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The conceptual relationship between ontogeny and phylogeny

William L. Fink

Abstract.—Studies of ontogenetic processes are fundamentally dependent on hypotheses of phylogeny. The model of Alberch et al. (1979) is reformulated in terms of phylogenetics and used to describe how heterochronic ontogenetic processes can be detected in nature. Heterochronic processes producing paedomorphosis can result in morphologies which resemble primitive (retained ancestral) traits; the conditions under which paedomorphic and primitive features can and cannot be distinguished are described. The utility of ontogeny for determination of evolutionary character transformations and character polarity and for detection of convergence and parallelism are considered. The ontogenetic criterion for assessing polarity is independent of hypotheses of phylogeny and may be as effective as outgroup comparison. Ontogenetic analysis may aid in the detection of convergence but not in the detection of parallelism.

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I. Introduction

One avenue towards the elucidation of evolutionary mechanisms that has recently received much attention is the study of ontogeny. This renewed interest in ontogenetic phenomena is a response to the failure of classical population genetics alone to account for evolutionary diversity. Reassessment and refinement of early evolutionary models emphasizing the importance of development, and a synthesis of these models with those of population genetics, promise to provide fundamental new insights into the study of the origins of morphological and phylogenetic diversity.

Most recent research concerning ontogeny (e.g., Løvtrup 1974; Gould 1977; Alberch et al. 1979) attempts to apply evolutionary explanations to observed patterns of morphology and morphological change. As one reads this literature, it becomes apparent that the study of ontogeny is considered a special tool in the study of evolution. One systematist (Nelson 1973) even suggests ontogeny to be an independent criterion for the evaluation of evolutionary transformations. Other authors have touched upon the problems that some forms of ontogenetic development, particularly neoteny, pose for systematic analysis (Eldredge and Cracraft 1980; Wiley 1980). My purpose here is to delimit more clearly both the assumptions underlying onto-

genetic research as it is applied to evolutionary biology and the implications of this research for systematic biology.

II. Detection of Heterochrony

A major focus of recent ontogenetic work is heterochrony. Briefly, changes in developmental rates or timing and their epigenetic consequences are suspected of being instrumental in the acquisition of evolutionary novelties, including those often major changes associated with large scale cladal diversity. The two general forms of heterochrony thought most likely to be associated with such diversity are paedomorphosis, traditionally defined as a process that produces a descendant with adult morphology similar to juvenile morphology of an ancestor (see Gould 1977) and peramorphosis, production of descendants whose form transcends that of an ancestor (Alberch et al. 1979). Although Gould (1977) and Alberch et al. (1979) discuss at length various heterochronic processes and methods by which the morphological results of such processes might be described, they do not provide explicit descriptions of the procedure for detecting those results in nature. This omission may reflect the focus of these authors on evolutionary process, per se, but it leaves unexplained a significant problem. Heterochrony is discussed by these authors in the context of “an-

cestral" ontogenies, but it is obvious that for the overwhelming majority of species, ancestors are not specifiable, much less their ontogenies.

In the absence of direct observation of an ancestor, how can the results of heterochronic developmental processes be recognized? Inferences about ancestral traits are provided by comparisons of characters and their ontogenies in the taxon of interest with their equivalents in genealogically closely-related taxa. Some phylogenetic context, however crude, is a fundamental prerequisite for a hypothesis of heterochrony since any such hypothesis is a comparative statement. A change in timing requires a standard from which deviation can be measured. Thus it is not logically possible to detect heterochrony by looking only at the development, or physiology, or ecology of a single taxon. In analyzing salamander ontogeny, Alberch and Alberch (1981, p. 250) use as a "prototypical ancestral *Bolitoglossa*" two Recent species in the genus, chosen on the basis of their relatively unmodified ("generalized") morphology. The two were selected from different "subgenera" in an attempt to sample two "independent" assessments of primitive growth patterns. Thus, these authors proceeded by assuming some, rather imprecise, phylogeny and chose their taxa accordingly. While in this particular instance the authors may have sufficient data for their case, I will argue below that a more precise phylogeny allows a more precise assessment of evolutionary patterns and thus a potentially more accurate analysis of evolutionary mechanisms.

McNamara's (1978, 1982) work exemplifies a paleontological analog to the neontological work just cited. McNamara (1982) proposes that heterochrony may be a factor in producing "directional" morphological changes in speciation. However, his bases of comparison are either appearance in stratigraphic sequence or alignment into morphological sequences, or both. Heterochrony is then invoked to explain the trends thus determined. Both of these procedures for "detecting" trends are of doubtful validity, as discussed, for example, by Cracraft (1981). The argument presented below is that both paleontological and neontological analyses of comparative ontogenetic phenomena should take place

in explicitly formulated hypotheses of phylogenetic relationship.

