

Do Frogs Come from Tadpoles?

Understanding Development as Creative Activity

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Where does a frog come from? The answer seems obvious. It comes from a tadpole. But does it?

Surely, without the tadpole the frog does not develop. But just as surely, nowhere do we find the frog in the tadpole. The frog comes into existence as the tadpole disappears out of existence. We need to be keenly aware of what we mean, and what we don't mean, when we say, "A frog develops out of a tadpole"—or a tadpole out of an embryo, or an embryo out of a fertilized egg, or an adult human being out of a child.

As we will see, when we give careful attention to what is actually happening when a new phase of life develops out of a previous stage, there are large implications for our overall understanding of developmental processes. New and exciting questions arise about how we conceive of development—including that trans-species developmental process we call evolution.

One caveat: I will be limiting my descriptions to those tadpoles that develop into frogs (not the tadpoles that

develop into salamanders). I will focus on pond-dwelling tadpoles and their metamorphosis into land-dwelling frogs, as exemplified by many species that live in temperate climates. There is an astounding variety of ways in which different species of frogs develop—some have no tadpole phase, some have tadpoles that are carnivorous rather than herbivorous, some frogs remain aquatic for their entire life cycle, and so on. Because of this, for probably every characteristic I describe there are exceptions. They are fascinating and warrant consideration when you really want to understand the peculiarities of given species or genera and the variations within the amphibians. But my aim here is to provide a general picture of metamorphosis.

The Life of a Tadpole

Most of you have probably seen tadpoles in ponds and vernal pools. With a thick squat body that abruptly tapers to a long finned tail, a tadpole definitely does not resemble a fish. And yet, tadpoles are fish-like in many of their characteristics. They remain submerged in water and breathe through their skin and gills. They have no limbs, and swim through water via undulating movements of a long boneless tail fin. Like fish, tadpoles have a lateral line organ, which runs along each side of its body and tail, through which they sense movements in water.

Figure 1. Metamorphosis of the European common frog (*Rana temporaria*). Pictured to scale. (Photographs by Tim Hunt, reprinted with permission; <http://www.timhuntphotography.co.uk/>)





Figure 2. Tadpoles (European common frog; *Rana temporaria*). (Photo by Friedrich Böhringer; wikimedia commons.)

A tadpole typically grazes off of algae that grow on plants, rocks, or at the surface of the water. Tadpoles have a “beak” and rows of denticles in their mouth that function like rasps to scrape off the algae. The denticles do not consist of bone and enamel but of keratin—a protein substance that, for instance, also makes up our fingernails and hair.

The tongue-less tadpole sucks the algae into its throat and the food enters the long intestine where it is digested. There is no stomach. The intestine can be more than ten times longer than the tadpole itself and is its largest internal organ, making up over half of its body mass. Tightly coiled, the intestine takes up about half the space within the tadpole’s ovoid-shaped body and is visible through the translucent belly skin.

How long a tadpole lives before it metamorphoses into a frog is dependent on the species and on outer conditions. A wood frog tadpole (*Rana sylvatica*), for example, usually metamorphoses into a froglet within two or three months after hatching in the northeastern United States. The time is shorter when there are higher water temperatures and ample food, and longer when there is colder water and little food. Bullfrog tadpoles (*Rana catesbeina*) grow large—often around four inches (10 cm) long—and, depending on circumstances, can sometimes metamorphose into frogs in

Figure 4. Tadpole metamorphosing into frog (Northern leopard frog; *Rana pipiens*). 1a, 2a, 3, 4 & 5 are drawn to scale, at about 1.2 times natural size. 1b and 2b are enlargements of 1a and 2a respectively. Numbers next to drawings indicate the developmental stages as given by Witschi. (Adapted from Witschi 1959, p. 80-1.)

