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OTOPHRYNE (ANURA: MICROHYLIDAE) FROM THE HIGHLANDS OF GUYANA: REDESCRIPTIONS, VOCALISATIONS, TADPOLES AND NEW DISTRIBUTIONS

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ABSTRACT

*Recent collections are used to expand existing descriptions of adults of *Otophryne robusta* and *O. steyermarki*. The calls of *O. pyburni* and *O. robusta* are compared. Tadpoles of *O. robusta* and *O. steyermarki* are described. Characters for distinguishing among adults and tadpoles of these two species and *O. pyburni* are provided. *Otophryne* is a Guiana shield endemic; *O. pyburni* is widespread at lower elevations, whereas *O. robusta* and *O. steyermarki* occur in southeastern Venezuela and western Guyana, the former at moderate elevations and the latter at higher elevations.*

KEYWORDS: *Otophryne robusta*, *Otophryne steyermarki*, tadpoles, Guiana Shield.

INTRODUCTION

The neotropical microhylid genus *Otophryne* possesses a number of unique characters, especially larval features (Pyburn, 1980; Campbell & Clarke, 1998). These have led some authors to award the genus a unique position among the Microhylidae (Wassersug & Pyburn, 1987; Wild, 1995). Frost *et al.* (2006) proposed a new arrangement for the Microhylidae, although *Otophryne* was left *incertae sedis*. Recently, Meijden *et al.* (2007) resolved *Otophryne* as basal to the Old World Microhylidae.

In a comprehensive work, Campbell & Clarke (1998) reviewed the genus, described adults and tadpoles of *O. pyburni* and elevated *O. steyermarki* to species status. *Otophryne* is a Guiana Shield endemic containing three species: *O. pyburni* widespread at lower elevations, with *O. robusta* and *O. steyermarki* at higher elevations in western Guyana and southeastern Venezuela (Campbell & Clarke, 1998; Señaris & MacCulloch, 2005).

At the time of Campbell & Clarke's (1998) publication, only a few specimens of *O. robusta* and *O. steyermarki* were available. Recent collections in the Pakaraima region of Guyana include specimens of

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adults, juveniles and tadpoles of these species. These collections allow us to expand the descriptions of *Otophryne robusta* and *O. steyermarki* from the region, using specimens of *O. pyburni* for comparison. Advertisement calls of *O. robusta* and *O. pyburni* were also recorded.

MATERIALS AND METHODS

Specimens were collected from the vicinity of Mount Ayanganna (05°24'N, 59°57'W), Mt. Wokomung (05°06'N, 59°49'W), Partang (05°56'N, 60°07'W) and the headwaters of the Meamu River (06°12'N, 60°29'W), Guyana. These locations are in the eastern part of the Pakaraima Mountain region of the Guiana Shield. Coordinates and elevations were determined using a Global Positioning System (GPS).

Specimens were euthanized according to approved protocols. Specimens were fixed in 10% formalin; tissue (liver) was removed and preserved in 95% ethanol.

Descriptions are based on recently collected specimens and specimens from existing collections (Appendix). Some information was taken from published accounts. All measurements of specimens were made using digital calipers. Interdigital webbing is described using the formula of Lescure (1975) and Myers & Duellman (1982), as refined by Savage & Heyer (1997). Descriptions of adults follow the format used in Campbell & Clarke (1998). Tadpole stages are those of Gosner (1960); tadpole mouth characters follow Wassersug & Pyburn (1987). Photographs of tadpole mouths were taken with a JVC KY-F75U Digital Camera (3 CCD) and processed with Archimed Pro software (GT Vision). Institutional abbreviations follow Leviton *et al.* (1985).

Advertisement calls of *O. robusta* were recorded at a distance of 2 m from a calling male using a Sony TCD5 Pro II tape recorder, a Sennheiser ME80 microphone and TDK D90 analog audiotape. Advertisement calls of *O. pyburni* were recorded at a distance of 60 cm using a Sony DAT TCD-D8 recorder and a Sennheiser K6 microphone. The calls were analysed at a sampling rate of 44100 Hz using Raven version 1.2.1 software (Charif *et al.* 2004). Temporal variables measured included: call duration (beginning of the first to the end of the last note; number of notes; note period (beginning of one note to the beginning of the next); note repetition rate (sec⁻¹). The frequency of the dominant (emphasized) harmonic was measured from a spectral slice taken through the portion of the har-

monic with the highest amplitude (using the Blackman window function at a 3 dB filter bandwidth of 50 Hz). Air temperature at the call site was measured with a BAT 12 digital thermometer.

RESULTS

Adults of *Otophryne steyermarki* and *O. robusta* were collected from the above locations, and tadpoles of *O. steyermarki* were collected on Mt. Wokomung. Specimens of *O. pyburni* were examined for comparison with *O. robusta* and *O. steyermarki*. The description of *O. pyburni* is expanded somewhat, to include additional characters that distinguish it from *O. robusta*. Species descriptions are in alphabetical order.

Otophryne pyburni Campbell & Clarke

Otophryne pyburni Campbell & Clarke 1998:309.

Campbell & Clarke (1998) provided a detailed description of this species based on a large sample of specimens. For purposes of this study, 10 adult *O. pyburni* were examined. Based on these specimens, the description of *O. pyburni* is expanded as follows.

The toe webbing formula is I 1½ – 2½ II 1½ – (3–3¼) III (2–2¼) – (3½–3¾) IV (3½–3¾) – 1½ V, with weak lateral dermal fringes on the outer edges of Toes II–IV (fringes most prominent on Toe IV). There

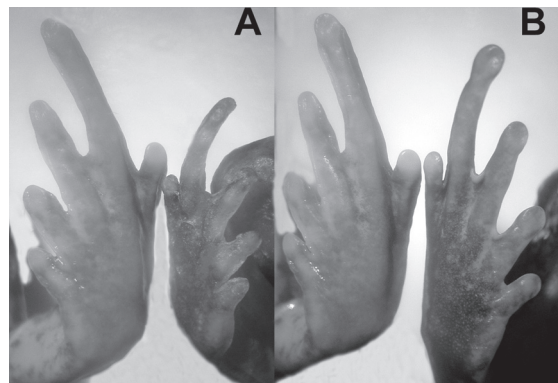


FIGURE 1: Plantar views of *Otophryne*. A. *Otophryne robusta* and *O. pyburni* illustrating relative length of toes. Left, *O. robusta* ROM 39679, male, 52 mm SVL; right, *O. pyburni* UTA 34527, male, 50 mm SVL. B. *Otophryne robusta* illustrating sexual dimorphism in toe webbing and fringes. Left, ROM 44054, female, 55 mm SVL; right, ROM 39679, male, 52 mm SVL.

is no difference in toe webbing between the sexes. Toes relatively shorter than those of *O. robusta* (Fig. 1A). Pharyngeal ridges straight or with posteriorly curved ends, the anterior ridge bearing 13-16 crenulae. The tympanum diameter: eye diameter ratio is 1.0-1.18 in males, 0.91-1.10 in females.

