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Development and Evolution in Amphibians

James Hanken

In Paris in 1865, an event occurred that rocked the intellectual centers of Europe and North America. Two years earlier, the first live specimens of the axolotl—a large, aquatic, gilled salamander endemic to the lakes and river drainages of the Valley of Mexico—had arrived in Paris courtesy of General Forey of the French Expeditionary Forces (Smith 1989). Of the 34 larval specimens that survived the trans-Atlantic voyage, six (five males and one female) were given to Auguste Duméril at the menagerie of the Musée d'Histoire Naturelle. Within the first year of Duméril's care, in January 1865, the axolotls, which until that time had been known only from preserved specimens, attained sexual maturity and bred. This apparently confirmed the status of the axolotl as a distinct species (and genus, *Siredon*) of "perennibranchiate" (permanently gilled) amphibians (Duméril 1865). Such species differ from other salamanders in which the gills are lost following a metamorphosis to a terrestrial stage. What happened later that year, however, was astonishing. Four of the laboratory-reared offspring, followed by several more the following year, did metamorphose into gill-less salamanders of a seemingly different genus, *Ambystoma*, which also had been formally described several years earlier (Duméril 1865, 1866).

> *The evolution of morphological diversity in amphibians has been achieved by modifications in development*

Announcement of this apparent developmental transformation between what for decades had been considered distinct species in different genera met with great skepticism from the scientific community, who felt that either the reported transformation was fabricated, or the taxonomy of these salamanders was incorrect. More significant, however, was the impact on the prevailing recapitulationist doctrine, which held that morphological evolution proceeds by the addition of novel features to an ancestral ontogeny, or developmental sequence, which is recapitulated in descendants (Gould 1977). Under the recapitulationist doctrine, perennibranchiate salamanders, such as the axolotl, were considered ancestral forms from which advanced species had evolved by adding a metamorphosis and a resulting nonbranchiate form. If, however, metamorphosing forms could also mature as larvae (thus eliminating later stages of their ontogeny), then the recapitulationist interpretation was clearly wrong.

Duméril's discoveries triggered, over the next several decades, a flurry of studies of both the developmental transformation known as metamorphosis and the validity of the recapitulationist doctrine as a model of organic evolution. (In the light of subsequent observations, Duméril's discoveries are no longer astonishing. All the salamanders he worked with are now known to belong to a single species, *Ambystoma mexicanum*. Moreover, larval reproduction has proved to be an extremely common mode in the life history of *Ambystoma*, which includes several species found in North America [Shaffer 1984].) Although intense interest in fundamental processes of development—both in amphibians and in other organisms—has continued unabated, by the early part of the twentieth century, evolutionary biologists were devoting less attention to development as an important influence in evolutionary change.

The last few years, however, have witnessed a resurgence of interest in the relation between development and evolution. A large number of studies conducted in this period have contributed enormously to our basic understanding of how developmental processes are modified in the evolution of structural diversity (e.g., Raff and Raff 1987). These studies have also revealed more clearly than ever before the dual role that developmental processes play as both a source of and constraint on morphological change (Alberch 1982; Roth 1982). This renewed interest in the role of internal or "structural" factors in mediating evolutionary change has restored a more balanced view of evolution and its causes, away from the strictly functionalist view—with its emphasis on adaptation in response to external processes such as natural selection—which has dominated much of evolutionary thought for the last 40 to 50 years (Lauder 1982). And again, as when Duméril made his dramatic discoveries more than a century ago, amphibi-

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ans occupy center stage. This can be attributed to the great structural and phylogenetic diversity of amphibians, their complex yet evolutionarily plastic life cycle, and their suitability for laboratory investigation, which is unmatched by other vertebrates. In this article I review the relation between development and evolution in amphibians, highlighting some of the more conspicuous and important features of this relation.

Hyla rufitella

Ensatina eschscholtzi

Ichthyophis kohtaoensis

Figure 1. The morphologies of the three living orders of amphibians have changed drastically since they last shared a common tetrapod ancestor. The three orders—Anura, Caudata, and Gymnophiona—are illustrated here by a frog, a salamander, and a caecilian. These modern amphibians provide clues to the relation between developmental processes and the evolution of morphology. (All photos are by the author except the caecilian, which is courtesy of David M. Dennis.)

