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Description of two dendrobatid tadpoles (Anura: Dendrobatidae: *Andinobates* and *Oophaga*) with comments on egg clutches

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Family Dendrobatidae is a taxonomically complex and diverse group subject to regular phylogenetic revisions and changes (e.g., Grant *et al.* 2017). Larval morphology proved useful in delimiting groups within dendrobatids (Myers & Daly 1980; Sánchez 2013; Grant *et al.* 2017), but more data on tadpole morphology is necessary to contribute to the development of new phylogenetic hypotheses for this interesting and highly diverse taxon (Sánchez 2013; Grant *et al.* 2017). The genus *Oophaga* was recognized through the division of the genus *Dendrobates* by Grant *et al.* (2006), whereas *Andinobates* was a proposed as a new genus by Brown *et al*. (2011) for a monophyletic group of species previously contained within the genus *Ranitomeya*.

Detailed tadpole descriptions are available for nine out of sixteen species of *Andinobates*: *A. abditus* (Myers & Daly 1976), *A. bombetes* (Myers & Daly 1980), *A. claudiae* (Brown *et al.* 2011), *A. daleswansoni* (Duarte-Marín *et al.* 2020), *A. minutus* (Silverstone 1975), *A. opisthomelas* (Silverstone 1975), *A. supata* (Chaves-Portilla *et al.* 2021), *A. tolimensis* (Bernal *et al.* 2007), and *A. virolinensis* (Ruiz-Carranza & Ramírez-Pinilla 1992). Additionally, Silverstone (1975) referred to *A. minutus*-like tadpoles with an indented oral disc and a dextral vent, purported to be *A. altobueyensis* and *A. fulguritus* tadpoles, without providing any further description. Several authors recognize them as tadpole descriptions and have provided additional information on a few features of both species (e.g., Brown *et al.* 2011; Duarte-Marín *et al.* 2020). Of the four *Andinobates* species from Panama, in addition to the partial description of *A. fulguritus*, only the tadpole of *A. minutus* has been fully described (Silverstone 1975). *Andinobates geminisae* is endemic to small area in the Caribbean lowlands of Panama (Batista *et al.* 2014), and the tadpoles of this species are unknown. On the other hand, there are currently 12 species of *Oophaga*, five of them present in Panama (Frost 2022). Tadpole oral morphology is believed to unite all *Oophaga* species, who share an egg-based diet (Myers *et al.* 1984; Grant *et al.* 2006); however, tadpole descriptions are only available for five out of 12 species: *O. arborea* (Myers *et al.* 1984), *O. granulifera* (van Wijngaarden & Bolaños 1992), *O. histrionica* (Silverstone 1975), *O. pumilio* (Silverstone 1975, Savage 1968), and *O. speciosa* (Jungfer 1985). With the exception of *O. histrionica* (Silverstone 1975), four of these species are found in Panama. *Oophaga vicentei* is endemic to central Panama (Jungfer *et al.* 1996). Except for an account by Jungfer *et al.* (1996) of a tadpole riding on the back of a nurse female, the tadpole of *O. vicentei* remains undescribed.

The Panama Amphibian Rescue and Conservation Project houses assurance populations for *A. geminisae* and *O. vicentei* at a facility of the Smithsonian Tropical Research Institute, located in Gamboa, Panama. As part of a study on tadpole health issues, tadpole deposition, development, and mortality, both captive populations kept in breeding tanks at this facility were monitored from May 2017 to July 2018. The frequency of the monitoring allowed us to find and preserve several dead tadpoles from baseline mortality events before their bodies decomposed (usually less than 24 h after death). We took advantage of this opportunity to describe the tadpoles of these two species, using specimens from a variety of life stages. We believe the use of dead specimens, rather than euthanized ones, is justified for this study due to the rarity of the species. We describe the tadpoles of *A. geminisae* based on n = 40 larvae ranging between Stages 25–43 (Gosner 1960), and those of *O. vicentei* using n = 11 preserved larvae between Stages 25–41 (Gosner 1960) and three live larvae at Stage 41. We also provide brief description of the eggs and embryos of these two species.

Andinobates geminisae tadpoles were preserved in 10% formalin or ≥ 70% ethanol. All *O. vicentei* tadpoles were

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preserved in 70% ethanol for future molecular studies. We took measurements of body length (BL) and total length (TL) using a dissecting microscope and 1 mm^2 graph paper under a petri dish containing each specimen. Due to ongoing research on tadpole development during the period of data collection, time limitations did not allow for the measurement of additional morphological features for the description. Terminology and labial tooth row formula (LTRF) follow that of McDiarmid & Altig (1999), Grant *et al*. (2006) and Sánchez (2013). Summary statistics of the mean and standard deviation for body and total lengths were calculated using R Statistical Software (R Core Team 2018). For *O. vicentei*, in addition to 11 preserved specimens, three live specimens were also examined in water under a dissecting microscope to confirm the morphological traits observed. For live specimen examination, we placed tadpoles in a small water-filled petri dish under a dissecting microscope and manipulated specimens with the aid of a plastic pipette. After examination, these tadpoles were returned to the same body of water in their parental breeding tank to complete their development.

