



<http://dx.doi.org/10.11646/zootaxa.3686.2.9>

<http://zoobank.org/urn:lsid:zoobank.org:pub:3E0BCF47-EC41-4623-99B2-29DEAEF58F8E>

Description of the previously unknown advertisement call and tadpole of the Colombian endemic glassfrog *Centrolene savagei* (Anura: Centrolenidae)

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Glassfrogs (family Centrolenidae) are a charismatic group that currently contains about 149 species biogeographically restricted to the Neotropics (Frost 2013). The advertisement call and tadpole has been described for less than 25% glassfrog species, 32 and 35 species respectively (e.g. Márquez *et al.* 1996; Ospina-Sarria *et al.* 2011). *Centrolene savagei* (Ruiz-Carranza & Lynch 1991; Fig. 1) is a species of relatively small size frogs (mean snout-vent length, SVL, females: 23.6 mm, males: 21.1 mm) occurring in both the Western and Central Andes (Cordillera Occidental and Cordillera Central) of Colombia, between 1400–2410 m a.s.l. (Ruiz-Carranza & Lynch 1991; Rojas-Morales *et al.* 2011). Although there is some information regarding egg attendance and natural history of *C. savagei* (Vargas-Salinas *et al.* 2007), neither the advertisement call or the larval morphology have been described.

This study was performed at three localities in Colombia. First, the Reserva Forestal Bosque de Yotoco, Western Andes (Cordillera Occidental), Valle del Cauca (03°53'18"N, 76°20'05"W; hereafter Yotoco); 1200–1600 m a.s.l.; annual precipitation and temperature mean 1100 mm and 22°C, respectively (Escobar 2001). Second, a remnant of riparian forest in the municipality of Filandia, Central Andes (Cordillera Central), Quindío (04°42'N, 75°38'W; hereafter Filandia); 1880 m a.s.l.; annual precipitation and temperature mean 2515 mm and 17°C (Mendoza *et al.* 2007). Third, Alto Bonito-El Águila, encompassed by the vereda Alto Bonito (05°07'27"N, 75°29'57"W) and the vereda El Águila (05°06'27"N, 75°29'30"W); municipality of Manizales, western slope of the Central Andes; 1950 and 2050 m a.s.l.; annual precipitation and temperature mean 2600 mm and 18°C (Corpocaldas 2002). Advertisement calls were recorded at all localities and tadpoles were collected only in Filandia.

Advertisement call. We recorded advertisement calls during one field trip to Yotoco (20–23 March 2009) and one to Filandia (5–7 April 2009). We positioned a unidirectional microphone (Shure B.G 4.1) connected to a digital recorder (Marantz PMD660) at 50–80 cm in front of a calling male. We recorded body temperature with an infrared thermometer Oakton Series 35629–00, captured the recorded individual and measured its body size (SVL) with a digital caliper. In Alto Bonito-Águila we recorded advertisement calls between October 2008–January 2011 using a shotgun microphone (Sennheiser ME64) connected to a digital recorder (Marantz PMD660). The microphone

was 50–150 cm away from the calling male; body temperature was measured using an infrared hygro-thermometer (Extech EA25) and body size was measured with a caliper. We did not collect vouchers in any locality, and all recordings were performed between 19:30–00:00 h.

We estimated the temporal and spectral parameters of the advertisement calls using the software RAVEN Pro 1.4 (Bioacoustics Research Program 2011). Recordings were digitized at 16 bits resolution and 44.1 kHz sampling rate. Oscillograms and spectrograms were analyzed with a Fast Fourier Transformation window of 256 points and Blackman algorithm. Low and high frequencies of the calls were measured at 20 dB (re 20 mPA) below the peak intensity of the dominant frequency, which is the value at which the signal energy could still be clearly distinguished from the background noise. Our unit of statistical analysis was the mean obtained from 10–18 calls per individual. Unless otherwise noticed, the terminology and procedures for measuring call traits followed Cocroft and Ryan (1995).