Phylogenetic analysis proceeds by the investigation of similarities, shared by some or all of the taxa under consideration, that might be evolutionary novelties. Whether or not a given similarity is a novelty (i.e., a synapomorphy, or derived similarity) is evaluated by the use of the ontogenetic criterion (Nelson 1973; see Section IV, below) or outgroup comparison. The latter approach, far more commonly used, is a search for the suspected novelty among taxa thought to be genealogically closely related to, but outside of, the group comprised of the taxa under consideration. Those similarities which are not present in outgroups are hypothesized to be evolutionary novelties—synapomorphies—each of which arose once, in a common ancestral species from which all taxa that share that similarity are descended. Thus one or more hypotheses of relationship among taxa may be formed on the basis of possible synapomorphies. The phylogenetic hypothesis of choice is that which provides the simplest explanation for the presence of the various possible synapomorphies. Because of the present paucity of knowledge about the probability of any given evolutionary novelty arising, the simplest explanation is usually that which requires the fewest evolutionary transformations in order to account for the possible synapomorphies. Thus, a biologist conducts an analysis by forming hypotheses that certain similarities are synapomorphous and then chooses among the possible phylogenetic hypotheses by means of logical parsimony (Beatty and Fink 1979; Eldredge and Cracraft 1980). Those similarities whose distributions are congruent with the simplest hypothesis are corroborated as synapomorphies, and those which are incongruent are called homoplasies and are usually thought to be the result of convergent or parallel evolution. Naturally, should new data cause a change in the hypothesis, the status of the characters may change, so that what was once thought a synapomorphy may be considered a homoplasy. When the data at hand do not allow a clear choice among alternative hypotheses, this fact must be accepted, presented as a result, and used to encourage more work on the group. The problems posed by homopla-

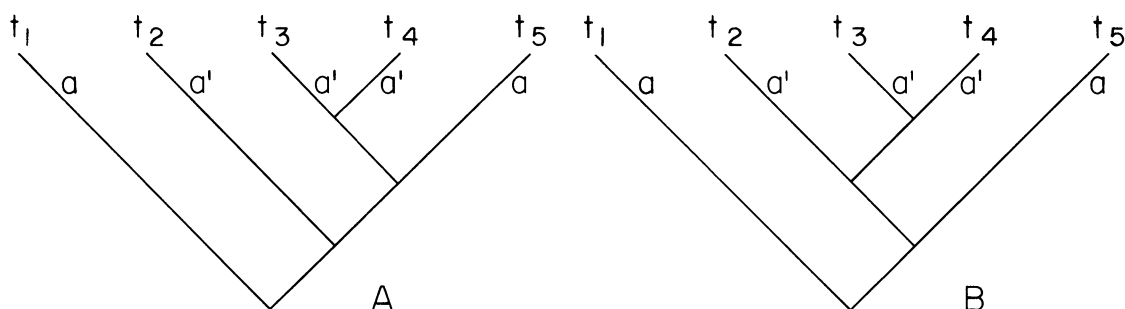


FIGURE 1. Alternative hypotheses of relationships of taxa t_1 through t_5 . In hypothesis A, presence of the primitive state of a in t_5 is anomalous and may be “explained” by heterochronic processes. In hypothesis B, presence of the primitive state of a in t_5 is due to retention of the ancestral feature and no hypothesis of heterochrony is called for.

sy for phylogenetic analyses are discussed in Section IV, below.

I must add here that there seems to be resistance among some biologists to the parsimony criterion as a guiding principle for hypothesis choice (see, e.g., Dunbar 1980), usually on the basis that the world is not “simple.” Yet as Beatty and Fink (1979) state, regardless of the assumptions underlying alternate hypotheses, a parsimony choice applies at the final stage of analysis. It is possible that data additional to the usual morphological characters, such as physiological or behavioral traits, or developmental information, might cause us to choose a hypothesis with a higher number of morphological transformations. Nevertheless, the preferred hypothesis would still be the one which most simply accounts for *all* the available data.

It is within the context of hypotheses of phylogeny that comparative analyses of ontogeny may take place. For example, given a phylogenetic hypothesis, one will occasionally find a taxon or taxa, some of whose characters more closely resemble those of more distantly related taxa than those of their closer relatives. That is, apparently primitive (“plesiomorphous”) characters rather than the expected derived ones are found at anomalous places in the chosen phylogenetic tree (Fig. 1A). Explanations of such discordances can take three forms: 1) an error has been made in the phylogenetic analysis and the phylogenetic hypothesis needs to be reconsidered, 2) heterochronic development in the form of peramorphosis has occurred, or 3) heterochronic development in the form of paedomorphosis has occurred. One of the latter ex-

planations can be considered correct only if the first has been rejected.

Figure 1 illustrates two alternative hypotheses of relationships. We are interested in interpreting the distribution of character a and its apomorphic condition a' . The primitive state is found in t_1 (and in outgroups) and in t_5 ; a' is present in t_2 , t_3 , and t_4 . In the context of hypothesis A, the presence of a in t_5 could be attributed to heterochrony, and a then should be denoted as a'' and is an apomorphy diagnosing t_5 . In the context of hypothesis B, the presence of a in t_5 can be attributed to retention of the ancestral condition, plesiomorphy—in evolutionary terms, “no change”—and no hypothesis of heterochrony need be invoked. To invoke heterochrony in the “explanation” of the presence of a in t_5 is to decrease the simplicity of the hypothesis by invoking an ad hoc explanation where none is called for.

