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Description of the tadpole of *Hyloxalus nexipus* (Anura: Dendrobatidae) with comments on geographic variation

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Poison frogs (Aromobatidae, Dendrobatidae) comprise a species-rich group of small Neotropical anurans. Over the last two decades, their systematics have been extensively studied (e.g. Grant et al. 2006, 2017). Especially, the colorful and toxic species have been the focus of studies (e.g. Brown et al. 2011, Guillory et al. 2020, Muell et al. 2022). The situation is different in the hyloxalines, a subfamily of the Dendrobatidae, especially in the genus *Hyloxalus* Jiménez de la Espada, 1870. This group is rich in both cryptic and morphologically distinct taxa (e.g. Grant et al. 2006, 2017) and many of them are highly threatened local endemics, making a better taxonomic understanding deeply needed (Guillory et al. 2019, IUCN 2023).

So far, some efforts have been made to disentangle *Hyloxalus* systematics using molecular markers. However, all share a yet incomplete sampling and the resulting topologies partially differ (e.g. Grant et al. 2006, 2017, Santos et al. 2009, Páez-Vacas et al. 2010, Anganoy-Criollo et al. 2022). More comprehensive approaches might not only aim for increased molecular sampling but also other data. In anurans, larval stages – commonly known as tadpoles – are morphologically and ecologically different to the adults (McDiarmid & Altig 1999). Hence, anuran larvae per se provide a large set of traits that can be informative in systematics in addition to the adults' characters (e.g. Haas 2003). Generally speaking, tadpole data have been neglected in many anurans (Candioti et al. 2023), but their value has been well demonstrated for instance in poison frogs of the genus *Ranitomeya* (Brown et al. 2011).

Of the approximately 80 known *Hyloxalus* species, larval stages have been reported from 27 taxa (Table 1). In this paper, we focus on the tadpole of *Hyloxalus nexipus* (Frost, 1986). This is one of the few, apparently conspicuously colored taxa (Fig. 1) allocated to the genus. It is a riparian species described from premontane forests in the Andean foothills of southern Amazonian Ecuador and adjacent Peru (Coloma 1995, Duellman 2004). Duellman (2004) provided a brief description of the tadpole of *H. nexipus* based on 12 specimens collected 14 km ESE Shapaja, Departamento San Martín, Peru (a series deposited at the Museum of Natural History at the University of Kansas, KU 215594). This material originates from the southern edge of the species' distributional range about 450 km airline from the Ecuadorian type locality (Los Tayos, Provincia Morona Santiago) (Frost 1986). We studied Ecuadorian material from Morona Santiago and captive-raised tadpoles from Peruvian parents collected in San Martín. We provide a detailed morphological description and examine variation over the geographic range of *H. nexipus*.

Methods: Specimens examined are deposited in CJ (Centro Jambatu de Investigación y Conservación de Anfibios, Quito) and QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito). A total of 17 specimens in stages 26–40 sensu Gosner (1960) were collected from the back of adult males and from small puddles near streams in the surroundings of Santiago de Méndez, Provincia Morona Santiago, Ecuador (at -2.744° S, -78.304° W: QCAZ 18499–18501 with 12 specimens; at -2.72364° S, -78.313° W: QCAZ 26280 and 26281 with 9 and 4 specimens, respectively), about 20 km from the type locality (Frost 1986). Specimens were fixed and preserved in 10% formalin. In addition, four captive-raised larvae in stages 27, 30, 35 and 36 from a research breeding colony at Trier University were fixed in 10% formalin and preserved in 50% ethanol (CJ 12363–12366). The parental stock originates from specimens collected along the Tarapoto-Yurimaguas road, NW of Pongo de Cainarachi. Founders were obtained via hobbyists in Germany. Tadpoles were raised in large planted aquaria at room temperature and fed ad libitum with spirulina powder and fish food, as described by Lötters et al. (2007).

