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HOMOPLASY: THE RESULT OF NATURAL SELECTION, OR EVIDENCE OF DESIGN LIMITATIONS?

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Abstract.—Similarity in morphological form may arise from common ancestry (failure to evolve), from parallel evolution, from convergence, or from reversal to an apparently ancestral condition. Homoplasy from convergence, parallelism, and reversal is common, and its ubiquity creates difficulties in phylogenetic analysis. Convergent evolution often is considered one of the most powerful lines of evidence for adaptive evolution. But an alternative explanation for convergence and other evolved similarities is that limited developmental and structural options exist. Identical forms can be obtained when particular developmental phenomena are triggered by very different kinds of stimuli or when constraints exist that shape external form or limit morphological expression to a few options. Examples from plethodontid salamanders are used to illustrate an approach combining internalist and externalist analytical methods. In order to explain how morphologies evolve in lineages, both functionalist and structuralist approaches are necessary, combined in a context in which phylogenetic hypotheses and their tests are continuously pursued. When homoplasy is rampant, as in salamanders, we can expect discordance with phylogenetic analyses based on nonmorphological data sets.

Recently Allan Larson and I argued that an understanding of the evolution of biological form—morphology—was unlikely unless one combined two distinct and independent approaches: neo-Darwinian functionalism and biological structuralism, in a context of rigorous phylogenetic analysis (Wake and Larson 1987). In this article, derived from my presidential address to the American Society of Naturalists, an organization dedicated to the conceptual unification of biological knowledge, I expand on this theme.

Our approach requires that structuralism, with its focus on organism-level phenomena such as the generation, self-organization, and transformation of specific form (see Piaget 1970; Webster and Goodwin 1982; Goodwin 1984; Rieppel 1989), and neo-Darwinism, with its focus on population-level phenomena and historical contingency, must be used concurrently, even while their differences and separate domains of explanation are retained. In this way, conflicts between the different modes of explanation are highlighted and interpreted, not simply argued away or ignored by default.

My central theme is the phenomenon of nondivergent evolutionary change among lineages, including convergent morphological evolution, parallelism, and some kinds of reversal—in other words, what phylogeneticists term homoplasy

(Simpson 1961; Hennig 1966; Wiley 1981; Patterson 1982). Convergence and parallelism (for a useful discussion of the distinction between these terms, see Patterson 1988) often are considered to constitute strong evidence of the functioning of natural selection. Patterson stated, "The general explanation for convergence is functional adaptation to similar environments" (1988, pp. 616–617), but I argue that alternatives must always be considered. In recent years increasing attention has been given to the possibility that parallelism is a manifestation of internal design constraints (see, e.g., Alberch 1989), and so both functionalist and structuralist constructs predict its occurrence.

The ubiquity of homoplasy is a major concern in phylogenetic analysis (e.g., Rieppel 1989; Sanderson and Donoghue 1989), which ironically is its primary means of detection. One assumes that homoplasy is sufficiently rare that, when parsimony is used in interpreting results of the application of cladistic methods to large data sets, an accurate assessment of genealogical relationships is obtained. But the level of homoplasy varies among taxa, and it is of interest to inquire why and to investigate causative factors. If homoplasy is rampant, existing cladistic methods fail.

To discuss homoplasy implies that one understands homology, one of the most ancient and difficult of biological topics. Homoplasy is essentially false homology, and Patterson (1982) proposes three tests for its detection: similarity, congruence (essentially phylogenetic analysis in the hands of most systematists), and conjunction. Parallelism fails only the congruence test, while convergence fails both the similarity (only "superficial" similarity, see below) and the congruence tests. Patterson does not specifically deal with reversal, but it seems likely that it would be considered a kind of parallelism in his scheme.

The taxon I study, the salamander family Plethodontidae, displays substantial homoplasy. The family includes well over 200 species, and the level of homoplasy is known to increase as the number of taxa included in a study increases (Sanderson and Donoghue 1989). I argue that both functionalist and structuralist explanations are necessary to explain the biological bases and evolutionary significance of the morphological homoplasy that is routinely encountered by me and other systematists.

My research focus is the family Plethodontidae, the lungless salamanders, and my examples all come from this group. Isolated cases lack the impact that arises when one must confront the often conflicting lines of evidence that arise from a long-term focus on the evolution of a diverse monophyletic taxon. My specific examples range from ecomorphology at the level of the whole organism to complex integrated systems, such as feeding, and even include alternative states of a single osteological character. I purposely take a broad perspective on biological form. For a morphologist such as myself, homoplasy is fundamentally a concept of form—two distantly related organisms are convergent if they have evolved similar features from nonhomologous ancestral states. The convergent forms may function similarly, but similarity in physiological performance or ethological or ecological biological role is neither assumed nor expected (Wake 1982a).

Several themes, not necessarily independent, emerge.

1. *The bauplan*.—There is a place in modern biology for the concept of the bauplan (cf. Rieppel 1988; Wagner 1989), which is manifest in design parameters that set limits to morphological variation, make reversion to developmental default states expected, and lead to evolutionary stopping points. The bauplan promotes parallelism, as well as reversal to ground plans.

2. *Heterochrony*.—Evolutionary changes in the timing of development among taxa can strongly influence form generation, and these become manifest in the morphological expressions of paedomorphosis and peramorphosis (Alberch et al. 1979). The evolutionary significance of paedomorphosis is debated, but salamander biologists, confronted by vivid examples such as the axolotl, are convinced of its importance. Permanently larval forms have evolved repeatedly within the order Caudata, and some of the most persistent phylogenetic questions concern the relationships of such genera as *Siren*, *Necturus*, and *Proteus* (Hecht and Edwards 1977). These larval forms represent parallel truncation of ontogeny by paedomorphosis. However, heterochrony is important in less dramatic but more pervasive and ultimately more significant ways. The most insidious effects are (1) paedomorphic homoplasy, the phylogenetic reversal of individual morphological traits to apparently ancestral states (from “backing down” ontogenetic trajectories in cases of prior recapitulatory evolution) or the parallel evolution of similar juvenile traits, and (2) peramorphic homoplasy, parallel phylogenetic extensions of ontogenies (McNamara 1986; Wake 1989). Parallelism is promoted when multiple features of organisms are affected simultaneously in species with direct development, which accordingly lack the telltale persistent larval state (Alberch and Alberch 1981).

3. *Genomic constraints on morphogenesis*.—Cellular and molecular phenomena have major implications for organismal and evolutionary biology in unexpected ways. Specifically, the enormous genome sizes of salamanders impose on them large cells and slow cell cycles, with many implications for biological form and evolutionary pattern. Plethodontid genomes range in size from about 12 to nearly 80 pg DNA per haploid genome (Sessions and Larson 1987) and are the largest genomes of any terrestrial vertebrate, exceeded among vertebrates only by those of lungfishes. Phenomena at the molecular level, such as increased genome size, can generate homoplasy at higher levels of organization.

4. *Adaptation and its consequences*.—Ecological specialization driven by natural selection can lead to severe tests of design limitations and to the dissolution of constraints on features quite unrelated to the specialization in question. Ecological specialization leads to convergence and, in the context of developmental constraints, to parallelism. Specifically, I examine microhabitat specialization, locomotion, miniaturization, age at maturity, and modifications of ancestral biphasic life cycles, all of which relate directly to different kinds of homoplasy.

5. *Interaction among constraints at different hierarchical levels*.—Hierarchical organization can have profound implications for homoplasy, especially in situations in which downward causation (such as population ecological limitations on body size) and upward causation (such as cell size) simultaneously affect a focal level (in this case, the individual organism).

THE PLETHODONTID SALAMANDERS

Herpetologists generally have considered the lungless salamanders of the family Plethodontidae to be the most highly derived of the 9 or 10 families of salamanders (see, e.g., Duellman and Trueb 1986). About two-thirds of living species of salamanders are included in the family. Plethodontids have a wide range of life histories and ecologies and occupy a full array of habitats, from strictly aquatic to fully terrestrial (Wake 1966). The relatively small subfamily Desmognathinae is restricted to eastern North America, but the large subfamily Plethodontinae, with three tribes, is more widespread.

Plethodontids are the only salamanders that have been successful in the tropics, in the sense that they are widespread (latitudinally, altitudinally, and ecologically) and represented by many species. All tropical species (salamanders occur only in the New World tropics) are members of a phylogenetic "twig," the supergenus *Bolitoglossa* of the tribe Bolitoglossini. This single lineage has undergone an extraordinary radiation, centered in Middle America. The supergenus includes about 45% of all species of salamanders, and their evolution has featured extreme specialization and adaptive radiation of a highly derived ancestral stock (Wake 1970a, 1987; Wake and Lynch 1976). The tropical salamanders have evolved with substantial homoplasy, and my attempts to solve the formidable phylogenetic problems that result have been a driving force in the development of ideas presented in this article. Progress is being made in defining monophyletic taxa among the approximately 150 species (Wake 1966; Wake and Elias 1983; Wake and Johnson 1989), but problems remain.

