Two New Species of Myersiohyla (Anura: Hylidae) from Cerro De La Neblina, Venezuela, with Comments on Other Species of the Genus

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Two new species of *Myersiohyla* (Anura: Hylidae) from Cerro de la Neblina, Venezuela, with comments on other species of the genus

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ABSTRACT

Two new species of *Myersiohyla* are described from the 1984–1985 Cerro de la Neblina Expedition in southern Venezuela, together with notes on the genus and a test of its monophyly, which has been challenged in recent studies. The inclusion of new sequences results in a monophyletic *Myersiohyla* that is better supported than in earlier analyses. One of the new species is similar to *M. inparquesi*, with which it has been confused previously. This newly described species has, like *M. inparquesi,* a tadpole with a dorsoventrally flattened body and the largest labial toothrow formula so far reported for anuran larvae (16/21). It differs from *M. inparquesi* in larval characters, adult coloration, and vocalization. The other new species is unique in having a color pattern composed of stellate melanophores over a greenish ground color. Comments on the holotype of *M. loveridgei* provide details overlooked in previous references to this rare species and stress the need to establish diagnostic characters that might differentiate it from *M. aromatica*. Furthermore, we report one specimen not assigned to any species from Huachamacary Tepui, only 25 km from the type locality of *M. loveridgei*. So far, all studied species of *Myersiohyla* have relatively large (2.8–3.2 mm), yolky ovarian eggs, a character state shared with several other frogs in Cophomantini (*Hyloscirtus, Aplastodiscus,* the *Hypsiboas benitezi* species group), and likely a

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plesiomorphic character state for the tribe. We report and illustrate the occurrence of a mental gland in some species of *Myersiohyla* and present a short discussion on odorous volatile secretions reported in some species of this genus.

The following species are described or discussed herein: *Myersiohyla chamaeleo* new species, p. 8, *M. neblinaria* new species, p. 25, *M. loveridgei* (Rivero), p. 38, *Myersiohyla* species inquirenda, p. 40, and *M. kanaima* (Goin and Woodley), p. 42. Following the International Code of Zoological Nomenclature, the nominal type species of *Myersiohyla* is changed from *Hyla inparquesi* to *Myersiohyla neblinaria* (p. 42).

INTRODUCTION

The former *Hyla aromatica* group was erected by Ayarzagüena and Señaris ("1993" [1994]) for two species from the Guiana highlands, *H. aromatica* and *H. inparquesi*. Faivovich et al. (2005) presented a phylogenetic analysis of Hylidae, with emphasis on the subfamily Hylinae. In their analysis, they included a single species of the group that they identified as *H. inparquesi*. Their results supported a sister-group relationship between this species and former *H. kanaima*, a species previously included in the former *Hyla geographica* group. Furthermore, these two species are the sister taxa of a pectinated series that includes four genera of Hylinae: *Hyloscirtus* (a resurrected name for the former *Hyla armata*, *H. bogotensis*, and *H. larinopygion* groups), *Bokermannohyla* (a newly described genus for the former *Hyla circumdata*, *H. claresignata*, *H. martinsi*, and *H. pseudopseudis* groups), *Aplastodiscus* (redefined to include also the former *H. albofrenata* and *H. albosignata* complexes of the former *H. albomarginata* group), and *Hypsiboas* (a resurrected name for several former species groups of *Hyla*). Because of its position, a new genus was erected to contain the former *H. aromatica* group, *H. kanaima,* and, tentatively, *H. loveridgei: Myersiohyla* (type species: *Hyla inparquesi*).

While *Myersiohyla* is supported by molecular data in the analysis of Faivovich et al. (2005), morphological data supporting its monophyly are still lacking. In the analyses by Wiens et al. (2006), which included most sequences from Faivovich et al. (2005) and Wiens et al. (2005), but analyzing them with different methods, *Myersiohyla* was not recovered as monophyletic, as its two available species formed a polytomy with the clade containing the remaining Cophomantini. A similar result is reported in Wiens et al. (2010), although they note that *Myersiohyla* is weakly recovered in their parsimony analysis, while it is not supported in their maximum-likelihood analysis.

In the definition of the former *Hyla aromatica* group Ayarzagüena and Señaris ("1993" [1994]) included several characters, most of which were also shared with species groups now included in *Hyloscirtus* (e.g., the small nasals, shared with the three species groups; labial toothrow formula [LTRF], shared with the *H. armatus* group; vomerine teeth smoothly S-shaped and more numerous, shared with the *H. larinopygion* group) or even with other hylids. One character state they included (strong odor) could support the monophyly of *Myersiohyla*, but it is still unknown in several species, and has been reported in some species of the *H. bogotensis* group, including *H. jahni* and *H. platydactylus* (La Marca, 1985). Faivovich et al. (2005: 89) warned that their sample of *Myersiohyla inparquesi* did not come from the type locality ("Cumbre del Tepuy Marahuaca-Sur. Estado Amazonas, Venezuela...") but from Cerro de la Neblina, ca. 400 km southward.

Our continuing work with these specimens shows that they are not *M. inparquesi*, but a new species described herein.

The former *Hyla loveridgei* was described by Rivero (1961) based on a single male specimen from Cerro Duida, and this description was supplemented by Rivero ("1971" [1972]) with a second male from the same locality. Since its description the species was rarely mentioned in the literature (see Rivero, 1963, and La Marca and Smith, 1982), until Faivovich et al. (2005) associated it with *Myersiohyla*. A reexamination of the holotype indicates that some comments are in order.

The goals of this paper are to (1) present a new test of the monophyly of *Myersiohyla*; (2) describe two new species of *Myersiohyla* from Cerro de la Neblina, one of which was included in the analysis of Faivovich et al. (2005), including descriptions of their tadpoles and advertisement calls and natural history notes; (3) discuss the status of *M. loveridgei* and complement the available descriptions given by Rivero (1961, "1971" [1972]); and (4) discuss nomenclature, taxonomy, and natural history of *Myersiohyla*.

Material and Methods

Measurements and Terminology: Webbing formula follows conventions of Savage and Heyer (1967) as modified by Myers and Duellman (1982). Measurements follow Duellman's (1970) standards. Abbreviations used throughout the text are: ED (eye diameter), EN (eye-nostril distance), FL (foot length), HL (head length), HW (head width), IND (internarial distance), IO (interocular distance), SVL (snout-vent length), TD tympanum diameter), TL (tibia length), TTL (tadpole total length). Sex was determined by examination of secondary sexual characters (nuptial pads, vocal slits, and expansion of the vocal sac) or, when in doubt, by examination of the gonads. We employ Luna et al.'s (2012) terminology for nuptial pads. Larval terminology follows Altig and McDiarmid (1999a, 1999b), while staging follows the system of Gosner (1960). Lateral line descriptions and terminology are based on the review in Lannoo (1987). Preserved museum specimens were available for *M. loveridgei, M. kanaima*, and *Myersiohyla* sp. All information regarding *M. aromatica* and *M. inparquesi* is that published by Ayarzagüena and Señaris ("1993" [1994]), supplemented with photographs of the type series kindly sent by Gilson Rivas. The information on tadpoles of *M. kanaima* is that provided by MacCulloch and Lathrop (2005).

Vocalizations: Calls were recorded using Sony TCM 5000 cassette tape recorders, with either an Electrovoice microphone (for USNM tapes) or mostly with TEAC ME 120 electrat or Sennheiser MKE 600 microphones (for AMNH tapes). Original tapes and digital copies are deposited in the tape archives of the Division of Amphibians and Reptiles (USNM) and the Department of Herpetology (AMNH). Tape recordings of frog calls were converted to electronic format and analyzed using either RAVEN 1.2.1 (Cornell Lab of Ornithology, 2004) or a Kay CSL 4500 16-bit analog-to-digital converter (sampling rate 22050 Hz). The waveforms and sound spectrographs in figures 11–13 and 24 were analyzed and printed using the CSL software (Kay Elemetrics Corp. [now KayPentax, Lincoln Park, NJ], also separately available as the Windows-based software, Multi-Speech). It has been pointed out by Myers and Donnelly (2008) that such

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

Tadpoles: In the field, tissues of both tadpoles and putative adults were preserved in liquid nitrogen. In the laboratory tadpoles were associated with adults based on absolute sequence similarity between the candidates with a fragment of 16S, the ribosomal gene employed for molecular identification by Thomas et al. (2005), Vences et al. (2005), and Randraniaina et al. (2007). Uncorrected pairwise distances (p-distances) of the static alignment of the same 16S fragment used by those authors, in our case delimited by the primers AR-BR (Palumbi et al., 1991), were calculated in PAUP* 4.0b10 (Swofford, 2002).

DNA isolation, PCR, and sequencing: Whole cellular DNA was extracted from liquid-nitrogen or ethanol preserved tissues with the DNeasy isolation kit (QIAGEN, Valencia, CA). Amplification was carried out in a 25 μl reaction using puRe Taq Ready-To-Go PCR beads (Amersham Biosciences, Piscataway, NJ) or Fermentas Master Mix, using the primers listed by Faivovich et al. (2005: table 2) plus those of Biju and Bossyut (2003) for CXCR4 and Wiens et al. (2005) for a PCR product including fragments of 16S, ND1, and intervening tRNAs. Polymerase chain reaction (PCR)–amplified products were desalted and concentrated using either GE GFX PCR purification kit or EXO/SAP (Fermentas) and labeled with fluorescent-dye labels terminators (ABI Prism Big Dye Terminators, v. 3.1 cycle sequencing kits; Applied Biosystems, Foster City, CA). The labelled PCR products were cleaned using cleanSEQ (Agencourt Biosciences, Beverly, MA). The products were sequenced with an ABI 3730XL (Applied Biosystems, Foster City, CA). All samples were sequenced in both directions to check for potential errors. Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher 3.0. (Gene Codes, Ann Arbor, MI). Complete sequences were edited with BioEdit (Hall, 1999).

Phylogenetic analysis: *Myersiohyla* is recovered by Faivovich et al. (2005) and Wiens et al. (2010, in their parsimony analysis) as the most basal taxon of the hyline tribe Cophomantini, which is the sister taxon of the other three hylid tribes (Dendropsophini, and Hylini + Lophiohylini). Considering the doubts surrounding the monophyly of *Myersiohyla* and differences among previous analyses, we would have preferred to design a phylogenetic analysis that differs as little as possible from those previous tests. However, in this paper we restricted ourselves to a compilation of all the relevant sequence data available for Cophomantini plus seven outgroups, to which we added new sequences for some of those same terminal taxa that were previously missing. For outgroups we included exemplars of Hylini (*Acris crepitans, Hyla cinerea*), Dendropsophini (*Dendropsophus nanus*, *Pseudis minutus, Scinax staufferi*), and Lophiohylini (*Phyllodytes luteolus, Trachycephalus typhonius*). *Phrynomedusa marginata*, a basal phyllomedusine (Faivovich et al., 2010) was used as the root. We will focus on the problem of the monophyly of *Myersiohyla*,

not on the several other issues of the systematics of Cophomantini, although the most obvious results of our analyses will be briefly mentioned, discussed, and further expanded in appendix 1. New sequences were produced for the genes CXCR4 and ND1, and these were added to sequences published by Faivovich et al. (2004, 2005, 2010), Salducci et al. (2005), Wiens et al. (2006), Antunes et al. (2008), Kohler et al. (2010), Lehr et al. (2010), and Coloma et al. (2012). See appendix 2 for list of Genbank numbers.

The rationale for using parsimony as an optimality criterion was advanced by Farris (1983) and discussed by, among others, Goloboff (2003) and Goloboff and Pol (2005). Kluge and Grant (2006), Grant and Kluge (2009), and Wheeler (2012) discussed its conceptualization in a dynamic homology framework (Wheeler, 1996). The phylogenetic analysis was done using POY4.1.1 (Varón et al., 2009) with equal weights for all transformations. Sequences of 12S, 16S, ND1, and intervening tRNA (valine, leucine, isoleucine) were preliminarily delimited in sections of putative homology (Wheeler et al., 2006), and equal-length sequences of nuclear protein-coding genes were considered as static alignments to accelerate the searches. These were performed using the command "Search." This command implements a "driven" search, building Wagner trees using random addition sequences (RAS), tree bisection and reconnection (TBR) branch swapping followed by Ratchet (Nixon, 1999) and tree fusing (Goloboff, 1999). The command (Search) stores the shortest trees of each independent run and does final tree fusing using the pooled trees as a source of topological diversity. Four 72-hour runs of Search were made in parallel at the American Museum of Natural History cluster using 32 processors. The resulting trees were submitted to a final round of swapping using iterative pass optimization (Wheeler, 2003).

We performed a multiple alignment with Clustal-W (Thompson et al., 1997) under default parameters. For the phylogenetic analysis using static parsimony we employed T.N.T., Willi Hennig Society Edition (Goloboff et al., 2008). Tree searches were done with a driven new technology search, using 100 as the search level. The strategy included sectorial searches, tree drift, and tree fusing (Goloboff, 1999). The driven search was requested to hit the minimum length 100 times. Gaps were considered as a fifth state. Parsimony Jackknife (Farris et al., 1996) absolute frequencies were estimated with T.N.T., generating 50 RAS + TBR per replicate, for a total of 1000 replicates. Edition of trees was performed with Winclada (Nixon, 2002).

Study Sites

Specimens of *Myersiohyla* were collected or recorded at seven of the 12 upland camps established during the Cerro de la Neblina Expedition (Brewer-Carias, 1988). Each of these camps is briefly described below and their relative locations are shown in figure 1. *Myersiohyla* was not found during extensive collecting around the Base Camp and in the adjacent lowlands. It clearly is an inhabitant of the highlands.

Camp I consisted of two sites located on the extreme southwestern part of the northern plateau between 1820–1880 m; 00°52′10″ N, 66°05′25″ W. The first site was visited between February 7 and 11, 1984, by William Buck, Charles J. Cole, and others, and located about 500

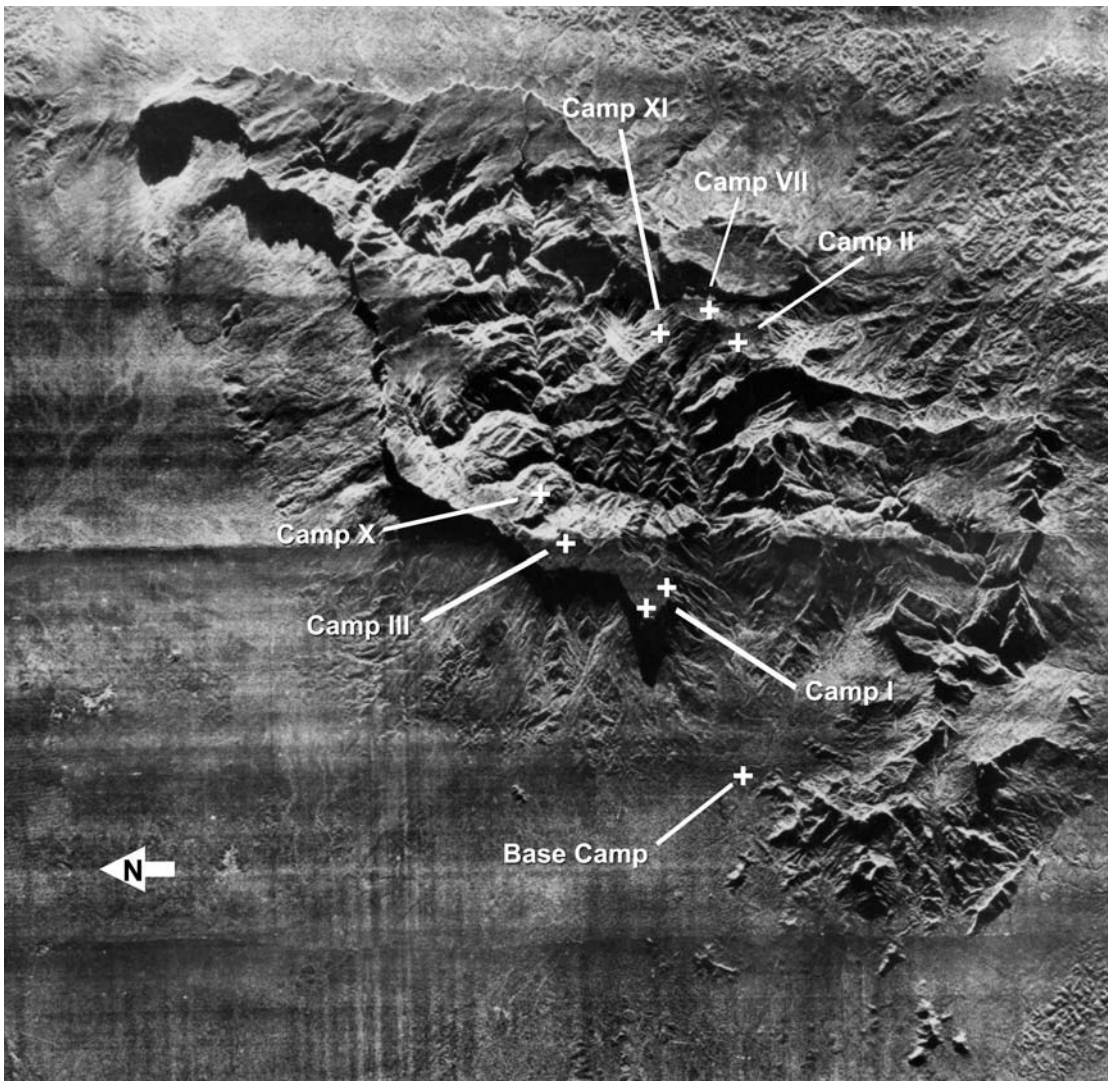

FIG. 1. Side-looking radar image of the Cerro de la Neblina massif showing lowland Base Camp and the seven collecting stations (numbered upland camps) for *Myersiohyla chamaeleo* new species and *M. neblinaria* new species. The Base Camp, at 140 m above sea level, lies below the mouth of the Cañon Grande, which is one of the world's deepest canyons and which separates the highland camps. Collecting stations I, III, and X lie on the westerly side of the canyon at 1820–2130 m; stations II, VII, and XI are on the easterly side at 1390–2100 m. Each nominal new species occurs on both sides of the Cañon Grande. Intercanyon vocalization differences between populations of *Myersiohyla chamaeleo* are striking (pulsatile vs. nonpulsatile) but conceivably related to call sites (unrestrained near streams or confined to plastic bags).

m east on the westernmost promontory (Pico Charles) that was visible from the western lowlands near the Base Camp. The second site was visited from January 31 to February 1, 1985, by Rex Cocroft and others and located closer to the margin of the Cañon Grande; 9.2 km NE of Base Camp (fig. 1). The habitat consisted of an open savanna dominated by species of *Stegolepis* (Rapateaceae), *Brocchinia* (Bromeliaceae), and *Heliamphora* (Sarraceniaceae), and inter-

spersed with exposed rocky areas supporting the endemic small shrub *Bonnetia maguireorum* (= *Neblinaria celiae*, see Huber 1995; Theaceae); two small streams drained the plateau to the northwest and southeast.

Camp II consisted of three sites all situated in an inundated savanna between 2.5 and 3.5 km NE of Pico Phelps between 2085 and 2100 m; 00°50′00″ N, 66°58′48″ W. Pitcher plants (*Heliamphora* sp.), clumps of a large bromeliad (*Brocchinia tatei)*, and various ericaceous and xiridaceous species and other bog plants were common in the area; two species of *Euterpe* palms, *Tyleria* sp. (Ochnaceae), and small bamboos grew in a gallery forest along a small stream that flowed to the west and eventually entered the eastern branch (Cañon Menor) of the Cañon Grande. South of the camp slopes with exposed rocks amidst shrubby *Bonnetia neblinae* (Theaceae) forest rose abruptly to Pico Maguire. McDiarmid, Mercedes Foster, and Richard G. Zweifel worked the site from February 17 to 25, 1984, and McDiarmid and Alfredo Paolillo were there from January 28 to 31, 1985.

Camp III was located in a moderately flooded savanna dominated by species of *Stegolepis*, *Brocchinia,* and *Heliamphora*; *Bonnetia maguireorum* occurred on exposed rocks and *Bonnetia* sp. formed a gallery along a small stream; about 5 km NE Pico Charles and 13.7 km NE Base Camp; 1820 m; 00°54′10″ N, 66°03′50″ W. Cole collected here from February 16 to 18, 1984.

Camp VII included two sites; the helicopter camp at 1850 m was located in a dense stand of a large terrestrial bromeliad (*Brocchinia tatei*) amidst rock outcrops, and the river camp was about 20 min. by trail to the east and along a stream that flowed into the Cañon Menor through cloud forest at 1730 m; the sites were near the edge of an escarpment, which to the south rose to about 2250 m, and were about 1 km NE Pico Maguire and 5 km NE Pico Phelps between 1730 and 1850 m; 00°50′40″ N, 65°58′10″ W. Myers and Alfred Gardner helped establish Camp VII on November 28, 1984; Myers worked there with Linda Ford until the camp was evacuated on December, 3, 1984. Gardner was again in the camp from January 27 to February 14, 1985; Cocroft and Paolillo collected frogs and tadpoles along the stream between February 10 and 14, 1985; Cocroft recorded frogs here as well.

Camp IX was occupied for only a single day because the terrain made helicopter landing difficult. The general area was steep and along a stream that formed the headwaters of the Río Baría and flowed SW into the Cañon Grande; David H. Benzing and Thomas J. Givnish worked the area on February 2, 1985, between 1780 and 1830 m; 1°00′00″ N, 65°53′00″ W; gallery forest bordered the stream which flowed through relatively dense scrub dominated by ericaceous and cyperaceous plants, species of *Brocchinia,* and an especially large *Heliamphora* sp. A single tadpole was taken in the stream.

Camp X was established near a burned area on the north side of the massif near the edge of Cañon Grande, 12.5 km NNW Pico Phelps, 00°54′40″ N, 66°02′30″ W. McDiarmid and Buck worked a rocky area between 1930 and 2130 m from February 12 to 14, 1985. The habitat was described by Givnish et al. (1986) and included large *Bonnetia maguireorum* on the rocky ridges and hillsides and smaller ones in the bottoms; three small creeks anastomosed to form a small stream that emptied abruptly into the Cañon Grande at about 1690 m.

Camp XI was a major camp established on the east slope facing the Cañon Menor about 2.5 km NNW Camp VII and 6.2 km NNE Pico Phelps between 1390 and 1515 m (00°51′45″ N, 65°58′52″ W). Four distinct habitats were accessible: the heliport was on a large flat rock on the slope at 1515 m in the midst of dense scrub forest of *Tyleria* (Ochnaceae) and *Brocchinia*; the camp itself was in this scrub forest at about 1490 m; a rocky stream (1–4 m wide) with large boulders, pools, and cascades flowed through dense gallery forest and was accessible at about 1450 m, and a dense cloud forest with large moss-covered rocks was reachable at lower elevations to about 1390 m. McDiarmid, Paolillo, Cocroft, and several others were there from February 25 to March 1, 1985.

RESULTS OF THE PHYLOGENETIC ANALYSIS

The phylogenetic analysis using direct optimization resulted in two optimal trees (length 25,161 steps) that were hit 974 times during the driven search. Our phylogenetic analyses including all relevant sequences for Cophomantini with additional evidence resulted in a supported *Myersiohyla* (91% jackknife absolute frequency in the static parsimony analysis with gaps considered as fifth state), with *M. kanaima* being the sister taxon of the two new species (fig. 2). Our results continue to support the position of *Myersiohyla* as the sister taxon of the remaining four genera of Cophomantini. Furthermore, the monophyly of *Aplastodiscus, Bokermannohyla, Hyloscirtus*, and *Hypsiboas* is corroborated, as are the relationships among these first hypothesized by Faivovich et al. (2005). See discussion for further reference to the phylogenetic results.

New Species Descriptions

Myersiohyla chamaeleo, new species

Figures 3–14

Hylid sp. nov. a – McDiarmid and Paolillo (1988). Species list.
Hylid sp. C (Neblina) – McDiarmid and Donnelly (2005). Species list.

Holotype: AMNH A-131173 (♂). Venezuela: Departamento Amazonas: Cerro de la Neblina: Camp I, 1820–1880 m, collected by C. J. Cole on February 7, 1984.

Paratopotypes: AMNH A-131174 (♂), USNM 562048 (♂), USNM 562054 (♂), USNM 562062 (♀), USNM 562063 (♂), USNM 562064 (♂).

Paratypes: Venezuela: Departamento Amazonas: Cerro de la Neblina: Camp II, 2085–2100 m: AMNH A-131176 (♀), USNM 562051 (♂). Camp III, 1820 m: AMNH A-131178 (♂, recorded). Camp VII, 1730-1850 m: USNM 562065 (♂, recorded), AMNH A-123709 (♂), USNM 562055 (♂); Camp X, 1690 m: USNM 562057 (♂), USNM 562058 (♂), USNM 562066 (♀), USNM 562067 (♂). Camp XI, approx. 1450 m: USNM 562059 (♂, recorded), USNM 562060 (♂, recorded), USNM 562061 (♀), USNM 562068 (♀).

