

## PHYLOGENETIC IMPLICATIONS OF ONTOGENETIC DATA

by

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## ABSTRACT

The controversy concerning the value of ontogenetic data for phylogenetic reconstruction is briefly reviewed. Examples to illustrate the problem are presented from data concerning plethodontid salamanders, and include an analysis of ontogenetic trajectories in the genus *Batrachoseps* and modifications of early ontogeny in bolitoglossine salamanders. Some workers advocate using ontogenetic data to establish the polarity of characters that vary among taxa. This view is rejected. The entire ontogeny of a character is the focus of interest, for ontogenies evolve as wholes and any part is subject to change. Only outgroup analysis is of value in determining character polarity, and ontogenetic data alone can be misleading. Nevertheless, examples presented show that ontogenetic information can serve as the basis for the establishment of hypotheses concerning the history of groups and can provide insight into evolutionary dynamics.

## RÉSUMÉ

La controverse concernant la valeur des données ontogénétiques pour l'établissement de reconstructions phylogénétiques est brièvement résumée. Des exemples ont été choisis pour illustrer ce problème au sein du groupe des salamandres plethodontidés. Ces exemples comprennent notamment des analyses de trajectoires ontogénétiques au sein du genre *Batrachoseps* ainsi que des modifications affectant l'ontogenèse précoce chez les salamandres bolitoglossines. Quelques auteurs ont prôné l'usage des données ontogénétiques pour la mise en évidence de la polarité des caractères entre plusieurs taxa. Ce point de vue est rejeté. L'ontogenèse complète d'un caractère est le centre d'intérêt, les ontogenèses évoluent en effet comme des ensembles complexes et chacune des parties est sujette au changement. Seule l'analyse "outgroup" est valable pour la détermination de la polarité alors que la prise en compte des seules données ontogénétiques peut induire des interprétations erronées.

Toutefois les exemples présentés montrent que l'information ontogénétique peut servir de base lors de l'établissement d'hypothèses relatives à l'histoire des groupes et peut également fournir des arguments précieux pour la compréhension de la dynamique évolutive.

KEY-WORDS : ONTOGENY, PHYLOGENY, ONTOGENETIC TRAJECTORY, SALAMANDERS, PLETHODONTIDAE.

MOTS-CLÉS : ONTOGÈNESE, PHYLOGÈNESE, TRAJECTOIRE ONTOGÉNÉTIQUE, SALAMANDRES, PLETHODONTIDAE.

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## INTRODUCTION

The relation of ontogeny to phylogeny is one of the oldest issues in evolutionary biology. Flurries of scientific interest in the topic have been followed by long periods of dormancy. We now live during a period of ferment. Some of the central issues in modern phylogenetic analysis involve debates over the value and meaning of ontogenetic data, especially their role in *a priori* determination of the direction of character state transformation.

The history of the notion of a parallelism between ontogeny and a natural hierarchical ordering of living

things, or phylogeny, has been reviewed recently (Gould 1977 ; Nelson 1978 ; Rieppel 1985), so I will focus my attention on the interpretation of ontogenetic data for phylogenetic analysis. This, too, is a topic that has received much recent attention. A sampling of the literature devoted to this topic includes : Alberch (1985), Alberch & Gale (1985), Brooks & Wiley (1985, 1986), David & Fouray (1984), de Queiroz (1985), Kluge (1985), Kluge & Strauss (1985), Mc Namara (1982), Nelson (1978, 1985), Nelson & Platnick (1981), Patterson (1982), O'Grady (1985) and Rieppel (1979).

### I - ONTOGENY AND PHYLOGENETIC ANALYSIS

A central question - what evolves and is classified ? - is addressed in different ways by Rieppel (1985) and de Queiroz (1985). The answer, both argue, is the whole ontogeny. One cannot know *a priori* that a given part of the organism is more conservative, and therefore possibly more informative than another, concerning the evolutionary history of the group. Accordingly, one should not expect to gain direct insight concerning the ancestry of an organism, or its parts, merely from a close study of its ontogeny.

The methodologies of cladistics are in wide use for phylogenetic analysis, whether or not workers follow cladistic principles in their classifications. One of the most fundamental of cladistic principles (Hennig 1966) is that only derived states of characters contain information of any value in assessing genealogical relationships, and accordingly the foremost tasks of a student of phylogeny are to recognize characters that show intergroup variation and to determine the pattern character state transformation. Methods for estimating the direction of character state transformations stem ultimately from the nonevolutionary three-fold parallelism that was perceived by nineteenth century scientists - comparative anatomy (the out-group method), paleontology (the geological time method), and embryology (the ontogenetic method).

We must select characters before proceeding. If we wish to determine the genealogical relationships of organisms using cladistic methods we start by identifying discernable features - characters - and their variations, or states, in adults. Once this is accomplished we turn to the issue of polarization of the character states, so as to hypothesize a transformation series. If we take the organismal view, mentioned above, that

the whole ontogeny has evolved, we immediately face a problem.

