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The Tadpoles of Two Atelopus Species (Anura: Bufonidae) from the Sierra Nevada de Santa Marta, Colombia, with Notes on their Ecology and Comments on the Morphology of Atelopus Larvae

José Luis Pérez-Gonzalez¹,², Marco Rada³, Fernando Vargas-Salinas⁴, Luis Alberto Rueda-Solano¹.5.*

Abstract. We describe for the first time the tadpole of two endemic harlequin frogs of the Sierra Nevada de Santa Marta, north of Colombia: Atelopus nahumae and A. laetissimus. In addition, we provide further morphological data for a third species, A. carrikeri. We also discuss some external morphological features for the tadpoles of these species and compare them with data currently available in the literature for the genus and with other larvae deposited in the amphibian collection of the Instituto de Ciencias Naturales of the National University of Colombia. The examined characters comprise eight morphometric variables and many traits of external morphology related with the oral apparatus, abdominal disc, fins, and dorsal color pattern. The tadpoles of A. nahumae and A. laetissimus are gastromyzophorous and morphologically similar, sharing a great number of features with their congeners. The tadpoles of A. nahumae, A. laetissimus, and A. carrikeri contrast morphometrically; total length and tail width are the morphometric traits that are useful to differentiate among them. They are also differentiated by the size of the abdominal sucker and spiracle. In A. carrikeri, the abdominal sucker is large relative to that of A. nahumae and A. laetissimus; the spiracle of A. laetissimus and A. carrikeri is not visible in ventral and dorsal view, whereas it is large and conspicuous in A. nahumae. The tadpoles of the species from Sierra Nevada de Santa Marta differ from most of their congeners found in the Cordillera Oriental and Central of Colombia by lacking a dark band on the fins and caudal musculature. We recorded abiotic factors of the microhabitat where tadpoles of A. nahumae were observed (temperature, dissolved oxygen, and water depth). Our results indicate that the probability of finding A. nahumae tadpoles depends on the depth of the stream.

Keywords. Atelopus carrikeri; A. laetissimus; A. nahumae; Gastromyzophorous; Larval features; Microhabitats; Ontogeny.

INTRODUCTION

Atelopus Duméril and Bibron, 1841 (commonly known as harlequin frogs) is one of the most threatened amphibian genera on the planet due to several non-exclusive factors, including infection by the pathogen fungi Batrachochytrium dendrobatidis, climate change, and habitat destruction (La Marca et al., 2005; Stuart et al., 2008;...
Species of this genus inhabit a wide variety of ecosystems ranging from Tropical rain forests at sea level to paramos at approximately 4800 m above sea level (asl) and are distributed from Costa Rica in Central America to Bolivia in South America (Gawor et al., 2012; Frost, 2018). During the breeding season, it is common to observe solitary or amplexed individuals alongside streams; at the time of oviposition, the females attach a string of eggs to submerged rocks and vegetation. Tadpoles are usually found on sandy substrates or attached to rocks in streams (Starrett, 1967; Löters, 1996; Karraker et al., 2006; Crump 2009). To date, 94 species of *Atelopus* are recognized, of which 46 are found in Colombia (Frost, 2018). However, although Colombia is inhabited by the greatest number of species of *Atelopus*, the tadpoles of only five Colombian species have been described or illustrated, including *A. subornatus* Werner, 1899 (Lynch, 1986; Enciso-Calle et al., 2017), *A. mittermeieri* Acosta-Galvis et al., 2006 (tadpole described and illustrated in the species description), *A. carrikeri* Ruthven, 1916 (Rueda-Solano et al., 2015), *A. spumarius* Cope, 1871 (Duellman and Lynch, 1969), and *A. ardila* Coloma et al., 2010 (Gómez Castillo, 1982, 1993).

Here, we describe the external morphology of tadpoles of *Atelopus nahumae* Ruiz-Carranza et al., 1994 and *A. laetissimus* Ruiz-Carranza et al., 1994. Both species inhabit forests between 1,500–2,800 m asl and are endemic to the Sierra Nevada of Santa Marta (SNSM), an isolated mountain range located in northern Colombia. We compared external morphological features of the tadpoles of *A. nahumae* and *A. laetissimus* with those of *A. carrikeri*, another species endemic to the SNSM but distributed at higher elevations (2,900–4,500 m asl; Rueda-Solano et al., 2015) and with larval descriptions available in the literature. In addition, the distribution of some characters/states related to dorsolateral color pattern and some oral disc structures are reported and discussed for the tadpoles described herein and for some undescribed *Atelopus* tadpoles deposited in the Instituto de Ciencias Naturales of the National University of Colombia in Bogotá. We explore diagnostic information useful to delimit *A. nahumae* and *A. laetissimus* species, which will serve as a basis for future comparative studies that seek to elucidate the diversity of morphological characters within *Atelopus*. Finally, we recorded microhabitat preferences of these two species.