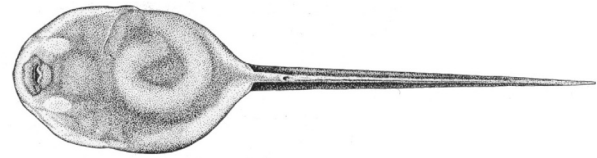
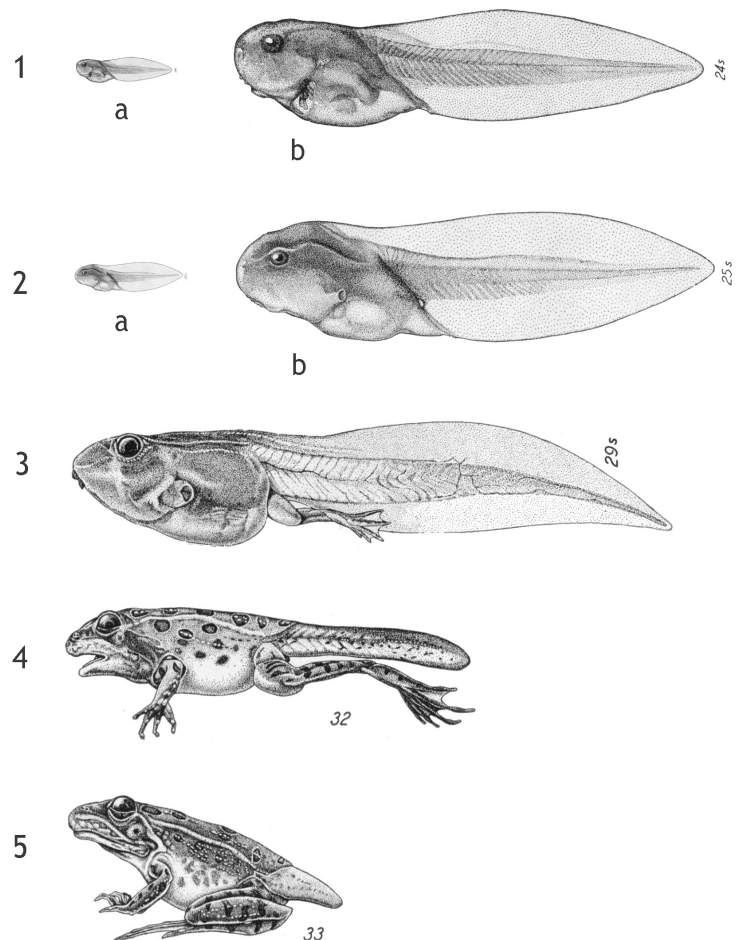


Figure 3. Northern leopard frog tadpole (*Rana pipiens*) viewed from below (ventral; stage 25). Note the coiled intestine visible through the belly skin. (From Witschi 1956, p. 80.)

the fall (four to five months after hatching). But, more typically, they live as tadpoles for two to three seasons before metamorphosing.

Metamorphosis

If you only observed, side-by-side, a tadpole and an adult frog, you would have no idea that the two animals have any connection with each other. The fully aquatic, herbivorous tadpole bears no resemblance to the tailless, four-legged, carnivorous croaking and leaping frog. And yet the two are inextricably connected; the one cannot exist without the other.



The first external sign that a tadpole will not always remain a tadpole appears in the gradual development of hind limbs. They originate as little buds from the rear of the torso, grow into paddle-like structures and then elongate into muscular, articulated limbs at the base of the still-existing tail. While the hind limbs grow, the tadpole also grows and the tail remains the primary means of locomotion. The legs come fully into action only after metamorphosis is completed.

While the hind limbs develop over many weeks or even months (this gradual transitional phase is often called “prometamorphosis”), the further transformation of tadpole into frog occurs within a short period of time—often a week. Virtually nothing in the tadpole remains untouched—organs and body parts are wholly broken down and disappear, others are refashioned, and wholly new organs and body parts arise. While it is easy to say “everything changes,” we gain a much richer sense of what such a transformation entails when we look at it in more detail. In this case, it is not the devil that is in the details; it is the beauty and awe-inspiring transformative ability of life itself.

Externally, the most marked transformation is the disappearance of the tadpole’s tail and the concomitant rapid development of the forelimbs and the growth of the hind limbs. The tail does not fall off. Rather, all its skin, muscle, cartilage, blood vessels, and nerves are internally broken down. The substances arising out of the self-digestion of the tail can be transformed and used to build up new body parts. Being tailless, a young frog is at first considerably smaller than the tadpole was. Depending on the species, it remains small or will grow larger than the tadpole.

A tadpole breathes mainly by taking in oxygen through the thin and highly vascularized skin of its tail. The skin has been compared to fetal skin in mammals. The gills play a lesser role in respiration. Already prior to metamorphosis the tadpole begins to develop lungs and in some species you can see—especially when the water is warm and stagnant—tadpoles swimming to the surface to gulp air into their lungs.