Referred Specimens: Venezuela: Departamento Amazonas: Cerro Neblina: Camp II, 2085–2100 m.: USNM 562049–562050, 562052–562053, AMNH A-131175, 131177 (juveniles). Camp

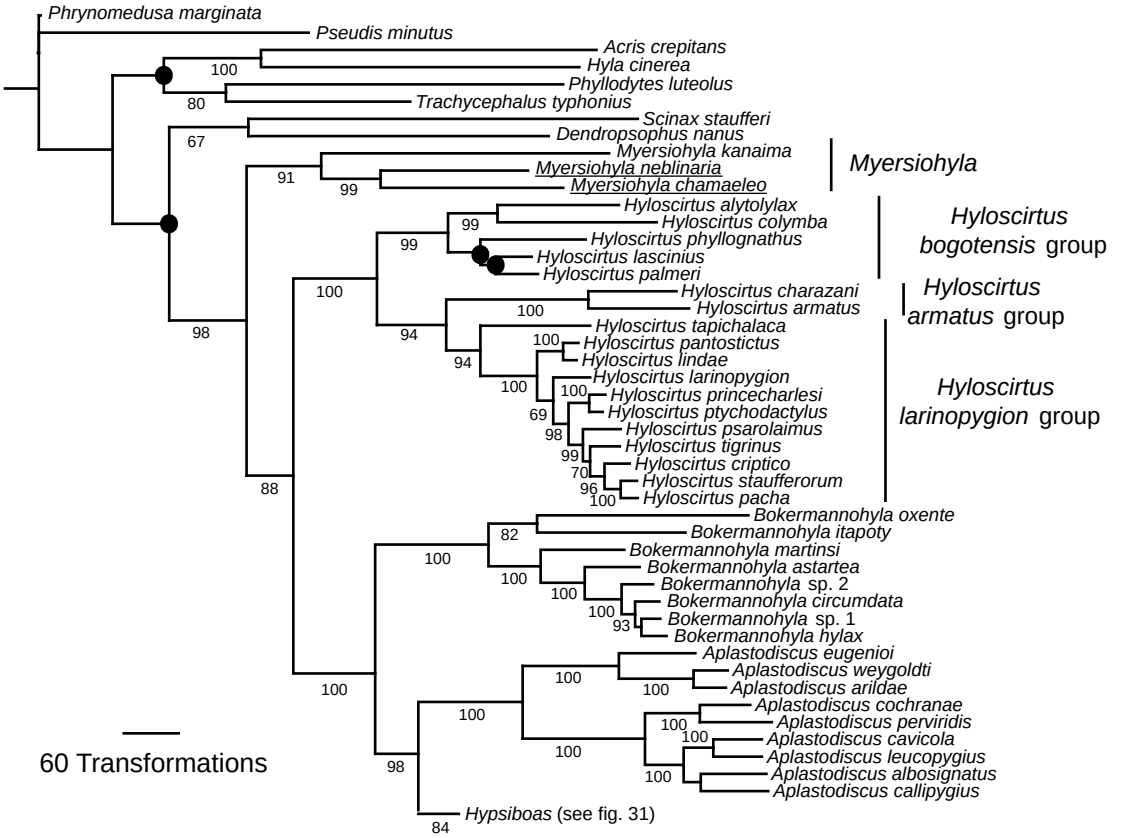

FIG. 2. One of the most parsimonious trees obtained with direct optimization (length 25161 steps). Differences with the topology obtained with static parsimony are minimal and involve poorly supported nodes. The circle indicates the nodes that collapse in the strict consensus. The new species of *Myersiohyla* are underlined. Values around nodes are jackknife parsimony absolute frequencies calculated using the static parsimony analysis. Nodes lacking values have < 50% absolute jackknife frequencies. The internal relationships of *Hypsiboas* are shown in figure 31.

VII: USNM 562056 (juvenile).

Etymology: The species name *chamaeleo* is a noun in apposition. It is derived (like that of the lizard genus *Chamaelo*) from Latin *chamaeleon* < Greek *chamaileōn*, a kind of lizard—in reference to this frog's similar ability to change coloration.

Diagnosis: A species of *Myersiohyla* characterized by (1) SVL of male 44.6–49.6; female 46.0–56.9; (2) presence of two nuptial pads; (3) absence of a row of tubercles along the ventrolateral edge of the arm; (4) an externally evident mental gland in males; (5) thighs and shank without longitudinal bars; (6) dorsal color pattern with stellated melanophores over a ground color; (7) presence of a slip of m. depressor mandibulae that originates on the dorsal fascia at the level of the m. levator scapulae; (8) unpigmented eggs; (9) tadpoles with globular body; (10) fins reaching the base of the tail; (11) labial tooth row formula (LTRF) 4/7 to 6/11.

Comparison with other species: The new species differs from *Myersiohyla inparquesi*, *M. kanaima*, *M. loveridgei*, and *M. neblinaria,* n. sp., by having two nuptial pads, and by its dorsal color pattern (stellated melanophores over a ground color), with yellowish flanks in life, the

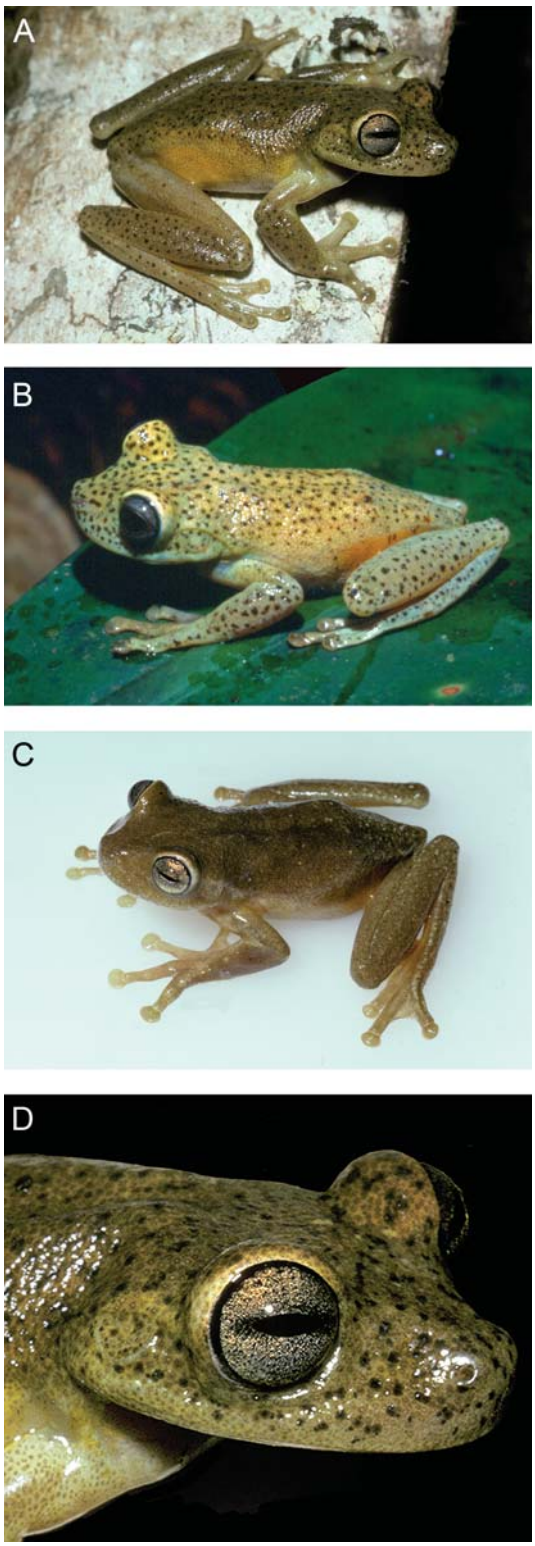

FIG. 3. **A.** Holotype of *Myersiohyla chamaeleo* (AMNH A-131173, Camp I). Photograph by R.W. McDiarmid. **B.** Paratype of *Myersiohyla chamaeleo* (AMNH A-131178, Camp III). Photograph by C.J. Cole. **C.** Paratype of *Myersiohyla chamaeleo* (USNM 562051, Camp II). Photograph by R.W. McDiarmid. **D.** Magnification of fig. 3A showing detail of the head.

absence of a row of tubercles along the ventrolateral edge of the arm, and the presence of a slip of m. depressor mandibulae that originates on the dorsal fascia at the level of the m. levator scapulae (absent on *M. kanaima*, and *M. neblinaria*; unknown in *M. aromatica*, *M. inparquesi*, and *M. loveridgei*). The color pattern differentiates the new species from *M. aromatica* (marbled with copper and dark brown; dark brown bars on arms, thighs and shanks). The new species can also be differentiated from *H. kanaima* because of its larger males (44.6–49.6, vs. 37.0–37.8 mm, $\bar{X}$= 37.4, *n* = 5, in *M. kanaima*), more robust body (slender in *M. kanaima*), more developed prepollex (proportionally reduced in *M. kanaima*), and its unpigmented eggs (eggs completely pigmented in *M. kanaima*). Furthermore, tadpoles of *M. chamaeleo* have a more reduced labial tooth row formula than those of *M. aromatica* and *M. neblina* (maximum 6/11 vs. a minimum of 10/17 in *M. aromatica*; tadpoles unknown in *M. loveridgei*), but larger than in *M. kanaima* (2/4; MacCulloch and Lathrop, 2005, but see discussion).

Description of the holotype (figs. 3A, 4–5): Body robust; head barely longer than wide; as wide as body; head width 34% SVL; head length 36% SVL. Snout in dorsal view rounded, in profile truncate; canthus rostralis rounded; loreal region concave; lips not flared; nares slightly protuberant, directed dorsolaterally, and posterior to anterior margin of lower jaw. Internarial region and top of head slightly depressed. Interorbital distance less than eyelid. Eye prominent; diameter 90% of eye-nostril distance. Tym-

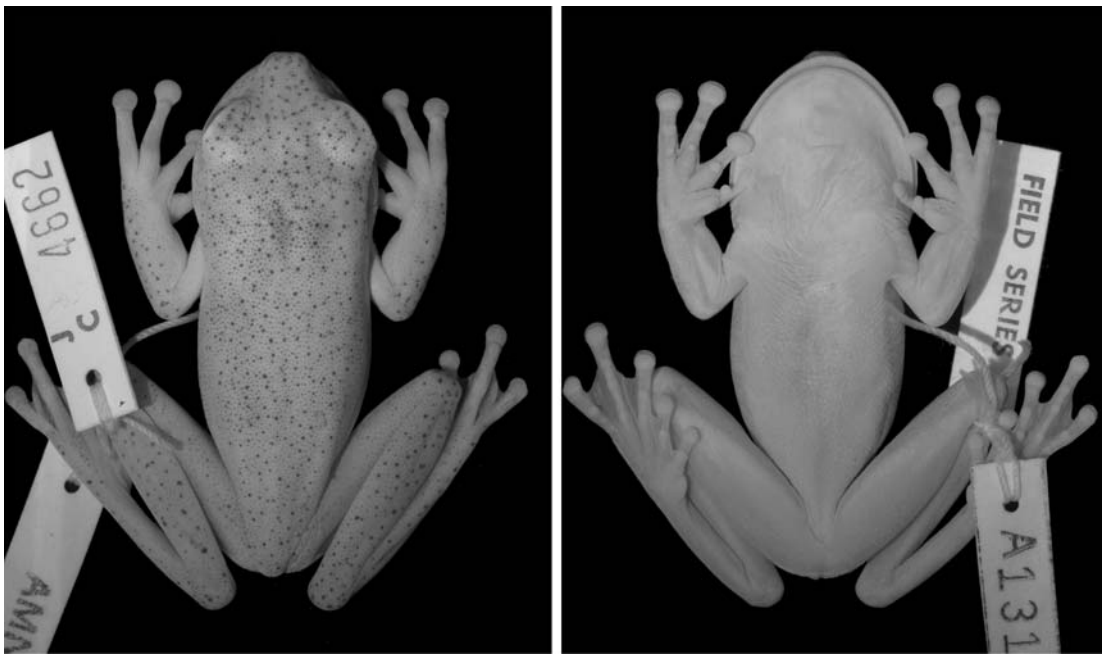

FIG. 4. Dorsal and ventral view of the holotype of *Myersiohyla chamaeleo* (AMNH A-131173, 47.4 mm SVL).

panum rounded, diameter 63% of eye diameter. Supratympanic fold thin, starting behind the eye and extending to the posterior margin of the insertion of the arm, obscuring dorsal margin of tympanic membrane.

Vomerine teeth in two medially convergent series that contour the posterior margin of the choanae and give a slight S-shape to each series. Each series bears 14 (right) and 15 (left) teeth. Choanae kidney shaped; separated by a distance greater than their maximum diameter. Tongue ovoid, attached overall (narrowly free around lateral and posterior margin), posterior margin notched. Vocal slits present, longitudinal, originating on the sides of the tongue and extending to the corner of the mouth. Vocal sac single and subgular. Macroscopically evident glandular tissue irregularly distributed in the mental area, extending posteriorly up to the beginning of the vocal sac.

Forearm robust and prominent. No row of tubercles along ventrolateral edge of forearm. Fingers long and slender, bearing large, ovoid discs, with its circumferential groove clearly defined by the size difference between the disc and the smaller pad; width of disc on third finger 88% tympanum diameter. Relative lengths of fingers 1<2<4<3. Fingers webbed basally, without dermal fringes; webbing formula of outer fingers **II** 2⅓–3½ **III** 3–3 **IV**. Subarticular tubercles large; the distal tubercle of finger IV ovoid, the others are round. Large supernumerary tubercles, flat and irregularly shaped on the base of fingers III, IV, and V. Outer metacarpal tubercle small, nearly round and bifid, barely noticeable. Inner metacarpal tubercle large, elliptical. Prepollex enlarged, semicircular. Nuptial excrescences in two contiguous, discrete pads, one along the medial margin of the prepollex, and the other medially and dorsally in the area between the distal margin of the

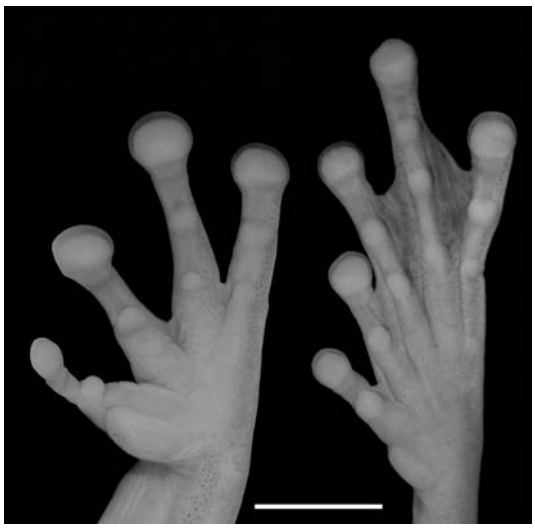

FIG. 5. Ventral view of hand and foot of the holotype of *Myersiohyla chamaeleo* (AMNH A-131173). Scale bar = 5 mm.

prepollex and the subarticular tubercle; they are composed of a thin glandular pad, covered by minute dark epidermal projections.

Hind limbs slender; tibia length 51% of snout-vent length; foot length 36% SVL. Calcar absent; tarsal fold absent; subtle dermal ridge along the margin of the tarsus. Inner metatarsal tubercle large, elliptical; outer metatarsal tubercle round. Toes short, bearing discs smaller than those on fingers; disc of toe I smaller than others; relative length 1<2<3≈5<4; webbing formula **I** 2–2^{+} **II** 1^{+}–2½ **III** 1^{+}–2½ **IV** 2–1^{+} **V**. Subarticular tubercles large, round. Cloacal opening directed posteroventrally, at upper level of thighs; some flat, irregular, whitish tubercles scattered around and below cloaca. Dorsal skin smooth, granular ventrally. Pectoral fold absent.

Measurements of holotype (all in mm): SVL 47.4; HL 17.1; HW 16.1; IND 3.4; IO 5.3; ED 4.3; EN 4.8; TD 2.7; TL 24.3; FL 17.1.

Coloration of holotype in life: From field notes taken by Cole (Feb. 7, 1984): Dorsum reddish brown (as at night when caught) but sometimes changing to light green when awakened in daytime, with numerous scattered dark brown dots. Sides, anterior and posterior surfaces of thighs, and ventral surfaces of lower legs orangish gold, but much duller on legs than on sides (bright). Throat pale green. Ventral surfaces of arms, chest, and abdomen translucent, with pinkish purple showing through. Iris black with an intricate metallic copper reticulum.

Coloration of holotype in preservative: The dorsal ground coloration is light cream. The dorsum of body, forelimbs, and hind limbs are homogenously covered by two types of chromatophores that vary in size. The larger ones are brown and stellate, with creamy white centers. The smaller are round glossy white guanophorelike units. The fact that some of these have white stellated arms raises the possibility that these are early stages in the maturating process of the brown units described above, or considering that this species easily changes color in life, they could be just different physiologic stages of the same pigment unit. Pigment is nearly absent from the margins of the eyelid, where the background coloration is creamy yellow. The large chromatophores are less abundant or absent in the hidden areas of thighs, shanks and feet, as well as on the dorsal surfaces of the hands and feet. They are absent on the flanks of the body, where only small chromatophores are present. The ventral coloration of body, throat, and surfaces of limbs is slightly paler than the dorsal ground color.

Variation among paratypes: Morphological variation is relatively low. On specimens USNM 562051, 562054, 562060, 562062–64, which were fixed with their thumbs slightly deflected, the outer metacarpal tubercle is more obvious, as are several large, flat supernumerary tubercles on the proximal surfaces of the digits. With the exception of USNM 562061 and AMNH

A-131176, most paratypes, unlike the holotype, have a median notch on the subarticular tubercle of finger IV. Males show two discrete nuptial pads (fig. 6A), that in a few cases almost coalesce medially because of the proliferation of epidermal projections (fig. 6B) into the space separating the glandular pads.

Variation of the webbing formula can be expressed as: **I** (1½–2)–(2–2^{+}) **II** (1^{+}–1½)–(2^{+}–3^{-}) **III** (1–1½)–(2–2½) **IV** (2–2½)–(1^{+}–1½) **V**. Vomerine teeth (n = 17): 10–18 (right, $\bar{x}$ = 14.3) and 10–18 (left, $\bar{x}$ = 13.7).

Most evident variation involves the dorsal coloration and pattern (figs. 3, 7). Several paratypes, most of them from Camp I (USNM 562048, 562054, 562064, 562063, AMNH A-131174) but also from camps II (USNM 562051) and X (USNM 562058) have a larger number of dorsal chromatophores, which makes them appear brown. Of these USNM 562048 has dark brown irregular blotches covering the dorsum and dorsal surfaces of limbs. In USNM 562058 only the body is darker; chromatophores are few on dorsal surfaces of thighs, and almost lacking on dorsal surfaces of arms that are cream with the exception of a few isolated chromatophores.

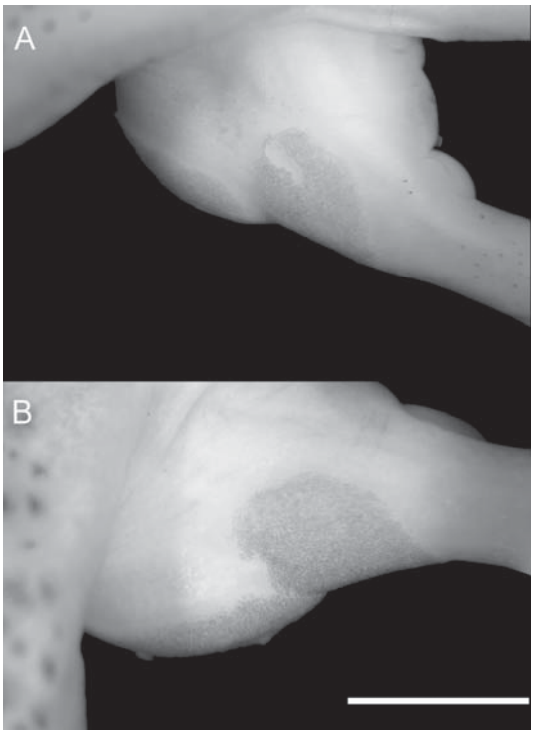

FIG. 6. Nuptial pad of *Myersiohyla chamaeleo*. (A) USNM 562058, (B) USNM 562059. Scale bar = 2 mm.

Coloration in life of some paratypes and referred specimens: We describe the variation in coloration and pattern based on descriptions of live specimens taken from field notes of McDiarmid, Myers, and Zweifel. Unless specified otherwise, notes were taken during the day and are presented here by camp number. **Camp II.** USNM 562049–50: Both went from bright grass green to brownish olive dorsally (brown specks on USNM 562049); sides bright yellow (USNM 562049) to very pale yellow (USNM 562050); yellow line on upper eyelid; blue green in all joints ventrally; center of chin and chest area blue green flesh; opalescent white where peritoneum shows; viscera visible in part through belly; iris bright coppery in bright sun. USNM 562051: Dorsally brown, light tan upper eyelids, bright yellow orange sides and anterior/posterior thighs; tan line along outer finger and toe; white rump patch; venter opalescent yellowish white on chin, pectoral area and belly; fleshy colored on forearms; toe pads whitish ventrally, pale greenish white dorsally; iris bright gold and brown (McDiarmid's field notes, Feb. 16, 1984). AMNH A-131176: The dorsal ground color of the head and body is light tan. The forearms and shanks are the same ground color, whereas there is merely a yellowish brown strip along the upper surface of the thigh. A pattern of small, yellowish, elongate spots is present over the head, body, lower arm and shank, extending along the foot. Webbing of the hind feet is sparse and tanish. The sides of the body, especially posteriorly, are an orange shade, which also extends onto the anterior and pos-

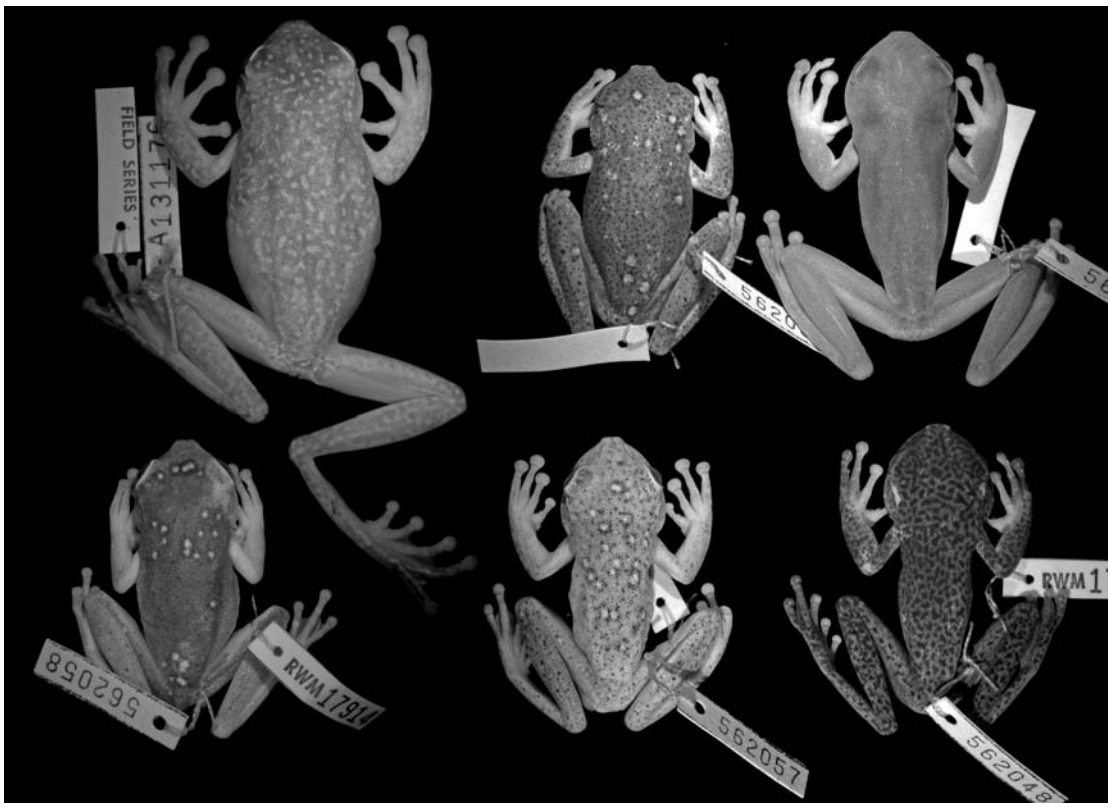

FIG. 7. Dorsal view of selected paratypes of *Myersiohyla chamaeleo* showing variation in pattern. Above, from left to right AMNH A-131176 (Camp II), USNM 562054 (Camp I), and USNM 562051 (Camp II); below, from left to right, USNM 562058 (Camp X), USNM 562057 (Camp X), and USNM 562048 (Camp I). AMNH A-131176 is a female, all other specimens are males.

terior surfaces of the thigh, but is less intense there. The chin is patternless with a yellowish tan tinge. The remaining ventral surfaces are grayish tan and translucent, so that the organs are at least dimly visible (Zweifel's field notes, Feb. 17, 1984). **Camp VII**. AMNH A-123709: Changing from brownish green to green above, speckled with black. Flanks rather bright orange; anterior and posterior faces of thighs yellowish orange. Ventral surfaces pale bluish green, except whitish on chest owing to underlying peritoneum. Iris pale bronze orange, dark banded by a fine venation (Myers' field notes, Dec. 1–2, 1984). **Camp XI.** USNM 562068: Back light green with brown spots (entire back appeared brown at night); turquoise in axilla, leg joints, groin, and behind eye (drawing in field notes); faint yellow on front and yellow on back of thighs; flanks orange; iris copper (McDiarmid's field notes, Feb. 25, 1985.) USNM 562061: Greenish with orange thighs (McDiarmid's field notes, Feb. 26, 1985.)

Measurements of the paratypes (all in mm, $\bar{x} \pm 1$ standard error): Males ($n = 15$). SVL 44.6–49.6 ($\bar{x}$= 46.1 ± 1.4); HL 13.8–17.5 ($\bar{x}$ = 16.3 ± 1.0); HW 15.7–17.2 ($\bar{x}$ = 16.2 ± 0.1); IND 3.3–3.8 ($\bar{x}$ = 3.6 ± 0.0); IO 4.8–6.1 ($\bar{x}$ = 5.3 ± 0.1); ED 4.2–5.2 ($\bar{x}$ = 4.6 ± 0.1); EN 4.4–4.8 ($\bar{x}$ = 4.6 ± 0.0); TD 2.7–3.3 ($\bar{x}$ = 2.9 ± 0.0); TL 22.3–25.0 ($\bar{x}$ = 23.4 ± 0.2); FL 16.0–19.3 ($\bar{x}$ = 17.0 ± 0.2). Females (n = 5). SVL 46.0–56.9 ($\bar{x}$ = 51.1 ± 2.0); HL 16.2–19.9 ($\bar{x}$ = 18.0 ± 0.7); HW

15.9–19.7 ($\bar{x}$ = 17.8 ± 0.7); IND 3.7–4.2 ($\bar{x}$ = 3.8 ± 0.1); IO 5.3–6.8 ($\bar{x}$ = 5.7 ± 0.3); ED 4.5–5.2 ($\bar{x}$ = 4.8 ± 0.1); EN 4.4–5.5 ($\bar{x}$ = 4.8 ± 0.2); TD 2.9–3.4 ($\bar{x}$ = 3.3 ± 0.1); TL 22.6–29.4 ($\bar{x}$ = 25.5 ± 1.2); FL 15.9–21.7 ($\bar{x}$ = 18.5 ± 1.1).