**MATERIALS AND METHODS**

**Collection sites**

We collected tadpoles from four localities distributed across an elevational gradient in the SNSM (Fig. 1). Tadpoles of *Atelopus laetissimus* were collected from two localities: the Estación Experimental San Lorenzo, San Lorenzo stream, northwestern slope of the SNSM, 2,100 m asl (11°06′54.96″N, 74°03′03.46″W; WGS84), 11 April 2015, and in the Serranía de Cebolletas San Pedro de la Sierra, Pascual stream, western slope of the SNSM, 2,200 m asl (10°54′03.70″N, 73°55′04.50″W), 31 March 2016. Tadpoles of *A. nahumae* were collected on 12 April 2015, at the headwaters of the Gaira river, Serranía de San Lorenzo, northwestern slope of the SNSM, 1,560 m asl (11°10′02.0″N, 74°10′41.5″W). Tadpoles of *A. carrikeri* were collected in the Serranía de Cebolletas on the western slope of the SNSM, 3,500 m asl (10°54′03″N, 73°55′05″W).

![Figure 1](https://bioone.org/journals/South-American-Journal-of-Herpetology-15-2020-47-62/48)

**Figure 1.** Geographic location and images of the study areas at Sierra Nevada de Santa Marta, northern Colombia, South America. The *Atelopus* species in each of the four study areas are indicated on the map.
Field sampling, identifications, and comparisons

We performed visual encounter surveys along four streams in the Sierra Nevada de Santa Marta to record *Atelopus* larvae (Fig. 1). The collected tadpoles were euthanized in lidocaine, fixed and preserved in 10% formaldehyde, and deposited in the herpetological collection of the Universidad del Magdalena CBUMAG, Santa Marta, Colombia (*Atelopus laetissimus*: CBUMAG-ANF: 0963 and CBUMAG-ANF: 0971; *A. nahumae*: CBUMAG-ANF: 0961; *A. carrikeri* CBUMAG-ANF: 0892).


Tadpole identification was based on the presence of adults occurring on the same area or stream as larvae, so we also collected postmetamorphic juveniles and adults of *Atelopus laetissimus* (Fig. 2A–D) and *A. nahumae*

![Figure 2. Individuals of *Atelopus laetissimus*. (A) Tadpole, CBUMAG: ANF 0963, stage 28–30 (sensu Gosner, 1960), (B) froglet, (C) juvenile, and (D) adult male (not collected).](https://bioone.org/journals/South-American-Journal-of-Herpetology)
which allowed us to assign the tadpoles to the corresponding species on the basis of external morphology.

**Microhabitat**

We recorded microhabitat preferences of tadpoles of *Atelopus laetissimus* and *A. nahumae*, using the methodology proposed by Rueda-Solano et al. (2015), but with the following modifications: we selected four streams in the Serranía de San Lorenzo, Quebradas San Lorenzo, Betoma 1, Betoma 2, and Cascada Río Gaira (Fig. 1), separated from each other by more than 300 m; in each stream, we established a transect 50 m long by 2 m wide. We divided each transect into 100 quadrants of one 1 m² each and then sampled half of them. In each sampled quadrant, we determined presence/absence of tadpoles, depth of the water column, level of O₂ dissolved (mg/L), and water temperature with a multiparameter sensor (3420 set G WTM 2FD46G). Water temperature in San Lorenzo Creek was also monitored with a HOBO Pro V.2 data logger U23–004 from 2014–2016, including a season of extreme drought in 2015.

**Data analysis**

Photographs used to obtain the morphometric variables of tadpoles were processed using ImageJ (Schneider et al., 2012). Two discriminant analyzes were performed to establish which variables have the highest weight in differentiating the tadpoles of *Atelopus carrikeri, A. laetissimus*, and *A. nahumae*. The first analysis included all tadpoles; the second analysis included only the individuals in developmental stages ≥ 29. This latter analysis was performed to control for the possible effect of small and morphologically undifferentiated tadpoles. In both analyses, we standardized morphometric variables by dividing them by TL. To determine interspecific differences in body size at the end of metamorphosis (Stage 46) for *Atelopus laetissimus, A. nahumae*, and *A. carrikeri*, we performed an analysis of variance (ANOVA). Finally, to evaluate microhabitat preferences for *A. nahumae* and *A. laetissimus* (using tadpole presence/quadrant), a binary logistic regression was performed using the environmental parameters (water depth, O₂ dissolved, and water temperature) as the independent variables and the presence/absence of tadpoles as the dependent variable. All analyses were done using the statistical software IBM SPSS Statistics for Windows, Version 23.0. (IBM Corp, 2015).

**Figure 3.** Individuals of *Atelopus nahumae*. (A) Tadpole, CBUMAG: ANF 0961, stage 33–35 (sensu Gosner, 1960), (B) froglet, (C) juvenile, and (D) adult (not collected).
Table 1. Measurements (in mm) of the tadpoles of Atelopus carrikeri, A. laetissimus, and A. nahumae (X ± SD; range in parentheses). BL = body length; TAL = tail length; TL = total length; IND = internarial distance; IOD = interorbital distance; MTH = maximum tail height; TMH = maximum tail muscle height; TMW = tail muscle width. Individuals in stage 46 (sensu Gosner, 1960) not included.

