

THE TADPOLE OF A DART-POISON FROG
PHYLLOBATES LUGUBRIS
(ANURA: DENDROBATIDAE)

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Abstract.—The tadpole of *Phyllobates lugubris* is described based on specimens collected from male nurse frogs in northeastern Costa Rica and northwestern Panama. *Phyllobates lugubris* tadpoles undergo ontogenetic changes in mouthparts, spiracle location, and vent tube location. The tadpole of *Phyllobates lugubris* is similar to those of *P. aurotaenia*, *P. terribilis* and *P. vittatus*, although absolute size varies among species.

The monophyletic genus *Phyllobates* is comprised of five neotropical species (*P. aurotaenia*, *P. bicolor*, *P. lugubris*, *P. terribilis*, and *P. vittatus*) that produce steroidal alkaloids (batrachotoxins) in granular skin glands (Myers et al. 1978, Myers 1987). *Phyllobates lugubris* inhabits humid lowland forests along the Atlantic versant of Costa Rica and western Panama (Silverstone 1976). Altig & Johnston (1986) summarized larval characteristics of *Phyllobates lugubris* based on a description provided by Savage (1968). Savage (1968) considered *Phyllobates vittatus* to be conspecific with *P. lugubris*, and described the tadpole based on material collected from the Golfo Dulce region of southwestern Costa Rica (J. M. Savage, pers. comm.). Silverstone (1976) considered *Phyllobates vittatus* to be a distinct taxon restricted to southwestern Costa Rica; therefore, the tadpole of *P. vittatus* has been described twice (Savage 1968, Silverstone 1976) and the tadpole of *P. lugubris* has not been described (Savage & Villa 1986). Here we describe the tadpole of *Phyllobates lugubris* based on material collected in northeastern Costa Rica and northwestern Panama.

Two male nurse frogs transporting tadpoles were captured by CG and MAD at the La Selva Biological Reserve (2.6 km SE of Puerto Viejo de Sarapiquí, Heredia Prov-

ince, Costa Rica). Two of five tadpoles collected on 25 May (stage 25 of Gosner, 1960) and four of six collected on 16 June (stage 25) were preserved on the date of capture. The remaining tadpoles were reared in the laboratory on a diet of algae; these were killed and fixed in 10% formalin at various stages of development following techniques described by Starrett (1960). The nurse frogs were released after the tadpoles were removed. The tadpoles were deposited in the Costa Rican Expeditions (CRE) collection at the University of Miami (CRE 6696, 6714).

Three lots of *Phyllobates lugubris* tadpoles and male nurse frogs, housed in the American Museum of Natural History (AMNH), were collected in Bocas del Toro, Panama by Charles W. Myers and his associates. One lot of four tadpoles (AMNH 86642) and the nurse frog (AMNH 86642) were collected on 21 January 1971 on the mainland about 5 km W Almirante (30–40 m), one lot of five tadpoles (AMNH 102253) and the nurse frog (AMNH 102246) were collected on 5 May 1977 on Isla Colón (near La Gruta, 10 m), and one lot of three tadpoles (AMNH 107237) and the nurse frog (AMNH 107231) were collected in forest on a ridge near Río Changuinola (near Quebrada El Guabo, 200 m) on 15 April 1980. All the Panamanian tadpoles taken from the

