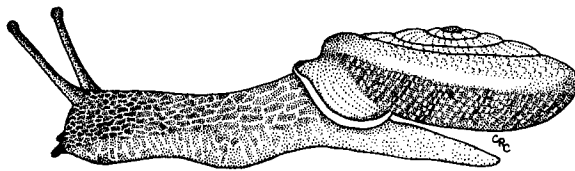


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DESCRIPTION OF THE TADPOLE**

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ABSTRACT.—The breeding habits of *Bufo coccifer* were studied in northwestern Costa Rica between 1971 and 1974. This species breeds during the rainy season, at least from May through August. Males chorus from areas of shallow water. Their calls resemble those of Mexican representatives of the species in pulse rate and duration, but are closer to those of other Costa Rican and Panamanian populations in dominant frequency. Thus, our data do not clearly support recognition of *Bufo cycladen* as a distinct species for the Mexican populations. Amplexus is axillary, and two strings of eggs are extruded simultaneously during oviposition. Tadpoles, described for the first time in this paper, are secretive and do not aggregate. Development to metamorphosis requires about 5 weeks.

Bufo coccifer Cope is a medium sized toad known from localities primarily along the Pacific versant of Mexico and Central America from sea level to about 2000 m elevation (Zweifel, 1965; Porter, 1964a, 1965; Meyer and Wilson, 1971). The mating calls of the Mexican and Central American populations of *Bufo coccifer* differ (Zweifel, 1965; Porter, 1965). These vocal characteristics, together with slight morphological differences, were used to justify recognition of the Mexican populations as a distinct species, *Bufo cycladen* (Lynch and Smith, 1966). Porter (1967) argued that *Bufo cycladen* was a *nomen dubium*. Although Smith and Smith (1976) recognized the distinctness of the Mexican populations, little information has been published on the species in the past 15 years. The tadpole has not been described.

During the course of our work on the reproductive ecology and behavior of frogs in the Tropical Dry Forest formation of northwestern Costa Rica, we obtained considerable data on the breeding biology of *Bufo coccifer*. Herein, we report our observations and describe the tadpole of this species.

STUDY SITE.—The study area was located on the property of Estación Experimental Enrique Jiménez Nuñez in Guanacaste Province, Costa Rica. This station, owned and operated by the Ministerio de Agricultura y Ganadería of Costa Rica lies about 13.6 km SW Cañas in a zone of Tropical Dry Forest (Tosi, 1969). General site descriptions of the area exist (e.g., Orians and Paulson, 1969; Holdridge et al., 1971; Sawyer and Lindsey, 1971; Janzen, 1973; McDiarmid et al., 1977). However, these papers refer primarily to the forested regions of the farm, particularly those in riparian areas. Although individual *Bufo coccifer* occasionally are found in forest habitats, these toads are located more commonly in areas where the forest has been cleared for pasture or cultivation.

Observations were made in two types of cleared areas. One was a pasture about 2.4 by 1.0 km located at the base of Cerro Eskameca and adjacent hills (Fig. 1). The somewhat irregular pasture (ca. 10 m elev.) is sown with various introduced forage grasses and supports small weedy herbs (e.g., Compositae, Malvaceae, Euphorbiaceae), vines (e.g., Cucurbitaceae, Leguminosae, Bignoniaceae), small saplings of various forest trees (especially *Enterolobium cyclocarpum*), and a number of leguminous shrubs. One of the shrubs, *Mimosa pigra*, grew in dense stands covering large areas. Usually, toward the end of each dry season, the pasture areas were plowed and all surface vegetation was turned under. With the first rains, new grass sprouted, and cattle and horses were turned out to graze. Within the pasture areas three ponds filled in May or June and, except in



FIG. 1.—Irrigation canal (above), flooded pasture (middle), and flooded roadside (below) at Estación Experimental Enrique Jiménez Nuñez, used as breeding sites by *Bufo coccifer*.

