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Intraspecific variation in the endangered frog *Mannophryne riveroi* (Anura, Dendrobatidae, Aromobatinae), with comments on coloration and natural history

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Abstract. We present new information about the morphology (body size and proportions, color in life), natural history (activity cycle, vocalizations), and incidence of malformation for the Venezuelan aromobatine frog *Mannophryne riveroi*. Our data show that inaccuracies in measurements and observations have obfuscated a variety of diagnostic characteristics for *M. riveroi*: its maximum size is 39 mm in males and 46 mm in females, its tympanum is distinct and possesses a tympanic annulus, and its first finger is always longer than the second. We provide additional details of the species' coloration in life, and we show this to be a sexually dimorphic feature with a greater amount of color variation than previously known. Vocalizations of this species are generally issued as trills with a dominant frequency at just over 3000 Hz. Two-thirds of our sample presented malformations of variable severity, with one-third of all limbs in the sample deformed in some way. Even though we are unable to pinpoint a cause of these malformations, they may represent an early warning of environmental degradation in the Península de Paria that requires a more detailed examination.

Keywords. Amphibia, morphology, vocalizations, malformations, Venezuela.

Introduction

The dendrobatid genus *Mannophryne* mainly comprises small (SVL ≤ 30 mm) diurnal or crepuscular frogs displaying characteristic color patterns including a combination of dull, mostly dark dorsal patterns, a set of dorsolateral and oblique lateral stripes, a bright yellow throat and/or venter, and a dark throat collar of variable shape and intensity. Among these variable patterns, ventrolateral stripes are conspicuously absent. The genus *Mannophryne* is limited in its distribution to primarily montane habitats in the Andes, the Cordillera de la Costa of Venezuela, northern and central Trinidad, and Tobago. *Mannophryne riveroi* Donoso-Barros 1964, classified as Endangered B1ab(iii) under IUCN criteria (Stuart et al., 2008), is an unusual member of this genus because it apparently possesses a series of characteristics that do not conform to some of the defining features of *Mannophryne*: atypically large size (up to 57 mm SVL), odd dorsal and ventral color pattern, and nocturnal activity. These oddities were all mentioned as diagnostic in the original description (Donoso-Barros, 1964) and the species has been mentioned in only a few publications since the original description (Edwards, 1974; Myers, Paolillo and Daly, 1991; La Marca, 1994; Grant et al., 2006). Since our own data contradict some of the information presented by Donoso-Barros (1964) and in the scarce literature, we here report observations made recently while conducting fieldwork in the Península de Paria in order to clarify the membership of the species within the genus *Mannophryne*, particularly with respect to the nonconforming features listed above. Even though Manzanilla, La Marca and García-París (2009) confirmed that the species *riveroi* belongs in the genus *Mannophryne* using genetic data, it is important to improve our knowledge of *M. riveroi* concerning its color in life, sexual dimorphism, intraspecific morphological variation including limb malformations, and daily activity cycle, in order to facilitate recognition in the field and future conservation management.

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Materials and methods

We made detailed field and laboratory observations on eight individuals of *Mannophryne riveroi*, collected in September 2001 and June 2002 at two localities on the Península de Paria, Estado Sucre, Venezuela. Measurements (Table 1) were made to the nearest 0.1 mm using digital callipers. The webbing formula follows Myers and Duellman (1982). Vocalizations were recorded with a Sony MZ-RH1 Mini Disc recorder using a Sony FV-5 microphone, and analyzed using SoundRuler version 0.960 (Gridi-Papp, 2007). Specimens were deposited in the Museo de Historia Natural La Salle, Caracas (MHNLS) and the Colección de Vertebrados, La Universidad de los Andes, Mérida, Venezuela (CVULA). Examined specimens and comparative material are listed in the Appendix.

Results

Our results were derived from detailed observations on two male and six female specimens of *Mannophryne riveroi*. All of these specimens appeared to be sexually mature, based either on observation of calling in the males or on the presence of developed or developing eggs in the females. In the following paragraphs we list those results that are relevant to the diagnostic characteristics of the species and we detail some heretofore unknown malformations.

Morphology

Whereas the snout–vent length of males ranges from 38.0–39.0 mm ($\bar{x}$ = 38.5 mm; Table 2), that of females has a broader range and a larger maximum (27.2–42.0 mm, $\bar{x}$ = 35.0 mm; Table 2). All specimens have a distinct tympanum whose diameter averages 41% of eye diameter in males and 36% of eye diameter in females (Table 2). A distinct tympanic annulus is present. Measurements of finger lengths show that the length of FI is always greater than that of FII in both sexes, averaging 6.7 vs. 6.5 mm in males and 5.9 vs. 5.3 mm in females (Table 2). The presence of rudimentary webbing between FII and FIII is variable in our specimens and not linked to sex. In some of our specimens (e.g. MHNLS 17455) this character is present, but only on the right hand. Similarly, the width of finger discs is also variable. Whereas some specimens (e.g., MHNLS 17455 and 17460) possess discs twice as wide as the adjacent phalanx, others have disc widths that conform more closely to the data of other authors (e.g., La Marca, 1994). Toe webbing is also variable. The webbing formula for a representative female (MHNLS 17460) is **I**1-2**II**1-3**III**2½-4**IV**4-2**V**, and for a representative male (MHNLS 17455) it is **I**1-2**II**1½-3**III**2½-3½**IV**3½-2**V**). A young female (MHNLS 17457) has a webbing formula of **I**1½-2**II**1-3**III**2-3½**IV**4-2**V**.