Remarks: The skin on the chin and anterior half of the gular area is glandular in all males when viewed with strong incident light and appears thicker than the loose skin of the vocal sac. On a few specimens the glands are evident externally without magnification (fig. 8). Superficial dissection of the skin of male paratype USNM 562058 reveals macroscopically evident glandular tissue (fig. 9). The prepollex is equally enlarged in males and females (figs. 5, 10). Two specimens partially dissected when tissue samples were removed (USNM 562061 ♀, and USNM 562057 ♂) show a parietal peritoneum partially covered with what seem to be iridophores at the level of flanks and dorsal body wall. The urinary bladder of the male is densely covered with the same putative iridophores (removed from the female when tissues were sampled), and the testes are ovoid, somewhat flattened, and unpigmented (left testis length 6.9 mm; SVL 46.6 mm). The female (SVL 51.2 mm) has large, unpigmented, ovarian eggs. The dissected left ovary (the right one was left intact) contained 54 eggs with largest diameter 2.9–3.1 mm ($\bar{x}$ = 3.02; s = 0.07; n = 15). Females are generally larger than males (SVL 46.0–56.9 mm; males 44.6–49.6 mm), with two (USNM 562066 and 562068) of the five females having SVL within the SVL range of the males. Superficial dissections in male USNM 562058 reveal the m. intermandibularis with a large diamond-shaped aponeurosis, through which the m. genioglossus is visible by transparency; no fibers of the m. intermandibularis contact the oval and araphic m. submentalis. Supplementary elements of the m. intermandibularis absent. Muscle depressor mandibulae with a differentiated slip that originates on the dorsal fascia at the level of the m. levator scapulae; tympanic origin contiguous with the belly that originates from the otic ramus of the squamosal.

We consider that the description of blue-green coloration described in the joints, and mental and ventral areas of living specimens, is very likely an indication of the occurrence of physiological chlorosis (Barrio, 1965a).

It is worth noting that the partial 16S sequences of juvenile referred specimen USNM 562056, and tadpole USNM 562723 from Camp VII are 1.1% different from those of specimens from the almost adjacent Camp XI (2.5 km SSE) and the more distant camps I and X (table 1). Interestingly, the vocalizations of USNM 562065 (USNM tape 68), also from Camp VII are indistinguishable from those of USNM 562060 (Camp XI); differences in vocalizations with specimens USNM 562054 (Camp I), and AMNH A-131178 (Camp III) are discussed below. Morphologically, all these adult specimens appear indistinguishable.

Ecology and natural history: Most specimens of *Myersiohyla chamaeleo* were found along or near streams. During the day, frogs were found in two types of plants, the leaves of which formed rosettes and held considerable water; at night they were found on vegetation and rocks along streams or in surrounding forest. Near Camp I, a male (USNM 562048) was found during the day hidden among the leaves of *Bonnetia maguireorum* growing along a stream. A snake (*Leptophis cupreus*) was photographed the following day (Feb. 11, 1984) as it searched the axils of these plants, presumably foraging for frogs (Albuquerque and McDiarmid, 2010). Two males (AMNH A-131173–74) had been previously located (Feb. 7, 1984) as they called from the leafy part of these plants, and another male (AMNH A-131178) was found 10 days later near Camp

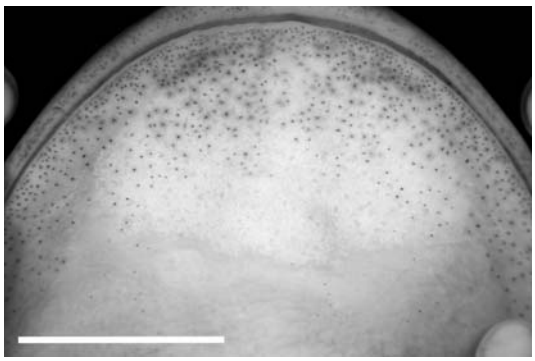

FIG. 8. Ventral view of the gular region of a paratype of *Myersiohyla chamaeleo* (USNM 562063) showing the external aspect of the mental gland. Scale bar = 5 mm.

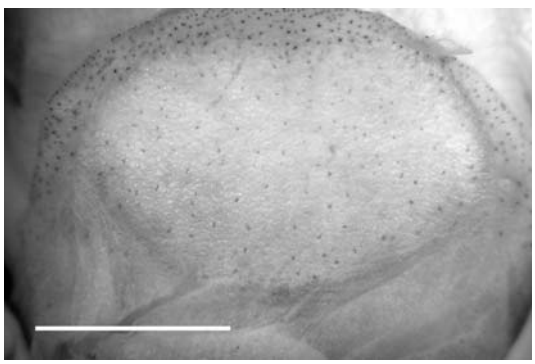

FIG. 9. The mental gland of *Myersiohyla chamaeleo* (Paratype USNM 562058) as seen through a superficial dissection exposing the internal aspect of the gular skin. Scale bar = 5 mm.

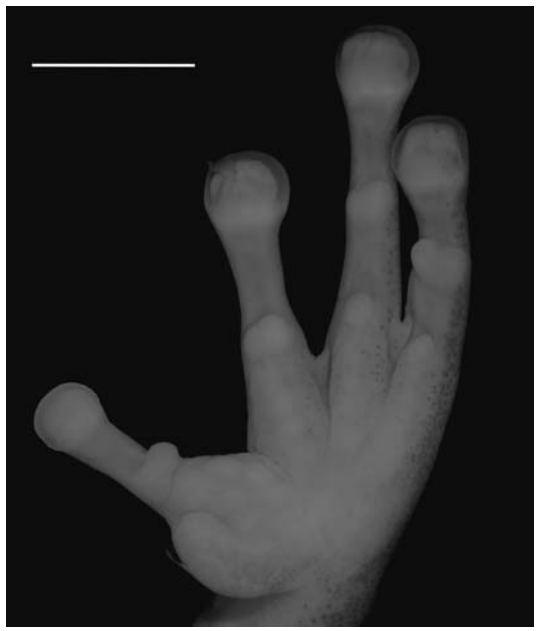

FIG. 10. Ventral view of hand of female *Myersiohyla chamaeleo*, USNM 562062. Note the size of the prepollex. Scale bar = 5 mm.

III also calling from a *Bonnetia* plant. Seven juveniles (SVL 28.6–34.0 mm) were collected from the large terrestrial bromeliad, *Brocchinia tatei*, which grew in large patches near Camp II and Camp VII. Three from Camp II (USNM 562049–50, USNM 562052) were collected during the day from the outer axils of a bromeliad growing along a small stream; both were in a head-up position. A fourth (AMNH A-131175) was hiding in a partly dead, rolled-up leaf and another (AMNH A-131175) was found in a bromeliad. Two other juveniles (USNM 562052–53) were found together in the central axil of a *Brocchinia* in the same area. A seventh juvenile was found at night (Feb. 12, 1985, 19:30–21:30 hr) on a leaf of a *Brocchinia* about 1 m above the ground near the heliport of Camp VII. A gravid female (USNM 562062) was found in the back of a cave adjacent to a creek ESE (above) of Camp I at 14:00 hr. Three frogs (USNM 562054, USNM 562063–64) formed a chorus around a 3 m wide and >1 m deep pool in the creek near Camp I (20:30–21:30 hr). One was taken from moss on a rock face 5 cm above the water, and two were calling from vegetation along the shore and about 10 cm above the water.

The five adult female *Myersiohyla chamaeleo* (SVL 46.0–56.9 mm) collected during the expedition were all found between January 31 and February 26, and all were gravid. Likewise, all adult

TABLE 1. Uncorrected pairwise distances between 16S sequences of available specimens of *Myersiohyla chamaeleo*. Those with an asterisk (*) are tadpoles.

	1	2	3	4
1-USNM 562718*-Camp I	—	—	—	—
2-USNM 562056-Camp VII	0.009	—	—	—
3-USNM 562057-Camp X	0.002	0.011	—	—
4-USNM 562061-Camp XI	0.002	0.011	0.000	—
5-USNM 562723*-Camp VII	0.009	0.000	0.011	0.011

males (SVL 44.6–49.6 mm, $n = 16$) had well-developed nuptial pads and were assumed to be in breeding condition. Calling males were heard at night along streams near camps I, III, VII, and XI during the same period.

Vocalizations: Recordings of calling males are available from four camps on opposite sides of the Cañon Grande (fig. 1). Recordings from east of the great canyon (camps VII, XI) are of males calling from along streams, whereas those from west of the canyon (camps I, III) are of frogs calling in camp from plastic bags. These segregate as two call types, one characterized by pulsatile notes (eastern camps), and the other is characterized by nonpulsatile notes (plastic-bag recordings from western camps). These are described separately and then compared.

Calls with Pulsatile Notes: A male was recorded calling on a vertical stem 1.5 m above streamside at Camp VII, at an air temperature of 14° C (USNM 562065 on USNM tape 68). Two males were recorded at Camp XI at an air temperature of 17° C (USNM 562059–562060 on USNM tape 70); the first was calling from the lower leaves of a bromeliad 1.5 m above a pool in the stream, while the second called from the lower, dead leaves of a bromeliad nearly 2 m above streamside.

The call is a short-to-long train of well-spaced, short notes given at a rate of about 1–2 notes/sec at 14°–17° C. Note duration is about 0.04 sec (32–51 ms, $\bar{x} = 44.3 \pm 5$ ms, $n = 29$). Each note is composed of several poorly resolved pulses that are indicated on wideband spectrograms (fig. 11B) but which are best visualized from expanded waveforms (fig. 11D). The individual note is a short "beep" composed of two harmonics, including a weak fundamental frequency at about 1100 Hz and a strong dominant frequency at about 2200 Hz.

Calls with Nonpulsatile Notes: One of three males was recorded calling from a plastic bag at Camp I at an air temperature of 17° C (recording of one of USNM 562054, 562063–562064 on USNM tape 67:17). A male collected at Camp III male was recorded in a plastic bag at the lowland Base Camp three days after capture, at an air temperature of 24° C (AMNH A-131178 on AMNH Herpetology Reel 250).

The calls of the frogs in plastic bags are given at rates of about 1.2 notes/sec at 17° C and up to about 4 notes/sec at 24° C. Note duration of the nonpulsatile notes is about 0.02 sec (17–27 ms, $\bar{x} = 22.3$ ms, $n = 18$). Most notes in the two recordings were examined by expanding the waveforms and were seen, without exception, to be nonpulsatile. The note is a short "beep" composed of two harmonics at about 950 Hz and 1900 Hz; the first or fundamental frequency is also the dominant frequency. The note is frequency modulated, with an initial increase followed by a steep decrease; owing to the shortness of the note, this modulation is barely indicated in figure 12C (but see fig. 13A′).

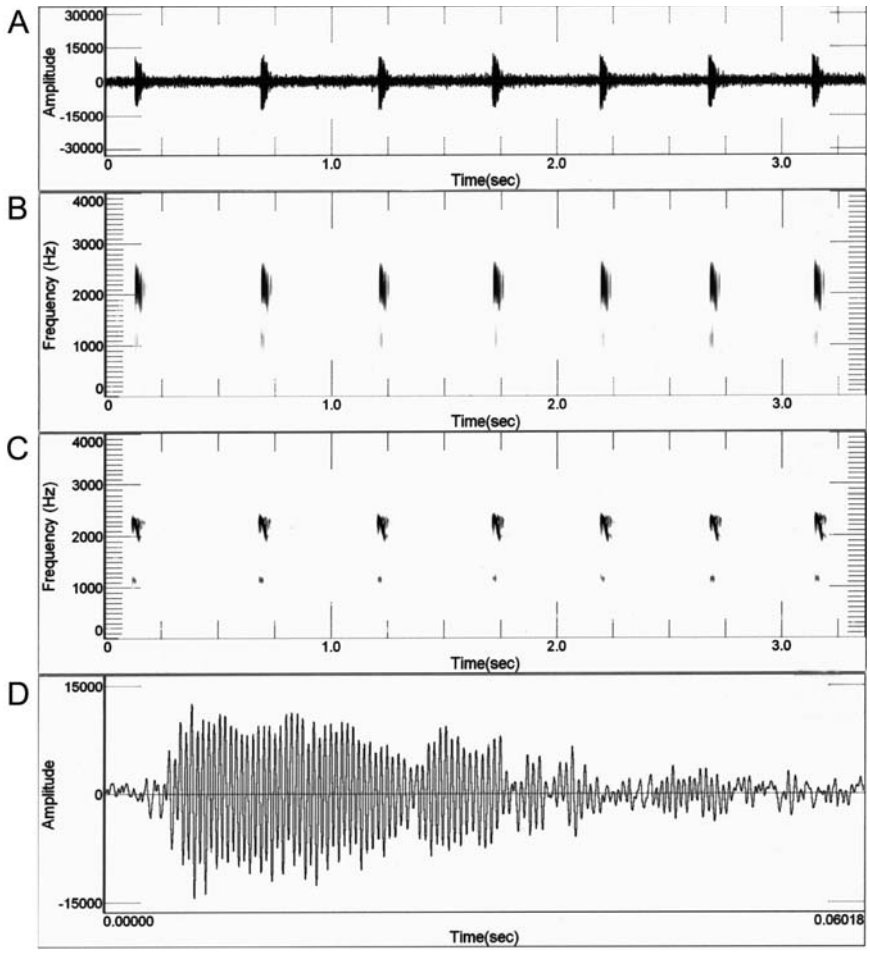

FIG. 11. Advertisement call of *Myersiohyla chamaeleo*. Seven pulsatile notes in 3.3 sec. (from 10-sec. segment of a longer train). **A**. Waveforms. **B.** Wideband (323 Hz) spectrogram. **C.** Narrowband (63.09 Hz) spectrogram. **D.** Expanded waveform of one note, showing poorly resolved pulses. Camp-XI specimen recorded February 25 1985, at an air temperature of 17° C (USNM 562059, paratype, on USNM tape 70).

Pulsatile and Nonpulsatile Notes Compared: The descriptions above and figures 11–12 show both similarities and differences in the notes. The pulsatile note is longer (about 0.04 sec) and has a weak fundamental frequency at about 1100 Hz, whereas the nonpulsatile (single-pulse) note is half as long (about 0.02 sec) and has a strong fundamental/dominant frequency at about 950 Hz. Each is frequency modulated in a similar way, with a sharp rise and subsequent sharp decline in the second harmonic; slight frequency modulation occurs also in the first harmonic of the nonpulsatile note.

Frequency modulation in the longer pulsatile note is evident in a standard narrowband spectrogram (fig. 11C), but not so obvious in the shorter nonpulsatile note (fig. 12C). However, it becomes evident in the shorter note when an exemplar is graphed at a different analysis size (fig. 13A′).

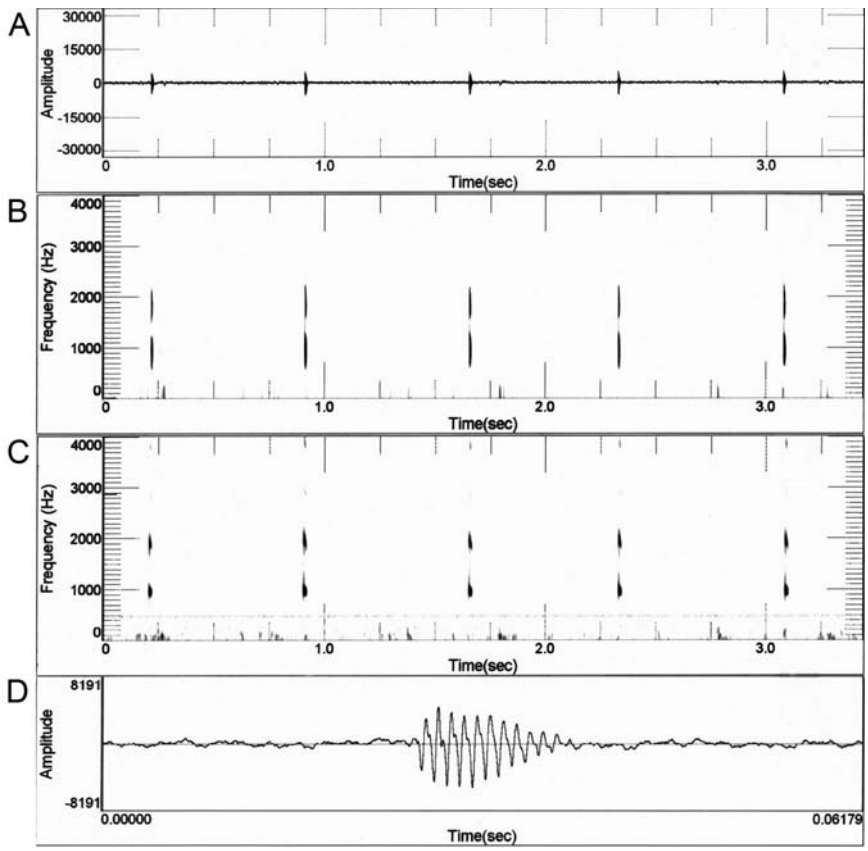

FIG. 12. Vocalization of *Myersiohyla chamaeleo*, calling from plastic bag. Five nonpulsatile notes in 3.3 sec. **A**.Waveforms. **B.** Wideband (323 Hz) spectrogram. **C.** Narrowband (63.09 Hz) spectrogram. **D.** Expanded waveform of one note, showing lack of pulsation. One of three Camp I specimens calling i n plastic bag, air temperature 17° C (either USNM 562054, 562063, or 562064 on USNM tape 67).

Clearly two different call types are involved, although their biological significance is uncertain. Slight divergence of the calls may have occurred on opposite sides of the great Cañon Grande of Cerro de la Neblina. On the other hand, perhaps confinement (in plastic bags) induced a call different from the normal advertisement call. In any case, we could find no external morphological differences among the specimens.

Tadpoles: The uncorrected pairwise distances of the 16S sequences (table 1), indicates that the sequence of tadpole USNM 562718 is similar (0%–0.2%) with those of the adult paratypes USNM 562048, 562057, 562061. All these have a 0.9%–1.1% uncorrected p-distance with sequences of a tadpole USNM 562723 and juvenile USNM 562056, these from Camp VII. Conversely, these are 12.5%–13.6% different from the sequences of available specimens of *Myersiohyla neblinaria*. Considering the small distances or identical sequences, we consider this tadpole and all others with the same general morphology (see below) to be larvae of *M. chamaeleo*. We describe a typical larva of *M. chamaeleo* (fig. 14) and then comment on the variation found in other available material.

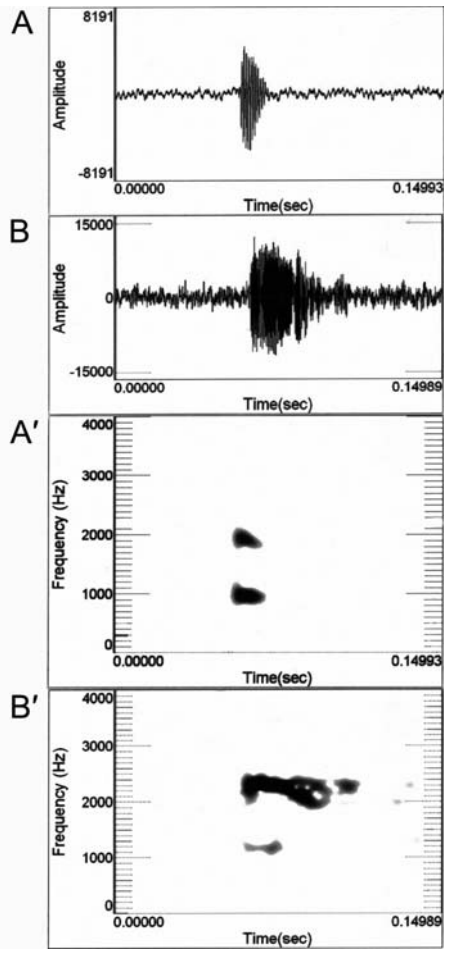

FIG. 13. Comparison of (A, A′) short non-pulsatile note and (B, B′) longer pulsatile note of *Myersiohyla chamaeleo*, n. sp. Spectrograms A and B above are graphed at an effective bandwidth of 107 Hz. (From same tape sources as figs. 12 and 11 respectively.)

Description: A tadpole (USNM 562727) in stage 25 from Camp XI (see below) has the following measurements (all in mm): total length 43.0; body length 16.6; basal tail muscle height 6.3; basal tail muscle width 4.3; maximum dorsal fin height 3.6, this point being 12.2 mm away from body; maximum ventral fin height 2.7, this point being 11.7 mm away from body; body width 9.5; body depth 8.3; eye diameter 1.9; pupil diameter 1.4; interorbital distance 4.1; internarial distance 3.7; snout to nostril distance 2.7; snout to eye 4.1; snout to spiracle 12.0; oral disc diameter 8.2.

Oral disc ventral, not emarginate but with posterior fold. Marginal papillae in a single row sometimes slightly offset, without gaps; submarginal papillae absent. LTRF 5(5)/9(1). Gaps in A-5 and P-1 small (~0.1 mm), posterior gap about 40% of anterior one. Labial tooth density 19–24 teeth/mm, with fewer teeth in rows proximal to jaw sheaths. Teeth in rows P-1 through P-4 more robust and about one-third to one-half longer than those of more posterior rows. Several (3–5), short tooth rows scattered lateral to primary tooth rows and on folded area of oral disc. Jaw sheaths pigmented; upper sheath narrow, slightly wider (M-shaped) medially, long and shallowly arched with short serrations; lower sheath moderately wide, V-shaped with small, pointed serrations, that are larger than those on upper jaw sheath.

Body ovoid; snout rounded in dorsal view, sloping in profile. Eyes dorsolateral, not visible in ventral view. Nostrils oval, with low, medial, fleshy projection and darker fleshy rim. Spiracle sinistral with its medial wall fused with the body wall, and the lateral wall shorter than the medial wall; spiracular opening directed slightly dorsad. Vent tube dextral, twice as long as wide. Dorsal fin arises just anterior to body-tail juncture; lower fin arises at base of tail and masked by vent tube; fin tip pointed, transparent. Neuromasts present, whitish, visible beneath and posterior to eyes, on top of head, and dorsolaterally on body. Melanophores rod shaped.

Head and body brown with irregular pigment; a pair of pale, elongate marks visible dorsolaterally. Coloration slightly paler on snout, around oral disc, and on spiracle. Venter brown, gut visible through body wall. Tail and fins brown except for anterior 20% and posterior 15% which are pale, giving a bicolor appearance to the tail; tail tip transparent. Other specimens from the same locality are entirely brown or bicolored and some from camps I and III are completely black

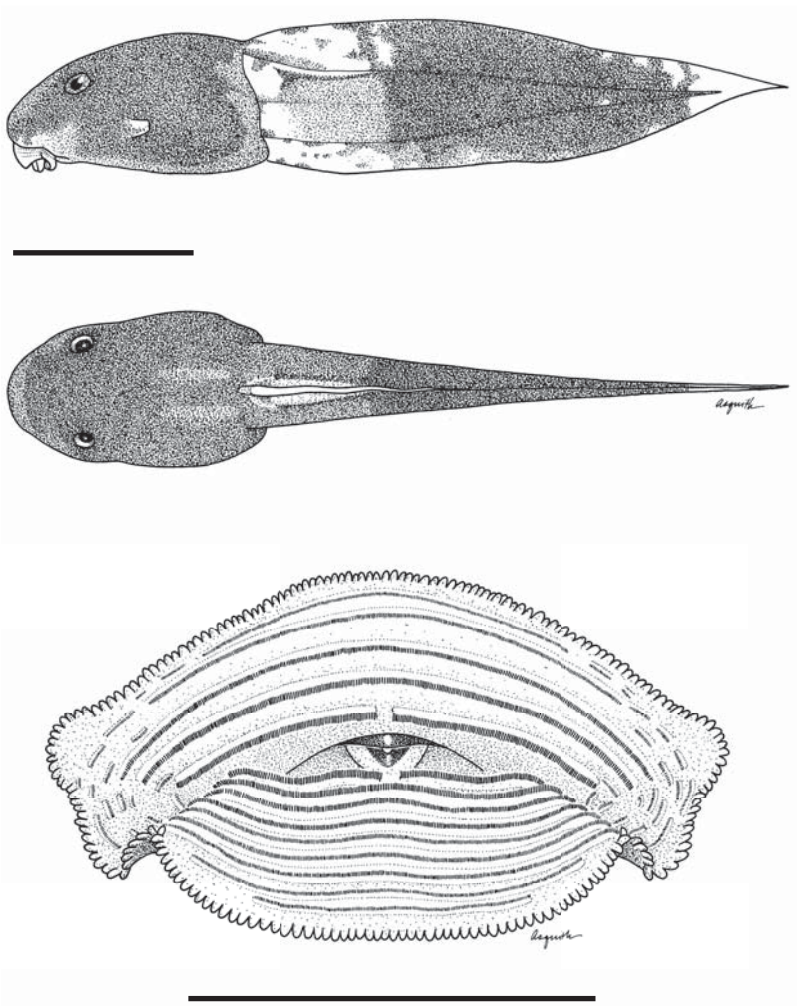

FIG. 14. Tadpole of *Myersiohyla chamaeleo* (USNM 562727) from Camp XI, Gosner stage 25. Lateral and dorsal views, and oral disc. Scale bar = 10 mm (upper) and 5 mm (lower).

(see below). Fins may be transparent, variably mottled, or completely black. Smaller tadpoles are generally paler overall.

Neuromasts are usually visible in tadpoles of *Myersiohyla chamaeleo* and appear as lines of round, whitish dots on the head, body, and tail. Their topography is complex and most obvious in darkly colored specimens from Camp III (USNM 562721); they are difficult to see in pale or bicolored specimens. In the Camp III tadpoles, the supraorbital line includes 13–15 neuromasts that converge anteriorly on the head between the nares and continue anteroventrally onto the snout where it approaches the anterior extent of the infraorbital series of 15–19 neuromasts; occasionally a single preorbital neuromast is visible. The oral series is indistinct and variable (also noted for many species by Lannoo, 1987). In some tadpoles it consists of a longitudinal row of 4–6 neuromasts and an anterior, ascending line, sometimes V-shaped, of 3–5 neuromasts; in others, only a few scattered neuromasts occur in the oral region. An angular

series of 4–5 neuromasts is visible below the eye. A postorbital series consists of two dorsal (supra-) and two ventral (infra-) neuromasts. A row of 8–10 neuromasts located dorsolaterally on the body is continuous with 4–5 neuromasts in the dorsal row at the base of the tail fin; on the body this dorsolateral series forms a loop and joins a lateral series of 10–12 that continues onto the tail as the middle caudal series consisting of 6–8 neuromasts. About halfway along the tail this middle series projects dorsally (3–4 neuromasts) and continues posteriorly (11–13 neuromasts) along the tail-fin juncture to near the tail tip. A ventral body row of 13–14 neuromasts extends from near the vent tube anterodorsally above the spiracle to a point between the dorsal loop and the postorbital series.