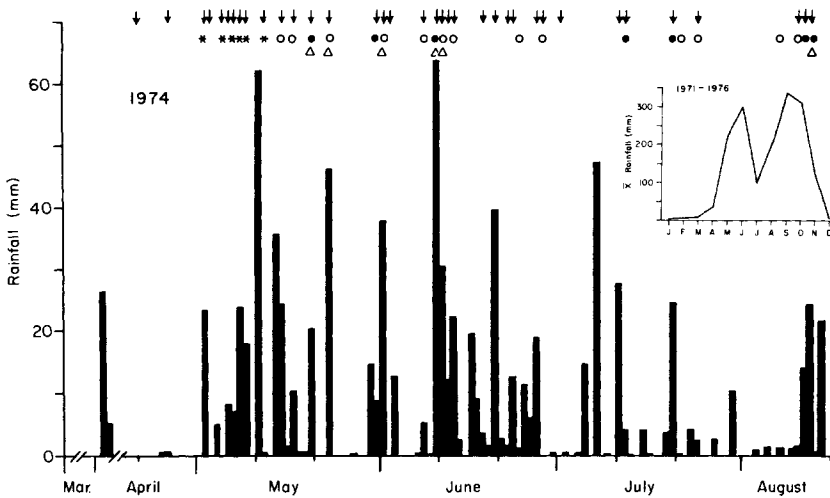


FIG. 2.—Schedule of nighttime visits, rainfall, and *Bufo coccifer* activities between 1 March and 15 August 1974 at Estación Experimental Enrique Jiménez Nuñez. Arrow = nighttime visit to all study sites. *B. coccifer* activities: asterisk = frogs active but not calling; circle = few individuals calling; dot = chorus; triangle = amplexing pairs. Inset depicts mean monthly rainfall at Estación Jiménez, 1971-1976.

drought years, contained water at least through October. In addition, certain areas of pasture, as well as a system of irrigation canals of varying depth, flooded with every rain to form shallow temporary ponds persisting from one day to several weeks. Puddles also formed in small, but relatively deep, depressions scattered throughout the pasture.

Observations were made also in shallow ditches adjacent to a dirt road (Fig. 1) running from the station headquarters along the side (ca. 65 m elev.) of Cerro Eskameca down to the Rio Higerón (5 to 10 m elev.) following the contour of the hills. The hillside above the road was covered with vegetation very similar to that described as Janzen's (1973) Taboga primary hill. The lower hillside was mostly cleared and covered with pasture plants. Rainfall in this region of Guanacaste is highly seasonal (Fig. 2). The wet period extends from May through October, but is interrupted by a short dry period in July. Even during the rainy season, however, rain does not fall every day (see Methods section below and Fig. 2).

METHODS.—Daily inspections of potential breeding sites began in early March or April and indicated that sites were completely dry until mid-late May. Systematic nighttime observations were initiated after the rains began but before the breeding sites became available. A nighttime observation unit included one complete loop of the study area during which the entire lengths of the road and the pasture area were traversed, all ponds and flooded areas were visited, and irrigation canals were checked at intervals along their lengths. The location of any toads observed was noted and their behavior recorded. Nighttime observations were made between 1800 and 0500 h for a period of from 1 to 5 h, depending on frog activity (occasionally two or three loops were made at different times during a single night). Complete loops were made on 73 nights, 7 between 20 May and 13 June 1971, 13 between 9 May and 12 July 1972, 17 between 2 May and 13 July 1973, and 36 between 20 April and 13 August 1974 (Fig. 2). Additional observations were made on other nights in the vicinity of the station headquarters and in other areas of the farm. Yearly observations were terminated in mid-July or August when we left the study area or when frog reproductive activity was minimal.

On 20 of the 73 nights on which loop visits were made, the rainfall (measured over a 24-h period beginning at 0700 h) exceeded 25 mm; on 22 nights it ranged from 10.1 to 25 mm, and on 31 nights it measured 0 to 10 mm. In the periods from 1 March to 15 July in 1971 through 1973 and from 1 March to 15 August 1974, more than 25 mm of rain fell on only 36 days and between 10 and 25 mm on an additional 51 days. Therefore, reproductive activity was adequately sampled

under all conditions of rainfall, especially as more than 10 mm of rain fell on several days during the transition from the dry to wet season and did not result in any standing water.

