124 (field no. CWM 19665), an adult female from the summit of Cerro Yaví, 2150 m elevation, Amazonas, Venezuela; obtained on February 19, 1995, by the AMNH–TERRAMAR Expedition.

PARATOPOTYPES: AMNH 141342, a male caught on February 21, and EBRG 3125, a female obtained February 25–28; all other data same as holotype.

ETYMOLOGY: The epithet *yavi*, a noun in apposition, is the name of the type locality. The name *Thamnodynastes yavi* thus parallels the name of another tepui endemic, *T. chimanta* Roze, to which it is compared.

DIAGNOSIS: A small, smooth-scaled *Thamnodynastes* about 300–400 mm total length, similar to the larger *T. chimanta* (430 mm known maximum) and *T. duida* (455 mm in ♂), but distinguished by 19 dorsal scales in midsection of body (vs. 17) and by a different color pattern on the anterior venter. *Thamnodynastes chimanta* and *T. duida* have a set of four dark ventral stripes anteriorly, whereas *T. yavi* lacks the median pair (compare figs. 27, 29). *Thamnodynastes yavi* further differs from *T. chimanta* and *T. duida* in having an unbifurcated hemipenis (weakly bilobed in the others). See Remarks.

DESCRIPTION

The type series comprises two females and one male (fig. 27). The female holotype is sexually mature at 340 mm total length (262 mm SVL); it contains ovarian eggs up to 3.5 mm long and has enlarging oviducts, which are about 0.7 mm wide and anteriorly convoluted. A paratopotype female 296 mm total length (227 mm SVL) is judged to be subadult because the largest ova on each side are only 2 mm long and the oviducts only 0.3 mm wide. A male paratopotype has well calcified hemipenial spines and is therefore considered adult at 390 mm total length (296 mm SVL).

Some individual comparisons of the type specimens are given in table 4. The following description is a composite.

PROPORTIONS AND SCUTELLATION: Small snakes less than 400 mm total length, of which the tail comprises 23–24 percent. Body slightly wider than high, ventrolaterally rounded but nearly angulate. Head slightly wider than neck, about as wide as body. Greatest head width across temporal region 52–66 percent of head length (tip of snout to end of mandible). Diameter of eye greater than distance from its anterior edge to edge of naris, going 1.3–1.4 times into length of snout. Pupil of eye elliptical (catlike, but capable of becoming round as in fig. 25).

Rostral plate visible from above, wider than high. Paired internasals wider than long, narrowed in front, more than half as long as prefrontals. Paired prefrontals about as wide as long, each in contact with its mate and with frontal, supraocular, preocular, loreal,



Fig. 25. *Thamnodynastes yavi*, new species. Paratopotypes in life. **Upper.** AMNH 141342♂. **Lower.** EBRG 3125♀, not to same scale.

nasal, and internasal. Frontal pentagonal or slightly hexagonal owing to tendency for small anterior apex (two specimens), slightly concave laterally, twice as long as its greatest (anterior) width and 1.4–1.7 times longer than distance from its anterior edge to tip of snout. In the two females, especially the holotype

(fig. 26), the posterior end of the frontal extends posteriorly past the transverse plane between posteriormost ends of supraoculars, but in the male, the end of the frontal lies even with the ends of the supraoculars. Supraocular large, about 75–90 percent of frontal length, anteriorly narrowed, posteriorly

TABLE 4
Measurements (in mm), Counts, and Proportions of Type Specimens of *Thamnodynastes yavi*, new species

Character ^a	Holotype ♀ EBRG 3124	Paratype ♀ EBRG 3125	Paratype ♂ AMNH 141342
Total length	340	296	390
Tail length	78	69	94
Head length (snout to end of mandible)	15.1	13.3	16.1
Greatest head width	8.0	8.8	9.2
Eye diameter	2.5	2.5	3.0
Eye/head length	0.166	0.188	0.186
Head width/head length	0.523	0.662	0.571
Tail/total length	0.229	0.233	0.241
Maxillary teeth (left side)	16 + 2	15 + 2	16 + 2
Dorsal scale rows	19-19-15	19-19-15	17-19-13
Ventrals	131½	130	135
Anal plate	÷	÷	÷
Subcaudals (pairs)	57	61	66
Supralabials	8	8	8
Supralabials touching loreal	2-3	2/2-3	2-3
Supralabials touching eye	4-5	3-5	4-5
Preoculars	1	1	1
Postoculars	2	2	2
Temporals	1 + 2 + 3/2 + 4	2 + 3	2 + 3
Infralabials	9/10	10/9	9
Infralabials touching anterior genials	1-5	1-5	1-5
Infralabials touching posterior genials	4-5/5-6	5-6/5	5

^a Differences between left and right sides indicated by solidus (left/right).

wider than adjacent part of frontal plate. Parietals 1.4–1.5 times longer than broad; interparietal suture 65–85 percent of frontal plate, longer than distance from snout to frontal.

Nasal plate long, nearly twice as long as high, in contact with supralabials 1–2, entire, grooves above and below posterior end of naris absent or very weakly developed. Loreal plate tipped forward, higher than long. Single large preocular (partially divided from anterior edge, midway up, on right side of EBRG 3125). Two postoculars, lower smaller than upper. Tendency for 2 + 3 temporals but some minor variation in positioning; lower primary temporal barely reaching or noticeably failing to reach lower postocular; holotype with an azygous scale on right side, between lowermost temporals in first and second rows. Supralabials 8, with 2–3 or 2

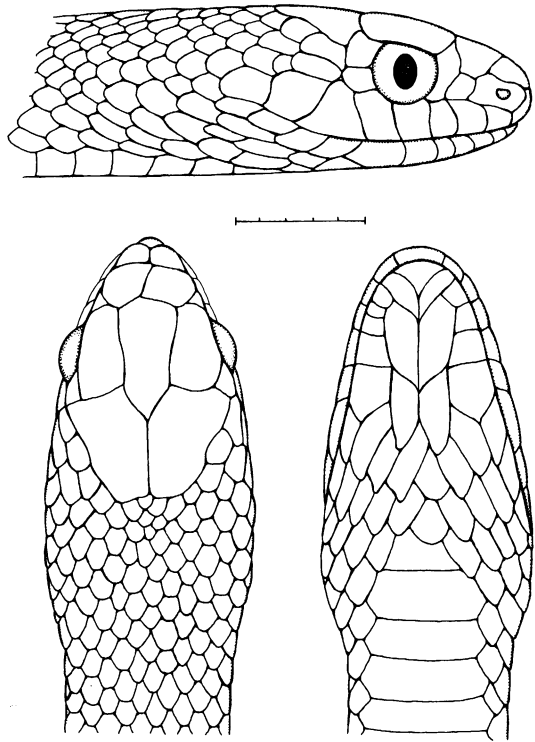


Fig. 26. *Thamnodynastes yavi*, new species. Lateral, dorsal, and ventral views of head of holotype (EBRG 3124). Scale line = 5 mm.

only (left side EBRG 3125) touching loreal and 4-5 or 3-5 entering orbit; supralabial 3 narrowly excluded from or (in EBRG 3125) barely entering orbit. Infralabials 9 or 10, 1-5 touching an anterior genial; if infralabials = 9, 4-5 or 5 only touching a posterior genial, if infralabials = 10, 5-6 touching posterior genial. Anterior genials noticeably wider than posterior ones but in length subequal or little longer than posterior genials. Minute, inconspicuous tubercles (presumed sensory organs) present on head plates and chin.

Moderate numbers of ventrals (130-135) and paired subcaudals (57-66); anal plate divided. Dorsal scales smooth, lacking apical pits or anal ridges, disposed in 19-19-15 rows in the two females and in 17-19-13 rows in the male. Simplified reduction formulae following (modified Dowling formula after Myers, 1974: 37).