Natural History: Tadpoles of *Myersiohyla chamaeleo* were collected in black water streams at six sites on Cerro de la Neblina. A series of 26 specimens (AMNH A-131171; stage 25; TTL 33–80 mm; LTRF 5/9) collected on February 7, 1984, by Cole from pools in a small stream near Camp I were black with globular bodies. Clear evidence of ontogenetic change from clear fins to black fins can be seen in this series. Tail tips were usually clear. Five other specimens from Camp I (USNM 562717 [4], USNM 562718, tissue voucher; stage 25; TTL 39–65 mm; LTRF 4/7–4/9) were collected by Cocroft from pools in another small stream (1–2 m wide, 10–30 cm deep) ESE of camp, January 31, 1985, between 10:00 and 13:00 hr. These tadpoles also were dark brownish black with clear tail tips.

Three tadpoles were collected from a small stream (0.6–1.2 m wide, 30–60 cm deep) near Camp II. One (USNM 562719; stage 25; TTL 40 mm; LTRF 4/9; Feb. 18, 1984) is light brownish with nearly transparent fins with small, scattered patches of melanin, a clear tail tip, and transparent belly. Two other pale specimens (USNM 562720; stage 25; TTL 54–56 mm; LTRF 5/9) were collected by Paolillo on January 30, 1985, from a small hollow beneath a rock; his notes indicate that they were feeding on the white sand bottom of the stream.

Six black specimens (USNM 562721; stage 25; TTL 56–71 mm; LTRF 4/7 [damaged mouth], 4/8-9 [broken series], 4/9, 5/9[3]) were collected in a stream near Camp III by Cole on February 18, 1984. Several of these had broken tail tips, but it is not clear whether this reflected attempted predation or collection damage; all intact tips were clear.

Cocroft and Paolillo collected tadpoles during the days of February 10–11 and on the night of February 12, 1985, at Camp VII. These 29 specimens (USNM 562722 [28], USNM 562723, tissue voucher; stage 25; TTL 23–71 mm; LTRF 3/4–5/11) were taken from quiet pools along the stream near camp; most were in water <1 m deep; several larger tads seen during the day in a large pool >1 m deep eluded capture. At night the tadpoles were sensitive to light and substrate vibrations and quickly took cover under rocks. The water temperature at 11:30 hr was 14° C. Two color phases were seen (Cocroft's field notes, Feb. 11–12, 1985): black, sometimes with a lighter tail, and greenish gray (we assume these greenish tadpoles were larvae of *Myersiohyla neblinaria* because adults of this species were collected here). Fin tips of the darker ones varied from clear to dark. One tadpole (TTL 35–40 mm estimate, tail broken at 29 mm) had a damaged tail that appears to have resulted from attempted predation. Another (TTL 45 mm) had a regenerated tail tip (distal 7 mm) that was transparent and slightly narrower. Several tadpoles in this series had irregular clumps of melanophores

on their bodies and tail, and one in poor condition had what appeared to be a fungal infection of the oral disc near the mouth.

Three other samples of tadpoles were collected by Myers and Ford on December 1–2, 1984, at the same site. Fifteen of 16 tadpoles (AMNH A-123713) were in stage 25 and measured 24–61 mm TTL; the largest from this series was 75 mm TTL at stage 35with an LTRF of 6/10, while the others ranged from 4/7 to 6/10. Two other specimens collected at the same time were metamorphs at stage 41; their tooth rows were starting to break up (AMNH A-123711 at 68 mm TTL had an LTRF of 5/10, and AMNH A-123712 at the same size had an LTRF of 4/7).

A single brownish tadpole was collected during the day (Feb. 2, 1985) in a stream that formed the headwaters of the Río Baría and flowed SW into the Cañon Grande (Camp IX; 1780–1830 m; 1°00′00″ N, 65°53′00″ W). The tadpole (USNM 562724; stage 25; TTL 29 mm; LTRF 4/7) has an obviously bicolored tail, similar to that illustrated in figure 14; the anterior third is light and the fins are transparent, while the posterior two-thirds is dark with densely distributed melanophores in the fins; the tail tip is transparent.

Several tadpoles collected in the stream below Camp XI are also in stage 25. A single specimen (USNM 562725; TTL 62 mm; LTRF 5/10) was taken in slow-moving water about 5 cm deep on February 25, 1985. Nine tadpoles (USNM 562726, USNM 562727 [described]; TTL 37-61 mm; LTRF 4/8[4], 4/9, 5/8, 5/10[2], 5/11) netted by McDiarmid on February 26, 1985 (19:30–21:30 hr), were uniform dark brown or bicolored; all had clear tail tips. Nine other specimens (USNM 562728; TTL 24–64 mm; LTRF 4/7[1], 4/8[4], 4/9, 5/9[2], 6/9) collected on February 27, 1985, by Paul Spangler during the day were all dark. Two other specimens (USNM 562729; TTL 47–49 mm; LTRF 5/9, 5/8) were both uniform dark. Most of the tadpoles from Camp XI had lateral tooth rows.

Comments: Twelve lots of 109 larvae of *Myersiohyla chamaeleo* were collected at six sites on Cerro de la Neblina. Even though the size ranged from 23 to 80 mm TTL, all but three specimens were in stage 25. A 75 mm TTL tadpole was in stage 35, and two 68 mm TTL individuals in stage 41; tooth rows in both of the latter were starting to fall out down. LTRFs varied from 4/7 to 5/11 and 6/10, with the lower numbers found in smaller individuals. No variation was observed in the positions or sizes of the toothrow gaps. All specimens from camps I and III were more globular (body shape) and densely pigmented, being nearly all black (body, tail, and fins) compared to most tadpoles from the other sites. Tadpoles from camps II, VII, IX, and XI were either uniform brown or bicolored with anterior part of tail pale. The latter specimens were usually found in smaller, often faster-flowing streams bordered by gallery forests that provided more shaded habitats. In contrast, the larger, black specimens generally were from open, exposed streams with larger, pool-type habitats. Intraspecific morphological differences among tadpoles have been noted by previous workers (Jennings and Scott, 1993; R.W.M., personal obs.), and we interpret the differences in coloration and body proportions of *M. chamaeleo* tadpoles as reflecting differences between habitats. Increased melanic pigmentation might counter the potential negative consequences of increased exposure to predation and solar radiation in more open habitats. Whether ontogenetic increases in melanism and larger body size reflect differences in food availability and growth (Altig and McDiarmid, 1999b) or are associated with distastefulness and aposematic coloration (Brodie and Formanowicz, 1987) remain to be demonstrated. See table 1 for 16S distances among samples from different

camps. The few samples available do not allow us to establish any significant association between these morphological differences and the p-distances that we observe.

In an effort to determine any ontogenetic change in LTRFs, we divided the Camp VII sample of 29 specimens (USNM 562722 [28], USNM 562723) into five size categories and recorded the LTRF for each tadpole in each size class (those with damaged oral discs or broken tails were not included). The results are as follows: **1.** TTL <30 mm: LTRFs 3/4 (*N*=1), 4/6(1); **2.** TTL 30–39 mm: LTRFs 4/7(3), 4/8(3), 4/9(1), 5/6(1), 5/8(1), 5/9(1); **3.** TTL 40–49 mm: LTRFs 4/8(1), 4/9(3), 5/9(4); **4.** TTL 50–59 mm: LTRFs 4/7(1), 4/8 (1), 5/10(2) 5/11(1); TTL >59: LTRFs 4/7(1). Though preliminary, three patterns emerge. First and not unexpectedly, smaller individuals generally have smaller LTRFs, and the smallest value (3/4) was in the smallest tadpole (23 mm). In contrast and in spite of the tendency for larger tadpoles to have more labial tooth rows, the largest LTRF value (5/11) was not in the largest tadpole (TTL 71 mm) but in a smaller one (TTL 59 mm); in this specimen the P-11 row was weakly developed and barely discernible. That all of these specimens were in stage 25 and showed more than a threefold increase[4] in size (TTL 23–71 mm) without a concomitant change in development suggests a long-lived tadpole. Another sample of 26 specimens from Camp I (AMNH A-131171) showed the same pattern; all were in stage 25 and ranged between 33 and 80 mm TTL. The low water temperatures (14° C) and relatively low nutrient content of most of the Neblina streams likely contributes to a relatively slow growth rate. The size range in a single developmental stage (stage 25) was surprising and reinforces previous observations of a decoupling of size, developmental stage, and age in many tadpoles. One of the largest *M. chamaeleo* tadpoles (AMNH A-123713) was also collected at Camp VII; it was in stage 35, measured 75 mm TTL, and had an LTRF of 6/10. That it was only 4 mm larger than the largest stage 25 individual collected from this same stream and smaller than the largest specimen (80 mm TTL) at the same stage from Camp I, suggests a larval growth curve in this species different from that reported for most other anurans for which data are available (e.g., see table and plots from Middle American hylids in Duellman, 1970). Why much of the growth is apparently concentrated in the earliest larval stage in this species, as contrasted to a less skewed and more evenly distributed size range with a typical sigmoid-shaped growth curve as reported for most tadpoles, is unknown. We saw no evidence of size-related predator pressure in these environments that might select for a faster growth and larger size early in development. A cursory review of growth data for Middle American tadpoles (Duellman, 1970) showed that 25%–50% of the maximum size is attained in pond tadpoles by stage 25, while stream species may reach more than 65% of their maximum size in the same stage. Together, these data imply a slower developmental rate for tadpoles living in stream compared to pond habitats. The lower productivity and generally cooler temperatures found in stream habitats may account for most of this pattern. Whether this is age dependent remains to be shown.

A second observation relates to the lack of a detectable pattern in either sequence or synchrony in the addition of anterior and posterior tooth rows. In the Camp VII sample, anterior rows increase by only a single row within a size class (e.g., 4–5 in categories 3 and 4) and two

[4] This size discrepancy may be greater as larger tadpoles were seen in the same habitats at the time but not collected.

rows overall (3–5), while posterior rows increase within size categories by up to four rows (6–9 in category 2) and as many as seven rows (4–11) overall. The smaller size of teeth in the distal rows (fig. 14) indicates that rows are added distally on both labia; this pattern was reported for many stream dwelling hylids by Altig and Johnson (1989) and has been observed in other forms as well (R.W.M., personal obs.).

Finally, we suspect that individual variation (either ecological or genetic) in growth rates of tadpoles of certain species, especially of long-lived, stream inhabiting forms, may override any ontogenetic pattern of toothrow addition, if such exists, and result in an LTRF in the largest specimen that is less than the maximum possible value. Accordingly, some individual larvae may reach a developmental stage (stage 41) approaching metamorphosis without ever having achieved the highest possible LTRF value for the population. Based on examination of all tadpoles of *Myersiohyla chamaeleo* taken on Cerro de la Neblina, the maximum possible LTRF value is 6(6)/11(1). No single specimen examined had that value. More detailed studies examining the trade-offs and interactions between size, developmental stage, and age, especially with species that have high LTRFs, are needed before we understand what is involved in the ontogeny of stream-breeding hylid tadpoles.

Myersiohyla neblinaria, new species
Figures 15–25

Hylid sp. nov. b – McDiarmid and Paolillo (1988). Species list.

Hylid sp. D (Neblina) – McDiarmid and Donnelly (2005). Species list.

Hyla inparquesi (non Ayarzagüena and Señaris, "1993" [1994]) – Faivovich et al. (2005). Misidentification of specimens from Cerro de la Neblina.

Myersiohyla inparquesi (non Ayarzagüena and Señaris,"1993" [1994]) – Faivovich et al. (2005). First combination with *Myersiohyla*.

Holotype: USNM 562071, adult ♂, with muscle tissue removed from left thigh. Venezuela: Departamento Amazonas: Cerro de la Neblina: Camp VII, 1730 m, collected by A. Gardner on February 1, 1985.

Paratopotypes: USNM 562072, AMNH A-123715 (♀♀).

Paratypes: Venezuela: Departamento Amazonas: Cerro de la Neblina: Camp I, 1820–1880 m: USNM 562070 (♀). Camp II, 2085–2100 m: AMNH A-131172 (♀). Camp XI, 1450 m: USNM 562073–562082 (♂♂).

Etymology: The species name *neblinaria* is an adjective derived from the mountain name *Neblina* plus the Latin suffix *-aria* (fem. to agree with *–hyla* of genus name), denoting a place or a connection to a place.

Diagnosis: *Myersiohyla neblinaria* is characterized by: (1) SVL of male 47.7–52.3; female SVL 54.0–61.6; (2) a single, thick, nuptial pad; (3) a row of tubercles in the forearm; (4) mental gland present but evident only through dissection; (5) thighs with longitudinal bars; (6) dorsum brown, with variable presence of a dorsal line and blotches; (7) m. depressor mandibulae without an origin on the dorsal fascia at the level of the m. levator scapulae; (8) unpigmented eggs; (9)

FIG. 15. **A.** Holotype of *Myersiohyla neblinaria* (USNM 562071. Camp VII). Photograph by Robert Noonan. **B**. Paratype of *M. neblinaria* (USNM 562075, Camp XI). Photograph by R.W. McDiarmid. **C**. Paratype of *M. neblinaria* (AMNH A-123715, Camp VII). Photograph by C.W. Myers. **D.** Magnification of figure 15A showing detail of the head.

tadpoles with a dorsoventrally flattened body; (10) fins reaching the base of the tail; (11) labial toothrow formula (LTRF) 16 (16)/21(1).

Comparison with other species: *Myersiohyla neblinaria* is most similar to *M. inparquesi* but differs in having: hand and toe discs without sagittal black lines (present in *M. inparquesi*); larvae with dorsal and ventral tail fins reaching the base of the tail (extending only a third in *M. inparquesi*); larvae with scattered submarginal papillae in the upper and lower labium (apparently absent in *M. inparquesi*); and larval oral disc with a single row of marginal papillae (three rows in *M. inparquesi*). Furthermore, the advertisement call of *M. neblinaria* is composed of a single note with 7–9 pulses and a duration of 295–382 ms; in contrast, the advertisement call of *M. inparquesi* is composed of two notes, one of 6 pulses and a duration of 90 ms, and the other with 7 pulses and a duration of 80 ms (Ayarzagüena and Señaris, "1993" [1994]). *Myersiohyla neblinaria* differs from *M. loveridgei* in its larger SVL (*M. neblinaria* 47.7–52.0 mm; *M. loveridgei* 42–45 mm; Rivero, 1961; "1971" [1972]), and in having a single nuptial pad (two in *M. loveridgei*). From *M. aromatica* it differs in having a single nuptial pad, instead of two (Ayarzagüena and Señaris, "1993" [1994]: 130); larger SVL (*M. aromatica*, 43.6–46.6 mm; *M. neblinaria* 47.7–52.0 mm); tadpole with dorsoventrally flattened body (globular in *M. aromatica*) and more rows of labial teeth (LTRF 10-13/14-18 in *M. aromatica*). *M. neblinaria* is distinguished from *M. kanaima* by its larger SVL (males: 37.0–37.8 mm, $\bar{X}$= 37.4, *n* = 5; females:

FIG. 16. Dorsal and ventral view of the holotype of *Myersiohyla neblinaria* (USNM 562071, 49.8 mm SVL), Camp VII.

46.3–48.0 mm, $\bar{x}$= 47.05, *n* = 4; Goin and Woodley, 1969, and this paper), more robust body (slender in *M. kanaima*), more developed prepollex (proportionally reduced in *M. kanaima*), more extensive and thick nuptial pad (reduced to the dorsal margin of the prepollex, and composed of a thin layer of glandular tissue, apparently without colored epidermal projections), unpigmented eggs (completely pigmented in *M. kanaima*), color pattern, tadpole with dorsoventrally flattened body (depressed in *M. kanaima*) and more rows of labial teeth (LTRF 2/4 in *M. kanaima*, but see discussion).

Description of the holotype (figs. 15a, 16–17): Body robust; head slightly longer than wide; as wide as body; head width 33% SVL; head length 36% SVL. Snout in dorsal view rounded, in profile truncate; canthus rostralis rounded; loreal region concave; lips not flared; nares slightly protuberant, directed dorsolaterally, and posterior to anterior margin of lower jaw. Internarial region and top of head slightly depressed. Interorbital distance shorter than eyelid. Eye prominent, its diameter 125% eye-nostril distance. Tympanum rounded, its diameter 39% eye diameter. Supratympanic fold heavy, beginning behind eye and extending to anterior margin of insertion of arm, obscuring dorsal margin of tympanic membrane.

Vomerine teeth in two medially convergent series that contour posterior margin of choanae giving shallow S-shape to each series; 16 teeth on right and 13 on left. Choanae kidney shaped; separated by distance larger than their maximum diameter. Tongue ovoid, attached overall (narrowly free around lateral and posterior margin), posterior margin entire. Vocal slits present, longitudinal, originating at sides of tongue and extending to corners of mouth.

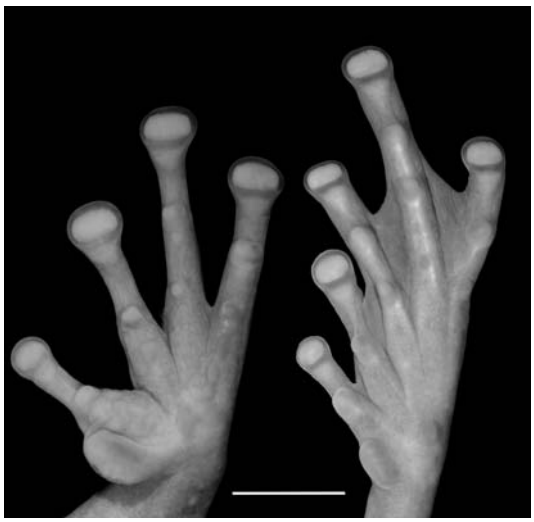

FIG. 17. Ventral view of hand and foot of the holotype of *Myersiohyla neblinaria* (USNM 562071). Scale bar = 5 mm.

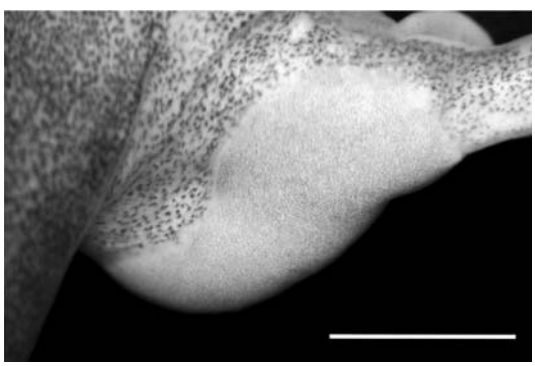

FIG. 18. Nuptial pad of *Myersiohyla neblinaria* (paratype USNM 562079). Scale bar = 2 mm.

Vocal sac not evident externally. Glandular tissue on mental area visible at 60×, but otherwise not evident externally.

Forearm robust and prominent. Row of low, irregularly spaced tubercles along ventrolateral edge of forearm. Fingers long and slender, with clearly defined circumferential groove, pad smaller (~75%) than disc; width of disc on third finger similar to tympanum diameter. Relative lengths of fingers 1<2<4<3. Fingers webbed basally, without dermal fringes; webbing formula of outer fingers **II** 2⅓–3½ **III** 3^{+}–3^{+} **IV**. Subarticular tubercles large; distal tubercle of finger IV irregularly shaped, others round. Large supernumerary tubercles, round or irregularly shaped. Outer metacarpal tubercle small and bifid, nearly round. Inner metacarpal tubercle large, elliptical. Prepollex enlarged, semicircular. Nuptial pad present, covering internal margin of thumb and dorsal margin of enlarged prepollex; consisting of thick, cream glandular pad, covered by minute dark epidermal projections (fig. 18).

Hind limbs moderately robust; tibia length 55% of SVL; foot length 43% SVL. Calcar absent; tarsal fold absent, but skin subtly thickened. Inner metatarsal tubercle large, elliptical; outer metatarsal tubercle round. Toes short, bearing discs smaller than those on fingers; disc of toe I smaller than others; relative length 1<2<3≈5<4; webbing formula **I** 2–2 **II** 1½–2½ **III** 2–3 **IV** 2½–1½ **V**. Subarticular tubercles large, round. Few flat supernumerary tubercles in longitudinal series at base of toes. Cloacal opening directed posteroventrally at midlevel of thighs; several flat tubercles scattered laterally and below cloaca. Dorsal skin smooth, finely granular on abdomen. Pectoral fold absent.

Measurements of holotype (all in mm): SVL 49.8; HL 18.0; HW 16.8; IND 4; IO 5.4; ED 5.9; EN 4.7; TD 2.3; TL 27.7; FL 21.3.

Coloration of holotype in life: No field notes are available for the holotype. Visible details from a color slide of RWM, here reproduced as figure 15A, differ little from the coloration in preservative.

Coloration in of holotype in preservative: Dorsally brown, turning darker brown toward the flanks, and with many large, irregular tan blotches; these blotches are smaller on the

sides. Thick dark brown to black uniform line from tip of the snout to approximately the distal tip of urostyle. Dark, poorly defined, diffuse canthal stripe. Discs dorsally dark gray, contrasting with the brown coloration of the limbs. Hind limbs dorsally and ventrally brown; each thigh with five tan dorsal longitudinal stripes with diffuse margins that extend into the hidden areas. Shank with irregular tan blotches, some of which look dorsally continuous with those on thigh, smaller blotches on the outer surface of the foot. The only pattern present on rear surfaces of thighs are the posterior margins of the tan bars. A few tan blotches surround the cloacal region. Paracloacal tubercles tan. Ventral surfaces of body and limbs brown; subarticular, palmar, and thenar tubercles light gray. Irregular series of small tan blotches across abdomen below the pectoral region.

Variation of paratypes: Morphologically the paratypes are similar to the holotype. The variation in toe-webbing formula can be expressed as: **I** (2–2½)–(2–2½) **II** (1^{+}–2^{-})–(2½–3) **III** (1½–2)–(2–3) **IV** (2½–3)–(1^{+}–2^{-}) **V**. Vomerine teeth (n = 12): 12-17 (right, $\bar{x}$ = 14.1) and 11-16 (left, $\bar{x}$ = 13.4). The structure that has been described in the holotype as a subtle dermal ridge along the tarsus is equally subtle in most paratypes, with the exception of three females (AMNH A-131172, USNM 562070 and 562072), where it is quite distinct, and proximally forms a few flat tubercles.

Most notable variation involves the coloration and color pattern, particularly regarding presence and extent of blotches (figs. 15, 19–20). We describe the variation according to the camps at which specimens were collected. Unless otherwise stated, all descriptions refer to preserved specimens. **Camp I.** The single specimen collected at Camp I (USNM 562070), an adult female, has a barely defined dorsal pattern, being light tan with a diffuse darker reticulum. Exposed surfaces of shank and foot are light tan as well, with diffuse brown blotches. Thighs dark brown with light tan blotches. Undersides of hind limbs and forelimbs reddish brown. Abdomen and throat creamy; areas surrounding the insertion of the arms dark brown. Diffuse line borders the lower jaw. An irregular brown line extends from the mandibular symphysis up to the beginning of the pectoral region. **Camp VII.** Coloration of two females differs notably from the holotype. USNM 562072 is dorsally tan, becoming brown on the sides. It lacks the dorsal line and other discernible pattern, with the exception of some irregular, small, tan blotches on the sides. Coloration of this frog during the day was noted by Cocroft (field notes, Dec. 2, 1985) as: iris coppery yellow with black reticulations; dorsal surfaces of fore- and hind limbs tan; dorsum from snout to vent brownish tan, fading to lighter tan laterally in center of body; feet mottled light tan and dark brown dorsally, toe pads dorsally dark brown, almost black in center outlined with light tan, brownish gray ventrally; sides and ventral surfaces lavender brown mottled with light tan; anterior and posterior thighs same as sides; toe webbing dark brown; light tan upper lips; tympanum coppery brown. In AMNH A-123715 the dorsal pattern is reversed with respect to the holotype, with the ground coloration being tan and the blotches, which are smaller and fewer, being brown. Middorsal dorsal dark line present. Seven longitudinal bars on the thighs. In his field notes Myers described this specimen in life as "Brown with vague darker blotching and blackish brown vertebral line. Flanks and thigh mottled and banded tan and purplish brown. Ventral surfaces purplish brown with suffusion of tan across chest. Iris golden yellow with black reticulation

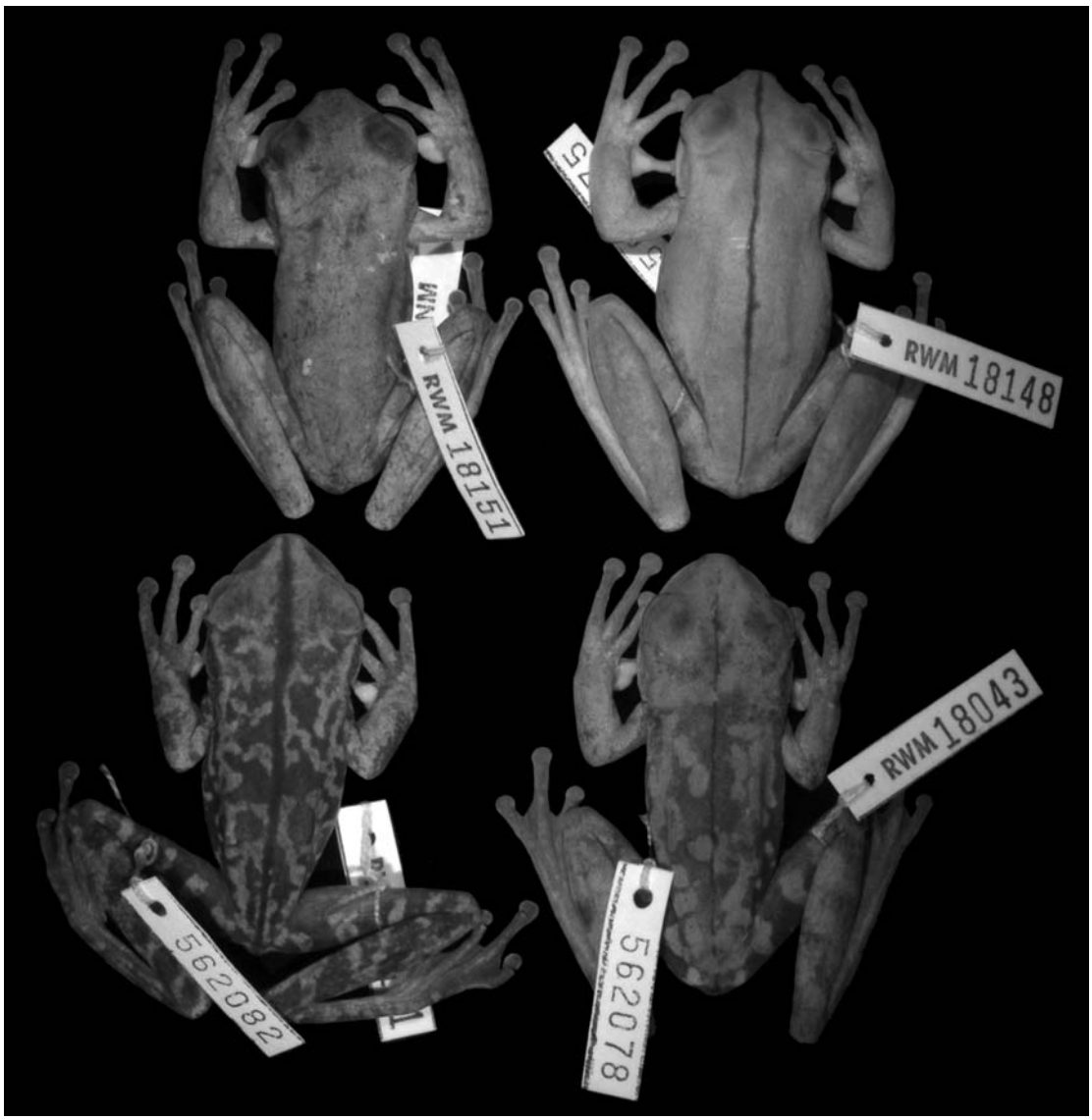

FIG. 19. Dorsal view of selected preserved male paratypes of *Myersiohyla neblinaria* showing variation in pattern; all from Camp XI. Clockwise, from top left, USNM 562080, USNM 562075, USNM 562078, and USNM 562082.