Amphibians were the first vertebrate class to colonize the terrestrial environment successfully and extensively, beginning some 400 million years ago in the Devonian period. From these archaic forms evolved the reptiles (and through the reptiles other amniotes—birds and mammals) as well as the amphibians alive today. Living amphibians, however, are a far cry from their Devonian prototype. They constitute three orders which have diverged substantially since they last shared a common tetrapod ancestor (Fig. 1). Indeed, it is easier to identify ways in which they differ from each other than to name the uniquely "amphibian" characteristics that they share (Hanken 1986). The frogs (Order Anura) and salamanders (O. Caudata) are probably more familiar to people than is the third order, the caecilians (O. Gymnophiona)—secretive, limbless burrowers found in many tropical regions. Collectively, these three orders display an impressive diversity in morphology, physiology, ecology, and behavior which has allowed them to occupy a wide range of environments worldwide, from wet Amazonian rainforests to dry Saharan deserts. In terms of the total number of described living species, which is 3,438 for frogs, 352 for salamanders, and 162 for caecilians (Duellman and Trueb 1986), they fall far short of extant amniotes, but they arguably match or even exceed these groups in their evolutionary diversity.

In analyzing the relation between development and evolution in extant amphibians, three features emerge as particularly important: phyletic size change; spatial and temporal repatterning; and paedomorphosis—the retention of juvenile characteristics of an ancestor in later stages of a descendant. These features, either singly or in combination, illustrate how development has been modified in the evolution of much of the morphological diversity in the group. They also help to pinpoint the specific developmental processes involved in each instance of morphological change. In the following sections each of these features is treated separately, although as will be apparent, they are often closely linked.

Phyletic size change

Living amphibians vary tremendously in size, from the tiny Brazilian rainforest frog *Psyllophryne didactyla*, which measures less than 1 cm from snout to rump, to Colombian caecilians, genus *Caecilia*, and the Asian salamander, *Andrias davidianus*, both of which measure over 1.5 m in length (Duellman and Trueb 1986; Taylor 1968). Some extinct species were even larger. Naively, we tend to consider large size or increase in size as being evolutionarily advantageous. Indeed, the evolutionary tendency for lineages to evolve to larger and larger body sizes is sufficiently widespread to be embodied in what is called Cope's rule, named after Edward Cope, the sensational and outspoken nineteenth-century vertebrate paleontologist who drew attention to the trend. Ironi-

Figure 2. The salamander *Thorius* is an example of evolutionary miniaturization; adults can be as small as 1.3 cm in length, snout to vent. The specimen shown is sitting on a blade of grass. At the time of hatching, these salamanders are less than half the size of the specimen shown.

cally, phyletic size decrease—and especially extreme decrease in size, or miniaturization—seems to be more important in the evolution of truly novel morphological features.