One amplexant pair was brought to the laboratory so that oviposition could be observed. The pair was maintained in a metal tank ca. 46 cm in diameter filled with water to a depth of 6 cm. Tadpole behavior was observed periodically in the field, and some individuals were sampled and preserved in 10% buffered formalin. An attempt to rear tadpoles in the laboratory in plastic dishes (19 by 12 by 8 cm) was not successful. They were fed Tetra Min, a commercial fish food, but grew poorly and did not metamorphose. These specimens and field-collected tadpoles and adults are in the collection of the National Museum of Natural History (USNM).

A Uher 4000 Report-L tape recorder and M 516 microphone were used to record vocalizations at a speed of 7.5 ips on 1 mil polyester tape. Ambient and water temperatures at the recording times were 26.7°C and 28°C, respectively. Body temperatures of calling frogs were not determined. Recordings were analyzed on a Kay Electric Co. Audio Spectrum Analyzer, Model 7029A at a wide band, 80 - 8,000 Hz setting. Lengths of calls were determined by timing the tape recordings with a stopwatch.

PRE-MATING ACTIVITY AND VOCALIZATIONS.—At the study site, *B. coccifer* breeds during the rainy season at least from May through August. Although the rains began in mid-April and toads were active at night between 15 April and 15 May, males did not start calling until mid-May (Fig. 2). Although calling occurred fairly regularly after mid-May, fewer individuals and less breeding activity were noted from mid-June to mid-July. Amplexant pairs were particularly common from mid-May to mid-June. No pairs were noted in the last half of June or in July in any year, but some were seen again in August (Fig. 2). The decrease in breeding activity during this period may reflect the reduced rainfall, or it may be indicative of a recovery period during which females yolk a second clutch of eggs.

A few individuals began calling at dusk, but maximum numbers were active between 2030 to 2300 h; number of vocalizations tapered off after 2300 h, although occasional individuals could be heard at any time during the night. Calling males were found at the periphery of shallow flooded areas, puddles, and less commonly, larger ponds. They usually sat half submerged in a few centimeters of water but occasionally called from the bank. The males were scattered around the small puddles (to ca. 3 m diameter), but seemed to cluster in areas along the perimeter of the larger bodies of water. They also called from open water or from dense growths of grass or herbs.

Males called in bouts lasting several minutes. During each bout, vocalizations of individuals in the group overlapped broadly. The chorus alternated with periods of silence 30 sec to several minutes long. Reinitiation of calling by one or a few individuals stimulated all the males in the group to resume calling. When a male *B. coccifer* called, his single central vocal sac was greatly inflated and appeared bright lemon yellow. We suspect calling males are especially vulnerable to predation. On 20 May an adult *Leptodeira annulata* in the shallows of a large puddle was found eating an adult *B. coccifer*. When captured, the snake regurgitated the partially swallowed, live toad which had been eaten head first. We suspect that many predators, including snakes, are attracted to males by their calls.

The shrill, buzz-like call of *Bufo coccifer* was described from individuals recorded from the Isthmus of Tehuantepec, Oaxaca, Mexico, by Porter (1964b), who noted its high pulse rate and high dominant frequency. Zweifel (1965) published an audiospectrogram of the mating call of *B. coccifer*

recorded near Nueva Gorgona, Panama Province, Panama. He commented on the slower pulse rate, lower frequency, and longer duration of the calls of the Panamanian population compared with those of the Mexican population. Zweifel (1965) mentioned that call differences of the magnitude observed usually were indicative of a specific relationship. The differences reported by Zweifel (1965) were confirmed by Porter (1965), who described the intraspecific variation in mating calls of 16 populations of *Bufo coccifer* from Guerrero, Mexico, southward to Guanacaste Province, Costa Rica. Toads from the Mexican populations had shorter calls with a faster pulse rate and a higher frequency than those from Central America. These data were used by Lynch and Smith (1966) to distinguish the Mexican populations, which they named *Bufo cycladen*, from *Bufo coccifer* in Central America. In response, Porter (1967) argued that additional experimental work with the call differences was necessary before species status for the Mexican populations was acceptable, especially in view of the inconsistent morphological differences between the two named taxa.