(conspicuous but not sharply defined)." **Camp XI.** Nine of the 10 specimens collected in Camp XI have the dark vertebral line. With the exception of USNM 562079, all are like the holotype in the dark brown flanks with tan blotches of variable size. Most variation involves the dorsal and thigh pattern, and the hues of brown and tan. On specimens USNM 562073–74, USNM 562076, and USNM 562079–80, the dorsal pattern is barely distinguishable. USNM 562075 is completely light tan without dorsal blotches. Specimens USNM 562077–78 and USNM 562081–82 have dorsal blotches, but their pattern is reversed from that of the holotype, with their ground coloration being tan or light tan and the blotches brown.

FIG. 20. Ventral of view of selected preserved male paratypes of *Myersiohyla neblinaria* showing variation in pattern; all from Camp XI. Clockwise, from top left, USNM 562080, USNM 562075, USNM 562078, and USNM 562082.

Measurements of the paratypes (all in mm, $\bar{x} \pm 1$ standard error): Males ($n = 9$): SVL 47.7–52.3 ($\bar{x} = 50.5 \pm 0.4$); HL 17.9–18.9 ($\bar{x} = 18.4 \pm 0.1$); HW 16.8.0 – 18.1 ($\bar{x} = 17.4 \pm 0.1$); IND 3.7–5.0 ($\bar{x} = 4.0 \pm 0.1$); IO 4.9–5.6 ($\bar{x} = 5.2 \pm 0.1$); ED 5.0 – 6.5 ($\bar{x} = 5.7 \pm 0.1$); EN 4.1 – 5.2 ($\bar{x} = 4.6 \pm 0.1$); TD 2.3 – 2.6 ($\bar{x} = 2.5 \pm 0.1$); TL 26.0–28.3 ($\bar{x} = 27.6 \pm 0.2$); FL 19.7 – 21.8 ($\bar{x} = 20.5 \pm 0.2$). Immature male (USNM 562081): SVL 40.0; HL 15.0; HW 14.0; IND 3.4; IO 4.7; ED

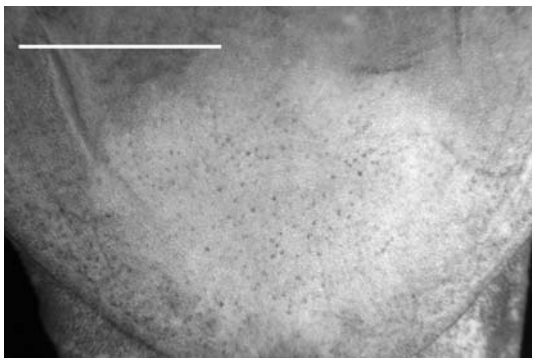

FIG. 21. The mental gland of *Myersiohyla neblinaria* (paratype USNM 562074) as seen through a superficial dissection exposing the internal aspect of the gular skin. Scale bar = 5 mm.

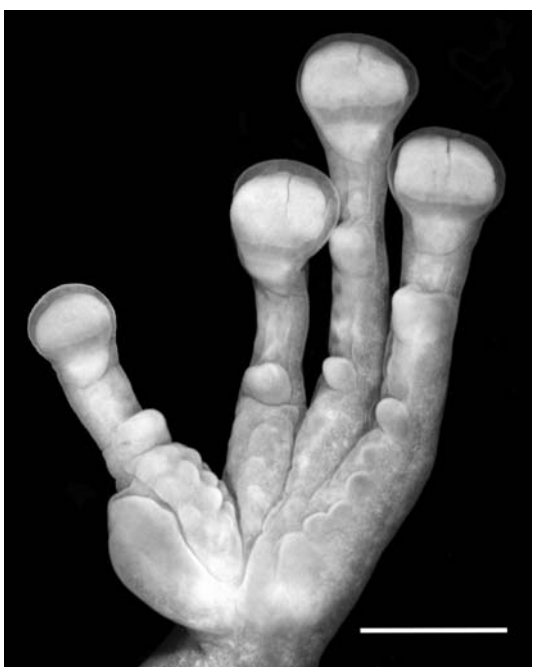

FIG. 22. Ventral view of hand of female *Myersiohyla neblinaria* (USNM 562072). Note the size of prepollex. Scale bar = 5 mm.

4.8; EN 3.9; TD 1.9; TL 23.1; FL 15.9. Females (*n* = 4): SVL 54.0 – 61.6 ($\bar{x}$ = 58.9 ± 1.7); HL 20.4 – 22.3 ($\bar{x}$ = 21.5 ± 0.4); HW 19.1 – 21.0 ($\bar{x}$ = 20.3 ± 0.4); IND 4.6 – 5.0 ($\bar{x}$ = 4.8 ± 0.1); IO 5.9 – 7.4 ($\bar{x}$ = 6.4 ± 0.4); ED 5.5 – 6.9 ($\bar{x}$ = 6.3 ± 0.3); EN 5.2 – 5.8 ($\bar{x}$ = 5.4 ± 0.1); TD 2.6 – 3.1 ($\bar{x}$ = 2.9 ± 0.1); TL 31.1 – 34.7 ($\bar{x}$ = 33.3 ± 0.8); FL 22.6 – 25.8 ($\bar{x}$ = 24.2 ± 0.7).

Remarks: The presence of a mental gland is not externally evident in male paratypes of *Myersiohyla neblinaria*, but is evident under high power magnification (60×) or through dissections. Superficial dissections in male USNM 562074 reveal a roughly circular patch of glandular tissue in the dermis of the mental region (fig. 21). A dissection of female USNM 562072 did not indicate the presence of a mental gland.

The vocal sac appears to be single and subgular, as indicated by the slightly distended sacs of USNM 562073, USNM 562076–77, and USNM 562080. The forearm is robust and prominent in all males, and proportionally slender in females. The prepollex is equally enlarged in males and females (figs. 17, 22). Two specimens partially dissected when tissue samples were removed (USNM 562072 ♀, and USNM 562077 ♂) show a translucent peritoneum and unpigmented urinary bladder. The female (SVL 60.2 mm) has large, unpigmented ovarian eggs. The dissected right ovary (left one not dissected) contained 119 eggs with largest diameter of 2.7–2.9 mm ($\bar{x}$= 2.8; s = 0.08; *n* = 15). The male has elongated, almost cylindrical, unpigmented testes. Females are proportionally larger than males (SVL 54.0–61.6 mm, males 47.7–52.3 mm). Superficial dissections in male USNM 562074 reveal that the m. intermandibularis has a large diamond-shaped aponeurosis; its fibers barely contact the oval and araphic m. submentalis. Supplementary elements of the m. intermandibularis absent. The m. depressor mandibulae originates from the zygomatic ramus of the squamosal, and, contiguously, from the posterior margin of the tympanic annuli; the tympanic fibers are not differentiated as a slip. There are no fibers originating from the dorsal fascia at the level of the m. levator scapulae.

FIG. 23. Adult female of *Myersiohyla neblinaria* (USNM 562070) asleep during the day in a leaf axil of *Bonnetia maguireorum* (Theaceae) on a small ridge NE of Camp I. Photograph by W. Buck.

Ecology and natural history: Near Camp I, Buck found an adult female (USNM 562070) asleep during the day in a leaf axil of *Bonnetia maguireorum* (Theaceae) on a small ridge northeast of Camp I (fig. 23). At Camp VII, a gravid female (USNM 562072) was collected on a vine in the forest and produced copious amounts of a milky white exudate on its back after capture. Specimens from Camp XI were collected by McDiarmid, Cocroft, and Paolillo along a small (1–4 m wide) forest stream with large boulders and cascades. On February 25, 1985, USNM 562073 was recorded as it called beside a cascade in a clump of grass growing out of a sloping, mossy rock face about 1 m from the water; three other males (USNM 562074, USNM 562077–78) were on leaves and in grass clumps near cascades on sloping rocks along the same stream. USNM 562075–76, USNM 562079–80, USNM 562082 were all collected from a rocky grotto along the same stream on the following night. An immature male (see below) was collected on a leaf of a small plant about 15 m from the stream that same night.

Two of three females (USNM 562070, SVL 59.8; USNM 562072, SVL 60.2) collected on February 10, 1984, and February 10, 1985, respectively, were gravid. A comparable-sized female

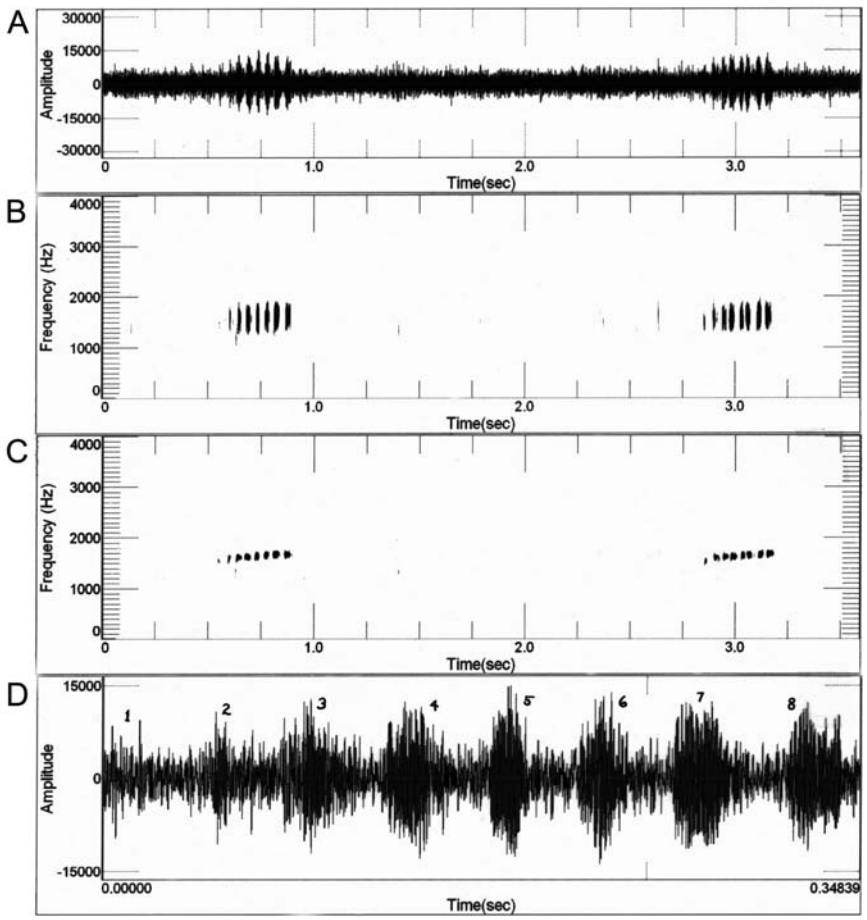

FIG. 24**.** Advertisement call of *Myersiohyla neblinaria*. Two notes in 3.6 sec., from a long continuous call > 1 min. duration. **A**. Waveforms. **B.** Wideband (323 Hz) spectrogram. **C.** Narrowband (63.09 Hz) spectrogram. **D.** Expanded waveform of first note, showing 8 pulses; the first pulse is weak (see also narrowband spectrogram above), being barely resolved above the background stream noise. Camp-XI specimen (USNM 562073) recorded February 25, 1985, air temperature 16.6° C (USNM tape 70, track 8).

(AMNH A-123715, SVL 61.6 mm) collected on November 29, 1984 also was gravid. The fourth female (AMNH A-131172), collected February 9–11, 1984, was smaller (SVL 54.0 mm) and had oocytes in very early stages of development, suggesting that she was approaching maturity. Most collected males (SVL 47.7–52.3 mm, $n = 10$) had well-developed nuptial pads and presumably were capable of breeding. Calling males were heard in late February 1985 at Camp XI. A single smaller male (USNM 562081, SVL 40.0 mm) collected at the same time and place lacked nuptial pads and likely was immature.

Vocalization: The advertisement call of a male paratype (USNM 562073) calling alone was recorded in February along a cascading stream near Camp XI (fig. 24). The frog was calling at the base of a clump of grass, about 1 m from the water. The recording includes 31 notes being continuously given in 80 sec of tape (the recording may contain only the terminal part of a long call).

TABLE 2. Uncorrected pairwise distances between 16S sequences of available specimens of *Myersiohyla neblinaria*. The one with an asterisk (*) is a tadpole.

	1	2	3
1- USNM 562071	—	—	—
2- USNM 562072	0.002	—	—
3- USNM 562074	0.000	0.002	—
4- USNM 562732*	0.000	0.002	0.000

The call is a long train of well-spaced notes given at a rate of 23.4 notes/min. Note duration is about 0.3–0.4 sec (295–382 ms, $\bar{x}$ = 338 ± 21 ms, n = 20). The individual note is composed of 7–9 pulses ($\bar{x}$ = 8.05 ± 0.69, n = 20 notes) that are resolvable even by narrowband analysis (fig. 24C). The individual note is a brief musical trill, being narrowly tuned with frequency rising about 113–151 Hz throughout the note from 1522–1560 Hz at initiation to 1673 Hz at the end (n = 9 notes analyzed).

Ayarzagüena and Señaris ("1993" [1994]) described the advertisement call of *Myersiohyla inparquesi* as a train of 240 ms, composed of two notes, the first with six pulses (90 ms) and the second with seven pulses (70 ms). The call was described as spanning the spectrum between 1200–2000 Hz, with a harmonic at 4400 Hz and the fundamental frequency at 1740 Hz. The call repetition rate was 20 notes/min. While no illustrations or temperature data were provided by Ayarzagüena and Señaris, their description suggests a call quite different from that of *M. neblinaria.*

Although *Myersiohyla neblinaria* and *M. aromatica* are readily diagnosable by several morphological characters (see diagnosis), the calls seem similar. The call of *M. aromatica* was described by Ayarzagüena and Señaris ("1993" [1994]), on the basis of recordings done at 19° C. The call was composed of single notes with an average duration of 420 ms, with 10–11 well-spaced pulses, a dominant frequency of 2000 Hz, and a bandwidth between 1250 and 2600 Hz. The note repetition rate was 44 notes/min.

Tadpole: The uncorrected pairwise distances of 16S sequences (table 2), between the tadpole (USNM 562732) and those of the holotype, and paratypes (USNM 562072, USNM 562074) are 0%–0.2%. Conversely, they are 12.3%–13.6% different from the sequences of available specimens of *M. chamaeleo*. Considering the identical or almost identical sequences, we consider this tadpole and all others with the same general morphology (see below) to be larvae of *M. neblinaria*.

Five larvae of *Myersiohyla neblinaria* in stage 25 were taken in the stream below Camp IX. They were found among rocks in shallow water (~5 cm deep) in slow-moving portions of the stream by day and night. A few tadpoles presumed to be of the same species (greenish gray) were seen at Camp VII (Cocroft, field notes) but none were collected. Specimens from Camp XI are quite fragile (possibly because of problems with the formalin [low pH?] at the time of fixation), especially the largest individual (USNM 562370) that was illustrated shortly after its capture and shown in figure 25. Since that time, the specimen has progressively deteriorated, particularly in that its tooth rows are separating from the tooth ridges; otherwise the remainder of the specimen is in good condition. Based on notes on the LTRF taken when the specimen

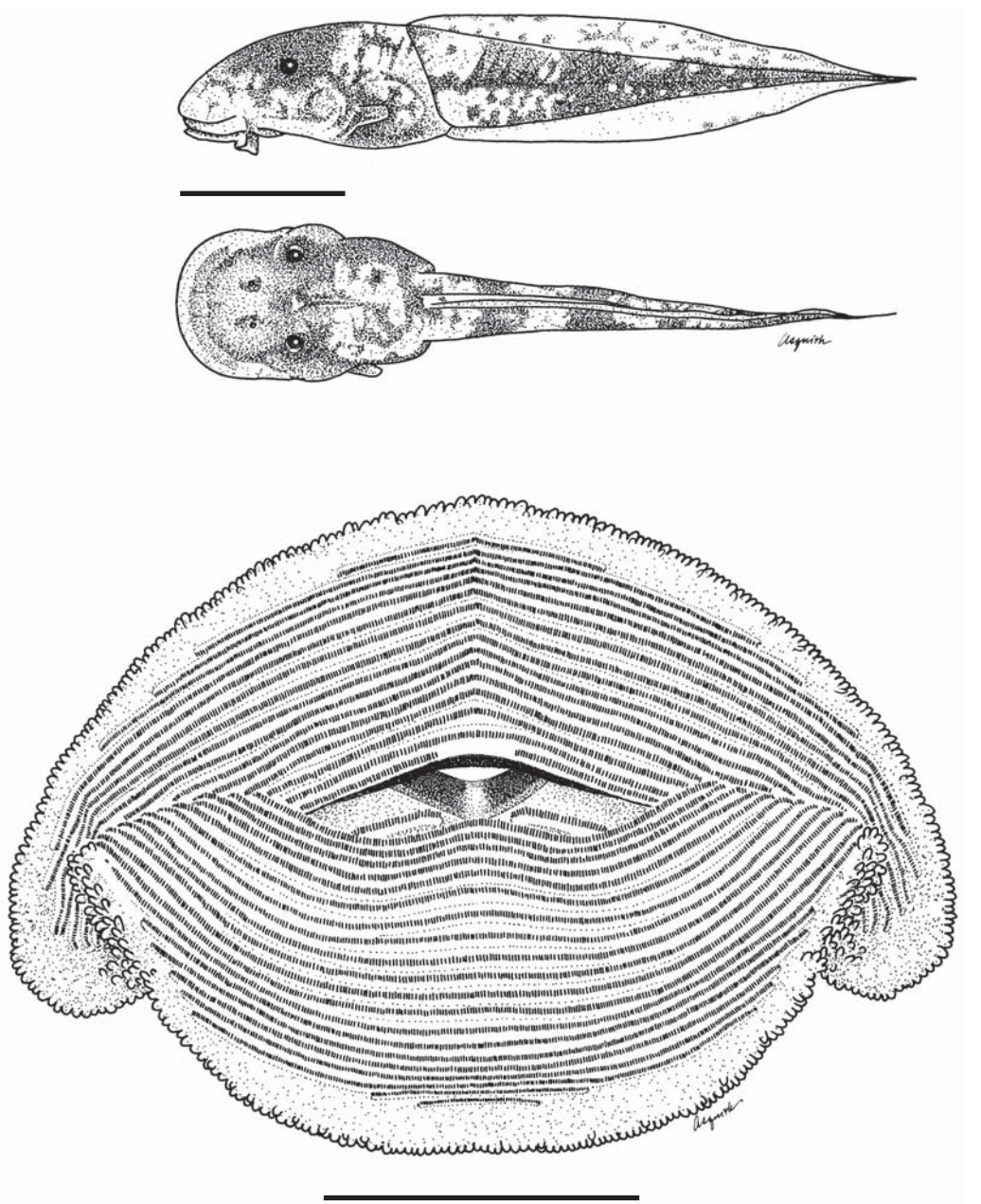

FIG. 25. Tadpole of *Myersiohyla neblinaria* (USNM 562370) from Camp XI, Gosner stage 25. Lateral and dorsal views, and oral disc. Scale bar = 10 mm (upper) and 5 mm (lower).

was illustrated and additional observations, we describe it below and compare it with other available specimens.

Description: A tadpole (USNM 562370, fig. 25) in stage 25 from Camp XI has the following measurements (all in mm): total length 76.0; body length 27.0; basal tail muscle height 7.8; basal tail muscle width 7.8; maximum dorsal fin height 2.8, this point being 20 mm away from body;

maximum ventral fin height 2.8, this point being 24.4 mm away from body; body width 16.7; body depth 12.1; eye diameter 2.0; pupil diameter 0.8; interorbital distance 5.0; internarial distance 4.9; snout to nostril distance 6.5; snout to eye 2.5; snout to spiracle 21.7; oral disc diameter 14.9.

Oral disc enlarged and ventral; marginal papillae in single row, with contiguous papillae in offset disposition, but sometimes also forming second row. Few submarginal papillae scattered between distal labial tooth rows and labial edge. LTRF 16(16)/21(1). Gaps in rows A-16 and P-1 small, of about equal width. Teeth on proximal (closest to mouth) rows wider than teeth on distal rows; distal teeth 2–3 times more numerous per mm. Tooth density on P-1 about 35 teeth/mm. Upper jaw sheath long and slender, with uniform and small serrations. Lower jaw sheath wide, V-shaped, about four times as wide as upper jaw sheath, and with low, rounded serrations.

Body dorsoventrally flattened anteriorly, ovoid posteriorly. Eyes small, dorsolateral. Snout slightly truncated in dorsal view, gently slopping in profile. Nostrils relatively small (about 60% of eye diameter), with fleshy rim and two medial, contiguous, triangular projections, anterior one quite prominent and about twice as large as the posterior one. Spiracle lateral, sinistral, its inner wall fused with body wall along its distal half; opening oriented slightly dorsally. Vent tube dextral, twice as long as wide, fused with lower fin; angular aperture. Dorsal fin originating on terminal eighth of the body, anterior to origin of tail; lower fin originating at base of tail. Neuromasts not visible but presumably present and undetected because of the almost complete loss of pigmentation as an artifact of fixation. Melanophores also not visible but presumably present (see below).

Some variation was observed in comparing the described specimen (USNM 562370) with four other smaller specimens also in stage 25 (USNM 562731: TTL 48 mm, LTRF 14/15; USNM 567732: TTL ? [tail taken for tissue], LTRF 14/18; USNM 562731[2]: TTL 41 and 22 mm, LTRF 13/15 and 9/10, respectively). We did not observe the second, minor triangular projection from the nostril rim in these specimens. Further studies will determine whether these projections are the same structures noticed by Mijares-Urrutia (1992) and Sanchez (2010) on several species of *Hyloscirtus*. Coloration of the body of USNM 567732 (a tissue voucher that was frozen in the field in liquid nitrogen) when it was thawed and preserved (Sept., 2005) was overall greenish with extensive concentrations of pigment on the head and body and patches of iridophores above the eyes; scattered patches of greenish color on the snout; neuromasts not visible and perhaps absent; melanophores (not visible in the other field-fixed specimens) visible and rodlike.

The LTRF of 16/21 reported for the largest tadpole (fig. 25) represents the largest labial toothrow formula known; it was erroneously reported as 17/21 and the largest value in hylids by Altig and McDiarmid (1999b: 308). The only tadpoles having large formulae that are close to the one reported here are those of *M. inparquesi* (a maximum of 14/21), *M. aromatica* (a maximum of 13/18), and the *Hyloscirtus armatus* group (a maximum of 14/17, Cadle and Altig, 1991; Lotters et al., 2005). Interestingly, the smaller tadpoles of *M. neblinaria* also have smaller formulae (ranging from 9/10 to 14/18). This apparent positive association between increased total length and LTRF could be related to a similar observation recently reported by Sanchez (2010) in tadpoles of *Hyloscirtus*; however, the underlying mechanism of ontogenetic increase in the number of labial tooth rows requires further study.

FIG. 26. Dorsal and ventral view of the holotype of *Myersiohyla loveridgei* (MCZ 28565, 38.2 mm SVL).

Myersiohyla loveridgei (Rivero, 1961)
Figures 26–28

Hyla loveridgei Rivero, 1961. Type locality: "Pico Culebra, Mt. Duida, 3000 ft., Territorio Amazonas."
Hyla ginesi Rivero, 1963. Replacement name for *Hyla loveridgei*, incorrectly considered a junior secondary homonym of *Nyctimystes loveridgei* Neill, 1954 (see La Marca and Smith, 1982).
Hyla loveridgei: La Marca and Smith, 1982.
Myersiohyla loveridgei: Faivovich et al., 2005. First combination with *Myersiohyla*.

Diagnosis: A species of *Myersiohyla* characterized by: (1) male SVL 38.2, females unknown; (2) two nuptial pads; (3) a row of tubercles along the forearm; (4) an externally evident mental gland in males; (5) thighs patterned with longitudinal bars; (6) dorsum with irregular brown blotches; (7) condition of the m. depressor mandibulae unknown; (8) eggs unknown; (9), (10), (11) tadpoles unknown.

