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The Tadpole of *Proceratophrys avelinoi* (Anura: Leptodactylidae)

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ly covered forest. Because of their greater deciduousness, upland habitats present a greater availability of gaps and may provide lizards with more thermal options to sustain activity during the dry season.

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The Tadpole of *Proceratophrys axelinoi* (Anura: Leptodactylidae)

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The genus *Proceratophrys* is poorly known. It consists of 14 currently recognized species (Frost, 2000) of medium-sized frogs distributed from northeastern Argentina and Paraguay to southeast Amazonia (Rondonia State), eastern and southern Brazil. *Proceratophrys axelinoi* was described from Misiones, Argentina (Mercadal de Barrio and Barrio, 1993). The larval stage of this species is unknown. Herein, we describe the tadpole and the characteristics of the internal oral anatomy of *P. axelinoi* using scanning electron microscopy (SEM).

Proceratophrys axelinoi tadpoles ($N = 6$) were collected at Estancia Hidromineral Santa Clara, Munic. Guarapuava, Paraná State, Brasil, in June 1998. The tadpoles were in a pond, about 5.0 cm deep; the surface of the pond was covered with aquatic vegetation. This pond was located about 100 m from the margin of the Jordão River. The specimens are deposited at the Museu de Historia Natural Capão da Imbuia, Curitiba, Paraná, Brasil, with number MNHCI 4198. Spec-

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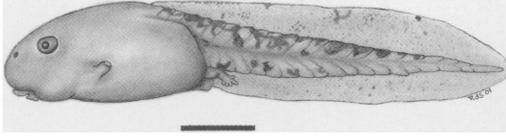


FIG. 1. Tadpole of *Proceratophrys axelinoi*, stage 36 MNHCI 4198. Bar = 5.0 mm.

imens were fixed in 10% formalin (commercial grade) and staged following Gosner (1960). Tadpoles were preserved during development, but two larvae were kept alive until they completed metamorphosis for species identification.

Measurements and terminology follow Lavilla and Scrocchi (1986) and Altig and McDiarmid (1999). Measurements were made using a Mitutoyo digital calliper under a binocular microscope with an ocular grid; average and standard deviation (\bar{x} , \pm SD) are given in the description. The description of larval external morphology is based on examination of specimens in Gosner's stages 30, 35, and 36. Tadpole illustration is based on a Gosner's stage 36 specimen. A tadpole in Gosner's stage 36 was dissected for SEM analysis. The specimen was prepared as follows: ultrasonically cleaned for 15 min, fixed in 3–4% solution of glutaraldehyde for 2 h at room temperature (rt), followed by three 15 min washes with 0.1 M phosphate buffer, postfixed for 2 h in a 1% solution of osmium tetroxide rt, three 15-min washes in 0.1 M phosphate buffer were repeated. Subsequently, samples were dehydrated using 15-min changes of the following graded ethanol series: 35%, 50%, 70%, 80%, 95%, and three 100% changes. Specimens were critical point dried in CO₂, mounted on aluminum stubs and sputter coated with gold/palladium, 22 nanometers thick, using a Hummer VII sputtering system. Internal oral anatomy was examined in a Hitachi S-2300 scanning electron microscope at 15 kV, 20 kV and 25 kV and photographed using Polaroid 55 positive/negative film. Morphological features were recorded using the methodology presented by Wassersug (1976) and Wassersug and Heyer (1988).

Tadpole Description.—*Proceratophrys axelinoi* tadpoles have an elliptical, slightly depressed, and elongated body (Fig. 1). In dorsal and lateral views, the snout is rounded; in lateral view, the snout slopes gradually anteriorly toward the oral disc. The eyes are large and directed laterally; eyes are positioned dorsolaterally on the body. The external nares are located half way between the eyes and the tip of the snout. Narial openings are small, rounded, laterodorsally positioned and have a well-defined marginal rim. A low papilla, with a dark pigment spot on its tip, is present on the inner (= medial) margin of the each nares. Tail fins are low, dorsal and ventral fins nearly parallel the tail musculature. Dorsal fin is slightly higher than ventral fin. The dorsal fin originates at the tail-body junction, and the ventral fin originates at the posterior ventral terminus of the body. Tail fins slope to a broadly rounded tail tip. Tail musculature extends to the posterior tip of the tail. The spiracle is sinistral and has a mid-lateral opening. The vent tube is large; vent tube and vent tube's apertures are dextrally placed relative to the ventral fin.

