

Papéis Avulsos de Zoologia

AN UNUSUAL ANURAN LARVA FROM THE VAUPÉS REGION OF SOUTHEASTERN COLOMBIA

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ABSTRACT

I collected eggs and larvae of an unidentified frog near the village of Yapima, Vaupés, Colombia in July 1974. The eggs and young larvae were large-yolked, without pigment and probably terrestrial. The older larvae were aquatic.

The tadpoles differ markedly from all other known anuran larvae. They have a single row of sharp, cornified teeth in the upper and lower jaws. The mouth is wide and the supralabial cartilage has a prominent flange at either end. There are no oral papillae, no beaks and no labial teeth. The spiracle is sinistral, but arises from the body posteriorly, near the base of the tail. Furthermore, in the oldest specimen the spiracle is extremely long and tubular, being about one-half the tail length. In its unusual mouth structure and peculiar spiracle, the Yapima larva differs from all four of Orton's basic larval types.

INTRODUCTION

Larval characteristics were generally disregarded by anuran systematists after Noble (1925, 1926, 1927) until Orton (1953, 1957) recognized four tadpole types based on differences in mouthparts, gill chamber and spiracle position (Fig. 1). Orton believed her four larval types to reflect basic divergences in frog evolutionary radiation and to be conservative indicators of major taxonomic groups. Orton's ideas, although controversial (see Griffiths and Carvalho, 1965; Kluge and Ferris, 1969) have nevertheless influenced anuran systematics by renewing interest in the importance of larval characteristics to phylogenetic classification. Her superfamilial groups based on larval types have been accepted by most anuran taxonomists (Wassersug, 1976). It is therefore of interest that tadpoles recently discovered in the Amazon Basin of Colombia are basically different from any known larval type. In this paper I describe the unique features of the Colombian larvae and discuss their relationship to Orton's larval types.

I obtained the specimens in southeastern Colombia about 6 km S of Yapima, a Guanano Indian Village on the Vaupés River. I attempted to raise one lot of the oldest larvae to metamorphosis, but without success. A second lot of 12 larvae preserved soon after collection is the basis of this report. I have made no dissections because of the small size and immaturity of the specimens. None had developed hind limb buds at the time of preservation. The oldest specimen, the only one that had depleted its yolk, was used in preparing scanning electron micrographs.

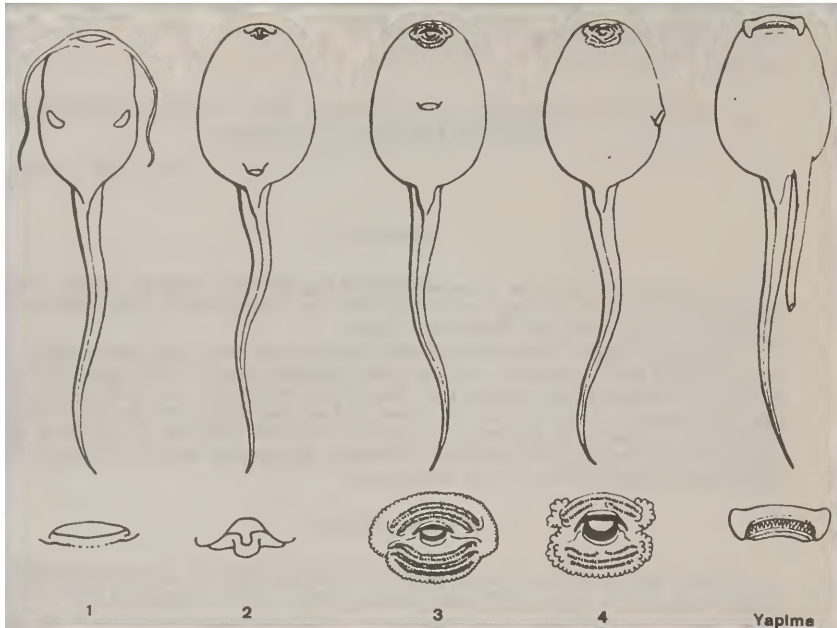


Fig. 1. Four larval types redrawn from Orton (1953) and the Yapima larva at far right. Not to scale.

EGGS AND LARVAE

On 12 July 1974 a villager brought to me several unpigmented eggs and whitish larvae that he had found at a seep in the forest. He had been attracted to the site in the late morning by the loud calls of the little-known microhylid frog, *Otophryne robusta*. In searching for the frog he inadvertently scattered both eggs and larvae in the leaf litter at the edge of the seep, making it impossible to determine whether their original position had been in or out of water. The next day we found additional eggs and larvae, probably scattered by the previous day's search, and captured a series of older, pigmented larvae hiding under leaves in the tiny streams that trickled from the seep. These little streams were 1-2 cm deep and flowed over sandy soil to a larger stream (20 cm deep) about 5 m away.