De Queiroz (1985) has contrasted what he has called instantaneous morphologies (the morphology of the stage one has chosen to study) and ontogenetic transformations (the entire course of development of the morphology in question). Those workers who advocate a focus on instantaneous morphologies, specifically, the pattern cladists such as Nelson & Platnick (1981) and Patterson (1982), find ontogenetic criteria (summarized by the famed aphorism of Haeckel : ontogeny recapitulates phylogeny) satisfactory for polarizing characters. They take an approach to systematics that attempts to be independent of evolutionary thinking, and ask whether evolutionary theory is necessary for systematics, and, if necessary, why so (Nelson 1985). But if we acknowledge that the diversity of organisms in the world is the result of evolutionary processes and that we are interested in evolutionary relationships among organisms rather than in relationships among instantaneous morphologies, phylogeny and evolution are fundamental elements of our thinking. Then it becomes appropriate to adopt a view in which, as de Queiroz (1985) has succinctly stated, "ontogenetic transformations are themselves the characters". Under this view, which I endorse, there are no ontogenetic criteria for determining character polarities, for the ontogenies themselves are the foci of interest.

I know of only one study that has explicitly examined the contrasting results one obtains from use of out-group and ontogenetic criteria. In a published abstract Mabee (1987) has shown that determination of character state transformation based on ontogenetic criteria are no better than chance when judged by a well-corroborated cladogram based on character state transformation determined by out-group criteria.

This large topic has received so much discussion in the literature that it no longer is possible to present a concise review of the various arguments and points of view. It is safe to say that most workers admit that *ontogenetic data have some intrinsic value, if only as a component of a very general outgroup analysis*. But approaches vary. Some workers view organisms as passing through discrete ontogenetic stages, each of which can be compared with comparable stages in related organisms (O'Grady 1985). Then, by using out-group analysis the individual characters can be polarized, and it can be determined where alterations in ancestral ontogenetic sequences occurred. Those interested in the role of heterochrony in evolution use an alternative approach - ontogenetic trajectories (Alberch *et alii* 1979). Both approaches depend rather heavily on the existence and relatively conservative nature of developmental sequences, but there is an important difference in that one need not identify comparable stages when comparing ontogenetic trajectories, for the trajectories themselves are the characters. Recently Alberch (1985) has argued that there is no good argument to assume *a priori* that ontogenetic sequences are conserved during phylogeny. He acknowledges that development is ordered, but he doubts that information relevant to the cause of the ordering is captured in ontogenetic sequences. Alberch presented several cases to illustrate his contention that the methodology of heterochronic analysis is not compatible with dynamic perspectives on the nature of developmental processes. As we focus more on detailed studies of comparative ontogenies we doubtless will find many instances in which there are deep modifications of early ontogeny that have persistent and multiple influences on later ontogeny. Later in this paper I briefly outline an instance of what I call

ontogenetic repatterning. The issue here is not whether ontogenetic data are of value in phylogenetic analysis, but rather that we must go beyond the perception of ontogeny as a sequence of discrete developmental stages if we are to gain success in our attempts to make connections between ontogeny and phylogeny.

If one denies that ontogeny provides direct evidence for polarization of character state transformations, some might question why we link ontogeny and phylogeny at all. The point, of course, is that it is the whole ontogeny that evolves, and thus a true phylogeny will be based on evolutionary transformations of ontogeny.

I share with Alberch (1985) a belief that a mechanistic approach to development is needed in evolutionary biology, so that development can play a role roughly comparable to, but doubtless less general than, that enjoyed by genetics (see also Hall 1984). Topics of interest include :

1) what factors are responsible for the regulation of morphogenesis, and,...

2) what limits the array of potential morphological variables in any given system ? To the degree that ontogenies are conservative and that development is an ordered process, one must seek the mechanistic basis in phenomena that control morphogenesis. Eventually we must consider the evolution of the processes controlling development, and incorporate such knowledge into our conception of the organism, so that our "characters" become not only the ontogenetic transformation but also the control system governing the process.

We cannot yet do as I advocate. Therefore, how can we deal with ontogenetic data in phylogenetic studies ? Some examples from my laboratory illustrate both pitfalls and opportunities.

## II - ONTOGENY IN RELATION TO THE EVOLUTION OF THE SALAMANDER GENUS *BATRACHOSEPS*

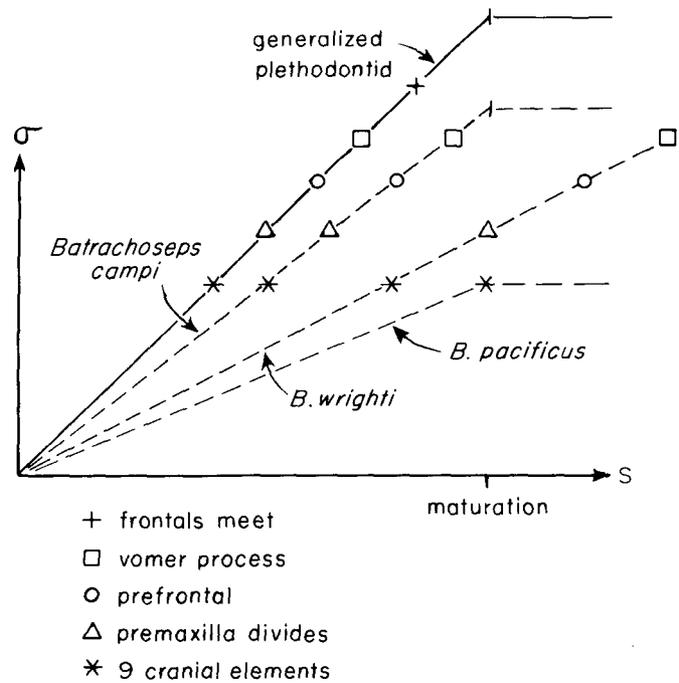
The plethodontid salamander genus *Batrachoseps* includes 8 species distributed in western North America. In the spirit of Gould (1977) and Alberch *et alii* (1979) I examined the possibility that heterochronic evolution might have played an important role in the phylogeny of the group. My data were generalized by plotting the first appearance during ontogeny of cranial elements (using the first sign of mineralization as the point of appearance) in four species, as if the patterns establish trajectories in size-shape space (fig. 1). An outgroup is essential (Fink 1982, made this explicit for the approach used by Alberch *et alii* 1979 ; earlier I also had made explicit use of outgroups in a heterochronic analysis, Wake 1966). In the figure, I have indicated an ontogenetic trajectory for an idealized common ancestor of the plethodontid tribe Bolitoglossini (to which *Batrachoseps* belongs).