Tests of hypotheses of heterochrony should take the form of an empirical study of ontogenetic changes of the characters in question within the organisms bearing the anomalous features, their putative sister taxon, and appropriate outgroups. This procedure is illustrated in Fig. 2. In Fig. 2A, we have a corroborated hypothesis of relationships and we wish to examine a particular character. In t_1 and in outgroups the ontogenetic sequence of the states of this character is 0-1-2; this sequence is therefore judged to be ancestral for the group t_{1-5} . In the more derived taxa t_{2-4} the sequence is 0-1-2-3, and in t_5 the sequence is as in the primitive taxa, 0-1-2. The character sequence in t_5 can be seen as an anomaly which merits further study, as

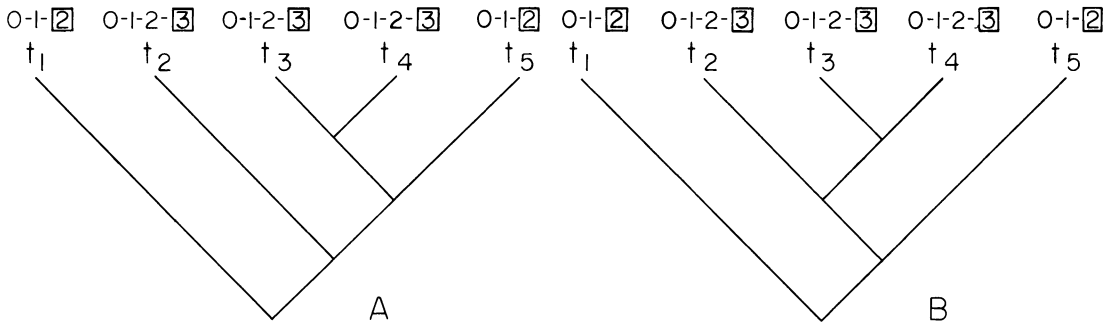


FIGURE 2. Procedure for detection of heterochronic development. Assume that the phylogenetic hypothesis is corroborated by numerous characters. We are interested in examining the distribution of a certain character whose ontogeny can be described. The terminal ontogenetic stage of the character in outgroups is Stage 2. A. In this hypothesis of relationships Stage 3 appears as a terminal addition in the ontogeny of t_{2-4} . Given this character stage distribution we would assume that Stage 3 is a synapomorphy of the group t_{2-5} and that Stage 2 in t_5 may result from pedomorphic development. Further study of the problem is indicated. B. In this hypothesis of relationships, Stage 3 in taxa t_{2-4} appears to be a synapomorphy of that group and the presence of Stage 2 in t_5 is clearly a plesiomorphy, equal to Stage 2 in t_1 . No further study is indicated.

described above. We rule out explanation 1, above, (an incorrect genealogical hypothesis) based on considerations of other characters. We can choose between explanations 2 and 3 by comparisons of the ontogenetic sequences. The presence of stage 2 as the termination of the sequence in t_5 and stage 3 in several successive sister taxa indicates that pedomorphosis is the explanation for presence of the character in t_5 . Should we find that the sequence appears to be 0-1-2-3-2 in t_5 , we would conclude that the final stage in t_5 is actually 4, but closely resembles stage 2; in this case the explanation would be peramorphosis. Figure 2B illustrates a situation in which investigation of character stage 2 would usually appear unwarranted, since its presence in t_5 does not appear anomalous and is most parsimoniously explained as plesiomorphy. However, there may be some circumstances in which further study would be desirable, for example, if other characters indicated that heterochronic development might have occurred during the evolution of t_5 . In this case, an examination of character stages would allow recognition of peramorphosis, as described above concerning the hypothesis in Fig. 2A, but one would not be able to discriminate between pedomorphosis and plesiomorphy by examining only character state sequences.

III. Models of Heterochrony

Alberch et al. (1979) developed a simple model by which heterochronic development of mor-

phology could be described. The model allows comparisons between ontogenies in ancestors and descendants, using what are essentially terminal developmental stages as reference points. There is a potential for confusion, however, since the authors use traditional definitions of heterochrony—definitions that employ developmental stages present in *adults* as reference points. There is a conflict here. While neoteny is defined in terms of *adult* vs. *juvenile* development in the text, in the model neoteny refers to changes that result in the presence of terminal ontogenetic stages that resemble pre-terminal stages in an ancestor, regardless of the stage of sexual maturity at which the terminal ontogenetic stage appears. Thus, in some cases terminal developmental stages will be attained at adulthood (sexual maturity), while in others terminal development may occur from well before to well after adulthood. The ontogeny of many features is altered relative to that of ancestral homologues in a manner not correlated with maturation of the gonads. Examples abound in organisms with indeterminate growth (many plants) and among features whose growth runs in cycles throughout life (e.g., tooth replacement in most gnathostomes). I will use the more general concepts described in the model, considering the traditional concepts as special, more restricted, cases. It may eventually be desirable to coin terms to differentiate between the traditional usages and the ones accepted here.

Alberch et al. (1979) describe the develop-

ment of a morphological system (either the entire organism or some subset of it) from its inception to its terminal form as an ontogenetic trajectory. These authors envision two major forms of morphological change, peramorphosis and paedomorphosis, each of which may result from underlying processes involving perturbations in onset of growth (α), offset of growth (β), size (S) at initiation of growth, and growth rate (k) of either size, S , or shape, σ . As noted above, the model has among its assumptions comparisons between ancestors and descendants. I will consider the comparisons in terms of genealogical hypotheses, specifying the taxon of interest (t_x), suspected of evolving through heterochronic processes, the sister taxon to t_x (t_y), and two or more outgroups (t_o). Thus, paedomorphosis is the presence in t_x of a truncated ontogenetic development in one or more features which results in a terminal stage similar to that found in pre-terminal stages of t_y and t_o . Peramorphosis is the presence in t_x of one or more features with an additional ontogenetic stage not found in t_y or t_o .