The eggs were roughly spherical, about 4 mm in diameter and when I obtained them were not enclosed in capsules. All appeared to be dead. Their large yolk content and lack of pigmentation indicated that the eggs were terrestrial.

Five young larvae in the preserved series have spherical, yolk-filled bellies, straight white tails and very little body pigment. In life they were pink. The series shows that the operculum develops from two folds, one across the mid-



Fig. 2 Left lateral view of oldest Yapima larva. Bar represents 1 mm.

ventral line directly below and behind the head, the other to the left of the first. The left-hand fold reveals the tips of gill filaments. Later the folds merge into a single ridge which grows diagonally backward on the left side eventually forming a circular opening (not yet a tube) at the posterior margin of the body to the left of the tail muscle. The head is small, rounded to truncated and the mouth is a terminal crescent-shaped slit. There is no oral disc (no oral papillae, keratinized external denticles or beaks). The unpigmented jaws are well defined and there is a deep rostral groove at either side of the mouth. The fins are translucent, the tail relatively narrow (maximum depth about 30% of tail length), and there is a short, median anal papilla. The intestine has begun to coil but it is filled with yolk and the larvae were obviously incapable of ingesting food.

Measurements of three young specimens in mm (mean followed by range) are: total length, 13.7 (13.0 – 14.3); tail length, 8.9 (8.3 – 9.7); tail depth, 2.7 (2.6 – 2.8); body width, 3.7 in all. Two damaged specimens were not measured.

Seven older larvae show further development of the spiracle from a posterior, circular opening to an enormous sinistral tube 33% of the total length. Arising from the body near the tail base the spiracle extends backward about half the length of the tail (Fig. 2). The mouth is subterminal. There is no oral disc and there are no external nares. The anal tube is midventral and in most specimens the coiled intestine is filled with yolk.

Measurements of the seven older larvae in mm (mean followed by range) are: total length, 19.9 (14.7 – 25.7); tail length, 13.4 (9.7 – 17.5); tail depth, 3.5 (2.7 – 4.5); body width, 4.0 (3.7 – 4.3).

The body of the largest specimen (Fig. 2) is slightly depressed dorsoventrally. Prominent flanges at the lateral ends of the supralabial cartilage partially conceal the deep rostral grooves. There are about 30 sharp, evenly spaced, internal teeth (Figs. 3, 4) in a single row in the upper jaw and a similar row of teeth in the lower jaw concealed by a fleshy fold of tissue. The teeth are translucent-white in formalin. Each tooth is composed of thin hard layers of cornified tissue, the outer layers apparently being shed as the tooth grows (Fig. 4). When the mouth is partly open the upper teeth project backward and are visible from below (Fig. 3). The small, laterally directed eyes are separated by a distance equal to the width of the lower jaw. The long, slender tail is 68% of the total length. Its narrow, upper fin begins posteriorly on the body and gradually widens to maximum depth at a point about 3/5 of the distance to the acute tip. At its greatest depth the upper fin is about twice as deep as the lower fin. A fine pattern of reddish-brown reticulations on the body grades into coarse reticulations on the tail; guanophores are scattered over the tail muscle and fins.

The lateral posterior spiracle, slender body and narrow tail fins make the free-swimming larvae well-suited to life in shallow, flowing streams. Their sharp, well-formed teeth indicate that the aquatic stages are predaceous.



Fig. 3. Drawing of head (ventral view) of formalin preserved Yapima larva. Bar represents 1 mm.

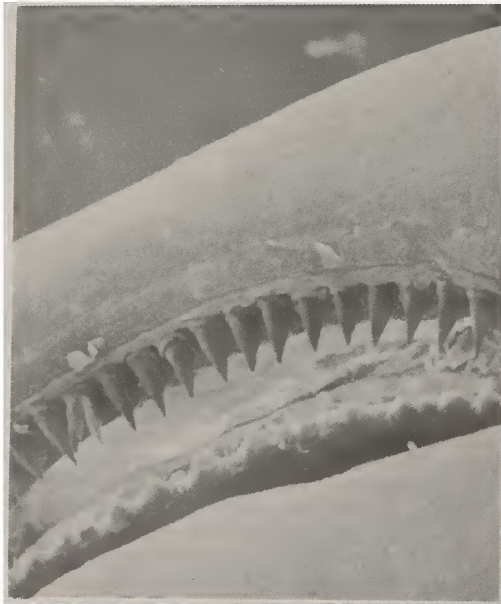


Fig. 4. Part of mouth and teeth of Yapima larva (X80). Note tooth shedding outer layer. Scanning electron micrograph by W. R. Fagerberg.

