Discussions of the origin and evolution of the oral apparatus of anuran tadpoles

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Abstract. Because studies of the oral apparatus of anuran tadpoles seem to be mired at the descriptive stage, a discussion based mostly on developmental concepts is presented as a primer to studies of developmental genetics and evolution. An oral configuration common among many ecomorphological guilds of anuran tadpoles is used as a morphological standard without ascribing evolutionary significance. Comments on the patterns of modifications of the jaw sheaths and labial teeth and other morphological patterns are presented.

**Keywords**.   Tadpole, mouthparts, development, evolution, systematics.

INTRODUCTION

Many morphological patterns in the oral structures common to specific taxa (e.g., wide dorsal and ventral gaps in the marginal papillae of *Bufo*) are recognized, but the description of the unusual tadpole of *Phyllodytes gyrinaethes* (Peixoto et al., 2003) shows that we do not yet fully understand tadpole morphological diversity and that generalizations can be misleading; other known *Phyllodytes* tadpoles are quite typical. Likewise, the development, genetic control, and evolution of these structures are understood in basic terms or often not at all. Studies of the anatomy of the jaw and associated muscular and their functions (e.g., Gradwell, 1972; Wassersug and Hoff, 1979; Larson, 2002; Haas, 2003) are available, but studies of the actual mouthparts seem to be inconveniently shackled at the descriptive level of research. Our understanding is further obscured by a confusing interplay of several poorly known areas: variations from micro- and macrogeography (e.g., Savage, 1960; Gollman and Gollman, 1996), ontogeny, development, and various forms of plasticity (e.g., Relyea and Auld, 2005).

This exploratory discussion does not present a unifying hypothesis, and I do not assert that the various ideas as necessarily correct; the intention was to stimulate new questions in a poorly studied field. The oral terminology of Altig and McDiarmid (1999a) was fol-

lowed, and four assumptions are made. (1) The tadpole stage is primitive within Anura. (2) The primitive tadpole had some kind of an oral apparatus. (3) Many changes in the oral disc represent adaptive morphologies associated with specific modes of feeding constrained by a large but poorly understood phylogenetic component. (4) The unique jaw complex (Gradwell, 1972; Svenson and Haas, 2005) was present in protoanuran larvae.