We analyzed the call characteristics (Fig. 3) of four *Bufo coccifer* from our study site and compared them with those reported by Porter (1965) from Costa Rica, by Zweifel (1965) from Panama, and by Porter (1965) from Mexico (Table 1). Our call data are similar to those for other Costa Rican toads (Porter, 1965) in pulse rate and dominant frequency but differ in call length. In this parameter our Costa Rican sample is more similar to the Mexican toads than to other Costa Rican and Panamanian samples (Table 1). Larger samples are needed to clarify these differences. The Costa Rican toads have a pulse rate slower than that of Mexican toads but much faster than the Panamanian animals (Zweifel, 1965). In dominant frequency the Panamanian and Costa Rican calls are similar but different from those of the Mexican sample. We agree with Porter (1967) that the call data do not clearly support specific recognition of the Mexican population and that clarification requires a more thorough analysis, possibly with the use of experimental playbacks to test the effectiveness of the call as an isolating mechanism.

AMPLEXUS AND EGG-LAYING.—As in other species in the genus, amplexus in *Bufo coccifer* is axillary. The male generally is much smaller than the female (three adult females with well developed eggs measure 55.6, 64.4, and 77.3 mm, and three adult males with nuptial pads measure 46.3, 52.8, and 53.7 mm SV lengths). He holds onto her back with his body tightly pressed against hers. The hind legs of the male are bent, and his feet rest on the female's dorsolateral body surfaces just anterior to her thighs. If amplexus occurs away from a suitable egg-laying site, the female carries the male until one is located. Eggs usually are deposited in water 5 to 15 cm deep. Once a suitable site is found, the pair remains in amplexus for some time before egg-laying begins. If the water is shallow, she sits on the bottom with her head almost completely exposed, whereas, at times, his may be partially to completely submerged.

Oviposition by one amplexant pair was observed in the laboratory. When egg-laying is imminent, the female floats in a slanted position with her posterior end lower than her head. The slightly bent front legs stretch out

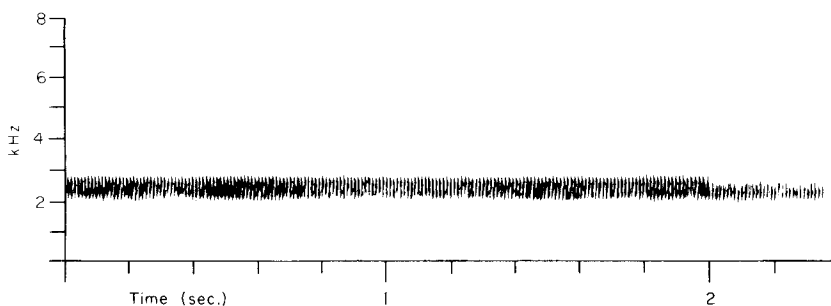


FIG. 3.—Sound spectrograph of calls from a chorus of *Bufo coccifer* recorded at Estación Experimental Enrique Jiménez Nuñez on 20 May 1974.

anterolaterally, and the slightly bent hindlegs slant posteriorly so her toes just touch the bottom. First one side of her body, then the other, is flattened as the lateral body muscles contract strongly. The contractions follow each other regularly, but at a low rate, each lasting ca. 1 to 2 sec and separated by intervals of several seconds. A series of 5 to 15 contractions is followed by a rest period of variable length (often as long as a minute or more). Throughout this time, the male remains perched on the female's back with his body and chin very tightly pressed against her, the tip of his nose just about reaching her midparotoid area. No eggs are extruded with these contractions; presumably she has just moved them into the ovisac. (Similar contractions occurred at irregular intervals in a female observed as she moved along carrying an amplexant male several hundred meters to a suitable egg deposition site). After a certain number of contractions, the female stops pumping, and the male moves his legs slightly so that his feet are closely situated

TABLE 1.—Characteristics of vocalizations of *Bufo coccifer* from Mexico, Costa Rica and Panama.