Within the tropics, ecological generalists and more ancestral lineages are found at middle and high elevations; ecological specialists occur in specific microhabitats and elevational zones, usually associated with cloud-forest bromeliads, lowland fossorial habitats, and lowland arboreal habitats. Because so little was known concerning these organisms—and in order to pursue the study of adaptation, morphological evolution, and phylogenetics outlined in the introduction—I established a series of elevational transects between Veracruz, Mexico, and western Panama (Wake 1987; Wake and Lynch 1976; Wake et al. 1991). As many as 23 species (the highest number anywhere in the world) are distributed along a single long transect. Morphological homoplasy is common in phylogenetically independent lineages occupying different regions (e.g., convergence in body form among small bromeliad-dwelling members of the genera *Chiropterotriton* in eastern Mexico, *Dendrotriton* in Nuclear Central America, and *Nototriton* in Talamancan Central America) and even within regions (as in the evolution of interdigital webbing in species of different groups of *Bolitoglossa*; Wake 1987). Some general features of the tropical salamanders, in addition to their relative morphological simplification, include specialized visual systems featuring large, frontally oriented eyes (Roth 1987), a highly projectile tongue used for feeding on terrestrial arthropods (Lombard and Wake 1977), and direct development in which eggs are laid at terrestrial sites and the aquatic, larval stage is bypassed. With one exception (an undescribed aquatic species from Mexico), all of the species appear to be strictly terrestrial throughout life.

The following examples of homoplasy in plethodontids exemplify my analytical approach. All examples arise from problems initially pursued in the bolitoglossines, but in every instance a broader frame of reference is required.

DESIGN LIMITATIONS AND HOMOPLASY

The Premaxillary Bone

My first example is a relatively well-understood, but very complex, case: the alternative forms of the premaxillary bone in plethodontid salamanders (Wake 1966, 1989; Wake and Larson 1987; Larson 1991). In most nonplethodontid salamanders, the bone arises as a paired structure at the front of the skull and remains paired throughout life. In some taxa the bones fuse during ontogeny. Parallelism and reversal have characterized the history of fusion and separation of the premaxilla in plethodontids.

A cenogenetic novelty inferred to have been inserted into the larval stage of a plethodontid ancestor suggests a functional interpretation: fusion associated with improved feeding performance in larvae became a fixed feature of the normal ontogeny and now constitutes a synapomorphy of the family. The plesiomorphous ontogeny in the family is for the larval or embryonic bone to separate at metamorphosis or, in direct developing forms, at about the time of hatching. This restores the plesiomorphous state (two separated bones) for the order Caudata; the bones essentially revert to the bauplan. This sequence of events persists even in the face of evolution of direct development and loss of the larval stage; this is significant, for it means that the ontogenetic trajectory stabilized once it was modified by cenogenesis. Subsequently, evolution of a single bone in adults has proceeded in parallel in different plethodontid lineages by paedomorphosis (retention of the larval or embryonic state, generally but not necessarily nonadaptive as far as the premaxilla is concerned) or by peramorphic fusion (adaptive evolution associated with strengthening of the jaws).

This example illustrates the phylogenetic persistence of bauplans and the existence of a default state associated with metamorphosis. The point is that an analysis of the potentialities and the limits of morphogenetic systems that characterize lineages may provide a unique perspective on how morphological evolution proceeds and on why patterns of change are so restricted and stable. It is not the adapted larval skull that influences adult skull form, but rather a default to ground plan, which restores an ancestral pattern. This example also illustrates the need for an appreciation of the whole ontogeny of a character, its holomorphology, as opposed to its instantaneous manifestation, say, in an adult (e.g., de Queiroz 1985).

Numbers of Digits

The ancestral condition for salamanders, found in the vast majority of living species and in fossil out-groups, is four digits in the forelimb and five in the hind limb (Shubin and Alberch 1986). However, species with four digits (toes) on the hind limb are found in several different families (e.g., Plethodontidae, Salamandri-

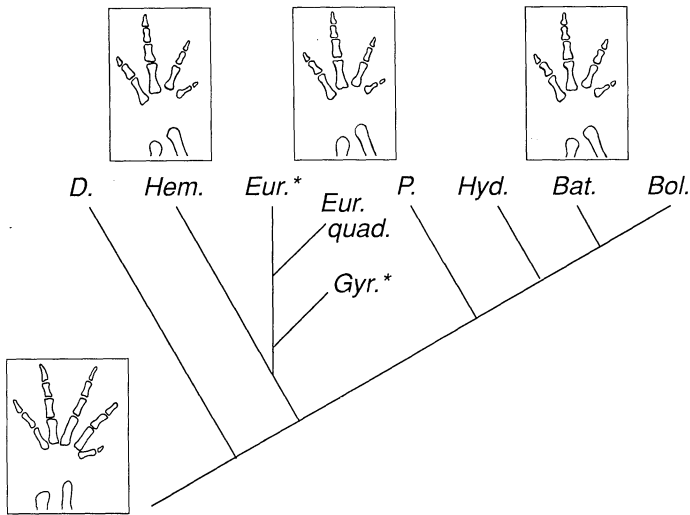


FIG. 1.—Scenariogram illustrating digital loss in the family Plethodontidae. The distal ends of the tibia and fibula, the metatarsals, and the phalanges are drawn; the tarsals and joints are cartilaginous in these species. The independent evolution of four toes from an ancestral five-toed state has taken place in three separate lineages. This is a collapsed cladogram (based on Lombard and Wake 1986) in which only the most inclusive relevant taxa are shown. *D.*, subfamily Desmognathinae; *Hem.*, *Hemidactylum*; *Eur.**, all members of the genus *Eurycea* except *Eurycea quadradigitatus*; *Eur. quad.*, *E. quadradigitatus*; *Gyr.**, all members of the tribe Hemidactyliini except *Hemidactylum* and *Eurycea* (*Gyr.** is probably paraphyletic); *P.*, tribe Plethodontini of the subfamily Plethodontidae; *Hyd.*, *Hydromantes*; *Bat.*, *Batrachoseps*; *Bol.*, supergenus *Bolitoglossa*.

dae, Hynobiidae). Figure 1 is a "scenariogram" (see Wake and Larson 1987), a collapsed cladogram (based on phylogenetic hypotheses discussed in Lombard and Wake 1986) in which only relevant taxa and otherwise most inclusive taxa are illustrated. Within the Plethodontidae, four toes occur in widely dispersed lineages: in the genera *Batrachoseps* and *Hemidactylum* and in one species in the genus *Eurycea* (Shubin and Alberch 1986; Wake and Larson 1987). Factors controlling limb and digit development have been studied extensively in salamanders, and many aspects are well understood (see reviews in Shubin and Alberch 1986; Bryant et al. 1987; Sessions and Larson 1987; Oster et al. 1988). In contrast to the situation in lizards, in which digital and limb reduction has evidently been a gradual process (Lande 1978; Lande also defined conditions under which limb loss in amniotes could occur rapidly), evolutionary modifications of developmental events in the limb bud of amphibians result in the production of entire (rather than partial) digits in the postaxial portion of the limb; experimental disruption of developmental regulation (e.g., with the mitotic inhibitor colchicine) mimics patterns seen in nature (Alberch and Gale 1985). Although cellular-level controlling factors remain to be discovered, there are important correlations between the number of digits in amphibians and such phenomena as cell size (di-

rectly related to genome size), cell number, and the number and size of cells in limb buds of different size.

The four-digitated feet of unrelated salamander taxa are nearly identical in structure, and they are produced independently by the operation of one of the two developmental options, which produce either four or five toes. This is a direct example of design limitations, in which alternative states are sharply defined. One might predict that four-toed variants would appear in species with small limb buds, in species with large genomes (and hence relatively few cells in limb buds), or both. The miniaturized species *Parvimolge townsendi* of eastern Mexico has five toes, but individuals with four have been found. The outer (postaxial) toe of the four-toed individuals is larger than the fourth toe of five-toed individuals. This toe contains either one or two skeletons (fig. 2), direct evidence of the existence of design limitations. Alberch and Gale (1985) found a similar phenomenon in a large species of *Bolitoglossa* that has a large genome.

A possible reverse example is a case involving *Batrachoseps wrighti*, a member of a genus that normally has four toes. A single individual more than 10% larger than any other member of the species so far reported has one hind limb bearing five toes (Brame 1964). However, there are only three, instead of the normal four, metapodial elements; two of these are much larger than normal, and each is bifurcated so that five digits appear distally (fig. 2). Only experimental studies will determine whether abnormalities such as this are more likely in relatively larger individuals (with correspondingly different balances between limb bud dimensions and cell numbers), as I suspect. Alternatively, this may be a case of abnormal regeneration following injury (although no other evidence of injury is present).

These examples show that homoplasy, in this case parallelism, can be a manifestation of design limitations in the form of developmental constraints, which are only indirectly related to adaptive processes. Thus, selection for very small size may have, as an incidental side effect, the loss of a toe. A functionalist interpretation would view this as a correlated response to selection; a structuralist would focus on design limitations.

Organization of Wrists and Ankles

The wrist and ankle (mesopodia) of plethodontids consist of a group of cartilages that arise during development by processes of condensation, segmentation, and bifurcation of blastemal masses (Shubin and Alberch 1986; Oster et al. 1988). There are many conceivable organizations for this complex set of elements (primitively, eight in the wrist and nine in the ankle), but variation is highly ordered, and only a few of the possible variant conditions are found, even in cases in which higher-than-expected amounts of variation are encountered (Hanken 1982, 1983a, 1985; Hanken and Dinsmore 1986). The ordering is sufficiently great that comparative anatomists have named each element and treated the named units as homologues, a procedure that has been challenged by some developmental biologists (e.g., Goodwin and Trainor 1983). Relatively few rearrangements of the ancestral patterns are found in plethodontids, but all that characterize species or genera have arisen more than once (Wake and Larson 1987).

