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A PRIMER FOR THE MORPHOLOGY OF ANURAN TADPOLES

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Abstract.—**There has been confusion or misuse of some morphological terminology of anuran tadpoles. I summarize the key measurements and terms from larger sources with an emphasis on North American taxa.**

Key Words.—**body, morphology, mouthparts, oral apparatus, tadpole**

There has been confusion and misuse of measurements and terms used to describe tadpole morphology. For example, proper understanding and uniform usage of terms is critical to assess the effects of chytrid fungi on tadpole mouthparts; see Altig (2007) for comments in this regard. I extracted a general view of morphological definitions and diversity from larger publications (e.g., Altig and McDiarmid 1999a, b; Altig, R., R.W. McDiarmid, K.A. Nichols, and P.C. Ustach. 1998. Tadpoles of the United States and Canada: a tutorial and key. http://www.pwrc.usgs.gov/tadpole/default.htm#families; also http://alpha.selu.edu/ch/.). Species identifications and the taxonomic distributions of characters are not discussed in detail.

Selected papers that discuss developmental aspects of oral structures include Kaung (1975), Kaung and Kollros (1976), Luckenbill (1965), Thibaudeau and Altig (1988), and Tubbs et al. (1993). Cannatella (1999) illustrates the odd anatomy (e.g., two joints in lower jaw) and musculature of the jaws of tadpoles. The many taxa that do not have a free-living, feeding tadpole in their ontogeny (i.e., endotrophs; Altig and Johnston 1989; Thibaudeau and Altig 1999) are not reviewed. While there are other schemes that address tadpole morphology, the terminology given below is derived from that of Altig and McDiarmid (1999a).

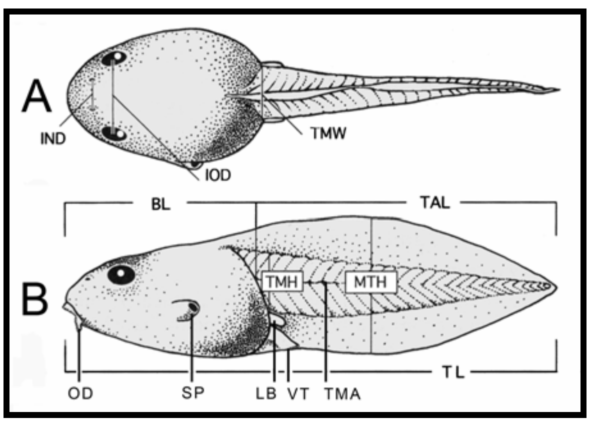

FIGURE 1. (A) Dorsal and (B) lateral views of a typical tadpole. Abbreviations: BL - body length, IND - internarial distance, IOD - interorbital distance, LB - limb bud, MTH - maximum tail height, OD - oral disc, SP - spiracle, TAL - tail length, TL - total length, TMA - tail muscle axis, TMH - tail muscle height, TMW - tail muscle width, and VT - vent tube. Modified with permission from Altig and McDiarmid (1999a).

BODY

Body.—A tadpole is composed of a body (Fig. 1A, B; also measurements below) and tail, and body shape correlates with habitat. The bodies of active, midwater forms are commonly compressed (higher than wide), and at least the snout region or all of the body of midwater, suspension-feeders and benthic forms, pronounced in fast-water forms, are depressed (wider than high).

Spiracle.—The opening(s) (Fig. 1A, B) through which water exits the buccopharyngeal chamber after being pumped in through the mouth and over the gills and food-gathering structures occur(s) in four general configurations with poorly defined subtleties: medial on chest; medial near vent; single on left side (sinistral; most common); and dual and lateral.

External nares.—The external nares are present throughout larval ontogeny in most taxa but appear only near metamorphosis in microhylids. These apertures may be nearer the snout than the eye, nearer the eye than the snout, or about equidistant between the two; narial diameter varies (e.g., notably large in bufonids, quite small in *Lithobates catesbeianus* group). The aperture often has a slight rim, and less commonly it has various papillae or ornamentations.

Eye. —The position, facing direction (= orientation), and size of the eyes vary among taxa. Regardless of their orientation, dorsal eyes (Fig. 2A) lie totally inside the dorsal silhouette. Some parts of lateral eyes (Fig. 2B) are included in the dorsal silhouette, and the eyes face laterally.

