CHAPTER 3

Larvae in Amphibian Development and Evolution

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I. INTRODUCTION

The tremendous intellectual excitement and activity that have attended the study of the relation between development and evolution over the past 20–25 years rival those characteristic of the "Golden Age" of zoology in the latter half of the 19th and early 20th centuries (Goldschmidt, 1956; Hall, 1992; Müller, 1991; Raff, 1996; D. B. Wake *et al.*, 1991). Then, as now, scientists strove to tease apart the complex relationship between ontogeny and phylogeny, including studies of both pattern and process (Churchill, 1997; Gould, 1977; Luckenbill-Edds, 1997). In both periods, amphibians—and especially amphibian larvae—occupy center stage. Evolutionary biologists have long

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appreciated that the presence of a free-living, aquatic larval stage, as well as the primitively complex (metamorphic) life history of which it is a part, confer on Recent amphibians a tremendous potential for adaptive diversification (Hanken, 1992; McDiarmid, 1978). This potential has been realized in the wide array of alternate life-history modes, developmental patterns, morphologies, and ecological relationships that are seen in both extinct and extant taxa (Duellman and Trueb, 1986; Lynn, 1961). At the same time, because of their relative accessibility, rapid external development, and ease of laboratory handling and experimental manipulation, amphibians offer many outstanding and practical opportunities to study animal development, including both features unique to amphibians as well as those characteristic of vertebrates in general (Armstrong and Malacinski, 1989; Cannatella and de Sá, 1993; Kay and Peng, 1991; Malacinski and Duhon, 1996; Shaffer, 1993). In short, amphibians and their larvae offer an excellent "system" to study the relation between development and evolution (Hanken, 1989).

The literature on larval amphibian biology is vast. It includes both classical and ongoing studies of morphology, physiology, ecology, behavior, genetics, and developmental biology. No attempt to offer a comprehensive review of this literature is made here. Instead, this chapter highlights several topics that are especially pertinent to contemporary studies of the development and evolution of amphibian larvae. In so doing, critical gaps in our knowledge and understanding of both the evolutionary history and developmental biology of modern amphibians, and especially their larvae, will be made evident. Hopefully, such an approach will help to guide or even initiate future research in these areas. The treatment begins with a short review of current ideas concerning the phylogenetic ancestry of amphibian larvae. This provides the historical context necessary for subsequent considerations of evolutionary trends in larval development and diversification involving Recent taxa. These are followed by a section that discusses two examples of the pervasive trend toward larval loss that is seen in many extant groups.

II. HISTORICAL CONTEXT: THE ANCESTRY OF AMPHIBIAN LARVAE AND THE COMPLEX, METAMORPHIC LIFE HISTORY

The free-living, aquatic larva is an ancient feature in amphibians. A complex, biphasic life history is phylogenetically widespread among Recent taxa and generally is accepted as the primitive condition for each of the three living orders (Duellman and Trueb, 1986). Interestingly, whereas a metamorphic ontogeny is characteristic of many species of frogs, salamanders, and caecilians, it is not the most frequent reproductive mode in all three groups. Most species

of living salamanders, for example, have direct development: courtship, mating, and oviposition occur on land, and the terrestrial egg hatches as a fully formed, albeit miniature, adult; there is no free-living larva (D. B. Wake and Hanken, 1996). All of these species belong to a single family, the Plethodontidae, or lungless salamanders. Members of four additional families (Sirenidae, Proteidae, Cryptobranchidae, and Amphiumidae) display obligate loss of both a discrete metamorphosis and the subsequent terrestrial adult stage. Consequently, sexually mature adults reproduce essentially as modified larvae.

Paleontology provides an additional, valuable perspective regarding the ancestry of amphibian larvae. Extinct salamanders with a larval morphology are known from both the Cretaceous (Evans and Milner, 1996; Evans *et al.*, 1996) and Triassic (Ivakhnenko, 1978, cited in Roček, 1996); some Paleocene fossils are assigned to extant genera (Naylor, 1978). Fossil tadpoles from the Cretaceous and Miocene are assignable to extant families (Estes *et al.*, 1978) or even genera (Wassersug and Wake, 1995; Fig. 1) of frogs. Stem members

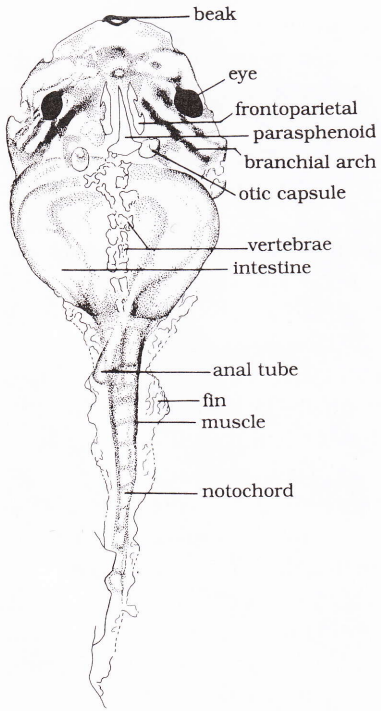

FIGURE 1 Reconstruction of a fossil tadpole from the Miocene of Turkey, which tentatively is assigned to the extant Eurasian genus *Pelobates* (Pelobatidae). Reprinted with permission from Wassersug and Wake (1995).

of the three Recent orders existed at least as far back as the early or middle Jurassic (Evans and Milner, 1996; Jenkins and Walsh, 1993; Shubin and Jenkins, 1995) or Triassic (Rage and Roček, 1989), but these clades likely had differentiated from one another by the end of the Permian, ca. 240 Myr BP (McGowan and Evans, 1995). If we accept the premise that a larval stage is a primitive characteristic in each order, then larvae also must date to at least this early.

The homology of amphibian larvae across all three Recent orders—that is, whether they represent just one versus two or more independent instances of the evolution of the metamorphic ontogeny among living taxa—is not fully resolved. Indeed, the topic has received surprisingly little attention. The most parsimonious interpretation of the presence of a larva (and metamorphosis) as a primitive trait in frogs, salamanders, and caecilians is that they represent the retention of this characteristic from the common ancestor of all three clades. This interpretation is supported by several lines of evidence. First, it avoids the vast amount of convergent evolution (homoplasy) of the many shared-derived, larva-specific traits that are common to all three groups that would be implied by positing two, or even three, independent origins of larvae. Second, morphological differences between larva and adult in the ancestral anuran likely were much less extreme—and metamorphosis much more gradual—than those typically seen in living frogs (Elinson, 1990; Fritzsch, 1990; Wassersug and Hoff, 1982). Thus, the ancestral anuran would have resembled urodeles much more closely than do living frogs. Finally, abundant fossil material documents the existence of a complex, biphasic life history, as adduced from larval and adult specimens, in many early tetrapod groups, including dissorophoid temnospondyls (Bolt, 1977, 1979; Boy, 1974; Carroll, 1986, 1988; Milner, 1982, 1990; Schoch, 1992, 1995; Werneburg, 1991; Fig. 2). Several dissorophoids have been variably proposed as outgroups to living amphibians (Bolt, 1969, 1977, 1991; McGowan and Evans, 1995; Milner, 1988, 1990, 1993; Schoch, 1995; Trueb and Cloutier, 1991), although this hypothesized relationship is not universally accepted (e.g., Carroll, 1988, 1992, 1995; Laurin and Reisz, 1997; Reisz, 1997).

Analysis of the larval homology problem is closely linked to ongoing debate regarding phylogenetic relationships among Recent amphibians. The debate centers around the claim that the three extant orders constitute a monophyletic group, Lissamphibia, which has a common ancestry distinct from that of all other living tetrapods and is derived from dissorophoid temnospondyls (see references in the preceding paragraph). New data bearing on these phylogenetic issues may have important implications for larval biology. For example, albanerpetontids are an additional group of salamander-like, "predominantly terrestrial," fossil amphibians (McGowan and Evans, 1995, p. 143). They have been proposed as a fourth lissamphibian lineage, closely allied with, but

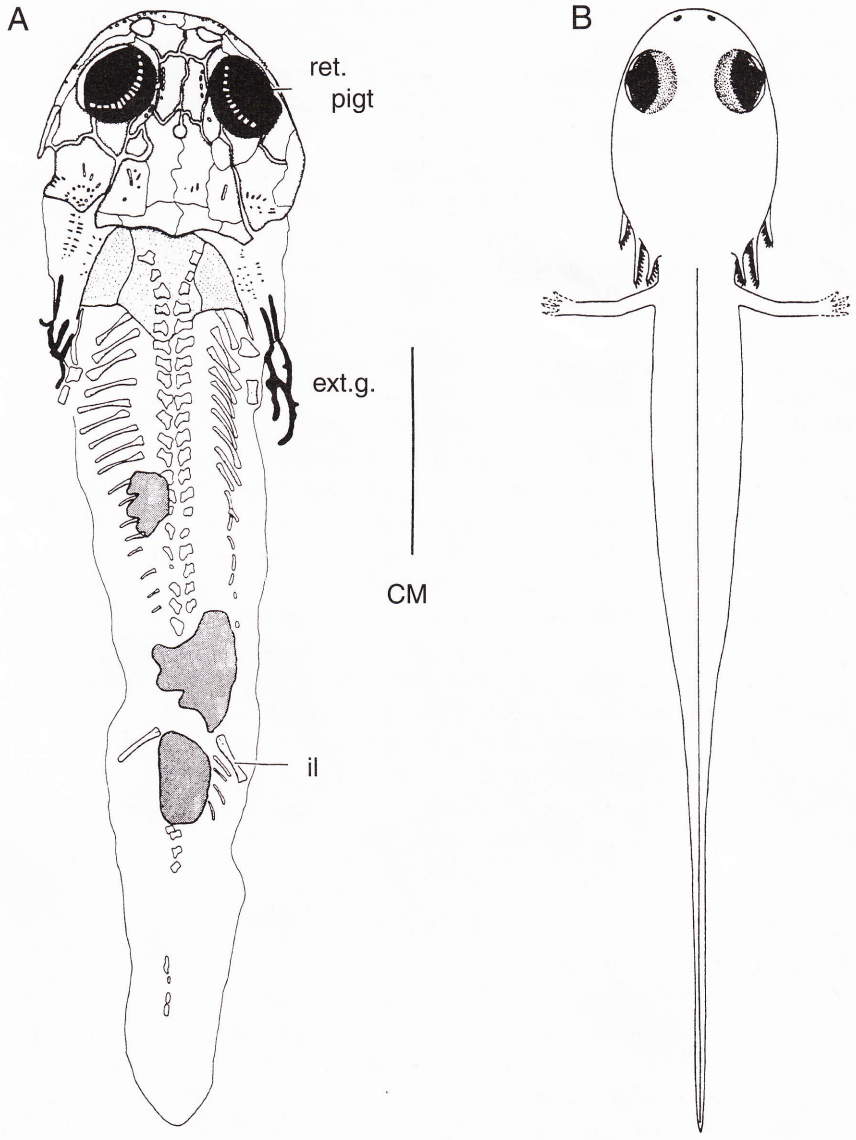

FIGURE 2 (A) *Saurerpeton* cf. *obtusum*, a basal temnospondyl amphibian (Saurerpetontidae) from the Middle Pennsylvanian of Illinois. The fossil is depicted in dorsal view; external gills (ext. g.) indicate a larval morphology. Abbreviations: il, ilium; ret, pigt, retinal pigment. Stippling denotes infilled intestines. Reprinted with permission from Milner (1982). (B) Larval specimen of *Branchiosaurus*, a temnospondyl amphibian (Branchiosauridae), reconstructed in dorsal view. Reprinted with permission from Boy (1974).

nevertheless distinct from, the three Recent orders. Larval albanerpetontids are unknown. If the presence of free-living larvae in living amphibians represents the retention of a primitive trait from dissorophoid ancestors, then larvae likely were either present in albanerpetontids as well or lost from this extinct lineage after it diverged from the three extant groups.