The oral apparatus of a typical, exotrophic, pond tadpole (Fig. 1A) includes an oral disc composed of an upper labium with free lateral edges and two tooth rows, a larger lower
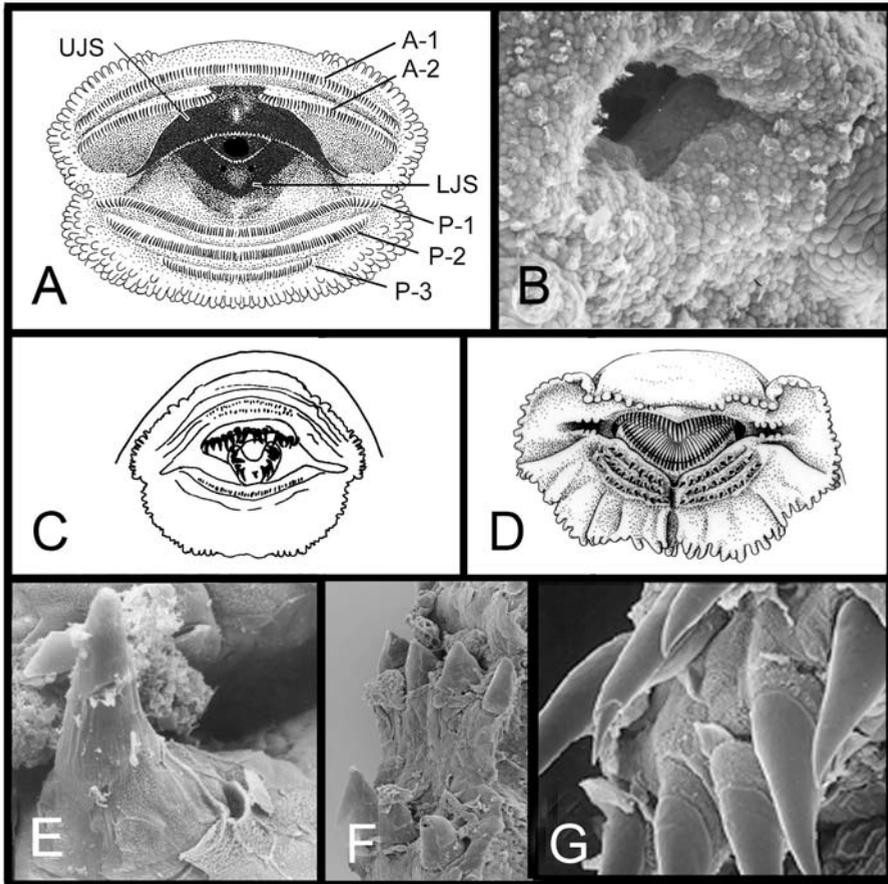
Fig. 1. (A) A typical oral apparatus of a pond tadpole (modified from Altig and McDiarmid, 1999a; Notations: A-1-2 = anterior tooth rows 1 and 2; P-1-3 = posterior tooth rows 1-3; LJS = lower jaw sheath; UJS = upper jaw sheath), the (B) oral disc of *Hyla chrysoscelis* at Gosner (1960) stages 21 showing the stomodeum and ciliated epidermal cells throughout the presumptive area of oral disc formation, (C) unusual. transient spike-like jaw sheaths of *Heleophryne* (modified from Visser, 1985), (D) somewhat similar jaw structures that persist throughout larval life in *Mantidactylus lugubris*, and unusual labial "teeth" in (E) *M. lugubris* (from rows on lower labium in panel D), (F) *Phyllodytes gyrinaethes*, and (G) *Hoplobatrachus rugulosus* (also note biserial construct)

labium with free marginal edges and three tooth rows, unmodified jaw sheaths, a wide dorsal gap in the marginal papillae, and submarginal papillae laterally and ventrolaterally. We have little idea of the characters of the primitive tadpole, and this oral configuration is used as a comparative standard without implying that it is primitive (e.g., Cannatella, 1999).

Less plastic structures than mouthparts probably will prove to be the most phylogenetically informative; nonetheless an understanding of the evolution of mouthparts would contribute immensely to understanding anuran larvae and this complex suite of oral characters. While acknowledging the issues concerning the use of ontogenetic data in phylogenetic inference (e.g., Krause, 1988; Mabee, 1989), those points where developmental data appear to give the only available signals are pointed out. Haas (2003) presented a recent phylogenetic analysis based on larval characters. Pervasive models involving larval characters will be devised only after we understand the developmental mechanisms and homologies of larval features and can interpret observed patterns in a phylogenetic framework.

After presenting ideas on the origins of the tadpole oral apparatus, I consider other patterns of modification of the oral features. I attempt to describe evolutionary trajectories within lineages that support the argument that larval traits have phylogenetic value. A proper analysis of the interactions between the gathering (oral apparatus) and filtering (buccopharyngeal structures) components would be informative, but the utility of this poorly understood link cannot be fully explored until we understand the evolution and function of the mouthparts. Changes in the oral apparatus as a consequence of the evolution of the "tadpole stage" and the highly specialized anatomy and life history of anurans are discussed.