Vent tube.—This tube is not the anus of an organism with a cloaca. It occurs in two major configurations with poorly documented subtleties. A medial tube (Fig. 2C) has the opening lying in line with the edge of the ventral fin, and a dextral vent (Fig. 2D) tube has the opening lying at various places to the right of the plane of the ventral fin.

Tail.—The tail is composed of a central, myotomic musculature and a notochord but usually lacks vertebrae. Dorsal and ventral fins extend along the upper and lower midlines of the

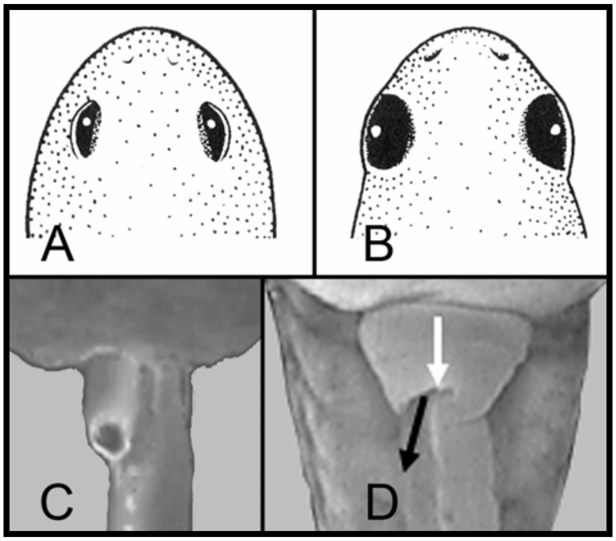

FIGURE 2. Eye positions (A - dorsal, B - lateral) and vent tube configurations (C - medial and D - dextral; white arrow - sagittal plane of ventral fin; black arrow - exit trajectory of vent. A and B modified with permission from Altig and McDiarmid (1999a).

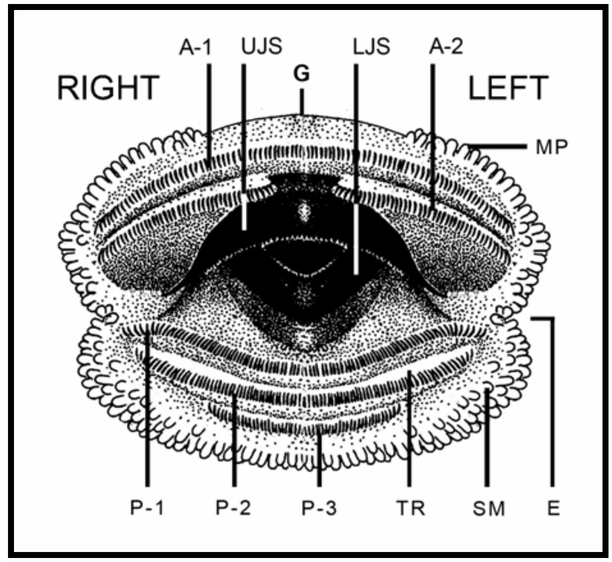

FIGURE 3. Face view of a typical oral apparatus of a taxon with 2/3 tooth rows. Abbreviations: A-1 and A-2 - first and second anterior tooth rows, E - lateral emargination of oral disc, G - dorsal gap in marginal papillae, LJS - lower jaw sheaths, MP - marginal papillae, P-1-3 - first through third posterior tooth rows, SM - submarginal papillae, TR - tooth ridge for tooth row P-2, and UJS - upper jaw sheath. Modified with permission from Altig and McDiarmid (1999a).

tail muscle. The origination of the dorsal fin varies from near the plane of the eyes to the dorsal surface of the tail musculature well posterior of the body. Those that originate well forward on the body occur in midwater, pond-dwelling tadpoles, those that originate near the tail:body junction occur in benthic forms and midwater suspension feeders, and those that originate well posteriorly on the tail muscle occur in stream or semiterrestrial forms. The heights of both fins vary from very high to very low in correlation with habitat. High fins occur in midwater forms, whereas midwater suspension-feeders and benthic forms, especially stream forms, have low fins.

The ventral fin usually originates at or near the vent tube, anterior to the vent tube uncommonly, and sometimes on the tail muscle well posterior to the vent. The tail tip takes various rounded shapes, and a particularly narrow terminal part (= flagellum), that is sometimes mobile independently of the rest of the tail, occurs in various midwater forms.

