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DEVELOPMENT AND EVOLUTION OF PLETHODONTID SALAMANDERS: A REVIEW OF PRIOR STUDIES AND A PROSPECTUS FOR FUTURE RESEARCH

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RECENT years have witnessed a dramatic increase in literature dealing with the relation of development to evolution, and there is a widespread impression that great progress is on the horizon (e.g., Hall, 1992; Wake and Roth, 1989; Wake et al., 1991). The possibility of productively combining developmental and evolutionary or phylogenetic studies of plethodontid salamanders has been evident at least since the demonstration by Emerson (1905) that *Typhlomolge rathbuni* is a perennibranchiate, or permanently larval, plethodontid rather than a close relative of proteiid genera. This simultaneous demonstration of homoplasy and paedomorphosis sets the stage for our review of progress to date, and our prospectus for a renewed focus on comparative developmental studies of plethodontid salamanders. There is a complex inter-relationship between development, evolution, and phylogenetics, and reciprocal illumination can result when the three approaches are pursued simultaneously within a single lineage. We believe that the family Plethodontidae is an appropriate taxon for such studies.

Although there are far more species of plethodontids than all other species of salamanders, there are more studies of development in members of the families Ambystomatidae, Salamandridae, and

Hynobiidae than there are of plethodontids. The reasons for this disparity are found in the life histories of the groups. In general, plethodontids are more secretive in their reproduction than are members of other families, and their clutch sizes are relatively small. Furthermore, more than two-thirds of the species of plethodontids, forming a majority of all salamanders, have direct development, a life history mode that further complicates use of these animals for routine studies of development. Species that undergo direct development usually have smaller clutch sizes than those with larval development, and their eggs are even more difficult to find. For these reasons, there have been no studies of the complete ontogeny of plethodontids, comparable to those for some other families. Plethodontids are far more diverse in their life history, ecology, and degree of taxonomic differentiation than the other families, and the opportunities for comparative developmental studies of plethodontids have gone untapped until recently. Hormonal methods for inducing oviposition have been developed for plethodontids (Collazo, 1990; Verrell, 1989). As a result, it is now relatively easy to obtain eggs, which means that the field of comparative ontogenesis now is wide open for students of plethodontid evolution. In this paper,

we review what has been accomplished and point out opportunities that exist for future studies.

DEVELOPMENT, EVOLUTION, AND PHYLOGENY

Our interests in the combination of these three traditions are illustrated by outlining some of the general issues that may be pursued with plethodontid salamanders. The first major area is the relation of development to the evolution of morphology. Plethodontids have a rich array of life histories, including perennibranchiate species (e.g., *Typhlomolge rathbuni*, *Haidetriton wallacei*), species that have multi-year larvae (e.g., *Gyrinophilus porphyriticus*, *Desmognathus quadramaculatus*), species with single season larvae (e.g., *Eurycea bislineata*, *Desmognathus fuscus*), species with extremely short larval periods (e.g., *Hemidactylium scutatum*), and species that undergo direct development (e.g., *Desmognathus wrighti*, tribes Plethodontini and Bolitoglossini). The fact that several to many species occur in each of these informal classes makes it possible to test hypotheses concerning the importance of the larval stage to adult morphology. Does the existence of a larval stage impose limits on morphological evolution in adults? This apparently is the case in regard to the biomechanics and functional morphology of tongue projection (Lombard and Wake, 1977; Roth and Wake, 1985). The highest degree of morphological specialization for tongue projection (longest, fastest, most maneuverable tongues) is attained in clades that have direct development (*Hydromantes*, supergenus *Bolitoglossa*), but other genera (e.g., *Eurycea*) also have projectile tongues. The bolitoglossines have achieved the apparent ultimate state of specialization by exercising a particular, biomechanically superior, developmental option—the use of the second rather than the first ceratobranchial as the force-delivering component in the system—from an array limited by physical considerations (Lombard and Wake, 1976). The existence of a functional larval state in hemidactyliines which entails a dual function (feeding in water and later on land) for the

hyobranchial system apparently limits them to a less specialized option (Wake, 1982).