Breeding tanks were monitored for the appearance of new clutches three times weekly. We placed freshly laid eggs at Gosner Stages ≤ 3 on laminated 1 mm^2 graphic paper and photographed them before returning them to their original deposition sites for their continued development. The diameter measurements for the embryos and jelly capsules represent the mean diameter of two diameter measurements that cross at a 90° angle. Egg embryo diameter and total egg diameter were measured using Fiji digital imaging software (Schindelin *et al.* 2012).

Andinobates geminisae

Body and tail length measurements of *A. geminisae* tadpoles are summarized in Table 1. The body is oval-shaped and depressed (Fig. 1A). Eyes and nares are positioned dorsally, oriented dorsolaterally. Nares are round without projection in the inner margin of the nasal rim. The spiracle is sinistral and vent tube is dextral. The oral disc is round with a very slight lateral indentation. The posterior labium is lined with a single row of oral papillae that extend the bottom lateral corners of the anterior labium. LTRF is 2(2)/3[1] in older tadpoles, but all Stage 25 specimens had only two posterior labial tooth rows. The jaw sheath is massive and serrate, and the mouth is oriented anteroventrally. The upper jaw sheath is U-shaped. In 10% formalin, *A. geminisae* tadpoles are greyish brown dorsally and light grey to transparent ventrally (Fig. 2A). A differentiated short gut in the abdominal area can be noticed. The tail fin is light grey or translucent and nearly reaches the body. Live tadpoles were dark grey to black dorsally, with a lighter grey ventral side. The tail tip is rounded and translucent.

Viable clutches of *A. geminisae* with eggs at Stage ≤ 3 were examined (n = 16). In our sample, the number of eggs per clutch was one (n = 14) or two (n = 2). While eggs from the same clutch were always in close contact, the translucent jelly capsules surrounding each egg (n = 18) were discrete in *A. geminisae.* The embryos were solid medium-dark grey in the animal pole with varying amounts of light grey at the vegetal pole (Fig. 2C). Average egg diameter was 6.2 mm (n = 18, SD = 0.85), with a mean embryo diameter of 2.4 mm (n = 18, SD = 0.23).

TABLE 1. Measurements of *Andinobates geminisae* and *Oophaga vicentei*, given in mm as range; mean (SD). Values marked with (*) were calculated with smaller n (6, 3, 4, and 3, respectively).

Species	Stage	N	Body length	Total length	Mean BL/TL
A. geminisae	25	8	3.4–4.6; 3.95 (0.54)	9.6–15.4; 11.37 (2.50)*	0.35
	27	3	4.6–6.0; 5.33 (0.70)	15–17; 16.07 (1.01)	0.33
	28	3	5.6–7.0; 6.20 (0.72)	16.8–19.2; 18.33 (1.33)	0.34
	30	2	6.0; 6.00 (0.00)	18.2–18.4; 18.30 (0.14)	0.32
	34	1	7.0	22.2	0.33
	35	2	7.0–7.6; 7.30 (0.42)	21.6–23.0; 22.30 (0.99)	0.33
	36	1	7.4	22.6	0.33
	37	4	6.0–8.0; 7.00 (0.82)	20.2–25.0; 21.93 (2.66)*	0.32
	41	8	6.6–8.0; 7.23 (0.47)	19.2–26.0; 21.55 (3.04)*	0.34
	42	5	6.8–8.0; 7.44 (0.43)	20.6–24.4; 23.07 (2.14)*	0.32
	43	2	6.4–7.4; 6.90 (0.71)		
O. vicentei	25	9	1.8–4.5; 2.5 (0.79)	7.0–13.0; 8.3 (1.92)	0.30
	33	1	6.5	16.0	0.41
	41	1	7.0	19.8	0.35