During metamorphosis, while the tail is shrinking in size, the skin of the remaining tadpole thickens. It develops a wholly new pattern of pigmentation and a variety of secretory glands, some of which keep the skin moist once the frog leaves water to live on land. A frog’s skin becomes less able to

take in oxygen and the lungs develop rapidly into the main organ of respiration while the gills are being broken down. Froglets begin floating near the surface with their nasal openings (nares) just above the water surface to take in air.

The circulatory system is intimately connected with respiration and experiences radical remodeling. All the vessels that serve the tail and gills are reabsorbed and new vessels are formed that connect the lungs to the heart. The blood itself becomes thicker in consistency as more serum proteins are formed. Larval red blood cells—which are formed in the kidneys and liver—die off as the smaller and more numerous adult red blood cells are generated. In frogs most of the blood arises out of stem cells in the bone marrow. Different types of hemoglobin—which bind oxygen in red blood cells—arise and they bind more oxygen than larval hemoglobins.

While tadpoles graze mainly on plant matter, frogs feed on other animals, often insects. This transition means a massive remodeling of its feeding and digestive organs. The tadpole’s beak is shed, its denticles are reabsorbed and the mouth as a whole widens. A highly articulated jaw allows the mouth to open wide and in many frogs true teeth form. In the mouth, secretory glands develop as does a tongue, which is muscular and can be quite long. A frog often captures its prey by flipping its tongue out of its mouth, enveloping the prey with its tongue and then pulling it into its mouth, holding it momentarily with its teeth and then swallowing it whole.

Many herbivores have long intestines in which they digest their food, and this is the case in tadpoles, as mentioned above. During metamorphosis, three-quarters of the intestine degenerates and the inner lining of the remaining intestine thickens, many folds arise in it, and a very large absorptive surface is created. As the intestine shrinks, a true stomach is formed that secretes pepsin, an enzyme that is important for digesting animal food. While the rapid

Figure 5. Changes in the shape of the head during metamorphosis (*Bufo valliceps*; Gosner stages 43, 44, & 45). Note the widening mouth. (Redrawn after McDiarmid and Altig 1999, p. 11.)



transformation of the digestive system occurs, the tadpole-becoming-frog hardly feeds.

If you picture a frog leaping—to catch a mosquito that is drifting by or a grasshopper resting on a plant—and you contrast this with the image of a tadpole scraping algae from a submerged stem, you have a sense of two very different ways of being and ways of relating to the surrounding world. This contrasting relation corresponds to a reorganization of the senses and sense organs during metamorphosis. The small, sideways-directed eyes of the tadpole grow into large, bulging eyes that let many frogs have a 360-degree field of vision and the ability to focus both eyes on one object. They gain the ability to move their eyes through the development of large external eye muscles. Eyelids allow frogs to open and close their eyes, which are kept moist by the newly developed tear glands and ducts. The eyes do not only grow but their inner structure and physiology changes. For example, the spherical tadpole lens flattens, the double cornea fuses into a single cornea, and in the light-sensitive retina rhodopsin becomes the dominant photopigment, as it is in most terrestrial vertebrates (and also marine fish).

Both male and female frogs can produce sounds and have a larynx with vocal chords that is not present in the silent tadpoles. Males are the dominant vocalizers in frogs—they are the ones we hear croaking loudly during the spring mating season—and they have, in contrast to females, a vocal sac. It is an outpocketing of the floor of the mouth that fills with air and serves as a resonating body when the male frog produces its sounds.

Anyone who hears a chorus of frogs during the mating season can realize that frogs must have an acute sense of hearing. An eardrum develops that is flush with the outer skin and a middle ear that connects via a bony stirrup (stapes or columella) with the inner ear, which is the only part of the ear that is developed in tadpoles. For a short time during this reconfiguration of the auditory organs the nascent frog is unable to hear sounds.

Manifold changes occur in other organs such as the brain, kidneys, liver, and pancreas. They are associated with the frog's different mode of perception, circulation, feeding, digestion, and movement. Therefore, as you can imagine by now, these organs also reconfigure both anatomically and physiologically.

The body of a tadpole is very flexible and most of its skeleton consists of cartilage and not bone. As the frog develops, the bone formation increases. The limbs are fully developed after metamorphosis and the muscular hind limbs allow the frog at first to swim well with forceful, rapid thrusts through the water, and then to lead a leaping life on land.

