Phyllomedusa 16(2):155–182, 2017

ISSN 1519-1397 (print) / ISSN 2316-9079 (online)
doi: http://dx.doi.org/10.11606/issn.2316-9079.v16i2p155-182

Redescription of the tadpoles of *Epipedobates narinensis* and *E. boulengeri* (Anura: Dendrobatidae)

Marvin Anganoy-Criollo[1,2] and Belisario Cepeda-Quilindo[1,3]

[1] Grupo de Cladística Profunda y Biogeografía Histórica, Laboratorio de Anfibios, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, A. A. 7495, Bogotá D.C., Colombia. E-mail: marvinanganoy@gmail.com.

[2] Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, 05508-090, São Paulo, SP, Brazil.

[3] Grupo Biología de Páramos y Ecosistemas Andinos, Departamento de Biología, Universidad de Nariño, Pasto, Nariño, Colombia.

Abstract

Redescription of the tadpoles of *Epipedobates narinensis* and *E. boulengeri* (Anura: Dendrobatidae). The larval morphology of poison frogs (Dendrobatoidea) has contributed to an understanding of the phylogenetic relationships within the superfamily. Nevertheless, our knowledge of larval morphology is incomplete. The larvae of the dendrobatids, *Epipedobates narinensis* and *E. boulengeri* are redescribed, diagnosed, and differentiated from three congeners, as well as sympatric dendrobatoids and closely related genera. Three larval developmental phases are described—viz., (1) back-riding tadpoles, (2) free-swimming tadpoles, and (3) metamorphosing tadpoles. Each larval phase is characterized by ontogenetic changes in external morphology, and there is also morphological variation within each developmental phase. Ontogenetic morphological changes are the most marked in back-riding and metamorphosing phases. The external features of free-swimming tadpoles do not change abruptly, but ontogenetic changes occur in the marginal papillae, stitches of the lateral line system, and tail coloration. Four features that have not been considered previously distinguish species-groups and/or genera—moderate A-2 gap; presence of shelf on back of the upper jaw sheath [UJS]; moderate notch on mid-UJS; and nostril size; these characters are putative synapomorphies of *Epipedobates.* Metamorphosing tadpoles have some adult features, such as the color pattern on the hind limbs and basal toe webbing, which facilitate identification of species.

Keywords: A-2 gap size, anteroventral coloration, Colostethinae, larval characters, nostril, ontogenetic variation.

Received 16 March 2017
Accepted 10 October 2017
Distributed December 2017

Resumen

Redescripción de los renacuajos de *Epipedobates narinensis* y *E. boulengeri* (Anura: Dendrobatidae). La morfología larvaria de las ranas venenosas (Dendrobatoidea) ha contribuido en el entendimiento de las relaciones de parentesco dentro de la superfamilia. No obstante, nuestro conocimiento de la morfología larvaria permanece incompleto. Por esta razón, en el presente trabajo se redescriben, diagnostican y se diferencian los renacuajos de *Epipedobates narinensis* y *E. boulengeri* desde sus congéneres, de otras especies simpátricas de Dendrobatoidea y de los géneros cercanos. Se describen tres fases larvarias—viz., (1) renacuajos de espalda, (2) renacuajos nadadores-libres y (3) renacuajos que inician la metamorfosis. Cada fase es caracterizada por cambios ontogenéticos en la morfología externa y también hay variación dentro de cada fase larvaria. Las características de los renacuajos de espalda y de los que están iniciando la metamorfosis son más afectadas por la variación ontogenética, a diferencia de la morfología de los renacuajos nadadores-libres que no cambia abruptamente, excepto por los cambios ontogenéticos en las papilas marginales, en las ranuras del sistema de líneas laterales, y en la coloración de la cola. Cuatro caracteres no habían sido considerados previamente para distinguir grupos de especies y/o géneros—brecha moderada en A-2, presencia de repisa sobre la parte interna del UJS, muesca moderada sobre la mitad del UJS y tamaño de la narina; estos caracteres son considerados como sinapomorfias putativas de *Epipedobates.* Los renacuajos que inician la metamorfosis presentan algunas características de adultos, tales como el patrón de coloración sobre los miembros posteriores y una membrana pedial basal que facilitan la identificación de especies.

Palabras clave: caracteres larvarios, coloración anteroventral, Colostethinae, narina, variación ontogenética, tamaño de la brecha en A-2.

Resumo

Redescrição dos girinos de *Epipedobates narinensis* e *E. boulengeri* (Anura: Dendrobatidae). A morfologia larvária dos sapos venenosos (Dendrobatoidea) tem contribuído para o entendimento das relações filogenéticas dentro da superfamília. Contudo, nosso conhecimento da morfologia larvária é incompleto. Os girinos dos dendrobatídeos *Epipedobates narinensis* e *E. boulengeri* são redescritos, diagnosticados e distinguidos dos girinos de três congêneres, bem como de outras espécies simpátricas de Dendrobatoidea e de gêneros intimamente aparentados. Descrevemos três fases larvárias—viz., (1) girinos transportados no dorso de adultos, (2) girinos livre-natantes e (3) girinos em processo de metamorfose. Cada fase é caracterizada por mudanças ontogenéticas na morfología externa, havendo também variação dentro de cada fase de desenvolvimento. Mudanças morfológicas ontogenéticas são mais marcantes nos girinos transportados no dorso e nos girinos em processo de metamorfose. As características externas dos girinos transportados no dorso não mudam abruptamente, mas ocorrem mudanças ontogenéticas nas papilas marginais, nos poros do sistema da linha lateral e na coloração da cauda. Quatro caracteres que não haviam sido considerados previamente distinguem grupos de espécies e/ou gêneros—fenda moderada em A-2, presença de projeção atrás da bainha da maxila superior (UJS), entalhe moderado na metade de UJS e tamanho da narina; esses caracteres são considerados como sinapomorfias putativas de *Epipedobates.* Os girinos em processo de metamorfose apresentam algumas características dos adultos, como o padrão de coloração dos membros posteriores e membranas interdigitais na base dos dedos dos pés, que facilitam a identificação de espécies.

Palavras-chave: caracteres larvários, coloração anteroventral, Colostethinae, narina, variação ontogenética, tamanho da fenda em A-2.

Introduction

Epipedobates Myers, 1987 included most of Silverstone's (1976) species of *Phyllobates* Bibron, 1840 with the exception of the *P. bicolor* Group (or *Phyllobates* sensu stricto of Myers *et al.* 1978). This genus grouped cis- and trans-Andean of then-*Phyllobates* species. Based on the total evidence analysis, Grant *et al.* (2006) redefined *Epipedobates* to include only Silverstone's (1976) *P. femoralis* Group and exclude *P. femoralis* (Boulenger, 1884) and *P. zaparo* (Silverstone, 1976); the latter two species were placed in *Allobates* Zimmerman and Zimmerman, 1988. *Epipedobates* sensu Grant *et al.* (2006, 2017) is a trans-Andean taxon distributed through the Pacific lowlands and foothills of the western Andes of Colombia, Ecuador, northern Peru, and one isolated species of doubtful provenance from western Panama (Myers 1982, Jungfer 2017). Currently, the genus includes eight species: *E. anthonyi* (Noble, 1921), *E. boulengeri* (Barbour, 1909), *E. darwinwallacei* Cisneros-Heredia and Yánez-Muñoz, 2011, *E. espinosai* (Funkhouser, 1956), *E. machalilla* (Coloma, 1995), *E. maculatus* (Peters, 1873), *E. narinensis* Mueses-Cisneros, Cepeda-Quilindo and Moreno-Quintero, 2008, and *E. tricolor* (Boulenger, 1899), two of which occur in Colombia (*E. boulengeri* and *E. narinensis*; Silverstone 1976, Mueses-Cisneros *et al.* 2008).

The morphology of dendrobatoid (i.e., aromobatid and dendrobatid) tadpoles has been crucial to our understanding of the relationships of members of this superfamily. One of the first relevant contributions was that of Savage (1968) who used some larval characters to diagnose three groups of poison frogs—viz., *Colostethus* Cope, 1866, *Dendrobates* Wagler, 1830, and *Phyllobates*. Silverstone (1975, 1976) distinguished genera and species groups (e.g., *Dendrobates histrionicus* and *Phyllobates bicolor* species groups) on the basis of larval characters. Myers (1987) employed skin-alkaloid data and larval characters to diagnose *Epipedobates* and *Minyobates,* and Haas (1995, 2003) identified synapomorphies for *Dendrobates* and Dendrobatidae based on larval anatomy. In a total evidence analysis, Grant *et al.* (2006) identified unambiguous, optimized larval synapomorphies of *Silverstoneia* Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler, 2006 (presence of umbelliform larval mouth) and *Oophaga* Bauer, 1994 (numbers of anterior and posterior tooth keratodonts, and the papillae size). Sánchez (2013) described new larval external characters (e.g., upper jaw sheath shape, ornamentation on nostril and gut disposition) and explored their distributions in dendrobatoid phylogeny.

Despite these and other contributions (e.g., Dunn 1931, Caldwell *et al.* 2002, Castillo-Trenn 2004, Poelman *et al.* 2010, Anganoy-Criollo 2013), the knowledge of larval morphology of poison frogs (Dendrobatoidea) is far from being satisfactorily complete and understood because the few available descriptions are usually short and very general (*i.e.*, only include common and shared features of Dendrobatoidea tadpoles and lack important details), some are based only on back-riding tadpoles, others on single free-swimming larva, and others use free-swimming tadpoles of uncertain identification.

The tadpoles of five species of *Epipedobates* have been described (*E. anthonyi, E. boulengeri, E. espinosai, E. machalilla,* and *E. narinensis;* Table 1)—each of which has back-riding tadpoles; the morphological variation of free-swimming tadpoles is undescribed. Moreover, the descriptions neither provide larval characters to distinguish the species nor diagnose *Epipedobates.* Herein, we describe the external morphology of the free-swimming tadpoles of *Epipedobates narinensis* and *E. boulengeri,* providing characters to distinguish these species from their congeners, as well as other sympatric dendrobatoids that inhabit Colombian and Ecuadorian Pacific lowlands.

Table 1. Common larval features of back-riding tadpoles of *Epipedobates*. Abbreviations and symbols: (A-1 and A-2) first and second anterior tooth rows, (A-2 gap) medial gap in A-2, (AL gap) anterior lip gap, (BL) body length, (BW) body width, (Dfin) dorsal fin, (END) eye–nostril distance, (Eye) eye diameter, (IND) internostril distance, (IOD) interorbital distance, (LJW) lower jaw sheath width, (LTRF) labial tooth row formula, (*N*) number of tadpoles, (ODW) oral disc width, (P-1 and P-2) first and second posterior tooth rows, (SND) snout–nostril distance, (TAL) tail length, (TL) total length, (TMW) tail muscle width, (TMH) tail muscle height, (UJW) upper jaw sheath width, (Vfin) ventral fin, (VT) vent tube length, (?) undetermined or not specified in the literature, (+) only three tadpoles preserved of 8–12 tadpoles carried by the adult (Silverstone 1976), (*) only one tadpole described from a lot of two tadpoles, (**) one tadpole from 15 larvae, (β) Coloma (1995: 40) stated that P3 is interrupted; however, it is an anomalous condition in Dendrobatoidea and this gap exists because of a lack of teeth on the row in the early stages, (1) the figure of other back-riding tadpoles of *Epipedobates* available to us shows that all species have a wide A2-gap.