A larval plethodontid starts to function relatively early in development, at a small size. Furthermore, life in flowing water, the way of life hypothesized to be ancestral for plethodontids (Wilder and Dunn, 1920), imposes rather rigorous demands on the young animals. When stream-adapted larvae hatch, they must immediately use limbs for locomotion, while demands on pond larvae are less rigorous in this regard. Feeding also differs in flowing and standing water. These functional requirements may feed back on developmental systems, accelerating limb development, for example, and consequently constraining evolution. Assuming that ancestors of direct-developing groups were stream-adapted, we hypothesize that the evolution of direct development might provide a release from these functional and developmental constraints. If so, new evolutionary opportunities might arise. Ontogenetic repatterning, the establishment of new sets of morphogenetic processes resulting from heterochronic events (Wake and Roth, 1989), appears to be associated with the origin of direct development in plethodontids, as it was much earlier in the origin of amniotes. Metamorphosis in vertebrates is less dramatic than in some other groups (e.g., insects), and the changes that occur may be insufficient to replace fully the morphological and physiological states necessary for larval function.

A second set of studies that has special relevance is the reconstruction of phylogenetic history. There are serious reservations to the use of ontogenetic information for ordering character states, especially in salamanders, where heterochrony has been demonstrably important (we always have before us the specter of the Axolotl!). To assume that the morphology that appears earliest in ontogeny is the ancestral state of a character can lead to error, for in plethodontids there are examples of larval and embryonic innovations that revert to apparently ancestral states (based on out-group analysis) later in ontogeny. The single premaxillary bone

of larvae and embryos, which metamorphoses to a paired structure in some plethodontid genera, is an example of such a caenogenetic character (Wake, 1966). However, because characters are appropriately full ontogenies of the characters (de Queiroz, 1985), phylogenetic analyses that make use of such ontogenies will be able to inform us as to how common recapitulation is within a given group.

A third major theme is the use of developmental studies for understanding characters and their transformations. A particularly thorny problem facing salamander systematists is the ubiquity of homoplasy (Wake, 1991)—derived similarity resulting from convergence, parallelism, or reversal. Fewer developmental options may exist than there are ecological opportunities, and homoplasy is the result. But developmental analysis may inform us that some homoplasies are more likely than others, or more likely in some taxa than in others. In the neotropical bolitoglossines, loss or gain of septomaxillary bones is an extremely common homoplasy, but in the tribe Plethodontini, the bones are invariably present and complex in their development, even though small. When a toe is missing in plethodontid salamanders, it is invariably the fifth. Development might also help us determine whether characters are homoplastic or homologous. For example, some workers considered the free-tongued condition of different plethodontids to have evolved once (i.e., to be homologous: Dunn, 1926), but comparative morphological and developmental data show that free tongues have evolved as many as *six times* independently (Lombard and Wake, 1986) within the family.

Homoplasy is so common in the family Plethodontidae and in other salamanders (Larson, 1991; Sever, 1991) that development of a robust phylogenetic hypothesis has been elusive (e.g., Lombard and Wake, 1986). The supergenus *Bolitoglossa*, which includes about two-thirds of the species in the family, has been especially difficult because of extensive homoplasy (Wake and Elias, 1983). Perhaps our problems with homoplasy could be resolved if we developed cladograms based on character ontogenies. We may be able to obtain on-

togenetic data for sufficient numbers of plethodontid taxa, representing at least the major monophyletic groups, to make such undertakings feasible.

REVIEW OF DEVELOPMENTAL STUDIES OF THE PLETHODONTIDAE

The literature on plethodontid development has never been reviewed, so we present an overview here in order to illuminate what is needed and what opportunities exist for further studies. We selected literature to make specific points, and we do not claim to present a complete reference list.

Early Development and Normal Tables

While there is a long history of studies of early development in plethodontids, there is as yet no formal normal table of development available for the family. The first description of the eggs of plethodontids dealt with *Eurycea bislineata* (Verrill, 1862), which is a relatively well studied species (Goodale, 1911; I. Wilder, 1924a,b, 1925). The most extensive studies of early development have used *Desmognathus fuscus* (Hilton, 1904, 1909; H. Wilder, 1904; I. Wilder, 1913). Cleavage and gastrulation were studied in *Hemidactylium scutatum* by Humphrey (1928), but few other such studies were undertaken until the work of Collazo (1990). Montgomery (1901) presented the first detailed information on a direct developing species (*Plethodon cinereus*). Ritter and Miller (1899) published initial observations on egg deposition sites (in tree cavities) and direct development in *Aneides lugubris*, but the detailed observations of Miller, which started before the turn of the century, were only published much later (Storer, 1925, quoted extensively from Miller's unpublished manuscript, and finally Miller, 1944, published his own work). The closest approximation to a normal table for a direct developing salamander is the treatment of *Plethodon cinereus* by Dent (1942). Marks and Collazo (1988) described ontogeny of the direct developing species *Desmognathus aeneus*, and Collazo (1990) described many stages of development in *Ensatina eschscholtzii* and *Batrachoseps attenuatus*.