EBRG 3124 ♀:

$$19 \frac{-4(77)}{-4(77)} 17 \frac{3+4(96)}{3+4(100)} 15 (= 131\frac{1}{2})$$

EBRG 3125 ♀:

$$19 \frac{3+4(79)}{3+4(77)} 17 \frac{3+4(95)}{3+4(95)} 15 (= 130)$$

AMNH 141342 ♂:

$$17 \frac{\div 3(23)}{\div 3(18)} 19 \frac{-4(72)}{3+4(74)} 17 \frac{2+3(90)}{2+3(91)} \\ 15 \frac{-P(81)}{-P(83)} 13 (= 135)$$

COLORATION: Appearing dark in life (fig. 25), being brown dorsally with ill-defined darker markings and turning grayish brown on sides. Top of head from snout onto parietals brown, patterned with small dark brown blotches, from which two short, parallel dark stripes extend onto nape. In the male, the nape stripes break into two dorsolateral rows of small, irregular spots, which fuse on rear of body into a pair of narrow dorsolateral lines that fade towards the end of the tail. In the two females, the dorsolateral lines of small spots are extremely vague on the body and form only a faint trace of dark lines atop the tail. Grayish brown sides slightly darker than dorsum and edged above with

a faint, narrow blackish line, which extends mainly along row 5 anteriorly and row 4 posteriorly.

Tip and sides of snout brown with small blackish blotches. Supralabials pale brown above, white on lower parts, with black markings. A blackish brown postocular stripe extends across the suture between upper and lower postocular and drops obliquely to the end of the ultimate supralabial, with a short horizontal extension behind the mouth nearly connecting with the faint lateral line.

Underside of head and throat white in life, with black markings, with rest of ventral and subcaudal surfaces gray and densely speckled with black. There is one pair of ill-defined blackish stripes, situated ventrolaterally and most distinct anteriorly (fig. 27).

Upper third of iris tan, lower two-thirds brown. Tongue black, including fork.

MAXILLARY DENTITION: There are 15 or 16 recurved subequal maxillary teeth, followed by a distinct diastema and two grooved fangs about $1\frac{1}{2}$ times longer than the prediastemal teeth. The ultimate prediastemal socket lies anterior to the front edge of the ectopterygoid process. The fangs are grooved along the anterior face for about three-quarters of their length, with the tips being laterally compressed and knifelike. The ultimate fang is offset slightly laterad.

HEMIPENIS: The everted hemipenes of AMNH 141342 are single (undivided) stubby organs, extending to the level of the sixth pair of subcaudals; they are spinose and calyculate but noncapitate. The right organ was inflated with red petroleum jelly and removed for detailed study and illustration (fig. 28).

The straight-line measurement of the slightly reflexed hemipenis is 10 mm in side view, or 9.5 mm if measured in sulcate or asulcate view. Approximately the distal half of the noncapitate organ is covered with calyces; the distal calyces are ornamented with tiny papillae or spinules, whereas the proximal calyces are markedly spinulate. The sulcus spermaticus divides in the calyculate region, about three-fifths the distance from the base; the short branches extend in centrolateral orientation, ending on the sulcate side well below the apex of the everted organ. The basal fourth of the organ is nude except for

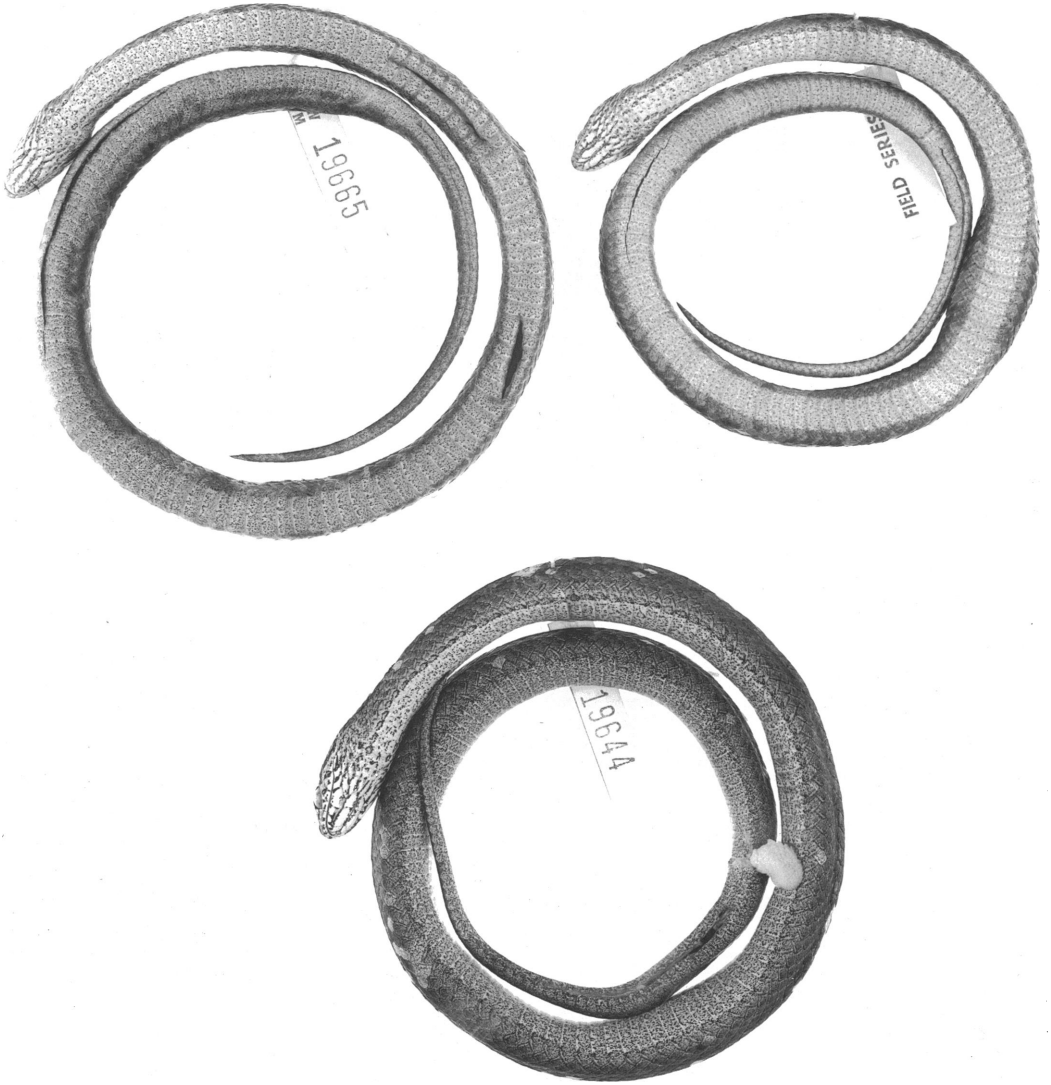


Fig. 27. *Thamnodynastes yavi*, new species. Ventral color pattern of type specimens. Upper left, EBRG 3124 (holotype); upper right, EBRG 3125; lower, AMNH 141342.

very scattered spinules; there is no basal pocket. The second fourth or midsection is heavily spinose; in addition to small spines on the sulcus lips, there are over 50 small to medium-sized stout spines vaguely arranged in oblique rows. There are no particularly enlarged spines; the largest spines are proximal in each row and there is a progressive

decrease to the small spines at the edge of the calyculate area.

HABITAT AND NATURAL HISTORY

All three specimens were found in open summit habitats, although this snake presumably also occurs in the patches of forest.

