

Amphibian Ecology and Conservation

A Handbook of Techniques

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Morphology of amphibian larvae

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3.1 Background

The larvae of amphibians are non-reproductive and usually aquatic. Most undergo metamorphosis prior to attaining an adult morphology and sexual maturity. Species within each amphibian order that develop by other modes (e.g. direct development; Altig and Johnston 1989; Thibaudeau and Altig 1999) have non-feeding larvae or embryos, and we do not discuss them in this chapter.

Amphibian larvae have some generalized morphological features that are useful for identification. In contrast to fish, they lack bony supports in the tail fins, and the vent is a longitudinal slit (not obvious in tadpoles). Amphibian larvae also lack eyelids, and most have external gills that are visible at some stage in their ontogeny.

Most caecilians (Gymnophiona) whether terrestrial or aquatic as adults, have aquatic larvae that look grossly like the legless, elongate adults. The larvae of salamanders (Caudata) look much like the adults. Unlike the condition in caecilians and frogs, salamanders may occur in larval (i.e. larval morphology, non-reproductive, and metamorphic) or larviform (i.e. larval morphology, reproductive, may or may not metamorphose) states. Larviform salamanders may exist as pedotypes (i.e. larval relative to the normal developmental trajectory of the taxon, reproductive, will metamorphose if the environmental conditions change to the detriment of being in the larval environment; some ambystomatids and salamandrids; terminology of Reilly *et al.* 1997) or pedomorphs (i.e. larval relative to the developmental pattern of their ancestors, do not metamorphose; all amphiumids, cryptobranchids, proteids, sirenids, and some plethodontids). Larval and larviform salamanders grossly resemble metamorphosed individuals in general body form but retain a number of larval features. Pond-adapted forms have a more bulky body and larger gills and tail fins than the more streamlined, stream-adapted forms.

The larvae of frogs and toads (Order Anura), called tadpoles, are grossly different from adults and have many developmental (Altig and Johnston 1989) and morphological (e.g. Altig and McDiarmid 1999a; also various morphologies documented in staging tables, see Duellman and Trueb 1986, pp. 128–9) features not seen in other amphibian larvae. Tadpoles live in many kinds of habitats; the most common types of tadpoles are found in lentic or lotic water, spend most of their time on the bottom, and feed by rasping material from submerged surfaces.

Because amphibians are ectotherms, their inherent developmental rates are modified by temperature and other environmental variables; size is thus an inaccurate estimator of chronological age. Consequently, biologists describe tadpole ontogeny using a staging table that divides their development into recognizable stages based on the attainment of specific morphological landmarks. With such a table the degree of development of morphological features of tadpoles can be compared among populations and across taxa occurring in the same or different habitats regardless of chronological age or attainable size.

Larval amphibians are exceptionally variable within and among species, although the degree and patterns of that variation are poorly documented and their sources rarely investigated. The many papers on induced morphological changes published in recent years (e.g. Relyea and Auld 2005, among many others) have made it abundantly clear that every tadpole of a given taxon collected at any site is a variant within the broad phenotypic range of its taxon. Although results from mesocosm experiments with controlled combinations and densities of species provide some insight into understanding phenotypic variation, predicting morphological variation from random samples of ponds is highly unlikely. The presence of different sets of predators in natural situations complicates the picture even more, and one has to keep these factors in mind when evaluating the morphology of tadpoles.

We mention in passing that less is known about amphibian eggs (e.g. Altig and McDiarmid 2007), hatchlings (Gosner stages 21–24; Altig 1972), and metamorphs than is known about tadpoles (stages 25–41) and other amphibian larvae. We urge workers to preserve and describe positively identified samples of these stages. Here we summarize data on the morphology, ontogeny, and diversity of larvae in each amphibian order.