In figure 1 the species *Batrachoseps pacificus*

represents several of the more familiar species : *B. aridus*, *B. attenuatus*, *B. nigriventris*, *B. simatus*, and *B. stebbinsi*. All are identical to *B. pacificus* in terms of data presented. The vertical axis represents generalized shape, simply the changing appearance of the skull resulting from the sequential appearance of mineralized elements. The horizontal axis represents size. Although the species plotted do not differ greatly in adult size, I have normalized them by indicating the size at which sexual maturation is attained. Note that the comparison is intended to begin at the point in ontogeny at which all species already have fairly well developed skulls, including most cranial elements. Thus the focus is on relatively late ontogenetic stages. *Batrachoseps*, and all other members of the tribes Bolitoglossini and Plethodontini (totalling about half the living species of urodeles), are fully terrestrial and have abandoned the aquatic larval stage. Eggs are laid on land and development is direct.

Figure 1 - A generalized representation of four ontogenetic trajectories for the cranium of plethodontid salamanders of the genus *Batrachoseps* and a postulated ancestor. Vertical axis is shape, horizontal axis is size. Size is normalized relative to size at sexual maturity. See text for details.

Représentation simplifiée des trajectoires ontogénétiques du crâne de trois salamandres plethodontides du genre *Batrachoseps* et de leur ancêtre supposé. L'axe vertical représente la forme, l'axe horizontal la taille. Le paramètre de taille est normalisé par rapport à la taille atteinte à la maturité sexuelle. (voir le texte pour plus de détails).



In order to interpret the ontogenetic data in figure 1 it is necessary to briefly present some information concerning four ontogenetic events in outgroups of *Batrachoseps*. These events are indicated by the top four shape symbols in the figure, and include : 1) in all plethodontids there is a single premaxilla in larvae (or encapsulated embryos, when larvae are absent). A single bone occurs in adults of some species, but in others the bone divides at hatching or metamorphosis. Outgroup analysis indicates that the divided bone is plesiomorphic for adults. An ontogenetic analysis which simply made the assumption that the earliest appearance of the bone is primitive would indicate that the divided bone is a reversal, and a synapomorphy of those species showing it. But outgroup analysis also indicates that an *ontogeny* in which a single bone is present first, and a division occurs later, is plesiomorphic. Fusion of the two premaxillae in larvae of the ancestral stock was a caenogenetic event which became a conservative component of the ontogeny (Wake 1966), and is now a synapomorphy for the family. Division of the bone is approximately coincident with metamorphosis in those species with larvae, and with hatching in those species with direct development. Paedomorphic species would retain a single bone (e. g., *Typhlomolge*), but if the particular process underlying the paedomorphosis was neoteny (a reduction in the rate of change of shape in relation to age) division of the bone may be delayed until relatively late in life. Failure of the bone to divide can also occur for other reasons unrelated to

paedomorphosis ; for example, the undivided (probably secondarily fused) premaxilla of the strongly-jawed species of *Aneides* and *Desmognathus* probably arose as a component of adaptation for increased jaw strength in these peramorphic groups (Wake 1966 ; Wake *et alii* 1983 ; Wake & Larson 1987).

2) A prefrontal bone appears late in ontogeny. This bone is absent in a number of species in the family Plethodontidae (Wake 1966). Alberch (1983) attributes the rare appearance of tiny, unarticulated spots of bone in species which normally lack prefrontals to atavistic reversal.

3) The larval vomer is reorganized at metamorphosis and a small, tooth-bearing process grows laterally behind the internal naris. The process is absent in a number of small tropical species, thought, on the basis of other data, to be paedomorphic (Wake 1966), but it is also absent in the western species group of *Aneides*, a group thought to be relatively peramorphic (Wake 1963 ; Wake *et alii* 1983).

4) Frontal and parietal bones are widely separated from their bilateral counterparts in larvae and embryos, but in adults the bones typically come into contact on the dorsal midline. A gap, or fontanelle, is retained in a number of plethodontid species throughout life (Wake 1966 ; Hanken 1984), and a large fontanelle is characteristic of all members of *Batrachoseps* (Marlow *et alii* 1979).