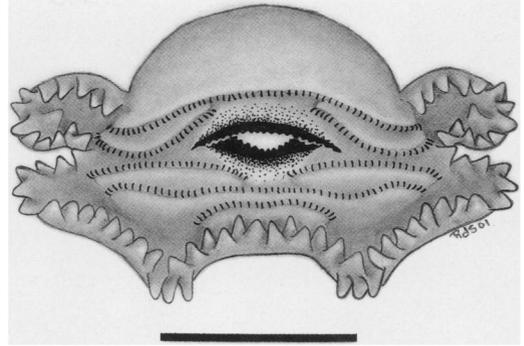


FIG. 2. Oral disk of *Proceratophrys axelinoi*, stage 36 MNHCI 4198. Bar = 1.0 mm.

Measurements in Millimeters (N = 4).—Sensu Altig and McDiarmid (1999): body length (\bar{x} \pm SD): = 12.2 \pm 0.62; tail muscle height: 3.1 \pm 0.3; fin height: 5.8 \pm 0.54; sensu Lavilla and Scrocchi (1986): total length: 32.6 \pm 3.2; eye diameter: 1.1 \pm 0.05; interorbital distance: 2.6 \pm 0.35; body maximum width: 7.9 \pm 0.64; body width at eyes: 6.1 \pm 0.37; body width at nostrils: 4.2 \pm 0.06; body maximum height: 6.5 \pm 0.72; rostrospiracular distance: 6.6 \pm 0.34; frontonasal distance: 2.2 \pm 0.24; naso-ocular distance: 1.1 \pm 0.21; nostril diameter: 0.38 \pm 0.05; eye diameter: 1.1 \pm 0.05; inter-narial distance: 1.6 \pm 0.13; width of oral disc: 2.2 \pm 0.17; width of dorsolabial gap: 1.4 \pm 0.12.

Coloration of Fixed Specimens.—Specimens in 10% formalin are overall brown, with tail musculature being light yellowish. The myotomes of the caudal musculature are visible, but they are not strongly marked. The tail fins and tail musculature are speckled with dark melanophores. Large, irregular-shaped, dark brown spots are scattered over the tail musculature, particularly close to the dorsal edge of the epaxial musculature. Melanophores are more abundant on the dorsal fin than on the ventral fin. The dorsal and dorsolateral surfaces of the body are homogeneously brown, grading continuously to a light brown and almost translucent ventral surface.

Oral Disc.—The oral disc is positioned ventrally, deeply emarginate and has two large folds of the posterior labium. The oral disc has a single row of large and conical marginal papillae with blunt tips (Fig. 2). This row of marginal papillae has a large dorsal gap occupying most of the upper labium. Furthermore, two sets of three slightly larger papillae project from the lower labium at the level of labial folds. These larger papillae are not entirely aligned with the row of marginal papillae; when the oral disc is closed, these papillae seem to form a second, outer, row of papillae. This arrangement is not quite visible in an open, extended, oral disc where it appears as a single row of marginal papillae. A single submarginal papilla is found laterally on the upper labium. The labial tooth row formula (Altig, 1970) is 2(2)/3(1), with the lower third row being the shortest. Upper and lower jaw sheaths are wide, pigmented for about one-third of their width, and their edge is serrated.