The following description is based on 238 calls recorded from 23 males. The advertisement call of *Centrolene savagei* consists of 1–3 “peep” notes, each with amplitude and frequency modulation (Fig. 1). Notes last 16.65 ± 2.98 ms (mean \pm SD, range = 10–22 ms) and consecutive notes are separated by silent intervals of 348.77 ± 33.67 ms (302–442 ms). Mean call duration was 0.501 ± 0.26 s (0.018–1.057 s) and, as expected, call duration increases with the number of notes per call. All frogs at Yotoco and Filandia gave one-note or two-note calls, whereas frogs at Alto Bonito-Águila gave up to three-note calls. Call rate was 0.112 ± 0.03 calls/s (range = 0.061–0.198 calls/s). The dominant frequency of the call was 6.214 ± 0.334 kHz (range = 5.822–7.211 kHz), the low frequency was 4.867 ± 0.498 kHz (range = 4.082–5.800 kHz) and the high frequency was 6.768 ± 0.392 kHz (range = 6.211–7.246 kHz). Besides the frequency band with the highest energy (see above), we registered a harmonic band with a mean dominant frequency of 11.498 ± 0.909 kHz (range = 10.552–15.021 kHz). The maximum sound pressure level (re 20 μ Pa, sound level meter Roline RO-1350) of the advertisement call measured at 50 cm in front of two males in Yotoco reached 75.4 and 78.6 dB. A summary of call features per locality is given in Table 1.

TABLE 1. Summary of advertisement call features for frogs of *Centrolene savagei* recorded at three localities in Andes of Colombia: Yotoco (Cordillera Occidental), Filandia, and Alto Bonito-Águila (Cordillera Central). Data are mean values \pm standard deviation and range where pertinent. Male body size corresponds to snout-vent length.

Locality	Yotoco	Filandia	Alto Bonito-Águila
Sample size (number males recorded)	4	2	17
Number calls per male recorded	10.50 ± 1.29 (9–12)	9.50 ± 2.12 (8–11)	10.41 ± 4.09 (7–17)
Male body size (mm)	22.68 ± 1.47 (21.38–24.17)	22.47 ± 0.18 (22.34–22.59)	21.65 ± 1.06 (20.02–24.10)
Male Temperature (°C)	18.55 ± 0.77 (17.80–19.60)	17.00 ± 0.57 (16.6–17.4)	15.94 ± 0.85 (15.0–17.6)
Call duration (s)	0.07 ± 0.03 (0.02–0.09)	0.36 ± 0.01 (0.35–0.37)	0.62 ± 0.16 (0.43–1.06)
Number of notes/call	1.12 ± 0.10 (1–2)	1.82 ± 0.26 (1–2)	2.14 ± 0.38 (1–3)
Note duration (ms)	18.0 ± 0.8 (17.0–19.0)	19.0 ± 0.0	16.06 ± 3.25 (10.0–22.0)
Internote interval (ms)	329.67 ± 11.68 (317–340)	325.50 ± 12.02 (317–334)	354.88 ± 35.86 (302–442)
Low frequency (kHz)	5.60 ± 0.23 (5.33–5.80)	5.46 ± 0.07 (5.51–5.41)	4.62 ± 0.30 (4.08–5.41)
Dominant frequency (kHz)	6.23 ± 0.21 (5.99–6.46)	6.05 ± 0.10 (5.98–6.13)	6.23 ± 0.38 (5.82–7.21)
High frequency (kHz)	6.70 ± 0.28 (6.42–7.04)	6.42 ± 0.68 (6.37–6.47)	6.83 ± 0.42 (6.21–7.45)
Harmonic dominant frequency (kHz)	11.40 ± 0.92 (10.55–12.22)	11.62 ± 0.92 (11.55–11.68)	11.51 ± 0.99 (10.58–15.02)

Combining the available information (Table 1), we find the advertisement call of *C. savagei* to be clearly diagnosable from other species of *Centrolene* for which the advertisement call have been described. Considering the role of advertisement calls as mate-recognition signals, we would expect greater similarity among more closely related species (Gerhardt & Huber 2002; Hutter *et al.* 2013). Not surprisingly, the call of *Centrolene savagei* is similar to the call of its sister species, *Centrolene daidaleum*; internote intervals was the only call trait that differ between the two species (Cardozo-Urdaneta & Señaris 2012). This comparison should not be considered definitive because most of the acoustic parameters listed above vary with environmental temperature (Gerhardt & Huber 2002). Nevertheless, in our data there was not relationship between temperature and internote interval (Pearson correlation $r = -0.22$; $p = 0.317$).