Species	Source and description of tadpole (s)	Locality of the tadpole (s) described	Type of tadpole (s) employed	stage	*N*	LTRF	A-2 gap size	Emargination of oral disc	Marginal papillae	Spiracle	Vent tube	Measurement
Epipedobates anthonyi	Silverstone 1976	Quebrada Angostura, Pozo Azul, Túmbez, Peru	Back-riding	25	3+	2(2)/3	?	Lateral emarginated	Lateral and posterior lips	Sinistral, ?	Dextral	?
Epipedobates boulengeri	Silverstone 1976	Isla Gorgona, Cauca, Colombia	Back-riding	28	9	2(2)/3	Wide (34% of OD)	Lateral emarginated	Lateral and posterior lips	Sinistral, Lateral	Dextral	TL and BL
Epipedobates espinosai	Silverstone 1976	9 km West of Santo Domingo de los Colorados, Ecuador	Back-riding	26	3	2(2)/3	Wide (36% of OD)	Lateral emarginated	Lateral and posterior lips	Sinistral, Lateral	Dextral	TL and BL
	Funkhouser 1956	9 km West of Santo Domingo de los Colorados, Pichincha, Ecuador	Back-riding	?	3	2(2)/3	Wide (28% of OD)	Lateral emarginated	Lateral and posterior lips	Sinistral, Lateral	Dextral (see Silverstone 1976: 30)	TL (as body length)
Epipedobates machalilla	Coloma 1995	17 km NE Naranjal, Guayas, Ecuador; 10 m	Back-riding	25	1**	2(2)/3β	Narrow (1)	?	Lateral and posterior lips	Sinistral, Lateral	Dextral	TL, Eye, Dfin, Vfin, ODW
Epipedobates narinensis	Mueses-Cisneros *et al.* 2008	Reserva Natural Biotopo Selva Humeda, El Berlín, El Diviso, Barbacoas, Nariño; 600 m	Back-riding	25	1*	2(2)/3	Wide (37% of OD)	Lateral emarginated	Lateral and posterior lips	Sinistral, Lateral	Dextral	TL, BL, BW, SND, IND, END, Eye, IOD, VT, TAL, TMW, TMH, MTH, ODW, AL gap, UJS, LJS, A-1, A-2, A-2 gap, P-1, P-2

Materials and Methods

Tadpoles

A total of 144 tadpoles was examined—94 larvae of *Epipedobates narinensis* and 50 larvae of *E. boulengeri* (Appendix I). Tadpoles of *Epipedobates narinensis* were collected in July 2006 from the type locality of the species—Reserva Natural Biotopo Selva Húmeda, Barbacoas, Nariño, Colombia. They were collected with the type series in pools close to streams, and subsequently deposited in the Colección de Anfibios, Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN). The tadpoles of *E. boulengeri* are from southwestern Colombia, in the municipality of Tumaco, Nariño, Colombia (housed in ICN, and in the Colección Zoológica de la Universidad de Nariño, Pasto, PSO) and from Pacific lowlands of central to northern Ecuador, in the provinces of Carchi, Esmeraldas, Imbabura, and Santo Domingo de los Tsáchilas. These specimens are housed in the Museo de Zoología, Pontificia Universidad Católica de Ecuador (QCAZ). The larvae of *E. boulengeri* from Nariño were collected in a flooded pasture or small pools at the edge of an oil palm plantation in the village of Llorente, and in a flooded pasture adjacent to small remnants of forest and with lentic water to in the heavily modified areas surrounding the village of Chilvi. All tadpoles were preserved and stored in formaldehyde (10%).

Among tadpoles of *Epipedobates narinensis* are 3 back-riding tadpoles, 89 free-swimming tadpoles, and 2 metamorphosing tadpoles. Tadpoles of *E. boulengeri* are represented by 8 back-riding tadpoles, 41 free-swimming tadpoles, and 1 metamorphosing tadpole. To establish the species identifications of the tadpoles, we used the methods proposed by Anganoy-Criollo (2013), as follow. For *E. narinensis,* we examined all free-swimming tadpoles of dendrobatoid frogs captured with the type series of this species and the back-riding tadpoles described by Mueses-Cisneros *et al.* (2008). We compared the features of metamorphosing tadpoles (such as the oblique lateral stripe, features of the feet, and the color pattern of legs) with those of adult *E. narinensis* to verify our identification. All larval characters discussed in Anganoy-Criollo (2013; e.g., upper jaw sheath, nostril, stitches, papillae and caudal fins) were examined. The same protocol was used to identify tadpoles of *E. boulengeri* based on the description and illustration of back-riding tadpole of Silverstone (1976), the tadpoles from the backs of adults, and the metamorphosing tadpoles.

Redescription and Variation

Larvae were assigned Gosner (1960) stages, and the format of the descriptions follows that of Anganoy-Criollo (2013), thereby providing comparable morphological data for free-swimming tadpoles (Stages 25–39) of *Epipedobates narinensis* and *E. boulengeri.* Proportional measurements of *E. narinensis* were taken at Stage 33 ($N = 8$); those of *E. boulengeri* are from Stages 34–36 ($N = 7$). Measurements and proportions of other stages of both species are provided (Tables 2, 3). The total and body lengths of 91 free-living tadpoles (Stages 25–41) of *E. narinensis* and 39 free-living tadpoles (Stages 26–41) of *E. boulengeri* were measured (Figure 1A, B). The measurements (range, mean ± SD) are those of Altig and McDiarmid (1999).

The tadpoles of *Epipedobates narinensis* and of *E. boulengeri* have three developmental phases: (1) back-riding tadpoles (Stages 25 and 26); (2) free-swimming tadpoles (Stages 25–39); and (3) metamorphosing tadpoles (Stages 40 and 41). Ontogenetic variation between each phase and within each phase is described.

Marginal papillae of *Epipedobates narinensis* and of *E. boulengeri* were counted on the right side of the anterior labium and on the posterior labium (for a 1-mm section) in larvae that were measured. Variation in rows of marginal papillae of free-swimming tadpoles was quantified following the method of Anganoy-Criollo

Table 2. Measurements (in mm) and proportions (%) of the free-swimming tadpoles of *Epipedobates narinensis* in Stages 26, 33, 35–36, and 39–41. The range, mean and standard deviation for measurements and the range for proportions are reported. Abbreviations as in Table 1; other are as follow: (BH) body height, (P-AL) papillae on the right side of anterior lip, (P-PL) papillae on posterior lip/mm, (SH) spiracle height at its base, (SL) spiracle length, (SOH) spiracle opening height, (SSD) snout–spiracle distance.

Measurements	Stage 26 (*N* = 12)	Stage 33 (*N* = 8)	Stage 35–36 (*N* = 8)	Stage 39–41 (*N* = 4)
TL	12.5–17.9 (15.4 ± 1.8)	18.7–22.8 (20.6 ± 1.4)	22.5–26.6 (23 ± 1.8)	22.1–25.8 (23.6 ± 1.6)
BL	4.1–7.2 (6.1 ± 0.9)	7.1–8.7 (8 ± 0.6)	7.9–9.6 (8.6 ± 0.5)	8.2–9.9 (8.9 ± 0.7)
BW	3.2–4.8 (4.2 ± 0.5)	4.7–6.1 (5.5 ± 0.5)	5.5–6.8 (5.9 ± 0.5)	5.1–6.5 (5.7 ± 0.6)
BH	2.2–3.8 (3.1 ± 0.5)	3.3–4.6 (3.9 ± 0.5)	3.8–5.1 (4.3 ± 0.5)	3.5–4.5 (4.1 ± 0.4)
TAL	7.1–10.7 (9.2 ± 1.1)	10.5–14.4 (12.6 ± 1.4)	12.4–17 (14.4 ± 1.4)	13.9–17.1 (15.5 ± 1.6)
Eye	0.6–0.7 (0.7 ± 0.04)	0.8–0.9 (0.8 ± 0.04)	0.9–1.1 (1 ± 0.1)	1–1.2 (1.1 ± 0.1)
Nostril	0.2–0.3 (0.2 ± 0.02)	0.2–0.3 (0.3 ± 0.02)	0.3–0.4 (0.3 ± 0.03)	0.2–0.4 (0.3 ± 0.1)
IOD	1.6–1.9 (1.7 ± 0.1)	1.8–2.5 (2.2 ± 0.2)	2.2–2.9 (2.6 ± 0.2)	2.3–2.8 (2.6 ± 0.2)
IND	1–1.4 (1.2 ± 0.1)	1.3–1.7 (1.5 ± 0.1)	1.5–1.8 (1.6 ± 0.1)	1.4–1.7 (1.5 ± 0.1)
SND	0.4–0.8 (0.6 ± 0.1)	0.6–0.9 (0.7 ± 0.1)	0.6–0.9 (0.7 ± 0.1)	0.5–0.8 (0.6 ± 0.1)
END	0.4–0.7 (0.6 ± 0.1)	0.7–0.8 (0.7 ± 0.04)	0.7–0.8 (0.8 ± 0.1)	0.7–0.9 (0.8 ± 0.1)
SL	0.6–1.2 (0.9 ± 0.2)	1.1–1.5 (1.3 ± 0.2)	1.2–1.7 (1.4 ± 0.2)	1.2–1.5 (1.3 ± 0.1)
SH	0.4–0.8 (0.6 ± 0.1)	0.7–0.9 (0.8 ± 0.04)	0.8–1 (0.9 ± 0.1)	0.7–0.8 (0.7 ± 0.01)
SOH	0.2–0.4 (0.2 ± 0.1)	0.2–0.4 (0.3 ± 0.1)	0.2–0.4 (0.3 ± 0.1)	0.2–0.4 (0.3 ± 0.1)
SSD	3.4–4.8 (4 ± 0.5)	4.6–5.8 (5.1 ± 0.4)	4.9–6 (5.3 ± 0.5)	5.2–6.1 (5.6 ± 0.4)
VT	0.7–1.0 (0.8 ± 0.1)	1–1.7 (1.2 ± 0.2)	1–1.9 (1.4 ± 0.3)	1.4–1.7 (1.6 ± 0.1)
TMW	1–1.7 (1.2 ± 0.2)	1.5–1.9 (1.8 ± 0.2)	1.8–2.5 (2.1 ± 0.2)	1.9–2.6 (2.2 ± 0.3)
TMH	1.2–1.9 (1.5 ± 0.2)	1.8–2.3 (2 ± 0.2)	2–2.7 (2.3 ± 0.2)	2.1–2.6 (2.3 ± 0.2)
ODW	1.4–2.2 (1.8 ± 0.2)	1.7–2.3 (2.1 ± 0.2)	1.8–2.4 (2.2 ± 0.2)	1.8–2.6 (2.1 ± 0.4)
AL gap	0.9–1.4 (1.2 ± 0.2)	1.2–1.6 (1.4 ± 0.l)	1.2–1.5 (1.4 ± 0.1)	0.9–1.7 (1.3 ± 0.3)
UJW	0.8–1.1 (0.9 ± 0.1)	0.9–1.2 (1 ± 0.1)	1–1.3 (1.1 ± 0.1)	1–1.3 (1.1 ± 0.1)
LJW	0.4–0.7 (0.6 ± 0.1)	0.6–0.8 (0.7 ± 0.1)	0.7–0.9 (0.8 ± 0.1)	0.7–0.8 (0.7 ± 0.1)
A-2 gap	0.3–0.5 (0.3 ± 0.1)	0.3–0.4 (0.3 ± 0.05)	0.3–0.4 (0.4 ± 0.03)	0.3–0.4 (0.3 ± 0.1)
P-AL	8–15 (11 ± 2)	10–17 (14 ± 2)	11–14 (13 ± 1)	10–14 (11 ± 2)
P-PL	21–26 (23 ± 2)	21–26 (23 ± 2)	17–24 (21 ± 3)	16–22 (20 ± 3)

Table 2. *Continued.*

Proportions (%) and Range	Stage 26 (*N* = 12)	Stage 33 (*N* = 8)	Stage 35–36 (*N* = 8)	Stage 39–41 (*N* = 4)
BL/TL	32–44	34–45	35–40	34–43
BH/BW	61–80	67–77	69–76	68–75
BW/BL	64–79	59–75	64–73	52–75
SSD/BL	60–85	56–70	57–68	56–70
TAL/TL	56–68	55–66	60–65	63–66
VT/BL	10–17	12–20	12–20	16–20
Nostril/Eye	31–42	31–40	30–35	17–32
Eye/IOD	36–71	33–42	35–43	35–50
IOD/BW	23–45	36–45	40–46	39–53
IND/IOD	61–82	64–75	61–70	52–70
SH /SL	62–100	50–68	50–80	50–63
TMW/TMH	63–91	82–97	81–100	91–100
ODW/BW	37–48	31–44	32–44	35–39
AL gap/ODW	59–72	62–73	55–68	51–73
UJS/ODW	43–62	44–55	44–57	49–58
A–2 gap/ODW	13–23	11–19	14–19	10–19

(2013). Measurements were taken with a manual caliper (0.01 mm) and with an ocular micrometer on a Carl Zeiss Stemi 2000 stereomicroscope (0.001 mm). All measurements are reported in millimeters (mm).