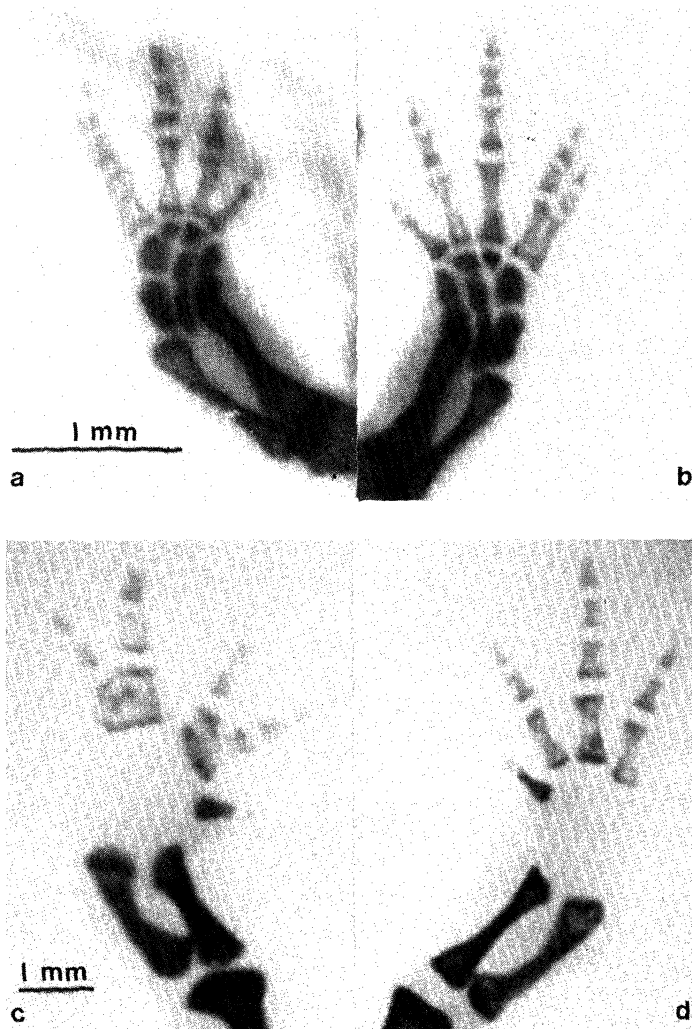


FIG. 2.—Hind feet of abnormal individuals of two species of plethodontid salamanders, printed directly from radiographs. *Above*, a specimen of *Parvimolge townsendi*, a normally five-toed species from Mexico. *a*, Its four digits and four skeletons on the left (the last digit of abnormally large diameter); *b*, the corresponding five skeletons, within a single external fourth digit on the right (the tarsals are often ossified in this species, as in the specimen radiographed). *Below*, a specimen of *Batrachoseps wrighti*, a normally four-toed species from Oregon. *c*, An abnormal pattern showing a bifurcation of two metapodial elements resulting in five digits; *d*, the normal pattern.

Functionally significant rearrangements associated with climbing have arisen independently in the genera *Aneides* (Wake 1963) and *Chiropterotriton* (Wake 1966). I restrict the treatment to the distal postaxial portion of the tarsus, in which the ancestral condition finds a large distal tarsal 4 (dt 4) contacting the fibulare, thereby preventing the small dt 5 from articulating with the centrale. In the derived condition, dt 5 is large and articulates with the centrale, thus excluding the relatively small dt 4 from articulating with the fibulare (fig. 3). The discovery of apparently atavistic variants in different species suggests a possible morphogenetic mechanism. In one variant (a specimen of *Pseudoeurycea anitae*) an extra element ("m") is present, and dt 4 and dt 5 are of approximately equivalent size (fig. 3). The tissue that in the variant forms a separate element is incorporated into dt 4 in the ancestral condition (and other individuals of this species), but a kind of developmental switch permits it to become associated with dt 5 to produce the functionally significant rearrangement. Recently Neil Shubin and I discovered the alternative variant in an adult *Aneides flavipunctatus*. In this specimen we also found element m, in this case disconnected from dt 5. This entire area remains undivided in a number of bolitoglossine genera, all of which have large genomes, small size, or both, and here the element has been termed dt 4-5 (but it also incorporates m); it is unclear how many times this derived failure to separate has evolved (Wake and Elias 1983).

The point of this example is that adaptively significant changes can arise from alternative developmental states, which themselves may be determined by phenomena that operate at different hierarchical levels, such as that of the whole organism (reduction in body size by paedomorphosis), at the molecular and cellular levels (by increases in genome and cell size), which lead to a reduction in the number of limb bud cells, or to a failure of blastemal masses to segment and/or bifurcate.

Vertebral Joints

The intervertebral joint varies in structure among salamanders in ways that have so far defied attempts at functional interpretation. In the majority of plethodontids, the intervertebral joints are not well differentiated. The notochord, which in adults contains cartilage and is an important skeletal element, persists throughout life. Between the husklike, ossified centra lies a spindle-shaped intervertebral cartilage, which is interrupted by invasive fibrocartilage so that a kind of ball-and-socket joint (functional opisthocoely) results (Wake and Lawson 1973). In distant out-groups, such as members of the family Salamandridae, as vertebral growth proceeds, the lateral walls of the developing centra move around longitudinally aligned blood vessels; as the blood vessels finally reach the cartilage inside the centrum, the intervertebral cartilage ossifies basally, producing a true bony condyle, capped with cartilage only in the joint region (Wake 1970b). The notochord disappears or is reduced to a crushed remnant. An identical phenomenon has evolved in the large plethodontid salamander *Phaeognathus*, a strong burrower, and it may well be that the strong intervertebral articulation of this form has adaptive significance. But bony condyles also are encountered as rare variants

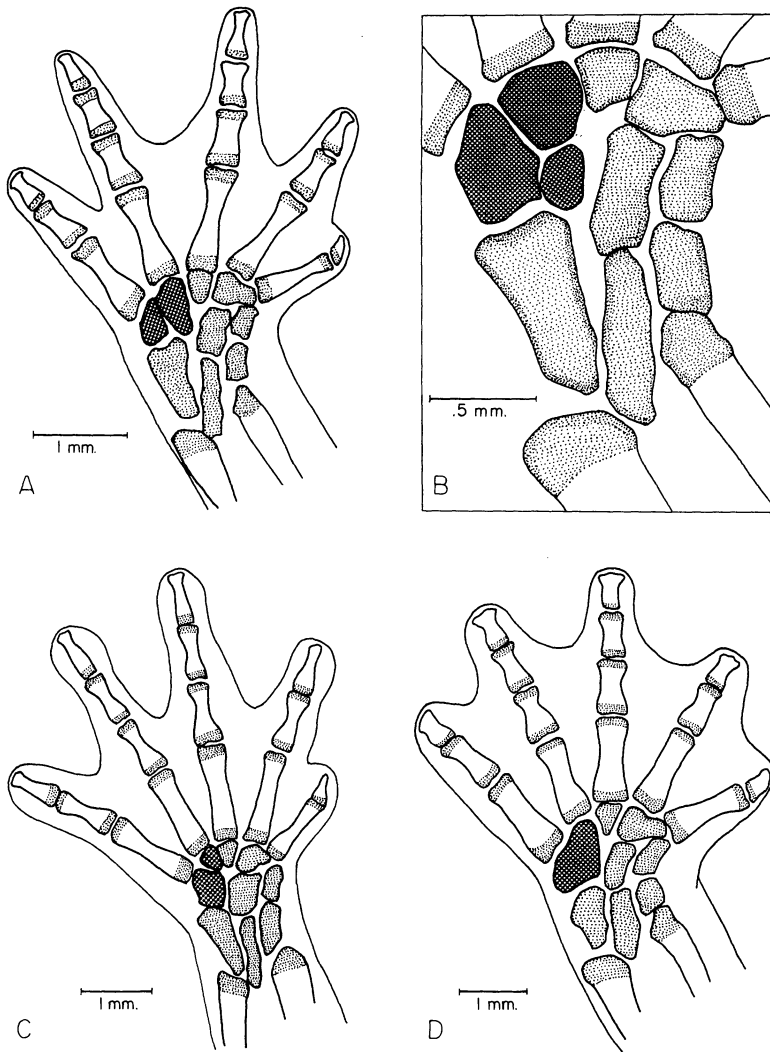


FIG. 3.—Mesopodial elements in some plethodontid salamanders. Bone is outlined, and cartilage stippled. The darkly stippled cartilaginous tarsals show different arrangements. A, Typical ancestral pattern, as seen in *Pseudoeurycea anitae* (dt 4 is large, and dt 5 is small); B, unusual pattern encountered in an adult *P. anitae* (bilaterally symmetrical), in which dt 4 and dt 5 are of equal size, and an atavistic additional element, “m” is present; C, typical pattern in *Chiropterotriton* (also seen in *Aneides*), in which dt 5 is large, and dt 4 is small; D, typical pattern in *Bolitoglossa* (also found in several other tropical genera, in which dt 4, dt 5, and possibly element m are combined in a single unit).