Colour in Preservative

Dorsum medium brown with dark brown middorsal stripe and other dark brown streaks, either symmetrical or random. In some specimens the dark brown markings are absent and the dorsal colour is uniformly medium brown. Colour pattern on dorsal part of thighs similar to that of dorsum. Dark brown patch surrounding vent. Rear of thigh brown with a series of white tubercles connected by a white line. Dorsolateral light stripe broad in females, narrow in males, in contrast to *O. robusta*, where it is narrow in both sexes. Colour in life, including photographs, is detailed in Wassersug & Pyburn (1987), Campbell & Clarke (1998) and Lescure & Marty (2000).

Advertisement Call (Fig. 2A, B)

The calls of *O. pyburni* from southeastern Colombia and Cerro Neblina, Venezuela, recorded at 25°C, were described and illustrated by Wassersug & Pyburn (1987), under the name *O. robusta*. These authors noted differences (in the Colombian population) between the advertisement calls of individuals calling alone and those calling in groups, and also described other types of calls produced by captive individuals.

In French Guiana, an isolated individual was recorded by P. Gaucher, 41 km NW of Saint Georges (04°02'05"N, 52°01'00"W): this recording is available on Audio CD (Marty & Gaucher 1999) and the call is illustrated and briefly described by Lescure & Marty (2000). P. Gaucher later recorded two males calling antiphonally at Haut Wanapi, French Guiana (02°30'46.4"N, 53°49'33.6"W). These recordings are assumed, on the basis of geographic location, to represent *O. pyburni*; *O. robusta* and *O. steyermarki* are not known from French Guiana.

We provide a detailed description of the calls recorded at the Saint Georges and Haut Wanapi localities in French Guiana. The recordings were made at 24-28°C (Lescure & Marty 2000, p. 344; P. Gaucher, pers. comm.)

Temporal structure

The Saint Georges recording of a single individual consists of two call bouts, of 26 and 25 notes respectively. The notes are closely spaced, with the note period and inter-note interval decreasing markedly towards the end of the bout (illustrated in Lescure & Marty 2000, p. 374). The mean note period is 324 ms and ranges from 260 ms at the beginning of the bout, to 589 ms at the end of the bout (N = 49). The note repetition rate is 182.9 and 187.7 notes/min for the first and second bout respectively. The mean note duration is 138 ms (range 129-159 ms; SD 8 ms; N = 46). Amplitude modulation of the notes produces pulses, but these are not evenly spaced and overlap to such an extent that it is not possible to count them accurately or measure the pulse rate. It is unlikely that this call parameter has a mate recognition function in *O. pyburni*.

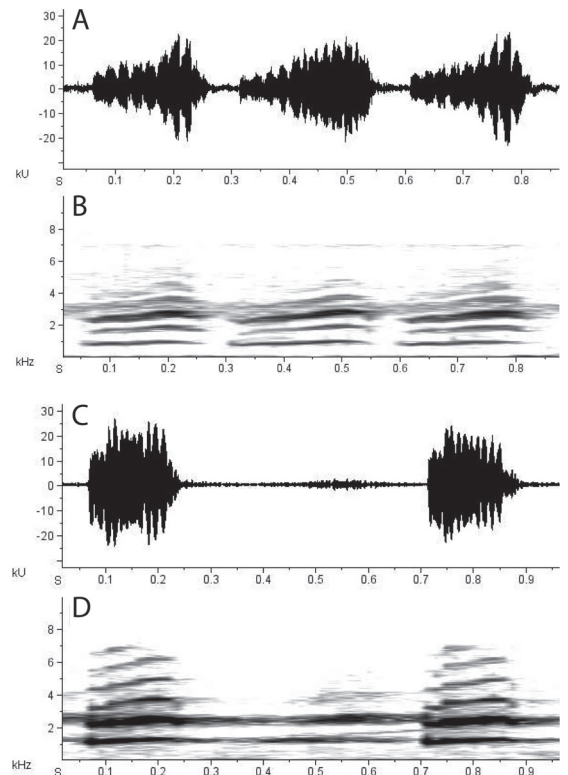


FIGURE 2: Waveform (A) and spectrogram (B) views of three notes of *Otophryne pyburni* from Haut Wanapi, French Guiana. The outer notes were produced by one male and the central note by another individual calling antiphonally with the first. Waveform (C) and spectrogram (D) views of three notes of *Otophryne robusta* from the Pakaraima escarpment, 7 km N of Marali Falls, Guyana. The outer notes were produced by one male and the central note (very low amplitude) by another individual calling antiphonally with the first.

The recording from the Haut Wanapi locality (21.5 s) appears to form part of a protracted bout of antiphonal calling between two males. During this alternating sequence, one of the males stopped calling on three occasions but resumed almost immediately, presumably in response to the calls of the other male. During these short interruptions the note period of the calling male increased slightly, but decreased when the second male resumed calling. During the uninterrupted parts of the antiphonal sequence, the note period and inter-note interval remain relatively constant. The mean note period for both individuals is 524 ms: in one individual this ranges from 500-548 ms (SD 15.3 ms; N = 18), while in the other it ranges from 498-569 ms; (SD 20.1 ms; N = 17). The note repetition rate for the two individuals is 114.6 and 114.5 notes/min. The mean note duration is 215 ms (range: 192-251 ms; SD 12.07 ms; N = 37). Although amplitude modulation is present within notes, it is not possible to count accurately the number of pulses or measure the pulse rate.

The marked differences in mean and range of the note period, note repetition rate and note duration in these recordings, is probably due to the fact that the St. Georges individual was calling alone whereas the Haut Wanapi recording involves two individuals calling antiphonally. In many chorusing frog species, males alter the timing and duration of their calls in the presence of other calling males (Klump & Gerhardt, 1992; Schwartz, 2001; Wells & Taigen, 1986; Zelick & Narins, 1985). Wassersug & Pyburn (1987) also noted a difference in note repetition rate, between individuals of *O. pyburni* calling alone and those calling antiphonally. The variation of temporal call parameters in different social contexts must therefore be borne in mind when comparing *Otophryne* calls both within and between species.

Spectral structure

No significant differences in spectral variables were observed between the Saint Georges and Haut Wanapi samples. Five to six harmonics are present, with most of the spectral energy concentrated in first four. The 1st harmonic (fundamental frequency) dominates at the beginning of the note but the emphasis shifts to the third harmonic, which dominates over the remainder of the note. The mean spectral energy increases from the 1st to the 3rd harmonic and then decreases through the 4th and 5th harmonic. For example, the mean spectral energy (measured in dB) of five harmonics of 20 notes from the Haut Wanapi

calls (taken at the region of highest amplitude, near the end of each note) was: 112.8, 116.2, 131, 109.6, and 100.1 dB. The frequency of the note is modulated, rising slowly to near the temporal midpoint, and falling very slightly at the end of the note. The mean modulation of 3rd harmonic is 451 Hz (range 420-496 Hz; SD 25 Hz; N = 19). The mean frequency of the 3rd harmonic measured in the region of highest amplitude, is 2786 Hz (range 2767-2824 Hz; SD 17 Hz; N = 19).