ORIGINS OF THE ORAL APPARATUS

This discussion focuses on oral morphology exclusive of the jaws and musculature. Is the face of an oral disc homologous with surfaces that surround the mouths of other vertebrates or is it derived from a reflexed surface as in extremely pouted lips? Developmental patterns (e.g., Thibaudeau and Altig, 1988) show that the oral disc initially is defined by an approximately circular furrow that forms peripherally to the stomodeum; the incipient tooth rows are dorsal and ventral to the stomodeum within the boundaries of the presumptive labia. The presence of ciliated epidermal cells characteristic of larval epidermis on the presumptive face of the disc (Fig. 1B) signals that the disc face is homologous with the general surfaces surrounding the mouth and that it is not a reflexed surface. This unusual growth pattern whereby the structure is delimited from, instead of growing out of, a local surface seems to resemble the growth pattern that produces the nose star of the star-nosed mole (*Condylura cristata*; see Catania et al., 1999). Intrinsic musculature of the oral disc is unknown, and extrinsic musculature originates on Meckel's cartilage and inserts at various sites, especially the bases of tooth ridges, within the oral disc (Gradwell, 1972; Carr and Altig, 1991).

Keratinized structures frequently occur in association with various feeding structures of chordates (e.g., cyclostomes, some teleosts, some larviform salamanders, some reptiles, and birds), and the propensity for keratinized tissues to occur on various surfaces suggests a conserved genetic background of a labile mechanism. Most tadpoles have the suprarostral and infrarostral cartilages covered by keratinized sheaths, and transverse rows of

labial teeth occur on each labium. The dense, pyncnotic tissue that is continually renewed mitotically adds strength and protection from abrasion during feeding activities. Comparative histological studies likely would show differences in the formation, maintenance, and structure of these keratinized structures.

In general, keratinized oral structures occur in organisms that lack calcified teeth. Keratin is lighter, less brittle, and more resilient than bone. It is probably cheaper to produce by organisms that sometimes discard these structures at some point, and it is readily developed by epidermal tissues. Keratinized structures may develop in response to abrasion; for example, keratin sometimes appears on nonworking surfaces of tadpole mouthparts where other keratinized structures make repeated contact (e.g., ventrolateral to robust lower jaw sheaths of the *Rana pipiens* group, personal observations; *Kassina senegalensis*, Noble, 1926). If such a mechanism initially produced keratinization on the jaw cartilages of tadpoles, selection might have resulted in the various shapes to improve specific functions and have given rise to the present ecological and morphological diversity (Altig and McDiarmid, 1999b). Typical jaw sheaths vary in every dimension, and further examinations of the cross-sectional shapes and the back surfaces (Altig and McDiarmid, 1999a) likely would reveal insights as to the function and interaction of these structures. Noteworthy developmental information probably could be gleaned by observing the development of jaw sheaths in tadpoles having atypical jaws (e.g., all stages of *Lepidobatrachus* [Ruibal and Thomas, 1988], young *Heleophryne* [Fig. 1C; Visser, 1985], *Otophryne* [Wassersug and Pyburn, 1987], and *Mantidactylus lugubris* (Fig. 1D). These various spikelike structures may be hypertrophied serrations with the sheath lacking or minimally developed and thus may be further evidence of a developmental relationship between jaw sheaths, papillae, tooth ridges and labial teeth (Thibaudeau and Altig, 1988).

Two arrangements seem possible for the original arrangement of labial teeth or their ancestral morphologies. There may have been a burr-like surface produced by rather rigidly attached, tooth-like projections over the entire face of the oral disc, or the projections may have originated in crudely arranged transverse rows but not on tooth ridges. Manipulations of embryos and later stages suggest that all surfaces of the face of the oral disc are totitpotent for tooth formation throughout most of larval life (e.g., Thibaudeau and Altig, 1988; D. Drake, unpublished data), and a multiserial, burr-like surface of firmly attached teeth is approximated in the distal rows of *Ascaphus truei*. The original spinules likely had short, weakly spatulate heads; cusps were small to lacking, and replacement teeth were absent. Teeth were attached strongly to the disc tissue and curved toward the mouth on each labium. Changes in orientation other than minimal modifications caused by changes in the shape of the entire disc during feeding strokes were minor. By interacting with substrate irregularities and the tangled array of periphyton, such a burred surface might have had the initial function of stabilizing the oral disc while the jaw sheaths worked as the primary food removal surfaces.