Finally, whereas there is widespread agreement that the presence of a free-living larva is a primitive life-history trait for living amphibians, alternate or divergent scenarios have been proposed. Bogart (1981) proposed that the primitive reproductive mode in anurans involved terrestrial, rather than aquatic, breeding. Although an aquatic larval stage still would have been present, it "probably had a relatively abbreviated free-swimming life" (Bogart, 1981, p. 34). This proposal has not been accepted by most subsequent authors (e.g., Duellman, 1989; Duellman and Trueb, 1986; Duellman *et al.*, 1988). Duellman and colleagues, however, have hypothesized that the free-living tadpole stage may have reevolved independently from a direct-developing ancestor as many as four times in a specialized group of South American marsupial frogs in the genera *Fritziana, Flectonotus,* and *Gastrotheca* (Duellman and Hillis, 1987; Duellman *et al.*, 1988; Wassersug and Duellman, 1984). Their hypothesis derives from a molecular phylogenetic analysis of these and related species, which was used to assess evolutionary trends in reproductive biology. Alternate hypotheses of life-history evolution in marsupial frogs have been offered by Haas (1996a,b) and Weygoldt and de Carvalho e Silva (1991). Similarly, the possibility of reevolution of the free-living, aquatic larval stage from direct-developing ancestors has been explored in plethodontid salamanders (Titus and Larson, 1996; D. B. Wake and Hanken, 1996; Fig. 3). In all of these studies, precise evolutionary sequences in relevant reproductive characters remain to be fully resolved.

III. EMBRYONIC DERIVATION OF LARVAL FEATURES

There is increased interest in resolving, with considerable precision, the embryonic derivation of both larval and adult (postmetamorphic) features in amphibians. These studies have been facilitated, if not promoted, by the advent of a variety of sophisticated molecular, experimental, and analytical tools for tracing embryonic cell and tissue lineages into postembryonic stages in animals generally (Collazo *et al.*, 1994; Gardner and Lawrence, 1986; Krotoski *et al.*, 1988; Le Douarin and McLaren, 1984; Thiébaud, 1983). Such techniques, although not infallible, offer considerable advantages over many comparable methods utilized by experimental embryologists earlier in this century to derive embryonic fate maps for various species, but especially amphibians, and to resolve

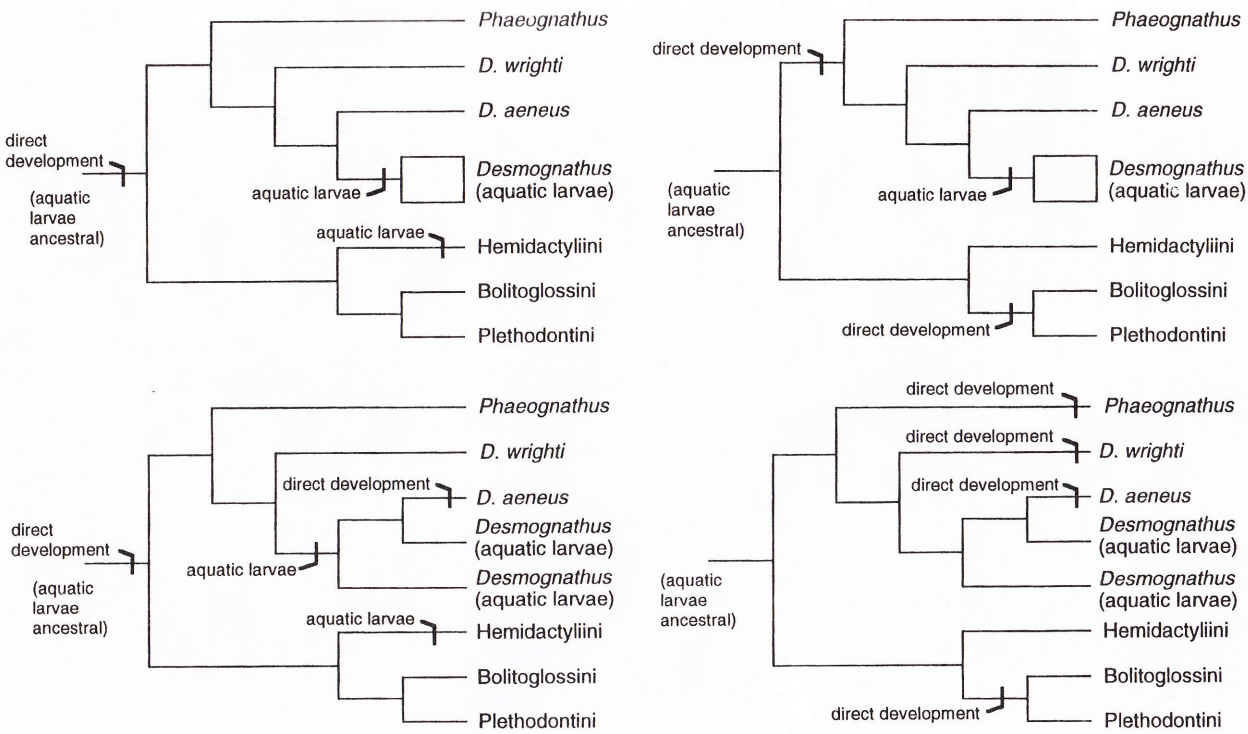

FIGURE 3 Four different scenarios for the evolution of aquatic larvae and direct development in lungless salamanders (Plethodontidae). Each scenario is a function of the particular scheme of phylogenetic relationships depicted and the parsimony method used to analyze life-history variation among the taxa. One consequence of the phylogenetic distribution of alternative life histories in these salamanders is that either aquatic larvae or direct development must have evolved more than once, and possibly several times, regardless of how the data are analyzed. Modified with permission from Titus and Larson (1996).

the embryonic derivation of particular organ systems (e.g., Hamburger, 1960). For example, a variety of fluorescent dyes will effectively label many cells and tissues for far longer than will traditional vital dyes, such as neutral red and Nile blue sulfate, and their use generally is not associated with many of the extreme developmental artifacts that are associated routinely with more invasive techniques, such as tissue ablation (e.g., Collazo *et al.,* 1993; Eagleson *et al.,* 1995; Olsson and Hanken, 1996).

In an evolutionary context, detailed knowledge of embryonic derivation can contribute much to our understanding of the developmental mechanisms that underlie the evolution of larval morphology per se, the extent to (and means by) which larval features mediate the evolution and development of adult features, and especially the reality and mode of operation of larval "constraints" on adult morphology. It can also contribute to more general discussions and controversies in evolutionary morphology, such as the developmental basis of homology (Abouheif, 1997; Hall, 1994, 1995). Nevertheless, most work on amphibians has been limited to the two standard, "model" amphibians, the clawed frog, *Xenopus laevis* (e.g., Collazo *et al.,* 1993; Eagleson and Harris, 1990; Krotoski *et al.,* 1988; Sadaghiani and Thiébaud, 1987), and the axolotl, *Ambystoma mexicanum* (e.g., Barlow and Northcutt, 1995, 1997; Northcutt *et al.,* 1994, 1995; Smith, 1996; Smith *et al.,* 1994); few studies focus on any of the large number of nonstandard species that display either the ancestral, biphasic ontogeny or some more derived reproductive mode. Moreover, most studies of *Xenopus* or the axolotl employ these species as model systems for understanding vertebrate development in general; they are not primarily interested in addressing larval specializations as such. One set of analyses that addresses the embryonic derivation of larval features in a comparative context focuses on the larval skull in anurans. These studies are reviewed briefly here.

Amphibians were the principal subjects of the large number of early studies that assessed the role of the embryonic neural crest in vertebrate development [reviewed in Hall and Horstädius (1988); Holtfreter, 1968]. These studies documented extensive contributions of the neural crest to many larval tissues and other features, especially the cartilaginous skull, spinal nerves, and pigmentation. In subsequent years, the focus of studies of neural crest biology moved to amniotes, and the use of amphibians was largely abandoned, at least for some organ systems such as the skull and skeleton. Embryonic derivation of the larval skull in anurans has been reinvestigated in several species of metamorphosing frogs. These studies provide an opportunity to confirm the results of earlier, classical studies by the use of alternate—and generally more sensitive and reliable—experimental and analytical methods. Moreover, by analyzing the data in a phylogenetic context, authors are beginning to assess various evolutionary topics, such as the relative lability versus conservatism of specific developmental characters.

For much of this century, the most comprehensive analysis of neural crest contribution to the tadpole skull was a study of the pickerel frog, *Rana palustris*, by Stone (1927, 1929). Phylogenetically, *R. palustris* (Ranidae) is a member of the so-called advanced frog clade, or Neobatrachia (Ford and Cannatella, 1993). Although *R. palustris* has a morphologically generalized tadpole, one can presume that it was chosen largely for reasons of practicality and availability; the species is widely distributed throughout much of eastern North America including New England, where Stone lived and worked (at Yale University). Stone assessed the extent of neural crest contribution to the exclusively cartilaginous larval skull of *R. palustris*, largely by ablating different portions of the neural crest before or soon after it began migrating from the neural folds and then identifying which cranial cartilages subsequently failed to form. By combining results from several ablated embryos, he inferred an extensive contribution of cranial neural crest to the larval skull. Indeed, all cranial cartilages were shown to be neural-crest-derived, except for posteroventral components of the skull proper and two small, median cartilages in the hyobranchial skeleton (Fig. 4).

Neural crest contribution to the tadpole skull has been assessed in three additional species of frogs. Sadaghiani and Thiébaud (1987) examined *Xenopus laevis* (Pipidae) by grafting cranial neural crest from a congeneric species,

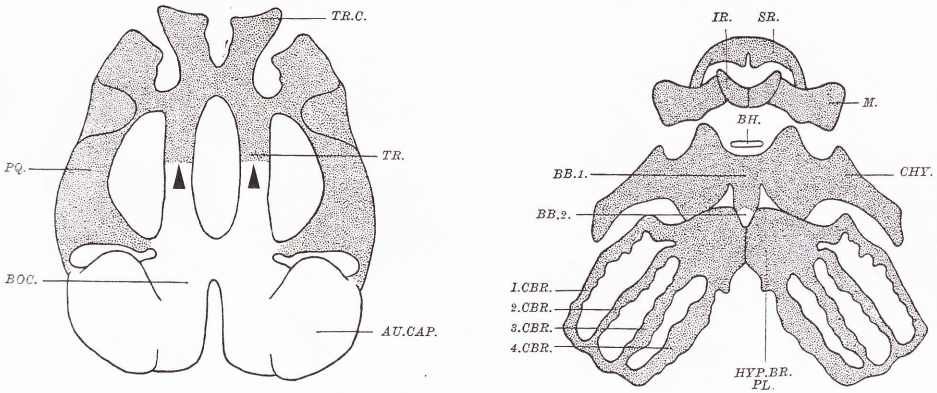

FIGURE 4 Neural crest derivation of the larval skull and hyobranchial skeleton of the pickerel frog, *Rana palustris* (Ranidae), seen in dorsal (left) and ventral (right) views. Crest-derived regions are stippled; arrows point to the boundary between crest- and non-crest-derived portions of the floor of the neurocranium. Anterior is at the top. Abbreviations: AU.CAP., auditory (otic) capsule; BB.1.–2 first and second basibranchials; BH., basihyal; BOC., basioccipital plate; 1.–4. CBR., ceratobranchials 1–4; CHY, ceratohyal; HYP.BR.PL., hypobranchial plate; IR., infrarostral; M., Meckel's cartilage; PQ., palatoquadrate; SR., suprarostral; TR., trabecular; TR.C., trabecular horn. After Stone (1929).

Xenopus borealis, to produce chimaeric embryos. Contrasting histological staining patterns by cell nuclei of these two species provide a permanent cell marker that can be used to distinguish donor from host cell lineages in differentiated tissues, such as the larval skull (Thiébaud, 1983; Fig. 5). Olsson and Hanken (1996) studied the Oriental fire-bellied toad, *Bombina orientalis* (Bombinatoridae), by labeling several different regions of premigratory neural crest with a fluorescent dye and following labeled cells into specific cranial cartilages (Fig. 6). Reiss (1997) mapped neural crest contributions in the tailed frog, *Ascaphus truei,* by following migrating crest cells, which can be distinguished histologically from non-crest (e.g., mesodermal) cell populations, at least during early developmental stages (Fig. 7). All three of these species are phylogenetically basal in comparison to all advanced frogs, including *R. palustris* (Ford and Cannatella, 1993). In this respect, each is more appropriate than any neobatrachian to serve as a source of "baseline" developmental data for evolutionary comparisons among anurans or between frogs and other vertebrates. Unlike *Bombina,* however, which has a morphologically generalized tadpole, larval cranial morphology in both *Xenopus* and *Ascaphus* is highly derived and unusual (Cannatella and Trueb, 1988; Gradwell, 1973; Trueb and Hanken, 1992). This at least potentially diminishes the suitability of *Xenopus* and *Ascaphus* as a baseline for anurans, in favor of *Bombina* (Cannatella and de Sá, 1993).