3.2 Larval caecilians

3.2.1 Morphology and ontogeny

The vermiform body (Figure 3.1) has primary annuli homologous to the costal folds of salamanders that form during early development; secondary and tertiary annuli may form later. External gills with branched rami (Figures 3.1a and c) are

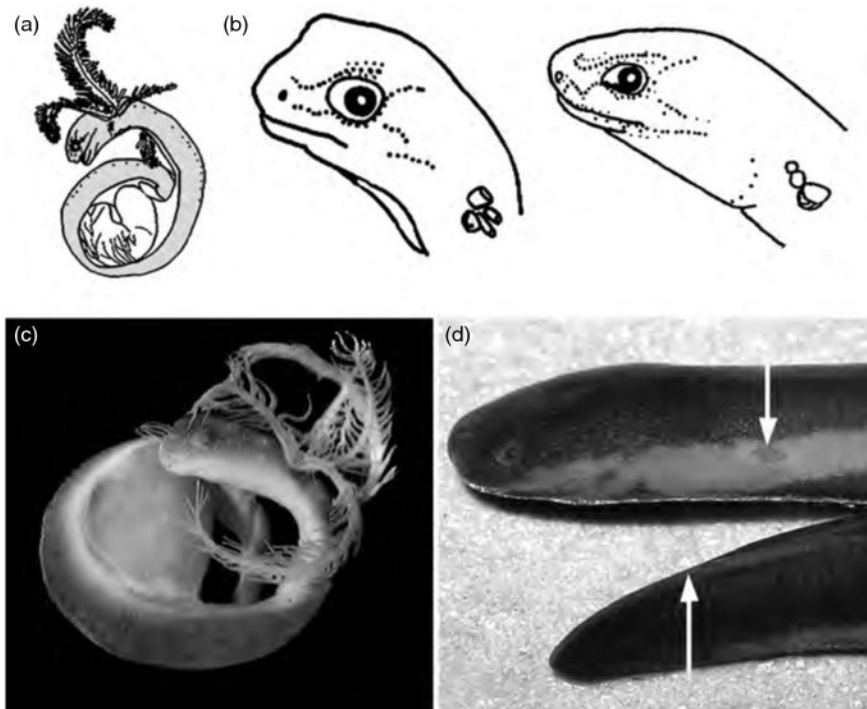


Fig. 3.1 Morphology of a larval caecilian. (a) Embryo of *Ichthyophis glutinosus*, modified from figure in Sarasin and Sarasin (1887–1890); (b) heads of embryos of *Ichthyophis kohtaoensis*, stages 27 (left) and 33 (right), modified from drawings in Dünker *et al.* (2000); (c) hatchling of *I. kohtaoensis*, modified from photograph by A. Summers on front cover, *Journal of Morphology* 2000, **243** (1); and (d) larva of *Ichthyophis banannicus* showing the gill slit (upper arrow) and tail fin (lower arrow), photograph by R. Nussbaum.

present during embryological development and lost at hatching (Figure 3.1b). The single gill slit (Figure 3.1d) closes at metamorphosis, and a small fin is present on a short tail (Figure 3.1d). The sensory tentacle, situated adjacent or anterior to the eye of caecilians, develops at metamorphosis. Some caecilians have small bony scales (i.e. osteoderms) embedded in the skin in the grooves between the annuli. These scales that are quite small when they first appear, get progressively larger as they develop, beginning in the posterior annuli and moving anteriorly. The definitive pattern of occurrence varies among species. Neuromasts, or lateral line organs, are present throughout larval life; labial folds, which modify the shape and size of the mouth opening during suction feeding, are present as they are in larval salamanders. The most complete information on early ontogeny can be found in Dünker *et al.* (2000) (also see Sarasin and Sarasin 1887–1890; Brauer 1897, 1899; Sammouri *et al.* 1990).

3.2.2 Coloration

Most caecilians are somewhat drab shades of gray, brown, black, or blue. A few species are more brightly colored and slightly banded or striped (terminology of Altig and Channing 1993).

3.2.3 Diversity

Larvae of species of caecilians in the families Rhinatrematidae, Ichthyophiidae, and some Caeciliidae that are known are similar to and grossly resemble adults in general morphology. The paucity of ontogenetic data, however, makes further comparisons impossible.

3.3 Larval and larviform salamanders**3.3.1 Morphology and ontogeny**

With the exceptions of pedomorphs in the families Amphiumidae (cylindrical, elongate body with four tiny limbs, each with one to three tiny digits) and Sirenidae (cylindrical, elongate bodies with front limbs only, each with three or four fingers), salamander larvae have a typical quadruped morphology (Figure 3.2a) similar to that of the adults once all four limbs develop. Costal grooves divide the myotomic muscle bundles of the trunk into costal folds. Gills of various shapes are often prominent (Figures 3.2a, b, and d), one to four gill slits open during larval life eventually close in metamorphic taxa, gill rakers are prominent to absent, and a gular fold that typically is free from adjacent throat tissue is usually present. Fleshy labial folds modify mouth size and shape during suction feeding, and neuromasts are present, although sometimes difficult to see without special techniques (Lannoo 1985). Major metamorphic modifications include the loss of tail fins, gills, gill slits, gular folds, and neuromasts, the development of eyelids, and many other integumentary, osteological, and physiological changes.