Why were teeth eventually arranged in linear transverse rows? Transverse tooth rows with the teeth facing the mouth seems intuitive based on the directions and presume functions of either removing or conveying materials toward the mouth or stabilizing the oral disc via a gripping action. A gripping or rasping surface that moves longitudinally would not function well if the effective structures also were arranged longitudinally. Even though a snail radula moves differently than a tadpole's oral disc, the power strokes basi-

cally are longitudinal in both cases, and radular teeth also are either arranged transversely or at a shearing angle to the direction of travel. Arrangement of spinules in rows with no particular alignment of teeth among rows may have been mechanically more effective and less subject to impediment or fouling with the available muscular forces. There were no grinding/crushing actions involved, so alignment of teeth between rows or special surfaces would not be required.

Why are the tooth rows on the tops of tooth ridges? Tooth rows positioned at the tops of ridges probably served two purposes. Tooth ridges vary in height and flexibility among taxa (e.g., shorter and less flexible in stream forms; taller and flexible in pond forms) but the ability to change the orientation and operation of the teeth at different parts of the operating cycle of the disc relative to the substrate would enhance their functions. Emlet (1991) analyzed an amazing parallel case. Ciliate protozoans have parallel rows of cilia positioned on ridges, and the movements of the cilia either move the organism forward or move water over the animal. Because they are positioned on ridges, the cilia move more fluid with a greater displacement per stroke than cilia on flat surfaces. During feeding actions, the rotation of the tips of labial teeth distally from the mouth at maximum disc excursion is caused by extrinsic musculature and tensions in the tooth ridges caused changes in disc shape. If all rows respond with simultaneous changes in orientation and shape during a feeding cycle, fluid-borne particles should be moved toward the mouth more effectively than if the teeth were on a flat surface. Tooth ridges and the connective tissues in their bases (Carr and Altig, 1991) also add "corrugations" on the face of the disc which keep the disc from buckling uncontrollably; this mechanism would enhance feeding activities in rasping tadpoles and substrate adhesion in fast-water forms. Teeth are reoriented by extrinsic muscles when the disc opens but return to their resting positions by elastic recoil of the connective tissues in the ridges.

Wear of keratinized mouthparts likely is a viable means to study function and warrants further attention in both ecological and developmental aspects. Wear can be assessed only in scanning electron microscope images, but the incorporation of generalities derived from studies of the wear of mechanical abrasive tools surely would improve our understanding of the morphological and ecological aspects of tooth function.

Extreme diversity in all aspects of labial teeth (e.g., tooth size, shape and cusping pattern; tooth density; number of replacement teeth; number and disposition of rows) suggests differential feeding functions. Correlations in tooth characteristics across taxa and ecological groups seem apparent (Altig and Johnston, 1989). However, even though factors associated with feeding during competitive interactions abound (Alford, 1999), specific actions or harvesting abilities provided by a given morphology have not been verified. As an extreme, it is curious that tadpoles that have lost all keratinized mouthparts from infections of chytrid fungi are not emaciated even though their growth trajectories lag that of intact controls (Parris, 2004). Do these individuals change the content and site of feeding, or in fact are the keratinized structures not that influential on feeding? If the latter were true, is the diversity of keratinized oral structures somehow pleiotropic to some other feature(s)? The fact that the first teeth to erupt ontogenetically have a simpler morphology than subsequent generations (M. Penuel-Matthews, unpublished data) of teeth may involve a phylogenetic signal. Thus, it remains unclear whether the primary function of labial teeth concerns food harvesting in general, a specific form or part of food harvest-

