

The Linkage between Ontogeny and Phylogeny in the Evolution of Complex Systems

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Abstract. Processes that modify ontogenies can have profound morphological consequences. Heterochrony is one means by which ontogenetic pathways can be changed to give large morphological changes in adults of related taxa with relatively little genetic change. On one hand, developmental interactions during development are so complexly integrated that they provide a stability to the characteristic morphology of lineages and give the impression of recapitulatory evolution. On the other hand, when the opportunities for modification of ontogenies arise, the results can be dramatic. Repatterning of ontogeny may be an important means by which evolutionary novelties are introduced. Both structuralist and functionalist perspectives, within a phylogenetic framework, contribute importantly to the understanding of the role of ontogenetic changes in the evolution of complex, integrated systems in vertebrates.

INTRODUCTION

Investigation of the relationship of ontogeny to phylogeny in the transformation of biological structure has a long history, and most of the fundamental embryological concepts (e.g., von Baer's laws) relevant to this relationship predate Darwin's *Origin of Species* (for general reviews see Gould 1977; Rieppel 1988). In this paper we treat only a subset of topics in the ontogeny–phylogeny relationship: how modifications in ontogeny relate to evolutionary transformations in complex, integrated systems, which become expressed in phylogeny. Deep intellectual conflicts are revealed by the approaches of different groups of biologists to these issues.

Biologists tend to fall into two loosely defined groups in regard to views on the evolution of complex integrated systems. The neodarwinists, proponents of the "evolutionary synthesis," have developed population-based models in the philosophical framework of functionalism to explain the evolution of complexity. Most neodarwinists are population geneticists and ecologists, but some are organismal biologists who have studied morphological and behavioral complexity (e.g., Bock 1988; Dawkins 1986; Williams 1966; Wilson 1975). For the most part, embryological concepts have been of little consequence in neodarwinism (de Beer 1930, is the main exception; see also Huxley 1942). The other group, less well defined, can be characterized generally as having the view that factors other than those stressed by neodarwinists, especially internal organismal features such as development, are needed to explain organismal diversity and complexity (e.g., Alberch 1980; Gould 1982b; Webster and Goodwin 1982). Many members of this group organize their research programs around the philosophical traditions of structuralism (e.g., Goodwin 1984; van der Hammen 1988; Webster and Goodwin 1982). The precedence of form over function is emphasized, and generative processes of development are stressed as the primary factor in the evolution of form. Both functionalist (neodarwinian) and structuralist (in a restricted sense, with a focus on principles underlying the generation and stabilization of form) perspectives are necessary for a full understanding of the evolution of complex integrated systems. Furthermore, historical contingency (i.e., phylogenetic factors) must be integrated with these approaches. In the resulting synthesis, the sometimes opposing elements of the different perspectives remain intact (cf. Schaefer and Lauder 1986; Taylor 1987; Wake and Larson 1987). We explore some ways in which a multidimensional analysis of evolutionary changes in ontogeny and phylogeny can contribute to an understanding of the evolution of complex integrated systems in vertebrates.

THE CONCEPT OF RECAPITULATION IN THE RELATION OF ONTOGENY TO PHYLOGENY

Haeckel's biogenetic law was obsolete by the time of the neodarwinian synthesis, and yet a more general kind of "recapitulation," based on von Baer's laws, has been perceived (Rieppel 1988). For example, while Løvtrup (1978) rejected Haeckelian recapitulation, he argued in favor of a more general "von Baerian recapitulation" ("during their ontogenesis the members of sister taxa follow the same course up to the stage corresponding to their divergence into separate taxa," Løvtrup 1986, p. 76). He has even gone so far as to assert that the above quotation is the "most parsimonious generalization ever stated in biology" (Løvtrup 1987, p. 228). In recent years, growing use of cladistic methods of phylogenetic reconstruction has led to rigorous attempts for hypothesizing polarity of character state

transformation, and there has been much debate concerning the value of ontogenetic information for such a determination (for contrasting views see Alberch 1985; Brooks and Wiley 1985; de Queiroz 1985; Kluge 1985; Nelson 1978, 1985; Patterson 1982; Rieppel 1988). Use of ontogenetic information for such purposes implies acceptance of some form of recapitulation.