Pond-inhabiting larvae (e.g. most species of Ambystomatidae and Hynobiidae) have robust bodies and heads, tall dorsal fins that can originate as far anterior as the back of the head, and long gill rami with plumose fimbriae. Stream-inhabiting larvae (e.g. certain species of Hynobiidae, Plethodontidae, and some Salamandridae) are more streamlined; they have low fins that usually originate near the tail/body junction, and shorter, less plumose gills. In species within the Rhyacotritonidae and desmognathine Plethodontidae, the gill rami are exceptionally short with few fimbriae. Gill rami are branched in species in the families Amphiumidae (gills lost soon after hatching) and Sirenidae (gills persist

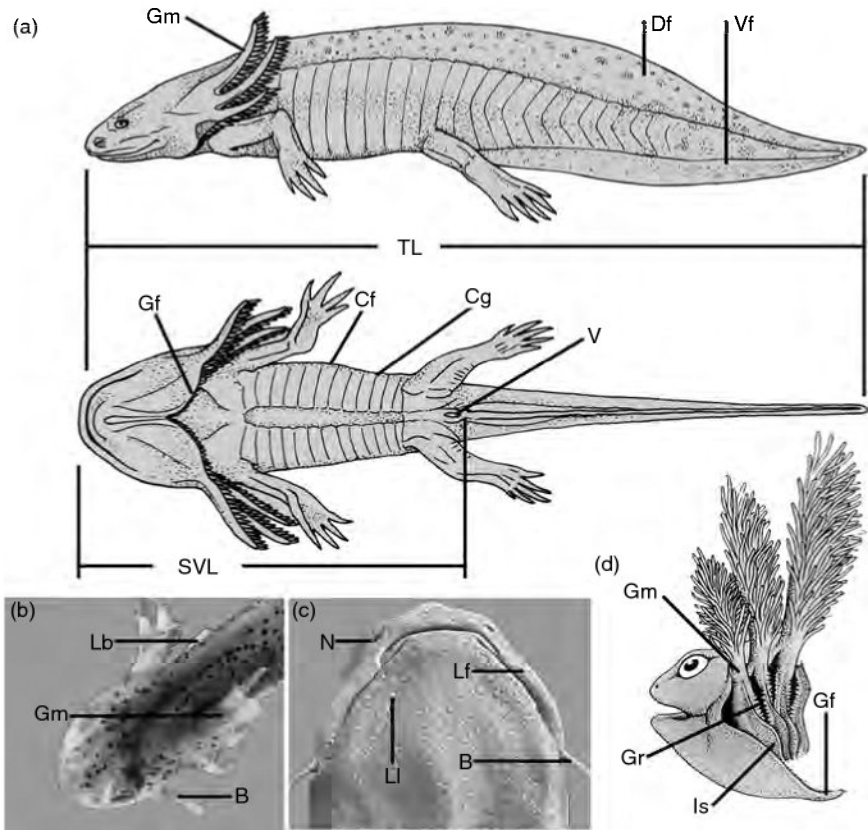


Fig. 3.2 Measurements and body parts of a larval salamander. (a) Lateral (upper) and ventral (lower) views of a typical *Ambystoma* salamander larvae, drawing by D. Karges; (b) dorsal view of the head and anterior body region of a hatchling *Ambystoma maculatum*, photograph by A.M. Richmond; (c) ventral view of head of *A. maculatum*; and (d) stylized drawing of gill structure of a larval salamander, modified from drawing in Pfungsten and Downs (1989). B, balancer; Cf, costal fold; Cg, costal groove; Df, dorsal fin; Gf, gular fold; Gm, gill ramus with fimbriae attached to posterior surface; Gr, gill rakers; Is, interbranchial septum; Lb, limb bud; Lf, labial fold; Ll, lateral line organs (neuromasts); N, naris; SVL, snout-vent length; TL, total length; V, vent; Vf, ventral fin.