Measurements were taken to the nearest 0.1 mm using a micrometer attached to a Leica MZ7s dissecting microscope for the QCAZ series and a scaled ocular attached to an Olympus SZ61 stereomicroscope for the CJ series. Where needed, the oral apparatus was stained with methylene blue for better visualization of oral disc structures. When more than one specimen was available per locality and per Gosner stage, measurements are given as mean ± SD in mm. In damaged specimens, morphometrics of impacted characters were excluded. Terminology of characters follows McDiarmid & Altig (1999). The description format follows Caldwell et al. (2002) and Caldwell & Lima (2003).

Taxonomic status of the Peruvian material studied with Ecuadorian *H. nexipus* populations was confirmed through mtDNA sequencing and ASAP, Assemble Species by Automatic Partitioning (Puillandre et al. 2021). For details see online supplementary data.

Morphology and morphometrics: The following description is based on a specimen in stage 28 from the surroundings of Santiago de Méndez, Provincia Morona Santiago, Ecuador (QCAZ 26280b) (Fig. 2). Type IV tadpole sensu Orton (1953). Larvae are assigned to the benthic ecomorphological guild as defined by Altig & Johnston (1989). Total length 21.5, body length 7.6 (35.3 % of total length). Body ovoid, longer than wide; body width at level of spiracle 5.1; body height posterior to eyes 3.6. Anterior margin of snout rounded with lateral oral papillae protruding anteriorly in dorsal view. Lateral-line system evident. Nostrils small, circular, protuberant, directed anterolaterally, opening 0.8 from tip of snout; internarial distance 1.6; distance from narial opening to anterior edge of eyes 0.7. Eyes situated dorsally, directed dorsolaterally, distance from anterior to posterior corner 1.2, from distal to proximal 0.4 in dorsal view; interorbital distance (measured between centers of pupils) 2.1. Spiracle sinistral, tube free, internal wall free; tube length 0.8, tube transverse width 0.8; spiracular opening directed posterodorsally; distance from tip of snout to spiracular opening 6.7. Vent tube free posteriorly, opening directed dextrally; tube length 1.0, tube transverse width 0.5. Tail length 13.9 (64.6 % of total length), height of upper fin at mid of tail 1.1, of lower fin at mid of tail 0.8; caudal musculature moderately robust, narrowing gradually until tail terminus; both upper and lower tail fins reach posterior end of body. Tail muscle width 1.6; tail muscle height 1.9; maximum tail height 2.5; dorsal fin height 0.4 and ventral fin height 0.5; upper fin starts slightly behind the juncture of caudal musculature and body; upper fin small with slight sigmoidal shape in anterior third, increasing in fin height only posteriorly; distal end of the tail rounded. Oral disc (Fig. 3) located ventrally, directed anteroventrally, emarginated on both sides; transverse width 2.0 (39.2 % of body width); oral disc surrounded by about 120 marginal papillae located distally and posteriorly; submarginal papillae absent; lengths of lateral papillae 0.4, width 0.2; length of ventral papillae 2.2, width 0.2; papillae gap on anterior region of the oral disc 3.6. Upper jaw sheath convex with a medial notch resulting in a W-shaped posterior rim; transverse width, including lateral processes 1.1 (55 % of oral disc width); lower jaw

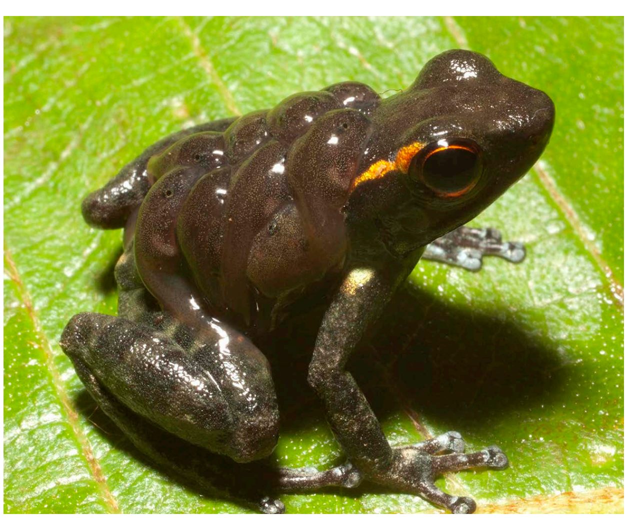

Figure 1. *Hyloxalus nexipus* male from Santiago de Méndez, Ecuador, carrying tadpoles. Photo: Luis A. Coloma.