Comparison with Other Species: *Myersiohyla loveridgei* is most similar to *M. aromatica*, from which it apparently differs by the presence of a distinct tarsal ridge (absent in *M. aromatica*; Ayarzagüena and Señaris, "1993" [1994]). The presence of two nuptial pads differentiates *M. loveridgei* from *M. inparquesi*, *M. kanaima*, and *M. neblinaria*. Dorsal color pattern and the presence of a row of tubercles along the forearm separate *M. loveridgei* from *M. chamaeleo*. The presence of an externally evident mental gland separates *M. loveridgei* from *M. kanaima* and *M. neblinaria*.

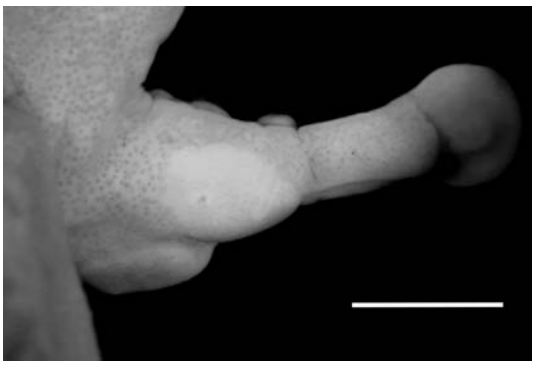

FIG. 27. Nuptial pad of the holotype of *Myersiohyla loveridgei* (MCZ 28565). Scale bar = 2 mm.

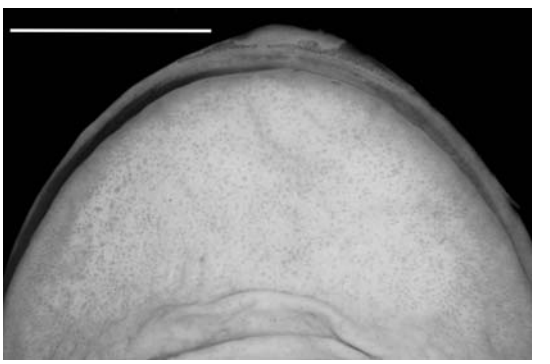

FIG. 28. Ventral view of the gular region of the holotype of *Myersiohyla loveridgei* (MCZ 28565) showing the external aspect of the mental gland. Scale bar = 5 mm.

Description: The descriptions provided by Rivero (1961, "1971" [1972]) are adequate, but a few details are worth noting. Rivero (1961) described the nuptial pad of the holotype as "male with a brown rugosity on the pollex and inner finger...." Later Rivero ("1971" [1972]) described the second specimen (UPR-M. 2854) as having "a smooth nuptial excrescence that extends up to the second finger." We had access only to the holotype MCZ 28565, an adult male (fig. 26). Like *M. aromatica* and *M. chamaeleo*, it shows two contiguous, discrete nuptial pads covered with minute epidermal projections. One of the pads is on the prepollex, and the other is on the medial-proximal surface of the first digit (fig. 27). The presence of a mental gland that occupies most of the gular region (fig. 28) is another characteristic overlooked by Rivero. Rivero (1961) reported that the holotype has the "vomerine odontoids forming a /--\ figure." Our study of the same specimen suggests that the expression used by Ayarzagüena and Señaris ("1993" [1994]), "slightly S-shaped" is quite appropriate to describe the disposition of each vomerine tooth series. There are 12 teeth on the right and 13 on the left. Rivero (1961) described a slight tarsal fold in the holotype; we consider it more appropriate to describe it as a distinct tarsal ridge. Foot-webbing formula for the holotype is **I** 2–2$^+$ **II** 1$^+$–2½ **III** 1½–2½ **IV** 2$^+$–1$^+$ **V**. Some approximate measurements of the holotype (the specimen is quite contorted, all in mm) are: SVL 38.2; HL 14.1; HW 13.3; IND 3.1; IO 4.8; EN 3.7; ED 4.2; TD 2.1; TL 22.0; FL 16.4. Note that Rivero (1961) reported the SVL of the same specimen to be 42.0 mm.

Remarks: The former *Hyla loveridgei* as described by Rivero (1961) was based on a single male specimen from Cerro Duida, and that description was supplemented (Rivero, "1971"

[1972]) with an additional male (SVL reported as 45 mm) from the same locality. Since its description, the species has rarely been mentioned in the literature (see Rivero, 1963; La Marca and Smith, 1982). While we still do not know any morphological synapomorphy for *Myersiohyla*, we find *loveridgei* to be very close morphologically (if not a senior synonym of *M. aromatica*, see below) to various species included in *Myersiohyla*, and for this reason we pose the testable hypothesis that *loveridgei* is congeneric. As morphological synapomorphies are discovered for *Myersiohyla*, or tissues of *loveridgei* become available, its generic status should be reevaluated.

We did not study specimens of *Myersiohyla aromatica*. Based solely on the thorough description provided by Ayarzagüena and Señaris ("1993" [1994]), the only character states differentiating this species from *M. loveridgei* seem to be the presence of a distinct tarsal ridge in the latter (Ayarzagüena and Señaris, "1993" [1994]). Since the distinctiveness of this ridge as described earlier in this paper is variable in *M. neblinaria*, the diagnostic value of the character is tentative and needs further evaluation. Furthermore, Ayarzagüena and Señaris ("1993" [1994]) reported 30–34 total vomerine teeth, whereas the holotype of *M. loveridgei* has 25. However, the lack of other specimens of *M. loveridgei* and potential variation in vomerine tooth counts precludes any conclusion regarding the diagnostic value of vomerine tooth number. Given that the type locality of *M. loveridgei* ("Pico Culebra, Mt. Duida, 3000 ft., Territorio Amazonas") is approximately 40 km (straight line) from the type locality of *M. aromatica* ("Cumbre del Tepui Huachamacari, Estado Amazonas, Venezuela"), and that Ayarzagüena and Señaris ("1993" [1994]) did not compare the species, we tentatively consider both species as valid, but suggest that their status deserves further study.

Ecology and Natural History: The holotype was collected during the day "as it sprang from beneath (or near?) a rock in a treeless, rocky area of Mt. Duida" (Rivero, 1961: 109). The other known specimen was collected on the mossy stones along a fast-running stream (Rivero, "1971" [1972]: 185).

Advertisement Call: Unknown.

Tadpole: Unknown.

Myersiohyla sp.
Figures 29–30

The second author collected an adult female specimen (USNM 550357) of *Myersiohyla* on the summit of Cerro Duida (1850 m, 03°25′N, 065°40′W). The point of capture is approximately 25 km SE (straight line) from Cerro Culebra, the type locality of *M. loveridgei*. The specimen has differences in pattern with the two specimens described by Rivero (1961; "1971" [1972]) and subtle morphological differences; for these reasons we are hesitant to assign it to *M. loveridgei* until more data on the variation of this species becomes available. The specimen (fig. 29) differs from the holotype of *M. loveridgei* and the specimen described by Rivero ("1971" [1972]) in having the thighs with irregular tan spots, instead of well-defined vertical bars, and in having the tympanic annuli more inclined medially. Some measurements of this specimen are (all in mm): SVL 47.2; HL 18.0; HW 17.4; IND 3.7; IO 6.0;

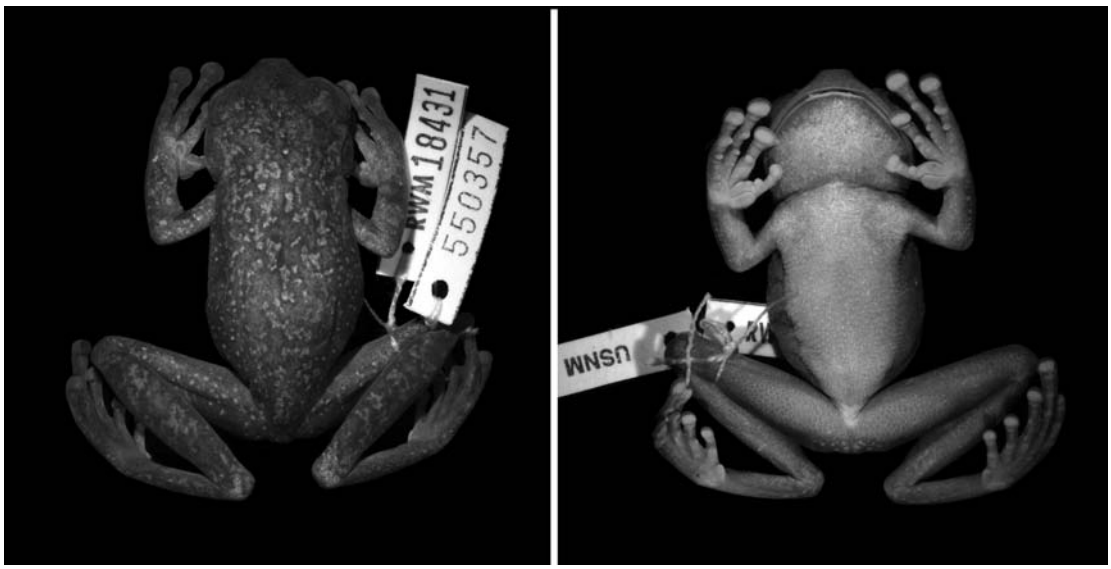

FIG. 29. Dorsal and ventral view of *Myersiohyla* sp. (USNM 550357, 47.2 mm SVL). This specimen was collected on Cerro Duida, approximately 25 km SE (straight line) from the type locality of *Myersiohyla loveridgei* (Pico Culebra). It differs from the two known specimens of *M. loveridgei* in having the thighs with irregular tan spots, instead of well-defined vertical bars, and in having the tympana inclined more medially.

ED 5.3; EN 4.5; TD 2.5; TL 26.4; FL 20.1. Other morphological characteristics include a row of tubercles along the arm, quite prominent palmar and plantar tubercles (including an enlarged inner metacarpal tubercle; see fig. 30), a well-developed ridge along the tarsus, and foot webbing formula **I** 2–2 **II** 1½–2 **III** 2^{+}–2½ **IV** 2½–1^{+} **V**. Dorsally the background coloration is dark reddish brown, with multiple, irregular tan mottling. The discs are pale gray. A superficial dissection reveals a group of fibers of the m. depressor mandibulae that originates on the sheath of connective tissue that extends from the dorsal fascia into the space between the head and the body, with a few fibers originating at the level of the suprascapulae. This morphology is different from that seen in *M. chamaeleo*, as in that species the fibers originating at the level of the suprascapula form a distinct fan over the suprascapulae, while in *Myersiohyla* sp, most of the fibers originate in the connective tissue between head and body, with only the proximal part of approximately half of the fibers marginally reposing on the levator scapulae. The specimen is a gravid female. The dissected right ovary (left one intact) contained 47 eggs with largest diameters of 2.5–3.0 mm $\bar{x}$ = 2.73; s = 0.15; n = 15), mostly unpigmented, with the exception of a reduced, pale brown animal pole.

Orejas-Miranda and Quesada (1976) referred to an unidentified hylid from the summit of Cerro Jaua and also mentioned tadpoles with numerous labial tooth rows. Further, they published a black-and-white photograph (their fig. 6) of an adult frog that unequivocally looks like a *Myersiohyla*. An adult male of *Myersiohyla* and some tadpoles with large LTRFs from Jaua are housed in the USNM (USNM 561349) and will be dealt with in a separate contribution.

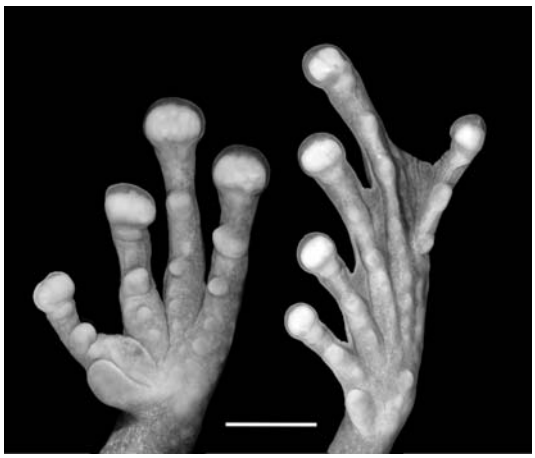

FIG. 30. Ventral view of hand and foot of *Myersiohyla* sp. (USNM 550357). Scale bar = 5 mm.

DISCUSSION

The Monophyly of *Myersiohyla*

Although morphological synapomorphies are still unknown, *Myersiohyla* is recovered as monophyletic in the present phylogenetic analysis and supported with 91% parsimony jackknife absolute frequency in the static parsimony analysis. Besides the monophyly of *Myersiohyla*, the results of the analysis conducted need extensive discussion, but that requires a separate paper (Faivovich et al., in prep.), so we provide here some general comments that are expanded in appendix 1.

Our results recover the individual monophyly of *Hyloscirtus, Bokermannohyla*, and *Aplastodiscus* with 100% of absolute frequency in parsimony jackknife in the static alignment, while the monophyly of *Hypsiboas*, however, has 84% in parsimony jackknife. Relationships among the five genera, which are the same as those resulting from the analysis of Faivovich et al. (2005) and minor additions in subsequent analyses by Wiens et al. (2006, 2010) and Pyron and Wiens (2011), have at least 93% in parsimony jackknife. The internal relationships of *Aplastodiscus* and *Bokermannohyla* are the same as those obtained by Faivovich et al. (2005), Wiens et al. (2006, 2010), and Pyron and Wiens (2011). For comments on *Hyloscirtus* and *Hypsiboas*, see appendix 1.

The Type Species of *Myersiohyla*

Faivovich et al. (2005) based the description of *Myersiohyla* on 48 molecular synapomorphies identified during their phylogenetic analyses of hylid frogs. The sample used for representing the former *Hyla aromatica* group was tissue of a frog collected by McDiarmid on Cerro de la Neblina and identified as *Hyla inparquesi* Ayarzagüena and Señaris, 1994. Because this specimen was an exemplar of their new genus, Faivovich et al. (2005) designated *Hyla inparquesi* as the type species of *Myersiohyla*. However, subsequent study has shown that the frog (USNM 562071 [= RWM 17688)]) was misidentified and not a specimen of *Hyla inparquesi,* but actually representative of a new species described herein as *M. neblinaria*. For this reason and following the International Code of Zoological Nomenclature (ICZN, 1999: article 70.3.2), we change the type species of *Myersiohyla* from *Hyla inparquesi* Ayarzagüena and Señaris, 1994, which was misidentified in the original designation by Faivovich et al. (2005), to *Myersiohyla neblinaria* Faivovich, McDiarmid, and Myers (this paper).

On *Myersiohyla kanaima*

MacCulloch and Lathrop (2005) reported on 23 specimens of *Myersiohyla kanaima* collected on Mount Ayanganna, Guyana. The authors reported that "enlarged black-and-white eggs, 1 mm

in diameter, were present in 13 of the 17 females; the remainder had small white ova." However, our dissection of female USNM 549311 (SVL 46.4 mm.) revealed 19 eggs in the left ovary (largest diameter 2.9–3.2, $\bar{x}$ = 3.07, s = 0.12); these eggs are densely pigmented overall, and the animal and vegetal poles are not distinguishable. This observation is more in line with Duellman and Hoogmoed's (1992) report for three female *M. kanaima*, which had "relatively large (1.8 mm diameter) ... pigmented oviducal eggs." Differences in egg size and coloration seem most likely to reflect state of maturity.

MacCulloch and Lathrop (2005) further described a series of tadpoles that they assigned to *Myersiohyla kanaima* on the basis of the presence of two subadults and two recently metamorphosed individuals (stage 45) on the bank of the stream, plus one metamorph (stage 43) collected along with the other tadpoles. These tadpoles differ from those of *M. aromatica*, *M. chamaeleo*, *M. inparquesi*, and *M. neblinaria* most notably in having an oral disc with a 2/4 LTRF.

On the basis of the taxonomic distribution of LTRFs in Cophomantini, Faivovich et al. (2005) suggested that an increase in the number of labial tooth rows is likely a putative synapomorphy of Cophomantini, because all known larvae of *Hyloscirtus* and *Myersiohyla* at that time had a minimum of 6/7 labial tooth rows. They stressed, however, that the minimum number of labial tooth rows that would be a synapomorphy was ambiguous because the tadpole of *M. kanaima* was unknown at that time.

Taking into account the position of *Myersiohyla kanaima* in our phylogenetic hypothesis, nested within a group where the minimum known labial toothrow formula is 6/7, a 2/4 LTRF is a stark contrast. This could well be simply another case of homoplasy, and as such it should be considered until new evidence is gathered. The possibility of a mistaken association between subadults, juveniles and metamorphs that led to the identification of these tadpoles should also remain open to question.

Material: The first author examined the following specimens that had been assigned to *Myersiohyla kanaima*: Guyana: Mazaruni-Potaro: northern slope of Mount Roraima: USNM 549311 ♀; Guyana: District 7: Mt. Ayanganna: ROM 39587 ♀, 39575–76 ♂♂, 39590 ♀, 43861 ♂, 43871 ♂, USNM 561828–29 ♀♀.

The Mental Glands

Mental glands[5] are known to occur in hylids in (1) the *Hyloscirtus armatus* and *H. bogotensis* group (Duellman, 1972, La Marca, 1985, Faivovich and De la Riva, 2006), (2) Several species of *Bokermannohyla* (Faivovich et al., 2009), (3) the *Hypsiboas benitezi* group (Faivovich et al., 2006;

[5] Barrio-Amoros and Brewer-Carias (2008: 32), while describing a new species of the *Hypsiboas benitezi* group stated: "*Hypsiboas tepuianus* apparently has a mental gland (sensu Faivovich et al., 2006). We did not consider this character in the diagnosis or description, because we consider that it is very subjective, and not easy to determine. For instance, while it is easily identifiable in *Hyloscirtus colymbus* [sic!], *H. palmeri* and *H. albopunctulatus* (see Fig. 4 in Faivovich et al. 2006), it is much less obvious in *Hypsiboas nympha* and *H. lemai* (same Fig. 4; Faivovich et al. 2006), and to us, an object of subjective appreciation. In two specimens of *H. lemai* examined (to be deposited in ERBG), the senior author could not distinguish the mental gland. In two more specimens of *H. jimenezi*, he either could see any gland (in accordance with Señaris and Ayarzagüena, 2006). Examining the mental zone of male paratypes of *H. tepuianus*, is possible to discern a whitish quadrangular area, but it is also present in the female. For this reason, we cannot conclude with confidence that this is the mentioned gland of Faivovich et al. (2006.)"

Myers and Donnelly, 2008), (4) *Hypsiboas granosus* and *H. punctatus* (Hoogmoed, 1979; Brunetti et al., 2012), (5) *Hypsiboas heilprini* (Trueb and Tyler, 1974), (6) *Duellmanohyla chamulae* and *D. ignicolor* (Duellman, 1961), and (7) *Litoria citropa, L. davisae*, and *L. subglandulosa* (Tyler and Anstis, 1975; Mahony et al., 2001). The occurrence of a mental gland in males of at least four species of *Myersiohyla* (*M. chamaeleo*, *M. kanaima*, *M. loveridgei*, and *M. neblinaria*) indicates that mental glands are more frequent than previously reported. Furthermore, the fact that these structures sometimes are evident only through superficial dissections suggests that they might be more widespread, but unnoticed.

A recent study on the mental gland of *Hypsiboas punctatus* (Brunetti et al., 2012) revealed that at least in that species, the male mental gland represents a region of accumulation of sexually dimorphic, specialized mucous and granular glands that occur as well on the flanks of the body. Whether this is also the case in the other Cophomantini remains an open question.

We did not study specimens of *Myersiohyla aromatica* or *M. inparquesi,* so we do not know whether a mental gland is present in these species. We had five males of *M. kanaima* available for study; all of these have scattered glandular units in the gular region, much less evident than in other species of *Myersiohyla*. Available data (McCulloch and Lathrop, 2005; Bruce Means, personal commun.) indicate that none of these males were collected while calling. For this reason, and considering that we have no knowledge regarding the physiological mechanisms involved in the development of the gland, at this stage it is unclear whether its occurrence as scattered units in the gular region of in apparently nonreproductive males of *M. kanaima* results from a real difference in the development of the gland in this species, or because of the physiological condition of the available males.

Reproductive Biology of *Myersiohyla*

Ovarian eggs in four species of *Myersiohyla* are relatively large (2.8–3.0 mm); they are unpigmented in *M. chamaeleo* and *M. neblinaria*, partially pigmented in *Myersiohyla* sp., and completely pigmented in *M. kanaima* (Duellman and Hoogmoed, 1992; this paper). Oviposition sites are unknown. Males of *M. chamaeleo* call from vegetation (e.g., stems of small shrub, fern frond,

(*Continued from previous page*) It is unnecessary to argue whether the mental gland being "easy" to determine invalidates its diagnostic value. However some clarifications are in order regarding the "subjective" nature of the gland, for which, at the histological level, the study of Brunetti et al. (2012) should be enough to dispel any doubt. Faivovich et al. (2006) included in their figure 4 photographs of mental glands of different species precisely to show what seems to be confusing for Barrio-Amorós and Brewer-Cárias: When they occur, mental glands do have different morphologies in different groups. The reference to a "whitish quadrangular area" rather than to the glandular units suggests confusion about the nature of the gland itself. It seems odd that the presence of the gland in females, as Barrio-Amorós and Brewer-Cárias apparently interpret in *Hypsiboas tepuianus* (on the basis of the "whitish quadrangular area"), could be taken as a reason to suspect that it is actually a gland, unless they were under the impression that mental glands occur only in mature males which is not the case. For example, Duellman (1972: 21, 25, 27) referred to mental glands occurring in both males and females of *Hyloscirtus colymba*, *H. phyllognathus*, and *H. platydactylus*. The reference to its absence in *Hypsiboas jimenezi*, a species of the *H. punctatus* group, is perplexing, as Señaris and Ayarzagüena (2006) explicitly stated that it was absent.

lower leaves of bromeliads) 0.1–2.5 m above the water or shore and up to 2 m from the water's edge, and from mossy rock faces about 0.5 m above the water; males of *M. neblinaria* call from leaves and grass clumps growing on sloping, mossy rock faces near cascades in the same stream near Camp XI. A gravid female *M. chamaeleo* was collected on a stem about 3 m above the ground along this same stream where males had been recorded the previous night. Known tadpoles of *Myersiohyla* (*M. aromatica*, *M. chamaeleo*, *M. inparquesi*, *M. kanaima, M. neblinaria*) are exotrophic and live in streams. No data are available regarding vocalization sites in *M. kanaima*, *M. loveridgei*, and *Myersiohyla* sp.

The presence of unpigmented eggs has commonly been associated with a spawn protected from direct solar light (Salthe, 1963; Altig and McDiarmid, 2007). Ova in *Myersiohyla* show three patterns of pigmentation. The presence of large, pigmented eggs in *M. kanaima* is remarkable in that the co-occurrence of large amounts of yolk (resulting in large-sized eggs) and dense pigmentation is quite unusual in anurans, as is the pigmentation of the vegetal pole. Furthermore, we have been unable to find records in the literature of other anuran species having comparable levels of pigmentation. Clearly the situation deserves further study. In *M. chamaeleo* and *M. neblinaria*, the eggs are completely unpigmented. In the specimen here referred as *Myersiohyla* sp., the eggs are mostly unpigmented, with the exception of a reduced brown animal pole.

Ova are known in only 10 of the 30 species of *Hyloscirtus*[6] (*H. antioquia*, *H. alytolylax, H. armatus, H. bogotensis, H. charazani, H. jahni, H. larinopygion, H. palmeri, H. phyllognathus,* and *H. platydactylus;* La Marca, 1985; Lang, 1995; Rivera-Correa and Faivovich, 2013; J.F. and R.W.M., personal obs.); they are unpigmented, and relatively large. La Marca (1985) noted that eggs of *H. jahni* have been found in turbulent waters, while those of *H. platydactylus* have been found deposited on leaves of certain streamside plants in the families Lauraceae and Melastomataceae, without providing any further details. Relatively large, unpigmented eggs are also reported in *Aplastodiscus* (Haddad and Sawaya, 2000; Haddad et al., 2005), and in the *Hypsiboas benitezi* group (Faivovich et al., 2006). In *Aplastodiscus* eggs are deposited in a subterranean nest built by the male (Haddad and Sawaya, 2000; Haddad et al., 2005); no data regarding oviposition site are available for species of the *H. benitezi* group. The diversity of reproductive modes, at least three (oviposition in lotic waters, on leaves, and on subterranean nests), associated with large and unpigmented eggs in groups closely related to *Myersiohyla*, preclude any prediction regarding its reproductive mode or modes.

A Comment on Odors and Exudates

Ayarzagüena and Señaris ("1993" [1994]) included "strong odor" as a diagnostic character of the former *Hyla aromatica* group, and Faivovich et al. (2005) considered this trait a potential synapomorphy of *Myersiohyla* if it were shown to be present in *M. loveridgei* and *M. kanaima*, in which a strong odor has not been yet recorded. We report here the presence of copious amounts

[6] Kizirian et al. (2003) reported large ovarian eggs (2.76–3.4 mm) in an eleventh species of *Hyloscirtus*, *H. tapichalaca*, but made no reference to their pigmentation. Cochran and Goin (1970) referred to unpigmented eggs in *Hyloscirtus bogotensis*, but provide no information on egg diameter.

of a milky white exudate in the back of a female of *M. neblinaria* (USNM 562072); unfortunately no reference to odors was recorded (Paolillo, field notes).

However, the possibility that strong odor and/or exudates could be synapomorphy of *Myersiohyla* deserves further scrutiny in the light of the phylogenetic context hypothesized by Faivovich et al. (2005) and of other published records of secretions with strong odors in other Cophomantini. So far, a strong odor has been reported for two species of the *Hyloscirtus bogotensis* group and three of the *H. larinopygion* group. Among the species included in the *H. bogotensis* group, La Marca (1985) reported a strong odor and smelly exudate in *H. platydactylus*, and La Marca (1985) reported a sticky exudate with a different smell in *H. jahni*. Taran Grant who actively smells every frog he collects (seriously) did not perceive any odor in *H. alytolylax* or *H. palmeri* (Grant, personal commun.). Lucas Barrientos (personal commun.) noticed a strong odor in several specimens of *H. bogotensis* from various localities in Colombia. Reynolds and Foster (1992) reported that an adult female of *H. armatus* produced copious skin secretions when handled, similar to "rubber-cement," but made no reference to its smell. Kizirian et al. (2003) reported a sticky white fluid with strong odor in *H. tapichalaca*, a member of the *H. larinopygion* group. Ronn Altig (personal commun.) noticed a strong odor associated with the three paratopotypes of *H. lindae*, another member of the *H. larinopygion* group that he collected in eastern Ecuador (Duellman and Altig, 1978), and recalled that the frogs seemed to produce a clear exudate that made them shine. Grant and Barrientos (personal commun.) also noticed a strong odor in several specimens of *H. larinopygion* from various localities in Colombia. Rivera-Correa and Faivovich (2013) recently reported the release of a white secretion with strong smell in *H. antioquia*.