Larval Development in Relation to Life History and Ecology

Larvae occur in the subfamily Desmognathinae and the plethodontine tribe Hemidactyliini. The most significant early work on larval development was that of I. Wilder on *Desmognathus fuscus* (1913) and *Eurycea bislineata* (1924a,b, 1925). Also important is the series of papers by Blanchard (e.g., 1923) on *Hemidactylium scutatum*. Bishop and Chrisp (1933) studied *Desmognathus ochrophaeus*, and, in his monograph on the salamanders of New York, Bishop (1941) presented much useful information and excellent illustrations for *Hemidactylium scutatum* (see also Bishop, 1919), *Gyrinophilus porphyriticus*, *Pseudotriton ruber*, *Eurycea bislineata*, *E. longicauda*, *Desmognathus ochrophaeus* and *D. fuscus*. Recent work has been increasingly ecological in nature and has included studies of *Leurognathus marmoratus* (Martof, 1962), *Desmognathus ochrophaeus* (Tilley, 1972), *Eurycea quadridigitata* (Semlitsch, 1980), and *Desmognathus fuscus* (Juterbock, 1990), as well as some other species. A long series of papers by Bruce (e.g., 1989, 1990) has dealt with desmognathines and hemidactyliines of the southern Appalachians.

Specific Organ Systems

Cope (1869, 1889) was the first systematist to make use of comparative osteological information, but the first detailed descriptions of cranial development and morphology were by Parker (1877, 1882). Houghton (1903) studied skeletal and muscular anatomy of *Eurycea longicauda*, but because he reported four epibranchials rather than the expected three, he may have worked with *Desmognathus* or a mixed species sample. Eigenmann (1909) and Besharse and Brandon (1974a,b, 1976) studied the eyes of *Typhlotriton*, Hilton (1913) the blood and vitelline vessels of "*Desmognathus*", P. Smith (1914) the central nervous system of *Desmognathus fuscus*, Reed (1920) the middle ear of many species, and Higgins (1921) the olfactory capsule of *Eurycea bislineata*. The hyobranchial apparatus of *Eurycea bislineata* was studied by L. Smith (1920), Alberch and Gale (1986), and Alberch et al. (1985).

Emmel (1924) investigated development of the blood cells of *Batrachoseps*, *Aneides*, and *Ensatina*. Wake and Lawson (1973) examined vertebral development of *Eurycea bislineata*, Shubin and Alberch (1986) and Shubin and Wake (1991) studied limb development (the latter in *Bolitoglossa subpalmata*), and Nishikawa et al. (1991) reported on the development of motor neurons of the anterior spinal cord in species of *Desmognathus*, *Eurycea*, *Plethodon*, and *Hydromantes*. Dentitional development and tooth replacement was studied by Lawson et al. (1971), Greven and Clemen (1976), and Mutz and Clemen (1992) in *Eurycea*, *Gyrinophilus*, *Hydromantes*, and *Plethodon*. Salthe (1963) described the egg capsules of a number of plethodontid species. Landacre (1921) described migration of the neural crest in salamanders said to be *Plethodon glutinosus*, but the embryos were obtained from egg clusters collected in a pond and thus are probably *Ambystoma*.

Stage-specific Accounts

Few studies of complete ontogenies have been published, but several workers have reported more limited information on eggs, or have described partial developmental sequences or focused on specific developmental stages. Among these studies are the following, arranged taxonomically: Desmognathinae—Bishop (1941), Goin (1951), Organ (1961), Pope (1924), Valentine (1963), Harrison (1967); Plethodontinae, Hemidactyliini—Bishop (1919, 1941), Goin (1947, 1951); Plethodontinae, Plethodontini—Bishop (1941), Cochran (1911), Emmel (1924), Miller (1944), Piersol (1910); Plethodontinae, Bolitoglossini—Bradford (1984), Burke (1911), Durand (1967, 1970), Emmel (1924), Gorman (1956), Hanken (1979), McDiarmid and Worthington (1970), Sessions (1977), Snyder (1923), Stebbins (1949), Vial (1968).