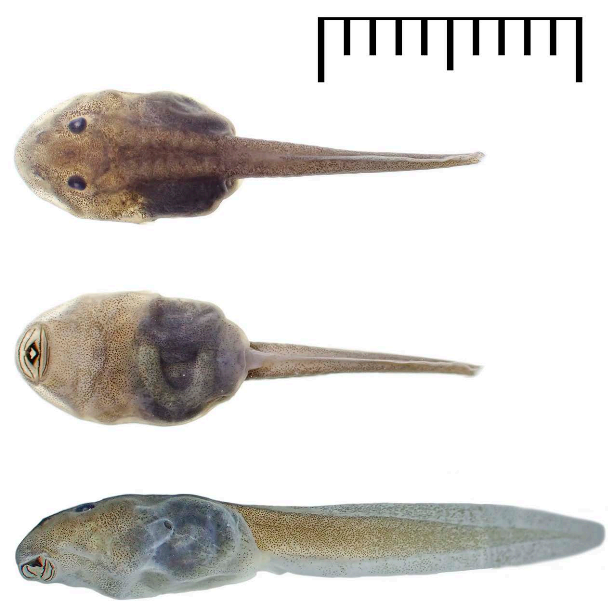

Figure 2. Tadpole of *Hyloxalus nexipus* (QCAZA 26280b) from Santiago de Méndez, Ecuador, in dorsal, ventral and lateral views. Broken tail tip attached in lateral view using Adobe Photoshop version 25.0; scale bar = 10 mm. Photos: AP.

Table 1. List of *Hyloxalus* species with described larval stages as an update to Anganoy-Criollo (2013). Descriptions based on one specimen only are indicated by as asterisk.

Species	Country	Collected from back of nurse frog	Free-swimming	Gosner stage(s)	Reference(s)
*H. anthracinus**	Ecuador		x	26	Coloma (1995)
*H. awa**	Ecuador		x	35	Coloma (1995)
H. azureiventris	Peru		x	37, 39, 40	Lötters et al. (2000)
*H. bocagei**	Ecuador	x		28	Páez-Vacas et al. (2010)
*H. chlorocraspedus**	Brazil		x	25	Caldwell (2005)
*H. craspedoceps**	Peru	x	x	34	Duellman (2004)
*H. delatorrae**	Ecuador	x		25	Coloma (1995)
H. edwardsi	Colombia		x	unknown	Lynch (1982)
H. elachyhistus	Ecuador, Peru	x	x	31–41	Edwards (1974), Duellman (2004)
H. eleutherodactylus	Peru	x		25	Duellman (2004)
H. exasperatus	Ecuador	x		23–25	Duellman & Lynch (1988)
H. fascianigrus	Colombia	x		25–26	Grant & Castro Herrera (1998)
*H. idiomelus**	Peru		x	34	Duellman (2004)
*H. infraguttatus**	Ecuador	x		24	Coloma (1995)
*H. insulatus**	Peru		x	34	Duellman (2004)
*H. italoi**	Ecuador		x	25	Páez-Vacas et al. (2010)
*H. leucophaeus**	Peru		x	28	Duellman (2004)
*H. maculosus**	Ecuador	x		28	Páez-Vacas et al. (2010)
H. nexipus	Ecuador, Peru	x	x	28, 37	Duellman (2004), this paper
*H. pulchellus**	Ecuador	x	x	25–26, 28–37	Edwards (1974), Coloma (1995)
*H. sauli**	Peru		x	25–26, 36	Edwards (1974), Duellman (2004)
*H. sordidatus**	Peru		x	25	Duellman (2004)
H. subpunctatus	Colombia	x	x	25–41	Stebbins & Hendrickson (1959), Anganoy-Criollo (2013)
*H. sylvaticus**	Peru		x	33	Duellman (2004)
*H. toachi**	Ecuador	x		25	Coloma (1995)
*H. vertebralis**	Ecuador	x		25	Coloma (1995)
*H. yasuni**	Ecuador		x	27	Páez-Vacas et al. (2010)