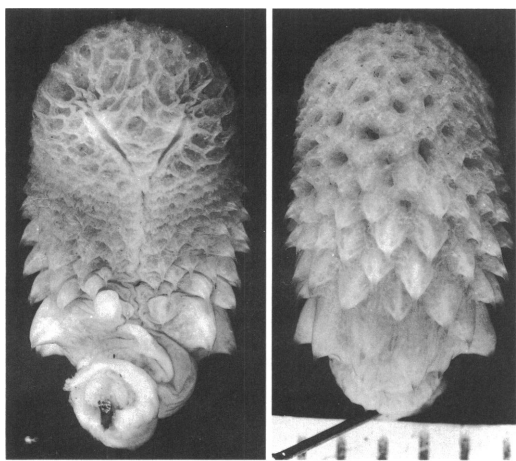


Fig. 28. Hemipenis of *Thamnodynastes yavi*, new species. Everted right organ of AMNH 141342, in sulcate (left) and asulcate view. Scale divisions in mm.

One specimen was found near the small lake, on the ground at night. The holotype was on the ground by day, among low sedges in an open seepage area. The male specimen was in the sun in late afternoon, stretched along a rock in a dry, open place. The last individual obviously had recently eaten and was made to regurgitate the tail of a small unidentified lizard (?*Arthrosaura*) and two fresh lizard eggs thought to be from *Euspondylus* (q.v.). The eggs are the size of *Euspondylus* eggs and probably were eaten at a nest site (see natural history notes under *Euspondylus*).

REMARKS

Thamnodynastes yavi most closely resembles *T. chimanta*, from which it is readily separated by dorsal scale row count, ventral color pattern, and in having an unbifurcated hemipenis. The last statement is based on everted hemipenes of *T. yavi* (fig. 28) compared with a retracted organ from *T. chimanta* (fig. 31B). As noted by Myers (1974: 31), "slight bilobation is not always detectable when the hemipenis is everted," which might conceivably be true for *T. yavi*. But the terminal bifurcation in *T. chimanta* looks sufficiently deep to be reflected in a markedly bilobate apex when the hemipenis is fully inflated. The retracted hemipenis of *T. yavi* is therefore predicted to be either single or bare-

ly bifurcated relative to *T. chimanta* and *T. duida* (fig. 31). Single hemipenes, which are thought to be derived relative to divided ones, sometimes retain a slightly divided insertion of the major retractor muscle as indication of their ancestry (Myers, 1974: 31).

Thamnodynastes yavi is unlikely to be confused with the several other, mainly lowland, species of *Thamnodynastes* that are already known from northeastern South America, namely *T. pallidus* and *T. strigilis* (Roze, 1966) and the recently described *T. gambotensis* (Pérez-Santos and Moreno, 1989). The last species does have 19 scale rows at mid-body like *T. yavi*, but it differs in having apical pits, more ventrals, fewer supralabials and infralabials, and is much lighter, with distinct lines running the length of the pale venter (Pérez-Santos and Moreno, 1989: color figs. 3–4).

Phylogenetic relationships among the named and unnamed species of *Thamnodynastes* remain to be elucidated, as do questions about species diversity and distributions on the tepuis. We are aware of the presence of *Thamnodynastes* on three tepuis—Chimantá in the eastern group of tepuis, Cerro Yaví in the northwestern group, 400 km west of Chimantá, and Cerro Duida in the western group, some 200 km south of Yaví. The genus was not taken during extensive fieldwork on Cerro de la Neblina (McDiarmid and Paolillo (1988), although we collected a specimen of *T. pallidus* (AMNH 134206) at 1270 m on Cerro de Tamacuari on the Brazilian border, 150 km northeast of Neblina.

Thamnodynastes pallidus, which has arboreal tendencies, may be regarded as an invader from lowland rain forest, whereas *T. chimanta* and *T. yavi* appear to be highland endemics. A specimen of this genus from Cerro Duida more resembles *T. chimanta* than its nearer neighbor on Cerro Yaví. This would seem an odd distribution, which requires a closer consideration of the Chimantá population.

NOTES ON *THAMNODYNASTES CHIMANTA* ROZE

Figures 29B, 30B, 31B

This species was described by Roze (1958) on the basis of two specimens (of which we

have examined the holotype)—and Gorzula (1992: 274, 308, photos 162–163) reported on 10 additional specimens—all from the summit of Chimantá Tepui at elevations of 1900–2600 m. Combined data for these 12 specimens, as derived from the papers cited above, are summarized below:

SIZE: The largest specimen, sex not stated (but a presumed female because of its size), is 430 mm total length (331 mm SVL + 99 mm tail); the next largest is a female 403 mm total length (321 mm + 82 mm), followed by the largest male at 376 mm (298 mm + 78 mm). Excluding a presumed juvenile male (191 mm total) and also excluding the large, probable female (430 mm total), six males are 280–376 mm total length (\bar{x} = 337.7 mm) and three females are 336–403 mm total length (\bar{x} = 360.7). The tail is 18.6–25.0 percent of total length in seven males (\bar{x} = 21.60%), and 18.5–21.0 percent in three females (\bar{x} = 19.93%).

SCALATION: Seven (usually) or eight supralabials; usually nine infralabials in a range of 8–11. Ventrals 125–135 in seven males (\bar{x} = 129.7), 125–129 in three females (\bar{x} = 126.67). Subcaudals 49–59 in seven males (\bar{x} = 54.6), 48–52 in three females (\bar{x} = 50.33). Dorsal scale rows 17–15 in 11 specimens, 17–13 in one. Roze (1958) noted that, in the holotype, reduction from 17 to 15 rows occurs by fusion of rows 3 + 4 on each side at the level of the 79th ventral.

COLOR AND PATTERN: Gorzula (op. cit.) gave color from life for a female 321 mm SVL (403 mm total): Dorsal scales reddish brown (*marrones*), being lighter along the middorsum in the vertebral and adjacent halves of paravertebral rows, and along the sides in rows 3½–5½ (these lighter areas lacking in two other females). Supralabials 5–7 with greenish spots. A photograph of the head in profile (Gorzula, op. cit.) shows the ground color of the dark-spotted supralabials to be basically brown from top to bottom, like the rest of the head. In the photograph, the iris is basically pale tan with dark speckling and orange-brown suffusion, the orangish color becoming predominant around the vertically slit pupil.

Gorzula described the ventral plates as being rosy in the center and changing to reddish brown laterally, but did not mention the darker ventral markings. Roze (1958) well

described the anterior venter of the holotype (fig. 29B) as having four obscure, somewhat irregular, dark lines produced by concentration of fine black dots; the dark lines expanding posteriorly, where the dark dots invade all the venter except a lighter, poorly defined median area.

MAXILLARY DENTITION: Roze recorded the maxillary dentition as 14 + 2 for both holotype and paratype. The holotype, however, has 15 + 2 teeth on the right maxilla (gum tissue undisturbed on left one), including the small anteriormost tooth that is frequently overlooked (Myers, 1974: 27).

HEMIPENIS: Roze (1958) briefly described the right retracted hemipenis of the holotype, this organ having been opened along its medial plane and freed at the base. The following new description is of the left hemipenis (fig. 31B).

The left retracted organ extended in situ to the end of subcaudal 10, being bifurcated from the end of subcaudal 10 and with the two slips of the major retractor muscle merging at the middle of subcaudal 11 (combined division of hemipenis tip and muscle less than two subcaudals in length). This organ, opened along its midventral surface and then removed and pinned out for study and illustration (fig. 31B), measures 11.7 mm from base to apex, 8.7 mm from base to division of sulcus spermaticus, 3.8 mm from beginning of calyces (on sulcate side) to apex, and 1.2 mm from base of lobe to apex.