Comparison with Other Species

The external morphology of free-swimming tadpoles was compared among five *Epipedobates* (*E. anthonyi, E. boulengeri, E. machalilla, E. narinensis,* and *E. tricolor*), as well as with other dendrobatoid frogs distributed in the Pacific lowlands of southwestern Colombia (departments of Valle del Cauca to Nariño) and northwestern Ecuador (provinces of Esmeraldas to Pichincha) (0–1000 m a.s.l.; Lynch and Suárez-Mayorga 2004). Our aim was to distinguish species of *Epipedobates* from other sympatric dendrobatoids (Table 4), in addition to larvae of closely related Colostethinae (Table 5). The larvae compared are from the zoological collections of ICN, QCAZ, and PSO-CZ (Appendix I) or descriptions of free-swimming tadpoles (Tables 4, 5). Comparisons are based only on free-swimming tadpoles because variation in larval morphology is minor in these stages (Anganoy-Criollo 2010, 2013).

The back-riding tadpoles of five species of *Epipedobates* are described (Table 1). Few interspecific comparisons of back-riding tadpoles have been made because their features are not

Table 3. Measurements (in mm) and proportions (%) of the free-swimming tadpoles of *Epipedobates boulengeri* in Stages 26, 34–36, and 39–41. The range, mean and standard deviation for measurements and the range for proportions are reported. Abbreviations as in Tables 1 and 2.

Measurements	Stage 26 (*N* = 11)	Stage 34–36 (*N* = 7)	Stage 39–41 (*N* = 4)
TL	12.5–16.7 (14.8 ± 1.6)	18.9–27.1 (23.5 ± 2.9)	24.5–25.6 (25 ± 0.6)
BL	4.5–7.1 (5.8 ± 0.7)	7.1–9.8 (9 ± 1)	8.9–9.7 (9.2 ± 0.4)
BW	3.3–4.2 (3.9 ± 0.3)	4.8–6.4 (5.9 ± 0.6)	6–6.9 (6.4 ± 0.4)
BH	2.1–3.1 (2.7 ± 0.3)	3.7–4.8 (4.2 ± 0.4)	4–4.8 (4.3 ± 0.4)
TAL	6.9–10.8 (9 ± 1.1)	11.8–17.6 (14.5 ± 2.1)	15.1–16.6 (15.7 ± 0.8)
Eye	0.6–0.9 (0.7 ± 0.1)	0.9–1.2 (1 ± 0.1)	1.2–1.3 (1.2 ± 0.02)
Nostril	0.2–0.3 (0.3 ± 0.05)	0.3–0.4 (0.3 ± 0.02)	0.3–0.4 (0.3 ± 0.02)
IOD	1.6–2 (1.8 ± 0.1)	2.3–3.3 (2.9 ± 0.4)	2.9–3.7 (3.3 ± 0.4)
IND	0.9–1.2 (1 ± 0.1)	1.4–1.8 (1.6 ± 0.2)	1.5–1.6 (1.5 ± 0.05)
SND	0.4–0.6 (0.5 ± 0.1)	0.6–0.8 (0.7 ± 0.1)	0.3–0.6 (0.4 ± 0.1)
END	0.5–0.6 (0.6 ± 0.1)	0.6–1 (0.8 ± 0.1)	0.7–0.9 (0.9 ± 0.1)
SL	1–1.5 (1.2 ± 0.1)	1.2–1.7 (1.5 ± 0.2)	1.3–2.1 (1.7 ± 0.4)
SH	0.5–1 (0.8 ± 0.2)	0.8–1.3 (1 ± 0.2)	1–1.2 (1.1 ± 0.1)
SOH	0.1–0.5 (0.2 ± 0.1)	0.3–0.6 (0.4 ± 0.1)	0.2–0.6 (0.4 ± 0.2)
SSD	3.3–4.5 (4.1 ± 0.4)	4.8–6.8 (6.2 ± 0.7)	5.7–6.2 (6 ± 0.2)
VT	0.4–1 (0.7 ± 0.2)	1–1.5 (1.2 ± 0.2)	1.3–1.6 (1.4 ± 0.2)
TMW	1–1.6 (1.4 ± 0.2)	1.8–2.9 (2.4 ± 0.3)	2.3–3 (2.5 ± 0.3)
TMH	2.3–3.0 (2.6 ± 0.2)	1.9–3.2 (2.5 ± 0.4)	2.2–2.6 (2.4 ± 0.2)
ODW	1.3–1.8 (1.5 ± 0.1)	1.6–2.5 (2.2 ± 0.3)	1.8–2.4 (2.1 ± 0.3)
AL gap	0.7–1.1 (0.9 ± 0.1)	1–1.6 (1.4 ± 0.2)	1.4–1.5 (1.4 ± 0.1)
UJW	0.7–0.7 (0.7 ± 0.03)	0.9–1.2 (1.1 ± 0.1)	1–1.2 (1.1 ± 0.1)
LJW	0.4–0.7 (0.5 ± 0.1)	0.6–1 (0.9 ± 0.2)	0.7–1 (0.8 ± 0.1)
A-2 gap	0.3–0.4 (0.4 ± 0.05)	0.4–0.5 (0.4 ± 0.04)	0.5–0.7 (0.5 ± 0.1)
P-AL	9–11 (10 ± 0.8)	8–17 (11.5 ± 3.3)	10–14 (12 ± 2.8)
P-PL	15–24 (21 ± 2.6)	17–21 (18.9 ± 1.8)	19–21 (20 ± 1.4)

Table 3. *Continued.*

Proportions (%) and Range	Stage 26 (*N* = 11)	Stage 34–36 (*N* = 7)	Stage 39–41 (*N* = 4)
BL/TL	35–45 (39 ± 3)	35–42 (38 ± 2)	35–39 (37 ± 2)
BH/BW	63–73 (68 ± 4)	59–81 (72 ± 2)	66–71 (68 ± 2)
BW/BL	55–75 (68 ± 6)	57–73 (65 ± 6)	64–75 (69 ± 5)
SSD/BL	63–78 (70 ± 4)	65–74 (69 ± 3)	63–68 (66 ± 2)
TAL/TL	55–65 (61 ± 3)	58–65 (62 ± 2)	61–65 (63 ± 2)
VT/BL	7–16 (13 ± 3)	10–15 (13 ± 2)	14–18 (15 ± 2)
Nostril/Eye	31–48 (41 ± 6)	29–37 (33 ± 3)	25–28 (27 ± 2)
Eye/IOD	33–49 (37 ± 4)	31–40 (36 ± 4)	33–44 (38 ± 5)
IOD/BW	40–54 (47 ± 4)	44–52 (49 ± 3)	44–59 (52 ± 8)
IND/IOD	53–62 (57 ± 3)	50–62 (56 ± 4)	43–54 (48 ± 6)
SH/SL	39–84 (66 ± 15)	50–81 (67 ± 10)	50–74 (63 ± 10)
TMW/TMH	83–123 (94 ± 11)	91–120 (100 ± 10)	99–115 (107 ± 7)
ODW/BW	33–44 (39 ± 4)	33–43 (37 ± 3)	30–35 (33 ± 3)
AL gap/ODW	45–74 (61 ± 8)	55–72 (62 ± 5)	62–63 (62 ± 1)
UJS/ODW	40–55 (47 ± 6)	46–56 (50 ± 4)	47–57 (52 ± 5)
A-2 gap/ODW	19–30 (24 ± 4)	16–23 (20 ± 2)	19–35 (25 ± 9)

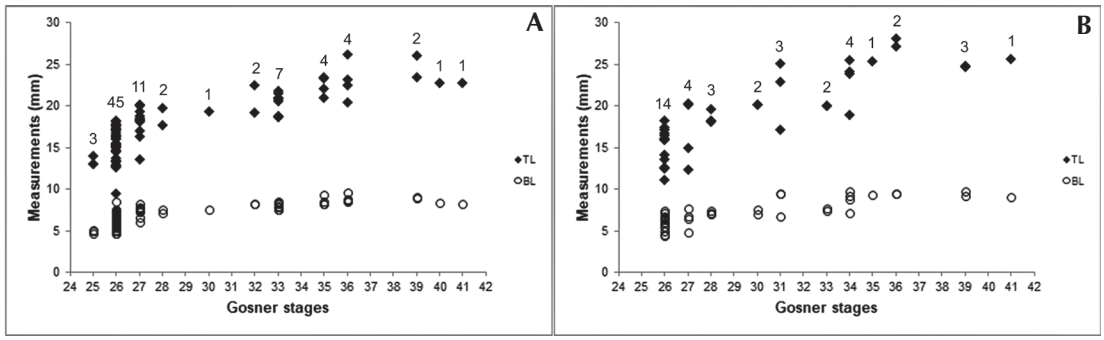

Figure 1. Total length (diamonds) and body length (circles) of the free-living tadpoles (i.e., free-swimming tadpoles and tadpoles initiating metamorphosis) of *Epipedobates narinensis* (**A**) and *E. boulengeri* (**B**). Numbers above total length are the number of individuals employed for the two measurements. No data are available for some stages.

Table 4. Morphological characters of dendrobatoid tadpoles in the Pacific lowlands of southwestern Colombia. Characters states apply only to free-swimming tadpoles. For abbreviation see the text and the Table 1 and 2. Symbols: (?) unknown or not specified in the literature; (-) no apply; (+) description based on back-riding tadpoles; (*) normal and umbelliform are refer in sense of Grant *et al.* (2006); (α) character proposed by Savage (1968); (¥) the figures of oral disc available in the literature (Ibáñez and Smith 1995: Figure 7B, Grant and Myers 2013: Figure 21D, and Savage 2002: Figure 7.121) shows "papillae" surrounding entire oral disc, but neither of the papers mentioned that there are marginal papillae; (**) tadpoles named as *Silverstoneia nubicola* in Savage (1968) are of *S. flotator* (see Savage 2002: 379 and Ibáñez and Smith 1995: 451); (†) the published illustrations of UJS of *S. dalyi* and *S. nubicola* (as for other species, see Ibáñez y Smith 1995, Grant and Myers 2013) and two tadpoles of *Silverstoneia* sp. (ICN 55313) from Río Quito, Chocó, Colombia no shows a medial notch, but Sánchez (2013: 576) stated that *Silvestroneia* has a small notch.