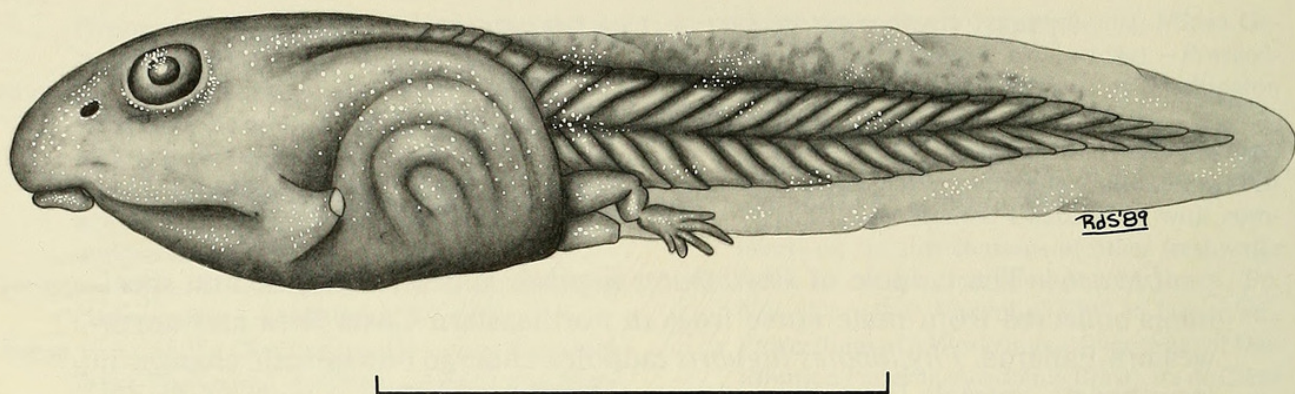


Fig. 1. Lateral view of a tadpole of *Phyllobates lugubris* in stage 37 (Gosner 1960) (CRE 6714). Bar = 10.0 mm.

backs of nurse frogs are in stages 24 or 25 (Gosner 1960).

We also examined tadpoles of *Phyllobates vittatus* (CRE 900, 903, 3152, 7234), *P. aurotaenia* (AMNH uncatalogued), and *P. terribilis* (AMNH 88979–88981). All tadpoles were measured to the nearest tenth of a millimeter under a dissecting scope with an ocular micrometer. The description of the tadpole of *Phyllobates lugubris* is based on two stage 37 specimens (CRE 6714).

Description of the Tadpole

Values are means. Body depressed (body width/body depth = 1.58); snout rounded in dorsal and lateral profiles (Fig. 1). Nostrils dorsal, directed laterally, opening 0.76 mm behind snout; internarial distance 1.75 mm. Eyes dorsal, directed dorsolaterally; diameter 0.95 mm; interocular plane 1.9 mm behind snout; interorbital distance 1.75 mm. Spiracle sinistral, low, opening 6.0 mm behind snout. Vent tube dextral to ventral fin.

Caudal musculature moderately robust anteriorly, gradually tapering posteriorly to near tail tip; height adjacent to body 2.0 mm, height at mid-tail 1.7 mm. Tail length 58% of total length. Tail height 15% of total length. Fins subequal in height; dorsal fin height 0.85 mm at mid-tail, not extending onto body; ventral fin height 1.0 mm at mid-tail. Tip of fin rounded (Fig. 1).

Mouth directed ventrally. Oral disc emar-

ginate (Fig. 2); oral disc width 2.35 mm. Labial teeth in two anterior and three posterior rows; tooth row formula 2(2)/3. Anterior rows equal in length, extending to marginal papillae; second row interrupted medially (A-2 gap = 0.35 mm). First and second posterior rows equal in length, slightly longer than third row. Upper jaw sheath moderately robust forming a broad arch with slender lateral processes; large pointed serrations present. Lower jaw sheath V-shaped, moderately robust; large pointed serrations present. Posterior lip bordered by one row of marginal papillae; one row marginal papillae extend onto lateral margins of anterior lip, one row submarginal papillae on lateral margins of oral disc.

In preservative, dorsal body color dark brown, lateral body color light brown, ventral body surface light brown with scattered white spots. Caudal musculature light brown. Fins transparent with brown blotches dorsally near musculature; ventral fin with brown spots near tail tip.