Heterochrony and Paedomorphosis

Cope (1889) and Dunn (1926) discussed heterochrony to a limited extent, and Emerson (1905) recognized that *Typhlomolge* was a perennibranchiate plethodontid. Several hemidactyliines, including some species of *Eurycea*, a species of *Gyrino-*

philus, and the genera *Typhlomolge* and *Haideotriton* (reviewed in Duellman and Trueb, 1985), are perennibranchiate, but this phenomenon has not been recorded in the Desmognathinae. Wake (1966) presented a detailed account of the significance of heterochrony for plethodontids. The most general treatment of the phenomenon is that of Gould (1977), whose models were made more formal and applied to plethodontids by Alberch et al. (1979). Alberch (1980) dealt mainly with bolitoglossines, and Alberch and Alberch (1981) specifically treated heterochrony in *Bolitoglossa*. Hanken (1982, 1983, 1984) presented detailed analyses of heterochrony in cranial and limb morphology of *Thorius*, Wake et al. (1983) examined the possibility that *Aneides lugubris* is peramorphic, and Wake (1989) focused on *Batrachoseps*.

Genome and Cell Size in Relation to Development

Variation in genome size within the family Plethodontidae greatly exceeds that for any other taxon of comparable rank, with values ranging from approximately 12 to nearly 80 pg DNA per haploid nucleus (Sessions and Kezer, 1991; Sessions and Larson, 1987). Huge genomes mean huge cells, and in organisms of small adult size there can be profound implications (Sessions and Larson, 1987), especially for the development of the nervous system and sense organs (Roth et al., 1990, 1993). Large cells appear to have less ability to migrate, and their proliferation rate is decreased. Large genomes slow down biological processes, and it may be impossible for large-genomed species to have a "normal" salamander life history, with an aquatic larval period and a terrestrial adult, because they may not be able to accomplish metamorphosis, which involves a speeding-up of metabolic processes. Large genomes may contribute significantly to the extensive homoplasy encountered in the family Plethodontidae (Wake, 1991). Given the many seemingly unfavorable consequences of evolutionary increases in genome size, it is unclear what mechanisms lead to the great increases in genome sizes,

and it is even more of a mystery why these large genomes, with their evident negative effects, remain large.

FUTURE DIRECTIONS

There are many compelling intellectual reasons for studying development and comparative ontogenies in plethodontid salamanders, and we believe that with the recent advances that have been made regarding inducement of oviposition (see above), the time is ripe for such studies. We suggest that research programs be planned so as to take advantage of the great diversity of life history modes and developmental patterns in plethodontids. Most features of special interest have evolved more than once in the family. The existence of such extensive homoplasy offers opportunities to test diverse developmental hypotheses. We will outline some promising topics.

Ontogeny and Phylogeny

Comparisons of ontogenetic trajectories are essential for phylogenetic studies. If we are to gain a full understanding of the role of heterochrony in the evolution of the family, we need not only extensive ontogenetic information, but also explicit phylogenetic hypotheses. Few full ontogenies are known (e.g., Alberch and Alberch, 1981; Wake et al., 1983), but there are many partial ones (e.g., Wilder, 1925). A focus on the development of normal tables (we still do not have a single one for plethodontids) is needed, for species with larval as well as direct development. At the same time, there is a need to provide as many full ontogenetic trajectories as possible. At least one of each of the major monophyletic assemblages should be included.

Direct development has evolved at least twice in the family, and possibly as many as five times, yet it has not evolved in any other family of salamanders. Opportunities exist to compare the direct development in different plethodontid taxa, in order to determine features held in common and thus possibly necessary for direct development to evolve. It is especially important to compare the phylogenetically

separate events, and to compare these with direct development in frogs and amniotes. Special attention should be given to such phenomena as condensation (the elimination of developmental events characteristic of ancestors), shifts in relative timing of developmental events, and the meaning of developmental time.

Homoplasy is common in plethodontids, and unusual opportunities exist for studying the developmental basis of homoplasy. The existence of particular developmental pathways and triggers associated with them may make certain developmental events and morphological outcomes far more likely than others, even in distantly related taxa.

Ontogenetic repatterning remains a promising topic, but more research is needed to determine if it is a definable general phenomenon, or if it is simply an extreme outcome of heterochrony. Wake and Roth (1989) treated it as a threshold phenomenon, in which a cascade of outcomes followed attainment of a certain level of reorganization during development. Research in progress focuses mainly on developmental neuroanatomy, but should be extended to other areas as well.