In Guyana, several males calling at 24°C, from leaf litter in a rocky stream bed in the headwaters of the Eping River, below the eastern scarp face of the Pakaraima range, were recorded by L. Minter. In these calls, spectral energy is initially concentrated in the first harmonic, shifting to the 3rd harmonic, as is the case in *O. pyburni*. However, the mean frequency of the emphasized third harmonic is 2382 Hz (range: 2309-2481 Hz; N = 10), considerably lower than the samples of *O. pyburni* from French Guiana, and barely overlapping the lower part of this call parameter's range in *O. robusta*. On the basis of the harmonic distribution of spectral energy, this population is tentatively assigned to *O. pyburni*.

Tadpole

Tadpoles of *O. pyburni* were described by Pyburn (1980), Wassersug & Pyburn (1987) and Campbell & Clarke (1998).

Otophryne robusta Boulenger

Otophryne robusta Boulenger 1900:55.

Nine adult and two juvenile *O. robusta* were examined. Measurements and other characteristics of *O. robusta* conform to those in Campbell & Clarke (1998) with the following additions.

In six adult males SVL is 48-54 mm, shank length 38-41% SVL. In three adult females SVL is 50-55 mm, shank length 38-40% SVL. Two juveniles measure 26 and 32 mm SVL, shank length 35-38% SVL. In adult males the toe webbing formula is I 1 - 2 II 1½ - 2½ III (2-2) - (2¼-2½) IV 2½ - 1+V, with strongly developed lateral dermal fringes. In females the webbing formula is less extensive than in males, I 1 - 2½ II 1¾ - (2¾-3) III (2-2¼) - (3+-3½) IV (3+-3½) - 1½ V (Fig. 1B). The lateral dermal fringes are also less pronounced in females than in males. Juveniles appear to have less webbing than adults, al-

TABLE 1: Characters useful for identification of adult *Otophryne*. Some information is from Wassersug & Pyburn (1987) and Campbell & Clarke (1998).

Character	<i>O. pyburni</i> (N = 10)	<i>O. robusta</i> (N = 11)	<i>O. steyermarki</i> (N = 11)
SVL (mm)	M 44-55; F 52-61	M 48-54; F 50-55	M 40-42; F 42-48
Shank length	34-39% SVL	38-41% SVL	38-43% SVL
Dorsal pattern	Medium brown with or without faint dark brown middorsal and lateral stripes	Medium brown with or without faint dark brown middorsal and lateral stripes	Typically black with pale spots; but some individuals may resemble <i>O. pyburni</i> or <i>O. robusta</i>
Ventral pattern	Orange with dark spots; throat dark in males and some females	Orange with dark spots; throat dark in most males	Yellow or orange with black mottling; throat dark in most males
Dorsolateral stripe	Narrow in males, broader in females	Narrow in both sexes	Narrow in males, broader in females
Dorsal surface of thigh	Not mottled; similar to dorsum	Mottled; different from dorsum	Black with pale spots; similar to dorsum
Rear of thigh	Brown with pale tubercles connected by a pale line	Mottled, with or without a pale line	Black with irregular yellow line
Toe webbing males	I $\frac{1}{2}$ -2 $\frac{1}{2}$ III $\frac{1}{2}$ -(3-3 $\frac{3}{4}$) III(2-2 $\frac{1}{4}$)-(3 $\frac{1}{2}$ -3 $\frac{3}{4}$) IV(3 $\frac{1}{2}$ -3 $\frac{3}{4}$)-1 $\frac{1}{2}$ V; weak fringes on outer edges of II-IV	I-2III $\frac{1}{2}$ -2 $\frac{1}{2}$ III(2-2)-(2 $\frac{1}{4}$ -2 $\frac{1}{2}$) IV2 $\frac{1}{2}$ -1*V; strong fringes	I $\frac{1}{2}$ -2II2-2 $\frac{1}{2}$ III(1 $\frac{1}{2}$ -1 $\frac{3}{4}$)-3 $\frac{1}{2}$ IV(3-3 $\frac{1}{4}$)-1V; weak fringes
Toe webbing females	Same as in males	I-2 $\frac{1}{2}$ III $\frac{3}{4}$ -(2 $\frac{3}{4}$ -3) III(2-2 $\frac{1}{4}$)-(3*-3 $\frac{1}{2}$) IV(3*-3 $\frac{1}{2}$)-1 $\frac{1}{2}$ V; fringes less than in males	I $\frac{3}{4}$ -2 $\frac{1}{2}$ II2-3 III(2-2 $\frac{1}{4}$)-3 $\frac{1}{2}$ IV(3 $\frac{1}{2}$ -3 $\frac{3}{4}$)-1 $\frac{1}{2}$ V; weak fringes
Tip of snout	Pointed	Rounded	Rounded
Glandular ridges on limbs	Distinct	Indistinct	Distinct
Anterior pharyngeal ridge	Straight; ends may curve posteriorly; 13-16 crenulae	Straight or concave; 13-19 crenulae	Concave; 14-17 crenulae

though it is difficult to quantify the webbing formula in small individuals. Phalangeal tips bluntly pointed. Toe II reaches base of penultimate phalange of Toe III, tip of Toe III reaches base of penultimate phalange of Toe IV; Toe V > II. Relative toe length greater than in *O. pyburni* (Fig. 1A).

The anterior pharyngeal ridge is straight or concave, bearing 13-19 crenulae. The tympanum diameter: eye diameter ratio is 1.08-1.17 in males, 0.80-0.92 in females, and 0.76-0.87 in two juveniles. The females have 9-12 enlarged unpigmented ova, 3 mm in diameter.

Colour in life

Dorsum variable, from dark orange with dark brown middorsal stripe and lateral bars to almost-uniform dark brown with faint orange mottling; narrow pale yellow dorsolateral stripe from snout tip passing above eye to groin, continuing onto anterior thigh in some individuals; lateral surfaces dark orange with small black spots, some with white centres; dorsal surfaces of arms dark brown with small white spots;

dorsal surfaces of thighs, shanks and feet dark orange with dark brown mottling and occasional dark brown bars; posterior thigh orange with variable dark brown mottling and a few white spots, often connected by a white line; throat and venter variable (see below); digits pink; upper third of iris pale yellow, matching colour of dorsolateral stripe; remainder of iris dark orange with black reticulations. A colour photograph is in MacCulloch & Lathrop (in press).

In preservative the darker orange changes to medium brown, while the lighter orange, pink and yellow become white. Figs. 2 and 3 in Campbell & Clarke (1998) are excellent renditions of dorsal pattern in preserved specimens of this species.

The photographs of specimens in the BMNH in Campbell & Clarke (1998:308) show a uniformly mottled pattern on the rear of the thigh that is not present in many specimens of *O. robusta* at ROM or UMMZ. Most of the latter resemble *O. pyburni* in having a series of white spots and line, but above this is the mottled pattern of the dorsal surface of the thigh, and below it is a narrow dark brown line; whereas in *O. pyburni* the thigh above the white line is uniform mid-brown, and below is a broad dark brown line.