throughout life although they atrophy during aestivation); rami in larvae of all other families are non-branched. Larvae of sirenid salamanders have low, fleshy, pigmented fins restricted to the tail, as in adults, and hatchlings have a transparent dorsal fin that originates well forward on the body. Amphiumid larvae have a very short, low caudal fin that is lost soon after hatching. All other salamander larvae have tail fins throughout their ontogeny. Regression of the

dorsal fin usually starts long before other metamorphic changes are noticeable. Fleishy flaps occur on the trailing edges of the hind legs of *Onychodactylus* larvae. Keratinized toe tips are found in a number of taxa but are most common in stream inhabitants. Sirenids have keratinized jaw sheaths (upper and lower) as do some ambystomatid larvae (lower).

Hatching occurs before the limbs are fully developed, and the front limbs usually develop faster than the hind ones. Some hatchlings (e.g. in the families Ambystomatidae and Salamandridae) have a balancer, a fleshy projection on each side of the lower part of the head (Figures 3.2b and c), that is lost soon after hatching. Staging tables (compilation in Duellman and Trueb 1986, p. 128) are available for several species (e.g. *Ambystoma maculatum*, Harrison 1969; *Ambystoma mexicanum*, Cano-Martinez *et al.* 1994; and *Hynobius nigrescens*, Iwasawa and Yamashita 1991).

3.3.2 Coloration

In contrast to *Stereochilus marginatus* (Plethodontidae), *Rhyacotriton* spp. (Rhyacotritonidae), and most pedomorphs, most of which retain something similar to the larval coloration as adults, larval salamanders often have a coloration distinct from that of the metamorph or the adult. Larval sirenids are jet black with contrasting stripes and bands of red or yellow, while adults have either a gray or black ground color usually overlain by speckles and small blotches of gold to greenish iridophores. Color and pattern (i.e. coloration) in larvae of most species can vary considerably during ontogeny, throughout a day, and among sites in response to substrate color, temperature, and water clarity. Colors are typically muted grays, browns, and blacks, and patterns range from none (unicolored), blotched, and mottled through striped (longitudinal or diagonal contrasting markings) and banded (transverse contrasting markings). The dorsum of the tail muscle of small *Ambystoma* is often banded, and the pattern may be retained throughout ontogeny (e.g. *Ambystoma talpoideum*) or change to a totally different pattern sometime after hatching and then again after metamorphosis. In some species and populations, larval *Desmognathus* (Plethodontidae) have a distinct pattern that is kept throughout life. Although colors are usually more muted, the adult patterns in other salamanders (e.g. *Ambystoma tigrinum* group, many plethodontids) may appear at metamorphosis or a different pattern may appear (e.g. most *Ambystoma*) after metamorphosis and slowly develop into the adult pattern, which is achieved long before sexual maturity.

3.3.3 Diversity

Larval salamanders show much less ecomorphological diversity than tadpoles. By definition, pedotypes and pedomorphs retain a larval morphology even

though they become reproductive, and species that metamorphose and are adapted for either pond or flowing water are the most easily recognized groups. Cannibal morphotypes with enlarged heads and altered dentition occur in some species (Ambystomatidae, Hynobiidae). Pond inhabitants often do not overwinter, whereas some stream inhabitants may grow as larvae for several years before undergoing metamorphosis. In some parts of their range *Notophthalmus viridescens* (Salamandridae) larvae metamorphose into a brilliantly colored eft that lives on the forest floor for several years before returning to the ponds for an aquatic existence as a reproductive adult.