<table>
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<tr>
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<th>Stage</th>
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<th>BL</th>
<th>TAL</th>
<th>TL</th>
<th>IND</th>
<th>IOD</th>
<th>MTH</th>
<th>TMH</th>
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<td>41</td>
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<td>42</td>
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<td>24.2 ± 2.7</td>
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A. laetissimus

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<th>IND</th>
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<th>MTH</th>
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A. nahumae

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<th>IND</th>
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<td>29–30</td>
<td>13</td>
<td>5.1 ± 0.3</td>
<td>8.4 ± 0.3</td>
<td>13.5 ± 0.5</td>
<td>0.9 ± 0.1</td>
<td>0.9 ± 0.1</td>
<td>2.1 ± 0.2</td>
<td>1.3 ± 0.2</td>
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<td></td>
<td>31–34</td>
<td>26</td>
<td>5.5 ± 0.5</td>
<td>9.1 ± 0.6</td>
<td>14.6 ± 1.0</td>
<td>1.0 ± 0.1</td>
<td>1.0 ± 0.1</td>
<td>2.5 ± 0.3</td>
<td>1.4 ± 0.2</td>
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<td></td>
<td>35–37</td>
<td>27</td>
<td>5.7 ± 0.5</td>
<td>9.8 ± 0.7</td>
<td>15.5 ± 1.0</td>
<td>1.1 ± 0.1</td>
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<td>39–45</td>
<td>5</td>
<td>7.2 ± 0.9</td>
<td>8.2 ± 4.8</td>
<td>15.3 ± 4.5</td>
<td>1.2 ± 0.2</td>
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<td>2.5 ± 0.1</td>
<td>1.7 ± 0.4</td>
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RESULTS

We collected 298 specimens, including 235 tadpoles and 63 froglets, divided among Atelopus carrikeri (n = 60), A. laetissimus (n = 105), and A. nahumae (n = 135). The tadpoles for the former two species represented 12 stages of development, while tadpoles of the latter species represented 17 developmental stages (Table 1, Appendix S2).

The tadpole of Atelopus laetissimus

The following description is based on three individuals in stage 35. Measurements (in mm) for Atelopus laetissimus are as follows (see also Appendix S2): TL = 23.9 ± 0.9; BL = 8.6 ± 0.5; TAL = 15.3 ± 0.4); IND = 1.8 ± 0.2; IOD = 1.7 ± 0.6; MTH = 3.7 ± 0.3; TMH = 2.4 ± 0.9; TMW = 2.0 ± 0.2. Body ovoid, elongate in dorsal view, depressed in lateral view; snout broadly rounded in dorsal view, rounded in lateral profile, chondrocranial elements not visible; eyes located dorsally; nostrils small, semicircular, with flat, non-protrusive margin, directed dorsolaterally, approximately equidistant between eyes and tip of snout. Spiracle small, single, sinistrally, 1/2 free, originating at midpoint of body, inconspicuous in dorsal and ventral views; opening of spiracle directed posterolaterally, diameter less than 1/2 of length of free tube. Vent tube short, medial; caudal musculature robust anteriorly, narrowing abruptly just posterior to midlength of tail. Dorsal and ventral fin originating on the tail, narrower than caudal musculature; tip of tail rounded. Mouth ventral, surrounded by well-developed labia forming complete oral disc; upper lip with bilateral anterior projections forming conspicuous M-shaped structure. Marginal papillae short, acuminate; one row of complete marginal papillae anteriorly; few submarginal papilla present, located on the medial and lateral regions of oral disc; posterior papillae absent. Labial tooth row formula 2/3, length of rows subequal. Upper jaw sheath strongly keratinized, arched; lower jaw sheath V-shaped. Both jaws slightly serrate. Abdominal sucker large, extending from posterior labium to midbody, forming complete, round structure (diameter 6.9 mm) with raised edge; abdominal sucker moderately extended (Fig. 4A–C).
In life, the tadpoles of *Atelopus laetissimus* (Fig. 2A) are almost uniformly black with very minute metallic blue or golden dorsal spots and a translucent to whitish border around the snout. In ventral view, the oral and sectorial discs are translucent. Tail musculature is cream with scattered black spots in dorsal and ventral view; some individuals have concentrated black spots in the dorsolateral area close to the body junction and towards the end of the tail in lateral view. The dorsal and ventral fins are translucent with very minute dark spots. Changes in coloration were observed during ontogenetic development: in early stages the individuals have uniform white coloration and the presence of light and dark bands interspersed with light brown or light green lines on the dorsum and limbs when the larva reaches stage 42 (Fig. 2B). The same color pattern was observed on forelimbs, once they had emerged in stage 43. In preservative, the color pattern is similar to that of living tadpoles, but it fades and loses its golden and blue/white iridescent tones. The tail musculature becomes light cream (Fig. 4A).