At maturity *B. pacificus* has a single premaxillary, lacks both prefrontals and vomerine processes, and has a large dorsal fontanelle. Division of the premaxillary is coincident with maturation in *B. wrighti*, but post-maturational development continues. Late in life tiny, unarticulated prefrontals appear and, finally, in the very largest and presumably oldest specimens, vomerine processes develop. The species retains a relatively large fontanelle. Division of the premaxillary bones occurs very early in *B. campi*, and by maturation the species has small but articulated prefrontals and a vomerine process. While a fontanelle is present, it is somewhat smaller than in the other species (data in Wake 1966 ; Marlow *et alii* 1979).

Phylogenetic analysis of these data is neither simple nor direct, and ontogenetic analysis alone without out-groups would be very misleading (Wake & Larson 1987). Two general categories of hypotheses are suggested. In the first, paedomorphosis increases with cladogenesis. In the second, extreme paedomorphosis is seen as a synapomorphy of the species in the genus and is reversed to differing degrees in derived species. It is

Fig. 2 — Hypothesis I, for the phylogenetic history of *Batrachoseps*.

According to this hypothesis, the ancestral stock was paedomorphic, and most species (represented by P, for the representative of these species, *B. pacificus*) have retained ancestral conditions. There is a peramorphocline which features a reversal of paedomorphosis (a gain of elements indicated by +). A synapomorphy for *B. campi* (C) and *B. wrighti* (W) is reversal of paedomorphosis, and reappearance of several bones and processes (see text for details).

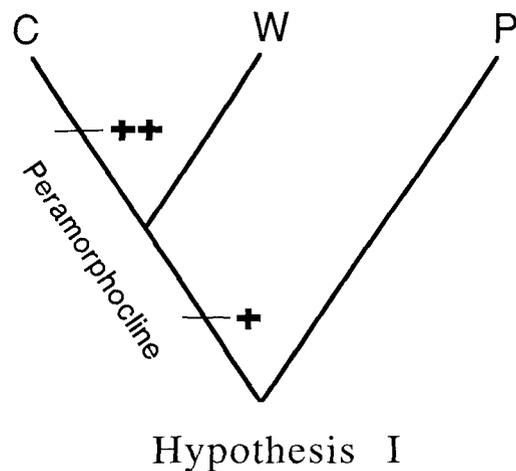
**Hypothèse 1, pour l'histoire phylogénétique de *Batrachoseps*.** Selon cette hypothèse le groupe ancestral est paedomorphique, et la plupart des espèces lui appartenant conservent des caractères ancestraux (elles sont représentées par P sur la figure car *B. pacificus* est représentatif de telles formes). On note un peramorphocline qui correspond à une réversion de la paedomorphose et qui s'exprime par des gains d'éléments symbolisés par (+). Une synapomorphie partagée par *B. campi* (C) et *B. wrighti* (W) marque une étape de réversion de la paedomorphose et correspond à la réapparition de plusieurs os et processus (pour plus de détails, voir le texte).

If extreme paedomorphosis characterized the ancestral stock of the genus, *B. pacificus* would represent the earliest branch (hypothesis I, fig. 2). The *pacificus* clade is speciose, with six (and several more undescribed) species, and it has a broad distribution. *B. wrighti* and *B. campi* would represent progressively more derived species that have undergone phylogenetic reversal of their ontogenies. This phylogenetic reversal produces a peramorphocline, with *B. campi* being the most peramorphic taxon (for guides to the terminology of heterochrony see Alberch *et alii* 1979 ; Mc Namara 1986a).

If paedomorphosis has been progressive, *B. campi*

possible that the situation is more complex, of course, and different kinds of paedomorphosis might be involved. But based on out-groups analysis (see Lombard & Wake 1986 ; Wake 1986) paedomorphosis must be invoked at some level.

Figure 1 presents *prima facie* evidence that paedomorphosis has occurred in *Batrachoseps*. Paedomorphosis is the simplest explanation as to why all species of *Batrachoseps* have a large cranial fontanelle. In addition, all species have but four digits in each hind limb, a paedomorphic trait associated with small size in amphibians (Alberch & Gale 1985). For clarity of illustration I have constructed figure 1 so that it appears that the three species of *Batrachoseps* show progressive neoteny - reduction in the rate at which they proceed through ontogeny. It may be that all species of the genus are neotenic to some degree, but such an interpretation of increasing neoteny is probably too simplistic in explaining the relationships of the species to one another, as I will show below.

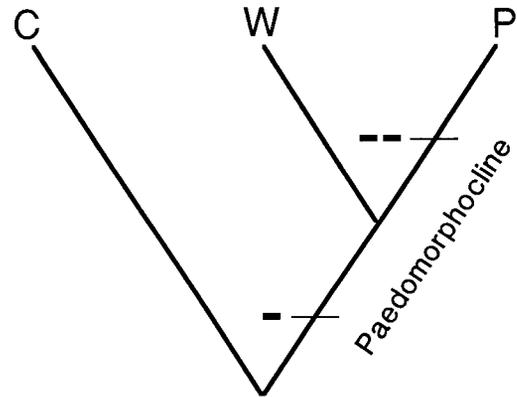


would represent the earliest branch (hypothesis II, fig. 3). Its ontogeny most closely resembles that of the ancestral ontogeny. *B. wrighti* and *B. pacificus* would represent progressively more derived and more paedomorphic species. Progressive phylogenetic paedomorphosis produces a paedomorphocline, with *B. pacificus* and relatives being the most paedomorphic taxa.