Despite the extensive phylogenetic and morphological diversity represented by these four species of anurans and the considerable differences among methods used to examine neural crest migration and fate, the general pattern of

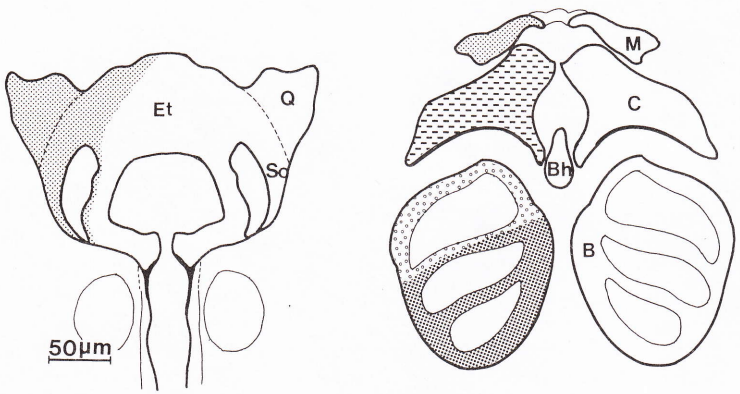

FIGURE 5 Neural crest derivation of the larval skull (left) and the lower jaw and hyobranchial skeleton (right) of the clawed frog, *Xenopus laevis* (Pipidae). Shading of crest-derived cartilages varies according to migratory stream; anterior is at the top. Abbreviations: B, ceratobranchials; Bh, basihyal; C, ceratohyal; Et, ethmoid–trabecular cartilage; M, Meckel's cartilage; Q, palatoquadrate; So, subocular. Modified with permission from Sadaghiani and Thiébaud (1987).

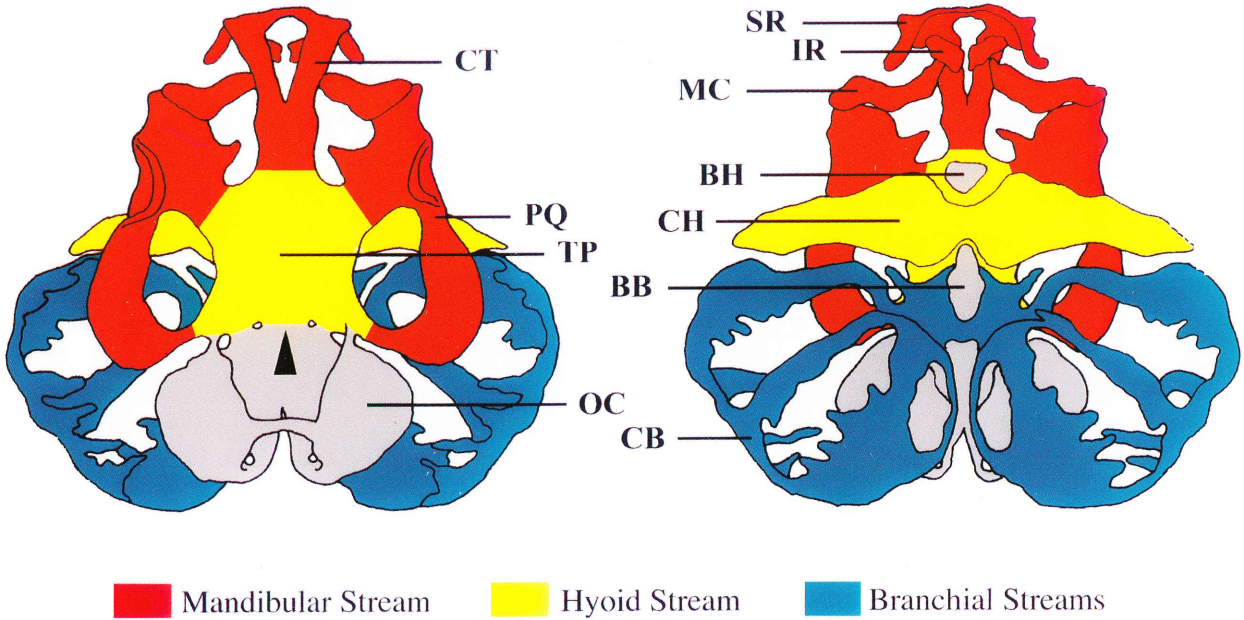

FIGURE 6 Neural crest derivation of the larval skull and hyobranchial skeleton of the Oriental fire-bellied toad, *Bombina orientalis* (Bombinatoridae), seen in dorsal (left) and ventral views. Cartilages are colored according to the cranial neural crest migratory streams(s) from which each is derived; non–crest-derived components are shaded gray. The arrow points to the boundary between crest- and non–crest-derived portions of the floor of the neurocranium. Anterior is at the top. Abbreviations: BB, basibranchial; BH, basihyal; CB, ceratobranchials I–IV; CH, certohyal; CT, trabecular horn; IR, infrarostral; MC, Meckel's cartilage; OC, otic capsule; PQ, palatoquadrate; TP, trabecular plate, SR, suprarostral. Olsson and Hanken (1996). Cranial neural crest migration and chondrogenic fate in the Oriental fire-bellied toad, *Bombina orientalis*: Defining the ancestral pattern of head development in annuran amphibians. *Journal of Morphology*.

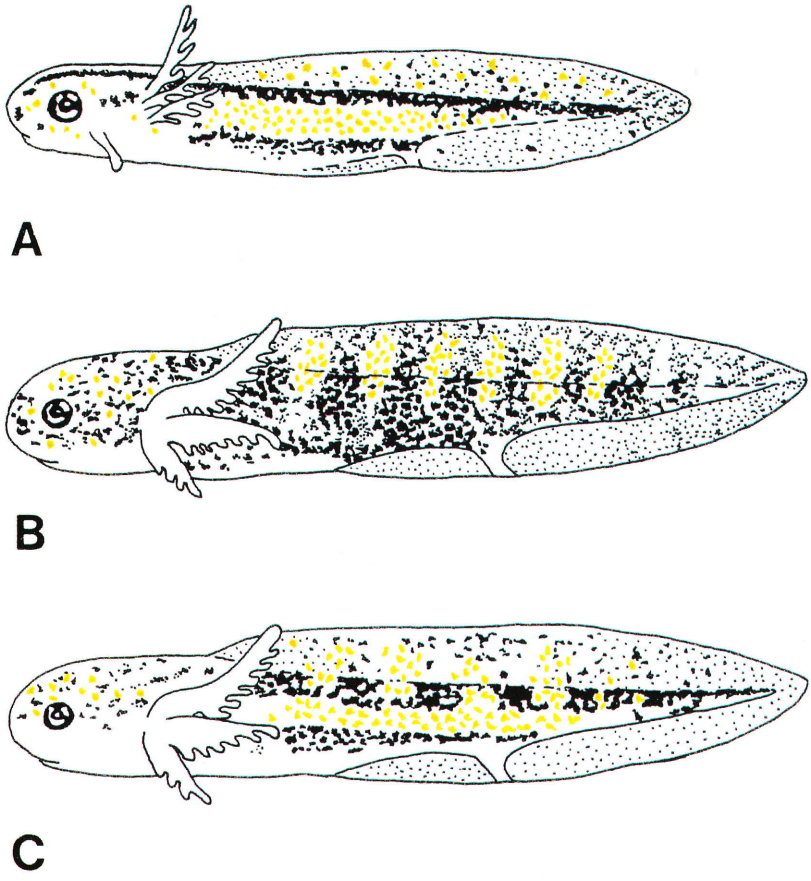

FIGURE 8 Variation in larval pigment patterning among three species of urodeles. (A) *Triturus alpestris* (Salamandridae) has a pattern of horizontal, lateral stripes above and below a melanophore-free region. (B) *Ambystoma mexicanum* has a series of vertical stripes or bars. (C) *Ambystoma t. tigrinum* has an intermediate pattern consisting of a series of vertical bars interrupted by a melanophore-free region. Reprinted with permission from Epperlein *et al.* (1996).

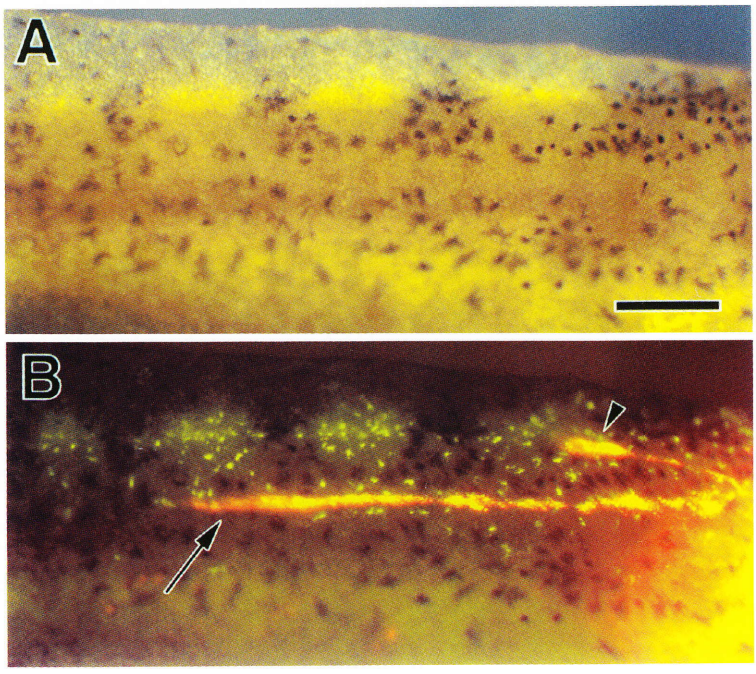

FIGURE 12 Interactions between pigment cells and the developing lateral line in the tiger salamander, *Ambystoma t. tigrinum*. (A) Brightfield photomicrograph of the lateral trunk region of an embryo. Dark melanophores are beginning to form a series of vertical bars, which are interrupted by a longitudinal, melanophore-free region. (B) Fluorescence double exposure of the same embryo shows dorsal aggregations of yellow xanthophores and dye-labeled, longitudinal lateral line primordia (arrow and arrowhead). The midbody lateral line primordium (arrow) lies within the melanophore-free region. Scale bar, 500 μm. Reprinted with permission from Parichy (1996a).

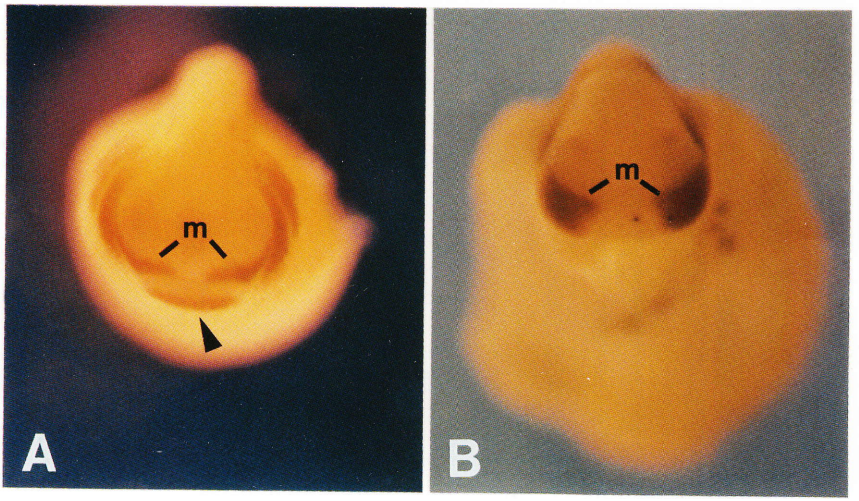

FIGURE 17 Distal-less gene expression in embryos of (A) the metamorphosing frog *Xenopus laevis* (Nieuwkoop–Faber stage 24) and (B) direct-developing *Eleutherodactylus coqui* (Townsend–Stewart stage 4) Both images are frontal views of the head; dorsal is at the top. Paired, dark areas on either side of the head in each embryo denote expression of homologous distal-less genes *X-dll4* (*Xenopus*) and *EcDlx2* (*Eleutherodactylus*) in migratory streams of cranial neural crest (m, mandibular stream). The arrow in A points to an additional, ventral site of distal-less expression in *Xenopus* that precedes embryonic differentiation of the larval cement gland in this species. The corresponding area of distal-less expression is absent from *Eleutherodactylus*, which also lacks a cement gland. Reprinted with permission from Fang and Elinson (1996).