**Natural history**

Adult male *Atelopus laetissimus* were observed during the day and night when calling, perched on vegetation at the border of streams, at a height of 20–100 cm from the water surface. Amplexus is axillary, and the unpigmented eggs are deposited beneath stones and in leaf litter accumulated in the backwater areas of streams. The egg string and jelly capsules are not attached to the substrate. The string is indented and each capsule clearly differentiated. Empty capsules occur at various points along the string, similar to those reported in *A. subornatus* by Lynch (1986). Tadpoles of *A. laetissimus* were abundant in San Lorenzo Creek, and they exhibited nocturnal habits (JLP-G, pers. obs, April 2015). Tadpoles developed at an

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**Figure 4.** Tadpole of *Atelopus laetissimus* in stage 27 (sensu Gosner 1960). (A) Lateral, (B) dorsal, and (C) ventral views. CBUMAG: ANF 0963.
average water temperature of 14.22°C ± 1.04 (n = 4,527, range = 11–29°C) and hatch in stage 19. Postmetamorphs and juveniles were found on vegetation bordering the ravines at a height of 40–100 cm from the ground level, after 4–5 months.

**The tadpole of Atelopus nahumae**

This description is based on 14 individuals in stage 35 (Fig. 5A–C). Measurements (in mm) for *Atelopus nahumae* are as follows (see also Appendix S2): TL = 14.9 ± 0.8; BL = 5.6 ± 0.4; TAL = 9.8 ± 0.5; IND = 1.1 ± 0.1; IOD = 1.1 ± 0.2; MTH = 2.6 ± 0.2; TMH = 1.6 ± 0.2; TMW = 1.2 ± 0.1. Body ovoid, elongate in dorsal view, depressed in lateral view; snout broadly rounded in dorsal view, rounded in profile; chondrocranial elements not detectable; eyes located dorsally; nostrils, small semicircular, with a flat, non-protrusive margin, directed dorsolaterally, equidistant between eyes and tip of snout. Spiracle, small, single, sinistral, 1/3 free, originating at midpoint of body, visible in dorsal and ventral views; spiracle opening directed dorsoventrally, diameter less than 1/4 length of free tube. Vent tube short, medial; caudal musculature robust anteriorly, narrowing abruptly just posterior to midlength of tail, terminating just anterior to end of tail. Dorsal fin originating on body; ventral fin originating on tail. Both fins narrower than caudal musculature, tip of tail rounded. Mouth situated ventrally, surrounded by well-developed labia forming complete oral disc; upper lip with bilateral anterior projections forming conspicuous M-shaped structure. Marginal papillae short, acuminate; one row of marginal papillae anteriorly; submarginal papillae present. Labial row formula 2/3, length of rows subequal. Upper jaw partially keratinized, arch-shaped; lower jaw sheath V-shaped. Abdominal sucker small, extend-

![Figure 5. Tadpole of Atelopus nahumae in stage 35 (sensu Gosner 1960). (A) Lateral, (B) dorsal, and (C) ventral views. CBUMAG: ANF 0961.](https://bioone.org/journals/South-American-Journal-of-Herpetology)
ing from posterior labium to midbody, forming complete round structure (4.7 mm in diameter) with raised edge; abdominal sucker slightly extended.

In life, the body is black with a conspicuous metallic blue transverse band behind the eyes and two bluish blotches between the nostrils and the snout tip. The snout is translucent with very small dark spots, clearing gradually towards the tip. The tail is black with dark brown spots and the distal-most portion is translucent (Fig. 3A); in ventral view, the oral and suctorial discs are translucent. The ventral and dorsal fins are translucent with tiny dark spots. In lateral view, the tail musculature is cream with scattered, minute, dark spots. During ontogeny, the dorsum becomes dark brown with dark brown blotches and small cream spots. Also, the hindlimbs are yellowish in early and middle stages (30–39) and become light brown by stage 42. The same color pattern was observed on forelimbs, once they had emerged (Stage 43). In preservative, the color pattern is similar to that of living tadpoles but fades and loses the bluish and iridescent tones. The tail musculature becomes light cream (Fig. 5A).

**Figure 6.** Morphological measurements according to the developmental stage (sensu Gosner 1960) of tadpoles of *Atelopus carrikeri* (black dots), *A. laetisimus* (green dots), and *A. nahumae* (orange dots). Some dots overlap. Dots indicate mean values, error bars indicate standard deviation.
Natural history

Breeding activity of *Atelopus nahumae* was observed from April to November at the headwaters of Gaira River. Adult males were detected in both day and night on rocks or vegetation beside the streams, ca. 0–50 cm from the water. Amplexus was axillary and tadpole and juveniles were observed over the entire year. The tadpoles were attached to rocks at the margins of the medium-sized streams (ca. 3–4 m wide), where the water flow was weaker. Unlike *A. laetissimus*, juveniles of *A. nahumae* were found on the ground on litter and rocks accumulated at the river edges. Juveniles and adults were abundant (JLP-G, pers. obs, April 2015).