Paedomorphosis is described by Alberch et al. (1979) as resulting from three possible processes: neoteny, progenesis, and post-displacement. Again, in the context of phylogenetic hypotheses, these may be recognized by changes in certain variables. Neoteny in t_x is development along a trajectory similar to that of t_o but at a slower rate (a negative perturbation of k). Progenesis in t_x is development along a trajectory similar to that of t_o but for a shorter period of time (a negative perturbation of β). Post-displacement in t_x is development along a trajectory similar to that of t_o , but with growth onset occurring after that in the other two taxa (a positive perturbation of α).

Peramorphosis is described by Alberch et al. (1979) as resulting from three possible processes: hypermorphosis, acceleration, and pre-displacement. These also may be recognized in the context of a phylogenetic hypothesis as changes in certain developmental parameters. Hypermorphosis in t_x is development along a trajectory similar to that of t_o , but passing beyond the terminal stage present in the latter taxon (a positive perturbation in β). Acceleration in t_x is development along a trajectory similar to that of t_o , but at a faster rate (an increase in k). Pre-displacement in t_x is development along a tra-

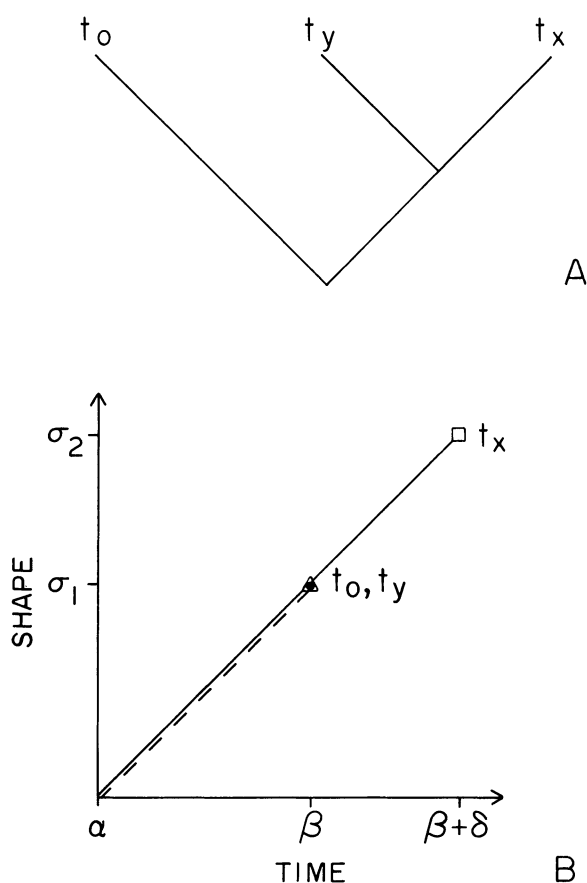


FIGURE 3. Example of the model of Alberch et al. (1979) for describing heterochronic development, modified for the examination of ontogenetic trajectories of sister taxa rather than ancestors and descendants. A. The given phylogenetic hypothesis. B. Projections of ontogenetic trajectories of shape (σ) in three taxa. In this case, development of σ in t_x proceeds along a trajectory similar to those of t_o and t_y but the offset time is positively displaced relative to that of the latter two taxa. The result is formation of σ_2 through hypermorphosis. Parameters (e.g., α , β) defined in text.

jectory similar to that of t_o , but development begins at an earlier time (a negative perturbation of α).

The model described above allows one to investigate which specific process or processes were responsible for the development of morphological features of interest, such as features thought to have been important in the evolution of a group. In addition, given a phylogenetic hypothesis as shown in Fig. 1B, one might wish to investigate the possibility that heterochrony was involved in the presence of a in t_5 if other features in t_5 appear to be the result of heterochrony. This situation would arise only if other