	Mexico (Porter, 1964b)	Costa Rica (Porter, 1965)	Costa Rica (this study)	Panama (Zweifel, 1965)
<i>Pulse rate per second</i>				
Mean	105.4	90, 95	9.48	66.0
N ¹	17	(8) (2)	(13) ²	
S.D.	5.6		4.25	
Range	97.33-115.99 ³		90.4-105.4	
<i>Call length in seconds</i>				
Mean	3.45	10.0, 1.5	4.4	13.0
N ¹	17	(8) (2)	(25) ²	(17)
S.D.	1.39		1.31	
Range	1.4-6.4 ³		1.2-5.7	8.0-17.0
<i>Dominant frequency, cycles per second</i>				
Mean	3026	2300	2402.5	2300-2500
N ¹	17	(10)	(22) ²	
S.D.	119		109	
Range	2800-3350 ³		2231-2539	2100-2600
Band of greatest energy			1900-2850	2100-2600

¹N = number of individuals recorded, or, in parentheses, number of calls recorded from one individual.

²N = number of calls recorded from four individuals.

³Range of means.

on either side of the female's cloacal opening. At the same time, the female straightens her hindlegs and brings them closer so that they almost touch. The legs and feet of the male and the most proximal part of the thighs of the female form a small chamber, presumably equivalent to the basket described by Miller (1909) for *Bufo americanus*, although the male *B. coccifer* observed did not hook his feet between the female's legs. At this point, the male begins to pump very rapidly up and down on the female with the hindmost part of his body and legs by alternately bending and straightening his knees. The relatively rapid pumps are given in short series of 7 to 10. As the male pumps, eggs are extruded from the cloaca of the female, though she usually does not exhibit any noticeable external movement or pumping action. Presumably, the rapid pumping by the male signals the release of sperm as in *B. americanus* (Miller, 1909).

Two strings of eggs are extruded simultaneously. This also was observed by Miller (1909) in *B. americanus* and Bragg (1937) in *B. cognatus*. During each period of extrusion, 5 to 7 cm of egg string containing ca. 40 to 50 eggs is released on each side. The egg strings sometimes curve upward, sometimes downward, but they remain irregularly coiled in the chamber from 60 to 90 sec. Presumably, this is when fertilization occurs. At the end of this time, the female relaxes and spreads her hind legs; the male then moves his feet and body forward to their previous positions, and the female moves slowly through the water. As she moves, the egg strings float out behind. After less than a minute, the entire process begins again, bouts of contractions alternating with egg extrusion. After extrusion of the last eggs, the male immediately breaks amplexus. The egg strings were still attached to the female when amplexus was broken and were dragged around for about a minute before becoming tangled in her feet and freed from her cloaca. The entire laying period from first to last egg lasted 95 min. Clutch size was 3755 eggs. On subsequent examination, 10 eggs were found in the female's ovisac. In addition, she had a large complement of ovarian eggs in various stages of development, indicating the potential for multiple clutches in a single season.

EGGS.—Small samples of eggs were collected in the field on 21 May and 2 and 11 June. The eggs formed a single row within a continuous gelatinous envelope. Eggs in developmental stage 11 (Gosner, 1960) are surrounded by a clear vitelline membrane, average 1.31 mm in diameter (S.D. = 0.032; $R = 1.26 - 1.37$; $n = 25$), and are heavily pigmented black over 80 to 90% of their surface. The outer envelope apparently is very fragile, as intact strings longer than 15 cm rarely are seen in the field. Often the strings catch on vegetation or debris in the water and break. The slow forward movement of the female following the periods of egg extrusion probably accounts for the short length of many strings.