Species/ Character	Oral disc type*	Emargination of oral disc	Marginal papillae on lips of oral disc	Medial notch and type notch on UJS	Shelf on UJS	A-2 gap size	P-1 gap	LTRF	Spiracle position$^{\alpha}$	Nostril size	Source
Epipedobates narinensis	Normal	Lateral emarginated	Lateral and posterior lips	Present and Notable	Present	Moderate (10–19% of OD)	Absent	2(2)/3	Lateral sinistral	Moderate (30–42% of eye)	This work
Epipedobates boulengeri	Normal	Lateral emarginated	Lateral and posterior lips	Present and Notable	Present	Moderate (13–21% of OD)	Absent	2(2)/3	Lateral sinistral	Moderate (34–42% of eye)	This work
Allobates talamancae	Normal	Lateral emarginated	Lateral and posterior lips	Present and Shallow	Absent	Wide (22–34% of OD)	Present	2(2)/3(1)	Lateral sinistral	Small (15–20% of eye)	Savage 2002 This work
Andinobates bombetes	Normal	Lateral emarginated	Lateral lips	Absent	Absent	Wide (30–38% of OD)	Present	2(2)/3(1)	Low sinistral	Moderate (25–30% of eye)	Myers and Daly 1980 This work
Andinobates minutus	Normal	Lateral emarginated	Lateral and posterior lips	Absent	Absent	Wide (40–50% of OD)	Present (in ICN) Absent (in Silverstone)	2(2)/3, 2(2)/3(1)	Low sinistral	Moderate (40–50% of eye)	Silverstone 1975 This work
Andinobates viridis	Normal	Lateral emarginated	Lateral and posterior lips	Absent	Absent	Wide (25–38% of OD)	Present	2(2)/3(1)	Low sinistral	Moderate (25–35% of eye)	This work
Hyloxalus awa	Normal	Lateral emarginated	Lateral and posterior lips	Present and Shallow	Absent	Narrow (10–12% of OD)	Present	2(2)/3(1)	Lateral sinistral	Moderate (35–36% of eye)	Coloma 1995 This work

Table 4. *Continued.*

Species/ Character	Oral disc type*	Emargination of oral disc	Marginal papillae on lips of oral disc	Medial notch and type notch on UJS	Shelf on UJS	A-2 gap size	P-1 gap	LTRF	Spiracle position[α]	Nostril size	Source
Hyloxalus infraguttatus	Normal	Lateral emargin-ated	Lateral and posterior lips	Present and Notable	Absent	Narrow (6% of OD)	Absent	2(2)/3	Lateral sinitral	Moderate (30 % of eye)	This work
Oophaga histrionica	Normal	No emarginated	Lateral and posterior lips	Absent	?	-	Absent	1(1)/1, 1/1	Low sinistral	Moderate (34% of eye)	Silverstone 1975 This work
Oophaga sylvatica	Normal	No emarginated	Lateral and posterior lips	Absent	Absent	-	Absent	1/1	Low sinistral	Moderate (38% of eye)	This work
Phyllobates aurotaenia	Normal	Lateral emarginated	Lateral and posterior lips	Present and shallow	Absent	Wide (23–30% of OD)	Absent	2(2)/3	Lateral sinistral	Small (23–27% of eye)	This work
Phyllobates terribilis	Normal	Lateral emarginated	Lateral and posterior lips	Present and shallow	?	Wide (25% of OD)	Absent	2(2)/3	Lateral sinistral	Small (24% of eye)	Myers *et al.* 1978 This work
Silverstoneia dalyi+	Umbelliform	Anterolateral slightly emarginated	No papillae in lips	Absent[†]	?	-	-	0/0	Lateral sinistral	?	Grant and Myers 2013
Silverstoneia nubicola	Umbelliform	Anterolateral emarginated	?[¥]	Absent[†]	?	Moderate (13–14% of OD)	-	1–2(2)/0	Lateral sinistral	?	Grant and Myers 2013 Ibáñez and Smith 1995 Savage 2002 **

Table 5. The shared characters of free-swimming tadpoles of five *Epipedobates* (*E. anthonyi, E. boulengeri, E. machalilla, E. narinensis,* and *E. tricolor*), and the features of larvae of other Colostethinae (Dendrobatidae). Symbols: (*) condition present in five *Epipedobates* species; (?) unknown or not mentioned in the description.

Species	Shelf on UJS	A-2 gap size (%)	Notch on UJS size	Nostril size	Transverse ventral bands	Sources
*Epipedobates**	Present	Moderate (11–23)	Moderate	Moderate	Present	This work
Ameerega altamazonica	?	Moderate (28)	Low	?	Absent	Twomey and Brown 2008
Ameerega bilinguis	?	Moderate (28)	Moderate	?	Absent	Poelman *et al.* 2010. This work
Ameerega braccata	?	Moderate (26)	?	?	Absent	Haddad and Martins 1994
Ameerega flavopicta	?	Moderate (28)	?	?	Absent	Haddad and Martins 1994
Ameerega hahneli	?	Absent	Shallow	?	Absent	Haddad and Martins 1994. This work
Ameerega parvula	?	Moderate (22)	Moderate	?	Absent	Poelman *et al.* 2010. This work
Ameerega petersi	?	Moderate (22)	?	?	Absent	Silverstone 1976
Ameerega picta	?	Moderate (26–37)	?	?	Absent	Haddad and Martins 1994, Silverstone 1976
Ameerega silverstonei	?	Moderate (24)	?	?	Absent	Myers and Daly 1979
Ameerega smaragdina	?	Moderate (24)	?	?	Absent	Silverstone 1976
Ameerega trivittata	?	Moderate (22–26)	Moderate	Moderate	Absent	Silverstone 1976. This work
Colostethus fraterdanieli group	Present	Small (7–12)	Shallow	Large	Absent	This work
Colostethus imbricolus	Present	Small (5–8)	Shallow	Large	Absent	This word
Colostethus inguinalis	?	Small (4)	Shallow	?	?	Savage 1968
Colostethus latinasus	?	Small (10)	?	?	?	Savage 1968
Colostethus ruthveni	Absent	Small (6–9)	Shallow	Large	Absent	This work
Silverstoneia dalyi	?	Absent	Absent	?	Absent	Grant and Myers 2013
Silverstoneia erasmios	Absent	Absent	Absent	Small	Absent	This work
Silverstoneia flotator	?	Absent	Absent	?	Absent	Dunn 1924, Ibáñez and Smith 1995, Grant and Myers 2013
Silverstoneia minima	?	Absent	Absent	?	Absent	Grant and Myers 2013
Silverstoneia nubicola	?	Moderate (13–14)	Absent	?	Absent	Dunn 1924, Ibáñez and Smith 1995, Savage 2002, Grant and Myers 2013

fully developed, they are undergoing ontogenetic changes, and only subtle differences exist (Coloma 1995, Poelman *et al.* 2010). Thus, caution should be taken in interspecific comparisons tadpoles in this development phase (Myers *et al.* 1978).

Terminology

Terminology for external larval morphology follows that of Altig and McDiarmid (1999), and that of the lateral line system is based on Schlosser (2002). The lateral line system, its pathway, and extension were determined by examining the stitches on the skin. The extension and pathways of most of lateral lines are the same as those of Lannoo (1987, 1999) and the putative homologies suggested for anurans by Schlosser (2002). Exceptions occur in the oral, jugal, mandibular, medial trunk, and dorsal trunk lines (Table 6, Figure 2). The phylogenetic arrangement of genera and families follows that of Grant *et al.* (2006, 2017).

Table 6. Lateral lines of *Epipedobates narinensis* and *E. boulengeri* with a different pathway from that proposed by Lannoo (1987: 117, Figure 1) and its respective homologue for anurans of Schlosser (2002: Figure 3. Tables 1 and 2). See Figure 2 for illustration.

Lateral line	Pathway
Oral lateral line	The line extends from the postero-lateral side of the oral disc, below the infraorbital lateral line, and runs posteriorly until below of eye.
Jugal lateral line	The line is assigned as in Figure 3 of Schlosser (2002), unlike what was reported in Table 1 (jugal lateral line = middle part of anterior oral line of Lannoo 1987), because in the *Epipedobates* studied, this line follows the pathway of oral lateral line, but it starts below the eye, behind the oral lateral line and it extends backward to the anterior spiracle, where the route changes ventrally.
Mandibular lateral line	The line starts from lateral side of oral disc where it meets the infraorbital and oral lateral lines, although none is in contact. The mandibular lateral line runs backward along the ventrolateral flank of body to before and below the spiracle.
Medial trunk line	This line begins immediately posterior to the temporal infraorbital line, extends rearward along the dorsolateral flank of body to the body-tail junction where the line is displaced to the longitudinal half of the myotomes and it extends to mid-tail, ascending obliquely to the dorsal edge of the myotomes. The line covers the most tail length.
Dorsal trunk line	The line extends from mid-body to the anterior one-half of the tail commonly.

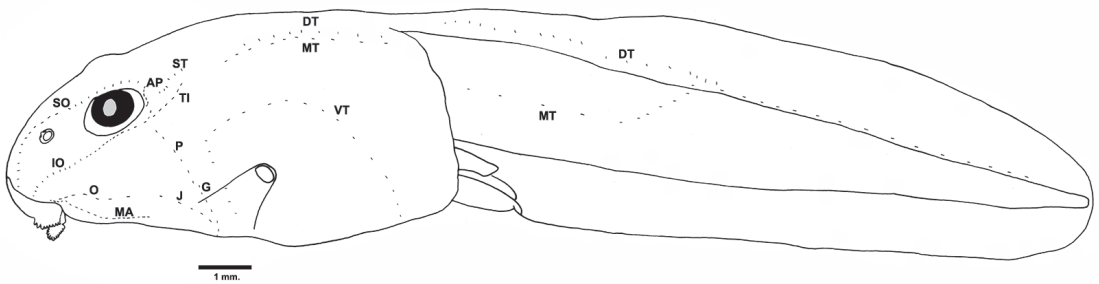

Figure 2. Lateral line system and stitches of larval *Epipedobates narinensis* at Stage 33 (ICN 55649).

Results

Redescription of the tadpoles of *Epipedobates narinensis* (Figures 3A, 4A–D, 5A)

Data were taken from 89 free-swimming tadpoles (Stages 26–39). Total lengths and body lengths per stage are plotted in Figure 1A, and measurements and proportions are given in Table 2. In Stage 33, body length 34–45% total length; body width 59–75% body length; and body height 67–77% body width. In dorsal view, body ovoid, widest at mid-body with rounded snout. In lateral view, body depressed, barely higher at intestines than oral disc level. Snout barely rounded to round, sloping anteriorly. Lateral line visible from Stage 26, with supraorbital, anterior pit, infraorbital, preopercular, gular pit, mandibular, oral, temporal infraorbital, supratemporal, dorsal, middle and ventral trunk lateral lines. In Stage 39, a pale line (sometimes located in skin depression) from eye to nostril. Equidistant stitches on all lateral lines. Pale white spot(s) (i.e., clusters of neuromasts) rarely present in the posteroventral region of some tadpoles in Stage 26.

Nostril rounded to ovoid (length 1–1.3 × height), dorsal, dorsolateral orientation, with marginal ring and low, dorsal fleshy projection. Nostril midway between eye and tip of snout. Nostril 31–40% eye diameter. Internarial distance 64–75% interorbital distance. Interorbital distance 36–45% body width. Eyes dorsal with dorsolateral orientation. Eye diameter equal to, or greater than, the nostril–eye distance. Eye diameter 33–42% interorbital distance. Spiracle sinistral, conical, directed posterodorsally, located below longitudinal midline and at vertical midline of body. Spiracle length equal to, or exceeding (× 1–2), spiracle height. Spiracle opening barely separated from body and located at 56–70% of body length (from tip of snout). Vent tube short, 12–20% body length, dextral, attached to ventral fin in A-type (commonly) or B-type (rarely, in one Stage-36 larva; Altig and McDiarmid 1999: Figure 3.5); opening with smooth edge.

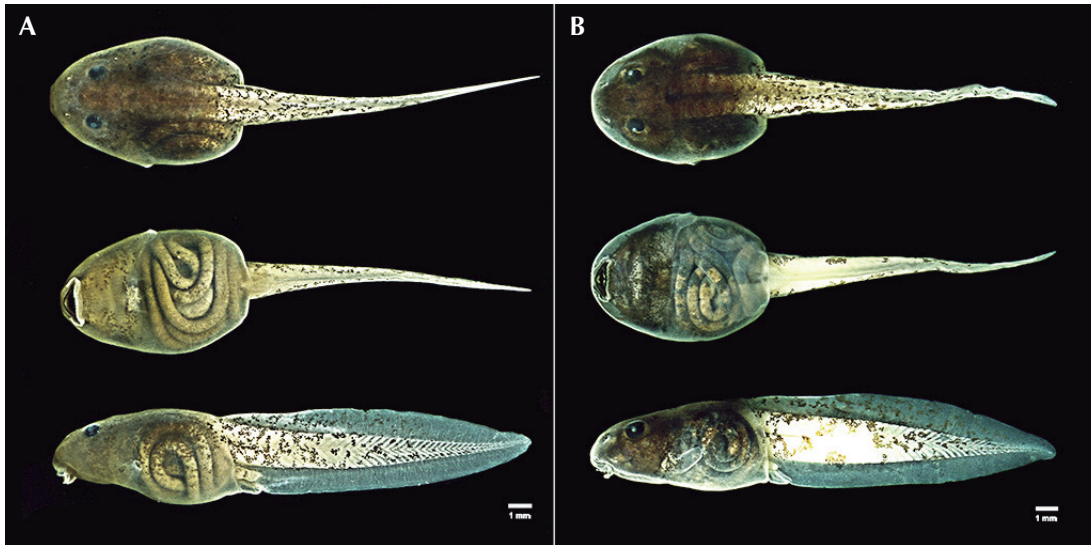

Figure 3. The free-swimming tadpoles of *Epipedobates narinensis* at Stage 33 in dorsal, ventral, and lateral views (**A**) (ICN 55646, TL = 20.8 mm) and of *E. boulengeri* at Stage 30 in dorsal, ventral and lateral view (**B**) (ICN 55653, TL = 20.1 mm).