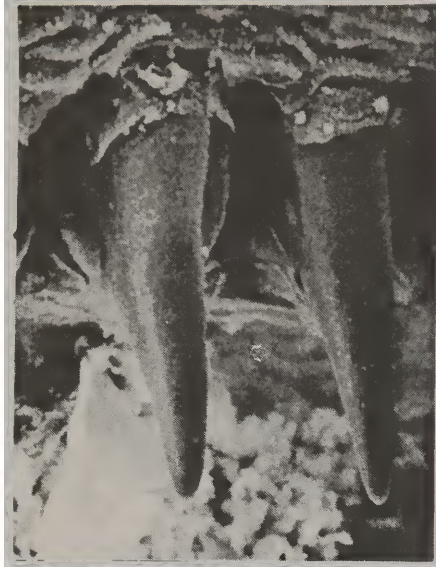


Fig. 5 Teeth of Yapima larva (X534). Scanning electron micrograph by W. R. Fagerberg.

DISCUSSION

Most recent authors agree with Orton (1957) that the type 2 larval form of microhylids is unique, although there is much disagreement about the phylogenetic significance and interpretation of larval characters. In supporting her hypothesis that the paired spiracles of type 1 larvae are primitive Orton (1953) pointed out that the opercula of fishes are basically paired structures and that among anurans only larvae of type 1 have paired opercular openings. Starrett (1973) found that all tadpole opercula develop from paired primordia but that the paired condition is retained only in larvae of type 1. Starrett therefore agreed with Orton that the bilateral spiracles of the Pipidae and Rhinophrynidae were primitive and that the single opercular openings of the other larval types were derived. Orton further argued that the simple mouths of types 1 and 2 larvae were primitive and that the complex oral discs of types 3 and 4, with their cornified beaks, external denticles and fleshy papillae were later evolutionary developments. Hecht (1963) and Starrett (1973) extended Orton's hypothesis; Savage (1973) and Goin *et al.* (1978) accepted Starrett's classification. Wassersug (1976) recognized Orton's four superfamilial groups based on larval types but did not use Starrett's names. Duellman (1975) continued the traditional practice of basing classification almost entirely on adult morphology, but used Orton's larval types in characterizing his superfamilial groups. Tihen (1965), Inger (1967), Sokol (1975) and others agreed with Orton that microhylid larvae (type 2) were distinct from those of all other families and that the asymmetrical spiracle of type 4 larvae was derived, but held that the characteristics of type 3 larvae were primitive whereas those of types 1 and 2 were derived.

In defense of his hypothesis that the simple mouths of larval types 1 and 2 were derived through loss of parts from a more primitive beaked mouth, Inger

(1967) cited examples of type 4 larvae (normally beaked) in which the beaks and denticles have evidently been reduced or lost. He was nevertheless mindful that frog larvae must have passed through a phase without cornified oral structures, possibly resembling the simple mouths of Orton's types 1 and 2.

According to Sokol (1975) larvae of type 3 are primitive because cranial nerves V (trigeminal) and VII (facial) emerge from the chondrocranium through foramina separated by the prefacial commissure; in all other larval types the pre-facial commissure is lacking, the ganglia of V and VII are fused and the two nerves emerge from the chondrocranium through a single foramen. The latter is a derived condition, which, according to Sokol (1977) is quite rare, having occurred "in a few sharks" and only once in the history of the Anura. Largely on this basis Sokol (1977) divided the Anura into two supposedly natural groups: (1) frogs with type 3 larvae, in which nerves V and VII emerge separately from the chondrocranium; (2) all other frogs, in which the ganglia of nerves V and VII are fused and the two nerves emerge from the chondrocranium through a single foramen. These frogs may have larvae of type 1, 2 or 4.

Examination of the literature suggests that loss of the prefacial commissure and emergence of nerves V and VII through a single foramen is not as uncommon as Sokol was led to believe. Sokol himself (1975, Fig. 14B) admitted that the event may have occurred more than once within the Anura, but later (1977) ignored this possibility. Among holostean fishes nerves V and VII emerge through separate foramina in *Pholidophorus* (Patterson, 1975, p. 333) but in *Amia* the prefacial commissure does not ossify and there are no separate foramina for the oculomotor (III), profundus, trigeminal (V), facial (VII) or palatine nerves (Patterson, 1975, p. 401). Similarly, one large opening transmits both trigeminal and facial nerves in *Lepisosteus* (Patterson, 1975, p. 402). In the chondrosteian *Acipenser*, all branches of the trigeminal and facial nerves emerge through the prootic foramen and the ganglia of the two nerves are fused (de Beer, 1937, p. 93, plate 31). The primitive teleost *Leptolepis* has separate foramina for the trigeminal and facial nerves (Patterson, 1975, p. 375) but in *Gymnarchus*, a somewhat more advanced teleost, the prefacial commissure is lost and these two nerves, along with the oculomotor, emerge from the chondrocranium through the same fenestra (de Beer, 1937, pp. 135, 391). Thus the prefacial commissure appears to be quite unstable; its loss, resulting in emergence of cranial nerves V and VII through the same foramen, is not uncommon and has occurred independently in some sharks, holosteans, chondrosteans, teleosteans and anurans. There seems little reason to assume that this often repeated event occurred only once in the long history of the frogs.