sheath V-shaped, 0.9 (45 % of oral disc width); both upper and lower jaw sheaths with serrated edges; serrations present over the entire length of sheaths; serration of the upper jaw becoming smaller towards corners. Labial tooth row formula 2(2)/3; only A-2 possesses a natural gap, P-3 possesses gaps on the right half caused by labial tooth losses. Length of A-1 1.8; number of teeth 167; length of A-2 1.7 (including medial gap at the level of upper jaw sheath), with 61 teeth right and 73 left; length of P-1 2.0; 72 teeth; length of P-2 1.9 with 146 teeth; length of P-3 1.7 with 123 teeth.

Coloration: In preservative (Fig. 2), dorsum and sides of body uniformly brown; ventrally, scattered brown spots present, becoming scarcer anteriorly; the gut is visible through the ventral skin in posterior half of the body; laterally, spiracle unpigmented; tail musculature whitish with brown spots; both dorsal and ventral fins translucent; dots extend uniformly in both dorsal and ventral fins. Oral disc and papillae translucent in ventral view. Brown spots on developing posterior legs. Live coloration unknown.

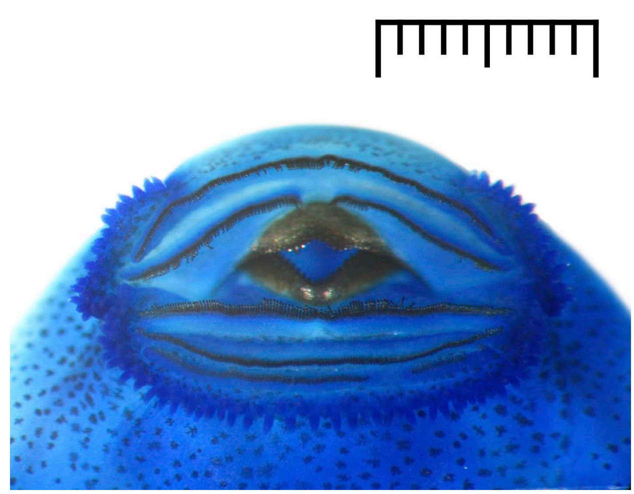

Figure 3. Mouthparts of the tadpole of *Hyloxalus nexipus* (QCAZA 26280b, specimen stained with methylene blue for better visualization); scale bar = 1 mm. Photo: SEL.

Table 2. Mean (for > 2 specimens) and range of measurements (mm) of *Hyloxalus nexipus* tadpoles from Ecuador (QCAZ series, excluding 26281a, c and d and four specimens from 18501 series which were decomposed by 2023 when reexamining the material) and Peru (CJ series). For definitions of measurements see references in text, abbreviations as follows. TL = total length, BL = body length, BH = body height, BW = body width, TAL = tail length, TH = tail height at mid of tail, UF = height of upper fin at mid of tail, LF = height of lower fin at mid of tail, IN= internarial distance, SND = apex of snout nostril distance, END = eye nostril distance, IOD = interorbital distance, ED = eye diameter, ODW = transverse oral disc width, SW = spiraculum width, SL = spiraculum length. Damaged characters indicated by an asterisk.