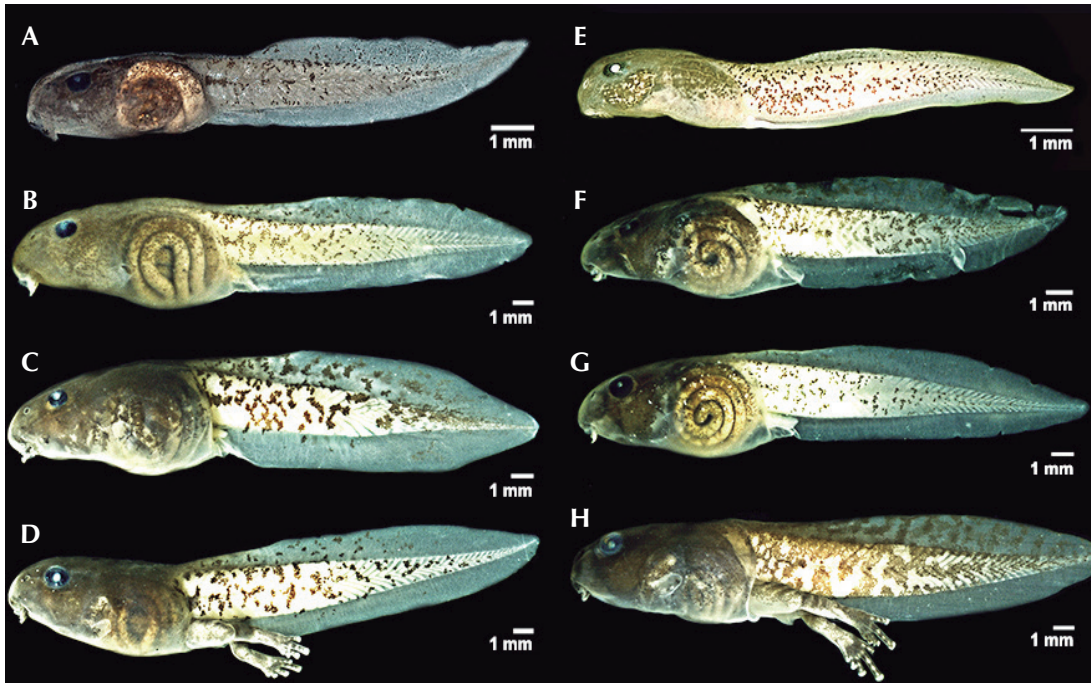

Figure 4. Ontogenetic variation of the tadpoles of *Epipedobates narinensis* (A–D) and of *E. boulengeri* (E–H): (**A**) back-riding tadpole at Stage 25 (ICN 55648, TL = 11.8 mm); (**B**) a free-swimming tadpole at Stage 26 (ICN 55646, TL = 25.2 mm); (**C**) another at Stage 32 (ICN 55649, TL = 22.5 mm); (**D**) at Stage 39 (ICN 55649, TL = 26.0 mm) of *E. narinensis;* (**E**) back-riding tadpole at Stage 26 (ICN-MAA 1059, TL = 9.2 mm); (**F**) a free-swimming tadpole at Stage 28 (ICN 55653, TL = 18.1 mm); (**G**) at Stage 33 (PSO-CZ 1773, TL = 23.2 mm); and (**H**) at stage 39 (ICN 55653, TL = 24.7 mm) of *E. boulengeri*.

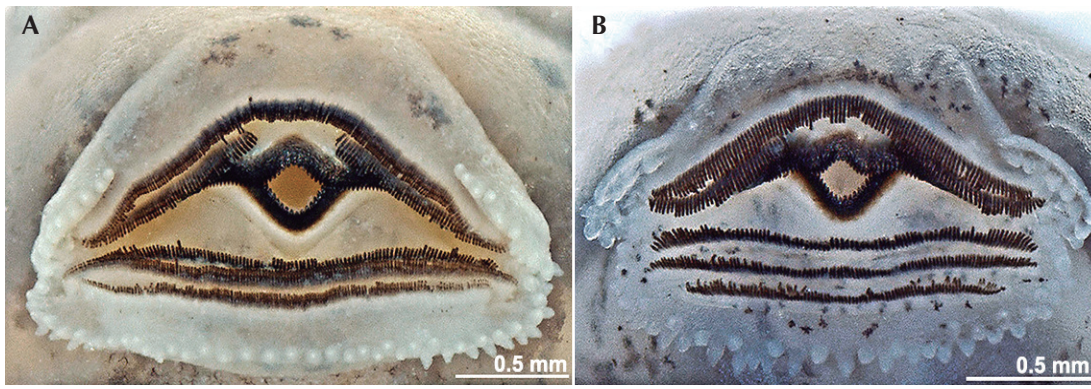

Figure 5. Oral disc of the free-swimming tadpole of (**A**) *Epipedobates narinensis* ICN 55646, Stage 36, ODW = 2.3 mm, and (**B**) *E. boulengeri* ICN 55653, Stage 27, ODW = 2.0 mm.

Intestines with sinistral, transverse (usually) or center-sinistral coils (in 2 Stage-26 larvae); 5–8 gut coils in ventral view. Tail length 55–66% total length. Height of caudal musculature 39–64% body height (at body-tail junction). Myotomes higher than wide (Stages 26–33) or as high as wide (Stages 35–39) at body-tail junction, narrowing gradually towards the tip of the tail. At mid-tail, dorsal fin higher than ventral fin and myotomes equal to, or higher than, dorsal fin. Dorsal fin arising at body-tail junction, lower on first anterior third of tail and of uniform height along length of tail, or sometimes higher at mid-tail length. Height of ventral fin uniform. Tip of tail rounded. Maximum tail height 80–121% body height.

Oral disc ventral, directed anteroventrally, laterally emarginate, bordered by marginal papillae except on anterior lip; sub-marginal papillae absent (Figure 5A). Width of oral disc 31–44% body width. Anterior lip gap 62–73% oral disc width. Marginal papillae arranged in 1 or 2 rows (Table 7) with 10–17 papillae on right side of anterior lip and 21–26 papillae/mm on posterior lip in Stage 33. Papillae low, narrow, slightly elongated on both lips, with rounded to sub-acuminate tips; papilla width (at base) ½ or slightly more than ½ of papilla height. Labial tooth row formula (LTRF) 2(2)/3; moderate A-2 gap, 11–19% oral disc width. A-1 and A-2 lengths equal; P-1 and P-2 lengths equal, usually slightly longer than P-3, or P-1–3 equal in length, or P-2 slightly longer than P-1 and P-1 slightly longer than P3 (rarely). Anterior tooth rows subequal or slightly shorter than posterior. Upper jaw sheath (UJS) keratinized; black or dark brown pigment covering half of UJS height, pigmented area height 9–16% UJS width, with notable medial notch (in depth and width; Figure 5A), 30–50% UJS height and shelf on back of the UJS (Figure 6A); lateral processes long and thin; UJS width 44–55% oral disc width. Anterior and posterior free edge of UJS well defined and sinuous. Low serrations on the UJS, except on lateral processes. Tips of serrations rounded at middle of UJS and acuminate towards ends. Lower jaw sheath (LJS) thin, V-shaped, black pigment covering one half of LJS height; LJS height (black pigmented area) 50–80% UJS height. Serrations on LJS low, with rounded tips.

Table 7. Variation of the rows of marginal papillae of the oral disc of *Epipedobates narinensis* and *E. boulengeri* through developmental stages. Variation is reported as range, average ± standard error, and the mode. Conventions: (1) one row, (2) one biseriate row, (3) two rows of papillae, (*N*) number of tadpoles, ([1]) the first number is for *E. narinensis*, followed by *E. boulengeri*, ([2]) only free-swimming tadpoles in Stage 26 for *E. boulengeri*.

Stages (*N*[1])	Parameters	Papillae on anterior lip		Papillae on posterolateral side of posterior lip		Papillae on middle of posterior lip	
		E. narinensis	*E. boulengeri*	*E. narinensis*	*E. boulengeri*	*E. narinensis*	*E. boulengeri*
25–26[2] (55, 14)	Range	1–2 (1 ± 0.03)	1–1 (1 ± 0.0)	1–3 (1.3 ± 0.07)	1–1 (1 ± 0.0)	1–3 (1.2 ± 0.06)	1–2 (1.3 ± 0.1)
	Mode	1	1	1	1	1	1
27–33 (24, 17)	Range	1–2 (1.1 ± 0.07)	1–2 (1.1 ± 0.07)	1–3 (1.5 ± 0.12)	1–3 (1.4 ± 0.2)	1–3 (1.4 ± 0.12)	1–2 (1.1 ± 0.08)
	Mode	1	1	1	1	1	1
35–39 (10, 11)	Range	1–1 (1 ± 0.00)	1–3 (1.4 ± 0.2)	1–3 (1.6 ± 0.20)	1–3 (1.4 ± 0.2)	1–3 (1.7 ± 0.19)	1–3 (1.6 ± 0.25)
	Mode	1	1	1	1	2	1

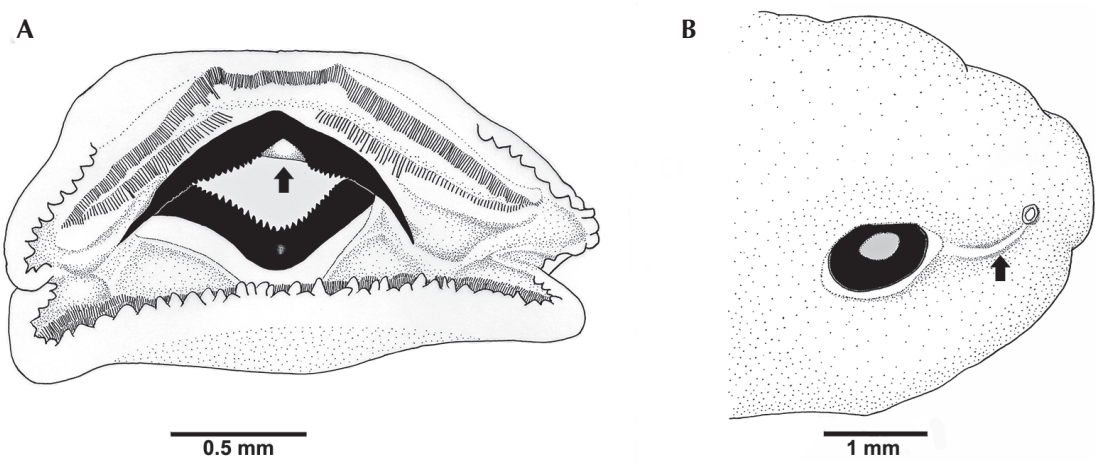

Figure 6. Posterior shelf concealed behind upper jaw sheath, and the pale line (arrow) between the eye and nostril of the tadpole of *Epipedobates narinensis*. (**A**) Stage 33 (ICN 55652); (**B**) Stage 41 (ICN 55652) in dorsolateral aspect.

Color in preservative (Figure 3A).—Skin of body translucent white, with abundant brown or dark brown dots dorsally and laterally; dots distributed uniformly or with dark spots between the snout and the eyes. Ventrally, body with few dark or pale brown dots, grouped between the oral disc and the anterior intestines, leaving the intermediate zone translucent (Figure 7B). Intestines dark brown. Myotomes cream or pale yellow. Fins translucent white with abundant brown dots forming brown spots that cover all tail, except ventral fin and tail tip, rarely the spots extend to the dorsal part of the ventral fin.

Variation.—Ontogenetic variation (i.e., variation between phases of development) affects many larval features of *Epipedobates narinensis,* with marked changes from one developmental phase to another (Table 8, Figure 4A–D). Moreover, there is variation within each developmental phase of development, described below.