Comparison with other *Atelopus* tadpoles of SNSM

In *Atelopus nahumae*, the abdominal sucker is short relative to body length (7.6%), whereas in *A. laetissimus* it is moderate (12.2%) and in *A. carrikeri* it is long (25%). In *A. laetissimus* (Fig. 4A, C) and *A. carrikeri* (Rueda-Solano et al., 2015), the spiral is small and less visible in ventral and dorsal views than the large, conspicuous spiral of *A. nahumae* (Fig. 5A, C). In all the stages of development, the dorsal fins of *A. laetissimus* and *A. carrikeri* originate at base of the tail, whereas the dorsal fin of *A. nahumae* originates on the posterior part of the body. In life, the dorsal coloration of *A. laetissimus* is mostly black with minute metallic blue or golden dorsal spots (Fig. 2A); however, they have a translucent or slightly whitish border around the snout that is maintained throughout larval development. The tadpole of *A. nahumae* is also black, but they have metallic blue dots and one transverse band behind the eyes; they are usually more colorful than their congeners found at SNSM and the translucent snout border observed in *A. laetissimus* is less evident. Additionally, *A. nahumae* has white spots of variable size distributed on the body, accompanied by small golden blotches (Fig. 3A). The tadpole of *A. carrikeri* is also uniformly black or dark brown with golden dots in all the stages of development (Rueda-Solano et al., 2015).

Among these three *Atelopus* species, *A. carrikeri* had the longest BL, TAL, and, therefore, TL in all stages of development (Fig. 6). However, TL for all three species was different in stage 46 (n = 63; F = 15.852; df = 2; P < 0.001). TL in *A. carrikeri* (n = 7; 14.0 ± 2.3 mm) and *A. laetissimus* (n = 6; 14.6 ± 0.9 mm) was similar (HSD Tukey P < 0.801), while TL in *A. nahumae* (n = 50; 11.3 ± 1.6 mm) was shorter than *A. laetissimus* (HSD Tukey P < 0.001) and *A. carrikeri* (HSD Tukey P < 0.001). Tadpole measurements and comparative data of *Atelopus* species from the literature are shown in Tables 1 and 2, respectively.

The first discriminant analysis performed with morphometric measurements of the entire sample (i.e., including all developmental stages) showed differences between *Atelopus laetissimus*, *A. nahumae*, and *A. carrikeri* (Fig. 7A). This analysis correctly separated 85.9% of the tadpoles measured for the predicted groups. Function 1 accounted for 92.1% of the variance, with TL having the

![Figure 7](https://bioone.org/journals/South-American-Journal-of-Herpetology/files/55/7.png)
Table 2. Summary of external morphological characters scored in tadpoles of *Atelopus*. Species in **bold** are those with published descriptions and/or illustration occurring in Colombia. * = data inferred from the tadpole’s illustration but not stated in the description by the author (pending corroboration); ** = new information; *** = modification from the source.