The entire ontogeny of *Batrachoseps* has evolved, and we cannot expect to find the means of rejecting either of the above hypotheses with ontogenetic data alone. Comparative studies of allozymes (Yanev 1980 ; Wake & Yanev in prep.) strongly suggest that *B. campi* and *B. wrighti* are sister taxa. A phenogram (fig. 4),

Fig. 3 — **Hypothesis II, for the phylogenetic history of *Batrachoseps*.** According to this hypothesis, the ancestral stock was fully developed, and the history of the group has been progressive paedomorphosis (a paedomorphocline, with loss of elements indicated by -). A synapomorphy for *B. pacificus* and *B. wrighti* is retardation of some osteological features (see text for details).

**Hypothèse 2, pour l'histoire phylogénétique de *Batrachoseps*.** Selon cette hypothèse le groupe ancestral possédait un développement complet et l'histoire du groupe correspond à une paedomorphose progressive (un paedomorphocline jalonné par la perte de caractères symbolisée par (-)). La synapomorphie partagée par *B. pacificus* et *B. wrighti* correspond à un retard dans l'ossification de certains éléments (pour plus de détail, voir le texte).



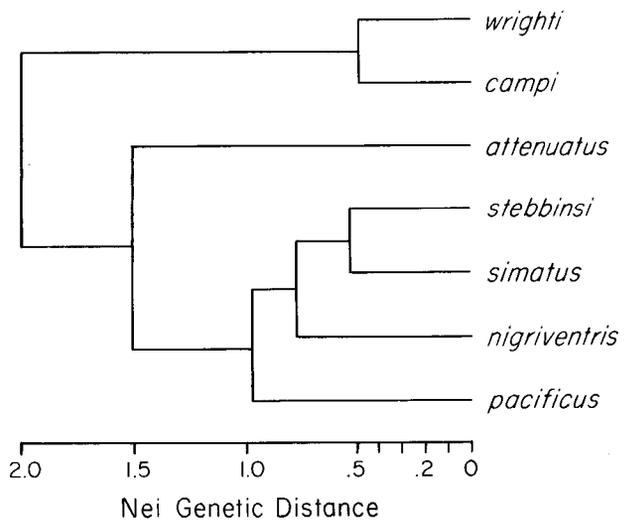
Hypothesis II

based on genetic distances, displays the hypothesized cladistic pattern. The genetic distances are large in this genus, but the genetic distance between *B. campi* and *B. wrighti* is relatively small. If genetic distance builds largely as a function of time since separation, a phenogram will contain useful phylogenetic information at the scale necessary for the present example. Because the genetic distances to out-groups are so great, it has

proven impossible to analyze the allozyme data cladistically. The probability that *B. campi* and *B. wrighti* are sister taxa is relatively great, since these two share 7 unique alleles as well as having a genetic distance between them that is on the same order as that found among different geographic segments of *B. campi* (Yanev 1980 ; and unpublished data).

Fig. 4 - **A simplified UPGMA phenogram based on Nei's genetic distance for the species of *Batrachoseps*, based on comparison of allozymes.** Modified from Yanev (1980). There are seven alleles uniquely shared by *B. wrighti* and *B. campi* which we accept as synapomorphies.

**Phénogramme UPGMA simplifié des différentes espèces de *Batrachoseps*.** Le phénogramme est construit d'après la distance génétique de Nei, basée sur la comparaison des alloenzymes, (modifié d'après Yanev, 1980). Il existe sept allèles uniquement partagés par *B. wrighti* et *B. campi*, nous les considérons comme des synapomorphies.



The data on which figure 4 are based contradict hypothesis II, and might be taken as support for hypothesis I, but there are alternatives. For example (hypothesis III, fig. 5), *B. wrighti* and *B. campi* might form a clade, but paedomorphosis might be preceding (rather than reversing, as in hypothesis I) in *B. wrighti*. The postmaturation appearance of new bones in this

species is novel, and may well represent a unique apomorphy. Under this hypothesis, *B. campi* has retained the most ancestral ontogeny, *B. pacificus* is prognetic (because its ontogeny is truncated), and *B. wrighti* is neotenic (because it continues to pass through the stages of ontogeny of the ancestor, but more slowly) (terminology of Gould 1977, and Alberch *et alii* 1979).

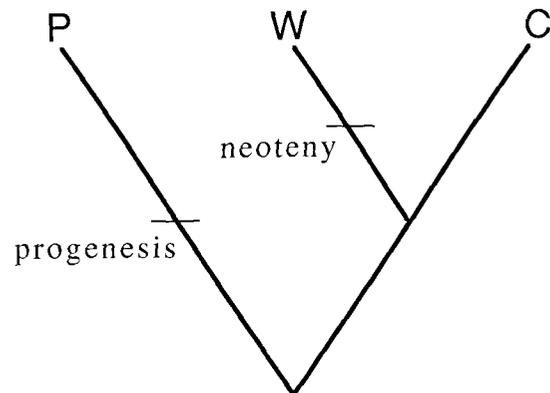
Tests of the above hypotheses would involve careful comparisons of the timing of ontogenetic events in the above species and outgroups, as well as experimental interventions such as speeding up or slowing down development through the use of hormones or other agents. Extrapolating in reverse from the results of Alberch & Gale (1983), perhaps augmentation of the size of hind limb blastema by adding cells from the bilateral organ early in development might even produce a 5-toed *Batrachoseps* (it may be significant that the

largest individual *B. wrighti* ever collected had 5 toes on one foot, Brame 1964 ; see also Wake & Larson 1987).