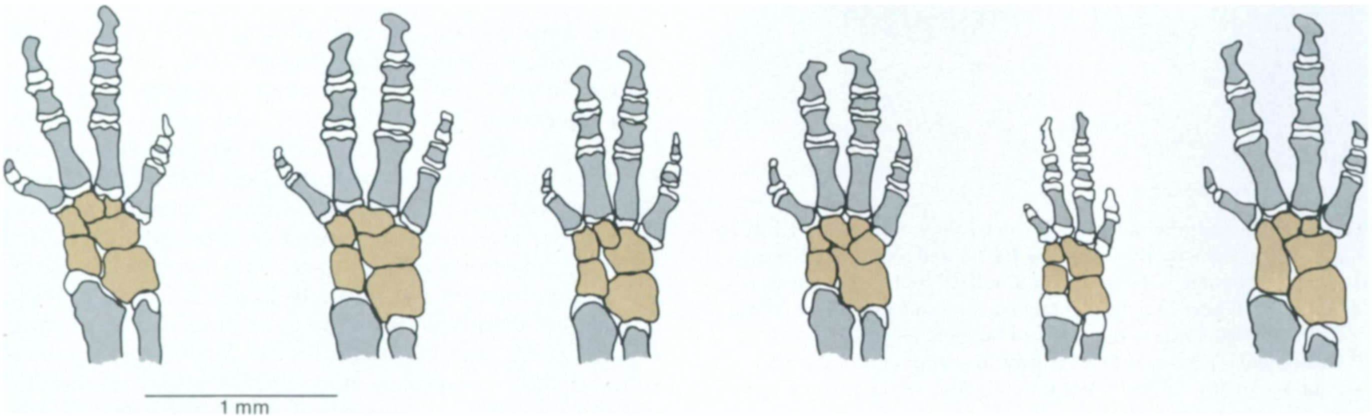
An excellent example of the role of miniaturization in the evolution of morphological novelty is the Mexican salamander genus *Thorius*, shown in Figure 2. The 15 species of *Thorius* (only nine are formally named) represent the smallest salamanders known. Sexually mature adults are as small as 1.3 cm, snout to vent (Hanken 1983a); they are clearly pushing the lower limit for body size in terrestrial vertebrates. They are found under logs or in leaf litter on the montane forest floor. Only after examining their internal anatomy by specialized staining procedures can one appreciate how unusual they are (Fig. 4). In the head, for example, the brain and the three paired, primary sense organs—the eyes, the (inner) ears, and the nose (olfactory organ)—predominate at the expense of the bony skull, which is reduced in many places to little more than thin scaffolding. Some bones are absent entirely (Hanken 1983b, 1984). Other cranial features, ranging from the branching pattern of nerve dendrites within the brain to musculoskeletal structures involved in feeding, are very different from those in closely related genera (Lombard 1977; Lombard and Wake 1977; Roth et al. 1988).

In the limbs, things are even more complicated. Most tetrapod species have a single, characteristic configuration of the wrist or ankle skeleton. *Thorius*, however, displays a total of 18 different skeletal patterns containing from as few as four to as many as nine separate cartilages (Fig. 3; Hanken 1982, 1985). A species typically will have several patterns, and as many as four different patterns in the forelimb alone are found in single populations of several species. Even individual salamanders commonly have different patterns on right and left sides. Many of these configurations are as different from one another as those that routinely distinguish other salamander genera.

Thus, in *Thorius* there is an obvious association between size change and the evolution of morphological novelty. But what links these two phenomena? The answer is development. Predominance of the brain and sense organs, for example, is largely an expression of the way that these structures scale to body size during ontogeny. In the development of virtually all vertebrates, absolute size of the brain and sense organs (especially the eye and inner ear) scales to body size with negative allometry; that is, the relative size of each structure is inversely proportional to body size. This relation holds for most comparisons among adults of different species as well. We typically think of negative allometry in terms of its consequences for size increase; for example, as an explanation for the relatively small eye in an elephant compared to a mouse, or for the relatively tiny brain in enormous dinosaurs compared to smaller, living reptiles. In *Thorius*, the mathematical relation is turned around so that a miniscule head (a skull length approximating 3 mm in adults of some species) contains a relatively enormous brain and sense organs.

Secondary changes also result. For example, another feature that distinguishes *Thorius* from larger salamanders is the orientation of the jaw suspension—that is, the bones, principally the quadrate, that connect the lower jaw to the skull in nonmammalian vertebrates. In larger salamanders, the jaw suspension descends ven-

Figure 3. In the case of *Thorius*, miniaturization has been accompanied by morphological novelty. Seen here are nine different forelimb skeletal patterns found in modern species. The patterns differ in the number and arrangement of the carpal, or wrist elements that lie at the base of the fingers.



trolaterally from the otic capsule (a bony chamber at the back end of the skull which houses the inner ear) to its articulation with the mandible at the jaw joint. In *Thorius,* the jaw suspension descends vertically from the otic capsule toward the mandible, a rearrangement that may have important functional consequences for the way the jaw is used in feeding. Reorientation of the jaw suspension during the evolution of *Thorius* may have been brought about by a relative increase in the size of the inner ear (Hanken 1983b); the articulation between quadrate and otic capsule—one of the most evolutionarily "conservative" joints in vertebrates—apparently moved laterally as the otic capsule increased in relative size to accommodate the expanding inner ear. The quadrate-mandible articulation, on the other hand, was not directed laterally. Unlike the otic capsule, the lower jaw does not enclose one of the primary sense organs and thus does not exhibit strong negative allometry. The lower jaw acted as a fulcrum about which the quadrate gradually pivoted during the evolution of small size.