Malformations

Specimen MHNLS 17456 presents a case of polymelia on toe **IV** (TIV) of the left foot, displaying an extra toe of length 3.5 mm originating at the proximal subarticular

Table 1. Abbreviations and definitions for measurements taken on eight specimens of *Mannophryne riveroi* from the Península de Paria, Venezuela.

Measurement	Abbreviation	Definition
Snout–vent length	SVL	straight length, measured from tip of snout to vent
Tibia length	TL	from outer edge of flexed knee to flexed heel
Foot length	FL	from proximal edge of inner metatarsal tubercle to tip of toe IV
Head length	HeL	from tip of snout to posterior edge of prootic, noted through the skin
Head width	HW	measured across the skull at angle of jaws
Upper eyelid width	UEW	measured along the widest part of the eyelid
Eye to snout distance	ETS	distance between the anterior edge of the eye to the tip of snout
Eye diameter	ED	measured horizontally across eye
Interorbital distance	IOD	measured between the medial edges of the orbits
Tympanum diameter	TD	measured horizontally across tympanum
Disc width of Finger III	F3D	measured across widest part of disc
Disc width of Toe IV	T4D	measured across widest part of disc
Length of Finger I	F1L	measured from inner edge of thenar tubercle to tip of disc
Length of Finger II	F2L	measured from inner edge of thenar tubercle to tip of disc

Table 2. Measurements (in mm) for 14 characters (Table 1) from adult male (n = 2) and female (n = 6) *Mannophryne riveroi*. Values listed include range and mean ($\bar{x}$) ± standard deviation (SD).

Character	Males		Females	
	Range	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$
SVL	38.0–39.0	38.5 ± 0.7	27.2–42.0	35.0 ± 6.1
TL	18.1–19.4	18.8 ± 0.9	13.0–20.0	16.6 ± 2.9
FL	18.5–19.8	19.2 ± 0.9	14.0–21.0	16.7 ± 3.8
HeL	13.2–14	13.6 ± 0.6	10.0–16.2	11.4 ± 1.5
HW	14.3–15.0	14.7 ± 0.5	11.5–17.0	14.5 ± 3.5
UEW	3.2–3.5	3.4 ± 0.2	2.5–4.1	3.0 ± 0.0
ETS	6.0–6.0	6.0 ± 0.0	4.5–7.2	5.0 ± 0.0
ED	4.5–4.6	4.6 ± 0.1	3.7–4.9	4.2 ± 0.6
IOD	4.0–4.5	4.3 ± 0.4	3.8–5.0	4.7 ± 0.6
TD	1.8–1.9	1.9 ± 0.1	1.2–2.2	1.5 ± 0.7
F3D	1.9–2.0	2.0 ± 0.1	1.0–2.0	1.3 ± 0.6
T4D	2.0–2.0	2.0 ± 0.0	1.2–2.0	2.0 ± 0.0
F1L	6.4–7.0	6.7 ± 0.4	4.6–7.5	5.9 ± 1.2
F2L	6.0–7.0	6.5 ± 0.7	4.0–7.0	5.3 ± 1.5

tubercle. MHNLS 17455 has a hypertrophied left thumb with a disc of 2.9 mm width (Fig. 1A), whereas the width of the normal disc of finger I (FI) on the right hand is 1.5 mm. The same specimen also has a case of polymelia, with TII of the left foot carrying an extra disc growing from the right side of the subarticular tubercle, and the disc on TV is abnormally reduced (Fig. 1B). MHNLS 17457, a young female, has a mutilated terminal phalanx of TIV on the left foot. The tip of FIV finger on the left hand of MHNLS 17458 is also mutilated. CVULA 6943 is missing the last phalanx of TIV and the entire TV of the right foot. In CVULA 7216, FIV on the left foot is well developed but conspicuously shorter (FL = 14.6 mm) than FIV on the right foot (FL = 16.0 mm).