Most frogs leave the aquatic environment and become land dwellers, although they thrive best in moist areas and often stay close to bodies of water. They return to water during the mating season. In the case of wood frogs (*Rana sylvatica*), for example, a female can lay over a thousand eggs, which are externally fertilized by sperm from the males. After fertilization the embryo begins to develop and forms into a tadpole that “hatches” out of its protective gelatinous ball and begins to live its tadpole life.

Thinking Development

In what follows I will be struggling with language. How can I adequately express what reveals itself during a study of amphibian metamorphosis? I don't want to fall back on standard phrasing that takes us away from the concrete richness and dynamism of what is showing itself. I want to stay close to the phenomena, not as a mere collection of facts, but as transformative process. So bear with me. Try to catch my meaning. I'm trying to articulate something about development that usually gets overlooked.

In the process of metamorphosis a way of being we call “tadpole” disappears while a way of being we call “frog” emerges. No investigation of the tadpole alone could ever lead us to the knowledge that it will develop into a frog. The frog does not, in this sense, come from the tadpole. During metamorphosis an organic activity is at work that brings the tadpole to disappear while it brings the frog into appearance. We are witnessing a creative transformative activity as the frog becomes flesh—literally incarnates—during metamorphosis.

What I want to emphasize here is that we are dealing with creative activity and not simply the unrolling of some genetic or developmental “program.” Development is not something automatic that just happens. What you find when you closely follow a developmental process is ongoing activity that cannot be accounted for by looking to what came before. You can't find the frog in the tadpole. This is self-evident as long as you attend to the actual process in its own terms.

But since we have been taught that science elaborates the causes of things—and causes, so we imagine, always lie in the past—then evidently the cause of the development of the frog must lie in the tadpole. Scientists start to investigate what substances—such as thyroid hormones—play a role in triggering the onset of metamorphosis, and what genes are turned on and turned off while the tadpole is transforming. This is all interesting, but it is actually just a further elaboration of the process itself at a molecular

level. When scientists discover new molecular processes that in turn influence other processes, they are uncovering fascinating details about how the frog is coming into being. They are not “explaining” it.

At the molecular level, processes and substances in very different kinds of organisms are remarkably similar. Many different organisms produce thyroid hormones and, clearly, a boost in their production doesn't turn them into frogs! Researchers may say that thyroid hormone “controls” metamorphic changes in the tadpole-becoming-frog, evidently believing that discovering a substance that may influence the realization of certain events is the same thing as understanding those events. But you don't understand maturation of the skeletal system in human beings or the transformations in the tadpole-becoming-frog by studying only the associated substance-based conditions (hormones or genes); you have to study the human being and the frog. In other words, the activity of hormones or genes can only be understood in the context of the given organism and the specific developmental process. The significance or meaning of the molecular events becomes clear when we understand how they are part of the actual manifestation of the frog, which we need to study in its fullness.

I'm wanting to counter the strong habit of thought that imagines the answer to developmental questions—the key that opens insights into the mystery of development—as lying in the past and in substances, i.e. in what one imagines as physical causes. No matter at what level we consider an organism and its development, we are always dealing with organizing activity or agency that is specific and that provides the context for any part-processes, such as molecular events, that are discovered.

This is not to deny the contribution of the past to a developmental process. I just want to try to think the relation in an adequate, close-to-the-phenomena way. The tadpole of a wood frog develops into a wood frog; the tadpole of a bull frog develops into a bull frog. That is the specificity that inheres in every aspect of a developmental process. In this sense what “is” constrains what can become. But every “is” is in essence activity. This is easy to see in the ongoing creative transformation from fertilized egg (zygote) into embryo into tadpole into frog.