There is an obvious association between size change and the evolution of morphological novelty

The proliferation of novel skeletal patterns in the limbs might also be a scaling effect of miniaturization on development. Many theoretical models of limb development emphasize the size-dependance of pattern formation in the limbs (e.g., Oster et al. 1985; Solursh 1984). The point is that the configuration and number of skeletal elements initially produced in the hand or foot are a consequence of the absolute size of the undeveloped limb, either directly or indirectly in response to other developmental parameters. These models predict that reducing the size of the developing limb would lead to a decrease in the number of rudimentary cartilages, which are among the first visible signs of limb skeletal pattern. This is exactly what is observed in *Thorius,* where the evolutionary trend is toward a smaller number of cartilages in the wrist and ankle (Hanken 1985). The relation between the size of the developing limb and the skeletal pattern has been demonstrated by comparisons among other amphibian lineages and by experimentation (Alberch and Gale 1983, 1985).

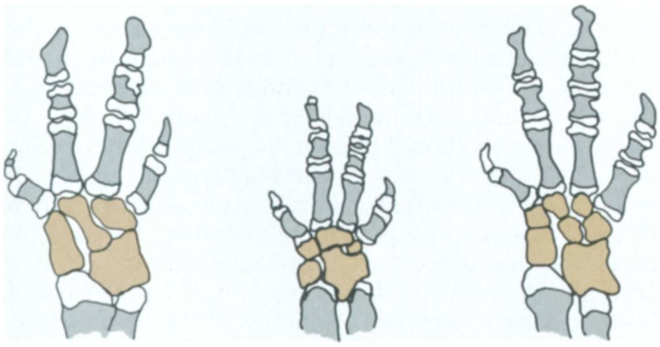


Figure 4. This stained lateral view of the head of an adult *Thorius* reveals a startling case of negative allometry: the brain and sense organs are disproportionately large compared to the tiny skull. Skeletal tissues are stained red (bone) or blue (cartilage). The cartilaginous nasal capsule encloses the olfactory organ; the transparent eye with inner lens appears yellow; the bony otic capsule, which encloses the inner ear, is on the right.

Spatial and temporal repatterning

At a basic level, every change of form is a change in pattern. Thus, morphological evolution can be thought of as phyletic alteration of the developmental mechanisms of pattern formation. Size change in *Thorius,* for instance, includes several examples of altered spatial patterning that are either a direct consequence of or at least closely correlated with miniaturization. Pattern change, however, need not always be tied to changes in absolute size. Repatterning also may involve change in the timing of development, or heterochrony (coined by the influential and highly controversial nineteenth-century German biologist Ernst Haeckel in the context of the recapitulationist doctrine, and later redefined by de Beer [1958]). Heterochrony is evolutionary change in the timing of developmental events. It may affect a wide range of developmental phenomena, from the sequence in which bones form in the skull, to the timing of earlier inductive events in the embryo (Gould 1977). Most important in the context of this article, repatterning may also affect evolutionary success. Some of the best examples of spatial and temporal repatterning and its evolutionary consequences are centered on amphibian metamorphosis, and especially an advanced life-history mode derived from it: direct development.

Metamorphosis is a critical event in the biphasic life history followed by many amphibians. Aquatic larval and terrestrial adult stages are well adapted for life in their respective environments, and this is reflected in the specialized features of their anatomy, physiology, and behavior. Metamorphosis effects an abrupt yet orderly transition between these two stages. Many amphibians, however, do not undergo this primitive transition. Earlier I described the Mexican axolotl, which routinely abandons metamorphosis and its resulting terrestrial