Variation within each phase of development.—Back-riding tadpoles: Total length 7.7–11.8 mm (9.4 ± 2.1, N = 3), body length 3.5–3.9 mm (3.6 ± 0.2, N = 3). Back-riding tadpoles with 3 or 4 gut coils (Figure 7A); 5 or 6 marginal papillae on the right side of anterior lip; 20–29 papillae on entire posterior lip (< 1 mm), arranged in one row; UJS unpigmented (occasionally) or with dark pigmentation on its margin. Some tadpoles with only supraorbital and anterior-pit lateral lines, contra Mueses-Cisneros' *et al.* (2008: 5) report of supratemporal lateral line and misnamed loreal line. Dorsal and lateral body cream with abundant brown spots; ventral body translucent with brown dots; intestines cream or light yellow; myotomes cream; fins translucent white; brown spots on myotomes and dorsal fin.

Free-swimming tadpoles: Spiracle sometimes higher than long in Stage 29 and 36 (× 1.1–1.2). Tail muscle height 39–64% body height in Stages 25–33, and 47–58% body height in Stages 35–39. Marginal papillae arranged one to two rows on each lip (Table 7). Stitches absent in Stage 25. In Stages 26–28, only anterior body lateral lines (supraorbital, anterior pit, infraorbital, jugal, mandibular, and oral) visible,

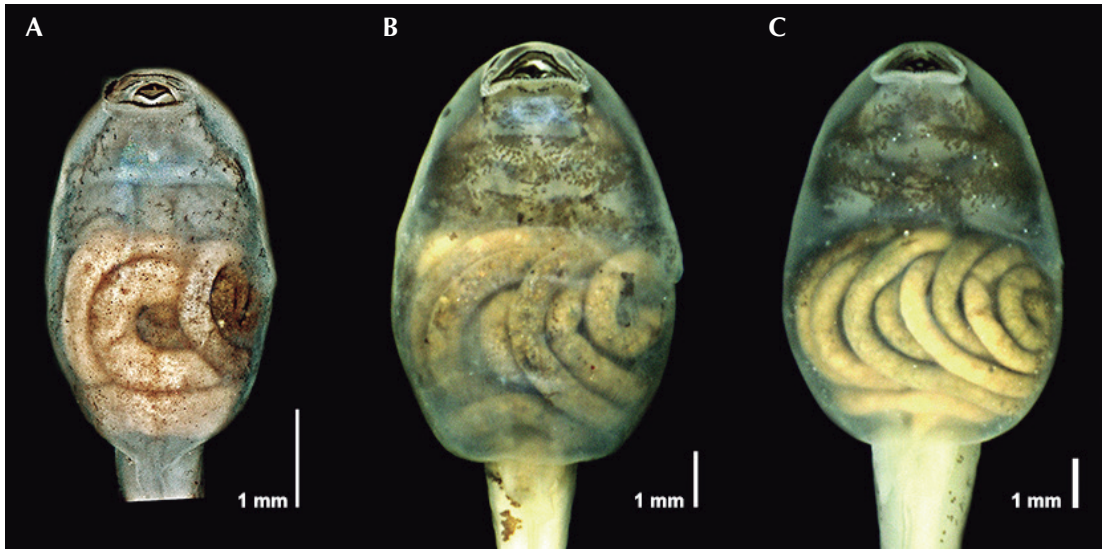

Figure 7. Ventral views of the tadpoles of *Epipedobates narinensis* and of *E. boulengeri,* showing the variation of the intestines between back-riding tadpole and free-swimming tadpole, and the dark transverse bands between the oral disc and intestines of free-swimming tadpole. Back-riding tadpole (**A**) Stage 25, ICN 55648, BL = 3.9 mm, and free-swimming tadpole of *E. narinensis* (**B**) Stage 33, ICN 55649, BL = 8.6 mm, and of the free-swimming tadpole of *E. boulengeri* (**C**) Stage 33, PSO-CZ 1773, BL = 7.6.

although sometimes preopercular, gular pit, temporal infraorbital, supratemporal, dorsal, middle, and ventral trunk lateral lines present; three latter lines not extending on tail. In Stages 30–39, all lateral lines present (Figure 2). Angular lateral line and pale line from eye to nostril present after Stage 38 (Figure 6B). The tail coloration changes from presence of few faint spots (Stages 25–28) to prominent, abundant spots (Stages 30–39) on myotomes and dorsal fin.

Metamorphosing tadpoles.—Total length 22.1–23 mm (22.6 ± 0.6, *N* = 2), body length 8.2–9.9 mm (9.0 ± 1.2, *N* = 2). Tadpoles have 10–11 papillae on right side of anterior lip, 16–22 papillae/mm on the posterior lip. In Stage 41, vent tube, UJS, LJS, and LTRF atrophied. Dorsal and lateral body dark brown, with faint, light cream incomplete oblique lateral stripe. Ventral body translucent white with brown spots between oral disc and intestines. Intestines dark brown, slightly visible. Myotomes pale yellow and fins translucent white, with abundant brown dots coalescing to form brown spots on entire tail except dorsal part of ventral fin. Legs cream with abundant (dorsally) or some (ventrally) brown dots distributed uniformly over thighs; toes brown with dark brown bands (Figure 8A).

Redescription of the tadpoles of *Epipedobates boulengeri* (Figure 3, 4E–G, 5B)

Data were taken from 41 free-swimming tadpoles between Stages 26 and 39. Total lengths and body lengths per stage are plotted in Figure 1B. Measurements and proportions are given in Table 3. In Stages 34–36, body length 35–42% total length; body width 57–73% body length; and body height 59–81% body width. In dorsal

Table 8. Ontogenetic variation in the tadpoles of *Epipedobates narinensis* and *E. boulengeri*. If variation is only present in one species, this is denoted with "En" for *E. narinensis* and "Eb" for *E. boulengeri*.

Feature	Back-riding tadpoles	Free-swimming tadpoles	Metamorphosing tadpoles
Body shape (in dorsal view)	Elongated and narrowed at the snout level	Ovoid	Ovoid, wider behind the eyes
Body shape (in lateral view)	The same height in the entire body (En)	Higher at level of intestines (En)	
Snout shape (in dorsal view)	Sub-truncate	Rounded	Rounded or Truncate
Snout shape (in lateral view)	Sub-truncate	Slightly rounded or rounded	Truncate
Nostril shape	Rounded or Ovoid (Eb)	Elongated (Eb)	Rounded (Eb)
Nostril direction	Anterolaterally	Dorsolaterally	Anterolaterally
Fleshy dorsal projection of nostril	Absent	Present	Absent
Eye direction	Dorsolaterally	Dorsolaterally	Laterally
Pale line between eye-nostril	Absent	Absent, but present in Stage 39	Present
Spiracle	Ventrolaterally located and weakly differentiable	Laterally located and differentiable	Laterally located and differentiable
Vent tube	Present		Atrophied
Tail muscle height/body height	80%	39–64% (En), 48–73% (Eb)	47–60% (En), 56% (Eb)
Dorsal/ventral fin	Equal	Higher	
Dorsal fin/myotomes	Lower	Equal (En, Eb), or slightly lower (En)	Equal
Origen of dorsal fin	At tail, in the first eighth of tail length	At body-tail junction	
Number of gut coils	3–4 (En), 5–6 (Eb)	5–8 (En), 5–7 (Eb)	5–8 (En), no visibles (Eb)
Oral disc direction	Ventrally (E.b)	Anteroventrally	
Papillae on anterior lip	5–6 (En), 5–8 (Eb)	8–17	10–11 (En), atrophied (Eb)
Arranged of papillae	1 row	1–2 rows	1 row (Eb), atrophied partially (Eb)
LTRF	2(2)/2 (En, Eb), 2(2)/3 (Eb)	2(2)/3 (En, Eb), 1/3 (Stage 39, Eb)	Atrophied (En), 1/1 (Eb)
A-2 gap (%)	Wide; 40–50% (En), 28–55% (Eb)	Moderate; 10–23% (En), 15–35% (Eb)	Moderate, 10–23% (En); atrophied (Eb)
Serrations of UJS	Absent	Present	Atrophied
Notch on UJS	Low	Notable	Atrophied (En), very low (Eb)

Figure 8. Tadpoles in late stages of (**A**) *Epipedobates narinensis* (Stage 40, ICN 55651, TL = 22.7, BL = 8.4) and (**B**) *E. boulengeri* (Stage 39, ICN 55653, TL = 24.7, BL = 8.15), showing the dorsal color pattern of the hind limbs; note uniformity of *E. narinensis* and distinct banded pattern in *E. boulengeri*.

view, body oval to ovoid, widest at mid-body. In lateral view, body depressed, barely higher at intestines than oral disc level. Snout rounded in dorsal and lateral aspects, sometimes slightly sloping anteriorly. Lateral line visible from Stage 26, with supraorbital, anterior pit, infraorbital, preopercular, gular pit, jugal, mandibular, oral, temporal infraorbital, supratemporal, dorsal, middle, and ventral trunk lines. In Stage 39, a pale line extending from eye to nostril. Equidistant stitches on all lateral lines. Neither angular lateral line, nor pale white spots (i.e., cluster of neuromasts) present.

Nostril elongated or ovoid (rarely, length 1.5–2 × height), dorsal, dorsolateral orientation, with a thick marginal ring and low fleshy projection dorsally. Nostril closer to eye than snout tip. Nostril 30–37% eye diameter. Internarial distance 50–62% interorbital distance. Interorbital distance 44–52% body width. Eyes dorsal with dorsolateral orientation. Eye diameter slightly greater than nostril–eye distance. Eye diameter 31–40% interorbital distance. Spiracle sinistral, cylindrical (i.e., spiracle height does not change), directed posterodorsally, located below the longitudinal midline and on vertical midline of body. Spiracle longer than high (× 1.4–2). Spiracular opening barely separated from body and ending at 58–65% body length (from tip of snout). Vent tube short, 10–15% body length, dextral, attached to ventral fin with slight ridge at union with the fin, as the B-type (see Altig and McDiarmid 1999: Figure 3.5); opening with smooth edge.

Intestines with sinistral, centro-sinistral, or transverse coils. Tail length 58–65% total length. Tail muscle height 48–73% body height (at body-tail junction). Myotomes higher than wide (Stages 26–33) or as high as wide (Stages 34–36) at body-tail junction, narrowing gradually toward tip of tail. At mid-tail, dorsal fin higher than ventral fin; myotomes higher than dorsal fin. Dorsal fin arising at body-tail junction, lower on first anterior third of tail and of uniform height along length of tail, or sometimes higher at mid-tail length. Ventral fin uniform in height along tail length. Tip of tail acuminate to subacuminate. Maximum tail height 88–117% body height.

Oral disc ventral, directed anteroventrally, laterally emarginate, bordered by marginal papillae except on anterior lip; sub-marginal papillae absent (Figure 5B). Width of oral disc 33–46% body width. Anterior lip gap 55–72% oral disc width. Marginal papillae arranged in 1 or 2 rows (Table 7) with 8–17 papillae on right side of anterior lip and 17–21 papillae/mm on posterior lip (Stages 34–36). Papillae on anterior lip low, narrow, with papillae width (at base) ¾ papillae height; papillae on posterior lip barely elongated, thin, with papillae width ½–⅔ papilla height. Papillae tips sub-acuminate to acuminate. LTRF 2(2)/3; moderate A-2 gap, 16–23% oral disc width. A-1 and A-2 lengths equal; P-1 and P-2 lengths equal and usually slightly longer than P-3, or P-1 longer than P-2 and P-3 (rarely). Lengths of anterior tooth rows equal to, or barely greater than, those of posterior tooth rows. Upper jaw sheath (UJS) keratinized with black or dark brown pigmentation; height of pigmented area 10–15% UJS width; notable medial notch

(Figure 5B); 30–50% UJS height and shelf on back of UJS; lateral processes long and thin. UJS width 46–56% oral disc width. Anterior and posterior free edges of UJS well defined and sinuous. Low serrations on the UJS, except on lateral processes. Tips of serrations rounded on middle of UJS and acuminate toward ends. LJS thin, V-shaped, black pigmentation covering half of LJS; LJS height (black pigmented area) 40–100% UJS height. Serrations on LJS low with rounded tips.