Ontogenetic data such as these challenge the phylogeneticist, and illustrate the difficulties of using ontogenetic data directly. It is likely that most cases involving paedomorphosis will prove to be complex, and that there will be alternative hypotheses concerning the ways in which the ontogenetic data can be interpreted.

Fig. 5 - **Hypothesis III, for the phylogenetic history of *Batrachoseps*.** According to this hypothesis, *B. campi* is most similar in cranial osteology to the ancestral condition, but both *B. pacificus* (progenesis) and *B. wrighti* (neoteny) have diverged by paedomorphosis. Only biochemical characters provide synapomorphies for the *B. wrighti* - *B. campi* clade (see text for details).

**Hypothèse 3, pour l'histoire phylogénétique de *Batrachoseps*.** Selon cette hypothèse, bien que *P. Campi* soit proche par son ostéologie crânienne des conditions primitives, *B. pacificus* (protogénétique) et *B. wrighti* (néoténique) sont supposés avoir divergé indépendamment par paedomorphose. Seules les données biochimiques indiquent qu'il existe des synapomorphies entre *B. wrighti* et *B. campi* (pour plus de détail voir le texte).



Hypothesis III

### III - ONTOGENETIC REPATTERNING IN BOLITOGLOSSINE SALAMANDERS

Gerhard Roth and I (1985a) briefly discussed a phenomenon we call ontogenetic repatterning, which contrasts with recapitulatory development. Ontogenetic repatterning involves modifications in early ontogeny that amplify during development to produce large differences between ancestral and derived morphologies in different lineages. This phenomenon counters the generally conservative nature of developmental systems, and has important phylogenetic implications, including the dissolution of what have been termed developmental constraints. Ontogenetic repatterning is distinct from heterochrony. Further, it cannot be treated simply according to the classification of ontogenetic changes presented by Brooks & Wiley (1985), in which it might appear as non-terminal addition or substitution. The reason is that ontogenetic repatterning destabilizes the apparently conservative ontogenetic trajectory, and impacts much of subsequent ontogeny. I will only briefly outline our findings here (additional research is in progress).

Members of the tribe Bolitoglossini demonstrate extreme morphological and behavioral specialization

for prey capture by tongue projection, including holding the body motionless during feeding and projecting the tongue at very high speed, at wide angles, and for great distances. Bolitoglossines differ from other tongue-projecting plethodontids in many details, but most importantly in lacking an aquatic larval stage and in having direct terrestrial development. In such non-bolitoglossine plethodontids as the hemidactylines and desmognathines, larvae hatch quickly and pass through a graded and conservative ontogeny, presumably constrained by the necessity to start and continue functioning in the external world at very small size. Why salamanders having a larval stage hatch so quickly is unknown, but may relate to the relative vulnerability of the developing egg to predation or other selective pressures in the semiaquatic habitats in which they are laid. In contrast, the embryonic period of bolitoglossines may be very long - in excess of 10 months in some tropical species. These eggs typically develop in well-hidden terrestrial sites. In part these eggs take so long to develop because of the enormous genome sizes of bolitoglossines, and the concomitant very low

rates of cell division (Sessions & Larson 1987). Because of this slow development there is adequate opportunity for ontogenetic repatterning, which has had profound consequences. The changes exceed the mere intercalation of a feature (or a non-terminal substitution) into the ontogeny, because of the cascading effects on a number of systems. Such phenomena seem to characterize many groups which have abandoned larval stages in favor of direct development of enlarged yolky eggs, an evolutionary process called embryonization that has many organismal-wide consequences (Matsuda 1986).

Among the elements of ontogenetic repatterning in these species are the following : 1) a great increase in eye frontality, which is difficult to accomplish in larvae in which dorso-lateral vision is important for predator detection ; 2) development of very strong ipsilateral in addition to the normal contralateral retinotectal projections, which, together with pronounced eye frontality, establish the necessary connections for high quality stereoscopic vision (Rettig & Roth 1985) ; 3) a

reorganization of the brainstem and cervical spinal cord, so that the class of large, spindle-shaped cells associated with quick movements in larvae is eliminated (Roth & Wake 1985b ; Wake *et alii* 1988) (this seems to make possible the motionlessness of the salamanders during feeding) ; 4) a reorganization of the hyobranchial apparatus so that the tongue projectile becomes relatively lighter and more versatile (Lombard & Wake 1977 ; Wake 1982).