3.4 Anuran tadpoles

3.4.1 Morphology and ontogeny

The transition between the body and tail across all stages and taxa of tadpoles is difficult to define. The demarcation between the two is most consistently and accurately described as the juncture of the axis of the tail myotomes with the posterior body surface (Figure 3.3a, bottom). The tails of most tadpoles lack vertebrae and are composed of dorsal and ventral fins and a long series of progressively smaller myotomic muscle bundles surrounding the notochord. The tadpoles of some species of Megophryidae do have tail vertebrae (e.g. Haas *et al.* 2006; Handrigan *et al.* 2007). The shapes and extents of the fins vary among taxa and habitats (i.e. tallest in pond dwellers, lowest in fast-water and semi-terrestrial forms). The eyes are either dorsal (i.e. lie totally within the dorsal silhouette; Figure 3.3b, left) or lateral (i.e. included as part of the dorsal silhouette; Figure 3.3b, right). All free-living tadpoles have a spiracle(s) through which water that has been pumped in through the mouth by the buccopharyngeal musculature and passed over the gills and food filtering system passes out of the body. In the vast majority of species, the spiracle is single and situated somewhere on the left side of the body (Figure 3.3a). Tadpoles of *Ascaphus* (Leiopelmatidae) have a single, ventral spiracle on the chest, while those of *Bombina* (Bombinatoridae) and *Alytes* and *Discoglossus* (Alytidae) have a single spiracle located almost midventrally on the abdomen. In microhylid larvae, the midventral spiracle is located at the posterior part of the abdomen or near the vent. The tadpoles of pipids, rhinophrynids and the leptodactylid genus *Lepidobatrachus* have dual lateral spiracles. The spiracles of *Lepidobatrachus* develop differently from the other two taxa (Ruibal and Thomas 1988).

Scent-laden water passes through the nares, over the olfactory epithelium of the nasal sacs, and into the buccal cavity via the internal nares. The shape of the external apertures varies from round to elliptical and may have a variety of papillae

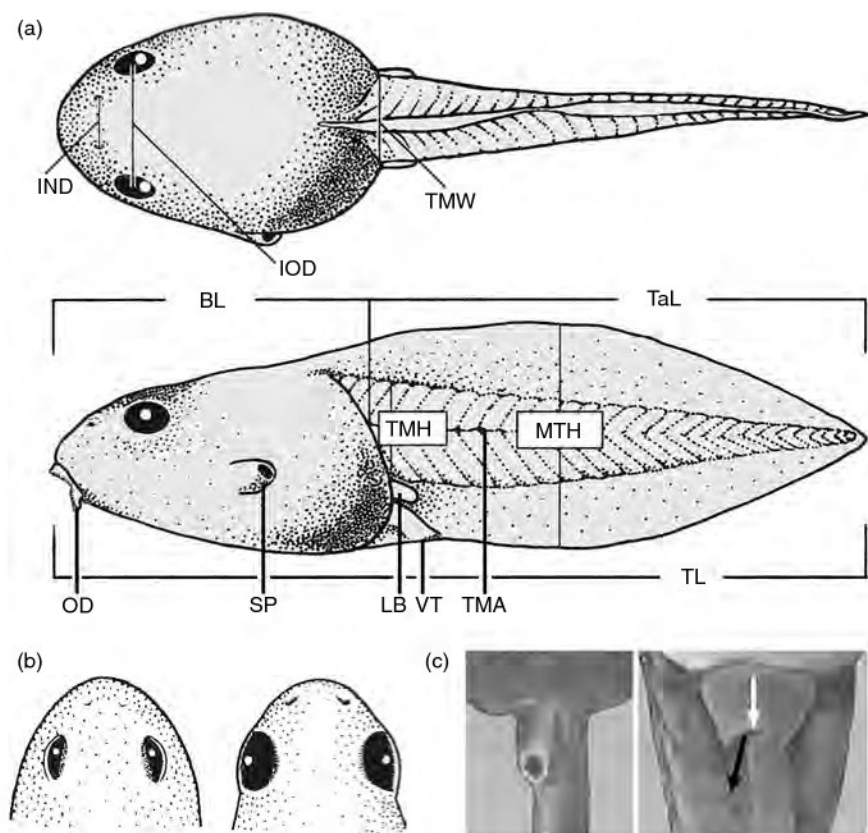


Fig. 3.3 Measurements and body parts of a tadpole. (a) Dorsal (upper) and lateral (lower) views of a typical tadpole, drawing of *Rana* sp. by D. Karges; (b) dorsal (left) and lateral (right) eye positions of tadpoles, stylized drawings by D. Karges; and (c) examples of medial (left, *Bufo boreas*) and dextral (right, *Rana catesbeiana*) vent tubes; white arrow, plane of ventral fin; black arrow, outflow of vent tube. BL, body length; IND, internarial distance; IOD, interorbital distance; LB, hind limb bud; MTH, maximum tail height; OD, oral disc; SP, spiracle; TMA, tail muscle axis; TMH, tail muscle height; TMW, tail muscle width; TL, total length; TaL, tail length; VT, vent tube.

associated with the margins. A vent tube extends posteriorly from the midventral abdomen. Two major types are recognized: dextral, where the aperture lies to the right of the sagittal plane of the tail fin (e.g. hylids and ranids), and medial, where the aperture lines parallel with the plane of the tail fin (e.g. bufonids and scaphi-podids; Figure 3.3c). As with the spiracular tube configurations, there are many subtle variations in the shape and position of the vent tube.