Advocates of von Baerian recapitulation accept exceptions and limitations (e.g., it takes place only within phyla or classes) but stress its generality. Rieppel (1988) recently has argued a point that has been discussed by others, i.e., that one cannot discuss evolutionary transformations without explicit phylogenetic frameworks ("Every hypothesis of transformation presupposes a hypothesis of relationship," Rieppel 1988, p. 160). A classification, when based on cladistic principles, forms a phylogenetic hypothesis. Rieppel sees classification as a process of logical subordination to be arrived at by methods of outgroup comparison (which he considers to be an indirect method) and ontogenetic comparison (based on von Baerian recapitulation, which he considers to be a direct method). The work of Garstang (1922) and de Beer (1930) showed that changes in timing and rates of development (heterochrony) could have important evolutionary consequences, and this approach has again become popular following Gould's (1977) review and analysis. Some relationship must exist between orderly ontogenies, a general kind of recapitulation, and heterochrony, but as yet there is little agreement (for example, between Gould and Løvtrup) on the nature of the relationship or even the relative importance of heterochrony in organismal evolution. For Rieppel (1988), heterochrony is a historically contingent statement about phylogeny and can only be determined from character incongruence (as revealed, in his view, by the ontogenetic method) in an explicit phylogenetic statement. While we agree with this view as a general statement, we disagree on how to detect character incongruence. For us, such incongruence is best revealed by outgroup comparison rather than by the ontogenetic method, for we see the reality of von Baerian recapitulation as an open research question. We agree, however, with his important point that because of the possibility of heterochrony, ontogeny cannot provide a direct clue to the phylogenetic process.

Some important research questions arise from these considerations: How general is von Baerian recapitulation? Does such recapitulation constitute a general constraint on morphological evolution within lineages? How important is heterochrony in morphological evolution, and what role does it play in major morphological transitions?

ALTERNATIVES TO NEODARWINIAN EXPLANATIONS FOR THE ORIGIN OF MORPHOLOGICAL NOVELTY

The view that some major change in morphogenetic processes is the principal means of morphological diversification is held by dissenters from standard

adaptationist explanations. Examples are Schindewolf's (1950) proterogenesis (in which novelties are introduced by some ill-defined but nondarwinian means into juvenile or embryonic stages of ancestors); Severtzov's (1931) idea that ontogenesis can be divided into phases, the earliest being the setting for innovation leading to the origin of higher taxa; Gould's (1977) focus on heterochrony; Matsuda's (1987) theory of environmental induction and subsequent genetic assimilation; and various genetically based concepts ranging from Goldschmidt's (1940) ideas on macromutation and Løvtrup's (1987) notion of epigenetic macromutations to current theories such as Dover's (1982) molecular drive. A now common expectation among molecular biologists is that some as yet unknown molecular developmental mechanisms underlie the generation of morphological novelty (for a contrasting view see Horder, this volume). Some who see "important" evolution as originating within the genome have taken aggressively negative stands toward neodarwinism (John and Miklos 1988, p. 292).

ONTOGENY AND THE INTRODUCTION OF MORPHOLOGICAL NOVELTY

Closely related taxa do have similar ontogenies. This fact makes it possible to analyze the implications ontogenetic changes have for the introduction of novelties into complex integrated systems and for the evolution of such systems. Such an analysis has as its point of departure a phylogenetic hypothesis. If taxonomies are grounded on evolutionary principles, and if one accepts (as we do) that most of the ontogeny of an organism is potentially subject to evolutionary modification (even though the overall ontogeny is conservative), it follows that ontogenetic information should not be used to determine direction of evolutionary change in a character. Our recommendation is that characters for cladistic analysis be ontogenetic transformations rather than instantaneous morphologies, and that polarity be determined by outgroup analysis (see de Queiroz 1985).

Explanations for the general conservatism of ontogenies vary greatly. For Løvtrup (1987), epigenetic "macromutations" are at the base of major evolutionary change. These have pervasive, integrative effects on development and organization of body plans. In contrast is the concept of an evolutionary ratchet, generating constraints in evolution through combinations of genetic, epigenetic and selectional events, that leads to a gradual "hardening of the developmental ground plan" (Levinton 1986, p. 257; see also Riedl 1978) in a strictly neodarwinian context. According to this view, bauplans may have arisen gradually, with occasional key innovations opening the door to establishment and radiation of groups.