These features, which are initiated in early ontogeny, profoundly change subsequent ontogeny and have had major phylogenetic impact. Again, the obvious point is that we must be concerned always with the entire ontogeny of an organism. In addition we can see that many different parts of the organism can be affected by a small suite of coordinated changes. Reorganization of the ontogeny goes well beyond heterochrony. But as with the example of heterochrony, how we interpret these changes, and what we choose to recognize as a character, have important implications for phylogenetic reconstruction.

## CONCLUSIONS

I have illustrated some of the problems and opportunities in the use of ontogenetic data for phylogenetic analyses. My principle message is that such data do not interpret themselves, as some would have us believe. Conservatism of ontogenetic trajectories among relatives may be more apparent than real, and evolution can affect literally every point along the trajectory. Ontogenetic trajectories themselves can be used as characters, but this raises the questions of what data we should collect and how we should organize them for analysis. One example dealt with heterochrony and the possibility that the cranium in the genus of salamanders under investigation might have to be viewed as an entity for analysis. By dealing with ontogenetic trajectories of characters, whether they be parts of organs or organ systems, and at the same time keeping alert to the possibility of organismal-wide phenomena (as Alberch & Alberch 1981, have shown), one can assemble the basic data. Then one must use outgroup analysis, and perhaps paleontological data in special instances (but this really is a kind of outgroup analysis as well) to determine character polarity. Other data sets, especially those generated by molecular methods, which appear to be remarkably independent of morphological data, may help reject some of these hypotheses (Wake 1981). Then, again, we can examine our ontogenetic data, and perhaps generate testable hypotheses to explore processes and explanations for the evo-

lution that has occurred. Another example outlined the phenomenon of ontogenetic repatterning, which can cause such extensive reorganization that ontogenetic trajectories can be profoundly changed. The trajectories nonetheless will appear to be conservative, largely because of the self-organizing nature of developmental processes, and the limited numbers of options available to developing systems (see Wessells 1982). We must be alert to the possibilities that many changes might stem from a common cause.

Ontogenetic approaches to phylogenetic analyses will continue to contribute much, but development is a complex phenomenon and we must be wary of attempts to oversimplify interpretation of ontogenetic data. As we continue to pursue ontogenetic studies we probably will gain more insight into the dynamics of evolutionary processes underlying genealogical transformations than of the simple interpretation of ontogenetic information for phylogenetic purposes.