The lateral line system (i.e. neuromasts; Hall *et al.* 2002; Lannoo 1985) is composed of many depressions in the skin with sensory cells in the center that

signal the patterns of water flow over various parts of the body and tail. The distribution and arrangement of neuromasts may be useful in distinguishing between closely related species. In darkly pigmented tadpoles these sites are often pale and obvious, but evaluation of stitch patterns in most tadpoles requires separating the epidermis from the underlying dermis, clearing in glycerin, and viewing the skin with dark-field illumination (see Lannoo 1985).

The oral apparatus, the composite of upper and lower labia and all keratinized mouthparts, is highly variable across taxa and ecological types. The most common oral apparatus (Figure 3.4a and c) occurs in many taxa in lentic and lotic sites. An assembly of the two infralabial and two Meckel's cartilages with three joints forms the lower jaw that is surmounted by a serrated, keratinized jaw sheath. The supralabial cartilage of the upper jaw is surmounted by a similar keratinized jaw sheath, and during a bite, the lower jaw passes totally behind the upper (Figure 3.4d). The interactions of the serrated margins of the sheaths serve as cutting/gouging surfaces when a tadpole feeds. The highly variable shapes of the jaw sheaths suggest different feeding abilities.

The face of the oral disc has fleshy transverse tooth ridges (Figure 3.4a, c, and d) surmounted by a row(s) of keratinized labial teeth. In most cases, several replacement teeth are interdigitated below a presently erupted tooth (Figure 3.4b, lower right), and they successively move into position as the erupted tooth wears out. The tooth rows are numbered from the anterior edge of the disc toward the mouth on the upper labium and from the mouth to the posterior edge of the disc on the lower labium. A fractional designation indicates the number of tooth rows on each labium; some rows have naturally occurring medial gaps denoted parenthetically. For example, a Labial Tooth Row Formula (LTRF) of 2(2)/3(1) indicates two upper rows with a gap in the second one and three lower rows with a gap in the first one (Figures 3.4a and c). Some tadpoles lack tooth rows (i.e. 0/0), and the maximum LTRF known is 17/21 in a tadpole of an undescribed hyloid frog from the Guayana Highlands of southern Venezuela.

The papillate margins of the oral disc may be complete and encircle the disc (e.g. tadpoles of Scaphiropodidae, Pelobatidae, and many stream-inhabiting tadpoles of several families), have a medial dorsal gap (most common; Figure 3.4a), or have both dorsal and ventral gaps (e.g. Bufonidae and those of some Hylidae, Mantellidae, Ranidae, and Rhacophoridae; Figure 3.4c). Although the number of rows of papillae on different parts of the disc margin may vary, the lengths of the papillae are typically somewhat uniform; several species of *Phrynobatrachus* (Ranidae) have exceptionally elongate papillae along the posterior margin of the disc. Submarginal papillae occur on the face of the disc away from the margin