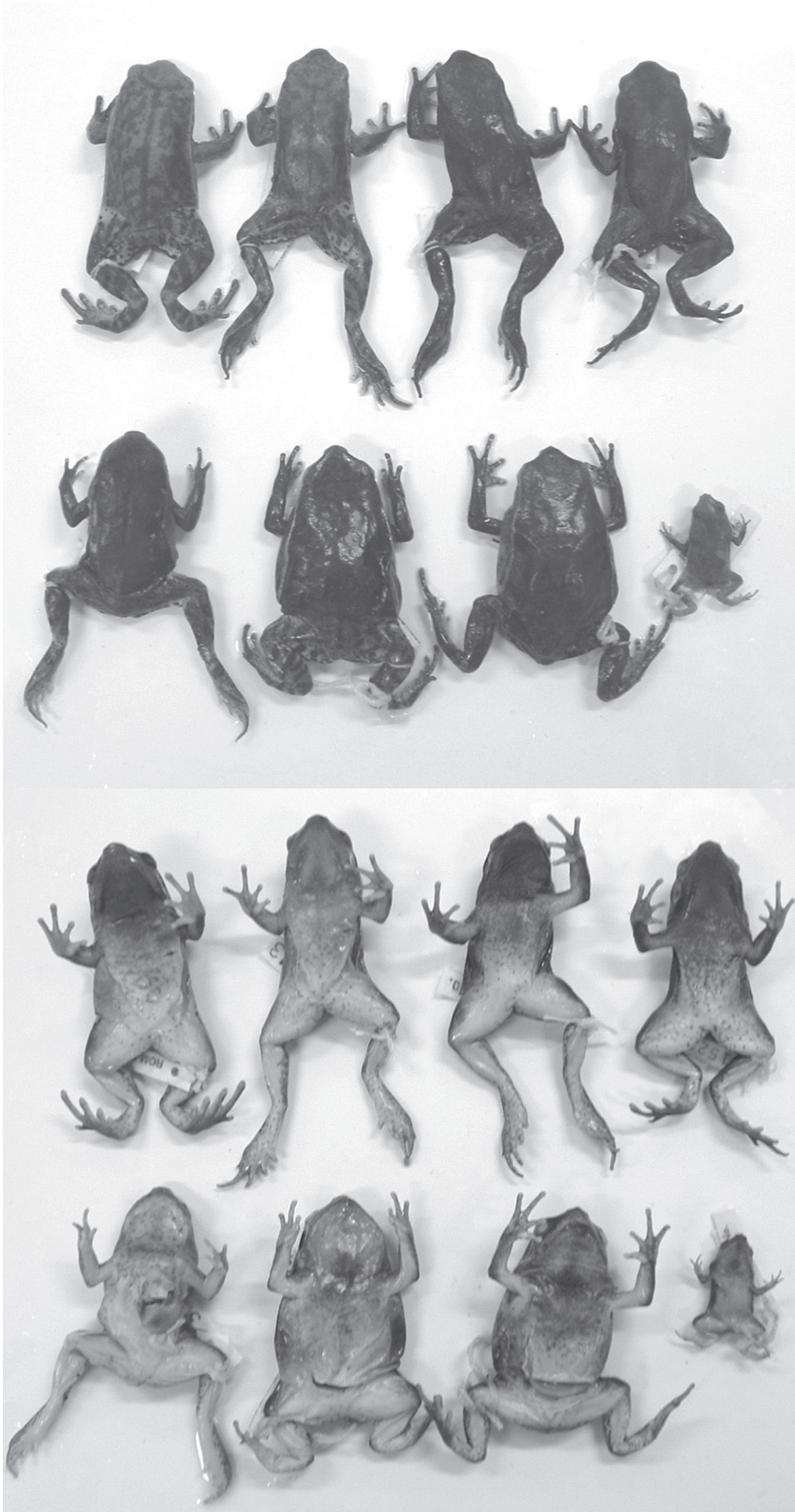


FIGURE 3: Colour pattern variation in *Otophryne robusta*. Males in upper row, females and juvenile in lower row. Dorsal (A) and ventral (B) views. Specimens are in the same locations in A and B.

The colour pattern on the dorsal surface of the thighs is one of the characters which distinguish *O. robusta* from *O. pyburni* (Table 1).

There is sexual dimorphism in colouration. The dorsal "leaf" pattern is more obvious in males than in females, which have a more uniformly dark dorsum. In males the throat is dark brown and the chest orange with dense brown speckles, decreasing in density posteriorly. In females the throat and venter are orange with variable dark speckling (Fig. 3). The lateral light stripe is narrow in both sexes, barely visible in one male.

Advertisement Call (Fig. 2C, D)

O. robusta is a diurnal species with a strident call that is easily heard at a distance of < 100 m in forest. Choruses were heard as early as 05:00, continuing into the late afternoon, even on hot, cloudless days. The following description is based on the calls of a male (not collected) calling from leaf litter alongside a stream at a locality on the northern end of the Pakaraima escarpment, 7 km N of Marali Falls, Guyana. The recordings were made between 12:30 and 13:00 on 5 November 2004, at an air temperature of 24°C. The chorus comprised a small group of at least four males that responded to one another's calls, resulting in distinct bouts of calling punctuated by short (< 30 s) periods of silence.

Temporal structure

Each bout of calling consists of a series of short, pulsed notes which alternate with those of the nearest neighbour. The notes are closely spaced and may form a single, uninterrupted series, but usually the series is punctuated by short pauses, as the male apparently adjusts the timing and number of his notes in response to the calls of his nearest neighbour. Nine call bouts from this individual have a mean duration of 10.8 s (range 3.6-18.9 s), and contain 5-28 notes. The mean note period is 604 ms (range 476-945 ms; SD 87 ms; N = 50), while the mean note repetition rate, in groups of uninterrupted calls, is 99.5 notes/min (range 94.3-111.7 notes/min; SD 7.6 notes/min; N = 5). Notes have a mean duration of 183 ms (range 149-207 ms; SD 11 ms; N = 50), and consist of 14-18 pulses (mean 15.6; N = 10). The pulses overlap to a varying degree and are not well defined at the end of the note. It is therefore unlikely that this call parameter plays a significant role in mate recognition in *O. robusta*.

Spectral structure

Six harmonics are present, with the spectral energy concentrated in the first two. Initially, the 1st harmonic (fundamental frequency) is slightly more energetic than the 2nd, but the latter is dominant over the remainder of the note. Spectral energy decreases progressively through the higher harmonics. For example, the mean spectral energy (measured in dB) of the six harmonics of 18 notes, taken at the temporal mid-point of each note, and beginning with the 1st harmonic, was: 124.6, 129.7, 95.6, 90, 83.1 and 81.4 dB. The frequency of the note is modulated, rising slowly over the initial 4/5 of the note, before falling slightly. The mean frequency modulation of the 2nd harmonic is 355 Hz (range 268-401 Hz; SD 36 Hz; N = 18). The mean frequency of the second harmonic, measured near the end of the note, at the point where the frequency reaches its peak, is 2505 Hz (range 2405-2538 Hz; SD 40 Hz; N = 18).