Specimen CVULA 7391 is a juvenile and stands out because it has deformities in each extremity. TIII of the left hand is extremely short, possibly mutilated, and appears to have regenerated, with a new, smaller disc (Fig. 2A). The right hand has only three fingers (Fig. 2B). FI appears normal. FIV is complete, but greatly hypertrophied in its entirety (including its subarticular tubercle and disc). The central element appears to be the result of a fusion of FII and FIII. There is no sign of subarticular tubercles on this element, but the disc is composed of a horizontal component on the left side of the disc that is merged with a vertical one on its right side. TIV of the right foot is reduced in length, to the level of TIII and TV, with a considerably expanded disc (Fig. 2C). The left foot has only four toes, apparently missing TI, and TV is substantially hypertrophied (Fig. 2D).

Coloration

The following descriptions are derived from photographs and detailed field notes of individuals in the wild and in captivity before preservation.

Male coloration (Fig. 3).

During the day, calling males appear dark chocolate brown to nearly black. The dorsum has no visible pattern throughout the day. At night the dorsal coloration shifts between shades ranging from olive green to light or dark brown, with a horizontal grayish upper lip bar (Fig. 3A). Discs on fingers and toes appear blue from above, and some small blue spots may be present on the upper surfaces of the hind limbs. The ventral coloration includes a gray to nearly black throat, an ill-defined but wide chocolate- to dark gray-colored collar on the posterior part of the throat (Fig. 3B), brightly colored spots in the axillary regions and in the groin, and a belly that is entirely pale gray or brightly colored posteriorly. The hidden surfaces of the thighs are brightly colored (sometimes with only a narrow longitudinal stripe), and brightly colored spots are on the undersides of the shanks. The bright coloration appears to be an individual characteristic, ranging from yellow in some individuals (e.g., Fig. 3C) to a deep orange color in others (e.g., Fig. 3B). Palms and soles are gray. The pupil is horizontally oval, with a pale golden pupil ring; the iris is a metallic pale brown to green with a finely dark gray reticulations.

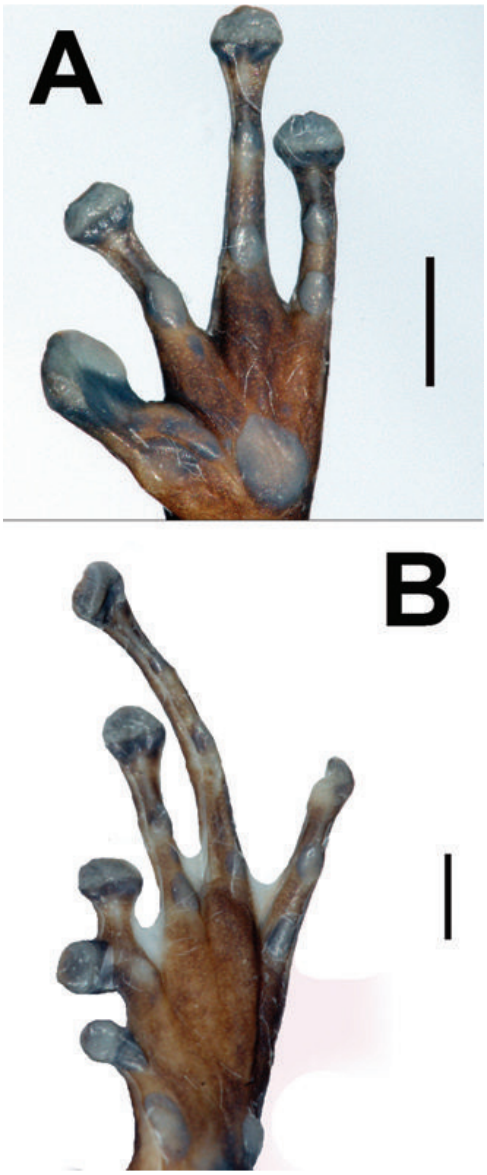

Figure 1. Limb malformations observed in a male *Mannophryne riveroi* (MHNLS 17455), showing a hypertrophied thumb on the left hand (A) and polymelia on TII and an abnormally reduced disc on TV on the left foot (B). Scale bar = 2.5 mm.

Female coloration (Fig. 4).

Females are colored quite differently from males, possessing a greenish gray dorsum (which may tend to olive, as noted by Donoso-Barros, 1964) devoid of any definite pattern. In some specimens we saw ill-defined dorsolateral and oblique lateral stripes (e.g., MHNLS 17460, Fig. 4A). The flanks are pale gray. There are ill-defined crossbars on the hind limbs; discs have a blue sheen when viewed from above. The ventral pattern on throat and chest, the undersides of the upper arms, the proximal half of the forearms, and the thighs are bright yellow (not orange), as is the posterior part of the belly (Fig. 4B). The throat collar is chocolate brown to grayish. The remainder of the venter is white. The hidden parts of the shanks are colored gray with white spots; soles and palms are gray. The iris is a coppery green.