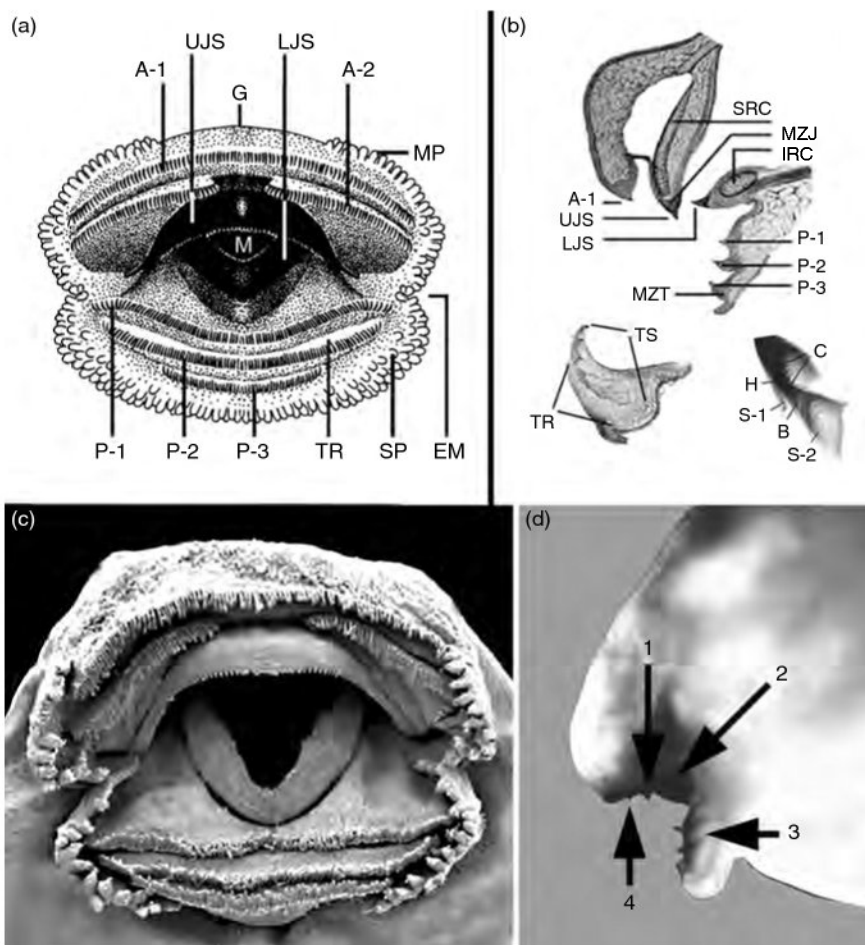


Fig. 3.4 Components of the oral disc of a tadpole. (a) Oral disc of a typical tadpole, schematic drawing by D. Karges; (b) sagittal sections of the oral apparatus of a common benthic tadpole (upper) and a tooth ridge (lower left), schematic drawings modified from ones in Heron-Royer and Van Bambeke (1889); two labial teeth of *Hyla chrysoscelis* (lower right) removed from a tooth series and in natural position; (c) scanning electron photomicrograph of the oral apparatus of a tadpole of *Bufo fowleri*, actual oral disc width, about 2.3 mm, photograph by M. Penuel-Matthews; and (d) lateral view of the mouthparts of *H. chrysoscelis* (1, upper jaw sheath; 2, lower jaw sheath; 3, lower tooth rows; 4, upper tooth row). A-1, A-2, anterior tooth rows 1 and 2; P-1, P-2, P-3, posterior tooth rows 1 to 3; S-1, S-2, sheaths of presently erupted (1) and first replacement (2) teeth; B, body of first replacement tooth; C, cusps on first replacement tooth; EM, lateral emargination in oral disc; G, dorsal gap in marginal papillae; H, head of presently erupted tooth; IRC, infraorstral cartilage; LJS, lower jaw sheath; M, mouth; MP, marginal papillae; MZJ, mitotic zone for production of jaw sheath; MZT, mitotic zone for production of labial teeth; SP, submarginal papillae; SRC, suprarorstral cartilage; TR, tooth ridge; TS, tooth series; UJS, upper jaw sheath.

and form various patterns (Figure 3.4a). The margin of the disc may be emarginate (i.e. indented; Figure 3.4a) or not.

Hatchlings (Gosner 1960; stages 21–24) usually have external gills but lack eyes and limb buds. The forelimb buds develop beneath the operculum after it closes, and the hind-limb buds grow from the posteroventral intersection of the body and tail muscle (Figure 3.3a, bottom). Staging tables have been made for a number of taxa (Duellman and Trueb 1986, pp. 128–129), but using a common table allows for meaningful comparisons among taxa. Gosner (1960; general) and Nieuwkoop and Faber (1956; *Xenopus*) are the two most commonly cited. Recent summaries of tadpole morphology and terminology are included in Altig (2007b) and Altig and McDiarmid (1999a, 1999b).

3.4.2 Coloration

Except for notations in descriptions, surprisingly little has been written about tadpole coloration. As in other larval amphibians, three basic populations of pigment-containing cells interact to produce both color and pattern. Melanophores contain melanins that produce browns and blacks, iridophores contain reflective guanine crystals that produce whites and silvers, and xanthophores contain carotenoids that produce yellows and reds. The pigments are retained inside the cells and can be dispersed in various patterns under the influence of temperature and light. Altig and Channing (1993) summarized the diversity of colorations in tadpoles, and Caldwell (1982) tested the functions of coloration in tadpoles experimentally.