Heterochrony

Heterochrony refers to morphological evolution resulting from changes in rates and timing of development. Several processes or mixtures of processes are included under the heading of heterochrony (e.g., neoteny, acceleration). Since the publication of Gould's (1977) major work on the topic, the relation of development to evolution, often with a focus on heterochrony, has enjoyed a rebirth of interest (e.g., see Bonner 1982; Goodwin et al. 1982). By presenting selected examples, we will show how evolutionary changes in ontogeny relate to the appearance of structural and functional novelties.

We limit our consideration of heterochrony to paedomorphosis and dissociation (terminology of Alberch et al. 1979; Alberch and Alberch 1981), both of which offer means of changing complex integrated systems without necessitating their decomposition. Paedomorphosis is the appearance of morphological traits in adults that were present only in earlier ontogenetic stages of ancestors. While paedomorphosis is widely accepted as an evolutionary phenomenon, its frequency and importance are challenging research questions.

Paedomorphosis can be a phenomenon of organismal-wide (global) expression, such as occurs by acceleration of gonadal development with retention of ancestral developmental timing and rates for the rest of the organism (termed progenesis), or by the slowing-down or truncation of most aspects of organismal development while gonads mature at the normal time (termed neoteny). Both result in adult morphology resembling that of juveniles of related groups (Gould 1977). The axolotl, *Ambystoma mexicanum*, is a vivid example of neoteny. It becomes reproductively mature at the time normal for related groups while retaining the overall morphology of a salamander larva, but has normal size for its age. Species in several other salamander families are neotenic, but to varying degrees, and not all look like larvae. In fact, most species of salamanders lack larvae and have direct development, and many of these are greatly affected by paedomorphosis (Wake 1966). The skulls of salamanders are relatively simple and have reduced numbers of bones compared with fossil outgroups; many parts of the body fail to ossify and remain cartilaginous, and the hyobranchial apparatus retains features characteristic of larvae and does not meld together during ontogeny as in anurans and other tetrapods.

Evidence of paedomorphic evolution is found in soft tissues as well as in the skeleton. The brains of adult salamanders are only slightly different in gross morphology from those of larvae. In most tetrapods cell migration in the embryonic brain is the basis for a laminar arrangement of cell bodies and fibers (e.g., in the cortex or the midbrain tectum) and the formation of distinct nuclei, but migration is slight in salamanders. There is little or no lamination in the tectum, and there are indistinct nuclei in the adult

brain, mostly “hidden” in the periventricular grey matter. The morphology of nerve cells in salamander brains remains larval-like, even though sensory functions typical of adults are attained (Roth 1987). There is a strong correlation between overall paedomorphosis and degree of differentiation of neural structures; the most highly derived salamanders, the paedomorphic members of the plethodontid tribe Bolitoglossini, have the least degree of nerve cell migration and differentiation (Roth 1987; Wake et al. 1988). Until recently, neuroanatomists mistook the salamander brain as representing the most primitive tetrapod condition (Kuhlenbeck 1967–1978; Herrick 1948), on the basis of the apparent lack of specialization. Recent studies on lungfishes have shown that many of the neural characters mentioned above are found in lepidosirenids (African and South American species), but in strong contrast the neoceratodids (Australian species) show most of the neural characters found in the coelacanth *Latimeria* and in vertebrates other than salamanders and caecilians (Northcutt 1986). These last two groups also have relatively simplified, paedomorphic brains. Despite the overall larval appearance of the brain, lepidosirenids, salamanders and caecilians all show different derived specializations of specific details of neural structure. Secondary simplification of brain structure by paedomorphosis has occurred independently at least twice (lepidosirenids and Caudata + Gymnophiona).

Paedomorphosis in a form that has less than global impact has been important in the evolution of fishes, frogs, and salamanders, in which the presence of larval stages often simplifies analysis. However, it also is important in direct-developing amphibians, and we believe in amniotes as well. Structural, functional and behavioral novelty in these groups may arise from ontogenetic dissociations, a less global kind of paedomorphosis that occurs in the absence of larval stages (Wake 1966 called this differential metamorphosis). Dissociation, i.e., changes in rates or timing of development of a particular morphological feature with respect to the global developmental process, decouples a feature from the overall ontogenetic sequence (Alberch and Alberch 1981). For example, in some small species of *Bolitoglossa* shape and growth of the foot are decoupled so that digit formation stops early, even though the overall foot continues to grow for an additional period of time. Gould (1982a) argued that ontogenetic trajectories are formed of blocks of covariant sets of morphogenetic mechanisms producing specific features, and that these blocks are dissociable from each other to some degree. Dissociation of these postulated blocks makes possible a shuffling that can lead to new morphological outcomes, and can establish a framework in which new ontogenetic couplings can occur.