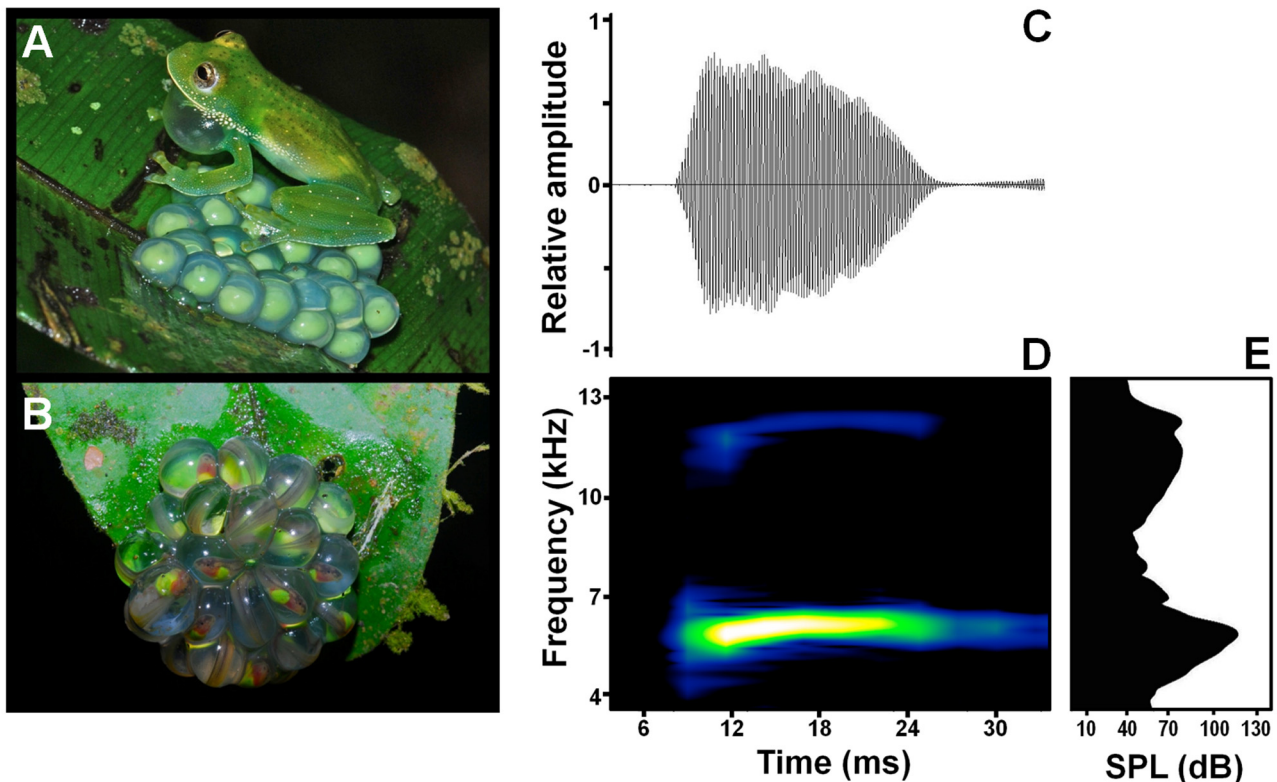


FIGURE 1. A: Calling male of *Centrolene savagei* with its putative egg clutch (eggs younger than 7 days); B: eggs older than 18 days age (not the same clutch than picture A); note the ontogenetic change in coloration of embryos inside egg capsules. Both pictures taken in Reserva Forestal Bosque de Yotoco, Cordillera Occidental, Colombia (Photo: F. Vargas-Salinas). C: Oscillogram; D: spectrogram; and E: power spectrum of one note advertisement call of *C. savagei*. Male body size = 22.59 mm, temperature of male calling = 16.6°C, Locality: Filandia, Central Andes of Colombia.