Natural history

Behavior

Our observations indicate that the activity cycle of *M. riveroi* primarily conforms to the diurnal pattern of other dendrobatid frogs. However, we have encountered these frogs at night and observed escape behaviors. One of us (GR) watched an adult female *M. riveroi* preying on an odonate larva (approx. length 30 mm) in darkness at 1940 h. Calling usually occurred during the daytime from dark crevices and from perches hidden in cascading streams. Males ceased calling when approached and escaped by jumping into the water. In the water, escapees usually descended to the bottom of the pool, stopped moving, and tried to remain as cryptic as possible. Adult females were more frequently encountered at the edges of quiet pools than in mid-stream, and in these calmer waters we have observed tadpoles.

Vocalizations

Our data show that notes of individual length 0.22 s are trilled with a frequency of 2.6 notes per second (Fig. 5A), and with a space between notes of 0.2 s. The fundamental frequency was observed to be 1618 Hz and the dominant frequency 3165 Hz (Fig. 5B).

Discussion

Morphology

Maximum size

The original description of *Mannophryne riveroi* (Donoso-Barros, 1964) was sufficiently thorough to prove its distinctiveness and to secure its taxonomic status, and this information has since been supplemented with a revised diagnosis (Edwards, 1974) and an updated species account (La Marca, 1994). However, there is a dearth of information regarding intraspecific variation and behavior of the species, and such information is usually critical when developing effective management

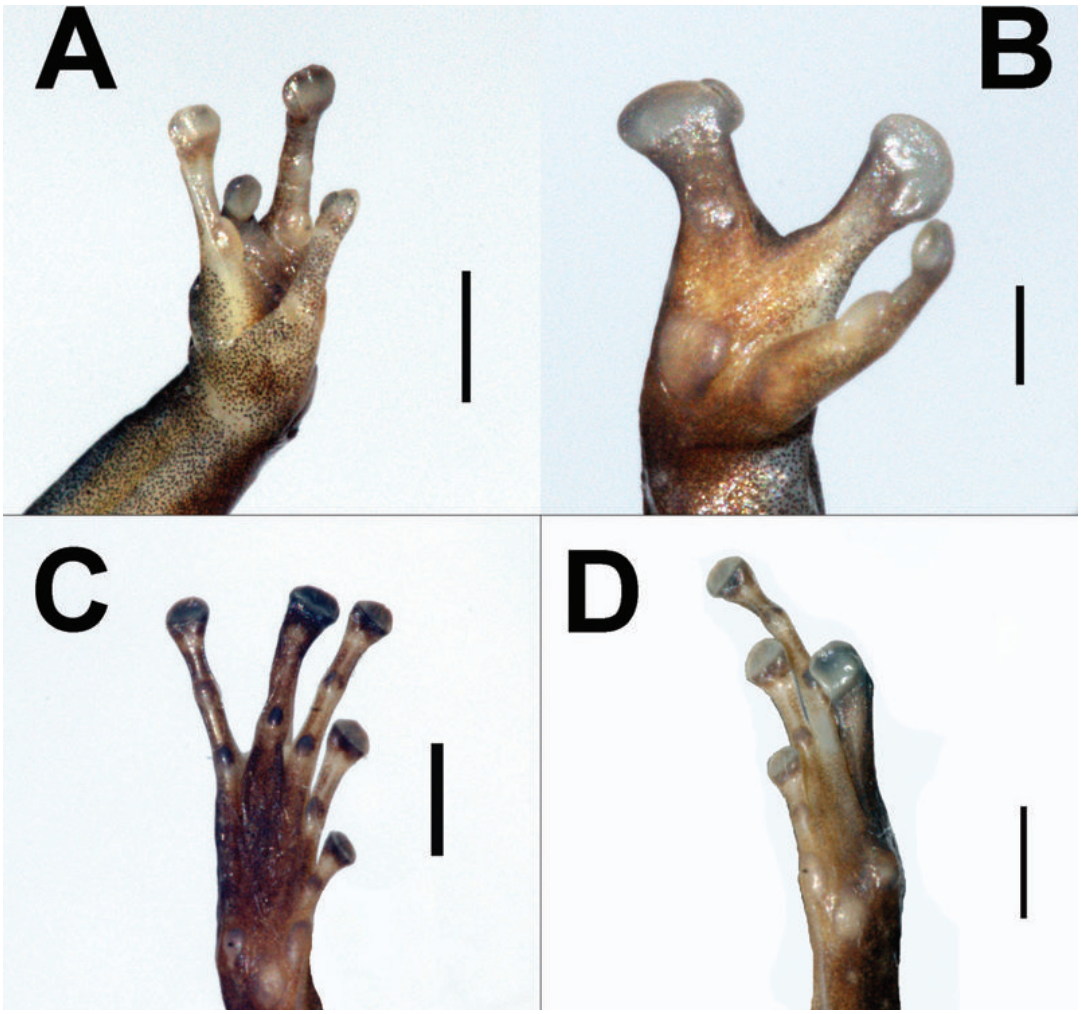

Figure 2. Multiple limb malformations observed in a female *Mannophryne riveroi* (CVULA 7391). This specimen presented with malformations on both hands and both feet, including an incompletely developed FIII on the left hand (A; scale bar = 2 mm), fused and hypertrophied fingers in the right hand (B; scale bar = 1 mm), a shortened TIV on the right foot (C; scale bar = 2.5 mm), and the loss of a finger on the left foot (D; scale bar = 2 mm).

strategies for species of conservation concern.