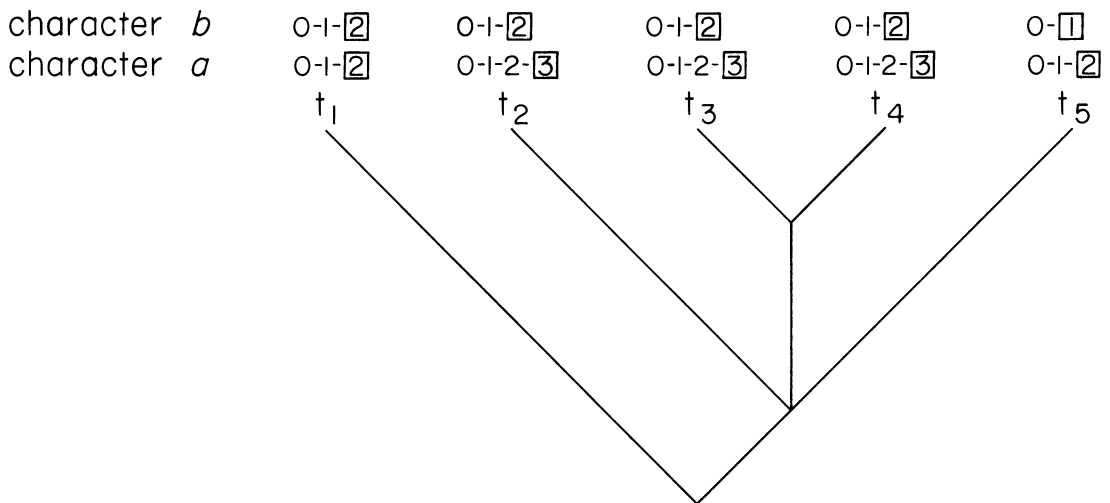


FIGURE 4. A situation in which one might wish to pursue a study of heterochronic development. The corroborated phylogenetic hypothesis is given. Stage 2 of character *a* is found in immediate outgroups and is primitive for the group. The distribution of ontogenetic stages is as in Fig. 2B, so that presence of Stage 2 in t_5 may be interpreted as a primitive feature. Given this phylogeny and no other character information, we might not wish to investigate further. However, the presence in t_5 of Stage 1 of character *b* suggests that paedomorphic development should be suspected in the evolution of t_5 and one might wish to investigate development of character *a* in t_{1-5} . Note that character stages of *a* and *b* in t_5 would not be useful in resolving the trichotomy of t_2 , t_{3-4} , and t_5 , since the conditions in t_5 are either unique to it or plesiomorphic.

terminal stage features in t_5 resembled pre-terminal stages found in outgroups.

A test of hypothesized heterochrony would consist of determining the values of the above-listed parameters in a taxon of interest, its sister group, and in outgroups, that is, evaluation of the variables in the context of a phylogenetic hypothesis. For example, in the context of the phylogenetic hypothesis in Fig. 3A, we project in Fig. 3B ontogenetic trajectories of shape (σ) for taxa t_x , t_y , and t_0 . We note that the trajectories for t_y and t_0 are similar and that the trajectory for t_x proceeds along those of t_y and t_0 but extends further along the morphological axis of those taxa. Further, we find that the time of initiation of the trajectory (α) and rate of development (k) are all equal in the three taxa, but that offset of development occurs later in t_x ($\beta + \delta$) than in t_y and t_0 (β). In this case we would postulate that σ_2 in t_x is the result of hypermorphosis. The other heterochronic processes can be detected in similar fashion.

We might also wish to investigate the processes that were responsible for σ_1 in t_y , i.e., whether σ_1 is due to retention of plesiomorphy or is the result of heterochrony. This problem can arise in several situations. We have decided

that σ_2 arose in t_x due to hypermorphosis. Since the ontogenetic trajectory and morphology of t_y are identical to those of t_0 , we are unable to tell whether heterochrony in the form of progenesis is involved in the presence of σ_1 in t_y . As mentioned above, because retention of plesiomorphy requires no evolutionary change and is thus the simpler hypothesis, we would in practice opt for that explanation.

Should some terminal features of an organism resemble juvenile or preterminal stages of the outgroup taxa, one might suspect that paedomorphosis was responsible not only for those features but perhaps also for some features that appear simply to be plesiomorphies relative to the homologous states in a presumed sister taxon (Fig. 4). It may be possible to base a choice on the model of heterochrony presented above, since in some cases the ontogenetic trajectories of t_0 and t_x will be different. These cases include the following:

- 1) When the common ancestor of t_y and t_x evolved σ_2 through hypermorphosis, and t_x evolved σ_1 through neoteny. In this case, the rate of development of σ in t_x would be slower than that of either t_y or t_0 . See Figs. 5A,B.
- 2) When the common ancestor of t_y and t_x

evolved σ_2 through hypermorphosis, and t_x evolved σ_1 through post-displacement. In this case, the rate of development of σ in t_x would equal that of σ in t_y and t_0 but development would begin later than in those taxa.

3) When the common ancestor of t_y and t_x evolved σ_2 through acceleration, and t_x evolved σ_1 through progenesis. In this case, the rate of development of σ in t_x would be similar to that of t_y , but offset time would be earlier and the morphology would resemble that of t_0 .

4) When the common ancestor of t_y and t_x evolved σ_2 through acceleration, and t_x evolved σ_1 through post-displacement. In this case, the rate of development of σ in t_x would equal that of σ in t_y , but development would begin later than in either t_y or t_0 .

5) When the common ancestor of t_y and t_x evolved σ_2 through pre-displacement, and t_x evolved σ_1 through neoteny. In this case, the developmental rate of t_x would be slower than that of t_y and t_0 .

6) When the common ancestor of t_y and t_x evolved σ_2 through pre-displacement, and t_x evolved σ_1 through progenesis. In this case, initiation of growth and growth rate of σ in t_x would equal that of σ in t_y , but development would cease at the same stage as in t_0 .

Apparent plesiomorphy due to paedomorphosis cannot be discriminated under certain conditions. These are:

1) When the common ancestor of t_y and t_x evolved σ_2 through hypermorphosis, and t_x evolved σ_1 through progenesis. See Fig. 5A,C.

2) When the common ancestor of t_y and t_x evolved σ_2 through acceleration, and t_x evolved σ_1 through neoteny.

