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Mini-review

Life history and morphological evolution

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Morphological evolution is influenced by a wide variety of processes, at levels that likely range from molecules to communities, or even ecosystems. The relative contributions of these processes and other biological properties to morphological evolution in individual lineages, and their ultimate role in mediating the evolutionary success of these groups, remain fundamental problems in evolutionary biology (e.g., Müller and Wagner, 1991; Nitecki, 1990; Roth and Wake, 1989). One underappreciated feature, at least with respect to its potential role in the evolution of morphology, is life history. Organisms with a complex life history comprising a series of discrete, free-living stages might be expected to possess more morphological adaptations than taxa with simple life histories, especially when successive stages occupy radically different environments. Also, the genetic and developmental mechanisms that underlie the sequential appearance of distinct phenotypes might be expected to allow, if not actually facilitate, morphological change at one stage without correlated effects at others to an extent not possible with a simpler life history (Elinson, 1990). On the other hand, the presence of fully differentiated, functional structures at one stage might be expected to constrain the morphology of structures that form earlier or later (D. Wake and Roth, 1989). Yet, ideas such as these remain largely unexplored in most groups.

Here I briefly review aspects of the relation between life history and morphological evolution in Recent amphibians, an especially good group for such an analysis. Many taxa retain the ancestral complex life history, which comprises discrete aquatic larval and terrestrial adult stages bridged by a sharply defined transition, or metamorphosis (Fig. 1A). In addition, there is a remarkable array of derived life history modes that can be used to test evolutionary hypotheses and illustrate phylogenetic patterns. When examined in this way, a complex life history can be seen to provide substantial opportunities for morphological evolution in these vertebrates. These opportunites are realized through a variety of evolutionary

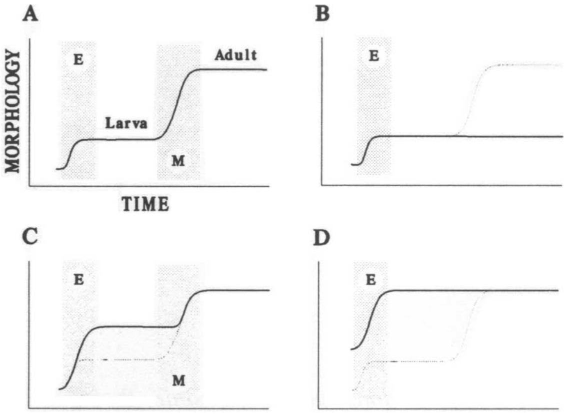

Fig 1. Alternative life-history/developmental patterns in amphibians. A: Ancestral biphasic pattern (also dotted line in B–D) B: Paedomorphosis. C: Precocious metamorphosis. D: direct development. Abbreviations: E, embryogenesis; M, metamorphosis.

modifications – some apparently quite simple – to the ancestral developmental program.

Developmental patterns

Notwithstanding characteristic differences in metamorphosis among the three extant orders – frogs (Anura), salamanders (Caudata), and caecilians (Gymnophiona) – a biphasic life history is regarded as the primitive mode for Recent amphibians (Duellman and Trueb, 1986; Fritzsch, 1990). The wide variety of derived life history modes seen in many extant taxa comprise recent variations on this ancestral theme; many of the modifications involve changes in the timing and extent of metamorphosis, and provide excellent examples of heterochrony (*sensu* Gould, 1977). Much of this diversity is representative of three basic developmental patterns – paedomorphosis, precocious metamorphosis, and direct development.

Paedomorphosis is the retention of ancestral juvenile features in an adult descendant as a result of precocious truncation of the ancestral ontogeny (Gould, 1977). It is extremely common in amphibians, including both living and fossil taxa, and has played a predominant role in morphological evolution in the group (Hanken, 1989; Milner, 1988). Effects range from the relatively minor elimination of individual traits from the end of the ancestral ontogeny, to the virtually complete elimination of metamorphosis and abandonment of the subsequent terrestrial, adult stage (Fig. 1B).

Because paedomorphosis is defined in terms of phyletic change in the time of appearance of ancestral traits, one is tempted to deny it a role in the evolution of significant morphological configurations new to a lineage. This qualification is not justified. Because of the dissociation of tightly correlated ancestral traits that is frequently seen in paedomorphosis, the descendant may in fact be conferred with a novel combination of these traits with potentially tremendous functional significance. In other cases, minor changes in the ancestral relation between morphological differentiation and body size can evoke functionally significant new structures ("morphological novelty" *sensu* Müller and Wagner, 1991) whose origin may represent little more than scaling effects realized from the vast potential of preexisting developmental systems (Hanken, 1983, 1989).