The largest size reported for the species is a SVL of 57 mm, given in the original description by Donoso-Barros (1964). This measurement is problematic since it was not tied to a voucher specimen. After their study of specimens from the type series, Myers, Paolillo and Daly (1991) reported that the 57-mm measurement was that of a tadpole and could not be associated with any of the adult specimens. La Marca (1994) provided the size range for nine females (SVL 41.3–46.2 mm) and the measurement for a single male (SVL 35 mm). Among our specimens, the largest female (MHNLS 17460) has an SVL of 42 mm, and the largest male (MHNLS 17455), the largest recorded for the species to date, measures 39 mm in SVL. We are therefore in agreement with Myers, Paolillo and Daly (1991) that the maximum size of 57 mm reported by Donoso-Barros (1964) is excessive, and we suggest that stating a size limit for females near 46 mm and for males near 40 mm SVL is more appropriate. Regardless of the revised maximum size, females of *M. riveroi* remain veritable giants among dendrobatid frogs, being surpassed in size only by *Aromobates nocturnus* (SVL up to 64 mm; Myers, Paolillo and Daly, 1991), *Ameerega trivittata*, and *Dendrobates tinctorius* (SVL up to 60 mm; Walls, 1994), and of about the same size as *Dendrobates auratus, Phyllobates bicolor,* and *P. terribilis* (Walls, 1994; Lötters et al., 2007).

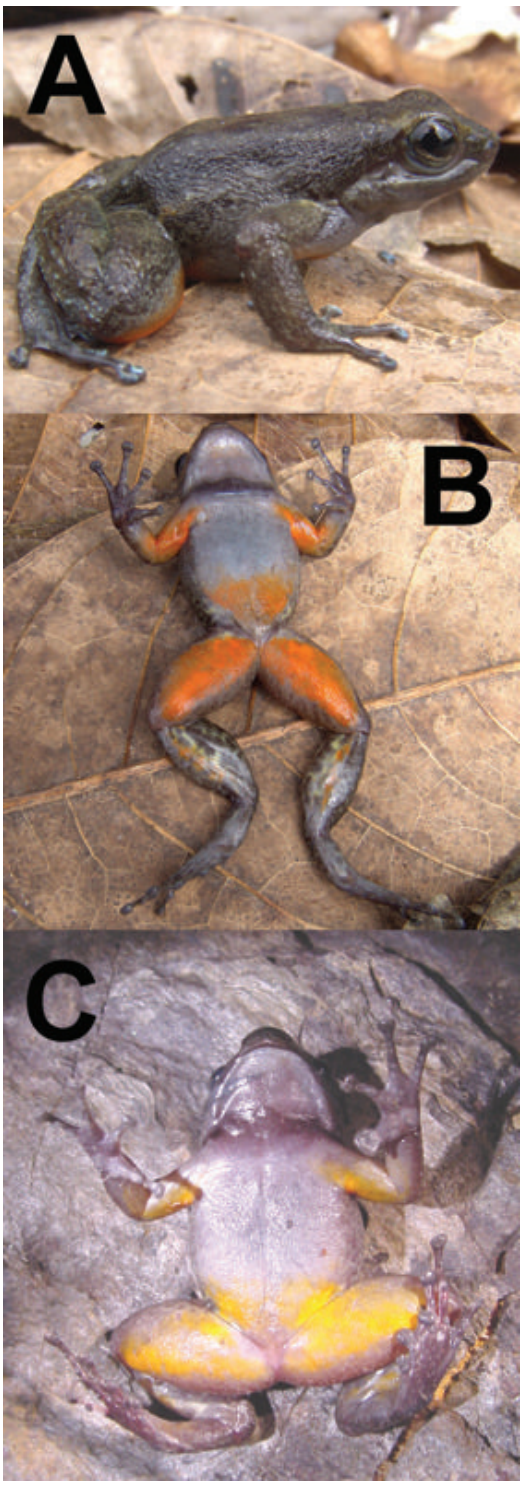

Figure 3. Examples for the coloration in life of male *Mannophryne riveroi*, showing typical daytime dorsal coloration (A), and the deep orange (B) or bright yellow (C) ventral coloration.