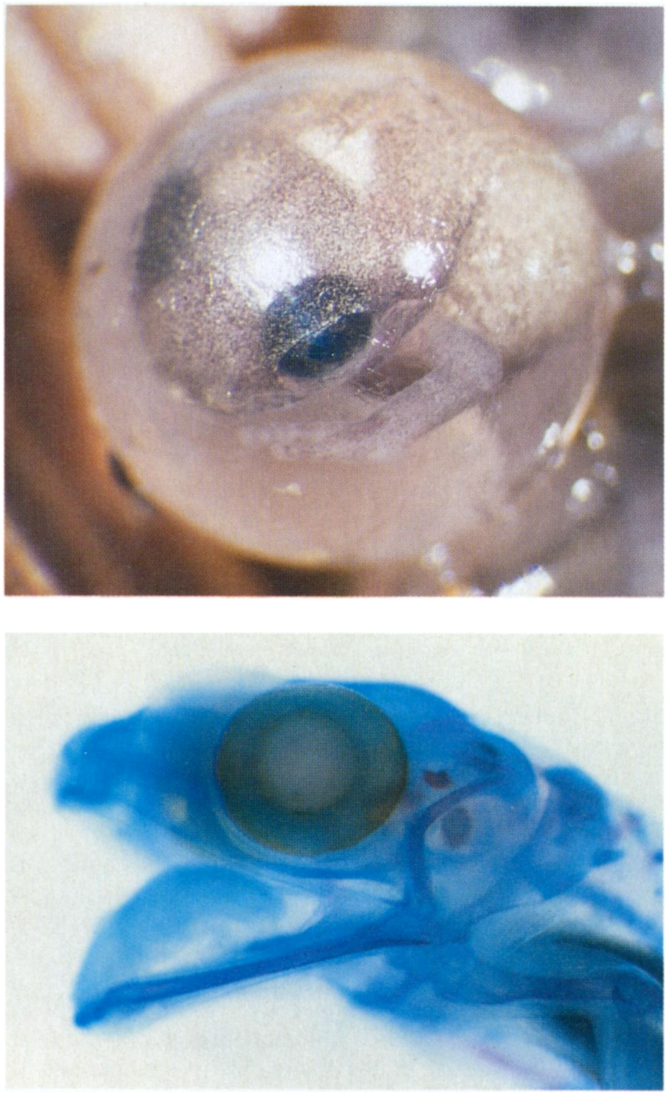


Figure 5. Direct-developing species such as the Puerto Rican frog coqui (*Eleutherodactylus coqui*) have eliminated the free-living, aquatic larval stage (the tadpole) and hatch from the egg as fully terrestrial frogs. In the developing fetus (*above*), note the well-developed forelimb, which never forms during embryogenesis in metamorphosing species. The cleared and stained head of a newly hatched coqui (*below*) reveals the lack of a distinctive larval skull characteristic of metamorphosing species.

stage, and consequently lives its life as a larva, albeit a sexually mature one. A far more common alternative, however, is direct development, in which the free-living, aquatic larval stage is "abandoned." In this case, eggs are laid on land (instead of in ponds or streams), and at the end of embryonic development a fully developed juvenile frog, salamander, or caecilian hatches, grows, and matures. Other reproductive modes are sometimes considered direct development, such as viviparity, or the retention of the developing embryo within the maternal oviduct until and beyond hatching.

Direct development is found in hundreds of amphibian species and has probably evolved repeatedly in each extant order (Duellman and Trueb 1986). It is also tightly linked with the evolutionary success of many groups. One obvious benefit that it confers is emancipation from aquatic breeding sites, thereby allowing the species to disperse across or even permanently occupy areas that do not contain such habitats. Not surprisingly, direct development has received a great deal of attention by biologists, but most of this has concerned the ecological factors that promote its evolution and the sequence in which it evolves (e.g., McDiarmid 1978). In contrast, the developmental basis of direct development has received little attention. For example, it is commonly assumed, and stated in many textbooks, that direct developers undergo a metamorphosis in the egg; that is, that direct developers recapitulate the ontogeny of ancestral metamorphosing species. Yet there are few studies that document this phenomenon, at least with respect to important internal features such as the skeleton, and there are other well-documented cases in which this phenomenon has been shown not to be the case. In fact, what one sees in groups such as frogs is a gradient of developmental patterns, from species that do at least superficially recapitulate the ancestral ontogeny (including forming a tadpole within the egg), to others that essentially bypass many ancestral stages and add new ones—a phenomenon called ontogenetic repatterning (Roth and Wake 1985).