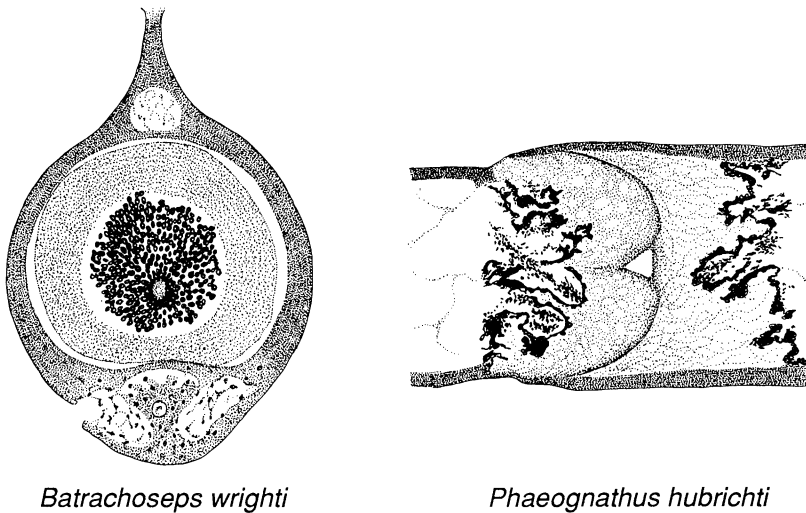


FIG. 4.—Unusual intervertebral joints in plethodontid salamanders. *Left*, cross-section of a trunk vertebra showing the large spinal cord filling the vertebral canal, and the small centrum underlying it. The centrum, normally filled with cartilage in plethodontid salamanders, has been invaded by lateral blood vessels and largely converted to bone, but a small notochordal remnant (circle) remains. *Right*, longitudinal section of a trunk vertebra through two centra in the region of an intervertebral joint in a stout-bodied, burrowing species. The condyle (to the left) and the cotyle (to the right) of adjacent centra are cartilaginous, but the cartilage rests on an ossified cap (dark black), such that an opisthocoelous condition is attained; anterior is to the right.

in species of moderate size, such as in a specimen of *B. wrighti* in which blood vessels have invaded the lateral surfaces of a few anterior vertebrae (fig. 4), with the posterior vertebrae retaining the apparently ancestral notochordal vertebrae.

A superficially similar but developmentally entirely different arrangement has evolved in several diminutive bolitoglossine genera (Wake 1970b). In *Thorius*, the nervous system is extraordinarily large compared with the skeletal system (Wake 1970b; Hanken 1983b; Roth et al. 1988, 1990). In hatchlings, the neural canal is relatively enormous, and the centrum is what one would expect in a salamander of its size. During later ontogeny, the neural canal is eroded from inside, and bone accretes to the outside, thereby accommodating the relatively rapid growth of the spinal cord. As a result, the dorsal surface of the centrum, which is also the ventral floor of the vertebral canal, erodes away, and the cartilage is exposed to the blood vessels lying inside the canal. Ossification of the intervertebral cartilage ensues, and a miniature duplicate of the condyle of large species such as *Phaeognathus* occurs, by cellular processes that I suspect are identical (inferred from work of Shapiro et al. 1988) but as a result of very different morphogenetic pathways. Thus, complex homoplasy results, with miniatures displaying parallel evolution that is simply an outcome of miniaturization, other

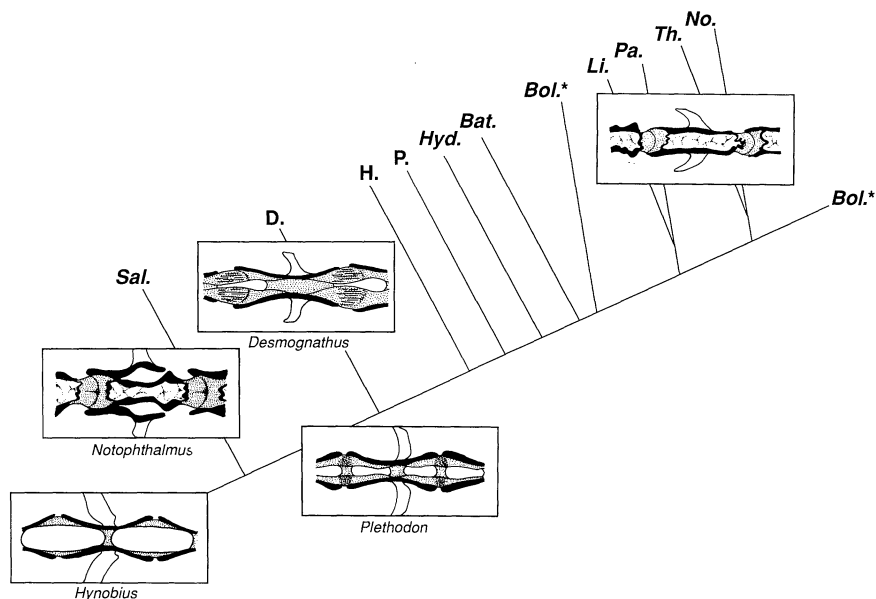


FIG. 5.—Scenariogram for the evolution of vertebral articulations in salamanders based on phylogenetic hypotheses of Duellman and Trueb (1986) and Lombard and Wake (1986). The boxes show longitudinal sections through one complete centrum and two intervertebral joints. Black, bone; stippling, cartilage. Anterior is to the right. The situation in *Hynobius* and *Plethodon* is ancestral and shows nonossified joint regions. Ossification has occurred in *Notophthalmus* by one mechanism, and in *Thorius* and species of three other genera by another. A third condition is seen in *Desmognathus*, in which the condyle is mineralized cartilage; the sister taxon of *Desmognathus*, *Phaeognathus* (fig. 4), has carried this one step further to ossification, in parallel with the situation in *Notophthalmus*. The condition in *Thorius* is convergent. *Sal.*, Family Salamandridae; *D.*, subfamily Desmognathinae of the Plethodontidae; *H.*, tribe Hemidactyliini of the plethodontid subfamily Plethodontinae; *P.*, tribe Plethodontini of the subfamily Plethodontinae; *Hyd.*, *Hydromantes*; *Bat.*, *Batrachoseps*; *Bol.**, members of the supergenus *Bolitoglossini* other than the bolitoglossines *Lineatriton*, *Parvimolge*, *Thorius*, and *Nototriton* (this is shown as a paraphyletic assemblage); *Li.*, *Lineatriton*; *Pa.*, *Parvimolge*; *Th.*, *Thorius*; *No.*, *Nototriton*.

species displaying convergent evolution (different morphogenetic pathways) that is itself subject to parallelism, and the family as a whole illustrating homoplasy in the form of reversal in comparison with distant out-groups (fig. 5).

This example shows that even in functionally highly significant structures such as joints, specific morphology can arise for entirely incidental reasons. A complex developmental trajectory may be abbreviated or truncated (as in the ancestral plethodontids compared with salamandrid out-groups, possibly by paedomorphic truncation), but this trajectory also can be "entered" at different points in ontogeny by different morphogenetic routes. Once again the need for a multidimensional analytical approach is evident.

ECOMORPHOLOGY AND HOMOPLASY

Elongation and Fossorial Specialization

Fossorial specialization in salamanders includes elongation, attenuation, and limb reduction. Most genera of tropical salamanders display no variability in numbers of trunk vertebrae, but in out-groups even intrapopulational variability is common. This fixed number of vertebrae appears to act as a constraint on elongation, precluding selection for increased vertebral numbers. In the Mexican genus *Lineatriton*, however, a unique developmental pattern has evolved in which the individual vertebrae have elongated to produce an extremely attenuate body form (Tanner 1950; Wake and Lynch 1976). This is a "giraffe-neck" solution to the problem of how to become elongated. The only genus of tropical salamanders showing vertebral variability is another fossorial genus, *Oedipina*, which occurs south and east of the Isthmus of Tehuantepec. Here a common homoplasy is encountered, one seen not only in bolitoglossines (e.g., *Batrachoseps*), but also in other plethodontid taxa (e.g., *Plethodon*, *Phaeognathus*) and in other salamander families (e.g., Amphiumidae, Sirenidae), in which an evolutionary alteration has affected segmentation during development, so that elongation is accomplished by adding trunk vertebrae. At one time, all tropical fossorial species (members of the currently recognized genera *Oedipina* and *Lineatriton*) were included in a single genus (Taylor 1944). This was bad taxonomy (corrected in Tanner 1950), for here is an example of a true convergence, which arises from different morphogenetic mechanisms. I envision only the two morphogenetic options that have been exercised to produce elongation in salamanders: one is common and expected; the other is unique and represents a novel response to selection. All close relatives of *Lineatriton* have a fixed number of trunk vertebrae; the only variation on which selection could work was in vertebral length, not vertebral number.

In this example, homoplasy is a phenomenon of the whole organism. Related lineages independently have adapted to similar microhabitats by assuming essentially identical ecomorphologies based on fundamentally distinct morphogenetic mechanisms (change in shape vs. change in number). Although convergence in this instance might be interpreted as evidence of natural selection (although not within the more rigidly defined criteria of Endler 1986), there also is evidence of design limitations (the oddly elongated vertebrae are unique to *Lineatriton*) that make certain responses (increases in numbers of segments) more likely than others. In short, there is a bias to the direction of evolution.

Tail Autotomy and Defense against Predation

All tropical salamanders are capable of autotomizing the entire tail as a defense against predators. Under attack, a salamander disengages the tail, which then whips back and forth in a violent and dramatic manner while the animal lies quietly. At least some predators are attracted by the active tail, and when they eat it they receive a distasteful if not poisonous dose of secretion from the abundant "poison" glands (Hubbard 1903; Brodie 1983).