In the direct-developing salamanders of the family Plethodontidae, paedomorphosis is manifest in a mosaic pattern, involving extensive dissociation. Some parts of an affected organism (typically the patterns are species-specific) show paedomorphic morphology, but other parts do not.

The two major direct-developing groups, the tribe Plethodontini and the tribe Bolitoglossini, are sister taxa (Lombard and Wake 1986). The former group has remained relatively generalized in morphology and ecology (with some interesting exceptions), and has moderate numbers of species; the latter is highly specialized in morphology and ecology, and is speciose. In the Plethodontini paedomorphosis is not a dominant factor. For the most part adult salamanders of this group have the appearance of metamorphosed members of other groups, with a full complement of digits, well-ossified skulls with all the bones that are present in close outgroups, and some species even have peramorphic traits such as hyperossification and large size (peramorphosis refers to "shapes beyond," and is usually characterized by recapitulatory ontogenetic trajectories that extend beyond ancestral stopping points [Alberch et al. 1979]).

In the Bolitoglossini, paedomorphosis is expressed in many different ways and at different taxonomic levels. For example, *Batrachoseps* has a number of paedomorphic traits, including attenuation of the body and limbs, digital loss, presence of a large frontoparietal fontanelle (Wake 1966), and the nearly complete suppression of myelination of the optic nerve (Linke and Roth, submitted). The incompletely ossified braincase contains a brain that is relatively much larger than in related genera, although the forebrain is smaller (Roth et al. 1988). These features are characteristic of embryos and juveniles of other species. Many species of the genus *Bolitoglossa* have pad-like hands and feet, with incompletely formed digits, which resemble embryonic stages of related species. These species display a general paedomorphic syndrome, with many manifestations (Alberch 1981, 1983; Alberch and Alberch 1981; Wake and Brame 1969).

Ontogenetic Repatterning

Ontogenetic repatterning refers to the establishment of new sets of morphogenetic processes resulting from heterochronic events (Roth and Wake 1985). It is an evolutionary and phylogenetic phenomenon, based on changes in developmental systems. "Patterning" in developmental biology usually means spatial patterning only, but our use of ontogenetic repatterning is more general and explicitly includes a temporal component as well. By establishing new networks of interactions at the same time that old ones are decoupled, ontogenetic repatterning establishes a framework for the introduction of novelty into complex integrated systems. We examined the evolution of the feeding system in plethodontid salamanders, including vision, neural control, functional morphology and biomechanics, within a framework of phylogeny and ecology (Roth and Wake 1985). The loss of the larval stage has been a necessary but not sufficient condition for the evolution of a long series of specializations associated with feeding.

Thus, in the *Plethodontini* development proceeds much as in ancestral groups, and the free-living larval stage is simply dropped out of the ontogeny, although such larval traits as three branchial arches are present embryologically. The feeding mechanisms are generalized. In contrast, in the *Bolitoglossini* the most highly specialized feeding systems in amphibians are found, featuring tongues that can be fired with great accuracy and for great distances at high speed. This highly developed feeding apparatus requires sophisticated mechanisms of depth and distance perception involving a high degree of eye frontality as well as specific patterns of retinotectal projections (Roth 1987). The *bolitoglossines* have achieved these novelties through ontogenetic repatterning. A dissociation of branchial arch development has led to the suppression of all but one epibranchial, and a new pattern of force transmission (Lombard and Wake 1977; Wake 1982) has evolved that does not contain the ancestral biomechanical "stopping point" that limits specialization in other tongue-projecting salamanders. Larval salamanders have laterally placed eyes, which rotate slightly during metamorphosis to gain some degree of frontality. In *bolitoglossines* eye frontality is more pronounced than in other amphibians, and occurs in embryos (Rettig, Roth, and Wake, unpublished). Overlap of direct projections from both eyes in the visual centers is a precondition for well-developed stereopsis. In all other salamanders investigated, and in frogs (as well as in most "lower vertebrates"), retinotectal projections are mainly to the contralateral hemisphere, and there is only a minor ipsilateral component that does not become evident until late metamorphosis, at which time it is associated with eye rotation. *Bolitoglossines* contrast strongly with this general condition and have extensive direct ipsilateral projections comparable to the condition in mammals (Rettig and Roth 1986). This pattern already is evident in late embryonic stages, which have more extensive ipsilateral projections than do adults of any other amphibian group (Rettig, Roth and Wake, unpublished). The *bolitoglossines* have a greater number of sites in the brain for retinofugal projection than do any other amphibians studied (Rettig and Roth 1986). Ontogenetic repatterning has other manifestations unrelated to feeding, and may have had global effects. For example, the cytoarchitecture (less differentiated cell morphology) and topography of the motor nuclei (lack of lateral motor column) in the cervical spinal cord probably result from ontogenetic repatterning (Wake et al. 1988).