A strong odor is known to occur as well in at least seven species of the *Hypsiboas pulchellus* group: *H. caipora, H. cordobae*, *H. curupi*, *H. prasinus*, *H. pulchellus, H. riojanus,* and *H. stellae* (Barrio, 1962, 1965b; Gallardo, 1958; Garcia et al., 2007; Antunes et al., 2008; J.F., personal obs.). Azevedo-Ramos (1995) reported that two out of 79 studied males of *H. semilineatus* (using the name *H. geographicus*) emitted a strong odor when defensive behaviors were elicited. Bokermann (1964) noticed that *Bokermannohyla martinsi* secretes a copious exudate when handled, but made no reference to its smell. Lutz (1973) noticed that *Bokermannohyla claresignata* smells like crushed plants, a suitable description of the smell of the species of *Hypsiboas* listed above, as well as that of *B. ahenea*, *B. circumdata*, *B. hylax*, *B. ibitiguara*, *B. izecksohni*, *B. luctuosa*, *B. martinsi*, *B. napolii, B. ravida,* and *B. saxicola* (Célio F.B. Haddad, personal commun.; J.F., personal obs.). However, species of *Bokermannohyla* have a stronger smell than *Hypsiboas* (J.F., personal obs.)

Besides the need for increased understanding of the taxonomic distribution of strong odor within *Myersiohyla*, the possibility that the strong odor could actually be more common in *Hyloscirtus* than currently known deserves some consideration. This is relevant because Faivovich et al. (2005) found *Myersiohyla* to be the sister taxon of *Hyloscirtus* plus the remaining Cophomantini (*Bokermannohyla*, *Aplastodiscus*, and *Hypsiboas*). Although it would ultimately depend on the internal topology of *Hyloscirtus*, if strong odor actually occurs in more species of *Hyloscirtus,* optimizing it as a plesiomorphic character state on its ingroup node, strong odor

might be a synapomorphy of a more inclusive clade (Cophomantini?), not just *Myersiohyla*. Unfortunately, additional speculation is hampered by the total lack of knowledge regarding the chemical nature of the odors and secretions and the scarce and anecdotal knowledge of their taxonomic distribution among hylines and other frogs. Another problem is the basis for determining what and how odors are to be considered homologous and how they are associated with secretions. Clearly the ideal situation would be to understand their chemical nature, but in the absence of this, one would expect that odors minimally would smell similarly (however, this might be a function of concentration; see below) or would be associated with secretions of similar consistency or appearance (i.e., milky, white, sticky, etc). Certainly no systematic effort to study the occurrence of odor in Hylinae has been made, as has been done in Pelodryadinae (Smith et al., 2003, 2004a, 2004b).

It should be realized that anurans and other amphibians secrete a great number of biologically active substances, mostly from integumentary granular glands. These substances include biogenic amines, peptides, bufodienolides, and more than (at last count) 800 chemically diverse alkaloids—bioactive organic nitrogenous ring compounds that until the latter half of the 20th century were generally thought to originate solely from plants. The chemistry and pharmacology of amphibian exudates was pioneered by our late colleague John Daly, whose bibliography includes over 200 papers on compounds found in amphibian skin (see Myers, 2009). But if the chemistry of such compounds is in its infancy (as Daly might have stated), the chemistry of volatile amphibian secretions is a science not yet born. The dendrobatoid genus *Aromobates* was named (Myers et al., 1991) for the strong mercaptan-like odor of the type species (*A. nocturnus*). Efforts to demonstrate mercaptans or other volatile compounds were unsuccessful; for Daly's protocols, see Myers et al. (1991: 14). The analytical difficulty for mercaptans and probably many other compounds is that the human nose is sensitive enough to detect mercaptans at the level of parts per billion. Compounds responsible for such odors may originate from much lower levels than suggested by vertebrate olfactory systems. Thus, the failure to detect seemingly diagnostic odors when handling or skinning frogs (e.g., other species currently assigned to *Aromobates*) provides no proof that the suspected compound is absent. Such "negative data" are worthy of note but currently lack phylogenetic usefulness.

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Representative specimens from the type series will be deposited in the Venezuelan collection at Museo de la Estación Biológica de Rancho Grande, Maracay (MBRG). Specimens from Myers' 1984 Neblina collections (including a specimen of *Myersiohyla neblinaria*) were deposited in the Museo Biología de la Instituto de Zoología Tropical, Universidad Central de Venezuela (MBUCV),

For helping to save or prevent delay of an important part of the Neblina Expedition, participants owe special thanks to Robert G. Goelet, former president and Chairman Emeritus of the Board of Trustees of the American Museum of Natural History. The Neblina Expedition was closed down between late July and November 1984, with subsequent notification from FUDECI that it could not be resumed before February1985. Some of the problems were standard political ones, but another involved the serious problem of funding for helicopter support. When informed of the latter, Mr. Goelet promised substantial support for chartering private helicopters. That promise notably uplifted the spirits of those engaged in expedition logistics and appeared to stimulate intragovernment cooperation. Chartering private aircraft proved, after all, not necessary and the Venezuelan Air Force (FAV) was able to resume its superb role in providing helicopter support for the montane camps. Goelet's financial support of other tepui expeditions is well known, but the pronounced impact of the support that he *offered* to the Neblina Expedition has not been publicized. (AMNH Dept. Herpetology Archives, Myers Collection. Formal Expeditions: Neblina Expedition 1984–1985, Folder II.)

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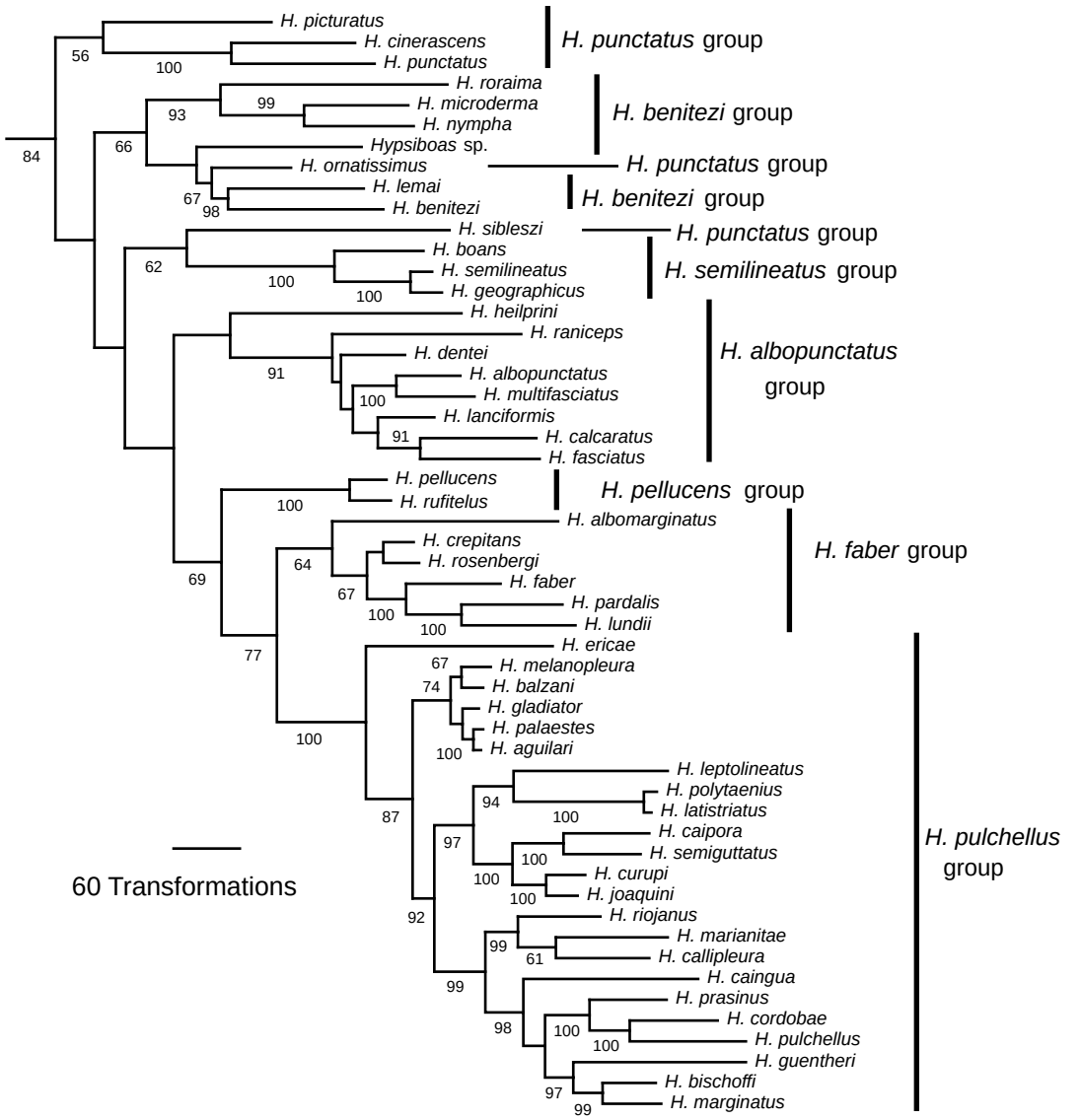

FIG. 31. Relationships of *Hypsiboas* recovered on the most parsimonious trees using direct optimization. Values around nodes are Jackknife parsimony absolute frequencies calculated using the static parsimony analysis. Nodes lacking values have < 50% absolute jackknife frequencies.

APPENDIX 1

Further Comments on the Phylogenetic Results

The results support the monophyly of the three species groups of *Hyloscirtus*, the *H. armatus, H. bogotensis,* and *H. larinopygion* groups (fig. 2). Eleven known species of the *H. bogotensis* group are absent from our analysis, so our results are not a stringent test of its monophyly. This is an important limitation considering that its only putative morphological

synapomorphy so far known, the mental gland in males, has been shown to be present as well in the *H. armatus* group (Faivovich and De la Riva, 2006). The relationships of the *H. larinopygion* group, from which we have a taxonomic sampling identical to that of Coloma et al. (2012), are the same as those obtained in that paper on their parsimony analysis. Differences with the topologies of their maximum likelihood and bayesian analyses only involve the position the *H. armatus* group and that of *H. larinopygion* (sister taxon of *H. lindae* + *H. pantostictus* on our analysis vs. sister taxon of a clade containing all species of *Hyloscirtus* excluding the former clade and *H. tapichalaca* on their analyses) and *H. tigrinus* (sister taxon of *H. criptico* + *H. pacha* + *H. stauferorum* on our analysis vs sister taxon of the latter clade plus *H. psarolaimus* on theirs). Coloma et al. (2012) on their maximum likelihood analysis obtain the *H. armatus* group as the sister taxon of the *H. bogotensis* group. However, on their Bayesian analysis (though with poor support), in the present analysis and those of Faivovich et al. (2005), Wiens et al. (2006, 2010), and Pyron and Wiens (2011), it is supported (Jackknife absolute frequency 94%) as the sister taxon of the *H. larinopygion* group. This difference could be related to the fact that Coloma et al. (2012) limited their analysis to mitochondrial sequences, as well as to the low density of outgroups employed by them.

Regarding the relationships within *Hypsiboas* our results are similar to those obtained by Faivovich et al. (2005) in terms of the monophyly of most of the species groups that they recognized, but relationships among them differ (fig. 31). Subsequent to Faivovich et al. (2005), sequences of a few more species of *Hypsiboas* became available in Genbank through the papers of Salducci (2005) and Wiens et al. (2005, 2006). Most of these sequences were included in the analyses of Wiens et al. (2010) and Pyron and Wiens (2011), who made no comments about relationships of *Hypsiboas*. These additions allow additional testing of the monophyly of the species groups recognized by Faivovich et al. (2005). The position of *H. dentei* in the *H. albopunctatus* group, and that of *H. rosenbergi* as sister taxon of *H. crepitans* in the *H. faber* group, corroborate the monophyly of those groups as defined by Faivovich et al. (2005). On the basis of the monophyly of *H. cinerascens, H. picturatus,* and *H. punctatus* in their analysis, these authors recognized the *H. punctatus* group, including all species that had been tentatively associated with those species available to them. The *H. punctatus* group, as recognized by these authors included *H. alemani*, *H. atlanticus, H. hobbsi, H. ornatissimus, H. cinerascens* (as *H. granosus*), *H. picturatus*, *H. punctatus*, and *H. sibleszi*, to which Señariz and Ayarzagüena (2006) added *H. jimenezi* and Kok (2006) added *H. liliae*. Only short sequences of *H. ornatissimus* had been added to the original sampling of the group by Faivovich et al. (2005). The *H. punctatus* group was not particularly well supported in their analysis, and the exemplars available to them are not monophyletic in our results. *Hypsiboas ornatissimus*, interestingly, is nested in the *H. benitezi* group, and should be included in that group. *Hypsiboas sibleszi* is the sister taxon of the *H. semilineatus* group, but this node is poorly supported. The remaining three exemplars of the *H. punctatus* group, the nominal species, *H. cinerascens* and *H. picturatus* are monophyletic, with low support. The non-monophyly of the *H. punctatus* group makes it imperative to include its remaining species (particularly *H. alemani, H. jimenezi, H. hobbsi, H. liliae*) in order to understand their relationships with the other groups of *Hypsiboas.*

APPENDIX 2

Genbank Accession Numbers for the Sequences Employed in the Phylogenetic Analyses and Estimation of p-Distances

Sequences were produced by Darst and Cannatella (2004), Faivovich et al. (2004, 2005, 2010), Salducci et al. (2005), Wiens et al. (2006), Antunes et al. (2008), Köhler et al. (2010), Lehr et al. (2010), and Coloma et al. (2012). See those papers for locality data and other voucher information. Sequences produced for this project are in bold

Voucher	Species	12S-tRNA val-16S	16S-tRNA leu-ND1-tRNA Ile-tRNA Gln	Cytochrome b	Rhodopsin Exon 1	RAG-1	Tyrosinase	SIAH 1	CXCR4	28S
LSUMZ H-2164	*Acris crepitans*	AY843559	**GQ366290**	AY843782	AY844533	AY844358	AY844019	AY844762	**GQ365976**	AY844194
CFBH 3184	*Aplastodiscus albosignatus*	AY843596	—	AY843817	AY844570	AY844385	AY844042	AY844796	—	AY844219
USNM 303022	*Aplastodiscus arildae*	AY843604	—	AY843825	AY844578	AY844392	AY844049	AY844803	—	AY844223
CFBH 3909	*Aplastodiscus callipygius*	AY843614	—	AY843840	AY844592	AY844402	AY844058	AY844813	—	AY844236
AF 0070	*Aplastodiscus cavicola*	AY843617	—	AY843843	AY844594	AY844405	—	AY844814	—	—
CFBH 3001	*Aplastodiscus cochranae*	AY843568	—	AY843790	AY844542	AY844365	AY844024	AY844770	—	AY844200
CFBH 5915	*Aplastodiscus eugenioi*	AY843669	—	AY843913	AY844660	AY844456	—	AY844875	**KF751465**	—
USNM 303038	*Aplastodiscus leucopygius*	AY843638	**KF794106**	AY843873	AY844622	AY844425	AY844084	AY844840	**KF751466**	AY844261
MACN 37791	*Aplastodiscus perviridis*	AY843569	**KF794107**	AY843791	AY844543	AY844366	AY844025	AY844771	**KF751467**	AY844201
AF 0068	*Aplastodiscus weygoldti*	AY843685	—	AY843931	AY844678	AY844467	—	AY844887	—	—
USNM 303032	*Bokermannohyla astartea*	AY549322	—	AY549375	AY844580	—	—	—	—	AY844225
CFBH 3621	*Bokermannohyla circumdata*	AY549328	**KF794108**	AY549381	AY844598	AY844409	AY844064	AY844817	**KF751468**	AY844242
USNM 303036	*Bokermannohyla hylax*	AY549338	—	AY549391	AY844614	AY844419	AY844077	AY844832	—	AY844254
CFBH 5652	*Bokermannohyla itapoty*	AY843677	**KF794109**	AY843922	AY844669	AY844461	—	AY844881	**KF751469**	AY844294
AF 414	*Bokermannohyla martinsi*	AY843641	—	AY843878	AY844626	—	AY844086	AY844844	—	AY844264
CFBH 5642	*Bokermannohyla oxente*	AY843676	—	AY843919	AY844667	AY844460	AY844118*	AY844879	**KF751470**	AY844292

Voucher	Species	12S-tRNA val-16S	16S-tRNA leu-ND1-tRNA Ile-tRNA Gln	Cytochrome b	Rhodopsin Exon 1	RAG-1	Tyrosinase	SIAH 1	CXCR4	28S
CFBH 5766	*Bokermannohyla sp. 1*	AY843673	—	AY843916	AY844664	—	AY844115	—	—	—
CFBH 5917	*Bokermannohyla sp. 2*	AY843674	—	AY843917	AY844665	AY844458	AY844116	AY844877	—	—
MACN 37785	*Dendropsophus nanus*	AY549346	—	AY843888	AY844634	AY844437	—	AY844852	—	AY844271
MVZ 145385	*Hyla cinerea*	AY549327	**KF794110**	AY549380	AY844597	AY844408	AY844063	AY844816	**KF751471**	AY844241
AMNH A-165163	*Hyloscirtus armatus*	AY549321	**KF794111**	AY549374	AY844579	AY844393	AY844050	AY844804	—	AY844224
AMNH-A 165132	*Hyloscirtus charazani*	AY843618	**KF794112**	AY843844	AY844595	AY844406	AY844061	—	—	AY844239
SIUC H-7079	*Hyloscirtus colymba*	AY843620	**KF794113**	AY843848	AY844599	AY844410	AY844065	AY844818	**KF751472**	AY844243
KU 181086	*Hyloscirtus lascinius*	DQ380359	—	—	—	—	—	—	—	—
KU 202760	*Hyloscirtus pacha*	AY326057	—	—	—	—	—	—	—	—
SIUC H-6924	*Hyloscirtus palmeri*	AY843650	—	AY843890	AY844636	AY844439	AY844095	AY844854	**KF751473**	AY844273
QCAZ 16704	*Hyloscirtus tapichalaca*	AY563625	**KF794114**	AY843925	AY844672	—	AY844121	—	**KF751474**	AY844297
QCAZ 24377	*Hyloscirtus alytolylax*	JX155798 JX155825	—	—	—	—	—	—	—	—
QCAZ 45466	*Hyloscirtus criptico*	JX155813 JX155840	—	—	—	—	—	—	—	—
QCAZ 41826	*Hyloscirtus larinopygion*	JX155817 JX155844	—	—	—	—	—	—	—	—
QCAZ 41232	*Hyloscirtus lindae*	JX155821 JX155848	—	—	—	—	—	—	—	—
QCAZ 45438	*Hyloscirtus pantostictus*	JX155819 JX155846	—	—	—	—	—	—	—	—
QCAZ 41032	*Hyloscirtus phyllognathus*	JX155801 JX155828	—	—	—	—	—	—	—	—
QCAZ 43654	*Hyloscirtus princecharlesi*	JX155807 JX155833	—	—	—	—	—	—	—	—
QCAZ 27049	*Hyloscirtus psarolaimus*	JX155808 JX155835	—	—	—	—	—	—	—	—
QCAZ 46030	*Hyloscirtus ptychodactylus*	JX155804 JX155831	—	—	—	—	—	—	—	—

Voucher	Species	12S-tRNA val-16S	16S-tRNA leu-ND1-tRNA Ile-tRNA Gln	Cytochrome b	Rhodopsin Exon 1	RAG-1	Tyrosinase	SIAH 1	CXCR4	28S
QCAZ 45967	*Hyloscirtus staufferorum*	JX155815 JX155842	—	—	—	—	—	—	—	—
QCAZ 41351	*Hyloscirtus tigrinus*	JX155810 JX155837	—	—	—	—	—	—	—	—
MTD 45203	*Hypsiboas aguilari*	HM444785	**KF794115**	HM444762	HM444766	HM444764	—	—	**KF751475**	KF751464
USNM 284519	*Hypsiboas albomarginatus*	AY549316	**KF794116**	AY549369	AY844568	AY844384	—	AY844794	**KF751476**	AY844218
ZUEC 12053	*Hypsiboas albopunctatus*	AY549317	—	AY549370	AY844569	—	AY844041	AY844795	—	—
CBF 2696 MNCN 543	*Hypsiboas balzani*	HM480432	—	HM535348	—	—	—	—	—	—
USNM 302435	*Hypsiboas benitezi*	AY843606	**KF794117**	AY843830	AY844583	AY844396	—	—	**KF751477**	AY844227
CFBH 3356	*Hypsiboas bischoffi*	AY549324	—	AY549377	AY844586	AY844398	—	—	—	—
RWM 17746	*Hypsiboas boans*	AY843610	**KF794118**	AY843835	AY844588	—	AY844055	AY844809	**KF751478**	AY844231
MLP-DB 1084	*Hypsiboas caingua*	AY549326	**KF794119**	AY549379	AY844591	—	AY844057	AY844812	**KF751479**	AY844234
CFBH 5738	*Hypsiboas caipora*	EU077268	**KF794120**	EU077267	EU077265	EU077266	—	EU077264	—	EU077263
NMP6V 71250	*Hypsiboas calcaratus*	AY843613	—	AY843839	—	—	—	—	—	AY844235
DLR 4119	*Hypsiboas callipleura*	AY549323	**KF794121**	AY549376	AY844582	AY844395	—	AY844806	—	AY844226
MAD 085	*Hypsiboas cinerascens*	AY549336	—	AY843861	AY844610	—	—	AY844828	**KF751480**	—
MACN 37692	*Hypsiboas cordobae*	AY549330	**KF794122**	AY549383	AY844600	AY844411	AY844066	AY844819	**KF751481**	AY844244
CFBH 2966	*Hypsiboas crepitans*	AY843621	—	AY843850	AY844601	AY844412	AY844067	—	**KF751482**	—
MACN 37794	*Hypsiboas curupi*	AY549359	—	AY549412	—	—	—	AY844880	**KF751483**	—
13mc	*Hypsiboas dentei*	AF467270 EF376018	—	—	—	—	EF376124	—	—	—
CFBH 3599	*Hypsiboas ericae*	AY549332	**KF794123**	AY549385	AY844605	AY844416	AY844071	—	—	—
MACN 37000	*Hypsiboas faber*	AY549334	**KF794124**	AY549387	AY844607	—	—	AY844825	—	—

Voucher	Species	12S-tRNA val-16S	16S-tRNA leu-ND1-tRNA Ile-tRNA Gln	Cytochrome b	Rhodopsin Exon 1	RAG-1	Tyrosinase	SIAH 1	CXCR4	28S
MAD 440	*Hypsiboas fasciatus*	AY549335	—	AY549388	AY844608	—	—	—	—	—
AMNH-A 141054	*Hypsiboas geographicus*	AY843628	—	—	—	—	—	—	—	—
DLR 4537 MNCN 5207	*Hypsiboas gladiator*	HM480405	—	HM535330	—	—	—	—	—	—
CFBH 3386	*Hypsiboas guentheri*	AY843631	**KF794125**	AY549390	AY844612	—	—	AY844830	—	AY844253
AMNH A-168405	*Hypsiboas heilprini*	AY843632	**KF794126**	AY843864	AY844613	—	—	AY844831	—	—
CFBH 3625	*Hypsiboas joaquini*	AY549339	**KF794127**	AY549392	AY844616	AY844421	—	AY844834	**KF751484**	AY844256
MJH 564	*Hypsiboas lanciformis*	AY843636	—	AY843870	AY844619	—	AY844081	AY844837	—	AY844258
MZUSP 111556	*Hypsiboas latistriatus*	AY549360	**KF794128**	AY549413	AY844668	—	—	—	—	AY844293
ROM 39570	*Hypsiboas lemai*	AY843637	**KF794129**	AY843871	AY844620	AY844423	AY844082	AY844838	**KF751485**	AY844259
CFBH 3848	*Hypsiboas leptolineatus*	AY549341	**KF794130**	AY549394	AY844621	AY844424	AY844083	AY844839	—	AY844260
CFBH 4000	*Hypsiboas lundii*	AY843639	—	AY843874	AY844623	—	AY844085	AY844841	—	AY844262
CFBH 3098	*Hypsiboas marginatus*	AY549342	**KF794131**	AY549395	AY844624	AY844426	—	AY844842	**KF751486**	AY844263
MV 0249	*Hypsiboas marianitae*	AY549344	**KF794132**	AY549397	AY844625	AY844427	—	AY844843	—	—
MTD 46350	*Hypsiboas melanopleura*	HM444779 HM444774	**KF794133**	HM444756	HM444766	—	—	HM444789	**KF751487**	—
NMP6V 71258/1	*Hypsiboas microderma*	AY843644	**KF794134**	AY843881	—	—	—	—	—	AY844267
AMNH A-141040	*Hypsiboas multifasciatus*	AY843648	**GQ366299**	AY843887	AY844633	AY844436	AY844093	AY844851	**GQ365986**	AY844270
NMP6V 71202/2	*Hypsiboas nympha*	AY843670	**KF794135**	AY843914	AY844661	AY844457	AY844112	—	**KF751488**	AY844289
51mc	*Hypsiboas ornatissimus*	EF376019 EF376056	—	—	—	—	EF376125	—	—	—
MHNC 6795 MNCN 23199	*Hypsiboas palaestes*	HM480418	—	HM535351	—	—	—	—	—	—
USNM 303046	*Hypsiboas pardalis*	AY843651	**KF794136**	AY843891	AY844637	—	AY844096	AY844855	—	—