ing, or stabilization of the tadpole while the jaw sheaths act as the primary food-removal structures. There is probably a wide latitude of functions that might be called into play only when crucial conditions demand interspecific differences in feeding ecology; that is, competition based on differential feeding abilities may occur only under specific and extreme conditions. Also, with the addition of more information on the feeding biology of tadpoles, we may find that a typical pond tadpole performs mostly as a carnivore (Schiesari, 2004) and perhaps employs three different feeding modes under specific circumstances. Perhaps the jaws function most effectively when a tadpole harvests a reasonably tall over-story without producing a particulate suspension (e.g., fibrous periphyton, 1-2 mm; personal observations), and the labial teeth would serve primarily in stabilization in this case. When a tadpole feeds on a very thin layer (e.g., diatom films), perhaps the labial teeth function most effectively, and at least part of the material is rendered as a suspension that is then captured by the buccopharyngeal structures. The third scenario involves the capture of naturally suspended particles (e.g., Seale, 1982) mostly by actions of the food traps.

If the labial teeth initially provided stabilization, one has to ask why the extreme diversity in tooth morphology occurs, but one has to assume that our present concepts of tooth diversity somehow includes ideas of the origins of these structures. The data on labial teeth are limited to snapshots of individuals, and additional data on intra- and inter-row and ontogenetic variations across many taxa, stages, and sites would be helpful. Searches for patterns and correlations among these data would promote informative ideas, and one has to consider that variations in tooth morphology may occur by genetic mechanisms other than selection for a given function. In any case, an explanation of the large diversity of labial tooth shapes and cusping patterns and the transverse topography of labial tooth rows requires further study.

There are "teeth" with aberrant morphologies and development that suggest that they may not be homologous with typical labial teeth. The tadpole of *Phyllodytes gyrinaethes* (Peixoto et al., 2003) has crowded rows of spade-shaped structures (Fig. 1F) that lie tightly flat against the local surface. The tadpole of *Mantidactylus lugubris* has conical, tooth-like structures in three transverse rows on only the lower labium (Glaw and Vences, 1992; Fig. 1E). Scanning electron microscopy shows that these structures are not typical teeth. These pigmented, pointed cones stand upon but not embedded in what appear to be flat-topped tooth ridges, and the heads are simple cones. One has to ask if they are ancestral to, or derived from, typical labial teeth or are they merely labial tooth analogs? If the latter were true, then the mechanisms that produced "labial teeth" likely differed. The presence of these seemingly abrasive structures only on the posterior labium again indicates that this surface is functionally more important than those on the upper labium. However, if posterior tooth rows were lost in the common ancestor of the group to which *M. lugubris* belongs, then selection may have promoted modification of submarginal oral papillae to take on the functional role of tooth rows on the posterior labium. Most other members of *Mantidactylus* in the *lugubris* group have typical teeth, although they are sometimes weakly developed. The ranid *Hoplobatrachus rugulosus* (Fig. 1G; Chou and Lin, 1997) is the third example of aberrant "teeth" and perhaps the second nonhomologous case, after bombinatorids and discoglossids, in which each tooth ridge has two lines of teeth (= biserial). This seemingly is the only case of biserial tooth structures in advanced frogs, but the occasional occurrence of sections of biserial teeth in species that normally have unise-

rial tooth rows shows that the developmental potential likely occurs throughout Anura. Also, the development of these large spiked teeth is entirely different than typical teeth (R. Altig, unpublished data). The intriguing fact that this configuration occurs within just one genus of ranids suggest that simple and labile genetic mechanisms control tooth morphology. Perhaps these structures are in fact modifications of typical teeth; compaction of the mitotic bed that produces labial teeth toward the surface of the tooth ridge (i.e., seemingly a developmental truncation) would seem to be a primary prerequisite.

Do biserial tooth rows represent any indication of being derived from the burred surface suggested above? Were the typical uniserial tooth rows seen in most extant tadpoles derived from the biserial condition either by fusion or the loss of some of the transverse, multilineal arrays? The alternative, of fission of uniserial rows to produce a biserial condition cannot be ignored *a priori*, and early embryological examinations of tooth and tooth ridge formation in representative taxa would likely indicate which case is likely.