Color in preservative (Figure 3B).—Skin of body translucent white, with many dark brown dots (dorsally) and mottling (laterally), distributed uniformly on body. Nostril pale white with scarce or abundant dark brown blotches. Ventral skin with few or many dark brown dots forming spots; spots covering entire venter or only region between the oral disc and the anterior intestines, sometimes leaving the intermediate zone translucent (Figure 7C). Intestines yellowish brown to brown, sometimes with small white spots (under the skin). Myotomes cream or pale yellow. Fins translucent white, with dark brown stipples or spots, covering the most tail, forming a reticulated pattern in Stage 39. Oral disc translucent white with dark brown stipples or spots.

Variation.—The ontogenetic variation of *Epipedobates boulengeri* is summarized in Table 8 (Figure 4E–H). Variation within each phase and between populations is described below.

Variation within each phase of development.—Back-riding tadpoles: Total length 7.8–9.4 mm (8.7 ± 0.6, N = 8), body length 2.8–3.3 mm (3.1 ± 0.2, N = 8). Back-riding tadpoles with 5 or 6 gut coils; 5–8 marginal papillae on right side of anterior lip; 17–27 papillae on entire posterior lip (< 1 mm wide) arranged in one row. UJS and LJS unpigmented or only darkly pigmented on distal edges. LTRF from 2(2)/2 (N = 6) to 2(2)/3 (N = 2). Body cream with abundant brown spots, forming reticulate pattern on flanks of body; venter white to translucent white with brown spots forming two diffuse transverse bands between oral disc and viscera; intestines cream or light yellow; myotomes cream or white; fins translucent white; brown spots cover the myotomes and the dorsal fin.

Free-swimming tadpoles.—Marginal papillae 8–17 on right side of the anterior lip, 16–24 papillae/mm on posterior lip, arranged in one or two rows (Table 7). A-2 gap size varying from 15–35% oral disc width. LTRF 1/3; A-2 absent in Stage 39. Stitches visible from Stage 26, more evident in Stages 31–33. In Stages 26–27, the supraorbital, anterior pit, infraorbital, temporal infraorbital, and middle body lines present; a few tadpoles with preopercular, gular pit, jugal, mandibular, oral, supratemporal, dorsal, and ventral trunk lines. In Stage 29, all lateral lines present except angular. In some tadpoles in Stages 26 and 27, supraorbital, infraorbital, middle, and ventral lateral lines shorter than those in later stages; extending from posterior oral disc to anterior nostril (supraorbital) or anterior eye (supraorbital and infraorbital), on only body (middle) or only anterior to and above the spiracle (ventral); later, line lengths maximized. Body with scarce (Stages 26–28) or abundant (Stage 30 onward) dark brown stipples. The dark brown color on tail composed of dots (Stages 26–28), spots (Stages 30–36), or reticulations (Stage 39).

Tadpoles initiating metamorphosis.—Total length 25.6 mm (N = 1), body length 9 mm (N = 1). Papillae only along posterolateral margin of posterior lip. Dark brown pigmentation only on margins of UJS and LJS. Dorsal and ventral body covered by dark brown mottling; no transverse bands between the oral disc and anterior gut. Tail with dark brown mottling configured into reticulations and line along dorsal margin of musculature. Legs with dark brown bands (Figure 8B).

Variation between populations of Epipedobates boulengeri.—The tadpoles of Ecuadorian populations (QCAZ) differ from those of

Colombian populations (PSO and ICN). The body is ovoid in Colombian tadpoles and oval in Ecuadorian tadpoles. The tips of marginal papillae are commonly subacuminate in Colombian tadpoles and predominantly acuminate in those from Ecuador. Brown dots on the tail are scarce in Colombian tadpoles, whereas they are abundant in Ecuadorian tadpoles. Some Colombian tadpoles lack dark colored anterior snouts (in dorsal view), whereas those from Ecuador have dark snouts.

Comparisons

Between species of Epipedobates.—The free-swimming tadpoles of *Epipedobates anthonyi, E. boulengeri, E. machalilla, E. narinensis,* and *E. tricolor* differ in the shape of the nostril, size of dorsal fleshy projection of nostril, spiracle shape, type of the vent-tube attachment, and shape of tail tip. Additionally, the tadpoles of *E. boulengeri* are distinguished from those of *E. narinensis* by the number of papillae on the posterior lip, internarial distance, and the color pattern of the thighs in late stages (Table 9).

Tadpoles of sympatric dendrobatoids.—The distribution of *Epipedobates narinensis* is restricted to its type locality (Nariño, Colombia), but *E. boulengeri* has broader range from the Pacific lowlands of southwestern of Colombia to the middle of Ecuador (Silverstone 1976, Frost 2016). In the Pacific lowlands where both species of *Epipedobates* occur, 22 species of other dendrobatoids are found (*Allobates talamancae* (Cope, 1875), *Andinobates bombetes* (Myers and Daly, 1980), *A. fulguritus* (Silverstone, 1975), *A. minutus* (Shreve, 1935), *A. viridis* (Myers and Daly, 1980), *Ectopoglossus absconditus* Grant, Rada, Anganoy-Criollo, Batista, Dias, Jeckel, machado, and Rueda-Almonacid, 2017, *E. confusus* (Myers and Grant, 2009), *E. lacrimosus* (Myers, 1991), *Hyloxalus awa* (Coloma, 1995), *H. breviquartus* (Rivero and Serna, 1991), *H. infraguttatus* (Boulenger, 1898), *H. toachi* (Coloma, 1995), *Paruwrobates erythromos*

Table 9. Comparison of larval morphological features of free-swimming tadpoles of five species of *Epipedobate*s.

Character/Species	*E. narinensis*	*E. boulengeri*	*E. anthonyi*	*E. machalilla*	*E. tricolor*
Nostril shape	Rounded (commonly) or ovoid (rarely), 1–1.3 times	Elongated (commonly) or ovoid (rarely), 1.5–2 times	Rounded	Rounded	Ovoid
Dorsal fleshy projection of nostril	Low	Notable	Notable	Low	Low
Spiracle shape	Conical	Cylindrical	Cylindrical	Cylindrical	Cylindrical
Attached type of vent tube	A-type	B-type	A-type	A-type	C-type
Tail tip	Rounded	Acuminated to subacuminated	Acuminated	Acuminated	Acuminated
Papillae on posterior lip	17–26 papillae/mm	15–21 papillae/ mm	-	-	-
Internarial distance/ interorbital distance	61–75%	50–62%	-	-	-
Pattern on thighs (Stages 39–41)	Uniform, not banded	Banded	-	-	-

(Vigle and Miyata, 1980), *P. whymperi* (Boulenger, 1882), *Phyllobates aurotaenia* (Boulenger, 1913), *P. bicolor* Bibron, 1840, *P. terribilis* Myers, Daly, and Malkin, 1978, *Oophaga histrionica* (Berthold, 1845), *O. occultator* (Myers and Daly, 1976), *O. sylvatica* (Funkhouser, 1956), *Silverstoneia dalyi* Grant and Myers, 2013, and *S. nubicola* (Dunn, 1924). *Hyloxalus chocoensis* Boulenger, 1912 also was reported from Valle del Cauca, Colombia (Lynch and Suárez-Mayorga 2004; ICN 13425–13426); however, the latter specimens are *E. lacrimosus* (Grant *et al.* 1997).

Some of these species are sympatric with either *Epipedobates narinensis* or *E. boulengeri.* For example: in Colombia, *E. narinensis* occurs with *Oophaga sylvatica* in Barbacoas-Nariño (Mueses-Cisneros and Moreno-Quintero 2012; considered as *O. histrionica*) and *E. boulengeri* with *Allobates talamancae, Andinobates minutus, A. viridis, Ectopoglossus lacrimosus, E. narinensis, O. histrionica, O. occultator, Phyllobates terribilis* in Timbiquí-Cauca (Myers and Daly 1976, Myers *et al.* 1978, Myers 1991, Grant and Myers 2013) and with *Silverstoneia* in Buenaventura-Valle del Cauca (likely *S. nubicola*, Grant and Myers 2013). In Ecuador, *E. boulengeri* is sympatric with *Hyoxalus awa* and *H. breviquartus* in Provincia de Pichincha and Carchi, respectively (Coloma 1995). The free-swimming tadpoles of 12 species were found in the zoological collections we reviewed or were described previously (Table 4).

The tadpoles of *Epipedobates narinensis* and *E. boulengeri* can be distinguished from these 12 species by the following combination of characters: presence of a notable notch on mid-UJS; shelf on back of the UJS; moderate-sized A-2 gap; and moderate-sized nostril (Table 4, Figure 5). These features are also present in *E. anthonyi, E. machalilla,* and *E. tricolor.* Additional differences are found in oral disc (type and emargination of OD), marginal papillae, P-1 gap, LTRFs, and spiracle position (Table 4).

Discussion

Published information about larvae of *Epipedobates* is based on back-riding tadpoles. The descriptions describe common features, without specifying the characteristics that distinguish species of *Epipedobates* (Table 1). The common features of *Epipedobates* (viz., LTRF 2(2)/3, wide A-2 gap, marginal papillae on lateral and posterior lips, oral disc laterally emarginated, spiracle sinistral, and dextral vent tube) also are shared with back-riding tadpoles of other species of dendrobatid frogs of the genera *Ameerega* Bauer, 1986 (Silverstone 1976: 5–7, Poelman *et al.* 2010), *Hyloxalus* Jiménez de la Espada, 1870 (Coloma 1995, Anganoy-Criollo 2013; except the A-2 gap size), and *Phyllobates* (Silverstone 1976: 5–7, Myers *et al.* 1978; except the vent tube direction), as well as the aromobatid genus *Allobates* (Silverstone 1976: 5–7, Coloma 1995).

In the transition from one developmental phase to another (e.g., from back-riding tadpoles to free-swimming tadpoles), many larval morphological features of *Epipedobates boulengeri* and *E. narinensis* change (e.g., body shape, the tail, the oral disc and its structures; Table 8). Thus, the condition of a structure changes through development and different developmental phases are not comparable between species.

The larval features characterizing free-swimming tadpoles of *Epipedobates boulengeri* and *E. narinensis* differentiate these species and distinguish them from other congeners and sympatric species. Therefore, tadpole morphology of *Epipedobates* is a useful systematic tool at species and generic levels—a fact that also was shown in *Allobates* (Caldwell *et al.* 2002, Castillo-Trenn 2004), *Ameerega* (Poelman *et al.* 2010), *Anomaloglossus* (Kok *et al.* 2010), *Hyloxalus* (Anganoy-Criollo 2013), and *Phyllobates* (Donnelly *et al.* 1990; see also Savage 1968, Silverstone 1975, 1976, Myers 1987, Grant *et al.* 2006, Sánchez 2013). Nevertheless, the shelf on back of the UJS, the moderate A-2 gap, the

moderate notch on mid-UJS, and the moderate-sized nostril are shared by *Epipedobates* (*E. anthonyi, E. boulengeri, E. machalilla, E. narinensis,* and *E. tricolor*). These four characters were not considered in poison frogs previously.

Epipedobates was placed in the dendrobatid subfamily Colostethinae (Grant *et al.* 2006, 2017), together with the genera *Ameerega, Colostethus, Leucostethus,* and *Silverstoneia*. The presence/absence of a UJS shelf and the size of nostril are unknown in most of these genera; however, the *C. fraterdanieli* Group and *C. imbricolus* Silverstone, 1975 have a shelf on the UJS and both species plus *"C". ruthveni* have large nostrils. The moderate A-2 gap of *Epipedobates* is found in some *Ameerega* and in *S. nubicola* (Table 5). Sánchez (2013) described a very small notch on mid-UJS in *Epipedobates;* however, the data are primarily based on back-riding tadpoles. The notch is moderate in free-swimming tadpoles of *Epipedobates* and in three *Ameerega—A. bilinguis* (Jungfer, 1989), *A. parvula* (Boulenger, 1882), and *A. trivittata* (Spix, 1824) (Table 5).