<table>
<thead>
<tr>
<th>Species</th>
<th>Gosner stage</th>
<th>Labial tooth row formula</th>
<th>Submarginal papillae</th>
<th>Spiracle position</th>
<th>Vent tube</th>
<th>Dorsal fin origin</th>
<th>Dorsal color pattern (ETOH)</th>
<th>Caudal band</th>
<th>Reference</th>
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<td><em>Atelopus balios</em></td>
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<td>2/3</td>
<td>Absent*</td>
<td>2/3</td>
<td>Short</td>
<td>Tail***</td>
<td>Reticulated, black, and cream</td>
<td>Absent</td>
<td>Coloma and Lötters, 1996</td>
</tr>
<tr>
<td><em>Atelopus carbonerensis</em></td>
<td>34, 37, and 38</td>
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<td>Absent*</td>
<td>Posterior (62.5%)*</td>
<td>Short</td>
<td>Tail</td>
<td>Reticulated, black, and cream</td>
<td>Absent</td>
<td>Mijarres-Urrutia and La Marca, 2005</td>
</tr>
<tr>
<td><em>Atelopus carrikeri</em></td>
<td>25–38</td>
<td>2/3</td>
<td>Present**</td>
<td>Posterior</td>
<td>Short</td>
<td>Tail</td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Rueda-Solano et al., 2015</td>
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<td>25–38</td>
<td>2/0</td>
<td>3/6</td>
<td>3/7</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>–</td>
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<td>Absent*</td>
<td>3/5</td>
<td>Short</td>
<td>Tail</td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Mebs, 1980</td>
</tr>
<tr>
<td><em>Atelopus exigus</em></td>
<td>31</td>
<td>2/3</td>
<td>Absent*</td>
<td>Posterior</td>
<td>Short</td>
<td>Tail***</td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Coloma et al., 2000</td>
</tr>
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<td>2/3</td>
<td>Present</td>
<td>Posterior</td>
<td>Median</td>
<td>Tail***</td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Lescure, 1981</td>
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<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
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<td>Tail***</td>
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<td>Boistel et al., 2005</td>
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<td>–</td>
<td>Short</td>
<td>–</td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Gómez Castilo, 1982, 1993</td>
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<td>Absent</td>
<td>This study</td>
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<td><em>Atelopus miroboensis</em></td>
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<td>2/3</td>
<td>Absent*</td>
<td>Posterior</td>
<td>Short</td>
<td>Tail***</td>
<td>Uniformly pigmented, black</td>
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<td>Lötters, 2001</td>
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<td>2/3</td>
<td>Present**</td>
<td>Posterior*</td>
<td>–</td>
<td>Tail</td>
<td>Reticulated, black, and cream</td>
<td>Present</td>
<td>Acosta-Galvis et al., 2006</td>
</tr>
<tr>
<td><em>Atelopus mucuajensis</em></td>
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<td>Posterior (73%)*</td>
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<td></td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Mijarres-Urrutia and La Marca, 2005</td>
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<td><em>Atelopus nahumae</em></td>
<td>35</td>
<td>2/3</td>
<td>Present</td>
<td>Posterior</td>
<td>Short</td>
<td>Body</td>
<td>Reticulated, black, and cream</td>
<td>Absent</td>
<td>This study</td>
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<td>2/3</td>
<td>Absent*</td>
<td>Posterior</td>
<td>Short</td>
<td>Tail***</td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Coloma, 2002</td>
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<td>25–32</td>
<td>2/3**</td>
<td>Absent*</td>
<td>Posterior**</td>
<td>–</td>
<td>Tail**</td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Gray and Cannatella, 1985</td>
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<td>2/3</td>
<td>Absent*</td>
<td>3/5</td>
<td>Median</td>
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<td>Reticulated, black, and cream</td>
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<td>Posterior (60%)*</td>
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<td>Tail</td>
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<td>Absent*</td>
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<td>Median</td>
<td>Tail***</td>
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<td>Absent</td>
<td>Duellman and Lynch, 1969; Lötters et al., 2002</td>
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<td>Present**</td>
<td>Posterior**</td>
<td>–</td>
<td>Tail***</td>
<td>Reticulated, black, and cream</td>
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<td>Lynch, 1986</td>
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<td>2/3</td>
<td>Absent*</td>
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<td>Short</td>
<td>Tail***</td>
<td>Reticulated, black, and cream</td>
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<td>Lavilla et al., 1997</td>
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<td><em>Atelopus varius</em></td>
<td>2/3</td>
<td>2/3</td>
<td>Absent**</td>
<td>2/3</td>
<td>Short</td>
<td>Tail***</td>
<td>Reticulated, black, and cream</td>
<td>Absent</td>
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<td><em>Atelopus zeteki</em></td>
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<td>2/3</td>
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<td>Posterior Median*</td>
<td>Tail***</td>
<td></td>
<td>Uniformly pigmented, black</td>
<td>Absent</td>
<td>Lindquist and Hetherington, 1998</td>
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</table>
The Tadpoles of Two *Atelopus* Species (Anura: Bufonidae) from the Sierra Nevada de Santa Marta, Colombia, with Notes on their Ecology and Comments on the Morphology of *Atelopus* Larvae
José Luis Pérez-Gonzalez, Marco Rada, Fernando Vargas-Salinas, Luis Alberto Rueda-Solano

Table 3. Summary of microhabitat variables (n = 104) for tadpoles of *Atelopus nahumae* in streams of the Serranía San Lorenzo, Sierra Nevada de Santa Marta, Colombia. * = *A. nahumae* tadpoles present; † = *A. laetissimus* tadpoles present.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Variable</th>
<th>Mean</th>
<th>SD</th>
<th>CV</th>
<th>Range</th>
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<td>Quebrada San Lorenzo †</td>
<td>Water temperature</td>
<td>13.8</td>
<td>0.0</td>
<td>0.0</td>
<td>13.7–13.8</td>
</tr>
<tr>
<td></td>
<td>Dissolved O₂ (mg/L)</td>
<td>8.1</td>
<td>0.1</td>
<td>0.0</td>
<td>7.9–8.2</td>
</tr>
<tr>
<td></td>
<td>Water depth (cm)</td>
<td>17.6</td>
<td>9.2</td>
<td>0.5</td>
<td>3.9–37.3</td>
</tr>
<tr>
<td>Betoma 1 2,100 m asl</td>
<td>Water temperature</td>
<td>14.8</td>
<td>0.3</td>
<td>0.0</td>
<td>14.5–15.3</td>
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<tr>
<td></td>
<td>Dissolved O₂ (mg/L)</td>
<td>7.3</td>
<td>0.4</td>
<td>0.0</td>
<td>6.6–7.7</td>
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<td>Water depth (cm)</td>
<td>4.6</td>
<td>1.2</td>
<td>0.3</td>
<td>2.5–6.4</td>
</tr>
<tr>
<td>Betoma 2 2,100 m asl</td>
<td>Water temperature</td>
<td>14.3</td>
<td>0.1</td>
<td>0.0</td>
<td>14.2–14.5</td>
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<td>Dissolved O₂ (mg/L)</td>
<td>8.0</td>
<td>0.1</td>
<td>0.0</td>
<td>7.2–8.0</td>
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<td></td>
<td>Water depth (cm)</td>
<td>4.8</td>
<td>1.0</td>
<td>0.2</td>
<td>2.5–7.6</td>
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<tr>
<td>Cascada Rio Gaira † 1,560 m asl</td>
<td>Water temperature</td>
<td>16.8</td>
<td>0.2</td>
<td>0.0</td>
<td>16.4–17.5</td>
</tr>
<tr>
<td></td>
<td>Dissolved O₂ (mg/L)</td>
<td>8.2</td>
<td>0.1</td>
<td>0.0</td>
<td>8.1–8.4</td>
</tr>
<tr>
<td></td>
<td>Water depth (cm)</td>
<td>14.1</td>
<td>6.8</td>
<td>0.5</td>
<td>5.9–30.5</td>
</tr>
</tbody>
</table>