Tadpole

Two tadpoles, determined to be *O. robusta* (Duellman, 1997; Campbell & Clarke, 1998), were collected at La Escalera, Venezuela (RMNH 27245-6). The following description is of RMNH 27245, an individual in Stage 26: total length (TL) 40 mm, tail length 27 mm (67% of TL). Body depressed (width 1.3 X height), oval in dorsal view; eye small, eye diameter 10% of interorbital distance; eyes dorsolateral, not visible from below; eye-snout tip 45% body length. External nares absent. Spiracle sinistral, its base located ventrolaterally at the rear of the body, projecting onto proximal part of tail; spiracle tube length 24% of tail length, 16% of TL. Vent tube caudal, medial, short. Caudal musculature extending to tail tip; myotomes visible anteriorly, barely visible posteriorly; dorsal fin originating at body/tail boundary; dorsal fin height 80% height of musculature at midpoint; ventral fin height 50% height of musculature at midpoint; tail tip rounded. Maximum tail height 25% tail length (Fig. 4A-C).

Oral disc absent. Supralabial cartilage expanded, bearing prominent lateral flanges with scalloped edges. A single row of 60 long, sharp keratinized teeth in each jaw; lower teeth slightly larger than upper teeth. Lower labium bordered by a single row of small papillae; a second row of larger papillae midway between lower labium and teeth. Denticles absent (Fig. 5A).

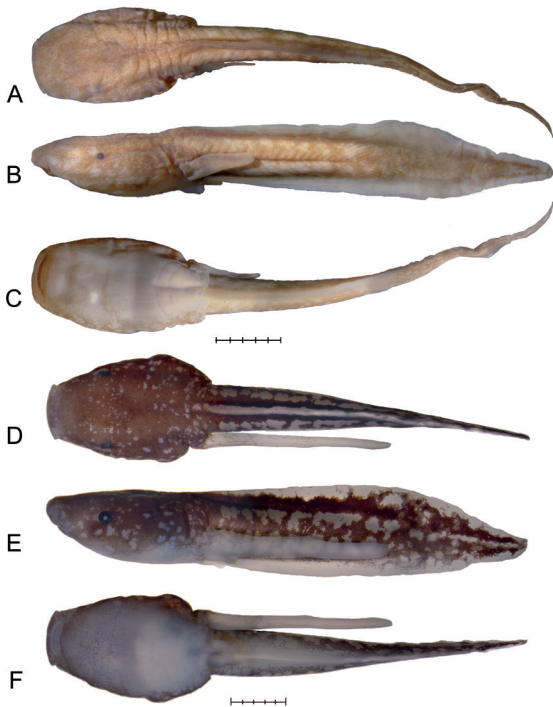


FIGURE 4: Dorsal (A), lateral (B) and ventral (C) views of the tadpole of *Otophryne robusta*, RMNH 27245. Dorsal (D), lateral (E) and ventral (F) views of the tadpole of *Otophryne steyermarki*, ROM 45271. Scale bars = 5 mm. Compare with illustrations of *O. pyburni* in Pyburn (1980) and Campbell & Clarke (1998).

Colour in Preservative

Dorsum and sides of body medium brown with small white flecks; venter white, intestine not visible. Tail musculature white with brown mottling dorsally and laterally, white ventrally; fins transparent with brown mottling, a brown line along base of dorsal fin; teeth reddish-brown (Fig. 4A-C). Colour in life was described by Duellman (1997).

Variation

One individual of Stage 25 measured 34 mm TL, body width 1.4 X height, spiracle tube 22% of tail length, 15% TL.

Tadpoles of *O. robusta* differ from those of *O. pyburni* by having 60 teeth in each jaw (30-35 in *O. pyburni*); spiracle short, < 25% tail length, 15-16% of TL (longer, up to 50% of tail length, 33% of TL); edge of the oral lateral flange scalloped (not scalloped). Tadpoles of *O. robusta* differ from *O. steyermarki* tadpoles by having 60 teeth in each jaw (38-50 in *O. steyermarki*); papillae in inner row larger

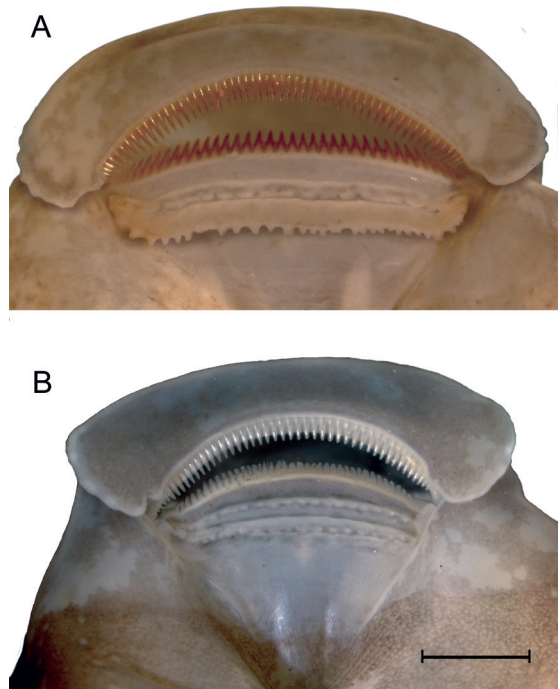


FIGURE 5: A. Mouth of tadpole of *Otophryne robusta*, RMNH 27245. B. Mouth of tadpole of *Otophryne steyermarki*, ROM 45271. Scale bars = 1 mm. Compare with illustrations of *O. pyburni* in Pyburn (1980) and Campbell & Clarke (1998).

than those in outer row (uniform size); spiracle short, < 25% of tail length, 15-16% of TL (longer, 47-68% of tail length, 33-47% of TL) (Table 2).

Distribution

Specimens of *O. robusta* were collected from the upper Potaro River, 680 m; Mount Wokomung, 690 m; Meamu River, 780 m; Mount Ayanganna, Guyana, 800 and 1100 m. In addition to these, *O. robusta* were heard calling at several locations along the eastern Pakaraima escarpment: edge of escarpment near the headwaters of the Perenong River, 615 m; northern end of escarpment, 7 km N of Marali Falls, 646 m; edge of escarpment near the Kurupung River (two locations), 695 m; 2 km W of Partang, 935 m; 5 km S of Partang, 1100 m. Specimens were encountered in the vicinity of small streams and seeps.

Otophryne steyermarki (Rivero)

Otophryne steyermarki Campbell & Clarke 1998:303.
Otophryne robusta steyermarki Rivero 1968:155.

TABLE 2: Characters useful for identification of *Otophryne* tadpoles. Some information is from Pyburn (1980), Wassersug & Pyburn (1987) and Campbell & Clarke (1998).

Species	Number of teeth in each jaw	Spiracle length as % of tail length	Spiracle length as % of total length	Edge of lateral oral flange	Tail tip profile
<i>O. pyburni</i> (N = 12)	30-35	up to 50	up to 33	smooth	pointed
<i>O. robusta</i> (N = 2)	60	22-24	15-16	scalloped	rounded
<i>O. steyermarki</i> (N = 18)	38-50	47-68	33-47	scalloped	rounded

Six males and five females were examined. Male SVL is 40-42 mm, shank length 38-43% SVL; female SVL 42-48 mm, shank length 38-42% SVL. *Otophryne steyermarki* is the smallest species of *Otophryne*; SVL is less than 50 mm in all individuals examined.