Take T. H. Huxley's beautiful description of a developing embryo, written in 1860 (Huxley was a colleague of Charles Darwin and one of the main early proponents of Darwin's theory of evolution):

The student of Nature wonders the more and is astonished the less, the more conversant he becomes with her operations; but of all the perennial miracles she offers to

his inspection, perhaps the most worthy of admiration is the development of a plant or of an animal from its embryo. Examine the recently laid egg of some common animal, such as a salamander or newt. It is a minute spheroid in which the best microscope will reveal nothing but a structureless sac, enclosing a glairy fluid, holding granules in suspension. But strange possibilities lie dormant in that semi-fluid globule. Let a moderate supply of warmth reach its watery cradle, and the plastic matter undergoes changes so rapid, yet so steady and purpose-like in their succession, that one can only compare them to those operated by a skilled modeller upon a formless lump of clay. As with an invisible trowel, the mass is divided and subdivided into smaller and smaller portions, until it is reduced to an aggregation of granules not too large to build withal the finest fabrics of the nascent organism. And, then, it is as if a delicate finger traced out the line to be occupied by the spinal column, and moulded the contour of the body; pinching up the head at one end, the tail at the other, and fashioning flank and limb into due salamandrine proportions, in so artistic a way, that, after watching the process hour by hour, one is almost involuntarily possessed by the notion, that some more subtle aid to vision than an achromatic, would show the hidden artist, with his plan before him, striving with skilful manipulation to perfect his work. (Huxley 1860)

It's interesting, and I believe significant, that Huxley is moved by the phenomena themselves to reach for the metaphor of the “hidden artist” sculpting the organism. Something creative—something I have referred to as “activity” or agency—is molding the developmental process. But it is not an artist creating something externally. It is the developing organism as artist creating itself. This gives richer meaning to the term “autopoiesis” (“self-creation”), which is often used to characterize the self-organizing capacity of living beings.

There's no need for dualism here. We don't need to think of some being or life force that is somehow outside the process working in. We just need to thoughtfully follow the process itself, and we see everywhere in organic life “being-at-work”—Joe Sachs's felicitous translation of Aristotle's term *energeia* (Sachs 2005).

Once we realize the activity-nature of a *developing* organism, we can see that the *mature* organism is also being-at-work. An adult frog carries out numerous activities—leaping with its long and powerful rear legs, catching a fly with its tongue, migrating to a vernal pool to mate, croaking at dusk. In all of these and many more activities we can point to a body and say “that is a wood frog.” In all

the changing activity there is a certain stability of form (shape, size, color pattern, etc.). While we can identify specific structures, the frog is always actively maintaining these and continually building up, breaking down, and transforming its bodily substances, all in relation to its needs and what it encounters in its surroundings. The frog never “is” in a static sense. It is continually producing and maintaining itself. Its body is the momentary result of ongoing creative activity.

To sum up: I’m encouraging a significant shift in attention. We habitually tend to consider an organism as “that which has become”—the organism as product that consists of a body, of heart and brain, of hormones and genes. We look at how these products are related and organized spatially and how they interact as products (this hormone affecting that organ). We conceive of everything as spatially bounded; we are tied to thingness in our minds, and the organism and its development appear in this light. Processes become the interactions of already existing substances, and development becomes the “chain reaction” sum of those interactions, the cascade of causal events. Time itself becomes “one thing after the other”—a sequence of events—and so also is atomized and made spatial.

Once we become aware of this grip of spatiality and “thingness” on our thinking, we can begin to loosen it when we attend to a developmental process. We attend to the process *as process*, follow closely the ongoing transformation, the coming-into-being and disappearing. We are no longer describing things, but flux and fluid movement. Huxley entered into this kind of attentiveness when observing the embryo, and he felt the need to characterize development as an artistic process. Development now shows itself as a true coming-into-being, the creative activity of life itself. Continuity lies no longer in the inertia of thingness but in the ongoing activity of life unfolding. This activity reveals itself as we move with the process in our thinking. As we observe, the continual flow in thinking is the means through which life-as-activity shows itself. In this mode of attentiveness, we no longer experience time as if from the outside, as a sequence of events, but rather as an ever-new-now, as ongoing creative activity.

This understanding of the organism and individual development (ontogeny) as creative activity opens up new territory and asks us to re-think all our notions that were based on a thing-centered, spatial way of viewing life processes. A biology of no-things—of activities—leads us into a science that takes seriously and strives to do justice to active, interpenetrating beings. And when we turn in this way of knowing to evolution (phylogeny)—the idea that

organisms develop into different types of organisms over long periods of time—we realize the limitations of conventional ideas that try to derive what has become out of what was present at earlier times. New challenges to our conceptualization of evolutionary processes emerge and new questions arise. How do we need to think about evolution once we begin to take organisms as beings-at-work seriously?

These are topics I will address in the future. And I’m grateful to frogs for helping me along the way.



Adult bull frog. (Photo: Bill Buchanan/USFWS)

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