These specific examples show that heterochrony is an important phenomenon in groups that lack larval stages. Further, they support our contention that heterochrony is a common mode of morphological evolution. Heterochronic analysis and investigations of ontogenetic repatterning should be undertaken with amniotes in more formal studies than have been conducted to date. Paedomorphosis long has been thought to underlie morphological transitions that are associated with the origin of higher taxa (Garstang 1922)

and to represent means of phylogenetic and evolutionary escape from specialization (Hardy 1954). While we believe that heterochronic analysis is an important adjunct of evolutionary morphological analysis, we emphasize that it is necessarily comparative in nature, and that direction of evolutionary change can be determined only by formal phylogenetic analysis (Fink 1982; Rieppel 1988).

How General is Ontogenetic Repatterning?

A complex network of causal developmental interactions, an epigenetic system, has been built through successive phylogenetic events (the "burden" of Riedl 1978). The existence of such causal relationships has led Løvtrup (1987) to assert that von Baerian recapitulation is a necessity within groups united by a common body plan (within phyla or classes), and that body plan formation was begun anew in many higher ("superior") animal taxa. Arguments that epigenetic evolution necessarily requires some nondarwinian evolutionary mechanism are unconvincing, but there is a need to enrich our view of evolution with embryological perspectives (see Horder, this volume; and Hinchliffe, this volume). For example, we suspect that ontogenetic repatterning has been important not only in the establishment of new body plans and the origin of higher taxa, but also in the introduction of novelties at lower taxonomic levels.

There are numerous examples of dissociation and divergence during early embryonic stages that lead us to question the generality of von Baerian recapitulation (e.g., Dohle 1988, 1989). Examples are the influence of egg size on cleavage patterns and subsequent development in echinoderms (Raff 1987) and frogs (Elinson 1987), and the different kinds of neurulation patterns of vertebrates (infolding vs. cavitation in formation of the dorsal hollow nerve cord). It no longer can be asserted that vertebrates have a common early ontogeny. There appear to be points of convergence during ontogenesis (e.g., gastrulation, neurulation, "pharyngula"), possibly because of the existence of some critical cell and tissue interactions that constitute developmental constraints. Periods of "relaxation" preceding and following convergence are times during which ontogenetic repatterning can occur (for alternative interpretations see Rieppel 1988; Horder, this volume).

Embryonization is the evolutionary incorporation in a given taxon of free-swimming ancestral larval stages (developed from small eggs) into the period of intraovular development from enlarged eggs (Matsuda 1987). There are many implications of such a phenomenon, and Matsuda (1987) has presented a theory which he identifies as neolamarckian (although he invokes genetic assimilation, a neodarwinian concept, to explain their evolution). He argues that very large, yolky eggs constitute highly stressful physicochemical environments for embryos, and that various phenotypic changes occur as a

result of new epigenetic interactions. While having reservations concerning his evolutionary hypotheses, we believe that Matsuda's epigenetic hypotheses merit careful consideration. For example, direct development usually entails increase in egg size, and this establishes a foundation for new patterns of interaction during development. Embryonization often is accompanied by acceleration of some developmental events (our example is the precocial development of ipsilateral retinotectal projections in bolitoglossine salamanders, cited above). Careful investigations are in order for different vertebrate taxa that have evolved direct development and enlarged eggs.