Toe webbing in *O. steyermarki* is more extensive in males than in females (Rivero, 1968). The webbing formula for males is I 1½ – 2 II 2 – 2½ III (1½-1¾) – 3 IV (3-3¼) – 1 V and for females I 1¾ – 2½ II 2 – 3 III (2-2¼) – 3½ IV (3½-3¾) – 1½ V. Toes have lateral dermal fringes on both sides, but these are less prominent than in *O. robusta*. Phalangeal tips bluntly pointed. Toe II does not reach base of penultimate phalange of Toe III, tip of Toe III reaches base of penultimate phalange of Toe IV; Toe V > II.

The anterior pharyngeal ridge is concave, typically with 14-17 crenulae. ROM 39677, a male from Ayanganna, has 11 crenulae, irregular in size and alignment.

Tympanum diameter: eye diameter ratio in males is 1.0-1.17; in females 0.93-1.05, with tympanum diameter exceeding eye diameter in only the largest female. There is apparent interpopulation variation in tympanum: eye ratio; Gorzula (1985) reported a range of 1.42-1.73 in four male *O. steyermarki* from Chimantá, Venezuela.

One female with SVL of 42 mm had eight enlarged ovarian eggs. The eggs are unpigmented, 4.5 mm in diameter, surrounded by a capsule 6.3 mm in diameter.

Colour in Life

Dorsum of body and limbs black or dark grey with irregular, variable yellow spots. A yellow line from tip of snout across eyelid to groin, continuing onto anterior thigh and sometimes onto shank. Lateral surfaces usually black or dark grey, occasionally dark orange, with yellow or orange spots, usually smaller than dorsal spots. Venter variable, ranging from black with small orange spots to orange with black or grey spots or mottling. Rear of thigh with a

thin horizontal yellow line, continuing onto shanks and feet. Forelimbs with a thin pale yellow line on the anterior and posterior surfaces, from insertion of arm to toes. Palms and soles dark yellow or orange. Upper third of iris gold with black reticulations, remainder of iris dark red with black reticulations. In preservative dorsal light spots and lines become white; venter becomes black and white; palms and soles are medium grey. Colour photographs are in Campbell & Clarke (1998), Gorzula & Señaris (1999) and MacCulloch & Lathrop (in press).

There is considerable variation in colour pattern. The dorsolateral light stripe is wider in females than in males, as in *O. pyburni* (Campbell & Clarke, 1998). Females generally have larger yellow dorsal spots than do males. The single male from Partang has only a few very small dorsal spots (Fig. 6A, second from left). Two males of 42 mm SVL from Mt. Wokomung have an atypical dorsal pattern; the dorsum in these two is medium grey-brown with dark mid-dorsal and lateral lines and a few faded yellow spots (Fig. 6A, upper right). This dorsal pattern bears a superficial resemblance to that of *O. pyburni* or *O. robusta*, although the ventral pattern is unmistakably that of *O. steyermarki* (Fig. 6B, upper right). Gorzula (1985) also found variability in dorsal colour pattern of this species.

Ventral pattern is also variable. In the four males from Wokomung the venter is mottled while the throat is dark grey with tiny yellow specks (Fig. 6B, upper row, third to sixth from left). The single male from Ayanganna has mottling on both venter and throat (Fig. 6B, upper left), while the male from Partang has very pale mottling, on the throat only (Fig. 6B, second from left). In females the throat and venter patterns are similar; either mottled or black with yellow specks. All females in Fig. 6 are from the same locality, Mt. Wokomung.

Tadpole

A series of tadpoles was collected in shallow streams at 1234 and 1411 m on Mt. Wokomung.

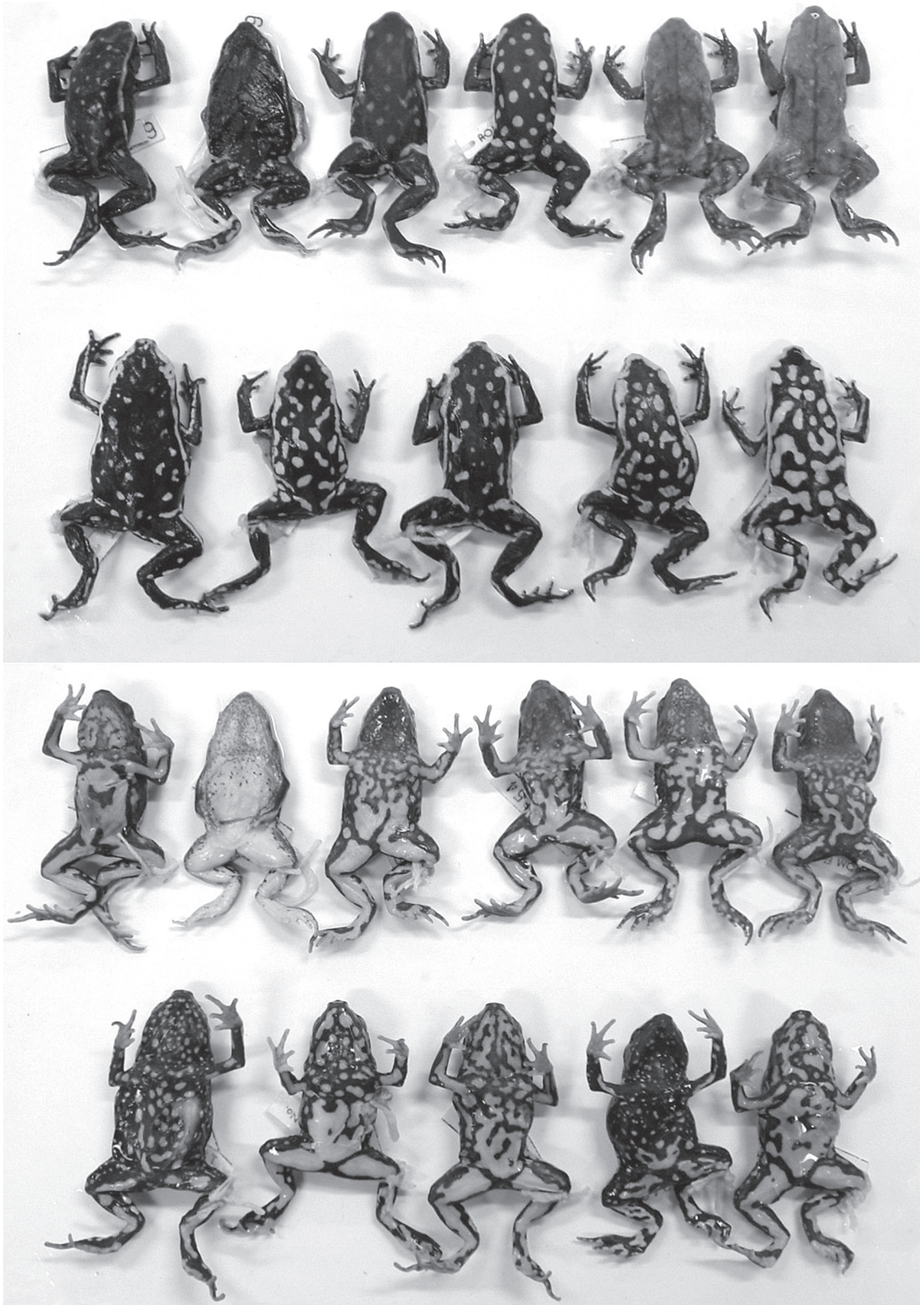


FIGURE 6: Colour pattern variation in *Otophryne steyermarki*. Males in upper row, females in lower row. Dorsal (A) and ventral (B) views. Specimens are in the same locations in A and B.