3.4.3 Diversity

Most morphological characters of tadpoles reflect their ecology. Suctorial tadpoles in a number of families have streamlined bodies and mouthparts modified to maintain position in fast-flowing water as they feed. A typical increase in the number of tooth rows, to a maximum of 17/21, is usually accompanied by a larger oral disc with complete marginal papillae. Other unusual morphological structures found in stream-inhabiting tadpoles include a belly modified as a sucker (a few bufonid and ranid species), and lateral sacs (or lymphatic sacs) on the ventrolateral parts of the body of other stream-dwelling tadpoles (Arthroleptidae). Tadpoles of *Mertensophryne* (Bufonidae) have a hollow crown on the head that encircles the eyes and nares, and tadpoles of *Schismaderma carens* (Bufonidae) have a semicircular, transverse flap of skin behind the eyes.

Suspension-feeding tadpoles in the families Microhylidae, Pipidae, and Rhinophrynidae have reduced, soft mouthparts that lack keratinized structures. They usually hang in midwater and capture suspended particles as water is pumped in through the mouth and out the spiracles. Even so, not all tadpoles

that lack keratinized mouthparts are suspension feeders, and tadpoles with keratinized mouthparts that are infected with the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) often lose most or all such structures.

Carnivores and other macrophagous feeders have a diversity of mouthparts related to how they feed. For example, tadpoles of the leptodactylid frog *Lepidobatrachus* have huge mouths but almost no soft or keratinized mouthparts; they engulf entire organisms, including other tadpoles. Tadpoles of other leptodactylid frogs, *Ceratophrys* spp., have huge jaws and many tooth rows and efficiently tear their victims to pieces. Carnivorous tadpoles of *Spea* (Scaphiopodidae) feed similarly. A number of other tadpoles (e.g. Hylidae: *Hyla leucophyllata* group; Ranidae: *Occidozyga*) lack all or most tooth rows but have huge jaw sheaths. Tadpoles that occupy tree holes and bromeliad tanks (e.g. some species of Dendrobatidae, Hylidae, and Rhacophoridae) are of several morphological types (Lannoo *et al.* 1987; Lehtinen *et al.* 2004) and have different diets; some are non-feeding, several are detritivores or macrophagous carnivores, many eat frog eggs (fertilized or not) of their own (cannibals) or other species, and some eat only trophic eggs supplied by their mother. Surface-film feeders have large oral discs, but keratinized structures are reduced or absent; the disc is turned upward (i.e. umbelliform) and captures material carried in the surface film. The oral discs of these surface-feeding tadpoles may be formed primarily from the lower labium (e.g. Microhylidae) or from parts of both labia (e.g. Megophryidae). This convergent morphology occurs in six families, and most tadpoles of this sort occur only in the slow reaches of streams.

Attempts have been made to define ecomorphological guilds or groups of taxa with suites of common morphological characters that are presumed to reflect a common ecology (e.g. Altig and Johnston 1989). Because of the lack of ecological data for many species and an incomplete understanding of how some of their morphologies actually function, we advise caution in assigning species to specific guilds without some knowledge of their natural history. For example, the morphologies of *Mantidactylus lugubris* (Altig and McDiarmid 2006) and of some taxa that occur in phytotelms suggest that one might find them in fast-flowing water. In fact, tadpoles of *M. lugubris* live in leaf packs in slow-flowing water.

3.5 Summary

Amphibian larvae show considerable morphological diversity from the relatively conserved forms of caecilians and salamanders to the unusual and often novel structures found in tadpoles of frogs and toads. The extreme variability of tadpoles is

almost certainly a product of ontogenetic challenges, the recently discovered influences of predators and competitors (e.g. Relyea and Auld 2005), and the selective effects of different habitats. The morphological variability manifest under these different conditions makes identifications and ecological evaluations especially difficult. This situation, combined with our lack of understanding of geographic variation in larval amphibians, especially tadpoles, emphasizes the relative poor state of our knowledge of larval biology. Much remains to be learned. The discovery of various anomalies (e.g. Drake *et al.* 2007), often with a weak understanding of their causes (Altig 2007a; see also Lannoo 2008), adds yet another impediment to our total understanding of larval morphology.

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