Tympanum morphology

Among the diagnostic characters listed by Donoso-Barros (1964) was and indistinct tympanum, which he reported as small (50% eye diameter). La Marca (1994) corrected this in his description by describing the tympanum as distinct and measuring 40% of eye diameter. La Marca's (1994) assessment corresponds well with our observations. Furthermore, the presence of a distinct tympanic annulus in *M. riveroi* has not previously been documented.

Finger length

A character that has been difficult to reconcile given the information provided by different authors is the relative length of FI compared to FII in *Mannophryne riveroi*. Donoso-Barros (1964) stated that FI was longer than FII and used this difference as one of the defining characters of the species. In direct contradiction, Edwards (1974) found FI to be shorter than FII. La Marca (1994) provided a third option, considering both fingers to be of equal length.

In anuran taxonomy the length relationship of fingers, with FI and FII taking a prominent position is often integrated into the diagnosis of species. When finger lengths are fairly similar, then the value of the character itself depends on the method, accuracy, and precision of the measurement (see discussion by Grant et al., 2006). Of the different methods employed to determine relative rather than absolute length of fingers, errors may be built into the method. We have informally tried several methods and instructed different individuals to make repeated measurements of FI and FII with similar lengths in selected species of dendrobatid, strabomantid, ranid, rhacophorid, and eleutherodactylid frogs. We found that moving FI and adpressing it to FII will most frequently let FII appear longer than FI in fingers of close length. The opposite movement, moving FII and adpressing it to FI, will generally make FI appear longer than FII. Finally, moving both fingers to a medial position (as generally used by Juan A. Rivero), results in highly subjective variation around what an individual researcher may consider "medial" and leads to inaccurate and unreliable measurements. Kaplan (1997) used the most objective method and measured both fingers from the closest edge of the palmar tubercle to the tip of the fingers, a method adopted by Grant et al. (2006). We measured both fingers in our specimens of *M. riveroi* accordingly (Table 2) and our measurements show conclusively that FI is always longer than FII.

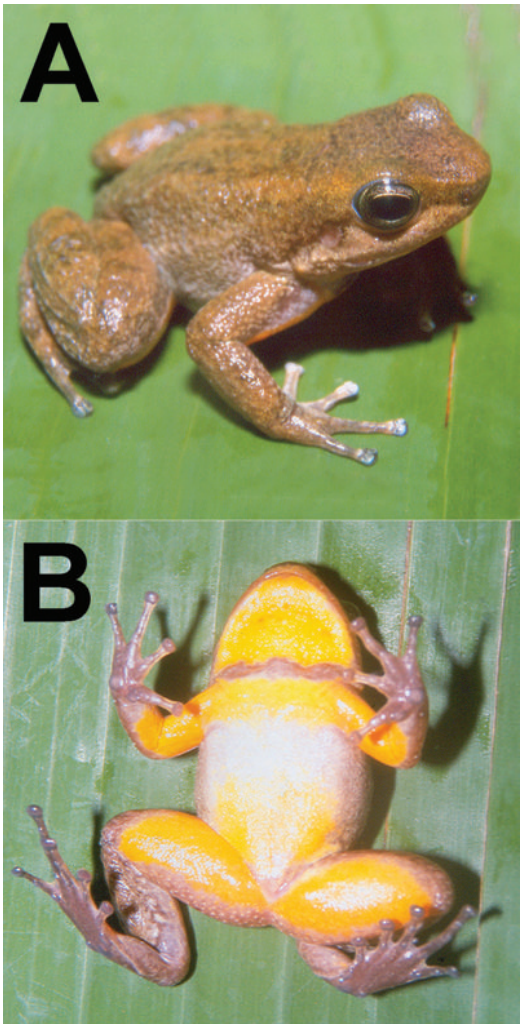

Figure 4. Examples for the coloration in life of female *Mannophryne riveroi*, showing typical daytime dorsal (A) and ventral (B) coloration.

Finger webbing

Grant et al. (2006) commented on the fact that Donoso-Barros (1964) listed the presence of rudimentary webbing between FII and FIII as a character of *Mannophryne riveroi*. Although La Marca (1994) did not report this character and Grant et al. (2006) did not observe it, we find that this character is present in some specimens (e.g., the right hand of MHNLS 17455). It is difficult to determine how much of this presumed webbing is a real feature of the living individual as opposed to an artifact of the preservation process.

Width of finger discs

La Marca (1994) stated that the width of the finger disc and toe disc ("finger pads" and "toepads" of some authors) of FIII and TIV in *M. riveroi* was 1.6 times wider than the adjacent phalanx. We find this character to be unreliable, since among our specimens MHNLS 17455 and MHNLS 17460 have slightly expanded discs that are twice as wide as the adjacent phalanges on FIII and 2.1 times as wide as those of TIV.

Toe webbing

The observed variation in webbing formula indicates that his feature should not be singled out as a stand-alone diagnostic feature.