The functional morphology of tail autotomy is relatively well understood (Wake and Dresner 1967). Typically, there is a constriction at the base of the tail where one finds one or two shortened vertebrae, a shortened muscular segment, and weakened connective tissue. In contrast to the well-known convergent situation in lizards, in which an autotomy plane exists within one or more vertebrae, the vertebrae of salamanders disengage without separating into two halves. A precondition for tail autotomy restricted to a single spot is a wound-healing specialization that is widespread in plethodontids. When the tail is forcibly broken in species with this specialization, the skin breaks a full segment behind the muscle, leaving a sleeve of skin that collapses over the wound, staunching the flow of blood and facilitating blastema formation and regeneration; a perfect tail, lacking only the notochord, is regenerated. In order for this mechanism to function, a precise coordination of parts is required.

Tail autotomy has evolved to a high degree of specialization in plethodontids (but in no other salamanders) at least three times (*Hemidactylium*, *Ensatina*, supergenus *Bolitoglossa*), each event featuring a unique combination of morphological specializations associated with basal constriction (fig. 6; Wake and Dresner 1967). A different kind of specialization has evolved in *Batrachoseps*; no basal constriction is found, but specialized points of separation occur at each segmental boundary in the tail. Furthermore, in *Lineatriton* and *Oedipina* (two unrelated bolitoglossines), secondary convergence has twice given rise to the condition seen in *Batrachoseps*.

In the ancestral condition there are three caudosacral vertebrae. Two exist in desmognathines and in the supergenus *Bolitoglossa*, and two or three are found in *Batrachoseps*. The independent points of acquisition of tail autotomy are indicated in figure 6. What appears to be a "key innovation" (Larson et al. 1981, pp. 415–419) is the evolution of a wound-healing specialization in the lineage leading to the tribes Plethodontini and Bolitoglossini. A different and less effective kind of wound-healing specialization has evolved (perhaps more than once) independently in the tribe Hemidactyliini (Wake and Dresner 1967). Because tail autotomy has evolved only in species that inherited some kind of wound-healing specialization, I conclude that some such specialization in morphology is a necessary, but not sufficient, condition for the evolution of true tail autotomy.

This example shows that discrete variations on a theme occur once a particular adaptation has become fixed. These variations are limited by specific functional and design constraints. A precise coordination of structural modifications at specific points in the segmented body is necessary, and in species in which variation in vertebral number occurs, maladaptive organization can result (e.g., in the *Ensatina*; Frolich 1991).

Foot Webbing, Locomotion, Development, and Ecology

Virtually all lowland species in the large tropical genus *Bolitoglossa* (which includes about 20% of the species of living salamanders) are arboreal to some degree, and they all have webbed hands and feet. Some of these species, usually the larger ones, have extensive interdigital webbing and are capable of generating suction (Alberch 1981). However, other species, usually miniaturized species that

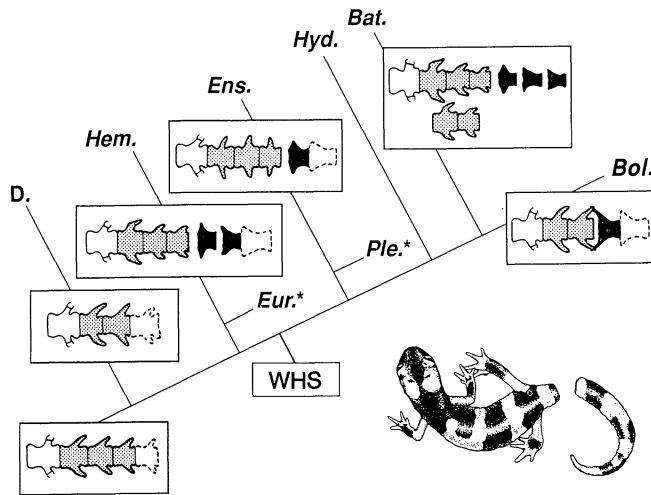


FIG. 6.—Scenariogram illustrating the evolution of tail autotomy in plethodontid salamanders. A collapsed cladogram (based on Lombard and Wake 1986) shows the distribution of specialized zones of separation of vertebrae in the tails of plethodontid salamanders. Anterior is to the left; the view is dorsal. *Open vertebrae with solid outlines*, sacrum; *stippling*, caudosacral vertebrae; *black*, vertebrae in front of which autotomy occurs; *open vertebrae outlined with dashed lines*, nonautotomic caudal vertebrae. *Eur.**, all members of the Hemidactyliini except *Hemidactylum*; *Ple.**, all members of the Plethodontini except *Ensatina*; *Ens.*, *Ensatiini*; *WHS*, wound-healing specialization. Other abbreviations are as in fig. 1.

are paedomorphic in much of their morphology, have apparently webbed feet that are in reality rather undifferentiated pads that cannot generate suction (Alberch 1981; Alberch and Alberch 1981). The limb buds of plethodontid embryos first produce a padlike structure, and as development proceeds the digits grow out of these pads. The paedomorphic species truncate development at the pad stage, and thus, as adults, they have feet that are superficially similar to the highly specialized webbed feet of congeners (fig. 7), which arise from secondary growth of skin between the nearly normally developed digits. The extremely complex phylogenetic pattern is slowly emerging as monophyletic groups are being identified (Wake and Lynch 1976; Larson 1983; Elias 1984). Often, in lowland areas (as in Nuclear Central America), two kinds of *Bolitoglossa* co-occur, one large with webbed feet and the other small with padded feet, and these may be close or distant relatives. When one examines another region (e.g., Talamancan Central America), one again finds this pattern, but the lineages represented are apparently independent (Wake and Lynch 1976).

In the caves of northern Mexico lives a strange salamander, *Chiropoterotriton magnipes*, unrelated to *Bolitoglossa* (Rabb 1965; Darda 1988) but resembling many species of that genus in having extensive interdigital webbing in its prominent hands and feet (fig. 7). Here webbing has evolved in complete independence of that in *Bolitoglossa*, apparently as an adaptation for clinging to wet, smooth walls and ceilings of caves.

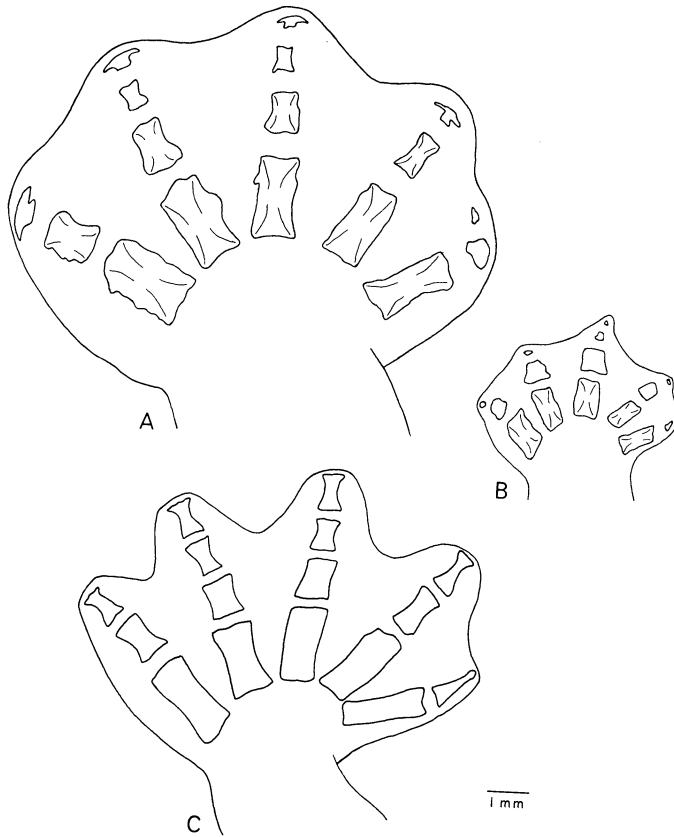


FIG. 7.—Fully webbed feet of three convergently derived taxa of tropical bolitoglossine salamanders. Only outlines of the entire foot and of the ossified parts of the digits are indicated. *A*, *Bolitoglossa salvinii*, a Guatemalan species with enlarged feet in which cutaneous webbing has grown between the digits. *B*, *Bolitoglossa rufescens*, middle American species with small, padlike feet that superficially appear to be webbed but are developmentally immature, pedomorphic structures. *C*, *Chiropterotriton magnipes*, a cave-dwelling species from northern Mexico with enlarged feet in which cutaneous webbing has grown between the digits.

The point of this example is that both direct adaptation (an increase in webbing associated with efficient production of suction that is used to maintain perch, or with increasing surface tension to cling to smooth, wet surfaces) and indirect effects of miniaturization achieved through pedomorphosis can produce superficially similar outcomes. Both of these outcomes can facilitate ecological specialization for arboreal life: large webbed feet produce suction, whereas miniaturized salamanders can move effectively along arboreal surfaces and hide in leaf axils. But neither is specific for arboreal life: some pedomorphs are upland terrestrial forms, and some webbed forms live in caves at middle elevations, not in lowland arboreal habitats. Foot shape in pedomorphs appears to be largely unrelated to specific function, even in arboreal microhabitats, and parallelism in pedomorphs

arises from design limitations (the nature of early development). In contrast, species with increased webbing are responding in parallel ways to generally similar selection for clinging ability, but in different ecological contexts.