The second of two scenarios mentioned above provides that teeth appeared in rows a priori and perhaps, if these teeth had replacement series in the subsurface tissue, these rows were on ridges merely because there had to be a place to house the mitotic beds that produce the teeth. Recall that the entire face of the oral disc appears to be potent for tooth formation and that tooth ridges and submarginal and marginal papillae may be homologs (Thibaudeau and Altig, 1988). Melanic pigmentation provides strength to structures, and labial teeth precursors may have been modified from papillae.

ORAL APPARATUS CHANGES

The paucity of descriptive information coupled with a lack of understanding of developmental mechanisms forces us to make predictions based mostly on fully developed structures. Heterochronic alterations of developmental trajectories are likely common genetic mechanisms of modification, and it seems that metamorphic reductions occur in reverse order of formation (Thibaudeau and Altig, 1988). Phylogenetic losses seem generally to follow the same sequence as metamorphic losses, but the mechanism of formation and comparisons of interspecific differences in row lengths, spacing, and gaps within and among parts of the oral disc needs attention. Parts of the presumed inductive events that produce an oral disc and the tooth ridges can be disrupted so that a disc with marginal papillae forms without tooth ridges and therefore, tooth rows (G. Thibaudeau, unpublished data). The generalized sequence of formation of oral structures for *Rana sphenocephala* proposed by Thibaudeau and Altig (1988) is noted: oral disc, jaw sheaths, marginal papillae, labial tooth ridges, labial teeth, and submarginal papillae. The ventrolateral margins of the lower labium are the first tissues of the oral disc to materialize from the surrounding body surfaces. Nascent marginal papillae subsequently appear in these same areas before they do on other margins of the disc, and they are the last to atrophy during metamorphosis. Most of the marginal papillae of the tadpoles of *Bufo* involve only these papillae. The corners of the mouth of a tadpole do not extend backwards to form a frog mouth until this tissue atrophies.

The mechanisms that account for the formation of marginal and submarginal papillae are unknown, although apoptosis surely is an important mechanism (e.g., Glückmann,

1951; Hammar and Mottet, 1971). Additional data are needed to determine the function and what controls the size, therefore number, of papillae/distance. These variables likely reflect an interplay of evolutionary history and functional demands (e.g., stream vs pond dwellers). A number of taxa have transverse rows of submarginal papillae distal to both upper and lower tooth rows that resemble either nascent or vestigial tooth ridges. The significance of the common pattern of submarginal papillae clustered in the lateral and ventrolateral parts of the disc is not known.

Vestigial, presumably not rudiments, tooth ridges occur in some members of the *Hyla leucophyllata* (*Dendropsophus leucophyllatus* of Faivovich et al., 2005) group (Thibaudeau and Altig, 1988) and some microhylids (e.g., *Nelsonophryne*, Donnelly et al., 1990; *Otophryne*, Wassersug and Pyburn, 1987) with reduced oral discs and no labial teeth. In the latter cases, these toothless ridges add credibility to the idea that the highly modified mouthparts of microhylids are derived from a more typical morphology and credence to the pattern of ontogenetic gain and loss of tooth rows that is mimicked phylogenetically. That is, the formation of tooth ridges is independent of, and occurs ontogenetically prior to, the presence of mitotic beds for tooth formation in the ridges. The potential to form teeth is likely not lost from the genome, but the regulation of the developmental program forbids the expression of this activity. Last, the idea that tooth ridges and at least submarginal papillae, which can form labial teeth at times, are homologs is supported. Because teeth seem to erupt on a ridge in a medial-to-lateral progression (e.g., Tubbs et al., 1993), I interpret a row that is shorter than expected as a developmental truncation. Likewise, the lack of row P-3 in a species (e.g., *Pseudacris crucifer*) or group (e.g., *Bufo debilis* group) whose close relatives typically have three posterior rows is also interpreted as developmental truncations.