Approximately the distal third of the non-capitate hemipenis is covered with calyces, including the short lobes that comprise the distal tenth of the organ. The distal calyces are ornamented with tiny papillae or spinules whereas the proximal calyces are conspicuously spinulate. The sulcus spermaticus divides in the calyculate region about three-fourths the distance from the base; one sulcus branch extends to the tip of the ventral lobe and the other disappears into and presumably extends to the tip of the unopened dorsal lobe. The basal third of the organ is spinulate; there is no basal pocket. The midsection is heavily spinose; in addition to small spines on the sulcus lips, there are over 60 small to moderate-sized spines vaguely arranged in about a dozen longitudinal rows. There are no markedly enlarged spines. The largest are proximal in each row, progressively decreas-

ing to the small spines at the calyculate area, which is not sharply set off from the spinose midsection.

HABITAT AND NATURAL HISTORY: Gorzula (1992: 274) gave five collecting stations for *Thamnodynastes chimanta* on Chimantá Tepui, which were described and mapped by Huber (1992: 31–33). The elevational range given by Huber is 1920–2600 m; the type locality is 2200 m (Roze, 1958).

Gorzula considered *T. chimanta* to be a diurnal species, which is partly true of *T. yavi*, and noted that two females contained two and three eggs. One of his specimens had eaten an *Anolis*, presumably *A. chrysolepis*, a largely terrestrial species that occurs on many tepuis.

REMARKS: Based on the above summary of *Thamnodynastes chimanta*, a single specimen of this genus collected on Cerro Duida, nearly 70 years ago, appears to represent a different species, named as follows.

***Thamnodynastes duida*, new species**

Figures 29A, 30A, 31A

HOLOTYPE: AMNH 36608 (field no. Tate 63), an adult male from the south end of the summit of Cerro Duida, valley between peaks 7 and 16, about 6610 ft (2015 m) elevation, Amazonas, Venezuela; collected January 27, 1929, by personnel of The Sidney F. Tyler, Jr. Duida Expedition of the American Museum of Natural History. The approximate coordinates are 3°20'N, 65°35'W (see comments under Habitat and Natural History).

ETYMOLOGY: From the type locality, a noun in apposition, in parallel with names of the other known tepui endemics (*T. chimanta* and *T. yavi*).

DIAGNOSIS: In having 17 midbody scale rows, four ventral stripes anteriorly, and a weakly bifurcated hemipenis, *Thamnodynastes duida* more closely resembles the distant (≈ 430 km) *T. chimanta* than it does the geographically closer *T. yavi*. But *T. duida* is a larger snake than *T. chimanta* (fig. 29); at 455 mm total length, the male holotype of *T. duida* is 79 mm (21%) longer than the largest known male *chimanta*. Other differences include a relatively large supraocular in *T. duida* (fig. 30A) and more vivid ventrolateral dark stripes that are distinct for the length of the body (see Remarks and fig. 29A).

DESCRIPTION OF HOLOTYPE

A male, considered adult because of well-calcified hemipenial spines.

PROPORTIONS AND SCUTELLATION: A small snake, 455 mm total length, of which the tail comprises 101 mm (22.2%). Body wider than high, ventrolaterally rounded. Head length about 19 mm from tip of snout to end of mandible; greatest head width across temporal region about 11 mm, or 58 percent of head length. Head wider than neck (6 mm) and body (8 mm). Diameter of right eye 3.2 mm, greater than distance from its anterior edge to edge of naris, going about 1.5 times into length of damaged snout. Pupil of eye elliptical (subcircular, higher than wide, presumably capable of becoming slitlike in life).

Rostral plate visible from above, wider than high. Paired internasals wider than long, narrowed in front, more than half as long as prefrontals. Paired prefrontals about as wide as long, each in contact with its mate and with frontal, supraocular, preocular, loreal, nasal, and internasal. Frontal (damaged) much longer than wide and longer than distance from its anterior edge to tip of snout; posterior end of frontal even with transverse plane connecting posteriormost ends of supraoculars. Supraoculars very large (3 mm wide \times 5 mm long), 87.7 percent of parietal length and at least 95 percent of frontal length, anteriorly narrowed, posteriorly much wider than adjacent part of frontal plate. Parietals 1.4 times longer than broad; interparietal suture shorter than frontal plate, longer than distance from snout to frontal.

Nasal plate long, nearly twice as long as high, in contact with supralabials 1–2. Single large preocular. Two subequal postoculars. Temporals 3+3/2+3; lower primary temporal not reaching lower postocular on left, barely reaching on right. Supralabials 8/8, with 2–3 touching loreal and 4–5 entering orbit. Infralabials 9/9, 1–5 touching an anterior genial and fifth only touching a posterior genial. Anterior genials slightly narrower than posterior genials (width 1.7 vs. 1.8 mm), 1.1 times longer than posterior ones. Minute, inconspicuous tubercles (presumed sensory organs) present on head plates and chin.

Ventrals 130 (first divided), subcaudals in 56 pairs; anal plate divided. Dorsal scales

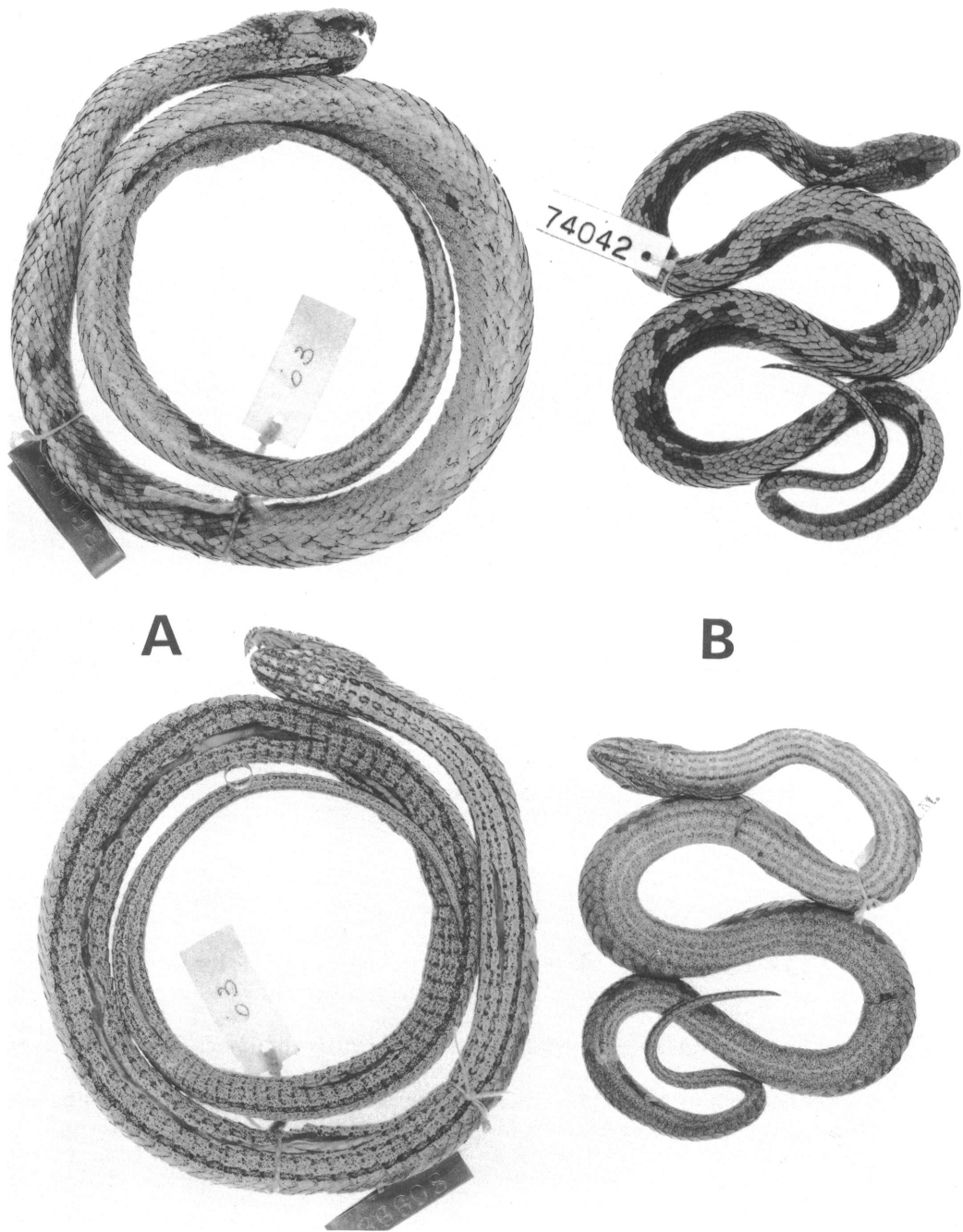


Fig. 29. Holotypes in dorsal and ventral view: A. *Thamnodynastes duida*, new species (AMNH 36608, adult ♂ holotype, 455 mm total length). B. *Thamnodynastes chimanta* Roze (FMNH 74042, adult ♂ holotype, 340 mm total length). Same scale, approximately $\times 0.9$.