Voucher	Species	12S-tRNA val-16S	16S-tRNA leu-ND1-tRNA Ile-tRNA Gln	Cytochrome b	Rhodopsin Exon 1	RAG-1	Tyrosinase	SIAH 1	CXCR4	28S
KU 202734	*Hypsiboas pellucens*	AY326058	—	—	—	—	—	—	—	—
KU 202737	*Hypsiboas picturatus*	AY326055	—	—	—	—	—	—	—	—
CFBH 5752	*Hypsiboas polytaenius*	AY843655	**KF894137**	AY843895	AY844641	AY844443	—	AY844859	—	—
CFBH 3388	*Hypsiboas prasinus*	AY549347	—	AY549400	AY844642	—	AY844100	AY844860	—	—
MACN 37788	*Hypsiboas pulchellus*	AY549352	**KF794138**	AY549405	AY844644	AY844445	AY844102	AY844862	—	AY844278
MACN 37792	*Hypsiboas punctatus*	AY549353	**KF794139**	AY549406	AY844645	—	—	—	—	—
MACN 37795	*Hypsiboas raniceps*	AY843657	**KF794140**	AY843900	AY844646	—	AY844103	AY844863	**KF751489**	—
MACN 37509	*Hypsiboas riojanus*	AY549355	**KF794141**	AY549408	AY844648	AY844447	—	AY844865	—	AY844279
ROM 39624	*Hypsiboas roraima*	AY843660	**KF794143**	AY843903	AY844650	AY844448	AY844104	AY844866	**KF751490**	AY844280
KU 217629	*Hypsiboas rosenbergi*	AY819438	**KF794142**	—	—	—	—	—	—	—
KRL 798	*Hypsiboas rufitelus*	AY843662	**KF794144**	AY843905	AY844652	—	AY844105	AY844867	—	AY844282
CFBH 3579	*Hypsiboas semiguttatus*	AY549357	**KF794145**	AY549410	AY844655	AY844452	—	AY844870	—	AY844285
CFBH 5424	*Hypsiboas semilineatus*	AY843778 AY843779	—	AY843909	AY844656	AY844453	AY844108	AY844871	**KF751491**	AY844286
ROM 39561	*Hypsiboas sibleszi*	AY843667	**KF794147**	AY843911	AY844658	AY844455	AY844110	AY844873	**KF751492**	AY844288
CWM 19512	*Hypsiboas sp.*	AY843671	—	AY843915	AY844662	—	AY844113	—	**KF751493**	AY844290
ROM 39582	*Myersiohyla kanaima*	AY843634	**GQ366307**	AY843868	AY844617	AY844422	AY844079	AY844835	**GQ365994**	—
USNM 562718[a]	*Myersiohyla chamaeleo*	KF751497	—	—	—	—	—	—	—	—
USNM 562056[b]	*Myersiohyla chamaeleo*	KF751498	—	—	—	—	—	—	—	—
USNM 562723[b]	*Myersiohyla chamaeleo*	KF751499	—	—	—	—	—	—	—	—

Voucher	Species	12S-tRNA val-16S	16S-tRNA leu-ND1-tRNA Ile-tRNA Gln	Cytochrome b	Rhodopsin Exon 1	RAG-1	Tyrosinase	SIAH 1	CXCR4	28S
USNM 562057[c]	*Myersiohyla chamaeleo*	KF751500	**KF794148**	KF751495	—	KF751496	—	KF751505	—	—
USNM 562061[d]	*Myersiohyla chamaeleo*	KF751501	—	—	—	—	—	—	—	—
USNM 562071[b]	*Myersiohyla neblinaria*	AY843672	**KF794149**	—	AY844663	—	AY844114	AY844876	**KF751494**	AY844291
USNM 562074[d]	*Myersiohyla neblinaria*	KF751502	—	—	—	—	—	—	—	—
USNM 562732[d]	*Myersiohyla neblinaria*	KF751503	—	—	—	—	—	—	—	—
USNM 562072[e]	*Myersiohyla neblinaria*	KF751504	—	—	—	—	—	—	—	—
CFBH 7613	*Phrynomedusa marginata*	GQ366234	**GQ366313**	GQ365924	GQ366110	GQ366078	GQ366199	GQ366167	—	—
n/a	*Phyllodytes luteolus*	AY843721	**GQ366314**	AY843966**	AY844708	AY844494	AY844150	AY844913	—	AY844324
MACN 37786	*Pseudis minuta*	AY843739	**GQ366339**	AY843984	—	AY844505	—	AY844929	**GQ366028**	AY844336
UTA A-50749	*Scinax staufferi*	AY843761	**GQ366340**	AY844006	AY844748	AY844523	AY844183	—	**GQ366029**	—
AMNH-A 141142	*Trachycephalus typhonius*	AY549362	**GQ366341**	AY549415	AY844707	AY844493	AY844149	AY844912	**GQ366030**	AY844322

*Due to an unfortunate offset during the layout of the appendix 2 of Faivovich et al. (2005) this number was incorrectly reported as AY844101. The same problem determined the mistaken report of the numbers for the tyrosinase fragment of *Isthmohyla pseudopuma* (actual number 844101, reported number 844075), *Plectrohyla* sp. 5 aff. *P. thorectes* (actual number 844117, reported number 844118), and the report of number AY844117 for *Isthmohyla rivularis*, for which the fragment was not amplified.

** Similarly this number was incorrectly reported in Faivovich et al. (2005) as AY843965. The same problem determined the mistaken report of the numbers for the cytochrome *b* fragment of *Phyllodytes* sp. (actual number AY843967, reported number AY843966), *Plectrohyla glandulosa* (actual number AY843976, reported number AY843967), *Plectrohyla guatemalensis* (actual number AY843977, reported number AY843976), *Plectrohyla matudai* (actual number AY843978, reported number AY843977), *Pseudacris cadaverina* (actual number AY843980, reported number AY843978), *Pseudacris crucifer* (actual number AY843981, reported number AY843980), *Pseudacris regilla* (actual number AY843983, reported number AY843982), *Pseudacris triseriata* (actual number AY843984, reported number AY843983), *Pseudis minuta* (actual number AY843985, reported number AY843984), *Pseudis paradoxa* (actual number AY843986, reported number AY843985), *Smillisca fodiens* (actual number AY843989, reported number AY843986), *Ptychohyla euthysanota* (actual number AY843990, reported number AY843989), *Ptychohyla hypomykter* (actual number AY843991, reported number AY843990), *Ptychohyla leonhardschultzei* (actual number AY843992, reported number AY843991), *Ptychohyla spinipollex* (actual number AY843994, reported number AY843992), and *Ptychohyla zophodes* (actual number AY843995, reported number AY843994).

[a, b, c, d, e] All specimens of *Myersiohyla chamaeleo* and *M. neblinaria* are from Venezuela: Departamento Amazonas: Cerro de la Neblina. [a] Camp I, [b] Camp VII, [c] Camp X, [d] Camp XI, [e] Camp II.

REFERENCES

Albuquerque, N.R., and R.W. McDiarmid. 2010. Redescription of *Leptophis cupreus* (Cope) (Serpentes, Colubridae), a rare South American colubrine snake. Papéis Avulsos de Zoologia 50: 375–384.

Altig, R., and G.F. Johnson. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. Herpetological Monographs 3: 81–109.

Altig, R., and R.W. McDiarmid. 1999a. Body plan: development and morphology. *In* R.W. McDiarmid and R. Altig (editors), Tadpoles: the biology of anuran larvae: 24–51. University of Chicago Press. xvi + 444 pp.

Altig, R., and R.W. McDiarmid. 1999b. Diversity: familial and generic characterization. *In* R.W. McDiarmid and R. Altig (editors), Tadpoles: the biology of anuran larvae: 295–337. University of Chicago Press. xvi + 444 pp.

Altig, R., and R.W. McDiarmid. 2007. Morphological diversity and evolution of egg and clutch structure in amphibians. Herpetological Monographs 21: 1–32.

Antunes, A.P., J. Faivovich, and C.F.B. Haddad. 2008. A new species of *Hypsiboas* from the Atlantic forest of Southeastern Brazil (Amphibia: Anura: Hylidae). Copeia 2008: 179–190.

Ayarzagüena, J., and J.C. Señaris. "1993" [1994]. Dos nuevas especies de *Hyla* (Anura; Hylidae) para las Cumbres Tepuyanas del Estado Amazonas, Venezuela. Memoria de la Sociedad de Ciencias Naturales La Salle 53: 127–146.

Azevedo-Ramos, C. 1995. Defense behaviors of the Neotropical treefrog *Hyla geographica* (Anura, Hylidae). Revista Brasileira de Biologia 55: 45–47.

Barrio, A. 1962. Los Hylidae de Punta Lara, Provincia de Buenos Aires. Physis 23: 129–142.

Barrio, A. 1965a. Cloricia fisiológica en batracios anuros. Physis 25: 137–142.

Barrio, A. 1965b. La subespecies de *Hyla pulchella* Duméril y Bibron (Anura, Hylidae). Physis 25: 115–128.

Barrio-Amorós, C.L., and C. Brewer-Carias. 2008. Herpetological results of the 2002 expedition to Sarisariñama, a tepui in Venezuelan Guayana, with the description of five new species. Zootaxa 1942: 1–68.

Biju, S.D., and F. Bossuyt. 2003. New frog family from India reveals an ancient biogeographical link with the Seychelles. Nature 425: 711–714.

Bokermann, W.C.A. 1964. Dos nuevas especies de *Hyla* de Minas Gerais y notas sobre *Hyla alvarengai* Bok (Amphibia, Salientia, Hylidae). Neotropica 10: 67–76.

Brewer-Carias, C. (editor). 1988. Cerro de la Neblina. Resultados de la Expedición 1983–1987. Caracas: Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales, 922 pp.

Brodie, E.D., Jr., and D.R. Formanowicz, Jr. 1987. Antipredator mechanisms of larval anurans: protection of palatable individuals. Herpetologica 43: 369–373.

Brunetti, A.E., G.N. Hermida, and J. Faivovich. 2012. New insights into sexually dimorphic skin glands of anurans: the structure and ultrastructure of the mental and lateral glands in *Hypsiboas punctatus* (Amphibia: Anura: Hylidae). Journal of Morphology 273: 1257–1271.

Cadle, J. E., and R. Altig. 1991. Two lotic tadpoles from the Andes of southern Peru: *Hyla armata* and *Bufo veraguensis*, with notes on the call of *Hyla armata* (Amphibia: Anura: Hylidae and Bufonidae). Studies on Neotropical Fauna and Environment 26: 45–53.

Cochran, D.M., and C.J. Goin. 1970. Frogs of Colombia. Bulletin of the United States National Museum 288: 1–655.

Coloma, L.A., et al. (+ 8 coauthors). 2012. Molecular phylogenetics of stream treefrogs of the *Hyloscirtus larinopygion* group (Anura: Hylidae), and description of two new species from Ecuador. Zootaxa 3364: 1–78.

Cornell Lab of Ornithology. 2004. Raven 1.2.1. Cornell Lab of Ornithology. Ithaca, NY: Bioacoustics Research Program.

Darst, C.R., and D.C. Cannatella. 2004. Novel relationships among hyloid frogs inferred from 12S and 16S mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 31: 462–475.

Duellman, W.E. 1961. Descriptions of two new species of frogs, genus *Ptychohyla*. Studies of American hylid frogs, V. University of Kansas Publications of the Museum of Natural History 13: 349–357.

Duellman, W.E. 1970. The hylid frogs of Middle America. Monograph of the Museum of Natural History, University of Kansas 1: 1–753.

Duellman, W.E. 1972. A review of the Neotropical frogs of the *Hyla bogotensis* group. Occasional Papers of the Museum of Natural History, University of Kansas 11: 1–31.

Duellman, W.E., and R. Altig. 1978. New species of tree frogs (Family Hylidae) from the Andes of Colombia and Ecuador. Herpetologica 34: 177–185.

Duellman, W.E., and M.S. Hoogmoed. 1992. Some hylid frogs from the Guiana highlands, northeastern South America: new species, distributional records, and a generic reallocation. Occasional Papers of the Museum of Natural History, University of Kansas 147: 1–21.

Faivovich, J., and I. De la Riva. 2006. On "*Hyla*" *chlorostea* Reynolds and Foster, 1992, a hylid of uncertain relationships, with some comments on *Hyloscirtus* (Anura: Hylidae). Copeia 2006: 785–791.

Faivovich, J., et al. (+ 5 coauthors). 2004. A molecular perspective on the phylogeny of the *Hyla pulchella* species group (Anura, Hylidae). Molecular Phylogenetics and Evolution 32: 938–950.

Faivovich, J., et al. (+ 6 coauthors). 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: Phylogenetic analysis and taxonomic revision. Bulletin of the American Museum of Natural History 294: 1–240.

Faivovich, J., J. Moravec, D.F. Cisneros-Heredia, and J. Köhler. 2006. A new species of the *Hypsiboas benitezi* group (Anura: Hylidae) from the western Amazon basin (Amphibia: Anura: Hylidae). Herpetologica 62: 96–108.

Faivovich, J., L. Lugli, A.C. Calijorne Lourenço, and C.F.B. Haddad. 2009. A new species of the *Bokermannohyla martinsi* group from central Bahia, Brazil with comments on *Bokermannohyla* (Anura: Hylidae). Herpetologica 65: 303–310.

Faivovich, J., et al. (+ 10 coauthors). 2010. The phylogenetic relationships of the charismatic poster frogs, Phyllomedusinae (Anura, Hylidae). Cladistics 26: 227–261.

Farris, J.S. 1983. The logical basis of phylogenetic analysis. *In* N.I. Platnick and V.A. Funk (editors), Advances in cladistics: proceedings of the third meeting of the Willi Hennig Society 2: 7–36. New York: Columbia University Press.

Farris, J.S., V.A. Albert, A.M. Källersjö, D. Lipscomb, and A.G. Kluge 1996. Parsimony jackknifing outperforms neighbour-joining. Cladistics 12: 99–124.

Gallardo, J.M. 1958. Observaciones sobre el comportamiento de algunos anfibios argentinos. Ciencia e Investigación 14: 291–302.

Garcia, P.C.A., J. Faivovich, and C.F.B. Haddad. 2007. Redescription of *Hypsiboas semiguttatus*, with the description of a new species of the *Hypsiboas pulchellus* group. Copeia 2007: 933–951.

Givnish, T.J., R.W. McDiarmid, and W.R. Buck. 1986. Fire adaptation in *Neblinaria celiae* (Theaceae), a high-elevation rosette shrub endemic to a wet equatorial tepui. Oecologia 70: 481–485.

Goin, C.J., and J.D. Woodley. 1969. A new tree-frog from Guyana. Zoological Journal of the Linnaean Society 48: 135–140.

Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15: 415–428.

Goloboff, P.A. 2003. Parsimony, likelihood, and simplicity. Cladistics 19: 91–103.
Goloboff, P.A., and D. Pol. 2005. Parsimony and Bayesian phylogenetics. *In* V.A. Albert (editor), Parsimony, phylogeny, and genomics: 148–159. Oxford: Oxford University Press.
Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.
Gosner, K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183–190.
Grant T., and A.G. Kluge. 2009. Parsimony, explanatory power, and dynamic homology testing. Systematics and Biodiversity 7: 357–363.
Haddad, C.F.B., and R.J. Sawaya 2000. Reproductive modes of Atlantic forest hylid frogs: a general overview and the description of a new mode. Biotropica 32: 862–871.
Haddad, C.F.B., J. Faivovich, and P.C.A Garcia. 2005. The reproductive mode of *Aplastodiscus perviridis* and its bearing on its generic status. Amphibia-Reptilia 26: 87–92.
Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis. Department of Microbiology. North Carolina State University.
Hoogmoed, M.S. 1979. Resurrection of *Hyla ornatissima* Noble (Amphibia, Hylidae) and remarks on related species of green tree frogs from the Guiana area. Notes on the herpetofauna of Surinam VI. Zoologische Verhandelingen 172: 1–46.
Huber, O. 1995. Vegetation. *In* P.E. Berry, B.K. Holst, and K. Yatskievych (editors), Flora of the Venezuelan Guayana, vol. 1, introduction: 97–160. St. Louis: Missouri Botanical Garden, xxii + 320 pp. [84 plates, accompanying topographical and vegetation maps]
ICZN. 1999. International code of zoological nomenclature, 4th ed. London: International Trust for Zoological Nomenclature.
Jennings, R.D., and N.J. Scott, Jr. 1993. Ecologically correlated morphological variation in tadpoles of the leopard frog, *Rana chiricahuensis*. Journal of Herpetology 27: 285–293.
Kizirian, D., L.A. Coloma, and A. Paredes-Recalde. 2003. A new treefrog (Hylidae: *Hyla*) from southern Ecuador and a description of its antipredator behavior. Herpetologica 59: 339–349.
Kluge, A.G., and T. Grant. 2006. From conviction to anti-superfluity: old and new justifications for parsimony in phylogenetic inference. Cladistics 22: 276–288.
Köhler, J., (+ 6 coauthors). 2010. Systematics of Andean gladiator frogs of the *Hypsiboas pulchellus* species group (Anura, Hylidae). Zoologica Scripta 39: 572–590.
Kok, P. 2006. A new species of *Hypsiboas* (Amphibia: Anura: Hylidae) from Kaiateur National Park, eastern edge of the Pakaraima mountains, Guyana. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 76: 191–200.
La Marca, E. 1985. Systematics and ecological observations on the Neotropical frogs *Hyla jahni* and *Hyla platydactyla*. Journal of Herpetology 19: 227–237.
La Marca, E., and H.M. Smith. 1982. The anuran named *Hyla loveridgei* Rivero. Caribbean Journal of Sciences 18: 91.
Lang, C. 1995. Size-fecundity relationships among stream-breeding hylid frogs. Herpetological Natural History 3: 193–197.
Lannoo, M.J. 1987. Neuromast topography in anuran amphibians. Journal of Morphology 191: 115–129.
Lehr, E., J. Faivovich, and K.-H. Jungfer. 2010. A new Andean species of the *Hypsiboas pulchellus* group: adults, calls, and phylogenetic analysis. Herpetologica 66: 296–307.
Lötters, S., S. Reichle, J. Faivovich, and R.H. Bain, 2005. The stream-dwelling tadpole of *Hyloscirtus charazani* (Anura: Hylidae) from Andean Bolivia. Studies on Neotropical Fauna and Environment 40: 181–185.

Luna, M.C., C.A. Taboada, D. Baeta, and J. Faivovich. 2012. Structural diversity of nuptial pads in Phyllomedusinae (Amphibia: Anura: Hylidae). Journal of Morphology 273: 712–724.

Lutz, B. 1973. Brazilian species of *Hyla*. Austin: University of Texas Press, xviii + 260 pp..

MacCulloch, R.D., and A. Lathrop. 2005. Hylid frogs from Mount Ayanganna, Guyana: new species, redescriptions, and distributional records. Phyllomedusa 4: 17–37.

Mahony, M.R., R. Knowles, and S. Donnellan. 2001. Systematics of the *Litoria citropa* (Anura: Hylidae) complex in northern New South Wales and southern Queensland, Australia, with the description of a new species. Records of the Australian Museum 53: 37–48.

McDiarmid, R.W., and M.A. Donnelly. 2005. The herpetofauna of the Guayana highlands: amphibians and reptiles of the lost world. *In* M.A. Donnelly, B.I. Crother, C. Guyer, M.H. Wake, and M.E. White (editors), Ecology and evolution in the tropics, a herpetological perspective: 461–560. Chicago: University of Chicago Press.

McDiarmid, R.W., and A. Paolillo O. 1988. Herpetological collections—Cerro de la Neblina, updated 1988. *In* C. Brewer-Carías (editor), Cerro de la Neblina. Resultados de la Expedición 1983–1987: 667–670. Caracas: Fundación para el Desarrollo de las Ciencias Físicas, Matematicas y Naturales.

Mijares-Urrutia, A. 1992. El renacuajo de *Hyla lascinia*, con aportes al conocimiento de los renacuajos de *Hyla jahni* e *Hyla platydactyla* (Hylidae) de los Andes venezolanos. Alytes 10: 91–98.

Myers, C.W. 2009. Memories of John William Daly (1933–2008): a biographical sketch and herpetological bibliography. Herpetological Review 40: 53–65.

Myers, C.W., and M.A. Donnelly. 2008. The summit herpetofauna of Auyantepui, Venezuela: report from the Robert G. Goelet American Museum–Terramar Expedition. Bulletin of the American Museum of Natural History 308: 1–147.

Myers, C.W., and W.E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. American Museum Novitates 2752: 1–32.

Myers, C.W, A. Paolillo O., and J.W. Daly. 1991. Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: phylogenetic significance of a new genus and species from the Venezuelan Andes. American Museum Novitates 3002: 1–33.

Nixon, K.C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15: 407–414.

Nixon, K.C. 2002. WinClada, vers. 1.00.8. Ithaca, NY: published by the author.

Orejas Miranda, B., and A. Quesada. 1976. Ecosistemas frágiles. Ciencia Interamericana 17: 9–15.

Palumbi, S.R., A. Martin, W.O. McMillan, L. Stice, and G. Grabowski. 1991. The simple fool's guide to PCR, Version 2.0. Privately published document compiled by S. Palumbi.

Pyron, R.A., and J.J. Wiens. 2011. A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. Molecular Phylogenetics and Evolution 61: 543–583.

Randrianiaina, R.D., et al. (+ 5 coauthors). 2007. Descriptions of tadpoles of two species of *Gephyromantis*, with a discussion of the phylogenetic origin of direct development in mantellid frogs. Zootaxa 1401: 53–61.

Reynolds, R.P., and M.S. Foster. 1992. Four new species of frogs and one new species of snake from the Chapare region of Bolivia, with notes on other species. Herpetological Monographs 6: 83–104.

Rivera-Correa, M., and J. Faivovich. 2013. A new species of *Hyloscirtus* (Anura: Hylidae) from Colombia, with a rediagnosis of *Hyloscirtus larinopygion* (Duellman, 1973). Herpetologica 69: 298–313.

Rivero, J.A. 1961. Salientia of Venezuela. Bulletin of the Museum of Comparative Zoology, Harvard College 126: 1–207.

Rivero, J.A. 1963. *Hyla ginesi*, a new name for *Hyla loveridgei* Rivero. Caribbean Journal of Sciences 3: 28.

Rivero, J.A. "1971" [1972]. Notas sobre los anfibios de Venezuela. I. Sobre los hilidos de la Guayana venezolana. Caribbean Journal of Sciences 11: 181–193.

Salducci, M.-D., C. Marty, A. Fouquet, and A. Gilles. 2005. Phylogenetic relationships and biodiversity in hylids (Anura: Hylidae) from French Guiana. Comptes Rendus Biologies 328: 1009–1024.

Salthe, S. 1963. The egg capsules in the Amphibia. Journal of Morphology 113: 161–171.

Sánchez, D.A. 2010. Larval development and synapomorphies for species groups of *Hyloscirtus* Peters, 1882 (Anura: Hylidae: Cophomantini). Copeia 2010: 351–363.

Savage, J.M., and W.R. Heyer. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa*. Beiträge zur Neotropischen Fauna 5: 111–131.

Señariz, J.C., and J. Ayarzagüena. 2006. A new species of *Hypsiboas* (Amphibia; Anura; Hylidae) from the Venezuelan Guyana, with notes on *Hypsiboas sibleszi* (Rivero, 1972). Herpetologica 62: 308–318.

Smith, B.P.C., M.J. Tyler, B.D. Williams, and Y. Hayasaka. 2003. Chemical and olfactory characterization of odorous compounds and their precursors in the paratoid gland secretion of the green tree frog, *Litoria caerulea*. Journal of Chemical Ecology 29: 2085–2100.

Smith, B.P.C., Y. Hayasaka, M.J. Tyler, and B.D. Williams. 2004a. ß-caryophyllene in the skin secretion of the green tree frog, *Litoria caerulea*: an investigation of dietary sourses. Australian Journal of Zoology 52: 521–530.

Smith, B.P.C., C.R. Williams, M.J. Tyler, and B.D. Williams. 2004b. A survey of frog odorous secretions, their possible functions and phylogenetic significance. Applied Herpetology 2: 47–82.

Swofford, D.L. 2002. PAUP*. Phylogenetic analysis using parsimony (* and other methods). Ver. 4.b.10. Sunderland, MA: Sinauer Associates.

Thomas, M., L. Raharivololoniaina, F. Glaw, M. Vences, and D.R. Vieites, 2005. Montane tadpoles in Madagascar: molecular identification and description of the larval stages of *Mantidactylus elegans*, *Mantidactylus madecassus*, and *Boophis laurenti* from the Andringitra massif. Copeia 2005: 174–183.

Thompson, J.D., T.J. Gibson, F. Plewniak, F. Jeanmougin, and D.G. Higgins. 1997. The CLUSTAL-X windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 25: 4876–4882.

Trueb, L., and M.J. Tyler. 1974. Systematics and evolution of the greater Antillean hylid frogs. Occasional Papers of the Museum of Natural History, University of Kansas 24: 1–60.

Tyler, M.J., and M. Anstis. 1975. Taxonony and biology of frogs of the *Litoria citropa* complex (Anura: Hylidae). Records of the South Australian Museum 17: 41–50.

Varon, A., V.S. Vinh, I. Bomash, and W.C. Wheeler. 2009. POY 4.1.1. American Museum of Natural History. Online resource (http://research.amnh.org/scicomp/projects/poy.php).

Vences, M., M. Thomas, A. Van Der Meijden, Y. Chiari, and D.R. Vieites, 2005. Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. Frontiers in Zoology 12: 1–12.

Wheeler, W.C. 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics? Cladistics 12: 1–9.

Wheeler, W.C. 2003. Iterative pass optimization of sequence data. Cladistics 19: 254–260.

Wheeler, W.C. 2012. Trivial minimization of extra-steps under dynamic homology. Cladistics 28: 188–189.

Wheeler, W.C., et al. (+ 9 coauthors). 2006. Dynamic homology and phylogenetic systematics: a unified approach using POY. New York: American Museum of Natural History.

Wiens, J. J., J.W. Fetzner, Jr., C.L. Parkinson, and T.W. Reeder. 2005. Hylid frog phylogeny and sampling strategies for speciose clades. Systematic Biology. 54: 719–717.

Wiens, J. J., C.H. Graham, D.S. Moen, S.A. Smith, and T. W Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog tree unearth the roots of high tropical diversity. American Naturalist 168: 579–596.

Wiens, J.J., C.A. Kuczynski, X. Hua, and D.S. Moen. 2010. An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. Molecular Phylogenetics and Evolution 55: 871–882.

Zweifel, R.G., and C.W. Myers. 1989. A new frog of the genus *Ctenophryne* (Microhylidae) from the Pacific lowlands of northwestern South America. American Museum Novitates 2947: 1–16.

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