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BIBLIOGRAPHY

- ALBERCH P. (1983) - Morphological variation in the neotropical salamanders genus *Bolitoglossa*. *Evolution*, Lawrence, **37** : 906-916.
- ALBERCH P. (1985) - Problems with the interpretation of developmental sequences. *Syst. Zool.*, Mobile, **34** : 46-58.
- ALBERCH P. & ALBERCH J. (1981) - Heterochronic mechanisms of morphological diversification and evolutionary change in the neotropical salamander *Bolitoglossa occidentalis* (Amphibia : Plethodontidae). *J. Morph.* New York, **167** : 249-264.
- ALBERCH P. & GALE E.A. (1983) - Size dependance during the development of the amphibian foot. Colchicine-induced digital loss and reduction. *J. Embryol. exp. Morph.*, London, **76** : 177-197.
- ALBERCH P., GOULD S.J. OSTER G.F. & WAKE D.B. (1979) - Size and shape in ontogeny and phylogeny. *Paleobiology*, Chicago, **5** : 296-317.
- BRAME A.H. Jr. (1964) - Distribution of the Oregon slender salamander, *Batrachoseps wrighti* (Bishop). *Bull. So. Calif. Acad. Sci.*, Los Angeles, **63** : 165-170.
- BROOKS D.R. & WILEY E.O. (1985) - Theories and methods in different approaches to phylogenetic systematics. *Cladistics*, Westport, **1** : 1-12.
- BROOKS D.R. & WILEY E.O. (1986) - Evolution as entropy. *Univ. of Chicago Press*, 335 p.
- DAVID B. & FOURAY M. (1984) - Variabilité et disjonction évolutive des caractères dans les populations des *Micraster* (Echinoidea, Spatangoida) du Crétacé Supérieur de Picardie. *Geobios*, Lyon, **17** : 447-476.
- DE QUEIROZ K. (1985) - The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. *Syst. Zool.*, Mobile, **34** : 280-299.
- FINK W.L. (1982) - The conceptual relationship between ontogeny and phylogeny. *Paleobiology*, Chicago, **8** : 328-334.
- GOULD S.J. (1977) - Ontogeny and phylogeny. Cambridge, Mass., *Belknap Press*, Harvard Univ, 501 p.
- HALL B.K. (1984) - Developmental processes underlying heterochrony as an evolutionary process. *Canad. J. Zool.*, Toronto, **62** : 1-7.
- HANKEN J. (1984) - Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia ; Plethodontidae). I. Osteological variation. *Biological J. Linnean Soc.*, London, **23** : 55-75.
- HENNIG W. (1966) - Phylogenetic systematics. *Univ. Illinois Press*, 263 p.
- KLUGE A.G. (1985) - Ontogeny and phylogenetic systematics. *Cladistics*, Westport, **1** : 13-28.
- KLUGE A.G. & STRAUSS R.E. (1985) - Ontogeny and systematics. *Ann. Rev. Ecol. Syst.*, Palo Alto, **16** : 247-268.
- LOMBARD R.E. & WAKE D.B. (1977) - Tongue evolution in the lungless salamanders, family Plethodontidae. II. Function and evolutionary diversity. *J. Morph.*, New York, **148** : 39-80.
- LOMBARD R.E. & WAKE D.B. (1986) - Tongue evolution in the lungless salamanders, family Plethodontidae. IV. Phylogeny of plethodontid salamanders and the evolution of feeding dynamics. *Syst. Zool.*, Mobile, **35** : 532-551.
- MABEE P.M. (1987) - Ontogeny as a predictor of phylogenetic polarity : an empirical assessment. *Amer. Zool.*, Thousand Oaks, **27** : 62A.
- MARLOW R.W., BRODE J.M. & WAKE (1979) - A new salamander, genus *Batrachoseps*, from the Inyo Mountains of California, with a discussion of relationships in the genus. *Contrib. Sci. Natur. Hist. Mus., Los Angeles Co.*, Los Angeles, n° **308** : 1-17.
- MATSUDA R. (1986) - Animal evolution in changing environments with special reference to abnormal metamorphosis. *John Wiley & Sons*, New York, 355 p.
- MC NAMARA K.J. (1986a) - The role of heterochrony in the evolution of Cambrian trilobites. *Biol. Rev. (Cambridge)*, **61** : 121-156.
- MC NAMARA K.J. (1986b) - A guide to nomenclature of heterochrony. *J. Paleo*, Tulsa, **60** : 4-13.
- NELSON G. (1978) - Ontogeny, phylogeny, paleontology, and the biogenetic law. *Syst. Zool.*, Mobile, **27** : 324-345.
- NELSON G. (1985) - Outgroups and ontogeny. *Cladistics*, Westport, **1** : 29-45.
- NELSON G. & PLATNICK N.J. (1981) - Systematics and biogeography : cladistics and vicariance. *Columbia Univ. Press*, New York, 567 p.
- O'GRADY R.T. (1985) - Ontogenetic sequences and the phylogenetics of parasite flatworm life cycles. *Cladistics*, Westport, **1** : 159-170.
- PATTERSON C. (1982) - Morphological characters and homology. In K.A. Joysey & Friday A.E. (eds) ; Problems of phylogenetic reconstruction, p. : 21-74. *Academic Press*, New York.
- RETTIG G. & ROTH G. (1985) - Retinofugal projections in salamanders of the family Plethodontidae. *Cell Tissue Res.*, Berlin, **243** : 385-396.
- RIEPPPEL O. (1979) - Ontogeny and the recognition of primitive character states. *Z. Zool. Syst. Evolutions f.*, Frankfurt am Main, **17** : 5-61.
- RIEPPPEL O. (1985) - Ontogeny and the hierarchy of types. *Cladistics*, Westport, **1** : 234-246.
- ROTH G. & WAKE D.B. (1985a) - Trends in the functional morphology and sensorimotor control of feeding behavior in salamanders : an example of the role of internal dynamics in evolution. *Acta Biotheoretica*, Leiden, **34** : 175-192.
- ROTH G. & WAKE D.B. (1985b) - The structure of the brainstem and cervical spinal cord in lungless salamanders (family Plethodontidae) and its relation to feeding. *J. Comp. Neurol.*, New York, **241** : 99-110.
- SESSIONS S.K. & LARSON A. (1987) - Developmental correlates of genome size in plethodontid salamanders and their implications for genome evolution. *Evolution*, Lawrence, **41** : 1239-1251.
- WAKE D.B. (1963) - Comparative osteology of the plethodontid salamander genus *Aneides*. *J. Morph.*, New York, **113** : 77-118.

- WAKE D.B. (1966) - Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. *Mem. So. Calif. Acad. Sci.*, Los Angeles, **4** : 1-111.
- WAKE D.B. (1981) - The application of allozyme evidence to problems in the evolution of morphology. In G.G.E. Scudder & Reveal, J.L. (eds), "Evolution today", p. 257-270. *Carnegie-Mellon Univ.* Pittsburgh.
- WAKE D.B. (1982) - Functional and developmental constraints and opportunities in the evolution of feeding systems in urodeles. In D. Mossakowski & Roth G. (eds). "Environmental adaptation and evolution", p. 51-66. G. Fischer, Stuttgart.
- WAKE D.B. & LARSON A. (1987) - Multidimensional analysis of an evolving lineage. *Science*, Washington, **238** : 42-48.
- WAKE D.B., NISHIKAWA K.C., DICKE U. & ROTH G. (1988) - Organization of the motor nuclei in the cervical spinal cord of salamanders. *J. Comp. Neurol.*, New York, **278** : 195-208.
- WAKE T.A., WAKE D.B. & WAKE M.H. (1983) - The ossification sequence of *Aneides lugubris*, with comments on heterochrony. *J. Herp.*, Lawrence, **17** : 10-22.
- WESSELLS N.K. (1982) - A catalogue of processes responsible for metazoan morphogenesis. In J.T. BONNER (ed.), "Evolution and development" ; 115-154. *Springer-Verlag*, Berlin, Heidelberg, New York.
- YANEV K.P. (1980) - Biogeography and distribution of three parapatric salamander species in coastal and borderland California. In D.M. POWER (ed.), "The California islands" : 531-550. *Santa Barbara Mus. Nat. Hist.*,.