Remarkably, the advertisement call of *Centrolene savagei* contains most of its energy at higher frequencies than other *Centrolene* species (e.g. *C. ballux* Márquez *et al.* 1996; *C. buckleyi* Bolívar *et al.* 1999; *C. geckoideum* Grant *et al.* 1998; *C. hesperium* Cadle & McDiarmid 1990; *C. lynchi* Dautel *et al.* 2011). Differences in dominant frequency between species may reflect covariation between larynx size and body size (reviewed by Gerhardt & Huber 2002). The small body size of *C. savagei* relative to other *Centrolene* supports this hypothesis. These arguments can also apply at the intra-specific level (e.g. Ryan & Wilczynski 1991; Wilczynski & Ryan 1999); hence, variation in some call features between populations of *C. savagei* could be due to the small sample size in Yotoco and Filandia (Table 1) or factors mentioned above.

Tadpole description. In April 2008, we manually collected two clutches of *Centrolene savagei*, each consisting of 24 eggs and embryos in Gosner stages 17 and 18 (Gosner 1960). We placed each clutch separately in a 30 x 50 cm glass aquarium with 10 cm of water level. The clutches were found attached to the upper side of a leaf. To simulate natural conditions, we attached the leaf petioles to an aquarium lid using sticky tape. To avoid the growth of bacteria and fungi, we installed an underwater air-flow pump, and added 0.3 mL of anti-chlorine and 0.3 mL of methylene blue (Rada *et al.* 2007b). To further improve water quality and to provide hiding places for larvae, we added live *Elodea* plants, twigs, and gravel to each aquarium. Once all eggs hatched, we fed tadpoles once per day with commercial fish food (Pescarina commercial product).

Tadpoles were sacrificed and later fixed at various developmental stages (following Gosner 1960) in 10% buffered formaldehyde solution. Voucher specimens were deposited in the tadpole collection of the Museo de Herpetología Universidad de Antioquia (MHUA-L 0197), Medellín, Colombia. The nomenclature of the lateral line system followed Lannoo (1987). We recorded 22 morphological measurements with a Vernier caliper in millimeters, (accuracy ± 0.1 mm) under a Zeiss dissecting stereo-microscope), following the terminology used to describe the larval characters by Mijares-Urrutia (1998) and Altig and McDiarmid (1999:26; including interorbital distances and internarial distances): total length (TL), body length (BL), body width (BW), body height (BH),

internarial distance (IND), eye diameter (ED), interorbital distance (IOD), eye–snout distance (ESD), spiracle–snout distance (SSD), tail length (TAL), tail height (TH), maximum tail height (MTH), tail musculature height at MTH (TMH), tail muscle width (TMW), dorsal fin height (DFH), ventral fin height (VFH), oral disc width (ODW), width of upper jaw sheath (WUJS), lower jaw sheath (LJS), labial tooth row formula (LTRF), cloacal tube length (CTL), and tube transverse width (TTW). Reported measurements are in millimeters.