In recent years the role of internal, or structural, influences on evolution has moved to the fore

One of the potentially most important examples of spatial and temporal repatterning is found in a group of tropical New World frogs, genus *Eleutherodactylus*. "Potentially," because these frogs have been studied very little compared to other groups. These frogs are a conspicuous component of the vertebrate fauna in most parts of their range, and would have to be considered an evolutionary success story by almost any criterion. Anyone who has found himself in the rain forests of Puerto Rico at night can attest to the deafening chorus of the coqui, *Eleutherodactylus coqui*. With more than 400 named species, *Eleutherodactylus* is the largest genus of vertebrates alive today (other, unnamed species await formal description). And from what is known, all species exhibit direct development, including *E. jasperi* from Puerto Rico, which is viviparous (see Fig. 5).

Cranial development in *Eleutherodactylus* illustrates well the extensive repatterning that has occurred in the evolution of direct development in the genus. If cranial development recapitulates the ontogenetic sequence typical of metamorphosing ancestors, then the skull of *Eleutherodactylus* should first form the distinctive tadpole skull, with its specialized, cartilaginous jaws and gill arches. This skull, while still in the embryo, should then abruptly "metamorphose" into an adult skull by a combination of resorption and remodeling of existing larval cartilages, and by the formation of new cartilages and bone. Instead, however, embryos of *Eleutherodactylus* never form the distinctive larval skull. Rather, from its earliest recognizable stage, the skull closely resembles that of the adult (Fig. 5; Hanken and Summers 1988; Lynn 1942).

Even the sequence in which the bones ossify is altered. In *Eleutherodactylus,* the first bones to form are the squamosal and angulosplenial, which together form the jaw joint. Precocious ossification of jaw elements, however, is not seen in any metamorphosing frogs (Trueb 1985). In fact, the only other amphibian that displays precocious ossification of these elements is the viviparous caecilian *Dermophis mexicanus,* which also has lost the free-living, aquatic larval stage (Wake and Hanken 1982; Fig. 6). In *Dermophis,* this feature is part of a suite of adaptations for nutrition of both the developing embryo and the fetus, which is retained in the mother's oviduct long after yolk reserves are exhausted. The developing fetus uses its developing jaws and teeth to scrape and ingest a milky secretion from the lining of the oviduct. In *Eleutherodactylus,* early ossification of the jaws probably assures their proper function in capturing prey soon after hatching, by providing both a well-developed joint and solid points of attachment for the jaw and tongue musculature.

Does spatial and temporal repatterning promote evolutionary success? In *Eleutherodactylus,* the association between extreme repatterning and proliferation of species is, pending additional study, no more than a correlation, albeit a striking one. Data from other amphibians, however, suggest that there may be a causal link. Perhaps the most compelling evidence comes from the lungless salamanders, family Plethodontidae. Plethodontids are by far the predominant group of salamanders alive today, comprising more than 220 species divided among 27 genera. The remaining eight living families of salamanders comprise 133 species (Duellman and Trueb 1986). A few plethodontids retain the ancestral biphasic life history with aquatic larvae that metamorphose into terrestrial adults. Most genera, however, have direct development. The bolitoglossines are such a subgroup; they are spread widely throughout the New World tropics (Wake and Lynch 1976). The tiny salamander *Thorius* is a bolitoglossine of Central America.

David Wake of the University of California has studied plethodontids extensively. With students and other collaborators, Wake has discovered a remarkable diversity in the structure and function of the feeding apparatus in many forms with direct development as compared to metamorphosing taxa (Lombard and Wake 1977; Wake 1982). The diversity includes novel arrangements of the skeleton, musculature, and nerves in the mouth and throat—the hyolingual apparatus—which allow the tongue to be extended to a distance of up to one-half the length of the body to capture prey. Among plethodontids, the greatest diversity, complexity, and functional versatility of the hyolingual apparatus are seen in the bolitoglossines, who also exhibit the most derived ontogeny compared to less specialized taxa.

Wake and colleagues argue that two sequential events permitted the observed repatterning (Roth and Wake 1985; Wake 1982). The first event was the loss of lungs, which occurred early in the history of the family (all living forms are lungless). Presumably this occurred as an adaptation to life in cool, aerated mountain streams, in which cutaneous respiration can accommodate modest respiratory needs and the buoyancy of lungs might be a hindrance. Because the two main functions of the hyolingual apparatus in adult lunged salamanders are lung ventilation and feeding, loss of lungs in plethodontids left feeding as the sole function. Moreover, this removed an important constraint on the morphology of the hyolingual apparatus, which in lunged salamanders represents a structural compromise between the conflicting demands for feeding and respiration.