TADPOLE.—The following description is based on 11 samples totaling 62 tadpoles in Gosner's (1960) stages 26 to 41 (Fig. 4); terminology follows Altig (1970).

Body ovoid, widest at point about two-thirds posterior on body, wider than deep; snout nearly semicircular in dorsal profile, rounded in lateral profile; eyes moderate in size, not part of dorsal

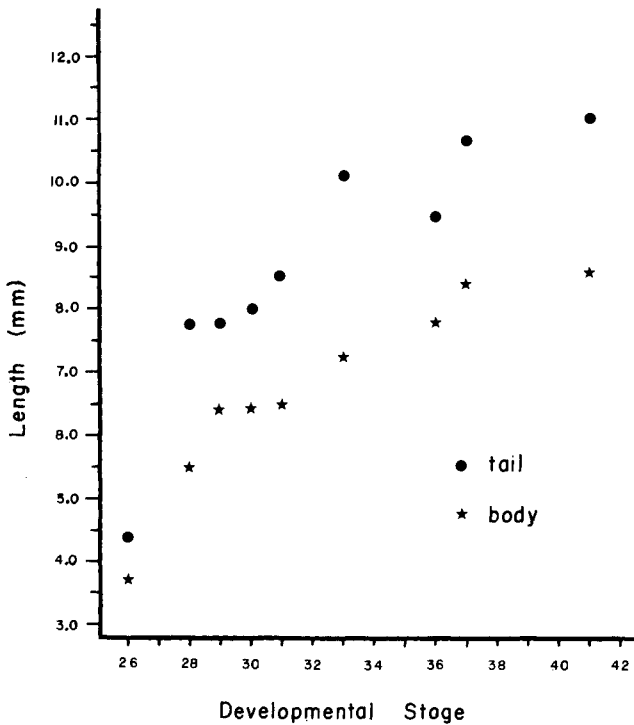


FIG. 4.—Distribution of mean body and tail lengths of tadpoles of *Bufo coccifer* during development. Stages follow Gosner (1960).

profile, directed dorsolaterally, separated by a distance about equal to 2 times eye width viewed from above; nostrils moderate in size, directed dorsally, slightly closer to eye than snout tip. Spiracle sinistral, opening near midbody slightly above midline, directed posterodorsally at about 45 degrees. Anal tube medial. Caudal musculature widest at base, gradually tapering to pointed tip, rises slightly near tip. Caudal fin moderately developed, extending to base of caudal musculature, tip subovoid to round; dorsal fin deeper than ventral, deepest just anterior to midpoint; ventral fin of nearly equal depth throughout its length (Fig. 5).

Mouth small, anteroventral in position; oral disc width about 1.2 times distance between eyes, emarginate with single row of small, truncate papillae laterally; anterior and posterior labium bare, lacking marginal papillae. Tooth row formula 2(2)/3. A₁ longest, slightly longer than P₁ and P₂ which are about equal in length, P₃ slightly shorter than P₂; A₂ gap wide, equal to one fourth length of A₁. Upper jaw moderately wide, finely serrate, medial part shallowly convex on oral edge, lateral processes taper abruptly posterolaterally; lower jaw about equal in width to upper, finely serrate, shallowly V-shaped (Fig. 6).

In preservative, body dark brown dorsally with small, scattered lighter spots; dark brown color extends laterally from half to two-thirds distance to venter; ventral surface without pigments, gut obvious. Caudal musculature with brown mottling throughout, darkest on upper third, faint and scattered on ventral third, often faintest along midline tending to form a light stripe; 5 to 8 distinct dark saddles separated by pigmentless gaps along the dorsal surface of caudal musculature. Small clumps of brown pigment scattered on dorsal fin and posterior half of ventral fin; faintest ventrally. In life, dark brown with darker mottling on body and tail, laterally with dark brown to nearly black markings, iridophores of iridescent copper and gold on back and sides.