Paedomorphosis is usually discussed with regard to differences among species, genera, or even higher taxa. Yet, one of the most interesting but least appreciated aspects of paedomorphosis in amphibians is that it may occur variably *within* species. This can result in discrete polymorphisms of adult phenotypes (e.g., larval vs. metamorphosed) or in nearly continuous variability across a broad morphological gradient (Reilly, 1987). This lability in developmental pattern is presumably related to the neuroendocrine mechanisms that mediate metamorphosis, which are sensitive to environmental perturbation and which may allow populations of at least some species to closely track environmental changes. Of perhaps ultimately greater evolutionary significance, it also confers the potential for substantial morphological change and local adaptation without speciation.

Unlike paedomorphosis, which is typically described in terms of consequences for adult morphology, **precocious metamorphosis** involves large-scale modifications to the larva. Characteristic features of the adult, which in the ancestral life history develop at metamorphosis, are advanced into the larval period (Fig. 1C). The resulting novel larval morphology is frequently associated with ecological specialization; it may or may not involve changes to the adult.

An excellent example of precocious metamorphosis is the remarkable tadpole of the South American frog genus *Lepidobatrachus*. Unlike "typical" tadpoles, which feed by filtering tiny pieces of plant matter from water currents passed over the gills, tadpoles of *Lepidobatrachus* are "megalophagous" carnivores, consuming large, live animal prey, which they swallow whole (Ruibal and Thomas, 1988; Fig. 2A). Associated with this shift of larval feeding guild is unique specialization of the trophic morphology, which is remarkably adult-like. Virtually the entire trophic apparatus is involved: jaws and visceral arches are enormous (Jennings et al., 1991; Fig. 2B), many of the oral integumentary adaptations for filter-feeding in microphagous herbivores are absent or highly reduced (Wassersug and Heyer, 1988), and the gut and associated digestive enzymes are modified to process animal food (Carroll et al., 1991).

What is the developmental basis of morphological and ecological specialization in larval *Lepidobatrachus*? Several of the most prominent features are consistent with the hypothesis that many metamorphic events in typical anurans have been advanced into the embryonic period. Yet, *Lepidobatrachus* does not simply recapitulate the ancestral ontogeny – first developing the typical anuran larval trophic morphology which subsequently undergoes precocious remodeling (metamorphosis) before or soon after hatching. Rather, the derived (adult-like) larval morphology is assumed virtually from the inception of morphogenesis; many typical larval features

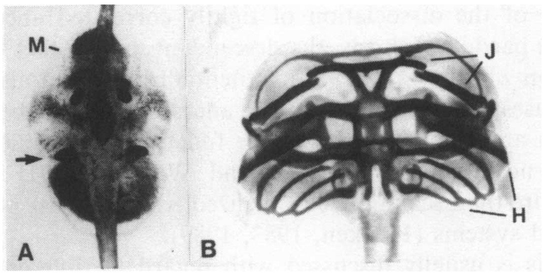

Fig. 2. Carnivorous tadpole of *Lepidobatrachus laevis* (dorsal view). A: Specimen fixed within minutes of eating another tadpole, whose abdomen and tail protrude from the mouth (M). Cannibalism is common in this aggressive species. The enlarged head (arrow denotes posterior limit) is also characteristic of the genus. B: Cartilaginous skull showing the hypertrophied lower jaw (J) and hyobranchial skeleton (H). The specimen, Gosner (1960) stage 27, is stained with Alcian blue.

never form. At metamorphosis, remodeling events similar to those in other frogs produce the more typical adult morphology. In *Lepidobatrachus*, evolution of a novel larval morphology has been achieved by dissociation of events that comprise the ancestral metamorphosis, by precocious initiation of some of these events during embryogenesis, and by elimination of many features characteristic of ancestral embryonic development.

The free-living, aquatic larval stage is also the primary target of evolutionary changes involving **direct development.** Unlike precocious metamorphosis, however, where the larva is retained, albeit highly specialized, direct development involves its evolutionary loss (Fig. 1D). In most cases, the aquatic phase of the ancestral life history is abandoned altogether (Duellman and Trueb, 1986). Typically, eggs are deposited terrestrially, from which emerge miniature versions of the adult.

While the existence of direct development as an alternative life history mode in amphibians is well known, its widespread occurrence is not. In fact, direct development has evolved independently in each of the three extant orders; in frogs alone it likely has evolved at least 12 times and characterizes well over 500 living species in at least 10 families (Duellman and Trueb, 1986). Consequently, direct development in amphibians offers an excellent opportunity to address a number of contemporary issues in evolutionary and developmental biology (Alberch, 1987; Elinson, 1990; Hanken, 1989; D. Wake and Roth, 1989). To date, however, most research has considered ecological and life-history aspects (e.g., McDiarmid, 1978); relatively little is known about the developmental patterns or mechanisms that underlie the evolutionary transition from the ancestral life history, and which are the subject of detailed examination in other chordates (Jeffery and Swalla, 1990) and invertebrates (Wray and Raff, 1991).