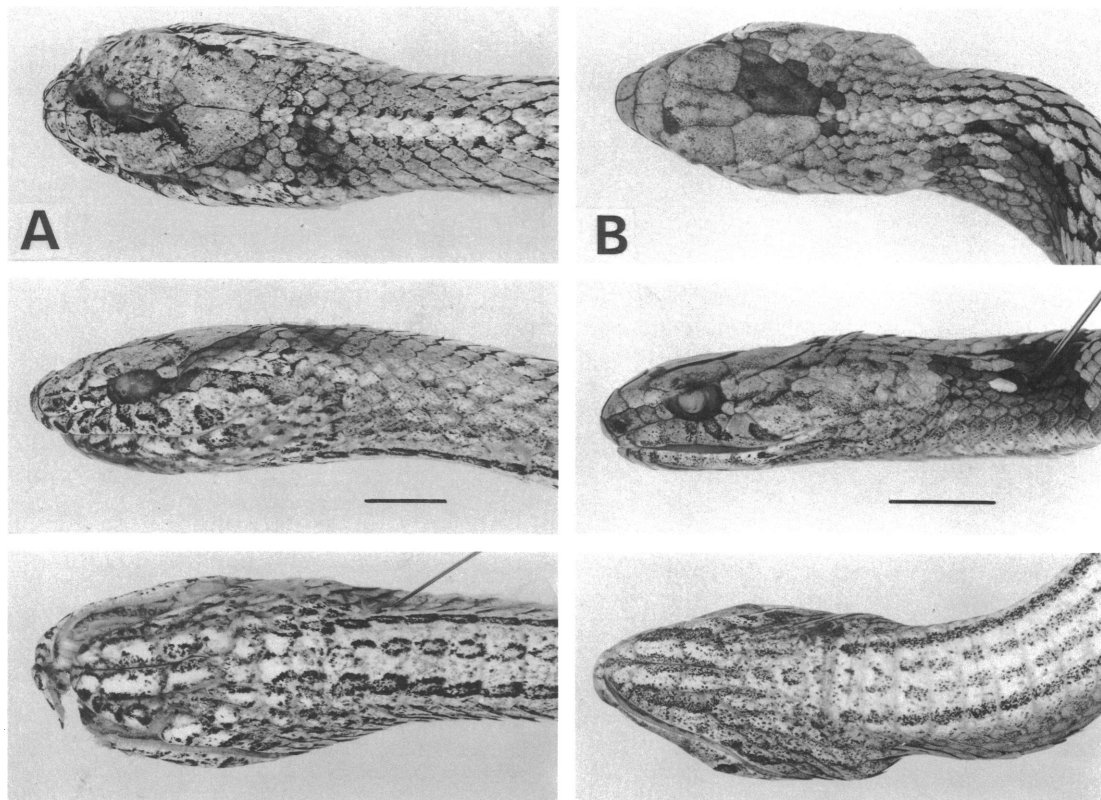


Fig. 30. Details of heads. A. *Thamnodynastes duida*, new species (AMNH 36608, adult ♂ holotype). B. *Thamnodynastes chimanta* Roze (FMNH 74042, adult ♂ holotype). Note relatively larger preocular in *T. duida* ($1.5 \times$ wider than posterior frontal width, about 95% as long as frontal) vs. *T. chimanta* ($1.1 \times$ wider than posterior frontal width, 85% of frontal length). Not to same enlargement, scale lines = 5 mm.

smooth, lacking apical pits or anal ridges, disposed in 17-17-15 rows. Reduction from 17 to 15 rows occurring by fusion of rows 3 + 4 at level of ventrals 81/80.

COLORATION: In preservative (fig. 29A) basically light brown, with darker sides, but turning shades of lighter and darker gray after loss of stratum corneum. Top of head from snout onto parietals indistinctly patterned with small irregular blackish and whitish markings. Head coloration extending onto the neck as a pair of broad (5 scales), black-edged dorsolateral stripes that soon lose the black edging and disappear into the body color. The short neck stripes enclose a white nape stripe on the vertebral and half of each adjacent row. Posteriorly, the vertebral scale row remains pale (melanophores reduced) onto the

base of the tail. The proximal, largely concealed edges of the dorsal scales are black, some of which shows as irregular black dorsal flecking.

Anteriorly, the lower $3\frac{1}{2}$ –4 scale rows are slightly darker than the dorsum, with no definite indication of lateral black line. Posteriorly, after scale row reduction (rows 3 + 4 past midbody), the lower 3 rows are noticeably darker than the dorsum and are edged above with a broken black line (on lower edge of row 4) that extends well onto the tail.

Tip and sides of snout and supralabials whitish, but much darkened by small black-edged gray blotches. A black-edged gray postocular stripe extends across the suture between upper and lower postocular and drops obliquely to the end of the ultimate supra-

labial, with a short horizontal extension behind the mouth being nearly confluent with upper edge of the slightly darkened sides. Above this, a whitish postocular stripe (perhaps merely unmarked or slightly pale ground color in life) extends posteriorly from the upper postocular.

Underside of head and throat yellowish white, heavily blotched with blackish. Rest of ventral and subcaudal surfaces gray, densely speckled with black. A pair of poorly defined but very conspicuous ventrolateral black stripes run the length of the body and extend well onto the tail. Between these, a less conspicuous pair of median stripes diverge from a point under the throat and run in parallel along the anterior third of the venter, being posteriorly lost in dense gray speckling.

MAXILLARY DENTITION: Left maxilla with 14 recurved maxillary teeth, broken at diastema, followed by deeply grooved fangs nearly twice as long as the prediastemal teeth. The fang remaining in place is deeply grooved along its anterior face for most of its length.

HEMIPENIS: The left retracted hemipenis extended in situ to the middle of subcaudal 9, being bifurcated from the end of subcaudal 8 and with the two slips of the major retractor muscle merging at the base of subcaudal 10 (combined division of hemipenis tip and muscle less than two subcaudals in length). This organ, opened along its midventral surface and then removed and pinned out for study and illustration (fig. 31A), measures 13.7 mm from base to apex, 11.2 mm from base to division of sulcus spermaticus, 4.5 mm from beginning of calyces (on sulcate side) to apex, and 0.9 mm from base of lobe to apex.

Approximately the distal third of the non-capitate hemipenis is covered with calyces, including the short lobes that comprise less than a tenth of the organ's length. The distal calyces are ornamented with tiny papillae or spinules whereas the proximal calyces are conspicuously spinulate. The sulcus spermaticus divides in the calyculate region about four-fifths the distance from the base; one sulcus branch extends to the tip of the ventral lobe and the other disappears into and presumably extends to the tip of the unopened dorsal lobe. The basal third of the organ is spinulate; there is no basal pocket. The mid-

section is heavily spinose; in addition to small spines on the sulcus lips, there are over 90 small to moderate-sized spines vaguely arranged in over a dozen longitudinal rows. There are no particularly enlarged spines. The largest are proximal, progressively decreasing to the small spines at the calyculate area, which is not sharply set off from the spinose midsection.