Their distinctive morphology allowed them to be conclusively identified as *Otophryne*. Because only *O. steyermarki* adults were encountered at these locations, we conclude that the tadpoles are of this species.

The following description is of ROM 45271, an individual in Stage 36: total length 43 mm, tail length 28.5 mm (66% of TL). Body depressed (width 1.5 X height), oval in dorsal view; eye small, eye diameter 15% of interorbital distance; eyes dorsolateral, not visible from below; eye-snout tip 35% body length. External nares absent. Spiracle sinistral, its base located posterolaterally on body, just above hindlimb insertion, projecting posteriorly to a point where the dorsal fin is highest; spiracle tube 61% of tail length, 41% of TL. Vent tube caudal, medial, short. Caudal musculature extending to tail tip; myotomes not visible; dorsal fin originating at body/tail boundary; dorsal fin height 80% height of musculature at midpoint; ventral fin height 50% height of musculature at midpoint; tail tip rounded. Tail height 30% tail length (Fig. 4D-F).

Oral disc absent. Supralabial cartilage expanded, bearing prominent lateral flanges with scalloped edges, the scalloping less than in *O. robusta*. A single row of long, sharp keratinized teeth in each jaw; 45 in upper jaw and 38 in lower; upper teeth longer than lower. Lower papillae in two rows; all papillae are approximately the same size. Denticles absent (Fig. 5B).

Colour in Life

Dorsum and sides of body dark grey with white flecks, the flecks larger on the sides; throat medium grey, belly white, intestine not visible. Tail musculature mottled white and dark grey laterally, white ventrally; fins transparent with grey mottling distally, a dark grey stripe along base of dorsal fin; teeth white. The colour changes little in preservative (Fig. 4D-F).

Variation

There is slight decrease in relative tail length, ranging from 70% of TL in the smallest individuals in Stage 25 (30 mm TL) to 66% of TL in the single individual of Stage 36 (43 mm TL). All other proportions are consistent throughout the range of tadpoles examined. Lengths of unbroken spiracle tubes ranged from 47-68% of tail length, 33-47% of TL, with no apparent correlation between TL and spiracle length. The spiracle tube was broken during capture or pres-

ervation in 4 of 19 individuals. Number of teeth 38-50; no apparent change in oral characters between stages 25-36. Dark mottling more prominent in larger individuals.

Tadpoles of *O. steyermarki* differ from *O. pyburni* tadpoles by having 38-50 teeth in each jaw (30-35 in *O. pyburni*); body more flattened; spiracle longer, 47-68% of tail length, 33-47% of TL (shorter, up to 50% of tail length, up to 33% of TL); tail rounded at tip (pointed). Tadpoles of *O. steyermarki* differ from *O. robusta* tadpoles by having 38-50 teeth in each jaw (60 in *O. robusta*); lower papillae of uniform size (papillae in inner row larger than those in outer row); spiracle long, 47-68% of tail length, 30-47% of TL (shorter, < 25% of tail length, 15-16% of TL) (Table 2).

Distribution

Specimens of *O. steyermarki* were collected from Partang, elevation unknown but probably not above 1000 m; Mount Wokomung, 1234 and 1411 m; Mount Ayanganna, 1490 m.

DISCUSSION

Morphology

The three species of *Otophryne* are similar in size, although *O. steyermarki* is slightly smaller, with no individuals attaining 50 mm SVL. The ratio of shank length to SVL has been used as a character to distinguish among species of *Otophryne* (Campbell & Clarke, 1998). Our data confirm interspecific differences in relative shank length, although there is some overlap among species (Table 1). In *O. robusta* juveniles, shank length is proportionally shorter than in adults. In a juvenile of 26 mm SVL the shank length is 35% SVL whereas in a juvenile of 32 mm SVL the shank is 38% SVL. Although only two juveniles were examined, it appears that shank length becomes longer with increasing body size, until it attains the typical adult size (40% of SVL).

Otophryne robusta juveniles also exhibit relatively small tympana. In a juvenile of 26 mm SVL the tympanum diameter: eye diameter ratio is 0.74; in a juvenile of 32 mm SVL it is 0.87. This suggests that tympanum diameter may increase relative to eye diameter with increasing SVL. This increase may depend on attainment of sexual maturity in males. This requires further study once additional specimens are available.

Campbell & Clarke (1998) found toe webbing to be most extensive in *O. steyermarki*, and least in *O. pyburni*. Our data confirm this, although the differences are slight (Table 1). Toe length in *O. robusta* is greater than in similar-sized *O. pyburni* (Fig. 1A).

Identification can be difficult in areas of species sympatry. Juvenile *O. robusta* have less mottling on the dorsal surface of the thighs and less webbing than adults, making them superficially resemble *O. pyburni*. Some *O. steyermarki* (Fig. 6) have reduced dorsal or ventral mottling, making them superficially resemble *O. robusta* or *O. pyburni*. In some *O. robusta* the pattern on the posterior surface of the thigh resembles that of *O. pyburni*. Additional characters for differentiating among species (especially *O. pyburni* and *O. robusta*) are toe webbing and fringes, toe length, snout profile and sexual dimorphism in width of dorsolateral stripe (Table 1).

Colour

Colour and colour pattern exhibit some variation in both *O. robusta* and *O. steyermarki* (Figs. 3, 6). Colour pattern on the upper surface of the thigh distinguishes *O. robusta* from *O. pyburni*. As noted by Lescure (1976), in *O. robusta* the upper surface is mottled, different from the pattern on the dorsum, although this difference may not be obvious on older preserved specimens which have darkened. In *O. pyburni* the upper thigh is not mottled, and is similar to the dorsum (Table 1).

In *O. steyermarki* from Guyana the dorsal spots are yellow, while in most specimens from Venezuela they are red (Gorzula, 1985; Campbell & Clarke, 1998; Gorzula & Señaris, 1999).

Advertisement Calls

Antiphonal calls of *O. robusta* from the Pakaraima escarpment and *O. pyburni* from Haut Wanapi differ in mean note duration, but the ranges of this character in the two samples overlap slightly. Given the apparent variability of note duration in different social contexts, and the small sample size, further investigation is needed to confirm the diagnostic value of this character.

Spectral characters seem to be of more diagnostic value, with a concentration of spectral energy in the 2nd harmonic in *O. robusta* and the 3rd harmonic in *O. pyburni* (Fig. 2). The mean frequencies of the

emphasized harmonics of the two species differ by 281 Hz and their ranges are separated by 229 Hz in the available samples (detailed descriptions of the calls are given in the species accounts).