The following description and measurements belong to one individual in Gosner's developmental stage 39 (MHUA-L 0197–1), but the variation through development is based on the other 17 tadpoles (MHUA-L 0197) in stages 25–46 (Table 2). Body elongate and depressed (wider than high) in lateral view (Fig. 2A) and oval in dorsal view (Fig. 2B); TL: 33.1; BL: 9.8 (33.7% of TL); BW: 5.9; BH: 4.8. Chondrocranial elements are not visible. Snout truncate in dorsal view and rounded in lateral view. Neuromasts of the lateral line system are evident, mainly in the frontal body, infraorbital line, angular line, and middle-lateral line. Eyes in dorso-lateral position; ED: 1.1; IOD: 1.3; ESD 3.0; very small narial apertures, elliptical, dorsally directed; IND: 2.1; distance from nostril opening to anterior edge of eye 1.1. Short spiracle, single, sinistral, at the postero-lateral region of the body; spiracular aperture with postero-dorsal orientation, inner wall present as slight ridge (*sensu* McDiarmid & Altig 1999: 33), aperture diameter: 0.7; SSD: 8.0; spiracle located slightly below the body midline at 61.6% of BL. Vent tube short and medial, free posteriorly, opening directed posteriorly; CTL: 0.8, TTW: 0.4. Tail long: 23.3 (70.4% of TL). Myotomes are visible across the tail. Medial line straight and visible, separating the dorsal and ventral myotomes; TMW: 2.9; MTH: 3.6; TMH: 3.0; DFH: 1.3; VFH: 1.1. Dorsal fin begins at the tail-body joint, increasing in size at the middle of the tail, and gradually ending with a rounded tip. Ventral fin originates almost at the base of the tail muscle in the posterior body region, slightly arched, and reaching its maximum height throughout the distal two-thirds of the tail.

TABLE 2. Measurements (in mm; mean±standard deviation) of *Centrolene savagei* tadpoles. Sample size (N), see text for other acronyms.

Character	Stage 25	Stage 26	Stage 28, 29,30	Stage 39	Stage 43	Stage 45	Stage 46
N	2	1	11	1	1	1	1
TL	17.2±0.4	19.4	22.3±1.0	33.1	25.6	12.9	11.6
BL	4.9±0.1	5.4	7.2±0.4	9.8	11.0	11.5	11.6
BW	2.6±0.1	3.3	3.5±0.5	5.9	5.6	4.7	4.5
BH	2.3±0.0	2.4	3.3±0.2	4.8	4.9	4.2	4.3
IND	0.8±0.0	1.1	2.9±0.9	2.1	1.3	1.1	1.2
IOD	0.9±0.1	1.0	0.7±0.1	2.0	3.3	3.3	3.6
ESD	1.45±0.1	1.5	2.1±0.1	2.6	1.6	1.4	0.3
SSD	4.2±0.1	4.7	5.8±0.3	8	-	-	-
TAL	10.6±3.0	13.7	15.5±0.8	23.3	15.9	4.2	-
TH	2.4±0.1	2.7	2.9±0.4	3	2.5	-	-
TMH	1.2±0.1	1.7	2.4±0.2	3	2.5	-	-
ODW	1.4±0.1	1.4	1.6±0.1	3.0	2.0	2.1	3.0
CTL	0.1±0.8	0.5	0.5±0.1	0.5	-	-	-

Oral disc (Fig. 2D) directed antero-ventrally, medium-sized; ODW: 3.0 mm (50.8% BW), not-emarginated; 32 marginal and uni-serial papillae, large and blunt, distributed around the oral disc, longest mainly on the lower labium; five submarginal papillae present on each side of jaw sheath (one papilla with a diminutive tooth rows); marginal papillae interrupted dorso-medially in the anterior labium forming a wide gap. Upper jaw sheath completely keratinized with serrated edge, and with a pronounced arch in middle; WUJS including lateral processes: 1.2 (40.0% ODW); LJS: 0.98 (32.6% ODW). Lower jaw sheath keratinized, V-shaped and with serrated edge. Broad-based serrations, short, oriented straight medially (serrated on the lower jaw sheath more pronounced in the distal region); LTRF: 1(1)/2(2); tooth row A-1 interrupted medially located at the sides of upper jaw sheath

forming a wide gap, length of each side: 0.6; P-1 and P-2 about equal in length and reaching the outer of the disc; longitude of tooth row P-1: 2.1; longitude of tooth row P-2: 1.9. Morphological variation was observed in the oral disc of just one individual in stage 26 (Fig. 2E): oral disc with 46 marginal papillae, those present on the lower labium not as long as in stage 39, submarginal papillae absent; LTRF 2(1)/3, A2 widely interrupted in the middle; P3 a little shorter than P1 and P2.