Stage	Series	TL	BL	BH	BW	TAL	TH	UF	LF
25	QCAZ 26280i, 18501 (1 specimen)	5.1–5.6	3.6–3.8	3.3–4.0	2.1–2.6	1.8	1.0	0.6	0.4
26	QCAZ 26280g,h	13.7–13.8	5.0–5.2	2.2–2.4	3.2–3.3	2.2–2.4	3.0–3.2	0.6	0.4–0.5
27	QCAZ 18500c; 26280f; 26281b	16.1 (15.8–16.5)	5.5 (5.3–5.7)	2.6 (2.4–2.7)	4.0	10.0 (9.7–10.2)	2.7	0.8 (0.7–0.9)	0.7 (0.6–0.8)
28	QCAZ 18499a; 26280b	21.5–21.7	7.6	3.6	5.0–5.3	13.8–14.0	1.6–3.5	1.1–1.3	0.8–1.2
29	QCAZ 18501 (1 specimen)	21.3	9.1	4.2	5.9	12.3	4.7	*	*
30	QCAZ 18500b	20.8	8.4	3.9	5.7	12.4	4.6	1.1	1.0
36	QCAZ 26280a	23.5	8.9	3.8	6.1	14.6	3.9	1.2	1.1
39	QCAZ 26280c,e; 18500a; 18499b	26.6 (26.0–27.3)	9.6 (9.3–10.0)	4.7 (4.6–4.8)	6.5 (6.3–6.8)	17.1 (17.0–17.3)	5.0 (5.0–5.1)	1.3 (1.1–1.6)	1.0
40	QCAZ 26280d; 18501(1 specimen)	24.5–25.1	8.3–9.1	3.6–4.0	5.3–5.6	15.1–16.0	3.6–4.0	1.1	0.9
27	CJ 12363	14.9	5.5	2.5	3.2	9.4	2.2	0.7	0.5
30	CJ 12364	23.7	87.4	4.3	5.0	15.3	3.3	1.0	0.8
35	CJ 12365	31.6	11.5	6.0	6.9	20.1	4.7	1.4	1.2
36	CJ 12366	29.9	11.2	5.2	6.7	18.7	4.2	1.3	1.0

Stage	Series	IN	SND	END	IOD	ED	ODW	SW	SL
25	QCAZ 26280i, 18501 (1 specimen)	0.3–0.4	1.1–1.2	0.8	1.6	1.5	1.6	0.7	0.7–0.8
26	QCAZ 26280g,h	1.1–1.2	0.9	0.5–0.6	0.7–0.8	0.4	*	0.4–0.5	0.7
27	QCAZ 18500c; 26280f; 26281b	1.2	0.5 (0.4–0.5)	0.4	1.7	0.6 (0.5–0.6)	1.8 (1.7–1.9)	0.5	0.8 (0.7–0.8)
28	QCAZ 18499a; 26280b	1.9–2.0	0.7–1.0	0.6–0.9	2.2–2.3	0.6–0.7	1.8–2.1	0.7–0.8	0.7–1.0
29	QCAZ 18501 (1 specimen)	0.9	2.1	1.0	0.8	1.0	2.6	1.1	1.4
30	QCAZ 18500b	1.8	1.1	1	2.0	0.8	2.4	1.2	1
36	QCAZ 26280a	1.8	0.9	0.6	2.6	0.7	2.3	0.9	1.0
39	QCAZ 26280c,e; 18500a; 18499b	2.0 (2.0–2.1)	1.0 (0.9–1.0)	1.0	3.6 (3.4–4.0)	1.1	2.7	1.1 (1.0–1.2)	0.7 (0.4–1.1)
40	QCAZ 26280d; 18501(1 specimen)	1.7–1.9	0.8–1.0	0.6–0.6	2.5–2.6	0.8–1.0	2.1–2.2	0.7–0.8	0.7–1.2
27	CJ 12363	1.0	0.5	0.8	1.7	0.5	1.7	0.3	0.8
30	CJ 12364	1.6	1.1	1.2	2.6	0.8	2.4	0.6	1.0
35	CJ 12365	2.2	1.2	1.8	3.3	1.1	3.2	0.8	1.3
36	CJ 12366	2.0	1.2	1.8	3.3	1.1	2.9	0.8	1.5

Variation: Generally, all specimens from Ecuador and those raised from Peruvian founders resemble the description provided above, except for stage-dependent differences and measurements, provided in Table 2.