Tadpoles

A distinguishing character of *Otophryne* tadpoles is the long sinistral spiracle. Length of this spiracle relative to tail length and TL seems to be useful in distinguishing among species. In order for this to be a valid character for identification, two criteria must be met: the spiracle must be unbroken and the spiracle length:tail length and spiracle length:TL ratios must be fairly constant. Specimens were examined with respect to these two criteria.

In unbroken spiracles, the tip is tapered (Pyburn, 1980: fig. 2; Wassersug & Pyburn, 1987: fig. 2; Campbell & Clarke, 1998: fig. 6). Spiracle tips of tadpoles of *O. robusta* and *O. steyermarki* were examined to ensure that only unbroken spiracles were included. In some tadpoles of *O. steyermarki* (N = 4) the spiracles were broken, and the end not tapered; these individuals were not included in the calculation of length ratios in *O. steyermarki*. In both *O. robusta* tadpoles the ends of the spiracle were tapered, so we conclude that the spiracles are unbroken, and that the short spiracle length in these two individuals is characteristic of this species (Table 2).

Pyburn (1980) and Campbell & Clarke (1998) stated that relative spiracle length increases in older tadpoles of *O. pyburni*. Such an ontogenetic change could lead to misidentification of tadpoles based on spiracle length. In 10 *O. steyermarki* tadpoles of Stage 25 (TL range 32-40 mm) with unbroken spiracles, no relation was found between TL and relative spiracle length. Apparently the increase in relative spiracle length noted by Pyburn (1980) and Campbell & Clarke (1998) occurs at earlier stages, prior to closure of the operculum. Conversely, Wassersug & Pyburn (1987) found that the spiracle begins to shorten in tadpoles of *O. pyburni* after Stage 40. Our measurements show that relative spiracle length is fairly constant from Stage 25 to Stage 36. We conclude that interspecific differences in relative spiracle length can be useful for identification of *Otophryne* tadpoles of Stages 25-36.

It should be noted that Wassersug & Pyburn (1987) and Altig & Johnston (1989) pointed out that the teeth in tadpoles of *Otophryne* are homologous to the jaws or beaks, rather than denticles, of other tadpoles.

Habitat of tadpoles of *O. steyermarki* at Mt. Wokomung was similar to that of *O. pyburni* tadpoles described by Pyburn (1980); very shallow forest streams with sandy substrate. Tadpoles concealed themselves under detritus by day. When disturbed, they swam rapidly for 15-20 cm, then buried themselves completely in the sand of the stream bed (Wassersug & Pyburn, 1987). By night they were observed resting on the substrate, but if disturbed swam rapidly and buried themselves with only the distal portion of the tail visible.

Distribution

Otophryne pyburni is widely distributed, from Amapá and Pará, Brazil to eastern Colombia at elevations from about 100 m to 1100 m (Campbell & Clarke, 1998; Barrio, 1999a; Lescure & Marty, 2000; Carvalho *et al.*, 2007). During this study one *O. pyburni* was recorded at the foot of the Pakaraima Escarpment near the headwaters of the Eping River, Guyana, 06°00'32"N, 060°11'28"W, 693 m. This was one of several locations along the escarpment where *Otophryne* were heard calling, but represents the only record of *O. pyburni*; all other calls were of *O. robusta*.

In addition to the locations mentioned above, *Otophryne robusta* has been collected from Kurupung River, Guyana, 700-750 m (Campbell & Clarke, 1998); Auyan-tepui, Venezuela, 950 m (Señaris & Ayarzagüena, 2006); Pratawaga, Venezuela, 960 m (Gorzula, 1985); La Escalera, Venezuela, 1000-1100 m (Duellman, 1997); Mount Roraima, Venezuela, 1067 m (holotype); Mount Roraima, Guyana, 1128 m (Campbell & Clarke, 1998); Arabopó, Venezuela, 1216 m (Campbell & Clarke, 1998) (Fig. 7). The species has an elevation range of 601 m

(615-1216 m). *Otophryne robusta* has also been heard but not collected in Kaieteur National Park, Guyana, approximately 35 km E of Mount Wokomung (P.J.R. Kok, pers. comm.). *Otophryne robusta* prefer rocky streambank or seep habitat in partially-closed canopy forest. They are notoriously difficult to locate, even when males are calling.

In addition to the locations in Guyana mentioned above, *Otophryne steyermarki* has been collected from Roraima, Venezuela, 1550 m (Gorzula & Señaris, 1999); Meseta de Jaua, Venezuela, 1800 m (Barrio, 1999b); Acopán-tepui, Venezuela, 1920-1980 m (Rivero, 1968; Gorzula, 1985); Chimantá-tepui, Venezuela, 1800-2140 m (Rivero, 1968; Gorzula, 1985; Gorzula & Señaris, 1999) (Fig. 7). The recent collections from Partang and Mt. Wokomung mark new low-elevation records for this species. Because the precise elevation for the Partang collection site is unknown, we use the lowest elevation on Mt. Wokomung, 1234 m, to extend the elevational range for the species to 1234-2140 m, a range of 906 m, greater than previously reported (McDiarmid & Donnelly, 2005). Although only a single specimen was collected at Partang, the low-elevation collections at Mt. Wokomung are not an isolated aberration because eight of nine adult *O. steyermarki* from Mt. Wokomung were collected at 1234 m, with only one from higher elevation at 1411 m. *Otophryne steyermarki* occurs in the vicinity of small streams in medium-canopy forest.

RESUMO

Coleções recentes de Otophryne robusta e O. steyermarki são usadas para expandir descrições existentes de adultos. Os cantos de O. pyburni e O. robusta são comparados. Os girinos de O. robusta e O. steyermarki são descritos. Os caracteres para distinguir adultos e girinos destas duas espécies e O. pyburni são fornecidos. Otophryne é endêmico do escudo Guianense; O. pyburni é comum em elevações mais baixas, enquanto O. robusta e O. steyermarki ocorrem no sudeste da Venezuela e Guiana ocidental, o primeiro em elevações moderadas e o último em elevações maiores.

PALAVRAS-CHAVE: *Otophryne robusta, Otophryne steyermarki, girinos, Escudo Guianense.*



FIGURE 7: Map showing the distribution of *Otophryne robusta* (circles) and *O. steyermarki* (triangles). Hollow symbols indicate type localities; solid symbols are other known localities. The asterisk indicates the location of the recording of *O. pyburni*.

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APPENDIX

Specimens Examined

Otophryne pyburni: Colombia, Vaupés, Yapima, UTA 5343-4, 5347, 34524, 34527, 34529, 34530, 40001; French Guiana, Paracou, AMNH A139211; Guyana, Mazaruni-Potaro (District 7), Kartabo, AMNH 71015.

Otophryne robusta: Guyana, District 7, Mount Ayanganna, ROM 39678-81; Meamu, ROM 44053-4; Makreba Falls, UMMZ 85140; District 8, Mount Wokomung, ROM 42962-3; Venezuela, Bolivar, Arabopó, UMMZ 85137-8; La Escalera, km 120, RMNH 27245-6 (tadpoles).

Otophryne steyermarki: Guyana, District 7, Mount Ayanganna, ROM 39677; Partang, ROM 44052; District 8, Mount Wokomung, ROM 42953-61, ROM 44778-9, 45271 (tadpoles).

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