During development, the mean body and tail lengths of field collected tadpoles increased at about equal rates (Fig. 4). Because sample sizes often were small (between 1 and 16 individuals/sample) and because tadpole sam-

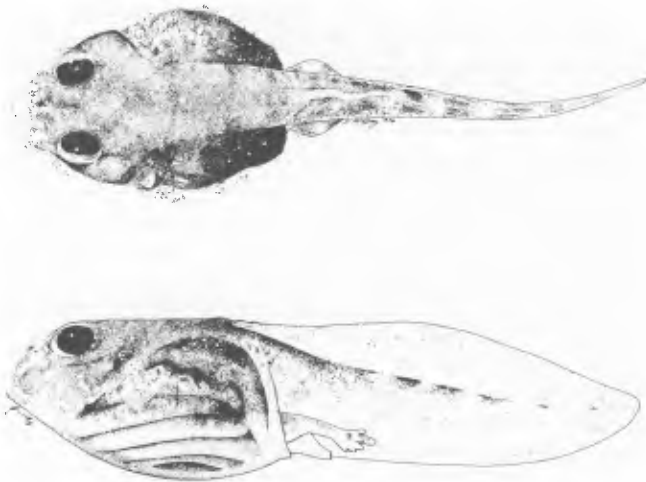


FIG. 5.—Dorsal and lateral views of the tadpole of *Bufo coccifer*, USNM 216499; total length, 18.6 mm, stage 37 (Gosner, 1960).

ples came from several different clutches and were taken from different breeding sites, the data were not treated statistically. Our best estimate of time to metamorphosis is about 5 weeks. Seven different samples of eggs and tadpoles were taken from a flooded roadside ditch between 11 June and 10 July. The eggs were deposited during the night of 10 June following a heavy rain, and the last sample (a single tadpole in stage 41) was taken on 10 July. We assume it would have metamorphosed about 3 days later for a total development period of 33 days. During this time, measured water temperatures ranged from 24° to 40°C.



FIG. 6.—Mouthparts of tadpole of *Bufo coccifer*, USNM 216499; distance between tips of upper jaw, 0.92 mm.

The tadpoles of *B. coccifer* do not show the conspicuous schooling or aggregating behavior characteristic of certain other anuran species (e.g., *Bufo marinus*, *Rhinophrynus dorsalis*, *Leptodactylus melanonotus*) at the study site. Rather, they are cryptically marked, usually occur singly, and often seek shelter in the grass or debris on the bottom of ephemeral, shallow-water habitats. Tadpoles in stages 20 and 21 move infrequently and remain attached to pieces of submerged vegetation. Some orient vertically, although the majority rest at about a 45° angle. Between hatching and stage 24, they are highly susceptible to predation by tadpoles of *Leptodactylus fragilis*, a species that occurs commonly in the same ponds. From stages 26 through metamorphosis, the tadpoles are highly mobile, widely dispersed, and relatively difficult to locate.

The tadpoles of *Bufo coccifer* can be distinguished from those of other species (except *B. marinus*) at the study site by a combination of the following characteristics: denticles and beak present; tooth row formula 2/3; oral disk emarginate, indented laterally; marginal papillae absent from anterior and posterior labium. The tadpoles differ from those of *B. marinus* (traits in parentheses) by having a clear belly (dark below), dark brown pigment on caudal fin (caudal fin clear), dorsal saddles on caudal musculature (uniform dark), and 1 row of lateral papillae (2 rows of lateral papillae). The tadpole of *Bufo leutkenii*, the only other toad occurring at the study site, is unknown.

In many ways, the tadpoles of *Bufo coccifer* resemble those of *B. valliceps*, a species known from northeastern Costa Rica and Nicaragua north to the southern United States. Although some of the apparent color differences between these two species may not be diagnostic, the tadpoles of *Bufo valliceps* generally are darker and have a heavily mottled, reticulate pattern on the caudal fin (Limbaugh and Volpe, 1957).

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