Development of Specific Organ Systems

Limb development of salamanders was long thought to differ greatly from that of frogs and amniotes (reviewed by Shubin and Alberch, 1986). Recent work is leading to a reinterpretation of these results. Shubin and Wake (1991) found that the direct developing species *Bolitoglossa subpalmata* has limb development that resembles that of frogs and amniotes more than that of non-plethodontid salamanders in the pattern of prechondrogenic bifurcation and segmentation. What long has been considered to be the general pattern of limb development in urodeles might be a larval adaptation associated with early use of the limbs. Frogs do not use their limbs until late in development, nor do amniotes, so direct developing salamanders may have reverted to the general vertebrate ground plan. More direct developing species, and plethodontids with larval stages, should be

investigated to determine if the pattern in *Bolitoglossa* is a general plethodontid pattern or if it is specific to direct developing taxa (studies of species of *Desmognathus* are in progress by Marks, Shubin, and Wake).

The development of nerve-tracing methods led to a new emphasis on comparative neuroanatomy of plethodontids (Roth and Wake, 1985; Roth et al., 1988; Wake et al., 1988). This has included developmental studies (Nishikawa et al., 1991). The combination of comparative and developmental neuroanatomy and phylogenetics has led to the proposal that salamanders in general, and bolitoglossine plethodontids in particular, have brains that are greatly simplified as a result of paedomorphosis, in comparison to outgroups (Roth et al., 1993). Comparative developmental studies are needed of more taxa, especially of those having direct development and very different genome sizes.

There are as yet no studies of urogenital development in plethodontids, and little attention has been given to internal organs. Studies of hyobranchial development and changes that take place in it and other systems during metamorphosis are in progress (Rose, 1991); these should be extended to additional taxa, especially of direct developing species.

Genetics of Development

There is a revolution in progress concerning the genetics of development. This rapidly developing field holds great opportunity for studying particular evolutionary radiations, such as that of the plethodontids. The role of regulatory phenomena in development, which has been so fruitfully explored using transgenic experiments, should prove to be of great interest for evolutionary and phylogenetic studies. Large numbers of embryos are required for such research, and attention must be given to captive breeding programs for plethodontids, which to date have been successful only for *Desmognathus ochrophaeus* (L. Houck, personal communication).

Some general questions in development might be profitably pursued using pleth-

odontid materials. Here we briefly mention some areas of special promise for combining genetic and developmental approaches.

The brain stem has attracted a great deal of attention because of the involvement of homeobox genes in its development (reviewed by Thorogood and Hanken, 1992). Because of the extensive knowledge that now exists concerning the anatomy of the brain stem region of plethodontids, the group is ideal for the application of these new methodologies.

Segmentation, its controls, and its evolution are the topics of intense study in modern developmental biology. Many species of plethodontids have variable numbers of trunk vertebrae (e.g., *Plethodon cinereus*, *Batrachoseps attenuatus*), but others have a fixed or nearly fixed number (most desmognathines and members of the supergenus *Bolitoglossa*, except for *Oedipina*). Some of the methods used for study of the brain stem could be applied to analysis of segmentation, for it may be that a general phenomenon is involved, and by studying one system we may be able to apply the information obtained to others (Thorogood and Hanken, 1992).

Molecular genetic methods may disclose what general developmental rules apply to limbs, which are more diverse in their morphology in plethodontids than in other families of salamanders. The availability of such a wide variety of species, with different patterns of development, different limb bud sizes, different adult sizes, different numbers of digits, and different functional requirements, makes the plethodontids especially attractive as research materials. Recent studies with chickens have suggested that homeobox expression might be involved in bifurcation processes during limb development (Morgan et al., 1992; Yokouchi et al., 1991), and the situation described earlier with respect to limb development in *Bolitoglossa* offers opportunities for studying such regulatory phenomena in a phylogenetic framework.

CONCLUSIONS

The combination of development and evolution has long held an allure for bi-

ologists, but to date the comparisons have been too broad to have much relevance to our understanding of patterns of phylogenetic transformations and evolutionary processes of morphogenetic change. Plethodontids have much to offer in terms of being a diverse and well known lineage. Studies of the significance of larval life and of direct development, of phylogenetic inertia and functional adaptation, and of the effects of differences in genome, ovum, cell, organ, and body size will contribute not only to our understanding of plethodontid evolution, but also will produce data of phylogenetic significance and provide insight into general problems of the developmental biology of vertebrates.

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