Internal Oral Anatomy.—Oral roof overall semicircular, with a narrow pre-narial arena. A transverse

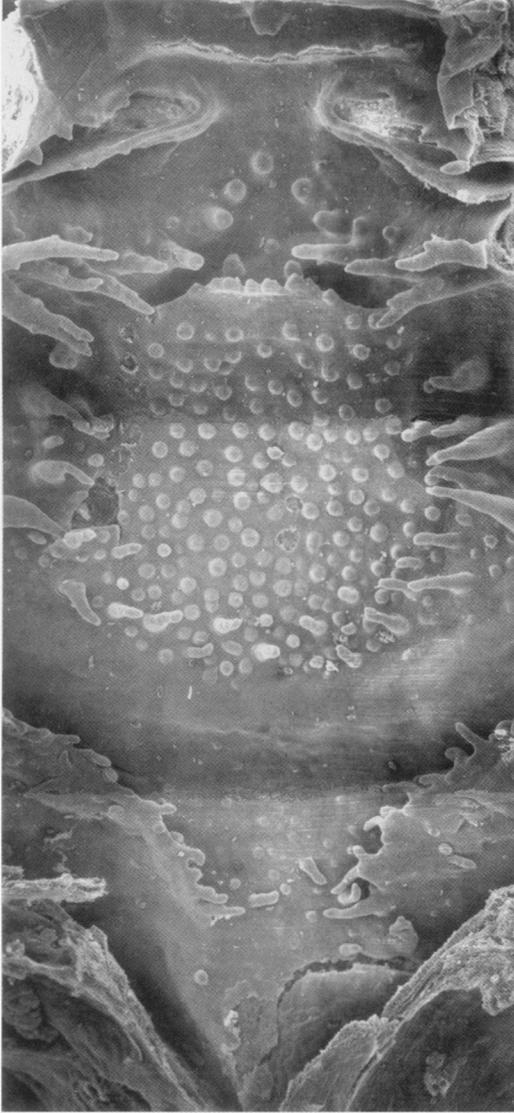


FIG. 3. SEM micrograph of roof of oral cavity of *Proceratophrys axelinoi*; Gosner Stage 36.

ridge is present in the prenarial arena, immediately in front of the internal nares. Nares are wide, obliquely oriented, and placed about one-fourth way back on buccal roof (Fig. 3). The anterior edge of each naris bears four or five prenarial papillae, whereas the posterior edge has a posteriorly convex narial valve, with a very small narial-valve projection. Postnarial arena complex. Two rows of postnarial papillae form a triangle in the postnarial arena, the apex of this triangle lies behind and between the internal nares. The postnarial papillae increase gradually in size posteriorly. Three or four additional papillae are found within this triangle of postnarial papillae. Median ridge large, trapezoidal, with large, pointed, papillae on its free edge. Lateral ridge papillae elaborate, oriented trans-



FIG. 4. SEM micrograph of floor of oral cavity of *Proceratophrys axelinoi*; Gosner Stage 36.

versely on each side of the median ridge and with long, fingerlike, papillae projecting medially. Buccal roof arena (BRA) rounded and bounded anteriorly by the median ridge and latero-posteriorly by about 30 elongate and pointed papillae, with largest papillae placed most laterally. An even field of large pustulations is present within the BRA. Dorsal velum long, curving gradually toward the midline, with a clear medial gap and a papillate margin. Glandular zone poorly defined or absent. Buccal floor overall triangular and broad (Fig. 4). Two pairs of infralabial papillae present, the most anterior pair is slightly oblique but almost perpendicular to the transversely oriented second pair. The first pair of infralabial papillae is deeply forked, with a larger posterior branch. The second infralabial papilla is divided into four blunt papillae connected basally. Four long and attenuate lingual papillae are present. Buccal floor arena (BFA) is U-shaped and bounded by about 20–25 long, attenuate, papillae. Large pustulations are homogeneously scattered within the BFA, a few smaller papillae are present among these pustulations. Velar surface free, long, and with continuous slightly jagged posterior margin. Median notch and secretory pits absent. Gill filters of moderate size with an average filter mesh.