Evolutionary significance of direct development may lie in its providing a release from developmental and functional constraints on adult morphology imposed by the larva in metamorphosing taxa. This view has been argued most stridently by D. Wake and colleagues, based on their studies of lungless salamanders of the family

Plethodontidae (Roth and Wake, 1989; D. Wake and Roth, 1989). They cite the striking correlation between direct development and morphological innovation in this group, particularly involving musculoskeletal components of the hyobranchial apparatus and its neural control. Yet, while this correlation is well established, there is little direct evidence that would either corroborate the larval constraint hypothesis, or refute it. If, for example, larval structures constrain adult morphology in metamorphosing taxa, then these structures should be absent from direct developers that show novel features in the adult; otherwise, the hypothesized constraint would still be present and adult morphology would not be expected to vary substantially. In other words, the ontogeny of direct developing taxa with a highly derived adult morphology should not simply recapitulate the ancestral biphasic pattern of development – including, for example, an embryonic "metamorphosis" – but should lack larval features.

For plethodontid salamanders, however, there are few embryological studies of direct-developing taxa, especially concerning the hyobranchial apparatus. Limited accounts for a few species support the view linking novel adult morphology with the absence of larval features (e.g., Alberch, 1987), but these claims remain to be fully documented. Ontogenetic data from other direct-developing amphibians complicate the situation even further. Here, a derived ontogeny involving substantial modification of the ancestral biphasic pattern, including the absence of many larval features, is not associated with any noticeable change in adult morphology.

This paradox is well illustrated by frogs of the Neotropical genus *Eleutherodactylus*. With approximately 450 described species (Hedges, 1989), *Eleutherodactylus* is the largest genus of terrestrial vertebrates. All species are believed to show direct development, including at least one in which the female parent retains developing embryos in her oviducts beyond hatching and gives birth to tiny froglets (M. Wake, 1989). Embryonic development in *Eleutherodactylus*, which is the best known of any group of direct-developing amphibians (Elinson et al., 1990; Lynn, 1961; Townsend and Stewart, 1985), is a complex mosaic of ancestral and derived traits. Many larval anuran features never form, including components of the skull, nervous system, and integument (Fritzsch, 1990; Hanken et al., 1992; Hughes, 1959; Lynn, 1942). In their absence, development of postmetamorphic structures is advanced into early stages. Indeed, *Eleutherodactylus* has long been regarded as the least recapitulatory of direct developing anurans, although individual species vary in this regard (Elinson, 1990; Lynn, 1961). At the same time, other features initially assume a mid-metamorphic configuration which is subsequently remodeled by hatching. In some cases, both loss and metamorphic remodeling may be seen in the same organ system or even anatomical unit (Fig. 3).

Perhaps the most remarkable – and paradoxical – aspect of direct development in *Eleutherodactylus* is that these and other changes to early ontogeny, which might otherwise be regarded as quite fundamental, have no apparent effect on adult morphology. *Eleutherodactylus* has a generalized morphology in comparison to that of other leptodactylid genera, including several metamorphosing taxa (Lynch, 1971), and only moderate interspecific variation (D. Wake and Roth, 1989). Thus, loss of larval features, and presumably any constraints on adult morphology

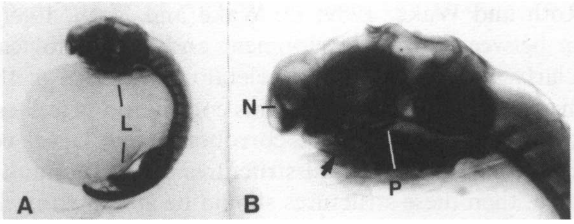

Fig. 3. Embryonic skeleton of the direct-developing frog *Eleutherodactylus coqui*, Townsend-Stewart (1985) stage 9, prepared using a monoclonal antibody against type II collagen. A: whole body, lateral view. B: close-up of head. The skeleton already shows many adult structures that don't form until metamorphosis in biphasic anurans, e.g., nasal capsules (N), and fore- and hind limbs (L). Many larval features are absent from the jaw suspension (palatoquadrate cartilage, P), which initially assumes a mid-metamorphic orientation. By hatching (stage 15), it will rotate through an arc of 60° about its dorsal tip, bringing the jaw articulation (arrow) posteriorly to produce the large mouth typical of adult frogs.