Ontogenetic Changes

The mouthparts of *Phyllobates lugubris* tadpoles undergo changes similar to those described for *P. terribilis* (Myers et al. 1978). Stage 24, 25, and 28 *Phyllobates lugubris* larvae have one row of submarginal papillae and one row of papillae on the posterior labium. In the stage 37 tadpole, there is a single row of papillae on the posterior la-

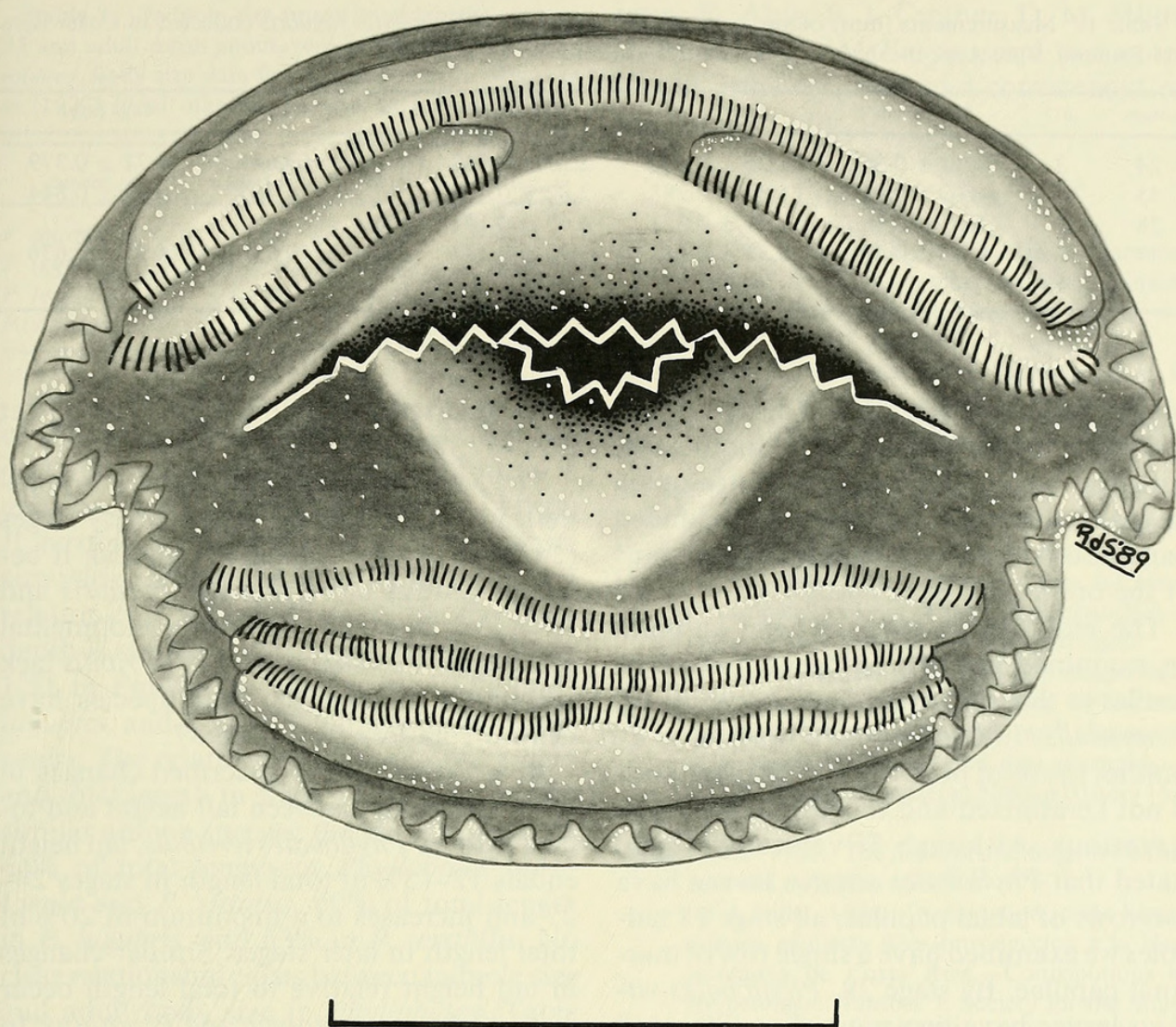


Fig. 2. Oral disc of a tadpole of *Phyllobates lugubris* in stage 37 (CRE 6714). Bar = 1.0 mm.