3) When the common ancestor of t_y and t_x evolved σ_2 through pre-displacement, and t_x

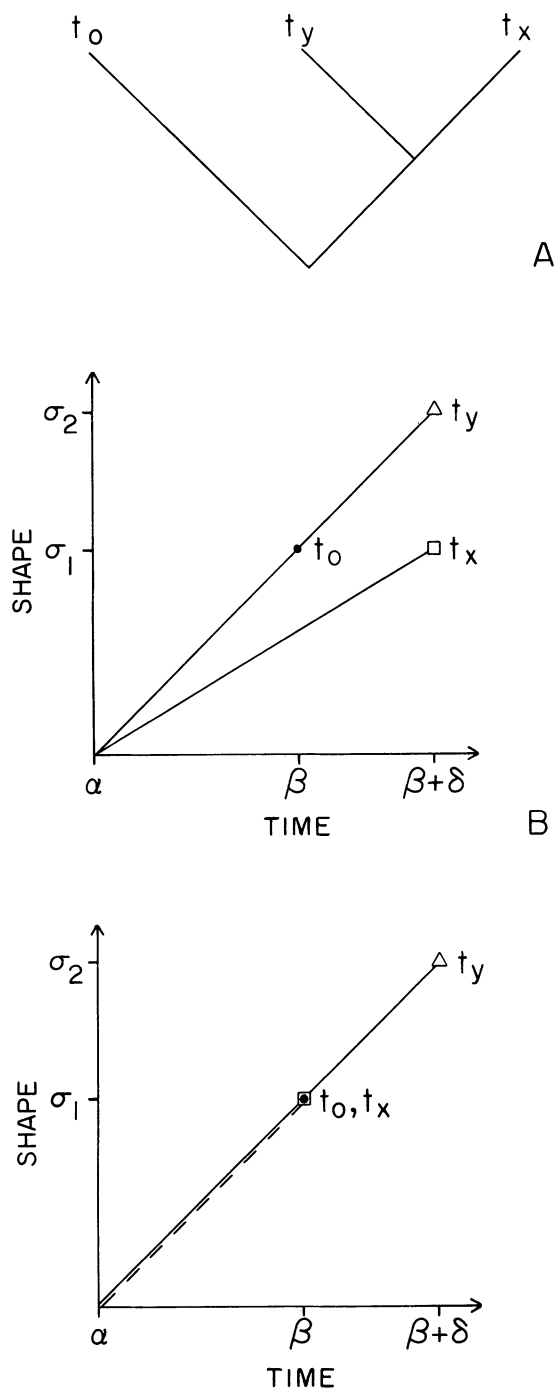


FIGURE 5. Examples of the use of the Alberch et al. (1979) model in detecting heterochronic development. A. The phylogenetic hypothesis is given. We assume that some characters cause us to suspect heterochronic development in the evolution of σ . Characters in t_0 are as found in outgroups. B. A case in which it is possible to choose between hypotheses of plesiomorphy and paedomorphosis to explain the presence of σ_1 in t_x . Although t_0 and t_x both have σ_1 as the terminal state, the developmental rate of σ in t_x is slower than in either t_0 or t_y , and the offset time in t_x (β) is equal to that of t_y . The common ancestor of t_y and t_x evolved

through hypermorphosis (there was a positive shift in offset time of development) and t_x evolved σ_1 through neoteny. C. A case in which it will not be possible to discriminate between paedomorphosis and plesiomorphy through examination of ontogeny. The common ancestor of t_y and t_x evolved σ_2 through hypermorphosis and then t_x evolved σ_1 through neoteny. The developmental rate of σ in t_x will be the same as that in t_0 . The rule of parsimony would cause us to choose a hypothesis of plesiomorphy in this case.

evolved σ_1 through post-displacement. In all these cases, the developmental trajectory and morphology will resemble those of the outgroups.

Although the circumstances in the latter three cases may not arise often in our analyses, they are nevertheless of significant interest. For example, the now classic explanation of human evolution as the result of neoteny falls into this category. Whether or not human morphology can be explained in terms of heterochrony depends on knowledge about the relationships and ontogeny of the great apes. Kluge (1982) deals with this problem in detail, so I will not pursue it here. Under some assumptions of hominoid relationships, the presence of many features of humans may be attributable simply to plesiomorphy, while under others neoteny might be invoked. Further, some hypotheses to explain many aspects of human morphology as due to neoteny require the complementary argument that the morphology of the great apes is the result of either hypermorphosis or pre-displacement.

While the model of Alberch et al. (1979) is of theoretical interest, it should be clear, as the authors themselves acknowledge, that "pure" cases of, say progenesis, or hypermorphosis, are rare. The sum of genetic, hormonal, cellular, tissue, and environmental interactions that produce an organism's morphology are complex. Terming whole organisms paedo- or peramorphic, as a linguistic shortcut, may obfuscate the real complexity of morphogenetic processes. As pointed out by Gould (1977), in the classic case of human evolution, far more is involved than neoteny—some subsystems show neotenic development while others develop by hypermorphosis or acceleration.

IV. Systematics and Ontogeny

Although varied interpretations may be placed on the historical role of ontogeny in systematic analysis (Nelson 1973, 1978; Gould 1973), it is nevertheless clear that considerations of ontogenetic processes and the frequency of heterochrony over the course of evolutionary history have played a major role in our attempts to discover the patterns of organic evolution. Systematists assess characters and phylogenetic hypotheses in light of their ideas about how

ontogeny reflects phylogenetic patterns and how some heterochronic developmental processes can obscure those patterns.