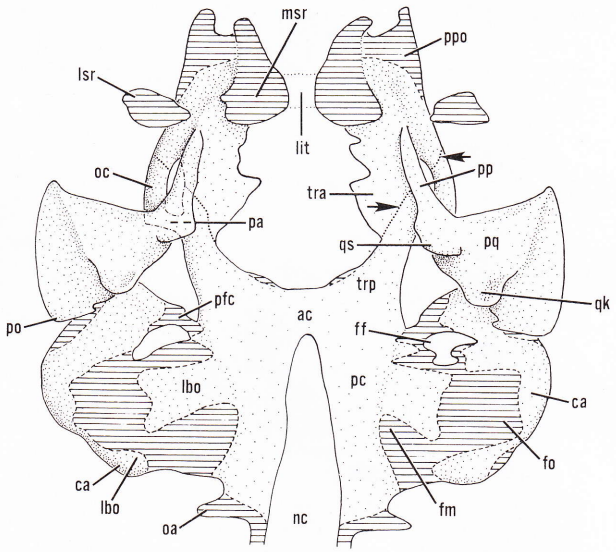

FIGURE 7 Larval skull of the tailed frog, *Ascaphus truei* (Ascaphidae), Gosner stage 23. Ventral view; anterior is at the top. Dotted lines (arrows) indicate the approximate boundary between neural crest and mesodermally derived tissues (all crest-derived tissues lie anterior to the boundary). Cartilage is stippled; undifferentiated mesenchyme is indicated by horizontal lines. Abbreviations: ac, acrochordal cartilage; ca, auditory capsule; ff, facial foramen; fm, mesotic fissure; fo, fenestra ovalis; bo, basiotic lamina; lit, intertrabecular ligament; sr, lateral suprarostral; msr, medial suprarostral; nc, notochord; oa, occipital arch; oc, orbital cartilage; pa, parachordal; pfc, prefacial commissure; po, otic process; pp, pterygoid process; ppo, pila preoptica; pq, palatoquadrate; qk, quadrate keel; qs, quadrate spur; tra, anterior trabecula; trp, posterior trabecula. Reiss (1997). Early development of chondrocranium in the tailed frog *Ascaphus truei* (Amphibia: Anura): Implications for anuran palatoquadrate homologies. *Journal of Morphology*, Copyright © 1997. Reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

neural crest derivation of larval cranial cartilages is highly concordant and consistent among them. Data for *Rana* and *Bombina* are the most extensive; these two species are compared in Table I (cf. Figs. 4 and 6). Patterns of derivation for these species are identical for 11 of the 12 discrete cartilages represented, which together constitute virtually the entire larval skull: seven are exclusively crest-derived, and four receive no contribution. Indeed, the sole apparent difference between these two species concerns the extent of neural crest contribution to the floor of the neurocranium (trabecular plate). In *Bombina*, the trabecular plate is entirely crest-derived. Consequently, the boundary between crest- and non-crest-derived regions of the cranial floor lies at the level of the anterior margin of the otic capsule (Fig. 6, arrow). In *Rana*, this boundary lies farther anterior, at a level corresponding to the middle of

TABLE I Neural Crest Contribution to the Skull of Larval Anurans[a]

Cartilage	*Bombina*	*Rana*
Cornua trabecula (trabecular cornu)	+	+
Suprarostral	+	+
Infrarostral	+	+
Meckel's	+	+
Palatoquadrate	+	+
Ceratohyal	+	+
Ceratobranchials I–IV	+	+
Trabecular plate (trabecular bar)	+	±
Basioccipital plate	−	−
Otic (auditory) capsule	−	−
Basihyal	−	−
Basibranchial (second basibranchium)	−	−

[a]A "plus" (+) denotes cartilages that are derived from neural crest; the embryonic origin of remaining cartilages (−) remains unknown, although it is presumed to be from cranial mesoderm. A "±" denotes dual origin. Data for *Bombina* and *Rana* are based on Olsson and Hanken (1996) and Stone (1929), respectively.

the orbit (Fig. 4, arrows). This results in a dual embryonic origin for the trabecular plate in this species (and in *Ascaphus;* Reiss, 1997). It should be noted, however, that accounts for these two species depict different larval stages: data for *Bombina* are mapped onto the skull of a "mature" larva (Gosner stage 36), whereas data for *Rana* depict a much smaller hatchling (ca. stage 23–25). Whereas the difference in derivation of the cranial floor noted previously may represent actual variation among species, it may also reflect ontogenetic change characteristic of both species.

Conserved patterns of neural crest derivation among anuran species also extend to the relative contributions of different migratory streams to specific cranial cartilages. The three principal cranial migratory streams—mandibular, hyoid, and branchial—exhibit the same basic pattern of cartilage derivation in both *Bombina* (Olsson and Hanken, 1996) and *Xenopus* (Sadaghiani and Thiébaud, 1987; cf. Figs. 4 and 5). The same general result even applies within streams. Thus, in both species the skeleton of the first branchial arch (ceratobranchial I) is derived exclusively from the anterior portion of the branchial crest stream, whereas posterior branchial arch elements (ceratobranchials II–IV) are derived principally from the posterior portion of the branchial crest stream.

Extensive similarity among anuran species in the preceding aspects of neural crest biology is of interest and significance in several respects. First, it likely

betrays extreme evolutionary conservatism of these (and possibly other) underlying features of cranial development. *Bombina* and *Rana,* for example, likely diverged from a common anuran ancestor no later than the Jurassic period, at least 144 Myr BP (Duellman and Trueb, 1986); the species *B. orientalis* may have differentiated as early as the Miocene (Maxson and Szymura, 1979). Yet, overall patterns of neural crest derivation of cranial cartilages are nearly identical in these two taxa (Table I; cf. Figs. 4 and 5). Second, whereas these features of neural crest biology have changed little, many of the crest-derived larval cranial cartilages have evolved extensive morphological differences among species. This suggests that the developmental basis of larval cranial diversification lies not in gross aspects of neural crest biology, such as the timing of cell emergence or migration, the number or configuration of the principal migratory streams, or possibly even migration pathways, but rather in more subtle features of neural crest biology related to pattern formation, such as cell behavior and commitment or gene expression (Moury and Hanken, 1995; Hanken *et al.,* 1997a).

These and other results provide important baseline data that facilitate studies of larval amphibian development and evolution. At the same time they reveal conspicuous gaps in our knowledge that hamper subsequent analyses. There are, for example, no published studies that assess neural crest contribution to the cartilaginous or bony skull in either salamanders or caecilians using modern labeling techniques comparable to those reviewed earlier for anurans. For that matter, there is very little direct evidence of a neural crest contribution to the bony skull in *any* of the three living amphibian orders. Whereas the extent of neural crest contribution to the osteocranium has been documented convincingly and precisely in at least some amniotes (Couly *et al.,* 1992, 1993; Köntges and Lumsden, 1996; Noden, 1986), comparable experimental data for amphibians are extremely scarce (e.g., de Beer 1947; Wagner, 1949, 1955). Certainly no one has yet produced a detailed map between particular cranial neural crest streams and individual skull bones for amphibians as is available for the chicken (e.g., Köntges and Lumsden, 1996). Indeed, a neural crest derivation of the amphibian osteocranium can only be assumed by extrapolating to amphibians the results obtained for other, distantly related taxa. Whereas generalization across major taxa in this manner may be justified by the empirical observation that many such features of neural crest biology are highly conserved among vertebrates (see previous discussion; Hall and Horstädius, 1988), direct assessment in each extant amphibian order is urgently needed. Similarly, the embryonic derivation of non-crest-derived portions of either the larval or the adult skull remains to be assessed directly in any amphibian. Ignorance of the embryonic derivation of the bony skull in Recent amphibians is especially surprising in light of the large number of studies that assess various aspects of cranial ossification during larval development and metamorphosis in the

context of broader analyses of heterochrony, functional morphology, and endocrinology (e.g., Hanken and Hall, 1984, 1988a, b; Maglia and Púgener, 1998; Púgener and Maglia, 1997; Reilly, 1986, 1994; Reilly and Altig, 1996; Rose, 1996; Trueb, 1985; D. B. Wake, 1980; Wild, 1997).

IV. HETEROCHRONY

The dominant paradigm for contemporary studies of the relation between development and evolution has been heterochrony, or change in the relative timing of developmental events (Gould, 1977; Hall, 1992; Raff, 1996). Originally formulated in the 19th century by Ernst Haeckel as a means of accounting for the many obvious (and to him, bothersome) exceptions to his biogenetic law—"ontogeny recapitulates phylogeny"—heterochrony was reformulated by Gavin de Beer in the 1930s in the context of then contemporary interest in rates of development and relative growth, or allometry [see reviews by Gould (1977) and Hall (1990, 1992)]. Widespread interest in heterochrony exploded anew in the 1970s, following Gould's (1977) "Ontogeny and Phylogeny," and this interest has continued virtually unabated ever since. Studies range from several conceptual and theoretical treatments that advocate one or another system of terminology, graphical depiction, or other methods of analysis (e.g., Alberch *et al.*, 1979; McKinney, 1988b; McNamara, 1986; Pierce and Smith, 1979; Reilly *et al.*, 1997; Shea, 1983, 1988) to a large number of empirical analyses that document or assess the existence and effects of heterochrony in particular groups of both animals and plants (e.g., McKinney, 1988a; McKinney and McNamara, 1991; Hart and Wray, this volume, Chapter 5).

Whereas there is virtually unanimous agreement that heterochrony is a prominent phenomenon in the evolution of organismal development, considerable disagreement remains regarding the extent to which heterochrony should be emphasized at the expense of other potentially important factors or explanations. In a general treatment of heterochrony, Reilly *et al.* assert that "heterochrony may underlie all morphological variation and possibly is *the* developmental phenomenon producing all morphological change" (1997, p. 120). Other authors take a more moderate view. Raff (1996), while conceding the pervasiveness of heterochronic changes in ontogenetic pattern and agreeing that such changes may offer important insights into underlying developmental processes, regards such an extreme emphasis on heterochrony as undeserved and, in some instances, even unhelpful. Indeed, "the uncritical attribution of so many of the phenomena observed in the evolution of development to heterochronic 'mechanisms' may be inhibiting a more penetrating investigation of the subject" (Raff, 1996, p. 259). Thomson (1988) and Hall (1990, 1992)

express similar reservations. As pointed out by several authors, and as illustrated by the preceding quotations, at least part of the problem or disagreement may stem from the frequent failure to distinguish heterochrony as a *pattern* from heterochrony as a *mechanism* of evolutionary change (Hall, 1990, 1992; Raff, 1996). Others emphasize the important yet underappreciated role of changes in spatial patterning, or heterotopy, as a complement to changes in developmental timing (e.g., Hanken and Thorogood, 1993; Zelditch and Fink, 1996).

Amphibians have been central players in the heterochrony "industry." Indeed in the larval axolotl, amphibians present what arguably represents the paradigmatic example of heterochrony among animals (Gould, 1977). This distinction is embodied in Garstang's (1951) classic poem, "The *Axolotl* and the *Ammocoete*," which was first penned around 1922:

> *Amblystoma's* a giant newt who rears in swampy waters,
> As other newts are wont to do, a lot of fishy daughters:
> These *Axolotls,* having gills, pursue a life aquatic,
> But when they should transform to newts, are naughty and erratic.
>
> They change upon compulsion, if the water grows too foul,
> For then they have to use their lungs, and go ashore to prowl:
> But when a lake's attractive, nicely aired, and full of food,
> They cling to youth perpetual, and rear a tadpole brood.
>
> And newts Perennibranchiate have gone from bad to worse:
> They think aquatic life is bliss, terrestrial a curse.
> They do not even contemplate a change to suit the weather,
> But live as tadpoles, breed as tadpoles, tadpoles altogether!
>
> Now look at *Ammocoetes* there, reclining in the mud,
> Preparing thyroid-extract to secure his tiny food:
> If just a touch of sunshine more should make his gonads grow,
> The Lancelet's claims to ancestry would get a nasty blow!