Relatively few species of frogs with direct development have been studied embryologically. Elinson (1987) summarized data for the two large and complex genera, *Gastrotheca* and *Eleutherodactylus*. Gastrulation in *Gastrotheca* is divergent from that in related taxa, while gastrulation in *Eleutherodactylus* is modified only slightly. However, in *Eleutherodactylus* development of the hyobranchial skeleton of embryos has been strongly repressed; the tail has become the major larval respiratory organ. Both genera show some major ontogenetic modifications, basically dissociations; however, too little information is available as to determine the extent of ontogenetic repatterning. Hanken (personal communication) has begun a long-term study of cranial development in *Eleutherodactylus*; he reports that initial data weigh heavily in favor of repatterning. During development, cartilaginous components do not form "larval" structures that are remodeled to form typical postmetamorphic structures, but adult patterns appear "de novo." The pattern of ossification also is highly derived.

Gastrotheca and *Eleutherodactylus* contrast in their diversity. Although neither is unusual in external morphology (which in frogs is highly conserved), both have atypical reproductive biology. *Gastrotheca* broods eggs in the skin of the back of the female, or inside a specialized pouch on the back, and direct development has evolved several times. Although the genus *Gastrotheca* has a modestly high number of species (ca. 40; Frost 1985), it contrasts with *Eleutherodactylus*, a highly speciose genus in which direct development is apparently universal. *Eleutherodactylus* shows a moderate degree of morphological diversity (in size, skin texture, coloration, skull shape, structure of digital tips, etc.), and it may be the most speciose vertebrate genus (over 400 species are listed by Frost 1985). The genus might be appropriate for testing the decoupling hypothesis of Lauder (1981), which predicts that the diversity of biomechanical pathways will be greater in speciose taxa than in morphologically conservative sister groups (see also Lauder and Liem, this volume).

Perhaps the most profound examples of ontogenetic repatterning are found in the Amniota, and in the species *Homo sapiens*. The evolution of the amniote egg established a framework for extreme embryonization, with a great deal of condensation and dissociation of ontogenetic trajectories.

Amniotes exemplify the effects of ontogenetic decoupling in many profound ways. Examination of amniote evolution within the framework of the decoupling hypothesis (see above) discloses increases in establishment of new couplings at many different taxonomic levels. Furthermore, the amount of parallel evolution is profound (e.g., in the evolution of viviparity, which has evolved *independently* at least 95 times in squamate reptiles alone [Shine 1985, this volume]).

The existence of heterochrony in the African great apes has been well documented; paedomorphosis accounts for the general morphology of the pygmy chimpanzee (Shea 1983a, 1983b, 1984). The once highly controversial theory that *Homo sapiens* evolved in part through the paedomorphic process of neoteny has again become widely accepted (for review see Gould 1977). The hallmark of modern man, enormously increased brain size and associated function (e.g., speech), has evolved in a short period of time. The parietal, temporal and frontal lobes of the cerebral cortex of man are associative centers that account for most of the difference in brain size compared with other mammals (Creutzfeldt 1983). These centers are not tightly connected to sensory and motor centers outside the cortex. Paedomorphosis may have led to an uncoupling of ontogenetic constraints, which facilitated the ensuing ontogenetic repatterning. Rapid brain growth followed, but it did not result in overall increase in volume. Rather, human brain evolution was highly channeled by intrinsic coupling properties of the brain into specific growth of the associative centers of the cortex, and these in turn may be the neural basis for the characteristic features of human behavior: abstract thinking, language and foresight (Changeux and Konishi 1987).

COMPONENTS OF A MULTIDIMENSIONAL ANALYSIS OF EVOLUTIONARY AND PHYLOGENETIC IMPLICATIONS OF ONTOGENY

From what principles does the unity of ontogeny arise? There appear to be two mutually exclusive answers: (a) that the unity of development and the whole organism might arise from pattern-creating forces that are universal and ahistorical (extreme structuralists, see below); proponents of this view doubt and some even heap ridicule on the concept that environmental forces (the neodarwinian view that novelties are built up gradually by natural selection acting on random variation) could play any consequential role; and (b) that the unity of organisms is determined by external selective forces that function continuously to unite parts of organisms. Without this unifying force the system would disintegrate (a functionalist approach, seen in neodarwinism). These views are neither mutually exclusive, nor can they simply be melded together or subsumed under a single concept (Wake and Larson 1987; Rieppel 1988). They arise from the paradox of organisms—

on the one hand organisms are autonomous self-constructing and self-maintaining entities (an der Heiden et al. 1985), and on the other hand these autonomous entities are completely dependent for the maintenance of their autonomy (i.e., for the continuation of their existence) on the external environment. These two approaches in less extreme form constitute a system of complementarity (Pattee 1978), and a broad synthesis should be sought in which the different perspectives are permitted to remain separated, yet joined together in a framework of historical contingency (Wake and Larson 1987).