HABITAT AND NATURAL HISTORY

The holotype of *Thamnodynastes duida* was taken by the Museum's 1928–1929 expedition in a summit valley between peaks 7 and 16—on the extreme southern end of the Duida massif (for account of expedition and original map, see Tate and Hitchcock, 1930; also Chapman, 1931). Examination of Tate's expedition journal (pp. 11.14, 12.5, and panoramic sketch 5) places the type locality on the southeastern side of the south end of the summit. The locality was on Tate's "SW trail," which extended from Valley Head Camp (5000 ft.) southwest to High Point Camp (6800 ft) on Peak 7 (7100 ft.). Peak 7 "forms a prominent corner of the mountain where the scarp face of the southwest side meets the south[east] facing precipices." Peak 16 is the terminus of the first major ridge to the northeast of Peak 7, one of several ridges that form "long, sweeping crests sloping gradually away from the southern cliff edge downwards towards the center of the mountain."

The type locality of *Thamnodynastes duida*—i.e., the "valley" between peaks 7 and 16—was described in one place in Tate's journal as a broad ravine at 6610 ft. (2015 m), and he characterized the general area as follows:

General Vegetation SW trail conforms astonishingly with that of the entire plateau. The ridge vegetation is generally dwarfed, but the species are pretty constantly the same as those of the lower parts of the same ridges: i.e. the *Broccinia* Hills vegetation [from the lower, interior part of the summit] in large part comes right to the very top along the crests. Similarly in the valleys. Many of the trees of Central Camp [interior of the summit, 4500 ft.] reach on up the gullies to the very brink of the fault scarp, though remaining much smaller. Even within a few feet of the point of #7 there are tiny ravines up which these dwarfed trees and bushes push their way. . . . What I want to bring out is that there is little change [in the

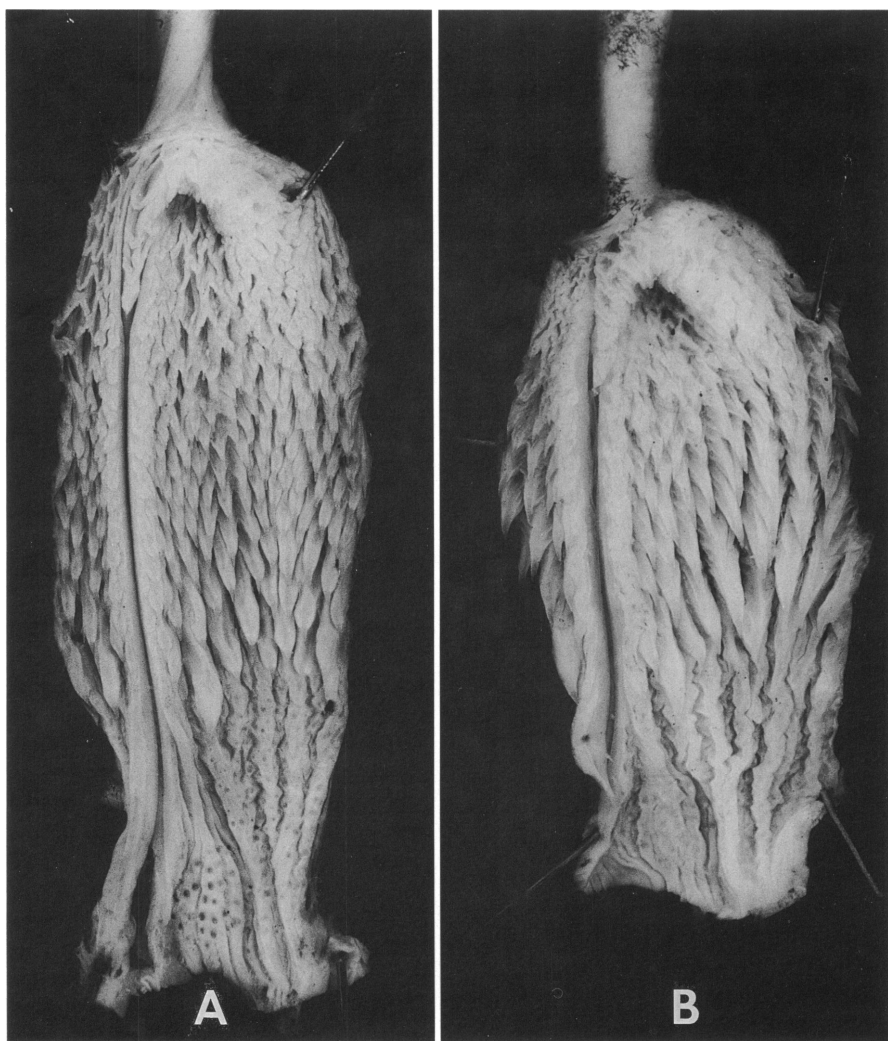


Fig. 31. Retracted hemipenes, $\times 8$. **A.** *Thamnodynastes duida*, new species (AMNH 36608, adult δ holotype). **B.** *Thamnodynastes chimanta* Roze (FMNH 74042, adult δ holotype).

summit vegetation] due to altitude on Duida, and that the significant changes that do signal themselves are due to the folding [of the sandstone], and give resultant forms specialized for valley, slope, stream, ridge, rock face, etc. types of environment. . . . To this folding, as contrasted with level bedded sandstones, is due the notable difference between the general forestation of the summits of Duida and Roraima.

The snake contained a rare lizard, *Rio-lama* sp. (see fn. 5), in its stomach. The lizard had been swallowed headfirst, but the tail obviously had been swallowed separately, tip-first, because the broken end of the tail was

at the stomach opening, barely out of the esophagus.

REMARKS

The three tepui species of *Thamnodynastes* are small snakes, under 500 mm in total length, with *T. duida* being the largest. They occur above 1900 m; the known elevational range of 1920–2600 for *T. chimanta* includes the elevation records for the other two species. At least *T. chimanta* and *T. yavi* are partly if not mostly diurnal, as might be ex-

pected for high-elevation snakes, and all three are known to prey on lizards and at least *T. yavi* feeds also on eggs of lizards.

DISCUSSION

With a summit elevation entirely above 2000 m, Cerro Yaví falls automatically into Huber's (1995a: 36) "homogeneous biogeographic complex, the tepui life zone." Huber (loc. cit.) redefined Mayr and Phelps' (1967) Pantepui as "a biogeographical province comprising all high-tepui ecosystems that are restricted to the Guayana Shield between 1500 and 3000 m elevation, but are best developed between 1800 and 2700 m." It is important to note, however, that the biotic homogeneity referred to by Huber is a relative concept that includes a large number of local endemics among plants (Berry et al., 1995: 166–167) and animals. The northwestern tepuis, including Cerro Yaví, are characterized by a high level of endemism among the plants (op. cit.: 180) and this conclusion also is certainly true of the herpetofauna of Cerro Yaví.

Cerro Yaví stands nearly isolated, rising from evergreen forest at the edge of savanna (fig. 2A). It is but narrowly continuous with Cerro Yutajé to the northwest by way of hills or ridges that probably attain elevations of 1000 m according to various maps. Frequent cloud cover and time restraints kept us from close examination of this area, but views on take off from Yutajé suggest that the hill and ridge connection is blanketed by continuous forest from the immediately adjacent lowlands. The open country on the upper half of the mountain is physically isolated from the open high-elevation formations on Cerro Yutajé.