Variation in developmental timing is a virtually ubiquitous phenomenon in amphibian evolution; it has played a pivotal role in the diversification of morphology, physiology, and ecology in both larvae and adults (Hanken, 1989, 1992). As stated by Milner, "The success of lissamphibians is very much a measure of the way in which adult and juvenile characters have been permutated by heterochrony and miniaturization to give new morphological combinations" (1993, p. 23). This variation has been couched explicitly in terms of heterochrony in numerous studies (Table II). Many of these studies principally are concerned with identifying changes in the timing or sequence of development of one or more individual characters, including those that underlie instances of evolutionary loss that are frequently associated with paedomorphosis (e.g., Hanken and Hall, 1984; Smirnov, 1989; D. B. Wake, 1980). Others constitute more comprehensive analyses that attempt to define, in terms of underlying developmental processes and mechanisms, particular pertubations

TABLE II Selected Examples of Studies of Heterochrony in Embryonic, Larval, and Adult Amphibians

Topic or feature addressed	Taxa[a]	Citation[b]
Origin and evolution of early and Recent amphibians	Temnospondyls, labyrinthodonts, lissamphibians (**F**, **S**, **C**)	9–11, 40, 41, 63
Skeletal morphology and dentition; progenesis and miniaturization, paedomorphosis, neoteny		
Paedomorphosis		
Phylogeny	S: *Ambystoma, Rhyacosiredon, Aneides, Batrachoseps*	34, 68, 84, 91
Genetic basis	S: *Ambystoma*	32, 65, 66, 70, 84, 85
Facultative	S: *Ambystoma, Notophthalmus,* others	6, 31, 33, 35, 64, 98, 99
Endocrine control		
Paedomorphosis, neoteny, perennibranchiation	S: *Ambystoma, Triturus, Proteus, Necturus, Pleurodeles, Eurycea,* others	54, 55
Direct development	F: *Eleutherodactylus*	30
Genome size and neoteny	S	83
Life-history evolution	C: *Siphonops, Gymnopis, Ichthyophis, Typhlonectes, Hypogeophis*	21
	S: *Salamandra*	17b
Population structure, diet, paedogenesis	S: *Eurycea, Gyrinophilus*	12, 13
Larval paedomorphosis	S: *Gyrinophilus*	15
Resource-based (trophic) polymorphism	S: *Ambystoma*	16, 95
Gonadal development, hemoglobins, nitrogen excretion, integument; neoteny	S: *Hynobius,* others	86–88
Embryonic development	C: *Typhlonectes*	60
	F: *Eleutherodactylus*	29, 61
	S: *Ambystoma, Gyrinophilus, Taricha*	14, 15, 44

Larval development and adult limb morphology	F: *Hyla, Rana, Bufo, Bombina*	8, 18–20
Larval pigment patterning	S: *Ambystoma*	37
	F: *Pseudis*	17a
Larval trophic morphology and behavior	F: *Lepidobatrachus*	27, 59
External morphology, size and shape; paedomorphosis	S: *Ambystoma, Rhyacosiredon, Notophthalmus, Bolitoglossa*	22, 31, 69
Cloacal anatomy; paedomorphosis	S: *Desmognathus, Phaeognathus, Leurognathus*	67
Neuroanatomy, sensory systems; paedomorphosis	C: *Epicrionops, Ichthyophis, Uraeotyphlus,* others	57, 62
	F: *Eleutherodactylus, Discoglossus, Bombina, Pipa, Ascaphus,* others	57, 61, 74
	S: *Batrachoseps, Plethodon, Thorius, Bolitoglossa, Hydromantes, Desmognathus, Ambystoma,* others	36, 44, 56–58, 77
Oral anatomy	F: *Gastrotheca, Ascaphus, Microhyla, Rhinophrynus, Scaphiopus, Alytes, Centrolenella, Colostethus,* others	96, 97
Larval and adult dentition	S: *Ambystoma, Rhyacosiredon, Hynobius, Eurycea, Gyrinophilus,* others	7, 42, 45
	F: *Pipa, Pyxicephalus, Pelobates, Uperoleia, Crinia, Pseudophryne*	17, 76
Cranial and hyobranchial morphology, ossification sequence and timing; paedomorphosis, neoteny, progenesis, peramorphosis, differential metamorphosis	S: *Batrachoseps, Notophthalmus, Thorius, Eurycea, Triturus, Aneides, Rhyacotriton, Siren, Cryptobranchus, Ambystoma, Rhyacosiredon, Necturus, Bolitoglossa, Salamandra,* others	1–5, 25, 39, 46–53, 89–92, 94
	F: *Rhinophrynus, Eleutherodactylus, Brachycephalus, Xenopus, Leiopelma, Uperoleia, Dendrobates, Ceratophrys, Bombina, Microhyla, Flectonotus,* others	17, 23, 24, 28, 29, 71–73, 75, 78–82, 100
	C: *Idiocranium*	93

(*Continues*)

TABLE II (*Continued*)

Topic or feature addressed	Taxa[a]	Citation[b]
Postcranial skeletal morphology, ossification sequence and timing; paedomorphosis, progenesis, neoteny	S: *Bolitoglossa, Thorius, Aneides, Necturus*	1–3, 26, 43, 94
	F: *Bombina, Leiopelma, Xenopus, Pseudophryne, Ceratophrys,* others	17, 38, 78, 79, 82, 100
	C: *Idiocranium*	93

[a]C, caecilians; F, frogs; S, salamanders.

[b]1, Alberch, 1980; 2, Alberch, 1983; 3, Alberch and Alberch, 1981; 4, Alberch and Blanco, 1996; 5, Alberch *et al.,* 1979; 6, Begun and Collins, 1992; 7, Beneski and Larsen, 1989; 8, Blouin, 1991; 9, Bolt, 1977; 10, Bolt, 1979; 11, Bolt, 1991; 12, Bruce, 1976; 13, Bruce, 1979; 14, Collazo, 1994; 15, Collazo and Marks, 1994; 16, Collins *et al.,* 1983; 17, Davies, 1989; 17a, de Sá and Lavilla, 1997; 17b, Dopazo and Alberch, 1994; 18, Emerson, 1986; 19, Emerson, 1987; 20, Emerson, 1988; 21, Exbrayat and Hraoui-Bloquet, 1994; 22, Green and Alberch, 1981; 23, Haas, 1995; 24, Haas, 1996a; 25, Hanken, 1982; 26, Hanken, 1984; 27, Hanken, 1993; 28, Hanken and Hall, 1984; 29, Hanken *et al.,* 1992; 30, Hanken *et al.,* 1997a; 31, Harris, 1989; 32, Harris *et al.,* 1990; 33, Jackson and Semlitsch, 1993; 34, Larson, 1980; 35, Licht, 1992; 36, Linke and Roth, 1990; 37, Löfberg *et al.,* 1989; 38, Maglia and Púgener, 1998; 39, Marconi and Simonetta, 1988; 40, Milner, 1988; 41, Milner, 1993; 42, Mutz and Clemen, 1992; 43, Naylor, 1978; 44, Northcutt *et al.,* 1994; 45, Pedersen, 1991; 46, Reilly, 1986; 47, Reilly, 1987; 48, Reilly, 1994, 49, Reilly and Altig, 1996; 50, Reilly and Brandon, 1994; 51, Reilly *et al.,* 1997; 52, Roček, 1996; 53, Rose, 1995; 54, Rose, 1996; 55, Rosenkilde and Ussing, 1996; 56, Roth and Schmidt, 1993; 57, Roth *et al.,* 1992; 58, Roth *et al.,* 1993; 59, Ruibal and Thomas, 1988; 60, Sammouri *et al.,* 1990; 61, Schlosser and Roth, 1997; 62, Schmidt and Wake, 1997; 63, Schoch, 1995; 64, Scott, 1993; 65, Semlitsch and Wilbur, 1989; 66, Semlitsch *et al.,* 1990; 67, Sever and Trauth, 1990; 68, Shaffer, 1984a; 69, Shaffer, 1984b; 70, Shaffer and Voss, 1996; 71, Smirnov, 1989; 72, Smirnov, 1990; 73, Smirnov, 1991; 74, Smirnov, 1993; 75, Smirnov, 1994; 76, Smirnov and Vasil'eva, 1995; 77, Smith *et al.,* 1988; 78, Stephenson, 1960; 79, Stephenson, 1965; 80, Trueb, 1985; 81, Trueb and Alberch, 1985; 82, Trueb and Hanken, 1992; 83, Vignali and Nardi, 1996; 84, Voss, 1996; 85, Voss and Shaffer, 1996; 86, Wakahara, 1996; 87, Wakahara and Yamaguchi, 1996; 88, Wakahara *et al.,* 1994; 89, D. B. Wake, 1966; 90, D. B. Wake, 1980; 91, D. B. Wake, 1989; 92, D. B. Wake and Larson, 1987; 93, M. H. Wake, 1986; 94, T. A. Wake *et al.,* 1983; 95, Walls *et al.,* 1993; 96, Wassersug, 1980; 97, Wassersug and Duellman, 1984; 98, Whiteman, 1994; 99, Whiteman *et al.,* 1996; 100, Wild, 1997.

to the presumed ancestral ontogeny that are associated with specific heterochronic changes (e.g., Rose, 1996; Shaffer and Voss, 1996). Effects of phylogenetic change in the relative timing or rate of character development in embryos and larvae range from subtle, yet functionally significant changes in adult body proportions (Blouin, 1991; Emerson, 1986, 1987, 1988) to large-scale shifts of entire suites of functionally integrated characters from one life-history stage to another (Carroll *et al.,* 1991; Hanken, 1993; Ruibal and Thomas, 1988). Heterochronic analysis has been especially important in suggesting the potential for relatively small changes in developmental processes to effect large-scale changes in larval and adult morphology by shifting development along evolutionarily conserved ontogenetic trajectories (Alberch, 1980; Alberch *et al.,* 1979; D. B. Wake and Larson, 1987).

There are, nevertheless, several difficulties in assessing the heterochrony literature in amphibians. First, it is vast; the 100 studies listed in Table II are only representative of a much larger number of analyses that address evolutionary changes in developmental timing in larval and adult amphibians, both living and extinct. A more fundamental problem, however, is the large and to some extent unwieldy terminology that has characterized the field, especially the diverse and sometimes contradictory use of terms such as neoteny, paedomorphosis, and paedogenesis. Frequently, the same term is used to describe vastly different evolutionary phenomena, which in turn likely reflect very different underlying developmental mechanisms. Conversely, several terms often are used in reference to the same phenomenon. Many endocrinologists and molecular biologists, for example, employ the traditional definition of neoteny as it applies to the numerous species of salamanders that typically retain a virtually intact larval morphology throughout life, such as the axolotl, *Ambystoma mexicanum,* and the mudpuppy, *Necturus maculosus* (e.g., Rosenkilde and Ussing, 1996; Vignali and Nardi, 1996; Wakahara, 1996). Whereas some contemporary comparative biologists endorse this definition (e.g., Reilly *et al.,* 1997), others favor a broader definition that emphasizes relative rates of development between ancestor and descendant taxa (Alberch *et al.,* 1979). They instead describe the extreme pattern of development in "neotenic" urodeles such as the axolotl and mudpuppy by the terms "larval reproduction" (Shaffer, 1984a), "paedomorphosis" (Voss and Shaffer, 1996), or "perennibranchiation" (Rose, 1996).

Such variable and inconsistent terminology complicates comparisons among studies; arguably it is retarding a synthesis of existing data. It also inhibits analyses of processes and mechanisms that underlie altered patterns of development. Although it may be unreasonable or even unnecessary to expect all authors to subscribe to and consistently employ the same, identical terminology for heterochrony, they should at least always define precisely how specific terms are being used.

V. DEVELOPMENTAL MECHANISMS OF MORPHOLOGICAL DIVERSIFICATION

Most studies of the evolution and development of amphibian larvae have focused on describing derived *patterns* of ontogeny in terms of the presence or absence of specific characters, or character states, and their developmental timing (i.e., heterochrony; see the previous discussion). Whereas such data have been used in some instances to generate hypotheses regarding the nature of specific perturbations to the ancestral ontogeny that underlie evolution of one or more derived patterns (e.g., Rose, 1996), there have been relatively few attempts to probe empirically and identify the actual developmental *mechanisms* involved. Among the notable exceptions are studies conducted over many years on the endocrinological basis of neoteny (larval reproduction) in the axolotl and other species of perennibranchiate urodeles (e.g., Rosenkilde and Ussing, 1996) and an embryological and molecular analysis of the evolutionary loss of the larval cement gland in the direct-developing frog, *Eleutherodactylus coqui* (Fang and Elinson, 1996). Many more such studies are needed.

Examples of the kinds of important insights into the developmental bases of evolutionary change that can be derived from such a mechanistic approach are provided by analyses of larval pigment patterning in urodeles. These analyses also demonstrate the additional benefits that accrue when comparative developmental studies are performed in an explicitly phylogenetic context. The studies address the extensive interspecific variation in external coloration that is found among urodele larvae. Notwithstanding the myriad subtle manifestations of pigment patterning in individual species, variation in larval coloration can be described largely in terms of two general pattern "elements:" vertical bars and horizontal stripes (Epperlein *et al.*, 1996; Olsson and Löfberg, 1992; Parichy, 1996a; Fig. 8). These pattern elements, in turn, form as a result of the migration and differentiation of three types of chromatophores, or pigment cells: black melanophores, yellow xanthophores, and, to a lesser extent, silvery iridophores. The two general pattern elements demonstrate a complex, overlapping distribution when superimposed on a scheme of phylogenetic relationships among urodele taxa (Parichy, 1996a; Fig. 9). One of the implications of the particular distribution of alternate character states (presence or absence) is that vertical barring has been acquired or lost two or more times independently in different lineages (Olsson, 1994; Fig. 10). Consequently, the absence of vertical barring that characterizes the salamandrid species *Triturus alpestris* and the ambystomatid species *Ambystoma maculatum* may not reflect simply the retention of a shared feature from the common ancestor of both species. Instead, it likely reflects the loss in *A. maculatum* of vertical barring, which evolved earlier in the common ancestor of all living ambystomatids (Olsson, 1993).