bium; the papillae alternate in orientation and it appears to be two rows rather than one. The jaw sheath edges are smooth in several stage 24 and 25 tadpoles, but they are serrated by stage 28. The labial tooth rows are not all keratinized at hatching; in many stage 24 and 25 larvae, the second anterior and the third posterior rows are not keratinized. The sequence of tooth row keratinization appears to be: P1 → A1 → P2 → A2 → P3. By stage 28, all tooth rows are keratinized. In our single stage 41 specimen, the A2 and P3 rows are reduced in length. The tail comprises 56% of the total length in stage 24 larvae and 60% of the total length in stage 41. The ratio of tail height to total length changes from 17% in stage 24 to 13%

in stage 41. In the early stages (24 and 25), the vent tube is medial and the spiracle is located at mid-body; in later stages, the vent tube is dextral and the spiracle is low on the left side of the body. Changes in body length, body depth, body width, tail length, and total length are summarized in Table 1.

Comparisons Among Species

We have not examined the tadpole of *Phyllobates bicolor* but we can compare the tadpole of *P. lugubris* to tadpoles of the remaining species in the genus. All *Phyllobates* tadpoles examined have: depressed bodies (width > depth), sinistral spiracles, dorsal eyes and nostrils, low-finned tails with

Table 1. Measurements (mm) of various stages of tadpoles of *Phyllobates lugubris* collected in Costa Rica and Panama. Values are means $\pm$ one standard deviation.

Stage	n	Body length	Body depth	Body width	Tail length	Total length
24	3	4.30 $\pm$ 0.361	2.00 $\pm$ 0.300	2.73 $\pm$ 0.252	5.47 $\pm$ 0.611	9.77 $\pm$ 0.379
25	15	4.16 $\pm$ 0.519	1.80 $\pm$ 0.288	2.82 $\pm$ 0.459	6.23 $\pm$ 0.466	10.39 $\pm$ 0.844
28	2	7.10 $\pm$ 0.566	2.95 $\pm$ 0.071	4.60 $\pm$ 0.141	—	—
37	2	10.30 $\pm$ 0.000	4.35 $\pm$ 0.212	6.90 $\pm$ 0.141	14.05 $\pm$ 0.636	24.35 $\pm$ 0.636
41	1	9.0	4.0	6.5	13.7	22.7

rounded tips, emarginate oral discs, two anterior and three posterior labial tooth rows, with the second anterior row interrupted medially, serrated jaw sheaths, and rounded papillae on the posterior and lateral margins of the oral disc.

The mouthparts of *Phyllobates* tadpoles we examined undergo ontogenetic changes similar to those observed in *P. lugubris* and *P. terribilis*. In some stage 25 larvae of *P. vittatus*, the third posterior row of labial teeth is not keratinized and the jaw sheaths lack serrations. Although Silverstone (1976) stated that *Phyllobates vittatus* larvae have two rows of labial papillae, all stage 25 tadpoles we examined have a single row of marginal papillae. By stage 28, *Phyllobates vittatus* larvae have two rows of papillae and all labial tooth rows are keratinized. In stage 25 *Phyllobates aurotaenia* tadpoles, the labial tooth rows are not keratinized, the jaw sheath edges are smooth, and there is one row of marginal papillae on the posterior labium and one row of submarginal papillae. By stage 37, *Phyllobates aurotaenia* tadpoles have keratinized labial teeth, serrated jaw sheaths, and two rows of papillae. Ontogenetic changes in oral papillae have

been reported for some hylids (Donnelly et al. 1987, Zweifel 1961).