Structuralist Perspectives

The structuralist perspective (Piaget 1970; van der Hammen 1988; Rieppel 1988) in relation to ontogeny is most evident in the causal networks of interactions that result in morphogenesis and delimit the forms that actually appear. Many workers in recent years have argued that epigenesis is the creative force in generating new morphologies. For example, Alberch (who prefers "internalist" to "structuralist"; 1989) argues that the internal rules of development define the realm of possible morphological variation, and, consequently, place limits on the process of adaptation. An example relevant to the present conference arises from a consideration of the evolutionary morphology of plethodontid salamanders, in which reversal of a morphogenetic gradient has led to a major reshaping of the hyolingual skeleton, and the consequent attainment of new functions and behaviors. Dissociation has led to a new generative pattern for the production of freely projectile tongues, and while both old and new patterns produce similar morphologies, the new pattern involves escape from a functional constraint and more extreme specialization is possible as a result (Roth and Wake 1985; Wake and Larson 1987).

Functionalist Perspectives

The functionalist perspective in biology is nearly equivalent to an externalist view, i.e., one based on the constructive role of natural selection in slowly building adaptive morphological novelties. This perspective was introduced in relation to ontogenesis by Garstang (1922), de Beer (1930), and Huxley (1942 and earlier). These workers observed that adaptive processes can introduce novelty at any point in ontogenesis. For example, caenogenesis is the phenomenon of larval adaptation, in which a novelty is introduced into a larval stage (or more generally, into any point in ontogeny other than the terminal stage), and it does not affect later stages. This example shows that selective processes can affect specific stages of the development of integrated systems without having broader consequences. Even if a given

morphological trait has been established by an adaptive process, however its subsequent fate might be better understood as a result of structuralist analysis. An example from our own work is the evolution of a single premaxillary bone in larvae of plethodontid salamanders from a paired condition as part of an adaptive process; the paired condition is restored at metamorphosis. However, in various lineages affected by paedomorphosis the larval condition is retained, and its retention in species that lack larval stages is understood by adding structuralist and phylogenetic perspectives (Wake 1966, 1989; Wake and Larson 1987).

Historical Contingency and Synthesis

The role of historical contingency cannot be disregarded in biology, so all concepts based on ahistorical reasoning alone are fundamentally inappropriate. There has been but one history of life, and historical contingency is a primary factor in evolution (Raup and Jablonski 1986). Not just in the case of catastrophes, such as those postulated in association with mass extinctions, but even in relation to life histories in groups of related species, for example, historical contingency plays critical roles. In respect to the examples presented in the two preceding sections, phylogenetic analysis shows how important historical contingency has been. The reorganization of the hyolingual apparatus in bolitoglossine salamanders seems to be a direct consequence of the loss of the larval stage in the ancestors not of this group but of the common ancestor of the Bolitoglossini and the Plethodontini. Thus, the loss of this larval stage is a necessary but not sufficient condition for the evolution of the highly specialized bolitoglossine tongue (Roth and Wake 1985). The caenogenetic evolution of a single premaxillary bone in ancestral plethodontids, and subsequent dissociated paedomorphosis, which can be detected only with phylogenetic analysis, is sufficient to explain the appearance of a single premaxillary bone in adults of many different bolitoglossine genera (Wake and Larson 1987), without the need for any specific functional role of the bone. The existence of stable ontogenies and the fact that closely related taxa share common ontogenies also have their explanation in a combination of internalist, externalist and historical factors.

SUMMARY AND CONCLUSIONS

Ontogenies are relatively stable, conservative phenomena that tend to characterize entire lineages. Within monophyletic groups, homoplasies alert workers to the possibility of heterochronic analysis to explain changes in morphology. Heterochrony is likely to remain a popular explanation for morphological changes in evolution. In the case of morphological novelties, the processes associated with heterochrony are attractive as possible

explanations for the establishment of new associations during ontogeny that can give rise to new causal generative patterns. At present, there is a debate between neodarwinist (functionalist) and developmentalist (structuralist) schools as to which mode of explanation has primacy in understanding the evolution of morphology. A dialectical synthesis in which the formally incompatible viewpoints remain separate while making their unique contributions offers the best opportunity for understanding the evolution of novelty within a framework of ontogeny and phylogeny.

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