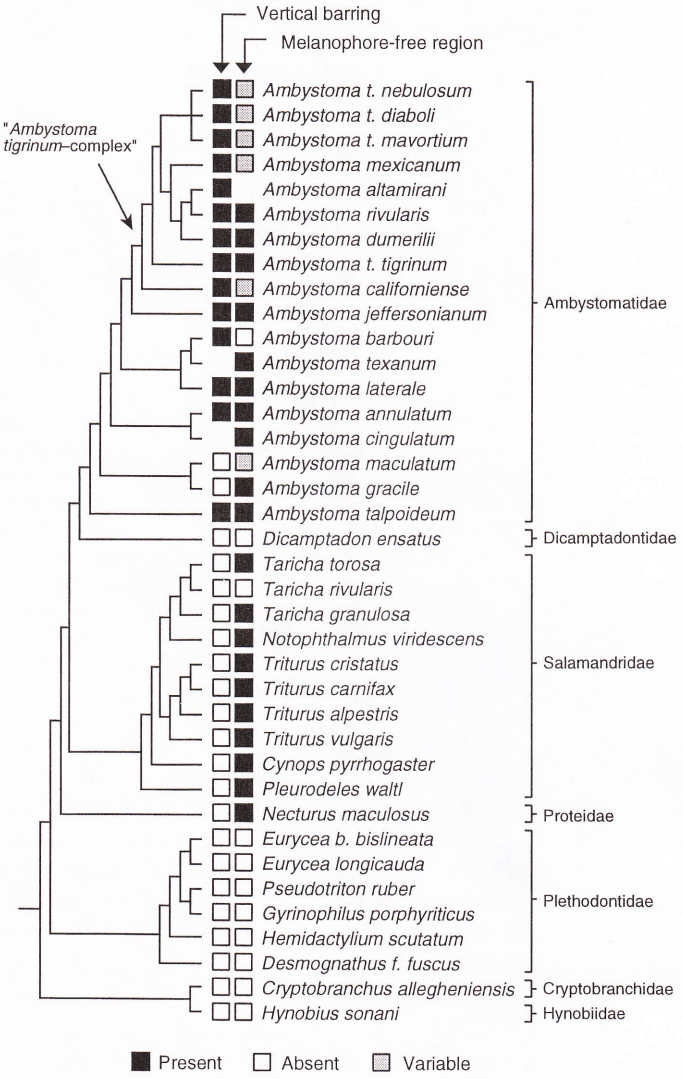

FIGURE 9 Phylogenetic distribution of the two general pigment–pattern elements—vertical barring and melanophore-free regions (horizontal stripes)—among urodele larvae representing several extant families. The particular scheme of phylogenetic relationships depicted is one of several alternate hypotheses derived from independent molecular and morphological analyses. Modified with permission from Parichy (1996a).

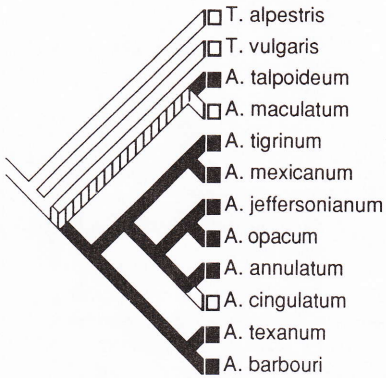

FIGURE 10 Evolution of vertical barring in the larval pigment pattern of urodeles. Black shading indicates that barring is present; in unshaded (white) areas barring is absent. Stripes indicate that the character state is equivocal (cannot be determined from existing data). T, *Triturus* (Salamandridae); A, *Ambystoma* (Ambystomatidae). The scheme of relationships among these 12 species is one of several possible phylogenetic hypotheses derived from consideration of both morphological and allozyme data. The particular distribution of character states shown here supports two equally parsimonious interpretations of the evolution of vertical barring: one gain and two losses, and two gains and one loss. Olsson (1994). Pigment pattern formation in larval ambystomatid salamanders: *Ambystoma talpoideum, Ambystoma barbouri,* and *Ambystoma annulatum. Journal of Morphology,* Copyright © 1994. Reprinted by permission of Wiley-Liss, Inc., subsidiary of John Wiley & Sons, Inc.

Whereas the mechanisms underlying pigment pattern formation in larval urodeles are far from understood completely, much fundamental information concerning the identity of and relationships among relevant components has been amassed in the last few years. In documenting the large number and diversity of developmental processes involved, these studies reveal the surprising complexity of mechanisms responsible for what might otherwise be regarded as a relatively simple patterning system. For example, development of vertical bars, one of the two basic patterning elements, occurs in two phases (Epperlein *et al.,* 1996; Parichy, 1996a). In the first phase, premigratory neural crest cells, from which pigment cells are derived, form a longitudinal series of cell aggregates dorsal to the neural tube (Fig. 11A). These aggregates eventually contain xanthophores, but not melanophores. While this "prepattern" is forming in the dorsal part of the embryo, melanophore precursors migrate out onto the dorsolateral portion of the flanks. In the second phase of vertical bar development, xanthophores migrate laterally from the cell aggregates atop the neural tube and invade regions of the flanks previously occupied by melanoblasts (Fig. 11B). Simultaneously, the melanophores aggregate among themselves and at a distance from the xanthophores. This results in a series of

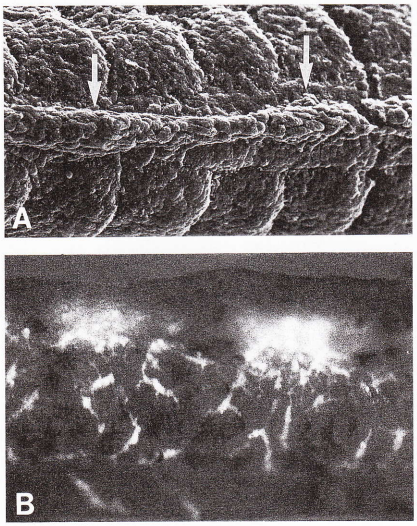

FIGURE 11 (A) Scanning electron micrograph of the trunk region of a stage 31 embryo of the ringed salamander, *Ambystoma annulatum* (Ambystomatidae). Dorsal view; surface ectoderm has been removed. Premigratory neural crest cells are beginning to form a longitudinal series of aggregates (arrows) dorsal to the neural tube and paired somites. (B) Lateral view of a slightly older, intact embryo (stage 38), viewed with fluorescence microscopy. Xanthophores (stained white with ammonia fluorescence) are beginning to migrate ventrolaterally from the crest cell aggregates. Olsson (1994). Pigment pattern formation in larval ambystomatid salamanders: *Ambystoma talpoideum*, *Ambystoma barbouri*, and *Ambystoma annulatum*. *Journal of Morphology*, Copyright © 1994. Reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

alternating bars, each principally containing one or the other of the two pigment cell types (Fig. 8). Factors governing the complex cell movements involved in these patterning events still are not well-understood, but likely include various kinds of cell–cell and cell–extracellular matrix interactions. Finally, there is compelling evidence that at least some of the preceding processes are directly involved in the evolution of pigment patterns (Epperlein *et al.*, 1996; Parichy, 1996a). In *A. maculatum*, for example, loss of vertical bars is correlated with the failure of premigratory neural crest cells to aggregate along the neural tube. Also, melanophores and xanthophores appear to migrate onto the flanks simultaneously in this species and not sequentially, as in species with vertical bars (Olsson, 1993).

Development of the second principal pattern element, horizontal stripes of melanophores on either side of a melanophore-free region, is mediated by processes that are both similar to and different from those involved in the development of vertical bars (Epperlein *et al.*, 1996; Parichy, 1996a). Especially

important are interactions between pigment cells and the developing lateral lines, which comprise a neurosensory system that provides a mechanoreceptive sense important to aquatic vertebrates (Parichy, 1996a,b,c; Fig. 12). This too is an ancient component of the pigment-patterning mechanism in salamanders; it likely was present in the common ancestor of the families Ambystomatidae and Salamandridae and appears to be retained in most living species. Interestingly, however, at least one salamandrid species (*Taricha torosa*) possesses horizontal stripes and a melanophore-free region, but lacks the close coupling between pigment patterning and lateral-line formation. The appearance of novel, extracellular cues for melanophore localization accompanies the apparent loss of this component of the ancestral patterning mechanism (Parichy, 1996b; Fig. 13).

Horizontal stripe formation adds to the growing list of examples from evolutionary developmental biology in which the same or similar phenotype in different, often closely related, species is produced by different underlying mechanisms (Hall, 1995; Raff, 1996). Evolution of developmental mechanisms need not lead to evolution of phenotypes. This demonstrates the difficulty of inferring the nature of developmental mechanisms from their end products. It also cautions against strict use of features of development as unambiguous criteria for assessing the homology of larval or adult characters.

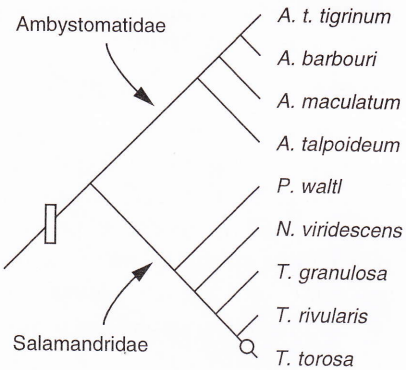

FIGURE 13 Hypothesis for the evolution of pattern-forming mechanisms underlying development of the horizontal stripe (melanophore-free region) in larval urodeles. This scenario posits the presence of a primitive, lateral-line-dependent pattern-forming mechanism in the common ancestor of the families Ambystomatidae and Salamandridae (open rectangle), which is retained in descendant taxa. A second, redundant, lateral-line-independent mechanism for stripe formation so far is known in only one species, *T. torosa*, and likely evolved much more recently (open circle). *A, Ambystoma; P., Pleurodeles; N., Notophthalmus; T., Taricha.* Reprinted with permission from Parichy (1996b).

VI. LOSS OF LARVAE

The presumed ancestral life history for all Recent amphibians comprises aquatic eggs and larvae and terrestrial adults. This biphasic, or metamorphic, ontogeny is retained in many living species of frogs, salamanders, and caecilians, although in many taxa embryonic and larval development has been altered to effect considerable morphological divergence among species. There are, however, a wide variety of alternate life histories and reproductive modes that have evolved independently within all three living orders (Altig and Johnston, 1989; Duellman and Trueb, 1986). Their distinguishing features range from virtually complete loss of the terrestrial adult (postmetamorphic) stage and obligate larval reproduction (e.g., the axolotl, *Ambystoma mexicanum*) to loss of the free-living, aquatic larva. Instances of larval loss are especially interesting, insofar as they can offer unique insights into the opportunities for adaptation and specialization that are conferred by the ancestral metamorphic ontogeny. They also provide opportunities to assess the possible role of larval features in mediating, or even constraining, the evolution of adult features. Two distinct examples of larval loss are discussed here: direct development and viviparity.