Malformations

The samples we studied are interesting from a conservation standpoint due to the high frequency (six of eight individuals; 75%) of malformations on fingers and toes. Three of our specimens (37.5%) present multiple malformations, and overall 31.8% of all extremities have deformed features. This may indicate an increased developmental predisposition of *Mannophryne riveroi* to malformations (from intrinsic genetic factors), or the presence of developmental sensitivity from external causes.

Cases with multiple limb abnormalities in a population can have a variety of causes, most prominently those related to as environmental degradation from pollutants or from climate change. Among the latter, increased parasitism or developmental irregularities, have been described for other tropical habitats (e.g., Pounds, Fogden and Campbell, 1999) and they have been linked to malformations (e.g., Blaustein and Johnson, 2003; Johnson and Lunde, 2005). Considering the particulars of the pristine, montane habitats in which we found *Mannophryne riveroi* populations, we feel comfortable with dismissing the possibility that man-made pollutants are the underlying cause for the observed deformities. Furthermore, such deformities are absent in our sample of *M. venezuelensis* from Las Melenas and from specimens of *Allobates caribe* (see Barrio-Amorós, Rivas and Kaiser, 2006) from the same general area. Absent further research, we are not in a position to link these deformities in *M. riveroi* to any particular cause. As we have observed deformities in specimens of *Mannophryne venezuelensis* from Macuro, near the eastern end of the Península de Paria, we suggest that the key to developmental deformities in these species may lie with microhabitat choice, especially considering that