HIERARCHICAL FACTORS AND HOMOPLASY

Tongue Evolution

Terrestrial salamanders feed exclusively by apprehending their prey, typically small arthropods for plethodontids, with the tongue. Plethodontid salamanders have the longest, fastest, and most accurate tongues among salamanders and can fire the tongue a distance equivalent to one-third the length of the body in 7.7 ms (Larsen et al. 1989). Different taxa display differences, often subtle, in the way in which tongues are projected. Three functional classes are recognized: attached protrusible (the ancestral condition), attached projectile, and free projectile (Lombard and Wake 1977). Whereas earlier workers thought that free projectile tongues had evolved only once (Tanner 1952; von Wahlert 1957), each of the derived functional classes is now thought to have evolved three times within the Plethodontidae (Lombard and Wake 1977, 1986). These arguments are based on biomechanical considerations (e.g., the recognition that there are two folding options for skeletal components during tongue projection, both of which have been used) and phylogenetic considerations (the hypothesis of a single origin of free projectile tongues is considerably less parsimonious than that of alternatives).

Elsewhere (Wake 1982*b*; Roth and Wake 1985; Wake and Larson 1987), it has been argued that the evolution of this complex, integrated system can best be understood by using both functionalist and structuralist perspectives. A series of necessary, but not sufficient, conditions establishes a framework within which homoplasy becomes increasingly probable (fig. 8). Loss of lungs, a synapomorphy for the Plethodontidae, frees the hyobranchial skeleton from the functional constraint of filling the lungs during respiration and makes extreme specialization possible. Loss of larvae, which has evolved independently at least three times in the Plethodontidae, frees the hyobranchial skeleton from the functional constraint of feeding in the larval stage and from the associated strongly cephalized development that is characteristic of species with larvae. As a result, the probability of heterochrony is increased. Ontogenetic repatterning (Roth and Wake 1985; Wake and Roth 1989) during direct development becomes increasingly likely as well, and this phenomenon is manifested in tongue projection in many kinds of extreme specialization in biomechanics (e.g., the appearance of a new option for folding tongue cartilages during protraction), neurophysiology (early and extensive development of ipsilateral as well as the expected contralateral retinotectal projections [Rettig and Roth 1986; Roth 1987]), and behavior (the uncoupling of forward lunging from tongue projection and the ability of salamanders to fire their tongues while maintaining a stationary body). Once specialization is initiated, it proceeds to a stopping point, often determined by biomechanical considerations, which can be overcome by a subsequent, usually novel, event. One such event is the disappearance of part of a skeletal element and the associated disarticulation of

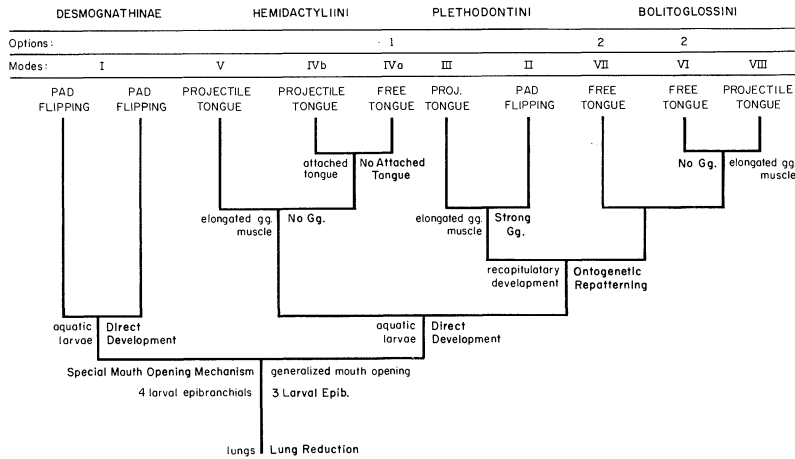


FIG. 8.—Flow diagram of tongue evolution in plethodontid salamanders, based on phylogenetic hypothesis favored by Lombard and Wake (1986) and arguments of Lombard and Wake (1977), Wake (1982*b*), and Roth and Wake (1985). Options 1 and 2 (the latter has evolved twice) are the two biomechanical options for free tongues identified by Lombard and Wake (1977). The modes are the different kinds of functional tongues identified by Lombard and Wake (1977). Boldface indicates synapomorphies. *Gg.*, genioglossus muscles.

the tongue skeleton in the diminutive Mexican genus *Thorius* (Lombard and Wake 1977). This produces a biomechanically efficient variation on the theme of the second folding option that is a direct outcome of miniaturization combined with large cell volume (the result of relatively large genome size).

The point of this example is that both functionalist and structuralist perspectives are necessary for a deep understanding of how complex systems evolve. Some events are best understood through the use of functionalist explanations (e.g., evolution of direct development, miniaturization), but these in turn lead indirectly (as in the evolution of a second folding option, which does not inevitably evolve in association with larval loss; Wake 1982*b*) or directly (as in the case of miniaturization in *Thorius*) to morphological changes that have functional implications but are independent of the original adaptation. It is at this point that structuralist interpretations enrich our understanding of historical events.

Miniaturization

Salamanders range in size from species more than 1.5 m long to species that become sexually mature at sizes as small as about 15 mm. Both extremes have been subject to homoplasy. Gigantism is associated with parallel neotenic trends in the families Cryptobranchidae, Amphiumidae, and Sirenidae. Miniaturization is less easily categorized. Within the family Plethodontidae, miniaturization has evolved repeatedly, in all major lineages, with concordant extensive homoplasy. Let us assume that miniaturization always is strictly adaptive and related to early sexual maturation and reproduction, the use of specialized microhabitats, escape

from predation, or other ecologically relevant phenomena. We can then examine the effects of organism-wide miniaturization on parts of the organism.

Often miniatures resemble each other in unexpected ways, for when miniaturization occurs in species with large cells (as a consequence of relatively large genomes), structural and design limitations are approached. Specific arrangements can be understood best within the analytical framework of structuralism. The phenomenon of miniaturization in plethodontids is receiving much recent attention by my colleagues James Hanken and Gerhard Roth (Hanken 1983*b*, 1984, 1985; Roth et al. 1988, 1990); here I present only a brief summary.

Within the bolitoglossine salamanders of the New World tropics, miniaturization has evolved independently many times; all members of the genera *Dendrotriton*, *Nototriton*, *Parvimolge*, and *Thorius* are miniaturized (i.e., sexual maturity of at least one sex is attained at a body size of less than 30 mm), and miniaturized species have evolved within the genera *Bolitoglossa* and *Chiropterotriton* (Wake 1987). In *Thorius*, some species become sexually mature at less than 15 mm, and one undescribed species does not exceed 20 mm (J. Hanken and D. B. Wake, unpublished data).

The bolitoglossines all have large to very large genomes (Sessions 1984; Sessions and Larson 1987), so one has an a priori expectation that design limitations might be reached in miniaturized species. For example, in *Thorius*, the organization of the head as a whole is affected (Hanken 1983*b*, 1984). Most species of *Thorius* inhabit small spaces under bark or surface cover, and their eyes do not protrude more than slightly beyond the limits of the head. But, because the cells are large (because the genome is large), the eye must be relatively large (in relation to the head) in order to achieve sufficient optic resolution for feeding and other functions. Therefore, the eyes must impinge on the space for the brain, which lies largely between the eyes, and the brain accordingly is deformed and displaced posteriorly (Hanken 1983*b*; Roth 1987).

The neurons, as well as the other cells of *Thorius*, also are large, and there are space constraints within the confined cranial vault. There are only about 25,000 photoreceptors in the eye of *Thorius* (there are about 450,000 in *Rana*; Szekely and Lazar 1976), but there are 26,000 retinal ganglion cells; thus, the whole retina is a functional fovea, with maximal visual acuity (Linke et al. 1986; Roth et al. 1988). The optic tectum, the main integration center in amphibian brains, which contains the cells that are directly related to visual function, contains only about 30,000 cells (Roth et al. 1990) in these extraordinarily tiny brains (there are about 800,000 in *Rana*; Szekely and Lazar 1976). Yet, although in relation to other salamanders the eye is small, visual acuity and distance perception remain at an effective level. Vision is important in *Thorius*, which uses the most extremely specialized (in a biomechanical sense) tongue-projection system known in salamanders (Lombard and Wake 1977). The relative size of the brain areas containing visual and visuomotor centers is greatly increased at the expense of other areas, especially the olfactory centers of the forebrain. Cell packing in miniaturized species with large genomes and large cells is increased at the expense of basal dendrites and glial cells and is especially great in hatchlings (Roth et al.

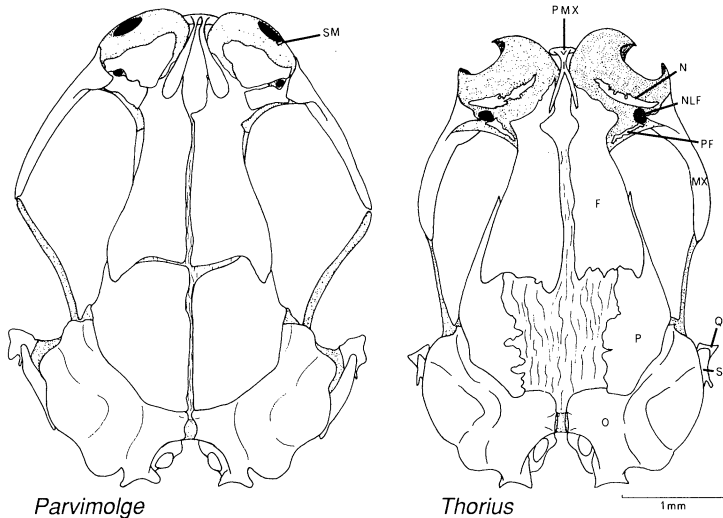


FIG. 9.—Dorsal views of the skulls of miniaturized species of tropical bolitoglossine salamanders. *Left*, an adult *Parvimolge townsendi* from Veracruz, Mexico; *right*, an adult *Thorius* (undescribed species) from Oaxaca, Mexico. *Stippling*, cartilage; *wavy lines*, fibrous tissues covering the brain; *SM*, septomaxillary bone; *PMX*, premaxillary; *N*, nasal; *PF*, prefrontal; *F*, frontal; *MX*, maxillary; *P*, parietal; *Q*, quadrate; *S*, squamosal; *O*, otic-occipital; *NLF*, nasolacrimal foramen.