Microhabitat preference

The tadpoles of *Atelopus laetissimus* and *A. nahumae* were collected in medium-sized, fast-flowing streams (Table 3). For *A. nahumae*, the logistic regression model accounted for 50–78% of the probability of finding tadpoles (Cox and Snell $R^2 = 0.50$; Nagelkerke $R^2 = 0.781$; Fig. 8). Water depth best predicted the presence of tadpoles, with the greatest probability of detection at 10 cm depth ($n = 107$, Wald = 5.23, $P < 0.022$), but this probability varies among streams. Water temperature ($n = 107$, $\bar{X} = 16.8^\circ$C, Wald = 1.65, $P = 0.19$) and dissolved oxygen ($n = 107$, $\bar{X} = 8.2$ mg/L, Wald = 2.88, $P = 0.090$) had no predictive power (Table 3). Data were insufficient to perform this analysis for *A. laetissimus*.

DISCUSSION

Our study increases to seven the number of *Atelopus* species in Colombia with described tadpoles (Table 2). Generally, *Atelopus* tadpoles are quite similar. For example, some of the most distinctive features observed in these gastromyzophorous tadpoles are a depressed body, robust caudal musculature, low fins, and a ventral mouth surrounded by well-developed labia that form a large and complete abdominal sucker (Lötters, 1996, 2001; Altig and McDiarmid, 1999; see Table 2). Despite these similarities, several authors have suggested that certain morphological traits, such as the relative size of the abdominal sucker, the relative size of the tail, the presence of submarginal papillae, and, in particular, the dorsal color pattern, are useful in distinguishing among species (Duellman and Lynch, 1969; Ruiz-Carranza and Osorno-Muñoz, 1994; Ruiz-Carranza et al., 1994; Coloma and Lötters, 1996; Coloma et al., 2000; Boistel et al., 2005).

The dorsal color pattern of *Atelopus laetissimus*, *A. nahumae*, and *A. carrikeri* is constant throughout stages 25–42. The black dorsal color pattern with large white or bluish-white spots, bands, or blotches in the tadpoles of *A. nahumae* is also known for tadpoles of other species of *Atelopus*, such as *A. certus* Barbour, 1923, *A. carbonerensis* Rivero, 1974, *A. subornatus*, *A. mittermeieri*, and *A. soria-noi* La Marca, 1983 (Duellman and Lynch, 1969; Lynch, 1974). The black dorsal color pattern with large white or bluish-white spots, bands, or blotches in the tadpoles of *A. nahumae* in streams of the Serranía San Lorenzo, Sierra Nevada de Santa Marta, Colombia.
Tadpoles of mid-elevation species like *Atelopus laetissimus* and *A. subornatus* tend to be larger than their lowland counterparts (Lynch, 1986; Gascon, 1989; Lavilla et al., 1997; Acosta-Galvis et al., 2006). Similarly, the tadpoles of high-elevation species (e.g., *A. carrikeri* and *A. ardila*) are larger than those of low and middle elevations (see Rueda-Solano et al., 2015). Among phylogenetically related species distributed on an altitudinal gradient, those that inhabit higher altitudes are usually larger (Ashton, 2002). According to our results and reports on *A. flavescens*, *A. balios* Peters, 1973, and *A. carrikeri*, larval growth, measured as TL, ceases at stage 42 in *A. balios* (Coloma and Lötters, 1996) and stage 43 in *A. carrikeri*, *A. laetissimus*, *A. nahumae* (Rueda-Solano et al., 2015) and *A. flavescens* (Gawor et al., 2012). Size then gradually decreases, so that by stage 46 larval length reaches the minimum values (14.5 mm in *A. laetissimus* and 11.3 mm in *A. nahumae*). According to published records, the values of *A. laetissimus* are equivalent to those reported for *A. carrikeri* (14.0 mm; Rueda-Solano et al., 2015) and *A. zeteki* Dunn, 1933 (14.0 mm; Lindquist and Hetherington, 1998). These differences between species/stages might have a genetic basis, but they might also be affected by biotic or abiotic pressures, such as predators, food sources, or temperature changes that cause development to vary (Dahl et al., 2012).