The circumstances of discovery of the Yapima specimens suggest that they may be the larva of the microhylid frog *Otophyryne robusta*, a species whose larval form is unknown. Aquatic microhylid larvae have a relatively simple mouth without oral papillae, cornified beaks or external denticles. The Yapima larvae also lack papillae, beaks and external denticles, but their mouth is much more complex than any known microhylid.

Microhylid larvae have a symmetrical opercular chamber and a midventral, posterior spiracle that opens near the anal tube. As in microhylids the operculum of the Yapima larvae extends far posteriorly and opens through a posterior spiracle tube, but unlike microhylids the opercular chamber is asymmetrical and the elongate spiracle is sinistral, not midventral, suggesting affinity with larval type 4.

Type 4 larvae have a sinistral spiracle and generally have a well developed oral disc with cornified beaks and denticles but secondary reduction of mouth parts has evidently occurred within some families having this larval type (Inger, 1967). The Yapima larval form could conceivably derive from type 4 larvae through

secondary loss of the oral disc and elongation of the opercular chamber and spiracle, but I think this derivation unlikely. The mouth of the Yapima larva is clearly not a simplified structure resulting from secondary loss of parts. Rather it is a highly evolved mechanism with prominent flanges on the supralabial cartilage and sharply pointed internal teeth that in no way resemble the external denticles or beaks of type 4 larvae. Any attempt to derive type 4 larvae from the Yapima type is met with a similar objection, namely the basic dissimilarity in mouth structure. Furthermore the mouth of the Yapima tadpoles does not resemble that of any other known larval type (Fig. 1).

Inger (1967) believed that the asymmetrical spiracle arose only once in the evolution of frogs because if it had arisen several times some frogs by chance should have a dextral spiracle. As he pointed out, none does. When the spiracle is asymmetrical it is always on the left side. Nevertheless spiracle position appears to be less stable than mouth structure, as has been commonly suggested in otherwise differing phylogenetic schemes (Inger, 1967; Starrett, 1973; Sokol, 1975). Types 3 and 4 larvae, usually thought to be related, have basically similar mouth parts but different spiracle positions (ventral in 3, lateral in 4). Instability of spiracle position is further indicated by the tendency of the sinistral spiracle to move ventrally in some pelagic forms (Starrett, 1973). The lateral spiracle of the Yapima larvae would seem to be advantageous over a ventral spiracle because these larvae live in very shallow streams that flow over an abrasive surface (quartz sand), habitat limitations that could also account for the narrow ventral fin. It may be unlikely that the sinistral spiracle arose "a number of times" (Inger, 1967), but even assuming no selective difference between right and left positions, I see no compelling reason why a left-side spiracle could not have evolved twice.

Whether the sinistral spiracle of the Yapima tadpoles is an independent adaptation to shallow water leading to convergence in spiracle position with larval type 4, or is a preadaptive retention of a conservative feature is not known. Late developmental stages and species identity of the Yapima specimens are also unknown. If they are the larvae of *Otophryne robusta*, their unique characteristics tend to confirm the conclusion of Bogart *et al.* (1976) that *O. robusta* is not closely related to other New World microhylids. The Yapima larvae are basically different in mouth structure and spiracle position from any presently recognized larval type.

ACKNOWLEDGMENTS

Field work in Colombia was supported at different times by travel grants from the National Science Foundation in support of U. S. participation in the International Biological Program, The American Philosophical Society (Johnson Fund) and The University of Texas at Arlington Organized Research Fund. I thank: Wanda Carl Pyburn, Jonathan Campbell, Harry Greene, Gayla Story and Natham Waltz for field or technical assistance; Ronald Heyer and Ronald Crombie for permission to examine preserved material at the United States National Museum; W. Frank Blair, Craig Nelson and Otto Sokol for reading and criticizing an earlier version of the manuscript. Officials of Inderena gave permission to collect specimens in Colombia.

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