1990). The close packing of cells in the brains of *Thorius* and other miniaturized bolitoglossine salamanders has many implications for such phenomena as cell migration (which might be strongly impeded as a result) and may well contribute, together with developmental phenomena (Hanken 1983*b*), to the general impression of paedomorphosis in these species.

The nervous system is only one of the systems affected by miniaturization. The entire skeletal system is affected as well, but in different ways in different taxa. In *Thorius*, the skull is retarded in development and appears to be shrunken around the components associated with the olfactory, visual, and auditory systems (fig. 9). The upper jaws in most species are toothless, and many bones simply “float” on top of cartilage or in fibrous sheets, with no articulations (Wake 1966; Hanken 1984). There is an enormous cranial fontanel, and the brain is largely not covered by bone.

In other miniaturized genera, design limitations are accommodated in different ways. In the genus *Parvimolge*, with a smaller genome than *Thorius*, the skull is not so deformed (fig. 9) and appears to be a smaller version of the skull of such out-group genera as *Chiropetrotriton* and *Pseudoeurycea*. Cell density in *Parvimolge* is much lower than in *Thorius* (G. Roth, unpublished data). In the western North American *Batrachoseps* (a member of the tribe Bolitoglossini) the cranial fontanel is even larger than in *Thorius*, and the brain shares many features, but the jaws are relatively strong and well supplied with teeth.

Some miniaturized plethodontids have small genomes (*Desmognathus wrighti* and *Desmognathus aeneus*). These species do not appear to have reached the limits that have been discussed, and they do not manifest the compromises that must be met in *Thorius* (G. Roth, unpublished data).

This example shows that, although miniaturization has occurred repeatedly, only when the organism as a whole is at its design limits must some structural-functional compromise occur. Genome and cell size are factors that mediate or exacerbate the consequences of changes in absolute body size. When compromise occurs, it often involves those features that are of apparently lesser adaptive significance—the forebrain and the teeth of *Thorius*, for example. But miniaturization also can affect structures that have no other developmental options; for example, the fifth toe is lost in some miniaturized taxa.

HOMOPLASY—THE DILEMMA

Is the extensive homoplasy in plethodontids typical or unique? For many years my attempts to hypothesize a robust phylogeny for the plethodontids, particularly the tropical bolitoglossines, have been frustrated by homoplasy. The problem appears to be general; homoplasy is so common in salamanders that, despite many efforts, there is no generally accepted phylogenetic hypothesis for the order Caudata. Each hypothesis requires extensive convergence and reversal (Hecht and Edwards 1977; Duellman and Trueb 1986). New data from aligned sequences of 18s and 28s ribosomal RNA, based on statistical analysis tests using parsimony, are in deep conflict with all phylogenetic hypotheses based on morphological data (confirmed by the independent analysis of the data of Larson and Wilson [1989] in Hillis 1991; see also Larson 1991), especially with regard to the phylogenetic position of the Plethodontidae. The sequence data have turned the accepted phylogenetic tree upside down by locating the plethodontids near the base of the tree and the cryptobranchoids rather far up in the tree, whereas morphologists always have concluded that plethodontids are a deeply nested taxon and the cryptobranchoids basal or nearly so. Larson (1991) has reanalyzed the morphological data and has shown that only slightly more nonmolecular homoplasy is required by his most parsimonious tree than is required by other trees.

The combined morphological and molecular data reveal an extraordinary amount of homoplasy. It may be that salamanders are special in this respect, but I doubt it. We simply do not as yet have adequate molecular information for such groups as neobatrachian frogs, teleost fishes, and others in order to have accurate estimates of the relative amount of homoplasy in different taxa. If salamanders are unique, we should investigate the basis for that uniqueness, but until more groups have been investigated in comparable detail we should not assume that salamanders are different from other vertebrate taxa.

The analysis by Sanderson and Donoghue (1989) of 60 recent cladistic analyses shows that, for both molecular and morphological data sets, levels of homoplasy (as measured by a consistency index) increase with increasing numbers of taxa. One obvious answer to the difficulty in finding a robust phylogenetic hypothesis

for bolitoglossine salamanders and neobatrachian frogs is that there are too many species, since the probability of character-state change increases with the total number of branches in a tree. However, the other side of the issue, as these authors made clear, is that the probability of homoplasy increases if the number of possible states of a character are limited. That is the major point of the present paper (and an important point in Rieppel 1989). When these two factors combine, as in the bolitoglossines, levels of homoplasy become so high as to frustrate analysis. Perhaps in the case of the bolitoglossines, DNA sequence data will provide a new perspective on the problem, but the risks are great that the results will be no more clarifying than in the case of the salamander families, for which all previous hypotheses were brought into question.

The relative balance of external (related to specific function and arising from interaction with environmental factors by means of natural selection) and internal (arising from such structuralist principles as wholeness, self-regulation and transformation, and manifested through form generation during ontogeny) factors in the determination of biological form has yet to be determined for any group of organisms. I advocate a research program in which both avenues of explanation are pursued simultaneously, without subjugation. The goal is an eventual synthesis, such as I have attempted, in which both functionalist and structuralist perspectives are presented to explain how the selective assembly of unit structures into more complex organism-level structures has evolved in a hierarchical manner, within a phylogenetic framework. Only when this is accomplished can the heuristic value of an analytical study of homoplasy be appreciated.

Homoplasy complicates phylogenetic analysis enormously, but at the same time it enriches our appreciation for the diversity of evolutionary processes.

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LITERATURE CITED

- Alberch, P. 1981. Convergence and parallelism in foot morphology in the Neotropical salamander genus *Bolitoglossa*. I. Function. *Evolution* 35:84–100.
- . 1989. The logic of monsters: evidence for internal constraint in development and evolution. *Geobios* (Lyon), *mémoire spécial* 12:21–57.
- Alberch, P., and J. Alberch. 1981. Heterochronic mechanisms of morphological diversification and evolutionary change in the Neotropical salamander *Bolitoglossa occidentalis* (Amphibia: Plethodontidae). *Journal of Morphology* 167:249–264.
- Alberch, P., and E. A. Gale. 1985. A developmental analysis of an evolutionary trend: digital reduction in amphibians. *Evolution* 39:8–23.
- Alberch, P., S. J. Gould, G. F. Oster, and D. B. Wake. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296–317.

- Brame, A. H. 1964. Distribution of the Oregon slender salamander, *Batrachoseps wrighti* (Bishop). Bulletin, Southern California Academy of Sciences 63:165–170.
- Brodie, E. D., Jr. 1983. Antipredator adaptations of salamanders: evolution and convergence among terrestrial species. Pages 109–133 in N. S. Margaris, M. Arianoutsou-Faraggitaki, and R. J. Reiter, eds. Adaptations to terrestrial environments. Plenum, New York.
- Bryant, S. V., D. M. Gardiner, and K. Muneoka. 1987. Limb development and regeneration. American Zoologist 27:675–696.
- Darda, D. M. 1988. Morphological and biochemical evolution within the plethodontid salamander genus *Chiropterotriton*. Ph.D. diss. University of California, Berkeley.
- de Queiroz, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Systematic Zoology 34:280–299.
- Duellman, W. E., and L. Trueb. 1986. Biology of amphibians. McGraw-Hill, New York.
- Elias, P. 1984. Salamanders of the northwestern highlands of Guatemala. Contributions in Science, Natural History Museum, Los Angeles County 347:1–20.
- Endler, J. 1986. Natural selection in the wild. Princeton University Press, Princeton, N.J.
- Frolich, L. 1991. Osteological conservatism and developmental constraint in the polymorphic “ring species” *Ensatina eschscholtzii* (Amphibia: Plethodontidae). Biological Journal of the Linnean Society (in press).
- Goodwin, B. C. 1984. Changing from an evolutionary to a generative paradigm in biology. Pages 99–120 in J. W. Pollard, ed. Evolutionary theory: paths into the future. Wiley, New York.
- Goodwin, B. C., and L. E. H. Trainor. 1983. The ontogeny and phylogeny of the pentadactyl limb. Pages 75–98, in B. C. Goodwin, N. Holder, and C. C. Wylie, eds. Development and evolution. Cambridge University Press, Cambridge.
- Hanken, J. 1982. Appendicular skeletal morphology in minute salamanders, genus *Thori* (Amphibia: Plethodontidae): growth regulation, adult size determination, and natural variation. Journal of Morphology 174:57–77.
- . 1983a. High incidence of limb skeletal variation in a peripheral population of the red-backed salamander, *Plethodon cinereus* (Amphibia, Plethodontidae) from Nova Scotia. Canadian Journal of Zoology 61:1925–1931.
- . 1983b. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thori* (Amphibia, Plethodontidae). II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. Journal of Morphology 177:255–268.
- . 1984. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thori* (Amphibia: Plethodontidae). I. Osteological variation. Biological Journal of the Linnean Society 23:55–75.
- . 1985. Morphological novelty in the limb skeleton accompanies miniaturization in salamanders. Science (Washington, D.C.) 229:871–874.
- Hanken, J., and C. Dinsmore. 1986. Limb skeletal variation in the red-backed salamander, *Plethodon cinereus*. Journal of Herpetology 20:97–101.
- Hecht, M. K., and J. L. Edwards. 1977. The methodology of phylogenetic inference above the species level. Pages 3–51 in M. Hecht, P. C. Goody, and B. M. Hecht, eds. Major patterns in vertebrate evolution. Plenum, New York.
- Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.
- Hillis, D. M. 1991. The phylogeny of the amphibians: current knowledge and the role of cytogenetics. In D. M. Green and S. K. Sessions, eds. Amphibian cytogenetics and evolution. Academic Press, New York (in press).
- Hubbard, M. 1903. Correlated protective devices in some California salamanders. University of California Publications in Zoology 1:157–170.
- Lande, R. 1978. Evolutionary mechanisms of limb loss in tetrapods. Evolution 32:73–92.
- Larsen, J. H., Jr., J. T. Beneski, Jr., and D. B. Wake. 1989. Hyolingual feeding systems of the Plethodontidae: comparative kinematics of prey capture by salamanders with free and attached tongues. Journal of Experimental Zoology 252:25–33.
- Larson, A. 1983. A molecular phylogenetic perspective on the origins of a lowland tropical salamander fauna. I. Phylogenetic inferences from protein comparisons. Herpetologica 39:85–99.