The historically recognized parallel between ontogeny and phylogeny suggests that information derived from study of ontogeny should provide insight into phylogenetic history. To the extent that evolutionary transformations are added to and retained in ontogenetic trajectories, information on those evolutionary events will be retained in individual ontogenies. To the extent that portions of trajectories are transmuted, such information will be lost. As Gould (1977) points out, recapitulation is a consequence of terminal addition. When terminal replacement occurs in evolution, ontogeny will follow von Baer's "law." Insertions of ontogenetic sequences into a trajectory will lead to violation of both Haeckelian and von Baerian principles of development, destroying the parallel between the sequences of evolutionary history and ontogenetic timing. Such insertions are nevertheless informative about particular evolutionary transformations when analyzed as synapomorphies and placed in the context of a genealogical hypothesis.

The fundamental contribution of von Baer to developmental biology is the concept that ontogeny usually proceeds from the more general to the less general. (Von Baer's principle is not a "law," since there are numerous examples of insertions of specialized sequences, such as larval features, into ontogenetic trajectories [de Beer 1940].) When cast into the context of evolutionary—i.e., genealogical—relationships among organisms, as by de Beer (1940), von Baer's notion provides a powerful approach to detecting the hierarchy of morphology and of phylogeny. Thus, phylogenetically more primitive character states (more general) often precede more derived ones during the ontogeny of an organism. Although the hierarchical structure of development has been known for many years (see e.g., Agassiz 1859), its full significance for unraveling phylogenetic history was not appreciated, with few exceptions, until Hennig (e.g., 1966) formalized the relationship between less general characters (synapomorphies) and the diagnosis of monophyletic groups (but see Nelson, 1973; Gould 1973).

Nelson (1973), in arguing for the importance

of ontogeny in phylogenetic analysis, considers ontogeny to provide an independent criterion for evaluating whether a character was derived or primitive for taxa under study. By "independent" Nelson means that polarity evaluations through ontogeny are not dependent on previous assumptions of relationship among the organisms involved. Nelson has been widely misunderstood on this point by authors who note that paedomorphosis can confound such analyses by making derived characters appear primitive, thus apparently necessitating outgroup analysis as a check on paedomorphosis (see e.g., Eldredge and Cracraft 1980; Wiley 1981). Nelson (1978) himself recognized the problem that paedomorphosis poses but failed to make a clear statement about its implications for the utility of the ontogenetic criterion. While any characters which resulted from truncated development could indeed cause incorrect assessment of character generality and lead to improper placement of a taxon, *other* characters in the same organisms, not truncated, could provide evidence for the appropriate position in the phylogeny. Outgroups are, in fact, not needed and provide no additional information; whether one uses ontogeny or outgroup comparison in an analysis, the placement of an organism will be the same provided one is using the same data base (and a valid outgroup hypothesis).

The models explicated in the previous section might allow one to differentiate independent paedomorphic (or peramorphic) evolution which could otherwise confound phylogenetic analyses. How frequently one might resort to such an approach will depend upon the degree of discordance in the character data, the perceived importance of the taxa, and/or the persistence of the investigator. I must stress that paedomorphosis can nevertheless lead one astray in a phylogenetic analysis unless a sufficient portion of the morphology remains non-truncated, or unless data external to the system, such as parasitological information, provides evidence that the characters are misleading.

Another aspect of systematic analysis in which concepts of development are important is the problem of estimating the "value" of a character, such estimates being used either explicitly or implicitly in character weighting. Two basic concerns are the evolutionary independence of

characters and the probabilities of convergence and parallelism.

Evaluations of the evolutionary independence of character states often are based on assumptions about ontogenetic processes, particularly paedomorphosis. One supposition has been that when a number of reductive traits are discovered in an organism they may all result from neoteny and hence may all represent a single evolutionary event. However, while numerous morphological traits might indeed be altered as a result of a single heterochronic change (such as loss of traits due to paedomorphosis), the fact remains that our recognition of the event and our interpretation of it must take place in the context of other characters and the groups they support. The first suggestion of character dependence is correlation; traits which appear together and which suggest groups contradicted by other characters deserve a closer look. If heterochrony appears to be a possibility, each character suspected of being related to the heterochronic developmental path can be reexamined ontogenetically and compared with its homologue in outgroups. Should a suite of characters be found to result from some heterochronic shift and thus appear causally linked, then that suite could be considered as a single transformation. However, simply because some number of traits in an organism can be attributed to progenesis, for example, it does not follow that *all* aspects of the organism should be interpreted as truncated in development. There is no reason that organisms with paedo- or peramorphic traits must be considered primarily paedo- or peramorphic since there appears to be a broad spectrum of effects from heterochronic development. Each trait must be examined in turn and analyzed in the usual way, in some cases supplemented by developmental studies using the model explicated above. No justification exists for judging a character a priori to be a product of some heterochrony detected in other characters.