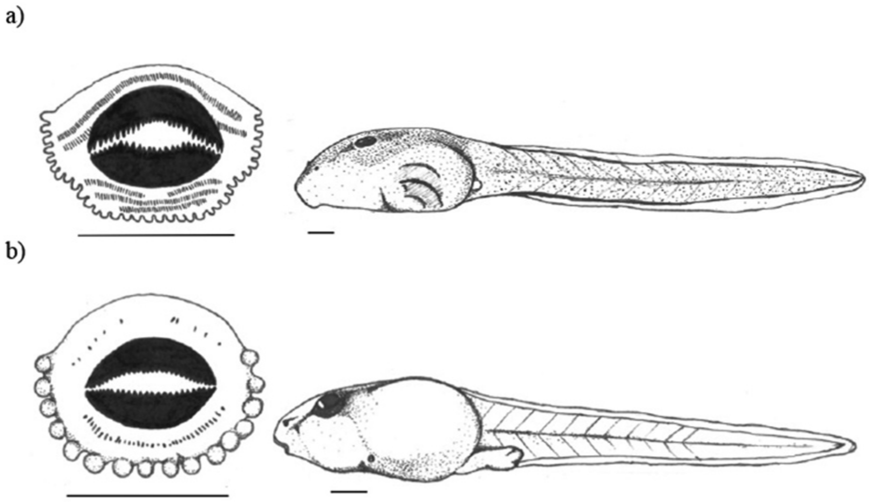

FIGURE 1. (a) Tadpole of *Andinobates geminisae* at Stage 28, oral apparatus and left lateral view; (b) Tadpole of *Oophaga vicentei*, combining the body shape at Stage 33 and the oral disc of a Stage 41 specimen to show the highest LTRF 1/1. Scale bars = 1 mm.

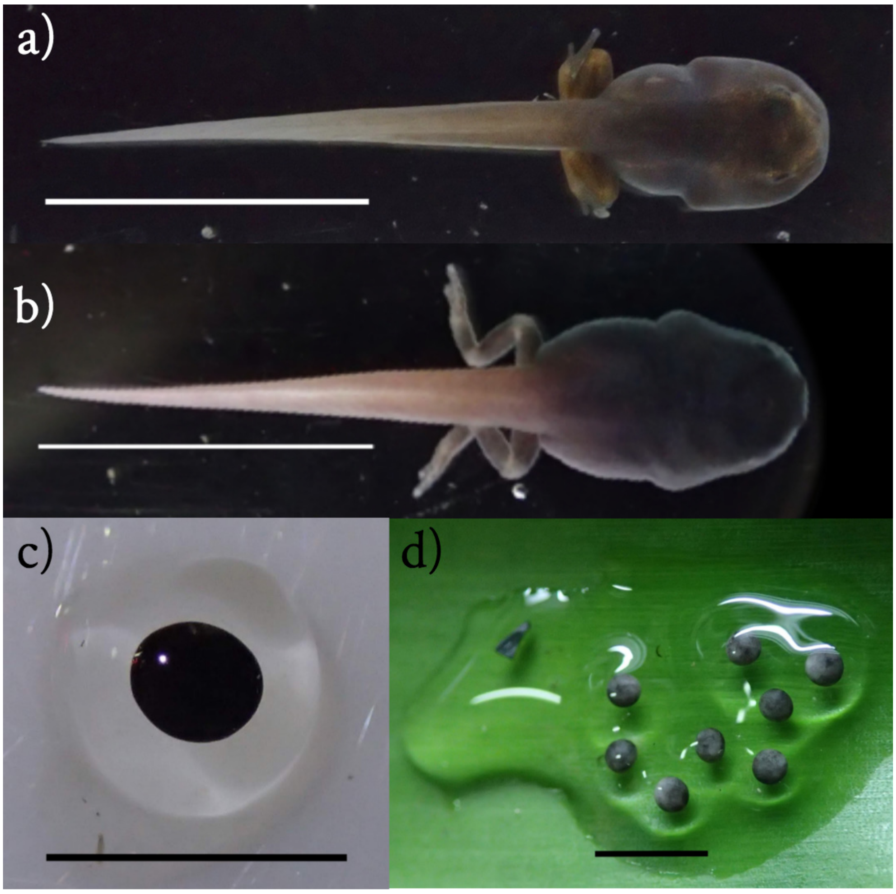

FIGURE 2. Stage 41 tadpoles of (a) preserved *Andinobates geminisae* and (b) live *Oophaga vicentei* and ≤ 3 Stage eggs of (c) *A. geminisae* and (d) *O. vicentei.* Scale bars = 10 mm (a,b) and 5 mm (c,d).