The configuration of the m. mandibulolabialis, an extrinsic oral disc muscle that originates on Meckel's cartilage and inserts at various places within the labia (Gradwell, 1972; Carr and Altig, 1991) also signals developmental truncations. The inferior slip of this muscle inserts within the lower labium and terminates where the tooth ridge for row P-1 would be expected if tooth rows were present in tadpoles of *Afrixalus brachycnemis*, *Hyla ebraccata* (*Dendropsophus ebraccatus*) and *Hyalinobatrachium eurygnathum* (Carr and Altig, 1991). The position and vestigial nature of this muscle suggest that the ancestors of these frogs had teeth, that toothlessness was derived by developmental truncation, and that P-1 was the last tooth row lost on the lower labium.

The position and size of the stomodeum within the presumptive field of the oral apparatus may be another marker. That is, might changes in the pattern of eruption of the stomodeum in the oral disc field influence the oral structures? For example, a change dorsally could produce a more terminal oral disc, and if the stomodeum changed in either actual size or developmental influence within the field that forms the oral disc, then the eventual size of the disc and the geography of its parts would differ. Tracking marked cells by time-lapse photography would reveal these patterns.

Data from hybridizations could provide a partial surrogate for molecular information on tooth-row formation, but no one has produced the more informative F_2 generation. Hybrids from reciprocal crosses between *Rana cascadae* [LTRF 3(2-3)/4] and *R. pretiosa* [2(2)/3(1)] had a LTRF of 2(2)/4(1) (Haertel and Storm, 1970). This hybrid with a LTRF of *pretiosa* on the upper labium and *cascadae* on the lower labial suggests a different genetic

control for tooth-row formation on each labium. Also, the size of the gap in A-2 and the presence of a gap in P-1 are *pretiosa* traits.

The absence of jaw sheaths and presence of labial teeth in tadpoles of *Heleophryne* superficially confutes the developmental sequence of appearance of oral structures outlined above, but knowing the developmental pattern (Visser, 1985) resolves the seeming contradiction. A few, isolated "fangs" presumed to be derived from jaw serrations form at the time and at the sites where jaw sheaths would be expected and then disappear. Even so, the absence of both sheaths confounds discussions of feeding in these suctorial tadpoles. These tadpoles and those of *Ascaphus* are superficially similar in morphology and habitat, and the large number of tooth rows made of very small, closely-spaced teeth in *Heleophryne* may be somehow compensatory for the absence of jaw sheaths. Even so, one must assume that the details of their feeding activities differ considerably.

CONCLUSIONS

Many morphological variations coupled with meager developmental data were used to develop speculative hypotheses on the evolution of tadpole mouthparts. Large amounts of descriptive (i.e., morphology and development coupled with descriptions of taxa to understand total diversity) and experimental (e.g., embryological manipulations and molecular genetics) research will be required before specific hypotheses concerning such a diverse and plastic series of structures can be formulated. Essays, such as Svenson and Haas (2005), are valuable bridges between herpetological and molecular perspectives. Researchers will benefit initially by figuring out a way to view the entire apparatus as a series of component parts and how they interact developmentally. Convergences surely have been common; major events (e.g., gains or losses of various components, which likely reflect heterochronic changes) likely have occurred multiple times throughout Anura, and this repetitiveness suggests reasonably simple genetic mechanisms have been conserved. Gene regulation rather than mutations or changes via selection is likely the more common developmental phenomenon. Other intra- and interfamilial convergences, such as umbelliform and suctorial oral discs and belly suckers (= gastromyzophory), are additional circumstances that need further study.

The following quote is a pertinent research insight for the complex subject of this discussion. "If you are a researcher you are trying to figure out what the question is as well as what the answer is. You want to find the question that is sufficiently easy that you might be able to answer it, and sufficiently hard that the answer is interesting. You spend a lot of time thinking and you spend a lot of time floundering around (E. Witten, physicist, Princeton University; CNN, 30 June 2005).

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