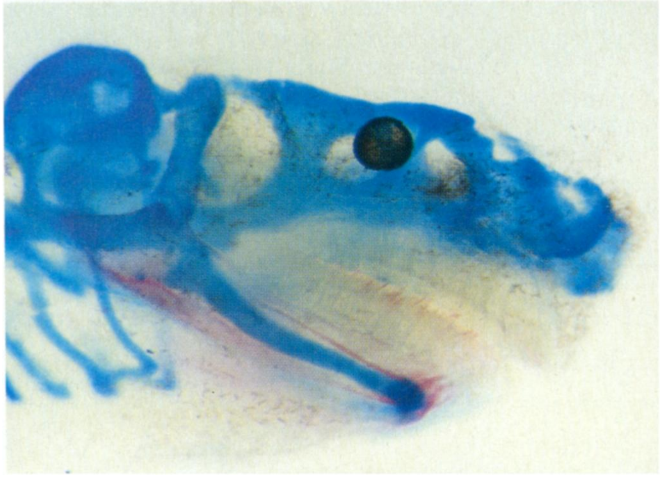


Figure 6. The Guatemalan caecilian, *Dermophis mexicanus*, is viviparous, that is, the developing young are retained in the maternal oviduct until and beyond hatching. Precocious ossification of the fetal jaws and early-formed teeth (*stained red*) allow the young to scrape a nutritive secretion from the lining of the oviduct.

The second key event was the evolution of direct development. With the loss of the larval stage, the need to form the larval hyobranchial apparatus (precursor of the adult hyolingual apparatus), which is anatomically specialized for aquatic feeding and respiration, was also removed (Fig. 7). Wake and his colleagues argue that the need to form a specialized, larval hyobranchial apparatus constrains the morphology of the adult hyolingual apparatus that forms from it in metamorphosing species; in other words, there is a limit to the extent of metamorphic transformation. When the larval constraint is removed,

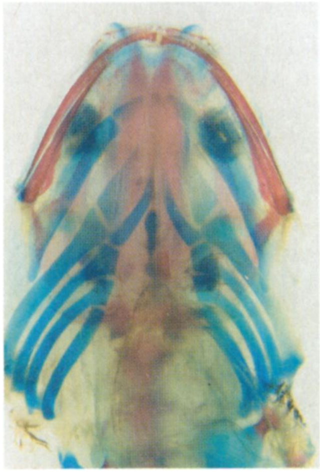


Figure 7. This stained skull of a larval long-toed salamander, *Ambystoma macrodactylum*, reveals the complex hyobranchial apparatus that will eventually be remodeled in metamorphosis—giving way to the adult hyolingual apparatus. The absence of a larval hyobranchial apparatus in some direct-developing species may eliminate constraints on the development of the hyolingual apparatus.

however, the adult structure is free to evolve, and this is what happened in bolitoglossines.

Thus two events seemingly far removed from feeding—lung loss and direct development—eliminated two constraints on the structure of the feeding apparatus. Bolitoglossines responded with spatial and temporal repatterning: in the embryo, the hyolingual apparatus initially assumes the derived, adult configuration, never recapitulating the ancestral larval structure (Alberch 1987). It should be noted that repatterning and consequent specialization of feeding structures did not follow these two events in all groups. For example, in another group of lungless, direct-developing plethodontids, the plethodontines (which include the common red-backed salamander of eastern North America), the adult hyolingual apparatus is not nearly as specialized, and development recapitulates, at least in part, the larval precursors (Dent 1942).

At a basic level, every change of form is a change in pattern

Paedomorphosis

The third principal feature characterizing amphibian development and evolution is a specific kind of heterochrony called paedomorphosis. In certain respects, paedomorphosis is far easier to understand than other kinds of temporal repatterning. Paedomorphosis is often not so much a change in ancestral developmental timing, as it is a failure to complete the ancestral sequence. In other words, the adult descendant retains "juvenile" characteristics of the ancestor.