The herpetofauna of nearby Cerro Yutajé, which is under study, shows only slight resemblance to that of Cerro Yaví. One presumably montane species of frog is similar if not identical to *Eleutherodactylus cantitans* of Cerro Yaví, and a single specimen of *Euspondylus* appears similar to but not identical with the type series of *E. goeleti*. Except for the occurrence of different species of *Eleutherodactylus*, no resemblance at all is seen between the herpetofauna of Cerro Yaví and that of Cerro Guanay, another mountain of the group here designated for convenience as

the "northwestern tepuis." Faunal differences among the northwestern tepuis reflect habitat differences (which correlate with differences in elevation and orographic rainfall) as well as the effects of isolation and all that implies (e.g., extinction events, speciation in situ, lack of dispersal opportunity).

So little is known about the highland *Eleutherodactylus* in the Guayana region that we can draw no further comparisons with the known anuran fauna of Cerro Yaví, except to note the apparent absence of bufonid, dendrobatid, centrolenid, or hylid frogs on the summit of Cerro Yaví. Representatives of most if not all these families probably occur at lower elevations, in the forested canyons, and we suspect that a representative of one or more of these (especially Hylidae) could be found on the summit during the rainy season. Tepui toads of the genera *Oreophrynella* or *Metaphryniscus*, which are restricted to some high tepuis (McDiarmid and Gorzula, 1989; Señaris et al., 1994), have not been found in the northwestern tepuis, although Cerro Yaví is within the elevational range. Absence of summit streams precludes some frogs that might otherwise occur, such as most centrolenids, riparian dendrobatids of the genus *Colostethus*, or a member of the *Leptodactylus rugosus* complex. No amphibians were sighted around the small summit lake (fig. 4) nor were tadpoles seen.

The reptiles of Cerro Yaví have phenotypically and ecologically similar counterparts¹¹ on other high tepuis, as mentioned under each species and summarized as follows:

The microteiid lizard *Euspondylus goeleti* has a counterpart on Cerro Jaua (*E. phelpsum*, 1917 m elev.) in addition to the one mentioned above from Cerro Yutajé (*E. sp.*, 1700 m). Although counterparts cannot be explicitly identified for the microteiid tail fragment tentatively referred to *Arthrosaura*, this genus is widespread in the tepuis as already indicated. The anoline lizard *Phenacosaurus bellipeniculus* has counterparts on Chimantá Tepui (*Phenacosaurus sp.*) and Cerro de la Neblina (*P. neblininus*, 1700–2200 m). The dwarf snake *Thamnodynastes yavi* has its counterparts on Chimantá Tepui

¹¹ This term is purposely vague. Although the species compared are very similar, degree of relatedness is unknown.

(*T. chimanta*, 1900–2600 m and Cerro Duida (*T. duida*, 2015 m).

The aforesaid tepuis and their approximate distances from Cerro Yaví are as follows:

CERRO YUTAJÉ, northwestern tepuis, 20 km northwest (*Euspondylus* sp.).

CHIMANTÁ TEPUI, eastern group of tepuis, 400 km east (*Phenacosaurus* sp., *Thamnodynastes chimanta*).

CERRO JAUA, east-central group of tepuis, 180 km southeast (*Euspondylus phelpsorum*).

CERRO DUIDA, west-central group of tepuis, 250 km south (*Thamnodynastes duida*).

CERRO DE LA NEBLINA, southern group of tepuis, 550 km south (*Phenacosaurus neblininus*).

Thus, one of the known counterparts occurs on nearby Cerro Yutajé, in the same tepui group. Otherwise, congeneric species similar to the lizards and snakes of Cerro Yaví are known as widely scattered highland endemics in the eastern, east-central, west-central, and southern groups of tepuis—approximately 180–550 km from Cerro Yaví (see foldout or pocket maps in Mayr and Phelps, 1967, and Steyermark et al., 1995).

These endemic highland reptiles may be perceived either as the result of (1) independent colonizations from unknown, lowland ancestors, or (2) as relicts of a widespread fauna. Individual tepuis certainly do show evidence of some geographic continuity with adjacent lowlands (e.g., Donnelly and Myers, 1991), although lowland elements seem to be absent on the summit of Cerro Yaví. But the fact that the summit reptiles of Cerro Yaví have counterparts widely scattered in Pantepui suggests to us that there was a widespread fauna, which probably also included such other reptiles as *Riolama* (see fn. 5) and

Liophis and various frogs including especially the *Oreophrynella*-like bufonids.

Inasmuch as this hypothesized herpetofauna seems unlikely to predate the erosional events that left the present-day tepuis, it seems probable that vicariance resulted from profound climatic and vegetational change. If that is the case, the present-day spotty occurrence of the faunal remnants doubtless has several reasons, including (1) woefully incomplete sampling of the small and depauperate montane faunas, (2) habitat differences among tepuis, (3) extinction events, especially on the smaller tepuis (such as Cerro Yaví), and (4) original, regional faunal differences within Pantepui.

Tropical herpetofaunas are difficult to sample thoroughly, in large part because species are often secretive and many seem to occur at low population density, characteristics that apply to the depauperate tepui faunas as well as to species-rich lowland faunas. Dry season collections such as ours are particularly likely to overlook parts of the fauna and only a few tepuis have been reasonably well sampled; clearly, collections should be repeated at different seasons, although this ideal is rarely practical. And more tepuis need to be sampled with some degree of intensity before theorizing gains substance. Nonetheless, we believe that emerging data are suggestive of some degree of historical unity for part of the present-day herpetofauna of Pantepui. Relatively widespread highland species are uncommon in this fauna, which we suggest is largely composed of sets of related endemic species. The precise relationships of these species will remain enigmatic so long as entire local faunas remain to be discovered.

REFERENCES

- Berry, Paul E., Otto Huber, and Bruce K. Holst
1995. Floristic analysis and phytogeography. In J. A. Steyermark, P. E. Berry, and B. K. Holst (general eds.), *Flora of the Venezuelan Guayana*, 1: 161–191. St. Louis: Missouri Bot. Garden.
- Chapman, Frank M.
1931. The upper zonal bird-life of Mts. Roraima and Duida. *Bull. Am. Mus. Nat. Hist.* 63(1): 1–135.
- Czeczuga, B.
1980. Carotenoids in some parts of certain species of lizards. *Comp. Biochem. Physiol.* 65B: 755–757.
- Donnelly, Maureen A., and Charles W. Myers
1991. Herpetological results of the 1990 Venezuelan expedition to the summit of Cerro Guaiquinima, with new tepui reptiles. *Am. Mus. Novitates* 3017: 54 pp.