A. Direct Development

In direct development, most adult features form in the embryo and are present at hatching; there is no free-living larva. It is so named to distinguish it from the ancestral, "indirect" mode of development, in which most adult features form during the (posthatching) metamorphosis that follows the larval stage. Direct development has evolved independently within each of the three living amphibian orders and characterizes many hundreds of species of frogs, salamanders, and caecilians (Duellman and Trueb, 1986; M. H. Wake, 1989). The neotropical anuran genus *Eleutherodactylus* alone includes more than 500 species (Duellman, 1993), all of which are believed to display direct development or some even more extreme modification thereof (e.g., ovoviviparity in *E. jasperi;* M. H. Wake, 1978, 1993). Yet, the three orders differ considerably with respect to the phylogenetic distribution of direct development among their component taxa. At one extreme are the anurans. Direct development occurs in one or more species in each of at least 10 different families or family-level taxa of frogs (Fig. 14). Each of these lineages is believed to represent an independent acquisition of direct development as all also contain metamorphosing taxa, which represent the presumed ancestral life history. Accordingly, direct development must have evolved at least 10 times just in anurans. This number represents a conservative estimate, as direct development likely evolved more than once in at least some lineages (Duellman, 1989; Duellman

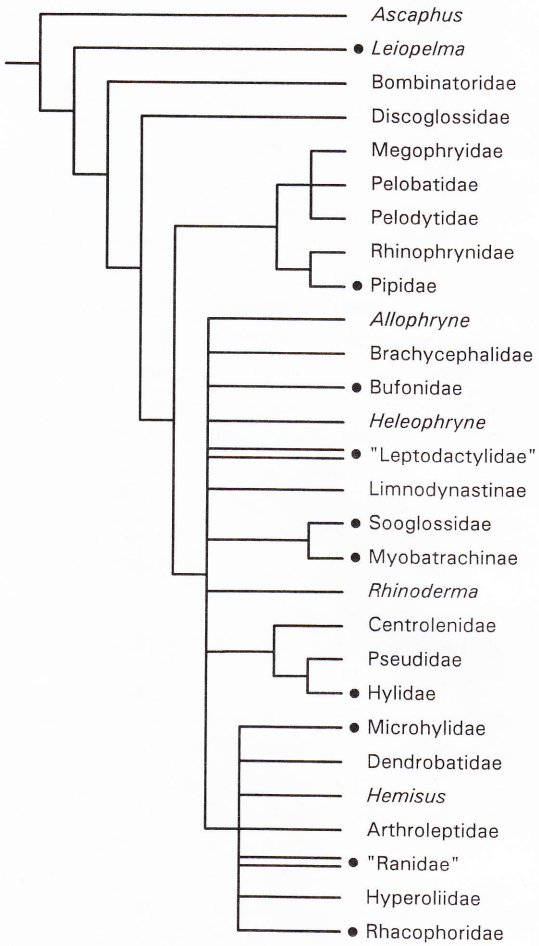

FIGURE 14 Phylogenetic distribution of direct development (●) among extant families and family level taxa of frogs [based on Duellman and Trueb (1986)]. Relationships depicted are based on Ford and Cannatella (1993). [Reprinted with permission from Ford and Cannatella (1993).]

and Trueb, 1986). Despite its repeated evolution and widespread distribution among anurans, direct development nevertheless is not the predominant reproductive mode in living frogs (Duellman, 1989).

At the other extreme are urodeles. Embryonic development outside the reproductive tract of the female parent that proceeds directly to a terrestrial hatchling without a free-living larval stage is restricted to just one of ten Recent families, the Plethodontidae, or lungless salamanders (D. B. Wake and Hanken,

1996; D. B. Wake and Marks, 1993; Fig. 15). However, because the Plethodontidae account for nearly two-thirds of all species of living salamanders and because most plethodontids have direct development, it is the predominant reproductive mode in urodeles.

Caecilians represent an intermediate condition. The biphasic life history, including free-living, aquatic larvae, is retained by some or all species in four of the six extant families (Duellman and Trueb, 1986; Nussbaum and Wilkinson, 1989; M. H. Wake, 1993; Wilkinson and Nussbaum, 1996). Direct development occurs in at least three families and includes many instances of viviparity (see the following section). Whereas general trends in life-history evolution in caecilians have been defined, detailed knowledge of evolutionary patterns in most clades awaits more robust phylogenetic hypotheses for the group and reliable life-history data for many more species (M. H. Wake, 1977a, 1982, 1989, 1993; Wilkinson and Nussbaum, 1996).

Whereas there is widespread acceptance that direct development has evolved many times independently within and among the major groups of living amphibians, determination of the exact number of times has proven much more difficult. Phylogenetic analyses of plethodontid salamanders, for example, implicate as few as one and as many as five separate instances of the evolution of direct development in this clade (Collazo and Marks, 1994; D. B. Wake and Hanken, 1996). Determination of the exact number and phylogenetic position(s) of instances of the evolution of direct development are not trivial issues. In plethodontids, some plausible phylogenetic scenarios for the evolution of direct development necessarily would imply that a free-living aquatic larva must have reappeared one or more times in the history of the group (D. B. Wake and Hanken, 1996). Similar scenarios exist for the so-called

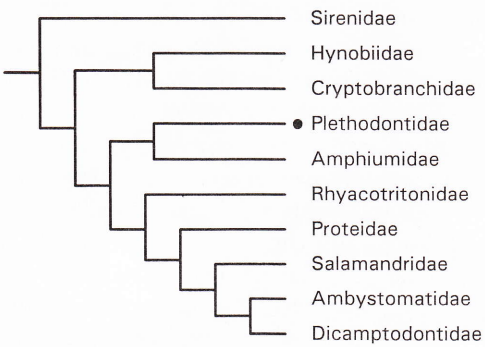

FIGURE 15 Phylogenetic distribution of direct development (●) among the 10 extant families of salamanders. Relationships depicted are based on Larson and Dimmick (1993). [Reprinted with permission from Larson and Dimmick (1993).]

marsupial frogs of South America (Hylidae: Hemiphractinae), which include both direct-developing and metamorphosing taxa (Duellman and Hillis, 1987; Duellman *et al.*, 1988; Wassersug and Duellman, 1984; but see Haas, 1996a,b). Resolution of these problems awaits more robust phylogenetic hypotheses than are available. Developmental data also may make an important contribution if it can be shown that "direct development" is not a uniform developmental mode wherever it exists within a particular clade, but instead comprises two or more distinct ontogenetic patterns. For example, preliminary evidence that direct development has evolved at least two or even three times within the Plethodontidae is seen in the contrasting patterns of embryonic development of several organ systems that distinguish several distantly related taxa (D. B. Wake and Hanken, 1996).

Almost by definition, direct development entails the precocious (embryonic) formation of adult features, which typically form during (posthatching) metamorphosis in species that display the ancestral, biphasic life history. Most studies of the embryology and developmental biology of direct-developing amphibians have been concerned primarily with assessing the extent to which larval features have been retained in or lost from this derived ontogeny (e.g., Orton, 1949; Wassersug and Duellman, 1984). As one might expect from a characteristic that has evolved repeatedly, there is considerable variation among direct-developing taxa with respect to the extent to which a given species or members of a particular clade either recapitulate or lack larval features (Fig. 16). The eastern North American urodele *Desmognathus aeneus* lacks a free-living, aquatic larva, but nevertheless it displays many larva-specific traits during embryonic or immediate posthatching development (Marks, 1994; Marks and Collazo, 1998). On the other hand, the many species of direct-developing *Eleutherodactylus* retain relatively few larva-specific features, either externally or internally (Hanken *et al.*, 1992; Hughes, 1959; Lynn, 1942). Indeed, *Eleutherodactylus* has long been regarded as among the most extreme examples of direct development in amphibians in terms of the great extent to which the species deviate from the ancestral, metamorphic ontogeny (Elinson, 1990; Orton, 1951).

Relatively few studies have attempted to probe the developmental mechanisms that underlie the evolution of direct development (Elinson, 1990). These mechanisms, however, are the subject of several analyses, which address both the loss of larval features and the embryonic formation of adult features. Although our understanding of the developmental basis of direct development is far from complete, the picture that is beginning to emerge is of a series of perturbations to developmental processes at several levels of biological organization, including gene expression, endocrine control, morphogenesis, and pattern formation (Callery and Elinson, 1996; Elinson, 1994; Moury and Hanken, 1995; Hanken *et al.*, 1997a,b; Jennings and Hanken, 1998; Richardson

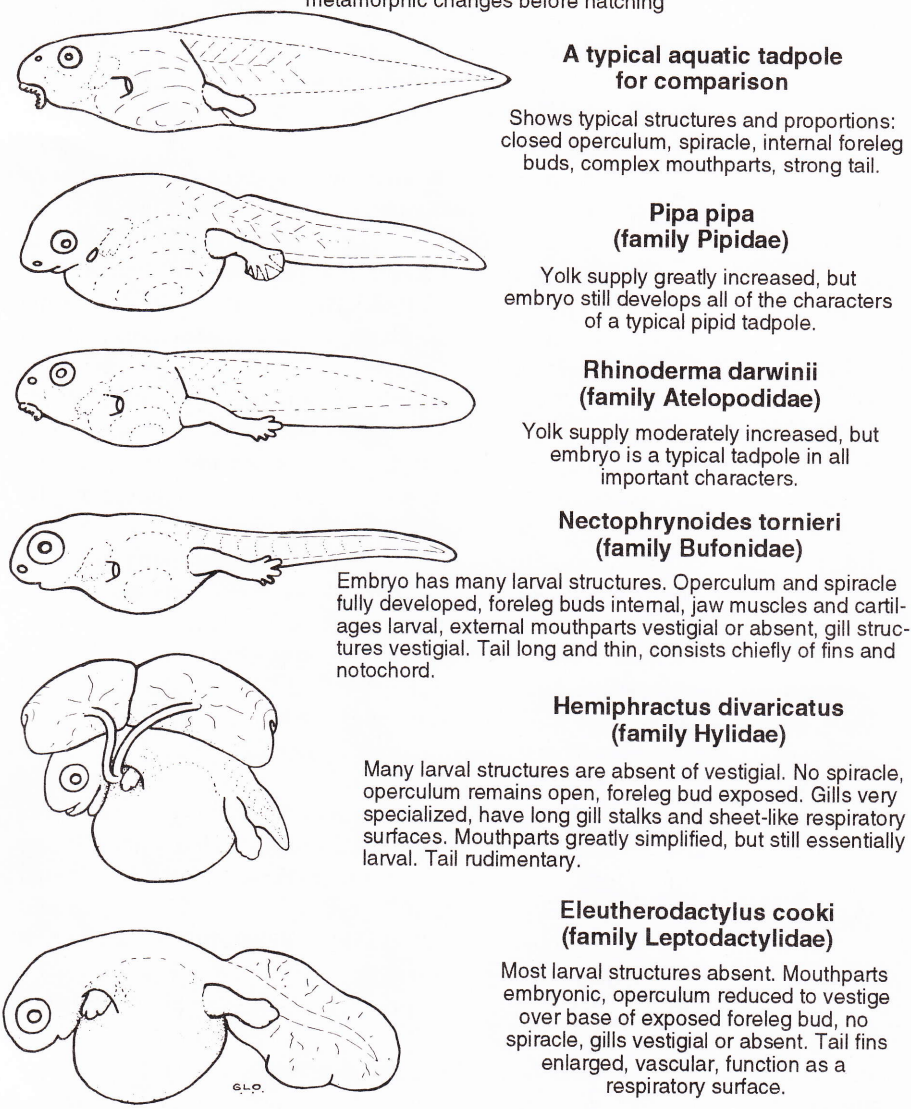

FIGURE 16 Direct development in frogs. Grace Orton's (1951) well-known illustration depicts the variable extent to which larval features have been lost during the evolution of direct development in different lineages of Recent anurans. Species are arranged in a cline from a typical tadpole (top), which represents taxa that retain the ancestral, biphasic life history, to *Eleutherodactylus* (bottom), which retains relatively few larval-specific features. Reprinted with permission from Orton (1951) courtesy of Ward's Natural Science Establishment, Inc.

et al., 1998). For example, evolutionary loss of the larval cement gland in direct-developing *Eleutherodactylus coqui*, a species native to Puerto Rico, is associated with altered spatial and temporal patterns of expression of distal-less genes during embryogenesis and modifications to the inductive interactions that mediate differentiation of the oral integument (Fig. 17; Fang and Elinson, 1996).

Direct development in plethodontid salamanders has been used to evaluate and support hypotheses regarding the existence of larval constraints on adult morphology in urodeles in general (D. B. Wake and Hanken, 1996; D. B. Wake and Marks, 1993). According to these hypotheses, the existence of fully differentiated, functionally specialized larval structures in metamorphosing salamanders limits, or constrains, the morphology of adult structures that can subsequently form at metamorphosis in these species (D. B. Wake, 1982; D. B. Wake and Roth, 1989). Because the evolution of direct development entails loss of the larva as a discrete, free-living, life-history stage, it also offers at least the possibility for loss of the larval constraint(s) on adult morphology. Direct-developing plethodontids offer at least circumstantial support for the larval constraint hypothesis, insofar as these species possess some of the most highly derived and complex functional systems found in any living salamanders. One example is the complex of muscular, skeletal, and nervous components that comprise the hyolingual apparatus, which mediates the tongue projection characteristic of many direct-developing species (Deban *et al.*, 1997; Lombard and Wake, 1977; Roth and Wake, 1985). If larval constraints have been relaxed or even lost in direct-developing plethontids, then we might expect to see the presence of derived adult morphologies correlated with novel developmental patterns of embryonic development that do more than simply recapitulate the ancestral ontogeny. Evidence for such "ontogenetic repatterning" in direct-developing plethodontids comes from several studies of the development of the limbs, the brain and cranial nerves, and the hyolingual skeleton (Alberch, 1987, 1989; Roth *et al.*, 1988; Shubin, 1995; Shubin and Wake, 1991; D. B. Wake and Roth, 1989; D. B. Wake and Shubin, 1994; D. B. Wake *et al.*, 1988).