Parallelism and convergence vex and fascinate many evolutionary biologists and are thought to be the scourge of systematics. It is difficult to decide how much these phenomena are the products of biological processes and how much the products of human psychology, since one person's "amazing case of convergence" may

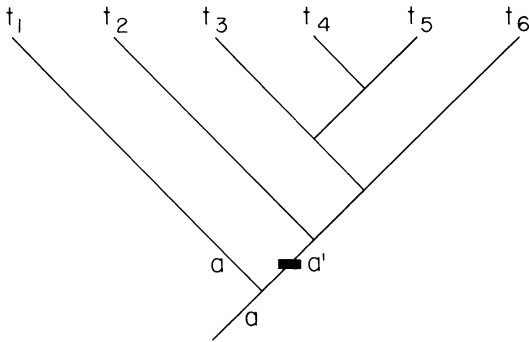


FIGURE 6. In a study of the evolution of character a' , examination of taxa t_4 and t_5 alone would be inappropriate since a' is present in their morphology as a plesiomorphy and may not be subject to conditions similar to those during the time when the ancestor of taxon t_2 - t_6 gained a' as an evolutionary novelty. A study of a' should include comparisons among the major clades within taxon t_2 - t_6 in order to assess any changes that may have transpired since the origin of a' . Thus, for example, examination of t_2 , t_4 , and t_6 would provide a better framework upon which to base an evolutionary study of character a .

be another person's vague similarity. Nevertheless, both terms imply multiple evolution of similarities, in parallelism through a similar genetic/epigenetic mechanism, in convergence through different genetic/epigenetic mechanisms (see Eldredge and Cracraft 1980, p. 71, for a summary of definitions of these terms). Recognition of either, like the recognition of heterochrony, requires some phylogenetic context. The problem for systematics lies in the possibility that these bogus similarities might be mistakenly used to diagnose unnatural groups. As long as there are more non-homoplasious characters than homoplasious ones, one should theoretically be able to find the proper phylogeny. However, as the proportion of homoplasy gets larger, the stability of the hypothesis can lessen. Clearly, if one were able to identify homoplasious characters before or during an analysis of relationships, that analysis would be easier and have a higher probability of being correct. Can we, as some authors maintain, move from assumptions about evolutionary processes to conclusions that certain character patterns resulted from particular processes, without any knowledge of the distribution pattern of those characters? I think not; notions about parallelism or convergence imply certain character distributions relative to a phylogeny and can hardly be regarded as having any support in the absence of information about

the actual distribution of features. Further, such information must be based on another line of evidence in order to provide an independent test of any process hypothesis. Hypotheses of process, then, gain their support from, rather than give their support to, hypotheses of pattern. Hypotheses of parallelism and convergence have merit only in the context of conflicting data, whether of intrinsic features or extrinsic information, e.g., biogeographical patterns or patterns of parasite evolution. Even experience in related groups suggesting that many characters should be expected to exhibit large amounts of homoplasy would serve more as a warning to expect incongruities in data than to propose hypotheses of homoplasy forthwith.

When, then, will ontogenetic analyses be useful in solving systematic problems? We wish to detect parallelism and convergence—can ontogenetic studies aid us? The answer lies in the definitions of the terms. Convergence, since it is similarity resulting from different genetic/epigenetic mechanisms, should be detectable through ontogenetic study; a search for further similarity should yield little return.

Since parallelism is by definition similar in ontogenetic detail, an ontogenetic analysis will not allow its discrimination from synapomorphy. Parallelism can be detected, if at all, only after parsimony assessment of the entire data set available.

V. Conclusions

Phylogenetic hypotheses play a fundamental role in any comparative analysis of ontogeny. This role is especially important to recognize in light of the recent emphasis on heterochrony as a factor in evolution, particularly in the evolution of speciose or persistent lineages (often, the so-called higher taxa of some schools of systematics). Such study tries to identify the conditions under which an evolutionary novelty appeared and then, often, attempts to explain the selective force that allowed the bearers of that novelty to become successful. As Lauder (1981) has pointed out, the acquisition of an evolutionary novelty is a singular event and it is not possible to provide a testable explanation for the origin of a unique feature. The best one can do is to find similar novelties in distantly related lineages to see if a general pattern of correlated

factors emerges. Obviously, the more precise the genealogical hypotheses for these comparisons, the stronger the basis for evolutionary suppositions. For example, should one wish to detect the conditions under which a certain kind of evolutionary novelty arose through heterochrony, the study should focus on taxa selected to provide as accurate a picture as possible of the "ancestral" condition (Fig. 6). Examination of poorly chosen taxa could result in the investigator proposing adaptive explanations where none are needed—i.e., where the trait is a primitive feature, present at least in part for historical reasons, and perhaps not subject to selection at all, or to selection very different from that present during the origin of the novelty.

Despite historical speculations that heterochrony is of fundamental importance as an evolutionary process and has occurred during the evolution of major phylogenetic groups (Gould 1977), empirical tests of these claims in the context of well-structured phylogenetic hypotheses remain to be done. Well-formulated studies are urgently needed to evaluate just how pervasive heterochronic ontogenetic changes are and have been during organic evolution.

One implication of this paper that may be especially dismaying to evolutionary theorists who are concerned with process rather than pattern is the necessity of well-documented patterns to which process analysis can be applied. The small number of phylogenies, especially at low taxonomic levels, now available is a reflection of the comparatively recent application of explicit methods to reconstruct those phylogenies (and the unsettling effect that application has had on systematic biology in general). Yet, as the acceptance of phylogenetic methods continues to grow, more patterns will become available. In the meantime, it would be well for all comparative biologists to keep in mind the potential problems of most current estimates of phylogeny.

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