Ventral pigmentation should be described in future treatments of the five *Epipedobates;* it forms transverse bands between the oral disc and anterior part of the intestine (one on the *interhyoideus* muscle and another between the branchial chamber and heart), as was show by Silverstone (1976: 7). This pigmentation is in a *subcutaneous fascia,* between the skin and the muscles. The character is not mentioned in tadpoles of Colostethinae, and we have not found the transverse band in *Ameerega* [*A. bilinguis, A. hahneli* (Boulenger, 1884), *A. trivittata,* and *A. parvula*], *Colostethus* [*C. fraterdanieli* group, *C. mertensi* (Cochran and Goin, 1970), and *C. ruthveni* Kaplan, 1997] and *Silverstoneia* sp. (Table 5).

Given that the five species of *Epipedobates* share character states (viz., shelf on back of the UJS, moderate A-2 gap, moderate notch on mid-UJS, moderate-sized nostril, and transverse ventral bands), these features may be putative synapomorphies for *Epipedobates*, with some convergences in related genera. However this hypothesis must be corroborated by evaluation of these characters in Dendrobatoidea and its relatives in a phylogenetic analysis.

The taxonomic status of *Epipedobates boulengeri* was questioned by Lötters *et al.* (2003, 2007), who stated that it is a complex of species based on calls, size, and color variation among populations, as described by Silverstone (1976). Lotters *et al.* (2003) found differences in calls from populations of northern Ecuador and those in the northernmost part of the range. Recently, Tarvin *et al.* (2017) reported cryptic species within of *E. boulengeri.* The tadpoles of *E. boulengeri* described herein represent the southern half of the range of the species. We detected some larval differences in body shape, tips of marginal papillae, and pattern of tail coloration between the populations of Ecuador and southwestern Colombia that support Lötters` hypothesis, thereby documenting the value of larval morphology as a taxonomic tool.

Acknowledgments

We thank J. D. Lynch, J. J. Calderon, and S. Ron for allowing us to access anuran larvae in the amphibian collections in their care (ICN, PSO-CZ, and QCAZ respectively). J. J. Mueses-Cisneros and V. Moreno invited us to participate in the field trip to the Reserva Natural Biotopo Selva Húmeda, Barbacoas, Nariño, in July 2006. We are grateful to J. D. Lynch, D. Sánchez, J. J. Ospina, P. Dias, T. Angarita, and R. Tarvin for comments and contributions to the manuscript. MAA thanks J. D. Lynch, D. Sánchez, R. Altig, B. Viertel, and G. Schlosser for sharing their valuable knowledge about tadpoles of dendrobatid frogs. MAA is indebted to V. C. Gutierrez and his family for support during the development of this project. Corponariño authorized collection of specimens (Resolution 356 of June 2007). Economic support was provided by Universidad Nacional de Colombia, the Programa de Estímulos a la Investigación Thomas van der Hammen del Jardín Botánico de Bogotá José Celestino Mutis (to MAA) and the University of Nariño, Pasto (to BCQ).

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Editor: Jaime Bertoluci

Appendix I. *Material examined.*
*For each species, the number of collection, the number of tadpoles by lot (N) and the range of Gosner (1960) stages of each lot and their locality is reported. *Denotes the back-riding tadpoles.*

Allobates talamancae. Colombia: ICN 55636, *N* = 21, stages 25–26; ICN 55637, *N* = 1, stage 27; Chocó, Quibdó, Pacurita, 48 m. ICN 55638, *N* = 33, stages 25–36; Chocó, Unión Panamericana, Salero. ICN 55639, *N* = 2, stage 26 and 27; ICN 55640*, *N* = 3, stage 26; ICN 55641, *N* = 2, stage 26–36; Chocó, Cantón de San Pablo, Victoria, 264 m. ICN 19805, *N* = 4, stages 33–42; ICN 19819, *N* = 2, stage 26 and 46; Valle del Cauca, Restrepo, vereda Alegra, campo Chancos, 460 m. ICN 46097, *N* = 12, stages 25–26; ICN 46098, *N* = 34, stages 25–34; Chocó, Quibdó, Pacurita, 6 km al Este de Quibdó. ICN 46099, *N* = 26, stages 25–36; ICN 46100, *N* = 17, stages 25–33; ICN 46101, *N* = 2, stage 28 and 43; ICN 46102, *N* = 4, stages 27–42; Chocó, Quibdó, 6 km al norte de Tanandó, Río Cabí, 70 m. ICN 55315, *N* = 12, stages 26–42; Chocó, Río Quito, Antadó–La Punta, 10 km noroccidente de Pato, 320 m.

Ameerega bilinguis: Ecuador: QCAZ 32194, *N* = 3, stages 33–39; QCAZ 32198, *N* = 2, stages 35–39; QCAZ 32206, *N* = 1, stages 34; Orellana, Yasuní National Park.

Ameerega hahneli: Colombia: ICN 53103, *N* = 1, stage 36; ICN 53104, *N* = 3, stages 28–31; ICN 53105, *N* = 32, stages 25–42; ICN 53106, *N* = 1, stage 25; Amazonas, Leticia.

Ameerega trivittata: Colombia: ICN 53107, *N* = 3, stages 29–38; ICN 53109, *N* = 1, stages 38; ICNMHN 53110, *N* = 1, stage 28; ICN 53113*, *N* = 17, stage 27–28; ICN 53114, *N* = 1, stage 35; ICN 53115*, *N* = 22, stage 27–28; ICN 53119, *N* = 1, stage 35; Amazonas, Leticia.

Ameerega parvula: Ecuador: QCAZ 32917, *N* = 1, stage 35; Napo, Archidona; QCAZ 32918, *N* = 4, stages 28–38; Napo, Río Arajuno.

Andinobates viridis. Colombia: ICN32698, *N* = 23 (plus 8 damaged tadpoles), stages 25–41; Valle del Cauca, Dagua, Queremal, Finca el Davis, 900 m.

Andinobates bombetes. Colombia: ICN 42287, *N* = 5, stages 25–29; Valle del Cauca, Yotoco, inspección Puente Tierra, km 18 Buga–Buenaventura. ICN 43922, *N* = 2, stages 42 and 43; Valle del Cauca, Yotoco, Reserva forestal Yotoco, km 18 Buga–Buenaventura, 1600 m.

Andinobates minutus. Colombia: ICN 46096, *N* = 3, stages 25–36; Choco, Quibdó, Pacurita (05° 41′ N, 76° 36′ W; datum = WGS84). ICN 55642, *N* = 1, stage 26; ICN 55643, *N* = 2, stage 26; Chocó, Quibdó, Pacurita, 48 m. ICN 55644, *N* = 1, stage 25; Chocó, Quibdó, hacia Tutunendo sobre la vía a Guadalupe, 100 m. ICN 55645*, *N* = 1, stage 25; Chocó, Quibdó, Pacurita, Pando.

Colostethus fraterdanieli group. Colombia: ICN 40800, *N* = 8, stages 25–26; ICN 40801, *N* = 27, stages 26–35; hacienda Agua Linda, vereda Piedra Alta, Betania, Antioquia. ICN 42290, *N* = 1, stage 28; ICN 42748, *N* = 1, stage 40; carretera Buga–Buenaventura km 18, Yotoco, Valle del Cauca. ICN 45920, *N* = 3, stages 34–40; campamento La Suiza, La Florida, Pereira, Risaralda. ICN 45927, *N* = 1, stage 43; ICN 45928, *N* = 6, stages 26–40; quebrada San Miguel, vereda San Miguel, La Unión, Antioquia.

Colostethus imbricolus. Colombia: ICN 55314, *N* = 41, stages 25–36; Choco, Río Quito, 320 m.

Colostethus ruthveni. Colombia: ICN 19776, *N* = 23, stages 25–28, Magdalena, Sierra Nevada de Santa Marta, Ciudad Perdida; ICN 33175, *N* = 35, stages 25–28, Magdalena, Sierra Nevada de Santa Marta, road from Santa Marta-Cerro San Lorenzo km 22.

Epipedobates anthonyi. Ecuador: QCAZ 18553, *N* = 4, stages 30–32; QCAZ 18555, *N* = 5, stage 27; El Progreso, El Oro. QCAZ 21130, *N* = 2, stage 33, Santa Isabel, Azuay.

Epipedobates boulengeri. Colombia: ICN 55653, *N* = 7, stages 26–39; palmera La Playa, southwestern de la variante, Llorente, Tumaco, Nariño, 95 m (01°25′ N, 78°37′ W; datum = WGS84). ICN 55654, *N* = 1, stage 34; palmera, 1 km to south "km 28", Tumaco, Nariño (01°37′30″ N, 78°44′ W; datum = WGS84). PSO-CZ 1773, *N* = 5, stages 31–39; finca Mar Agrícola, vereda Agua Clara, Chilvi, Tumaco, Nariño, 55 m. ICN-MAA 1059, *N* = 8, stages 25–26; Tumaco, Nariño.

Ecuador: QCAZ 10330, *N* = 1, stage 30; Eloy Alfaro, Esmeraldas. QCAZ 12751, *N*=1, stage 36; Alluriquín-La Florida, Santo Domingo de los Tsáchilas. QCAZ 16960, *N* = 18, stages 26–41; QCAZ 17893, *N* = 2, stages 27–28; Alto Tambo, Esmeraldas. QCAZ 23352, *N* = 3, stages 31–35; aprox., 4 km al oeste de Durango, Esmeraldas, 170 m. QCAZ 32153, *N* = 1, stage 27; San Francisco, vía a Urbina, Imbabura. QCAZ 40419, *N* = 1, stage 26; Caimito-Tachihue, Esmeraldas. QCAZ 40842, *N* = 2, stage 26; Río Baboso, Between Lita and Comunidad Awa de Baboso, Carchi, Ecuador.

Epipedobates machalilla. Ecuador: QCAZ 10329, *N* = 2, stages 35–36; Río Ayampe, Manabí. QCAZ 18508, *N* = 1, stage 27; Cabo Pasado y Río Ayampe, Manabí, 1550 m.

Epipedobates narinensis. COLOMBIA: ICN 55646, *N* = 32, stages 25–36; ICN 55647, *N* = 25, stages 25–36; ICN 55648, *N* = 1, stage 25; ICN 55649, *N* = 11, stages 26–39; ICN 55650, *N* = 8, stages 25–26; Nariño, Barbacoas, Berlín, Reserva Natural Biotopo Selva Humeda, 600–540 m. ICN 55651, *N* = 10, stages 26–40; ICN 55652, *N* = 5, stages 33–41; ICN 53341*, *N* = 2, stage 25; Nariño, Barbacoas, Berlín, Reserva Natural Biotopo Selva Húmeda, 600 m.

Epipedobates tricolor. ECUADOR: QCAZ 12197, *N* = 4, stages 30–31; Moraspungo, Cotopaxi.

Hyloxalus awa. ECUADOR: QCAZ 21350, *N* = 2, stages 28–31; La Unión de Toachi, Pichincha. QCAZ 45626, *N* = 2, stages 35–36; La Unión de Toachi, Santo Domingo.

Hyloxalus infraguttatus. ECUADOR: QCAZ 32187, *N* = 1, stage 35; El Mango, Cerro Masvale, Guayas. QCAZ 21179, *N* = 1, stages 39 via a Jipijapa, Puerto Cayo, Manabí.

Oophaga histrionica. COLOMBIA: ICN 55655, *N* = 1, stage 37; ICN 55656, *N* = 1, stage 35; raised in captivity at Zoológico de Cali, Valle del Cauca. Material prepared as skeletons.

Oophaga sylvatica. PSO-CZ 863, *N* = 1, stage 35. Nariño, Barbacoas, Junín, Reserva Natural de Aves El Pangán, 700 m.

Phyllobates aurotaenia. COLOMBIA: ICN 55658, *N* = 1, stage 25; Chocó, Quibdó, Pacurita, 48 m. ICN 55659, *N* = 2, stages 25–26; ICN 55660, *N* = 21, stages 25–35; ICN 55661, *N* = 4, stages 25–35; Chocó, Quibdó, en la via a Guadalupe, por la via Tutunendo, 100 m. ICN 55662, *N* = 4, stages 26–40; Chocó, Canto de San Pablo, Victoria, 264 m.

Phyllobates terribilis. COLOMBIA: ICN 55664, *N* = 1, stage 33; raised in captivity at Zoológico de Cali, Valle del Cauca. Material prepared as skeleton.

Silverstoneia sp. COLOMBIA: ICN 55313, *N* = 2, stages 28 and 33, Chocó, Río Quito, 360 m.