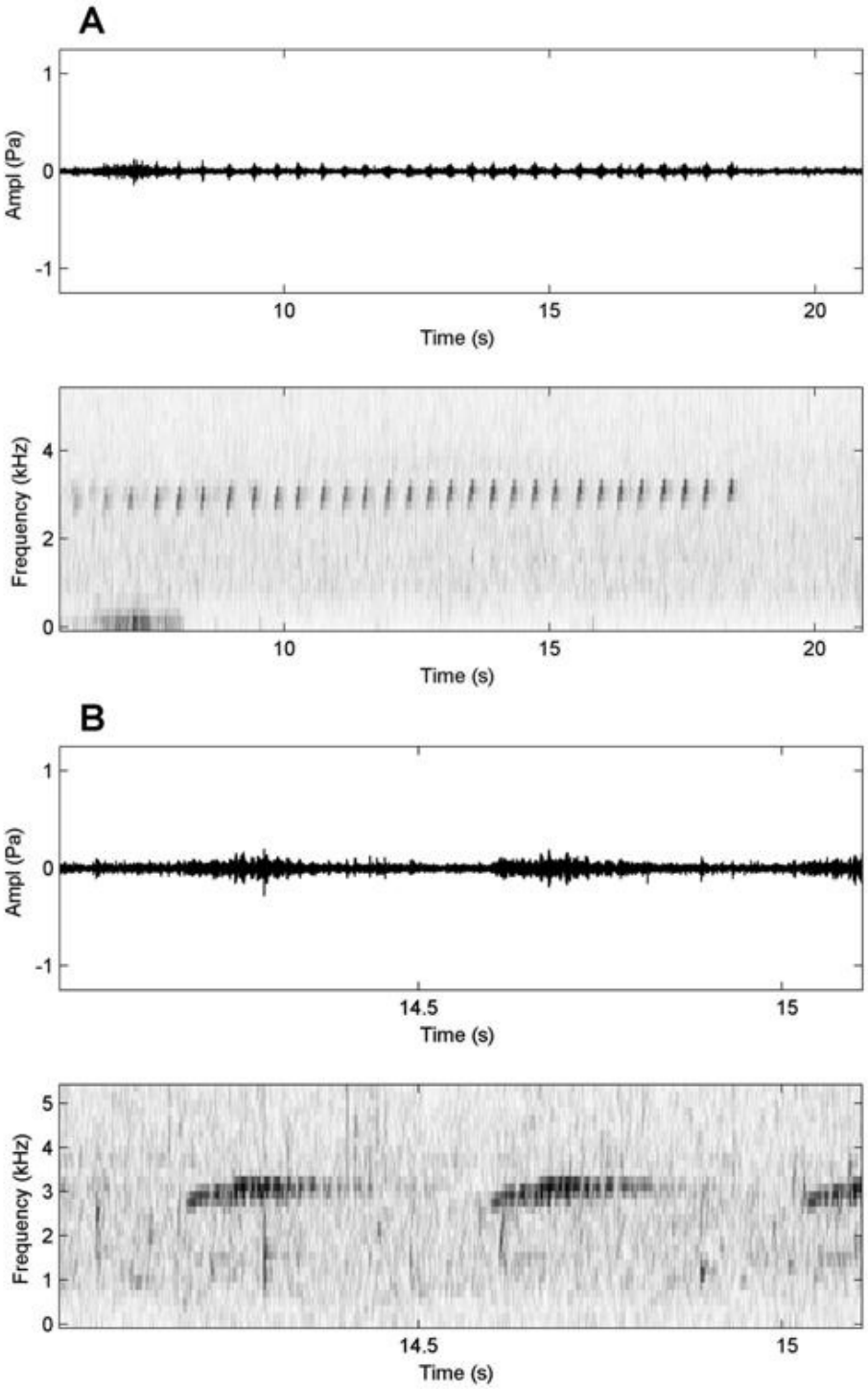

Figure 5. Audiospectrograms of vocalizations by an individual of *Mannophryne riveroi*, issuing a trilled call. (A) Oscillogram and sonogram of a single burst consisted of up to 30 individual notes produced at a rate of 2.6 notes per second. Notes were produced at a dominant frequency of 3165 Hz with a duration of 0.22 s, followed by a space of length 0.2 s. (B) Oscillogram and sonogram of two amplified notes chosen randomly.

these four dendrobatids share the same macrohabitat. Whereas *M. venezuelensis* and *A. caribe* are terrestrial and free from developmental deformities, the stream-dwelling confamiliars have them. Such a notion gains credence from the work of Molina (2003), who reported deformities on extremities (polydactylia, hypertrophy, missing arms) for *M.* aff. *herminae* from Caracas, another stream inhabitant.

Color in life

Color notes given by Edwards (1974), Myers, Paolillo and Daly (1991), and La Marca (1994) differ from our observations, most importantly in terms of sexual dimorphism. It is not easy to reconcile the differences in these observations with each other, but ontogenetic changes (e.g., dulling of colors as a function of ageing, brightening of colors during actual breeding) may play a role.

Natural history and vocalizations

Given the scarcity of published observations on this species in its habitat, it is not surprising that the original description (Donoso-Barros, 1964) contained an apparent error relating to the species' activity cycle that has been perpetuated in the literature (e.g., Grant el al., 2006). Donoso-Barros (1964) stated that *M. riveroi* is nocturnal (in contrast to all other dendrobatid frogs, including all other species of *Mannophryne* and *Aromobates*). We agree with Myers, Paolillo and Daly (1991) that finding active individuals of *M. riveroi* by night is distinctly possible, especially since they readily escape by jumping when disturbed. Such activity, however, does not by itself infer a nocturnal lifestyle. We observed several individuals escaping at night upon being disturbed, but once a disturbed animal reached a safe place following an escape episode, it generally remained there for an extended period of time. However, these frogs apparently do engage in some nocturnal activities unrelated to escape. More diverse behaviors in this species, however, are observed during the day. *Mannophryne riveroi* is much more aquatic than most other dendrobatids, certainly more so than its confamiliars found in the Península de Paria. This lifestyle is similar to that of other large aromobatines, such as *Aromobates nocturnus, A. meridensis, A. leopardalis*, and *Mannophryne oblitterata*. Even though Donoso-Barros (1964) considered *M. riveroi* to be sympatric with individuals of Paria populations of *M.* "*trinitatis"* (see Barrio-Amorós et al., 2006 for a discussion about the presence of *M. trinitatis* in Venezuela), we have never observed *M. riveroi* in microsympatry with any other dendrobatid. The species is syntopic with *M. venezuelensis* in Cerro Azul, but individuals of these species are not found in the same microhabitat. Whereas *M. riveroi* always inhabits small to medium-sized streams and was never found at distances > 1 m from flowing water, *M. venezuelensis* is a terrestrial species that is only occasionally found close to the running.

An audiospectrogram of the call of *M. riveroi* was presented by Edwards (1974), who showed two notes of length 0.14 s with a 0.37-s space between notes. These notes had a fundamental frequency of 1450 Hz and a dominant frequency of 2900 Hz. Differences between the recordings of Edwards (1974) and our own can be accounted for by differences in altitude and temperature.

Conservation

Stuart et al. (2008) listed *Mannophryne riveroi* as Endangered under IUCN criteria. We concur with this assessment not only because the species has a very limited range, but also because the unexpectedly high frequency of limb deformities may indicate a threat to the species. As of this writing, we have not observed any changes in the abundance of any of the species we have observed during our visits to the Península de Paria.

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Appendix

Mannophryne riveroi. MHNLS 17455–60, from a stream between Las Melenas and Cerro El Humo, Estado Sucre, Venezuela, elevation 800 m; CVULA 6942–43, from a path between Macuro to Cerro Azul, Estado Sucre, Venezuela, elevation 700 m.

Mannophryne venezuelensis. EBRG 299, CVULA 7265-70, MHNLS 17449–54, 17499–501, all from the southern slope of Cerro El Humo, Península de Paria, Estado Sucre, Venezuela, elevation 800 m.

Mannophryne aff. *venezuelensis.* CVULA 7331-42, from near Macuro, southeastern edge of the Península de Paria, Estado Sucre, Venezuela, elevation 0-40 m.

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