Do larval features constrain adult morphology in other amphibians either in the same way or to the same extent that they appear to do so in many urodeles? Studies of at least some direct-developing frogs suggest that the answer is no. In *Eleutherodactylus*, for example, pronounced evolutionary modifications to embryonic development, including the loss of many larval components, are not associated with the origin of novel morphologies that characterizes many direct-developing (plethodontid) salamanders (Hanken, 1992; Hanken *et al.*, 1992). Moreover, the developmental mechanisms that mediate anuran metamorphosis appear to confer much greater developmental independence between larvae and adults than do comparable mechanisms in most

metamorphosing urodeles (cf. Alberch, 1987, 1989; Elinson, 1990). Thus, in anurans, developmental mechanisms that mediate metamorphosis likely may facilitate, if not actually promote, the evolutionary dissociation of embryonic, larval, and adult features (Hanken *et al.*, 1997b).

B. Viviparity

Viviparity, or live-bearing, refers to an array of reproductive mechanisms for embryonic or fetal maintenance by either the maternal or paternal parent. Viviparity has evolved independently in many groups of animals, especially vertebrates, and specific definitions of the term vary widely among both taxonomic groups and authors (Altig and Johnston, 1989; M. H. Wake, 1989, 1992). In amphibians, viviparity entails the retention of embryos in the maternal oviducts through development to the adult (postmetamorphic) stage, with maternally derived nutrition provided or consumed following exhaustion of the embryo's yolk supply (M. H. Wake, 1982). Viviparous amphibians lack a free-living larva.

Viviparity has evolved one or more times within each of the three Recent amphibian orders (M. H. Wake, 1977a, 1989, 1993). As with direct development, however, the orders differ considerably with respect to the prevalence of viviparity and its impact on the evolutionary history of each group. Obligate viviparity is very rare in frogs and salamanders, accounting for less than 1% of extant species. One species of salamander exhibits "optional viviparity" associated with intrauterine cannibalism, in which prenatal young feed on unfertilized eggs and developing siblings within the mother's reproductive tract (Dopazo and Alberch, 1994). A few additional species are ovoviviparous; embryos are retained but nutrition is exclusively yolk-dependent and (in salamanders) the young may be born as larvae (Alcobendas *et al.*, 1996; Joly, 1968). In caecilians, however, viviparity is the predominant reproductive mode among the approximately 170 described species; it has evolved at least two and as many as four times.

Several aspects of the developmental biology of amphibian viviparity have received considerable attention, especially those that concern fetal–maternal relations. These include studies of reproductive endocrinology (Exbrayat, 1992; Exbrayat and Morel, 1995; Xavier, 1977, 1986), urogenital anatomy (Exbrayat, 1983, 1984; Hraoui-Bloquet *et al.*, 1994; M. H. Wake, 1970, 1977b), reproductive physiology (Toews and Macintyre, 1977), fetal nutrition and growth rates (Dopazo and Alberch, 1994; Exbrayat and Hraoui-Bloquet, 1992; Hraoui-Bloquet and Exbrayat, 1992; M. H. Wake, 1980a), and organogenesis (Hraoui-Bloquet and Exbrayat, 1994; Sammouri *et al.*, 1990; M. H. Wake, 1976, 1980b,c; M. H. Wake and Hanken, 1982; M. H. Wake *et al.*, 1985). The

taxonomic coverage of these treatments is spotty, however, and the comparative database for each topic is relatively small. Many do not concern larval biology per se and therefore are beyond the scope of this chapter. Interested readers are referred to several reviews and associated primary literature (see the references listed in this paragraph).

One important aspect of amphibian viviparity that does relate directly to larval biology and development is the evolutionary fate of larva-specific features. In general, there are two sharply contrasting fates. First, and as would be expected given that the neonate is born as a juvenile (postmetamorphic) adult, many larval features simply are lost. For example, several oral integumentary structures that contribute to the unique trophic apparatus that is characteristic of many anuran larvae are absent from embryos of the viviparous African frog, *Nectophrynoides occidentalis* (M. H. Wake, 1980c). These include the keratinized (horny) beaks and labial teeth. In lacking many larva-specific features, viviparous *N. occidentalis* exemplifies a predominant trend that is exhibited by several additional ovoviviparous or direct-developing species within the genus *Nectophrynoides,* all of which lack a free-living larva.

The second and arguably more interesting fate of larval features is their recruitment to perform new physiological functions in the developing embryo or fetus. Most of the examples offered to date center around apparent specializations for the transfer of nutrients and other substances from the mother to the fetus while it is still within the maternal oviduct. In *N. occidentalis,* for example, the fetal frog is believed to ingest uterine secretions orally as a supplemental food source following exhaustion of the embryonic yolk (Lamotte and Xavier, 1972; Vilter and Lugand, 1959; Xavier, 1973; cited in M. H. Wake, 1980c). Correlated with this novel feeding mode is the retention and, indeed, elaboration of the network of external buccal papillae, which surround the mouth and assist food gathering in typical tadpoles. In typlonectid caecilians, all of which are viviparous, embryos and larvae grow large, saclike, and highly vascularized external gills, which are resorbed or shed only at or soon after hatching (Hraoui-Bloquet and Exbrayat, 1994; Toews and Macintyre, 1977). The morphology and development of these gills differ considerably from those in viviparous species in other caecilian families, which are resorbed well before birth (M. H. Wake, 1993; Fig. 18). In free-living amphibian larvae, external gills provide sites for gas exchange that are used in aquatic respiration. In one typhlonectid species, *Typhlonectes compressicaudus,* the fetal gills and maternal oviduct have been posited to function as a "pseudoplacenta" that effects gas exchange and nutrient transfer between the mother and her offspring (Delsol *et al.,* 1981; Exbrayat and Hraoui-Bloquet, 1992; Hraoui-Bloquet and Exbrayat, 1994; Hraoui-Bloquet *et al.,* 1994; Sammouri *et al.,* 1990; Toews and Macintyre, 1977). However, despite extensive study of fetal–maternal relations in this species, evidence for this "placental" function is largely circumstantial. The

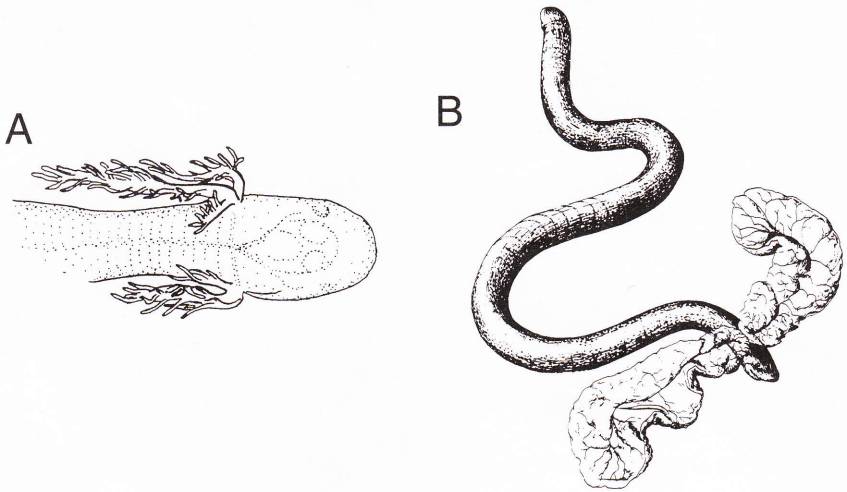

FIGURE 18 Fetal gill morphology in viviparous caecilians. (A) A pair of triramous, fimbriated, and relatively short gills are characteristic of nonviviparous and most viviparous species, such as *Dermophis mexicanus*. Reprinted with permission from M. H. Wake (1977a). (B) Viviparous typhlonectids, such as *Typhlonectes compressicaudus*, have a single, highly elongate, and saclike gill on each side of the head, which has been suggested to function as a "pseudoplacenta" (see text). Reprinted with permission from *Nature* (Toews and Macintyre, 1977) Copyright 1977. Macmillan Magazines Limited.

extent and mode of fetal–maternal exchange via the gills in this and other typhlonectid species await confirmation by direct observation and experiment (M. H. Wake, 1993).

Other features of the ancestral, complex life history may be recruited as well, including the biphasic pattern of development itself. For example, many viviparous caecilians possess a system for prenatal "food gathering" that is similar to but even more elaborate and complex than the one seen in *Nectophrynoides* described earlier; the fetus actively ingests secretions from the maternal oviducts (Exbrayat, 1984; Exbrayat and Hraoui-Bloquet, 1992; Hraoui-Bloquet and Exbrayat, 1992; M. H. Wake, 1977a,b). Associated with this novel feeding mode is the presence of highly specialized and unique fetal dentition (M. H. Wake, 1976, 1980b). The fetal teeth are shed at or shortly after birth, when they are replaced by the morphologically distinct and characteristic adult dentition. In effect, the biphasic pattern of tooth development and morphogenesis that is characteristic of the larval–adult transition in many metamorphosing amphibians is redeployed in the fetal–postnatal transition of viviparous caecilians.

Retention in viviparous amphibians of many larva-specific and related features of the ancestral, complex life history, despite loss of the corresponding, free-living larval stage, provides excellent examples of exaptation, i.e., the evolutionary cooption of preexisting adaptations in novel functional and ecological contexts (Gould and Vrba, 1982). Indeed, it seems likely that the existence of larval features, discrete from those in the adult, may have allowed, or even facilitated, the evolution of this novel reproductive mode in at least some instances. However, much greater knowledge of phylogenetic trends involving larval retention or loss, as well as their underlying developmental bases, is needed in order to accurately and reliably define the nature and role of such biases and constraints in the evolution of amphibian viviparity.

It also should be emphasized that the evolution of viviparity and other, related reproductive specializations in Recent amphibians involves much more than the simple retention, or even redeployment, of preexisting features of the ancestral ontogeny. For example, the morphology of individual teeth that comprise the fetal dentition in viviparous caecilians is unlike that seen in either the larval or the adult dentition of metamorphosing species (M. H. Wake, 1976). Many other aspects of early ontogeny, such as cranial ossification, similarly are highly derived in viviparous caecilians (M. H. Wake and Hanken, 1982) and salamanders (Alberch and Blanco, 1996) in comparison to the respective presumed ancestral ontogenies. In both instances, the sequence and timing of bone formation have been altered in similar fashion, apparently in response to similar functional demands imposed by precocious use of the jaws in feeding before birth. As with the evolution of most adaptations, viviparity comprises a complex mix of conserved and novel traits.

VII. CONCLUSION

The broad array of reproductive modes and life histories displayed by Recent amphibians constitutes a series of variations on the ancestral theme of metamorphosis (Hanken, 1992). These variations have allowed frogs, salamanders, and caecilians to diversify and adapt to a wide range of aquatic and terrestrial environments, as well as other ecological opportunities. A central element in this evolutionary success story is the free-living larva—retained or even amplified in many contexts and abandoned in others.

The evolution of larvae fundamentally involves modifications in development. Changes in developmental patterns, especially those concerned with the timing of developmental events, i.e., heterochrony, are well-documented. The mechanistic bases of these and other evolutionary changes in developmental pattern, however, generally remain poorly known. Both kinds of information are needed to reliably define the range of evolutionary opportunities and

constraints conferred by the ancestral, metamorphic life history, as well as to assess the extent to which these opportunities and constraints vary among different amphibian lineages.

Many of the most important evolutionary changes in larval development likely involve pertubations to earlier ontogenetic stages, especially the embryo. Yet, despite its long history, the comparative embryology of amphibians is relatively poorly known. Consequently, renewed interest in comparative studies of development has revealed an unexpected diversity of molecular, cellular, and developmental patterns and mechanisms among amphibian embryos (e.g., Del Pino, 1989; Del Pino and Elinson, 1983; Elinson and Del Pino, 1985; Novoselov, 1995; Purcell and Keller, 1993; Tiedemann *et al.,* 1995), including comparisons of close phylogenetic relatives (Minsuk and Keller, 1996). Comparative embryological studies need to be extended to define the consequences of these and other evolutionary modifications of early development for larval, as well as adult, features.

Finally, studies of larval development and evolution will be most effective and insightful when data are analyzed in a rigorous phylogenetic context, both as a means of deriving the likely sequences of character transformation and to most effectively integrate these studies with comparable and complementary analyses of amphibian phylogeny and larval biology.

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