- . 1991. A molecular perspective on the evolutionary relationships of the salamander families. *Evolutionary Biology* 25:211–277.
- Larson, A., and A. C. Wilson. 1989. Patterns of ribosomal RNA evolution in salamanders. *Molecular Biology and Evolution* 6:131–154.
- Larson, A., D. B. Wake, L. R. Maxson, and R. Highton. 1981. A molecular phylogenetic perspective on the origins of morphological novelties in the salamanders of the tribe Plethodontini. *Evolution* 35:405–422.
- Linke, R., G. Roth, and B. Rottluff. 1986. Comparative studies on the eye morphology of lungless salamanders, family Plethodontidae, and the effect of miniaturization. *Journal of Morphology* 189:131–143.
- Lombard, R. E., and D. B. Wake. 1977. Tongue evolution in the lungless salamanders, family Plethodontidae. II. Function and evolutionary diversity. *Journal of Morphology* 153:39–80.
- . 1986. Tongue evolution in the lungless salamanders, family Plethodontidae. IV. Phylogeny of plethodontid salamanders and the evolution of feeding dynamics. *Systematic Zoology* 35:532–551.
- McNamara, K. J. 1986. A guide to nomenclature of heterochrony. *Journal of Paleontology* 60:4–13.
- Patterson, C. 1982. Morphological characters and homology. Pages 21–74 in K. A. Joysey and A. E. Friday, eds. *Problems of phylogenetic reconstruction*. Academic Press, London.
- . 1988. Homology in classical and molecular biology. *Molecular Biology and Evolution* 5: 603–625.
- Piaget, J. 1970. *Structuralism*. Basic, New York.
- Oster, G. F., N. Shubin, J. D. Murray, and P. Alberch. 1988. Evolution and morphogenetic rules: the shape of the vertebrate limb in ontogeny and phylogeny. *Evolution* 42:862–884.
- Rabb, G. B. 1965. A new salamander of the genus *Chiropterotriton* (Caudata: Plethodontidae) from Mexico. *Breviora* 235:1–8.
- Rettig, G., and G. Roth. 1986. Retinofugal projections in salamanders of the family Plethodontidae. *Cell and Tissue Research* 243:385–396.
- Rieppel, O. C. 1988. *Fundamentals of comparative biology*. Birkhauser, Basel.
- . 1989. Character incongruence: noise or data? *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 28:53–62.
- Roth, G. 1987. *Visual behavior in salamanders*. Springer, Berlin.
- Roth, G., and D. B. Wake. 1985. 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* 34:175–192.
- Roth, G., B. Rottluff, and R. Linke. 1988. Miniaturization, genome size and the origin of functional constraints in the visual system of salamanders. *Naturwissenschaften* 75:297–304.
- Roth, G., B. Rottluff, W. Grunwald, J. Hanken, and R. Linke. 1990. Miniaturization in plethodontid salamanders (Caudata: Plethodontidae) and its consequences for the brain and visual system. *Biological Journal of the Linnean Society* 40:165–190.
- Sanderson, M. J., and M. J. Donoghue. 1989. Patterns of variation in levels of homoplasy. *Evolution* 43:1781–1795.
- Sessions, S. K. 1984. *Cytogenetics and evolution of salamanders*. Ph.D. diss. University of California, Berkeley.
- Sessions, S. K., and A. Larson. 1987. Developmental correlates of genome size in plethodontid salamanders and their implications for genome evolution. *Evolution* 41:1239–1251.
- Shapiro, I. M., E. E. Golub, B. Chance, C. Piddington, O. Oshima, O. C. Tuncay, and J. C. Haselgrove. 1988. Linkage between energy status of perivascular cells and mineralization of the chick growth cartilage. *Developmental Biology* 129:372–379.
- Shubin, N., and P. Alberch. 1986. A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evolutionary Biology* 20:319–387.
- Simpson, G. G. 1961. *Principles of animal taxonomy*. Columbia University Press, New York.
- Szekely, G., and G. Lazar. 1976. Cellular and synaptic architecture of the optic tectum. Pages 407–434 in R. Llinas and W. Precht, eds. *Frog neurobiology*. Springer, Berlin.
- Tanner, W. W. 1950. A new genus of plethodontid salamander from Mexico. *Great Basin Naturalist* 10:27–44.

- . 1952. A comparative study of the throat musculature of the Plethodontidae of Mexico and Central America. *University of Kansas Science Bulletin* 34(2):583–677.
- Taylor, E. H. 1944. The genera of plethodont salamanders in Mexico. I. *University of Kansas Science Bulletin* 30(1):189–232.
- von Wahlert, G. 1957. Biogeographische und oekologische Tatsachen zur phylogenie amerikanischer Schwanzlurche. *Zoologischen Jahrbüchern. Abteilung für Systematik, Geographie und Biologie der Tiere* 85:253–282.
- Wagner, G. 1989. The origin of morphological characters and the biological basis of homology. *Evolution* 43:1157–1171.
- Wake, D. B. 1963. Comparative osteology of the plethodontid salamander genus *Aneides*. *Journal of Morphology* 113:77–118.
- . 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. *Memoirs of the Southern California Academy of Sciences* 4:1–111.
- . 1970a. The abundance and diversity of tropical salamanders. *American Naturalist* 104:211–213.
- . 1970b. Aspects of vertebral evolution in the modern Amphibia. *Forma et Functio* 3:33–60.
- . 1982a. Functional and evolutionary morphology. *Perspectives in Biology and Medicine* 25:603–620.
- . 1982b. Functional and developmental constraints and opportunities in the evolution of feeding systems in urodeles. Pages 51–66 in D. Mossakowski and G. Roth, eds. *Environmental adaptation and evolution*. Fischer, Stuttgart.
- . 1987. Adaptive radiation of salamanders in middle American cloud forests. *Annals of the Missouri Botanical Garden* 74:242–264.
- . 1989. Phylogenetic implications of ontogenetic data. *Geobios (Lyon), mémoire spécial* 12:369–378.
- Wake, D. B., and I. G. Dresner. 1967. Functional morphology and evolution of tail autotomy in salamanders. *Journal of Morphology* 122:265–306.
- Wake, D. B., and P. Elias. 1983. New genera and a new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae). *Contributions in Science, Natural History Museum, Los Angeles County* 345:1–19.
- Wake, D. B., and J. D. Johnson. 1989. A new genus and species of plethodontid salamander from Chiapas, Mexico. *Contributions in Science, Natural History Museum, Los Angeles County* 411:1–10.
- Wake, D. B., and A. Larson. 1987. Multidimensional analysis of an evolving lineage. *Science (Washington, D.C.)* 238:42–48.
- Wake, D. B., and R. Lawson. 1973. Developmental and adult morphology of the vertebral column in the plethodontid salamander *Eurycea bislineata*, with comments on vertebral evolution in the Amphibia. *Journal of Morphology* 139:251–300.
- Wake, D. B., and J. F. Lynch. 1976. The distribution, ecology and evolutionary history of plethodontid salamanders in tropical America. *Science Bulletin, Natural History Museum, Los Angeles County* 25:1–65.
- Wake, D. B., and G. Roth. 1989. The linkage between ontogeny and phylogeny in the evolution of complex systems. Pages 361–377 in D. B. Wake and G. Roth, eds. *Complex organismal functions: integration and evolution in vertebrates*. Wiley, Chichester.
- Wake, D. B., T. J. Papenfuss, and J. F. Lynch. 1991. Distribution of salamanders along elevational transects in Mexico and Guatemala. In *Mesoamerican biogeography*. Tulane University Press, New Orleans (in press).
- Webster, G. C., and B. Goodwin. 1982. The origin of species: a structuralist approach. *Journal of Social and Biological Structures* 5:15–47.
- Wiley, E. O. 1981. *Phylogenetics*. Wiley-Interscience, New York.