The vent tube location changes ontogenetically in the four species. In early stages (24 and 25) the vent tube is medial; it becomes dextral in *Phyllobates lugubris* and *P. vittatus* by stage 28. The developmental series of *P. aurotaenia* and *P. terribilis* lack specimens in stage 28; both species have dextral vent tubes by stage 37.

Myers et al. (1978) described changes in the relationship between tail height and total length for *Phyllobates terribilis*; tail height equals 12–15% of total length in stages 24–27 and increases to a maximum of 20% of total length in later stages. Similar changes in tail height relative to total length occur in *Phyllobates aurotaenia* and *P. vittatus*. In *Phyllobates lugubris*, tail height does not increase relative to increasing total length.

Phyllobates tadpoles collected from male nurse frogs have been in stage 24 or 25; at this stage of development, the mouthparts of the species we examined were not completely developed. Measurements of stage 25 larvae for *P. aurotaenia*, *P. terribilis*, and *P. vittatus* are summarized in Table 2. The tadpole of *P. vittatus* is larger than tadpoles

Table 2. Measurements (mm) of stage 25 *Phyllobates* tadpoles. The following abbreviations identify the species: Pa = *P. aurotaenia*, Pt = *P. terribilis*, Pv = *P. vittatus*. Values are means $\pm$ one standard deviation.

Species	n	Body length	Body depth	Body width	Tail length	Total length
Pa	6	3.75 $\pm$ 0.138	1.57 $\pm$ 0.103	2.37 $\pm$ 0.121	6.73 $\pm$ 0.175	10.48 $\pm$ 0.306
Pt	12	4.38 $\pm$ 0.175	1.89 $\pm$ 0.131	2.98 $\pm$ 0.171	7.30 ^a $\pm$ 0.258	11.65 ^a $\pm$ 0.334
Pv	7	4.40 $\pm$ 0.883	2.04 $\pm$ 0.395	3.07 $\pm$ 0.170	8.08 ^b $\pm$ 0.898	12.70 ^b $\pm$ 1.138

^a n = 10.
^b n = 5.

Table 3. Tadpole size (mean total length) at stage 25 and adult mean snout-vent length (SVL) in *Phylllobates*. Body size data for *P. terribilis* from Myers et al. (1978), for all other species from Silverstone (1976).

Species	Tadpole total length (mm)	Male SVL (mm)	Female SVL (mm)
<i>P. aurotaenia</i>	10.48	26.9	30.4
<i>P. lugubris</i>	10.39	19.2	22.2
<i>P. terribilis</i>	11.65	41.1	43.2
<i>P. vittatus</i>	12.70	24.4	27.7

of the other species (Tables 1, 2); and its oral disc is wider (*P. vittatus*, 1.22 mm; *P. aurotaenia*, 0.80 mm; *P. lugubris*, 1.17 mm; *P. terribilis*, 1.09 mm). Although absolute size varies among the stage 25 tadpoles, the relationship between body width and body depth is similar (body width/body depth = 1.51 in *Phylllobates aurotaenia*, 1.57 in *P. lugubris*, and 1.58 in *P. terribilis* and *P. vittatus*). The relationship between tail length and total length in stage 25 tadpoles is also similar among species; the tail accounts for 64% of total length in *Phylllobates aurotaenia* and *P. vittatus*, 60% of total length in *P. lugubris*, and 63% in *P. terribilis*. No clear relationship exists between tadpole size and adult body size in *Phylllobates* (Table 3). Our observations agree with those of Myers et al. (1978); accurate identification of *Phylllobates* tadpoles in early (stage 24 or 25) developmental stages requires nurse frog identification. *Phylllobates* tadpoles in these stages exhibit little variation in larval characteristics other than absolute size. We expect that the tadpole of *Phylllobates bicolor* will resemble those of the other species.

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