Two instances of paedomorphosis have already been described: the axolotl becomes sexually mature while retaining an otherwise larval morphology; *Thorius* retains a flimsy skull which lacks many late-forming bones typically present in salamanders (Hanken 1984). Paedomorphosis in the axolotl, in which the rate of development of somatic tissues is slowed relative to that of reproductive structures, is commonly called neoteny, whereas that in *Thorius,* which probably involves precocious sexual maturation, is called progenesis (Gould 1977).

The significance of paedomorphosis for amphibians, and the reason I distinguish it from other instances of temporal repatterning, can be appreciated by considering two facts. First, paedomorphosis is an extremely common mode of evolutionary change. The extensive literature of amphibian morphology is replete with species, genera, and higher taxa—even the entire subclass Lissamphibia, to which living amphibians belong—that are paedomorphic compared to their ancestors or living relatives (e.g., Bolt 1977; D. B. Wake 1966; M. H. Wake 1986). Thus evolutionary change often represents variations on an ancestral theme. This, however, is not to say that novel changes, involving extensions beyond or drastic alterations to the ancestral ontogeny, never occur. Clearly, such events have occurred and some have been very significant. Nor should paedomorphosis be perceived as confining or limiting change. Rampant morphological novelty in *Thorius,* which is the product of paedomorphosis combined with extreme decrease in body size, proves the opposite. Rather, predominance of paedomorphosis illustrates the bold stamp that phylogenetic legacy leaves on morphological evolution in these vertebrates.

Second, paedomorphosis provides an alternative, or at least a complement, to strictly adaptationist explanations of trends such as convergent or parallel evolution. For example, several lineages of frogs have independently lost one or more bones in the skull, which apparently were present in their common ancestor. Among these is the columella, a small but important bone that conducts sound from the surface of the head to sensory cells in the inner ear. One might be tempted to interpret the repeated loss of the columella primarily as the result of natural selection for a particular kind of acoustical acuity. Indeed, such an explanation probably accounts for the loss of the columella in certain groups. A fuller understanding is achieved, however, when one considers that the columella is among the last bones to form in an anuran skull. If paedomorphosis occurred in a given lineage, for whatever reason, then there is a good chance that the columella would be lost as a consequence.

Thus paedomorphosis allows one to make specific, testable hypotheses of morphological change. In the case of the missing columella, for example, one might predict that additional late-forming bones would be absent as well, regardless of their role in hearing. This is indeed the case (Trueb 1985; Trueb and Alberch 1985). Loss of such bones in combination with the columella would be difficult to explain by purely selectionist explanations.

Evolution and development

Evolution is the net result of a series of influences, some promoting change, others limiting it. During much of this century, evolutionary biologists have tended to perceive the predominant influences as residing largely in the external environment of the organism. This functional, adaptationist approach has not been without success. It has contributed greatly to our understanding of many important evolutionary processes, such as natural selection. In recent years, however, the role of internal, or structural, influences on evolution has moved to the fore, a position occupied in earlier times both before and after Darwin (Goodwin 1984; Lauder 1982; Russell 1916). Development is one internal influence that can foster greater understanding of evolution.

The consideration of development need not deny an important role for external factors. Clearly, internal and external influences may be intimately related. In *Thorius,* miniaturization interacting with developmental phenomena such as allometry and scale-dependent patterning resulted in profound changes in the morphology of the head and limbs. Yet this provides no explanation for the trend toward small body size, a trend which probably results from natural selection for some life history or other ecological parameter (Gould 1977; Hanken 1984). And whereas features of limb development may promote the appearance of novel variants, these variants must function adequately or they will be quickly eliminated from the population. The path to greatest understanding of evolution entails an approach that considers the role of both internal and external influences in evolutionary change.

It is important to remember that while phyletic size change, spatial and temporal repatterning, and paedomorphosis may effectively describe characteristic features of the relation between development and evolution in amphibians, they reveal little of the molecular, cellular, and developmental processes that underlie the observed evolutionary changes. A major challenge for future research is to reveal the developmental and genetic bases of these features, and how they interact with evolutionary processes at the individual, population, species, and even community level.

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