Water depth had the greatest predictive power when the microhabitat preferences were evaluated in tadpoles of *Atelopus nahumae* (Fig. 8). This depth might be correlated with other factors like low speed of the current in which the tadpoles develop (Boistel et al., 2005). Likewise, a certain depth could increase the survival of tadpoles; however, this does not explain the absence of tadpoles in streams with similar depths (see Rueda-Solano et al., 2015). Alternatively, reproductive behavior could determine the presence/absence of the tadpoles (Rocha Usuga et al., 2017). Field observations suggest that *A. laetissimus*, *A. nahumae*, and *A. zeteki* (see Karraker, 2006; Rocha Usuga et al., 2017) use certain streams exclusively during the dry season for reproduction and oviposition. This behavior and the seasonality of the rain could determine the probability of detecting tadpoles of these species in the streams. In *A. balios*, *A. flavescens*, and *A. zeteki*, the variable that best predicts the presence of tadpoles is dissolved oxygen, because they require high oxygen concentrations for their development and survival (see Lescure, 1981; Coloma and Lötters, 1996; Lindquist and Hetherington, 1998). However, for *A. carrikeri* (Rueda-Solano et al., 2015) and *A. nahumae*, and perhaps *A. laetissimus* as well, dissolved oxygen has no predictive power to determine the presence of tadpoles in streams of the study area, because the concentration of dissolved oxygen in the water is always high and varies little.

The description of the tadpoles of *Atelopus laetissimus* and *A. nahumae* from the SNSM offers information
for the taxonomic delimitation of these two species, serves as a basis for future comparative studies that seek to elucidate the diversity of morphological characters within *Atelopus*, and enables knowledge about their ecology and reproductive behavior to be improved. To date, almost half of the known diversity of *Atelopus* (46 species) occurs in Colombia (Frost, 2018); however, the tadpoles of only seven species (including the present work) have been described or illustrated. Finally, in terms of future studies on *Atelopus* tadpoles, comparative revisions of internal morphology are needed; these studies would ideally include data on buccopharyngeal cavity structures, cranial muscles, and chondrocranium.

Figure 9. Presence of dark band on the fins and caudal musculature in *Atelopus subornatus* (arrow). (A) CZUT-A: 2256-4 in life, stage 36, (not to scale; photo: Marvin Anganoy Criollo); (B–C) ICN 31435, stage 31.
ACKNOWLEDGMENTS

This work is part of the project Atelopus: Monitoring harlequins frogs of the Sierra Nevada of Santa Marta, Colombia. We thank the Conservation Leadership Program for financial support. Thanks to John D. Lynch (ICN) for facilitating access to tadpole specimens under his care, and to Tarar Grant (USP) for his support and facilities during JLP’s stay at his laboratory. This research benefitted from discussions with Pedro H. Dias and Marvin Anganoy-Criollo and suggestion/corrections of Diego P. Cisneros-Heredia. Maria A. Pinto, Juan P. Ramírez, and Esteban Betancur clarified and shared valuable information about the dorsum color and catalogue numbers of some Atelopus species. Fieldwork was conducted in collaboration with Albertina P. Lima, William Magnusson, Teresa C.S. Avila-Pires, and Marinus Steven Hoogmoed, the students of the Herpetology group of the University of Magdalena (Los Progresos), Fundación Atelopus, and the administratores of the Sierra Nevada of Santa Marta Natural National Park (PNN, Caribbean territorial). María Camila Basto, Lilia Mejía, Lizeth Jiménez, and José Ángel Rincón provided technical support. Thanks to Molly Womack and Santiago Herrera, who reviewed or commented on early versions of the manuscript. Scholarship grant support to MAR was provided by Coordenación de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, PEC-PG) and PNPD programs (Proc. 2016.1.263.41.6). Fieldwork and other facilities of MAR were supported by a grant of FAPESP (Proc. 2012/10000-5 and Proc. 2008/50928-1). The collection of amphibians in Colombia was authorized by the Ministerio de Ambiente, Vivienda y Desarrollo Territorial of Colombia and Corporación Autónoma Regional del Magdalena (Resolución 0425 de 2015). This study was Jose Luis Pérez González’s undergraduate thesis directed by LARS (Beto Rueda).

REFERENCES


The Tadpoles of Two Atelopus Species (Anura: Bufonidae) from the Sierra Nevada de Santa Marta, Colombia, with Notes on their Ecology and Comments on the Morphology of Atelopus Larvae
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**Appendix S1.** Specimens examined for comparisons (tadpole lot).

**Appendix S2.** Morphological measurements (mm) and developmental stages (Gosner, 1960) for 60 tadpoles of *Atelopus carrikeri*, 103 of *A. laetissimus*, and 135 of *A. nahumae*, including larvae in stage 46.

**Appendix S3.** Species/specimens examined for occurrence of large dark band on the fins and caudal musculature.

**Appendix S4.** Species/specimens examined for the occurrence of submarginal papillae on the oral disc.