The larvae of eight only of the 14 species of *Proceratophrys* have been previously described. These are *Proceratophrys appendiculata* (Peixoto and Gonçalves da

Cruz, 1980), *Proceratophrys boiei* (Izecksohn et al., 1979), *Proceratophrys cururu* (Eterovik and Sazima, 1998), *Proceratophrys concavitimpanum* (Giaretta et al., 2000), *Proceratophrys laticeps* (Peixoto et al., 1981), *Proceratophrys moehringi* (Weygoldt and Peixoto, 1985), *Proceratophrys palustris* (Giaretta and Sazima, 1993), and *Proceratophrys precrenulata* (Peixoto et al., 1984, = *Proceratophrys schirchi* sensu Caramaschi and Velosa, 1997).

The larva of *P. avelinoi* is similar to other *Proceratophrys* larvae. *Proceratophrys* larvae have a slightly depressed body, more markedly depressed in *P. cururu*, *P. laticeps*, and *P. moehringi*. Tail length is about 1.5× body length in all larvae except *P. concavitimpanum*, *P. laticeps* and *P. moehringi*, where tail length is almost twice body length. The oral disk of *P. avelinoi* is surrounded by a single row of marginal papillae, although two sets of slightly larger papillae seem to form a second row projecting from the lower labium. This character has not been previously reported; however, this can be attributed to previous reports describing and illustrating an expanded, open, oral disk, in which the arrangement described herein for *P. avelinoi* is not clearly visible. A closer look at the figures of *P. boiei* (Fig. 4, Izecksohn et al., 1979) and *P. laticeps* (Fig. 4, Peixoto et al., 1981) do seem to mark larger papillae in the same position as those described for *P. avelinoi*.

Submarginal papillae are not reported for other species of *Proceratophrys*, except *P. concavitimpanum* that has submarginal papillae in the lower labium and posterolaterally. Furthermore, for *P. boiei* a "few" submarginal papillae were reported present ("...e unas poucas mais internas," Izecksohn et al., 1979), and for *P. cururu*, submarginal papillae were reported as "scattered laterally," but were not illustrated (Eterovik and Sazima, 1998). In *P. avelinoi*, we found a single submarginal papillae located laterally on the upper labium. Additional data on *Proceratophrys* larvae were presented in tables comparing *Proceratophrys* and *Odontophrynus* tadpoles by Rossa-Feres and Jim (1996) and Brandão and Batista (2000).

Besides the differences noted above, all *Proceratophrys* larvae, including, *P. avelinoi*, exhibit the following characters: (1) oval body; (2) low caudal fins; (3) ventral mouth; (4) sinistral spiracle with midlateral opening; (5) dextral vent tube and vent tube's opening; (6) labial tooth row formula 2(2)/3(1) (except *P. appendiculata*, which has a 2/3(1) formula); (7) oral disk emarginate and with two folds of the posterior labium; (8) a single row of marginal papillae with a large rostral gap; and (9) serrated, keratinized jaw sheaths.

The information available on the internal oral anatomy of *Proceratophrys* is limited to that reported for *P. appendiculata* and *P. boiei* (Wassersug and Heyer, 1988). The gill plates and density of filter mesh in *P. avelinoi* are similar to those of *P. boiei*, suggesting a generalized microphagous feeding diet. A few common characteristics in the three species are (1) large attenuate papillae present in the buccal roof and floor; (2) BFA and BRA with extensive amount of postulations; (3) four, long, lingual papillae; (4) large and elaborate lateral ridge papillae; (5) dorsal velum curving medially; and (6) glandular zone poorly defined or absent.