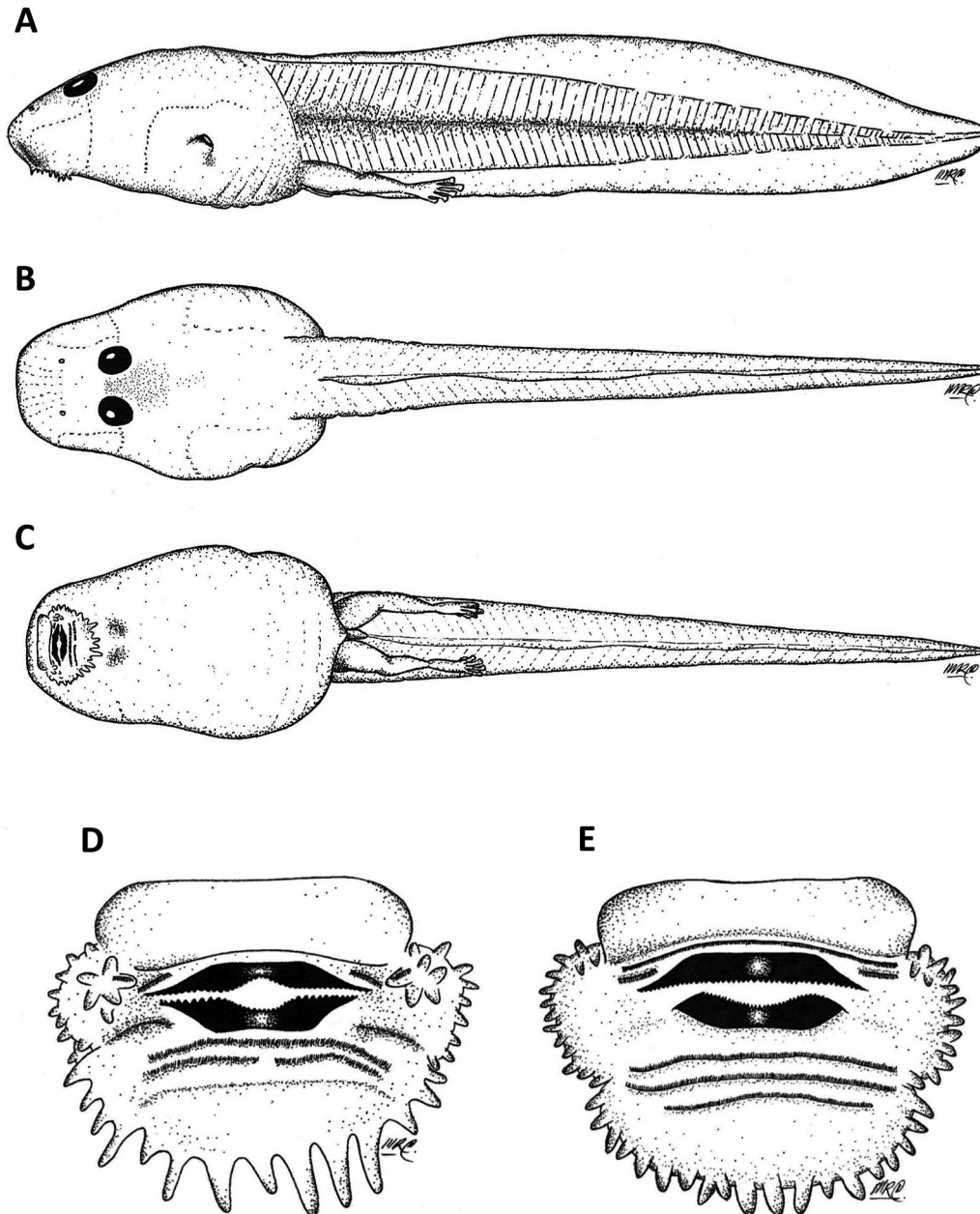


FIGURE 2. Lateral (A), dorsal (B) and ventral views (C) of the tadpole of *Centrolene savagei* at Gosner's stage 39 (MHUA-L 0197-1, total length = 33.1 mm); Oral disc at stage 39 (width = 1.4 mm; left) (D) and at stage 26 (width = 3.0 mm) (E). Illustration: M. Rivera-Correa.