Specimens from Peru are grey instead of brown in preservative and have the posterior half of the venter darker, which might be an artefact of preservation or captive conditions (Fig. 4). Number of papillae varies slightly between all specimens. In Peruvian specimens, the lateral line system is mostly inconspicuous. Our examined material further corresponds to the short account provided by Duellman (2004). However, they differ in preservative coloration (dark reddish brown, individuals in stage 41 with larger bluish-white lichenous flecks) and in labial tooth row formula (2(1)/3). We consider the formula provided by Duellman (2004) to be in error, however.

Captive raised tadpoles from Peru (CJ 12363–12366) in life were colored as follows: Dorsum and flanks brownish black to greyish black. Flanks and to a lesser extent dorsum covered with minute whitish to brownish golden dots. Spiraculum translucent. Nostrils whitish. Whitish halo running ventrally from anterior to posterior corner of eye. Ventrally, posterior half of body dark brown. Anterior portion lighter, partially brownish white to translucent with dark brown irregular markings. Mouthparts whitish translucent, tooth rows black. Vent tube translucent. Caudal musculature whitish cream with dense minute brownish to blackish dots, becoming scarcer towards distal end. Hind limbs dorsally colored as caudal musculature, ventrally whitish cream. Tail fins translucent with minute brownish black dots most densely on anterior part of upper fin. As derived from a photography from Ecuador (Fig. 1), dorsal and lateral coloration resembles the description of captive-raised tadpoles but presents more dense spotting on the dorsal surface. However, these specimens lack the whitish halo below the eye.

Remarks: As noted by Anganoy-Criollo (2013), there is considerable ontogenetic variation, as apparently tadpoles on the back of nurse frogs grow and begin to develop keratinized jaw sheaths and labial teeth (cf. Duellman 2004). Comparisons with free-swimming stages may be less informative when trying to distinguish taxa. The 14 species in which free-swimming larvae are described agree in overall morphology with moderately depressed body, rounded snout in lateral and dorsal views, nostril about mid-way between eyes and snout tip, eyes and nostrils on dorsum directed dorsolaterally, spiracle sinistral, vent tube short, caudal musculature moderately robust, fins low and often equal in height, oral disc emarginated without papillae on anterior lip, labial tooth row formula 2(2)/3 with A-2 gap among other characters (Anganoy-Criollo 2013). Differences are noted in the upper jaw sheath with most *Hyloxalus* species having a notch in the middle upper jaw sheath, absent only in *H. azureiventris, H. chlorocraspedus* and *H. sylvaticus* (Anganoy-Criollo 2013). *Hyloxalus nexipus* is among the species with a notch in the middle upper jaw sheath (Fig. 3). In lateral view, the upper fin in *H. nexipus* emerges only slightly behind the beginning of the caudal musculature increasing in fin height only further posteriorly (Figs. 2, 4), different to most other congenerics, in which the upper fin is well visible already at the tail-body junction (e.g. Coloma 1995: 11, Duellman 2004: 18, Anganoy-Criollo 2013: 215). However, detailed information is often available for single specimens in different developmental stages (Table 1), hampering intra- and interspecific comparisons.

Figure 4. Captive raised tadpole of *Hyloxalus nexipus* (CJ 12366) from a population from San Martín, Peru, in dorsal, lateral and ventral views; scale bar = 10 mm. Photos: Steven Guevara, Centro Jambatu de Investigación y Conservación de Anfibios.

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Supplementary data

The following data are available online:

Supplementary document 1. Detailed methods and results of mtDNA sequencing and Assemble Species by Automatic Partitioning.