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Diet of the Timber Rattlesnake, *Crotalus horridus*

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The diet of a species is one of the defining aspects of its ecology, and detailed information on food habits is often necessary to approach broader ecological or behavioral questions. This is particularly true for snakes: detailed dietary information has been the basis for studies of foraging behavior (Lind and Welsh, 1994), predator-prey coevolution (Brodie and Brodie, 1990; Downes and Shine, 1998; Heatwole and Powell, 1998), behavioral genetics (Arnold, 1980; Burghardt, 1993), optimal foraging theory (Arnold, 1993), community ecology (Cadle and Greene, 1993), and the evolutionary origins of specialized morphologies (Greene, 1983; Pough and Groves, 1983). However, despite its importance, detailed knowledge of food habits is often lacking, even in well-studied species, such as the timber rattlesnake, *Crotalus horridus*.

The timber rattlesnake is a widespread viperid in the deciduous forests of the eastern third of the United States. It is the model organism for numerous research programs (summarized in Brown, 1993), yet some basic aspects of its ecology, including its natural diet, are still relatively poorly known. Even though several accounts have been published (summarized in Table 1), they consist mainly of lists of prey taken by individual snakes from a localized area. Almost nothing is known about how diet varies ontogenetically, seasonally, or geographically.

I examined the feeding ecology of *C. horridus* by synthesizing previously published dietary records with new information about the stomach contents of museum specimens. Geographic variation in diet was assessed by comparing the food habits of snakes from the northern deciduous forest province with snakes from the southern coastal plain and mixed forest province. I also analyzed ontogenetic dietary variation by comparing the size of snakes that specialize on

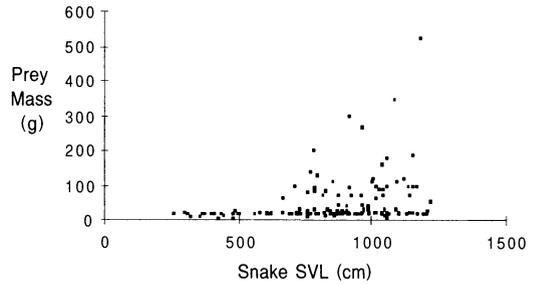


FIG. 1. Relationship between prey mass and snake body size (SVL) in *Crotalus horridus* ($N = 144$). The shape of the plot shows that larger snakes expand their diet to include larger prey items but do not eliminate small items from their diet as they grow.

specific prey taxa. The resulting dietary database not only fills a gap in our knowledge of the natural history of this species but may also serve as a foundation for further research on predator-prey interactions, foraging behavior, habitat use, and community structure.

I examined all available preserved specimens of *C. horridus* ($N = 1108$) in the collections of Cornell University, Carnegie Museum of Natural History, University of Michigan Museum of Zoology, Chicago Academy of Sciences, Field Museum of Natural History, University of Illinois Museum of Natural History, Illinois Natural History Survey, New York State Museum, National Museum of Natural History, North Carolina State Museum, University of Florida, Auburn University Museum, and University of Kansas Natural History Museum. I checked each specimen for stomach contents by making a midventral incision, omitting only fragile individuals and those specimens whose collection information indicated that they were not likely to contain stomach contents (i.e., there was a significant discrepancy between the date of collection and the date of preservation). For each snake with prey in its stomach, I recorded collection locality, snout-vent length ($SVL \pm 1$ cm), sex, body mass without stomach contents (± 1 g) and the number of items in the stomach. When possible, I also recorded direction of ingestion. All snakes were weighed after being blotted dry with paper towels. Stomach contents were identified to as low a taxonomic level as possible by comparison with museum specimens, or from microscopic examination of hair (Adorjan and Kolenosky, 1969). The mass at time of ingestion was estimated for relatively intact prey items by comparing them to conspecific specimens deposited in the Cornell University museum. This was not possible for several items, which consisted of only fur or feathers. Specimens that I suspected were fed in captivity were excluded from analysis.

When possible, I have incorporated previously published dietary records of *C. horridus* (listed in Table 1) in the analyses presented in this paper. However, most previously published dietary records contain only information on general locale and prey identity and so are of limited use.

For analysis of geographic variation in diet, I used a map of potential natural vegetation (Kuchler, 1985) to divide the specimens into two groups—one from