In life, dorsum is cream with some aggregations of brown melanophores mainly in the inter-ocular area; distal area of body is translucent cream, eyes are dark with a cream ring around the pupil. Venter is translucent cream, intestine light green, liver brown, heart and other parts of the blood system are bright red; tail musculature is cream with a stripe of melanophores arranged longitudinally, tail fins are transparent with melanophores mainly in the distal area. For color pattern of embryos before hatching see Figure 1. In preserved specimens, dorsum is white to

pink with brown melanophores, venter whitish with melanophores on posterior part, white internal organs, except the heart region with black coloration; tail musculature white to pink and tail fins transparent with melanophores on posterior end.

As expected, the tadpoles of *Centrolene savagei* is most similar to that of its sister species *Centrolene daidaleum* (Guayasamin *et al.* 2008). Among the distinctive morphological attributes of *C. savagei* (present study) compared to *C. daidaleum* (Rada *et al.* 2007a), we found differences in (characters of *C. daidaleum* in parentheses): oral disc size (larger in *C. daidaleum*), V-shaped (versus U-shaped) lower jaw sheath, snout shape dorsally truncated (versus dorsally subacuminated), eyes in dorso-lateral (versus dorsal) position, and tooth row formulae 1[1]/2[2] or 2[1]/3 (versus 1/2, 2/1 and 2/2 in *C. daidaleum*).

We observed that the tooth rows are acquired during early stages of development (i.e. 25–28), and gradually lost in the late Gosner stages, a pattern also present in *Centrolene daidaleum* (Rada *et al.* 2007a). Thus, we found no evidence of gradual acquisition of tooth rows in intermediate stages as reported for other frog species that inhabit streams (Sánchez 2010). This might suggest that developmental timing of tooth rows could depend upon phylogenetic constraints rather than ecological conditions, but this requires further testing.

Call features and tadpole morphology can be valuable characters for delimitation of anuran species and can also aid in the study of their phylogenetic relationships (Duellman 2007; Schneider & Sinch 2007). Despite advances in understanding the phylogenetic relationships among glassfrogs (i.e. Guayasamin *et al.* 2008, 2009), many uncertainties persist regarding both phylogenetic affinities and species limits. To better understand these relationships, it is necessary to combine information from several lines of evidence (e.g. molecular data, calls, adult and tadpole morphology, and additional observations of the natural history). We hope the information provided here will help to clarify phylogenetic relationships and to motivate further studies on other species.

Acknowledgements

Financial and logistic support in Filandia was provided by the Corporación Autónoma Regional del Quindío (CRQ) and the Unidad Municipal de Asistencia Técnica Agropecuaria, UMATA; in Manizales was provided partially by the Vicerrectoría de Investigaciones y Postgrados Universidad de Caldas (grant VIP-0224208). Fieldwork in the Reserva Forestal Bosque de Yotoco was possible thanks to the Universidad Nacional de Colombia, campus Palmira, to the Corporación Autónoma Regional del Valle del Cauca (CVC), and entities and people associated to the CIRNY. We are grateful to Hernando Rodríguez Correa y Enrique Arbeláez Cortés, for field assistance in Filandia. For the loan of specimens or access to collections we are indebted to Juan Daza (MHUA) and John Lynch (ICN-MHN). JARM and SEL are deeply indebted to the residents of the Alto Bonito-Águila villages, especially to Gilberto Bermeo, for allowing us to work in the areas neighboring to their houses. Previous versions of the manuscript were improved by C.R. Hutter, H. Hoffman, S. Castroviejo-Fisher and an anonymous reviewer. FVS research is supported by Faculty of Natural Sciences of the Universidad de los Andes and COLCIENCIAS funds for doctoral formation in Colombia. MRC and PDAGC receive Ph.D. scholarship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, proc. 141238/2009-7) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, proc. 5725/10-0), respectively. JAV receive a graduate from the Consejo Nacional de Ciencia y Tecnología (CONACYT). For academic support during different stages of this project, MRC thanks Taran Grant.

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