- Donnelly, Maureen A., Roy W. McDiarmid, and Charles W. Myers
 1992. A new lizard of the genus *Arthrosaura* (Teiidae) from southern Venezuela. *Proc. Biol. Soc. Washington* 105(4): 821–833.
- Estes, Richard, Kevin de Queiroz, and Jacques Gauthier
 1988. Phylogenetic relationships within Squamata. In R. Estes and G. Pregill (eds.), *Phylogenetic relationships of the lizard families*, pp. 119–281. Stanford, CA.: Stanford Univ. Press.
- Gorzula, Stefan
 1992. La herpetofauna del macizo del Chimantá. In O. Huber (ed.), *El macizo del Chimantá*, pp. 267–280 + 304–310 (= photographs 152–171). Caracas: Oscar Todtmann Editores.
- Harris, Dennis M.
 1985. Infralingual plicae: support for Boulenger's Teiidae (Sauria). *Copeia* 1985(3): 560–565.
- Hitchcock, Charles B.
 1947. The Orinoco-Ventuari region, Venezuela. *Geogr. Rev.* 37(4): 525–566 + foldout map.
 1948. La región Orinoco-Ventuari, Venezuela. *Bol. Soc. Venezolana Cien. Nat.* 11(72): 131–179 + foldout map (translation of 1947 paper).
- Huber, Otto
 1992. El área de estudio y su exploración. In O. Huber (ed.), *El macizo del Chimantá*, pp. 23–36. Caracas: Oscar Todtmann Editores.
 1995a. Geographical and physical features. In J. A. Steyermark, P. E. Berry, and B. K. Holst (general eds.), *Flora of the Venezuelan Guayana*, 1: 1–61. St. Louis: Missouri Bot. Garden.
 1995b. History of botanical exploration. In J. A. Steyermark et al., op. cit. 1: 63–95.
 1995c. Vegetation. In J. A. Steyermark et al., op. cit., vol. 1, pp. 97–160.
- Lancini V., Abdem R.
 1968. El género *Euspondylus* (Sauria: Teiidae) en Venezuela. *Publ. Ocas. Mus. Cien. Nat. (Caracas)*, Zool. 12: 8 pp.
- Lasser, Tobias, and Bassett Maguire
 1950. A report on the plants of the Phelps Cerro Yaví Expedition of 1947. *Brittonia* 7(2): 75–90.
- Lynch, John D.
 1976. The species groups of the South American frogs of the genus *Eleutherodactylus* (Leptodactylidae). *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* 61: 24 pp.
1979. Leptodactylid frogs of the genus *Eleutherodactylus* from the Andes of southern Ecuador. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* 66: 62 pp.
- 1980a. Systematic status and distribution of some poorly known frogs of the genus *Eleutherodactylus* from the Chocoan lowlands of South America. *Herpetologica* 36: 175–189.
- 1980b. Two new species of earless frogs allied to *Eleutherodactylus surdus* (Leptodactylidae) from the Pacific slopes of the Ecuadorian Andes. *Proc. Biol. Soc. Washington* 93: 327–338.
1984. A new species of *Eleutherodactylus* (Amphibia: Anura: Leptodactylidae) from southern Andean Colombia. *Herpetologica* 40: 234–237.
1986. The definition of the Middle American clade of *Eleutherodactylus* based on jaw musculature (Amphibia: Leptodactylidae). *Ibid.* 42: 248–258.
- 1992a. A new species of leptodactylid frog (*Eleutherodactylus*) from southwestern Colombia. *Ibid.* 48: 347–350.
- 1992b. Distribution and variation in a Colombian frog, *Eleutherodactylus erythroleura* (Amphibia: Leptodactylidae). *Stud. Neotrop. Fauna Environ.* 27(4): 211–226.
- 1992c. A new species of *Eleutherodactylus* (Amphibia: Leptodactylidae) from western Colombia with cranial co-ossification. *Copeia* 1992 (3): 826–831.
1994. Two new species of the *Eleutherodactylus conspicillatus* group (Amphibia: Leptodactylidae) from the Cordillera Oriental of Colombia. *Rev. Acad. Colombiana Cienc.* 19(72): 187–193.
- Lynch, John D., and William E. Duellman
 1980. The *Eleutherodactylus* of the Amazonian slopes of the Ecuadorian Andes (Anura: Leptodactylidae). *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* 69: [iv] + 86 pp.
- Lynch, John D., and Charles W. Myers
 1983. Frogs of the *fitzingeri* group of *Eleutherodactylus* in eastern Panama and Chocoan South America (Leptodactylidae). *Bull. Am. Mus. Nat. Hist.* 175(5): 481–568.
- Mayr, Ernst, and William H. Phelps, Jr.
 1967. The origin of the bird fauna of the South Venezuelan highlands. *Bull. Am. Mus. Nat. Hist.* 136(5): 269–327 + pls. 14–21 + foldout map.
- McDiarmid, Roy W., and Alfredo Paolillo O.
 1988. Herpetological collections—Cerro de la

- Neblina, updated January 1988. In C. Brewer-Carías (ed.), *Cerro de la Neblina. Resultados de la expedición 1983–1987*, pp. 667–670. Caracas: Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales.
- McDiarmid, Roy W., and Stefan Gorzula
1989. Aspects of the reproductive ecology and behavior of the tepui toads, genus *Or-eophrynella* (Anura, Bufonidae). *Copeia* 1989(2): 445–451.
- McDowell, Samuel B.
1979. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part III. Boinae and Acrochordoidea (Reptilia, Serpentes). *J. Herpetol.* 13(1): 1–92.
- Myers, Charles W.
1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. *Bull. Am. Mus. Nat. Hist.* 153(1): 1–262.
1982. Spotted poison frogs: descriptions of three new *Dendrobates* from western Amazonia, and resurrection of a lost species from “Chiriqui.” *Am. Mus. Novitates* 2721: 23 pp.
- Myers, Charles W., and William E. Duellman
1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *Am. Mus. Novitates* 2752: 32 pp.
- Myers, Charles W., Ernest E. Williams, and Roy W. McDiarmid
1993. A new anoline lizard (*Phenacosaurus*) from the highland of Cerro de la Neblina, southern Venezuela. *Am. Mus. Novitates* 3070: 15 pp.
- Pérez-Santos, Carlos, and Ana G. Moreno
1989. Una nueva especie de *Thamnodynastes* (Serpentes: Colubridae) en el norte de Colombia. *Boll. Mus. Reg. Sci. Nat., Torino*, 7(1): 1–9.
- Phelps, Kathleen D. de
1987. Memorias de Misia Kathy de un Yaví desconocido. Expedición Phelps al Cerro Yaví 31 de enero al 14 de marzo de 1947. Caracas: privately printed, 151 + iv pp. [reprinted 1994].
- Phelps, William H., Jr.
1947. The ornithological collections, pp. 559–560 in C. B. Hitchcock (see above).
- Presch, William
1983. The lizard family Teiidae: is it a monophyletic group? *Zool. J. Linn. Soc.* 77: 189–197.
- Rivero, Juan A.
“1982” [1984]. Los *Eleutherodactylus* (Amphibia, Salientia) de los Andes Venezolanos. II. Especies subparameras. *Mem. Soc. Cienc. Nat. La Salle* 118: 57–132.
- Roze, Janis A.
1958. Los reptiles del Chimantá Tepui (Estado Bolívar, Venezuela) colectados por la expedición botánica del Chicago Natural History Museum. *Acta Biol. Venezuelica* 2(25): 299–314.
1966. La taxonomía y zoogeografía de los ofidios de Venezuela. Caracas: Univ. Central Venezuela, 362 pp.
- Savage, Jay M., and W. Ronald Heyer
1967. Variation and distribution in the treefrog genus *Phyllomedusa* in Costa Rica, Central America. *Beitr. Neotrop. Fauna* 5(2): 111–131.
- Señaris, J. Celsa, José Ayarzagüena, and Stefan Gorzula
1994. Los sapos de la familia Bufonidae (Amphibia: Anura) de las tierras altas de la Guayana Venezolana: descripción de un nuevo género y tres especies. *Publ. Asoc. Amigos Doñana* 3: 37 pp.
- Steyermark, Julian A., Paul E. Berry, and Bruce K. Holst (general eds.)
1995. *Flora of the Venezuelan Guayana*. St. Louis: Missouri Bot. Garden, vol. 1, xxii + 320 pp. + 84 color pls. + 2 accompanying maps (topographic and vegetation).
- Tate, George H. H., and Charles B. Hitchcock
1930. The Cerro Duida region of Venezuela. *Geogr. Rev.* 20(1): 31–52.
- Uzzell, Thomas
1973. A revision of lizards of the genus *Prionodactylus*, with a new genus for *P. leucostictus* and notes on the genus *Euspondylus* (Sauria, Teiidae). *Postilla* 159: 67 pp.
- Vanzolini, P. E.
1986. Addenda and corrigenda to the Catalogue of Neotropical Squamata. *Smithson. Herpetol. Info. Serv.* 70: 25 pp.
- Walker, Charles F., and Frederick H. Test
1955. New Venezuelan frogs of the genus *Eleutherodactylus*. *Occas. Pap. Mus. Zool. Univ. Michigan* 56: 1–10.