***Measurements*.—**Landmarks used in measurements (Fig. 1A, B) must be accurately and repeatably located across taxa and stages. The use of different landmarks or landmarks that are not properly located causes noncomparable results. Measurements involving the nares, eyes, and spiracle as landmarks usually should be taken from the centers of those structures, and body terminus (Fig. 1B) is defined as that point where the axis of the tail myotomes contacts the body wall. Of the several options for measuring body length, the one illustrated uses an easily discerned landmark and gives the most comparable values among tadpoles of different shapes.

MOUTHPARTS

***Soft mouthparts*.—**All soft and keratinized structures surrounding the mouth (= opening between anatomical jaws as an entrance into the buccopharyngeal cavity; the oral disc is not the mouth) comprise the oral apparatus or mouthparts (Fig. 3). In most taxa, the oral disc is composed of upper (anterior) and lower (posterior) labia, each of which typically has transverse tooth ridges (Fig. 4A; see below) and submarginal papillae (Fig. 3) on the faces. Marginal papillae (Fig. 3) on the edges of the oral disc occur in three states: complete around entire disc, with a wide dorsal gap (most common; Fig. 3), or with wide dorsal and ventral gaps. All papillae vary in length, number, and number of rows among species. The lateral margin of the oral disc may be emarginated (laterally indented; Fig. 3) or not.

Light staining with Crystal Violet allows much enhanced views of these translucent soft tissues. Under unknown conditions, parts of the soft tissues of an oral disc, particularly of older specimens, become locally darkened, but they are not keratinized; I have heard this discoloration referred to as “formalin burn,” although I know of no proof that it is a function of the fixative.

There are a few cases of tadpoles having an oral disc but lacking keratinized mouthparts, and members of three families lack all keratinized structures and the soft structures that are present do not form an oral disc. Microhylids have hemispherical oral flaps pendant over the mouth and lack ventral labium derivatives and barbels. Pipids have a single, long, motile barbel at each corner of slit-like mouth and lack oral flaps, and rhinophrynids have several, short, non-motile barbels around a slit-like mouth that lacks oral flaps.

***Keratinized mouthparts*.—**The keratinized mouthparts include the multicellular, keratinized jaw sheaths with serrated cutting edges on the suprarostral (upper) and infrarostral (lower) jaw cartilages. Occasionally, areas on the tissues adjacent to the lower jaw sheath also are keratinized. The cutting edge of the upper sheath typically forms a smooth arc, and the lower sheath