Oophaga vicentei

Body length and total length measurements of *O. vicentei* tadpoles are summarized in Table 1. The body is ovate and slightly tapered at the anterior end (Fig. 1B). Eyes are located dorsally and oriented anterolaterally. Nares are round without projection in the inner margin of the nasal rim and are located dorsally. The vent tube is median, and the spiracle is sinistral. The oral disc is round and not indented, with enlarged oral papillae surrounding the posterior labium and the lateral margins of the anterior labium. LTRF is 1[1]/0 in all but one specimen in the sample, a Stage 41 tadpole that also has a posterior labial tooth row. We can not rule out the possibility that decomposition may have played a role in the number of specimens observed to lack a posterior labial tooth row. The anterior labial teeth are scarce and large, and the jaw sheaths are thick and serrate, the upper sheath U-shaped. The oral disc is oriented anteroventrally. In ethanol, *O. vicentei* specimens are uniformly gray in colour from above and below and translucent around the margins of the tail. A differentiated short gut in the abdominal area can be noticed. Live specimens are dark grey to black in colour, with darker speckling on the body and tail, and translucent along the margins of the tail (Fig. 2B).

Thirteen *O. vicentei* eggs from 5 different breeding pairs were examined in detail. In our sample, there was 1 clutch of 4 eggs, 2 clutches of 3 eggs, 1 clutch of 2 eggs (only 1 egg measured), and 2 clutches of 1 egg, but there may be anywhere between 1 and 12 eggs per clutch for this species, based on past observations. The clutches formed a cohesive transparent mass of eggs (Fig. 2D). The eggs (n = 13, embryo with jelly coat) measured approximately 3 mm in diameter. The embryos at Stages 0–3 had varying amounts of light grey at the vegetal pole, and dark grey at the animal pole, and had an average diameter of 1.6 mm (n = 13, SD = 0.10 mm).

Andinobates altobuyensis, A. claudiae, *A. fulguritus*, *A. geminisae* and *A. minutus* tadpoles have a complete row of oral papillae along the posterior edge of the oral disc. This feature distinguishes them from other species described, all which have a large medial gap interrupting the posterior row of oral papillae (Bernal *et al.* 2007; Brown *et al.* 2011; Duarte-Marín *et al.* 2020; Myers & Daly 1976, 1980; Ruiz-Carranza & Ramírez-Pinilla 1992; Silverstone 1975). Myers & Daly (1980) first proposed the medial gap in the posterior oral papillae as a synapomorphy, joining *A. abditus, A. bombetes, A. daleswansoni, A. opisthomelas, A. tolimensis* and *A. virolinensis* in the *A. bombetes* group (Brown *et al.* 2011; Duarte-Marín *et al.* 2020). Current distribution of this character is consistent with molecular phylogenetic hypotheses (e.g., Amézquita *et al.* 2013; Márquez *et al.* 2017). Nonetheless, the oral papillae along the posterior margin of the oral disc of *A. supata* tadpoles require further examination, since no gap has been reported for this species of the *A. bombetes* group (Chaves-Portilla *et al.* 2021).

Tadpoles from the genus *Oophaga* can be distinguished from tadpoles from other dendrobatid genera by their tapered egg-shaped body, reduced tooth rows (maximum one anterior and one posterior row) and the large size of the scarce oral papillae lining the entire posterior labium and the lateral regions of the anterior labium. However, we could not distinguish between described tadpoles of the genus *Oophaga* based on morphology alone. *Oophaga vicentei* tadpoles are indistinguishable from *O. arborea, O. granulifera*, *O. histrionica, O. pumilio* and *O. speciosa* for most observed traits (Jungfer 1985; Myers *et al.* 1984; Savage 1968; Silverstone 1975; Starrett 1960; van Wijngaarden & Bolaños 1992). *Oophaga vicentei* tadpoles differ from the only *O. speciosa* tadpole specimen described that lacks the anterior tooth row (Jungfer 1985).

Oophaga spp. tadpoles exhibit a reduced oral morphology that is typical of egg-eating dendrobatid tadpoles (van Wijngaarden & Bolaños 1992; Caldwell & De Araújo 1998). Furthermore, *Oophaga* spp. tadpoles share oral morphological features (i.e., an antero-ventrally positioned mouth, reduced tooth rows and tooth number, large jaw sheaths) that are considered to be adaptations to an egg-based diet in other groups of anuran larvae (Kishimoto & Hayashi 2017; Kuramoto & Wang 1987; Wassersug *et al.* 1981), and could be well-conserved in the genus *Oophaga* because they hold a similar adaptive significance.

Andinobates minutus eggs taken from the ovary of a dissected female were 3 to 4 mm in diameter (Silverstone 1975), but these had not likely acquired their full size yet. Information on eggs from other congeneric species is missing, except for a brief note of "brown eggs", of unknown stage or state of preservation, from *A. daleswansoni, A. dorisswansonae* and *A. tolimensis* (Bernal *et al.* 2007; Rueda-Almonacid *et al.* 2006). Our observations on the clutch size of *O. vicentei* eggs are consistent with reports from Jungfer *et al.* (1996), who indicated that a female laid 2-6 eggs after mating.

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