associated with them, has not led to morphological innovation in this taxon. In lacking substantial diversification of adult morphology despite significant change in early development, direct development in *Eleutherodactylus* is remarkably similar to that seen in many echinoderms (Wray and Raff, 1991; Strathmann, 1988). This paradox is eliminated, at least for anurans, if the tadpole represents an "evolutionary insertion" into the anuran life history and its development is largely independent of other stages (Elinson, 1990); changes to or even elimination of the larva would not be expected to have any effect on the adult. Proof of this hypothesis, however, requires further detailed examination of the development of metamorphosing taxa. Furthermore, even if larval features do constrain adult morphology, their loss need not invariably lead to morphological innovation, which is mediated by a variety of influences, both positive and negative (D. Wake and Roth, 1989). In other words, while removal of larval constraints may be a necessary condition for the evolution of adult morphology, it alone is not sufficient for substantial evolution to occur.

Developmental mechanisms

So far I've considered patterns of development in extant amphibians and the relation of these patterns to morphological evolution. But developmental patterns offer only a limited, albeit necessary, perspective on the evolution of morphology; one must also investigate underlying developmental mechanisms. One set of mechanisms especially important in the context of complex life cycles are those mediating cell lineage. The degree of independence of larval versus adult cell lines, as well as the developmental programs by which these cells differentiate into functional tissues, has direct bearing on the degree to which larval and adult structures may have divergent evolutionary fates. This applies to metamorphosing taxa as well as to those that have abandoned an ancestral complex life history. To date, these ideas have been developed most fully in invertebrates. Raff (1987), for example, apportions embryonic cell lineages in sea urchins among three categories: larval fate only; larval and adult fates; adult fate only (imaginal in larva). Subsequent studies document predictable changes in cell lineage and patterns of embryonic gene expression accompanying evolutionary change in life history (Wray and Raff, 1991).

The same categorization of cell lineage erected for sea urchins likely applies to amphibians as well (Fritzsch, 1990; Yoshizato, 1989), although the lineage of most adult structures has not been carefully followed. Larval-specific cells include those that make up the large number of larval organs that are resorbed at metamorphosis, such as the tail and many cranial cartilages in anurans, and the gills in all three orders. Cells that form both larval and adult structures probably represent the largest category. They contribute to the vast majority of organs that are functional at both phases of the life history and which, despite often substantial remodelling at metamorphosis, show no evidence of larval-to-adult cell turnover. Detailed cellular aspects of metamorphosis, however, are poorly known for most of these organs.

The third category – adult-specific cells (imaginal in larva) – is perhaps the most interesting of all with respect to the potential dissociation of larval from adult structures and its bearing on the question of evolutionary constraints. A number of discrete structures and even entire organs appear *de novo* during amphibian metamorphosis (Fritzsch, 1990; Yoshizato, 1989). For most of these, however, virtually nothing is known concerning the location or developmental state of progenitor cells in either the embryo or the larva. Possibly the best documentaed case of compartmentalization of an adult cell lineage in amphibians involves the jaw musculature in anurans (Alley, 1989). At metamorphosis, larval myofibers are destroyed coincident with recruitment of a secondary myogenic population from adjacent, and previously quiescent, satellite cells. This effects a virtually complete turnover of myofiber complement in the jaw. In at least one species, the clawed frog, *Xenopus laevis*, this morphological and cellular transformation is mirrored at the molecular level by an almost complete larval-to-adult replacement of creatine kinase isozymes in muscle (Robert et al., 1991). Analogous recruitment of quiescent larval cells in the *de novo* formation of postmetamorphic structures is seen in the hyobranchial skeleton of the urodele *Eurycea bislineata* (Alberch, 1987).

Summary and Conclusion

In amphibians, a complex life history provides unique opportunities for morphological evolution, which is achieved by modifications to the corresponding biphasic pattern of development. Derived developmental patterns may involve the loss of either the larval aquatic or the terrestrial adult phase; others involve more subtle modifications that retain the complex life history. Resulting changes in morphology facilitate ecological specialization and diversification by larvae or adults. Change in larval morphology may not affect the adult, and *vice versa*. This permits morphological evolution of larvae and adults to proceed independently, within limits defined by functional and possibly developmental constraints linking the two phases. Ontogenetic and morphological diversity in Recent amphibians is undoubtedly a function of the developmental mechanisms that underlie both embryogenesis and metamorphosis, but especially those involved in specifying larval versus adult cell lineage. Nevertheless, how these mechanisms mediate morphological evolution involving either phase of the primitive life cycle, and generate the specific changes in developmental pattern that accompany diversification in life history, remains poorly understood.

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