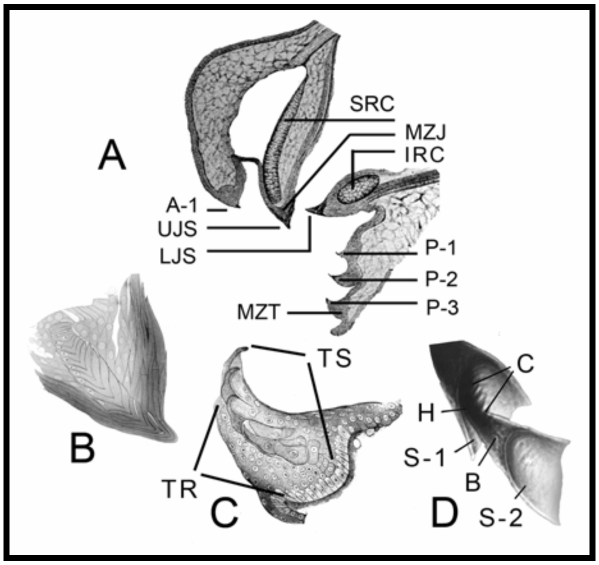

FIGURE 4. (A) Sagittal histological section of an oral apparatus showing 1 upper and 3 lower tooth rows, anterior to left. Abbreviations: A-1 - first anterior tooth row (sagittal section falls in the natural gap in row A-2 gap, so row A-2 not visible), IRC - infrarostral cartilage (lower jaw), LJS - lower jaw sheath, MZJ - mitotic zone that forms upper jaw sheath, MZT - mitotic zone that forms teeth in the base of the tooth ridge for tooth row P-3, SRC = suprarostral cartilage (upper jaw), and P-1-3 - first through third lower tooth rows. (B) Histological cross-section of jaw sheath (approximate keratinized portion darkened for emphasis) in same orientation as upper jaw sheath in panel A. (C) A histological cross-section of a (TR) tooth ridge and one (TS) tooth series comprised of 5 formative cells of various shapes at the base and 4 progressively older teeth, including the presently erupted tooth at the top. The tooth ridge extends transversely - in front of and behind the plane of this image; see Fig. 3) and is oriented like row P-3 in panel A. (D) A partial tooth series of *Hyla chrysoscelis* in the same orientation as row P-3 in panel A; the top tooth is presently erupted (head not shown), and the first replacement tooth in the tooth series is shown with its head interdigitated into the sheath of the erupted tooth. Abbreviations: B = body of replacement tooth, C = cusps on head of replacement tooth, H = head of replacement tooth, S-1 = sheath of erupted tooth, and S-2 = sheath of replacement tooth. Figures A-C modified from Héron-Royer and Van Bambeke (1889).

is most commonly V-shaped. Cells in each structure are continually produced by a basal mitotic zone, keratinize during their transit to the surface, and eventually slough. Some stream forms and some cannibalistic forms have variously modified jaw sheaths.

Tooth rows are numbered from the upper disc margin toward the mouth on the upper labium and from the mouth toward the lower margin on the lower labium (Fig. 3). The number of tooth rows/labium is shown by a fractional notation, where the numerator equals the number of upper tooth rows and the denominator equals the number of lower tooth rows. A labial tooth row formula (LTRF) of 2/3 is the most common configuration, but the number varies from 0/0–17/21 in many combinations throughout Anura. Natural gaps in rows formed during embryology are noted in parentheses. The LTRF 2(2)/3(1) (Fig. 3) denotes natural gaps in the second upper and the first lower row. Tooth rows are uniserial except in a few cases.

A labial tooth (Fig. 4D) is a single keratinized structure of various shapes among taxa and stage that is derived from the activities of one cell. Each tooth has a basal sheath, an intermediate body, and a terminal head of various shapes with or without projecting cusps (Fig. 4D). All teeth form successively in the base of the transverse tooth ridges (Figs. 3 and 4A, C) and move upwards as older teeth erupt and break or fall out. A tooth ridge is crudely analogous to mammalian ‘gums’ because they produce and support the labial teeth, but these structures are located on the face of the oral disc extraneous to the buccopharyngeal cavity and jaws. The presently erupted tooth and all its replacement teeth interdigitated below it form a tooth series; thus, a tooth row (Figs. 3 and 4A, C) is a transverse, linear group of labial teeth, or tooth series, on one tooth ridge; the erupted tooth is what one sees when observing an oral disc, but one usually can also see the replacement teeth through the translucent tissue of the tooth ridge. That is, the total height of what one sees when looking at a tooth row from the back or front is the height of the tooth series (i.e., typically 3-7 teeth/series), not that of an individual tooth. In summary, transverse, linear groups of individual, erupted teeth, each with replacement teeth below them (i.e., a tooth series) make up a tooth row produced and supported by a tooth ridge.

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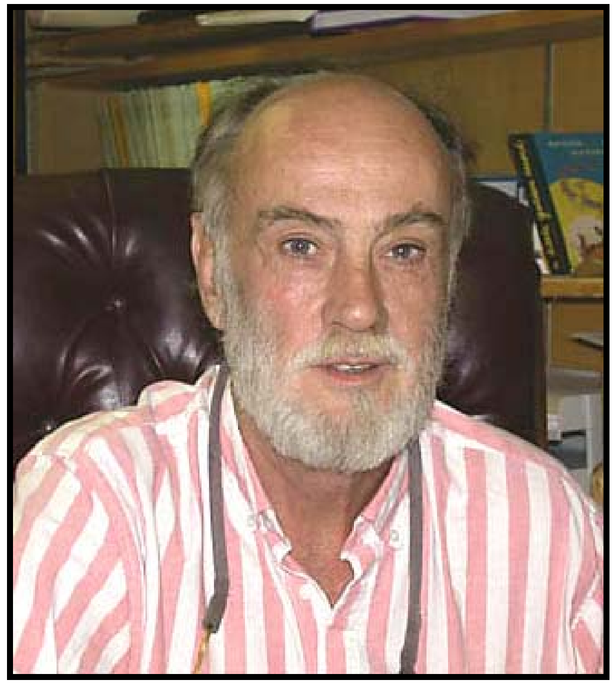

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