On the Problem of Stasis in Organismal Evolution

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One of the most challenging problems in evolutionary biology is morpho-
logical stasis—the maintenance of a standard morphology over vast periods
of time during which much environmental change has taken place. We
review empirical data for one well studied group of vertebrates, salaman-
ders of the family Plethodontidae. Despite much evolution at the level of
allozymes, proteins such as albumin, and DNA, morphological evolution
has been slow, and has been concentrated in relatively short spans of time.
The dominant theme has been morphological stasis. An important con-
tributing factor appears to be plasticity—behavioral, physiological, and
developmental—which allows organisms to compensate environmental,
and even genetic, perturbations without having to change morphologically.
Organisms are self-produced and self-maintained systems, and we argue
that the best measure of evolutionary adaptation is the persistence of this
autopoietic system. Internal dynamics of the organism determine what
change will occur and how it is to be expressed. Stable systems can be
established which transcend species borders, and the fossil record offers
no evidence with regard to speciation rates, or the relationship of speciation
events to morphological evolution. We urge that more emphasis be placed
on the organism in evolutionary studies.

Introduction

The concepts of fitness and adaptation are deeply entrenched within modern
evolutionary theory. Nonetheless, widespread discontent prevails con-
cerning these central concepts, though evolutionary biology is generally

perceived as a successful and dynamic field of science. In simple form, natural selection is seen to be an optimizing process whereby fitness increases and leads to greater adaptation. But there are many paradoxical results of evolutionary processes that require invocation of special circumstances in order to be understood. Evolution does not always optimize, and in fact when we apply concepts of fitness and adaptation to the whole organism (i.e. populations of organisms) level, we find that no general agreement exists as to what constitutes an objective measurement of either (Stearns, 1982a). No one thinks that the organism "knows" (by immediate insight) how to cope with challenges of changing environments, so one must admit the strict observer-dependence (hence subjectivity) of these concepts. Adaptation is then a phenomenon which we assess as an optimization process in a largely numerical (advantage of one phenotype relative to another or others, measured in relative numbers of surviving offspring) or technical (increase in efficiency) sense. However, this may have everything to virtually nothing to do with long-range evolutionary success, i.e. survival of the lineage of the organism.

Perhaps no phenomenon is as challenging to evolutionary biologists as what has been termed "stasis" (Gould & Eldredge, 1977). With natural selection operating in a changing environment as an agent of adaptation, we expect to see changes at the organismal, ultimately physiological and morphological, level. How, though, can we explain the paradoxical situation in which environments change, even dramatically, but organisms do not?

We will argue, from empirical data for one of the best studied groups of vertebrates—salamanders of the family Plethodontidae—that the long-term evolutionary progress of groups does not emanate from an optimization process. No one can deny that plethodontid salamanders are old, evolutionarily "healthy", and successful (there are many species; they have dense populations and wide distributions), yet they include (as is typical for many so-called adaptive radiations) both highly evolved specialists and little evolved, essentially static, generalists. To have survived for over 50 million years with little morphological change suggests that these organisms have not optimized; rather, they have persisted. From such observations we will argue that evolutionary biology lacks sufficient explanatory theory, and that the field would benefit from the introduction of a formulation from organismal biology which views the organism as a self-produced and self-maintained (autopoietic) system, which changes or stabilizes itself with respect to internal dynamics. We will further argue that the only meaningful and objective definition of adaptation is persistence. We see persistence as an active, dynamic process which incorporates genetic, developmental, and physiological variation in a largely self-maintaining and self-regulating system.

Our emphasis in this paper relates ultimately to the kinds of observations that are expected outcomes of autopoietic evolutionary systems. While we criticize some current evolutionary concepts, it is not our intention to produce a detailed critical analysis, for there have been many in recent years (Lewontin, 1974; Stearns, 1976, 1980, 1982a; Slobodkin & Rapoport, 1974; Gould & Lewontin, 1979, Saunders & Ho, 1979; Alberch, 1981a; Arnold &Fristrup, 1982).

Stasis in Evolution

The empirical observation that most fossil lineages experience long periods during which little morphological evolution occurs has led to much excitement in paleontology, as well as in evolutionary biology in general (Eldredge & Gould, 1972; Gould & Eldredge, 1977; Stanley, 1979; Olson, 1981). While attention initially was directed to the periods of relatively rapid change which punctuated the prevailing equilibria, more recent workers are focusing attention on the phenomenon of stasis itself (Levinton & Simon, 1980; Stearns, 1981; Wake, 1981; see also Anonymous, 1982). The founders of the concept of punctuated equilibria have boldly asserted that "stasis is data" (Gould & Eldredge, 1977), but in fact little is known concerning the basis for morphological stasis. By stasis we refer to an overall morphology—habitus—that persists for millions of years. Stasis has been judged to be the result of stabilizing selection of some sort (Charlesworth, Lande & Slatkin, 1982; Kirkpatrick, 1982), taking the form of developmental homeostasis (Rachootin & Thomson, 1981) or, using metaphors derived from ideas of Sewall Wright, getting in essence "stuck" on adaptive peaks (Templeton, 1982; Nanney, 1982). We do not reject ideas of stabilizing selection, but instead strive for a more explanatory framework focused on characteristics of organisms. Some potential explanations have emphasized genetic factors, such as genetic homeostasis (Lerner, 1954) or related phenomena (Mayr, 1982); our focus is on the phenotype *per se*. The examples we will use are plethodontid salamanders, but our conclusions have generality for many groups.

Central to our discussion is the concept of adaptation, which we here define as *the presence of a trait or set of traits that relatively increase the probability of survival and reproduction of members carrying it.* "Members" might be individuals of a species, but we conceive of adaptation more broadly, and apply the concept not only to populations, but even species and supra-specific groups.

Fitness is another concept that relates to survival and reproduction, and hence, adaptation. It has been a troublesome concept, because it was originally conceived in a population genetic context, but it has been applied

to adaptation at the organismal level. We restrict our consideration of fitness to the way the term has been applied to whole organisms, in the original Darwinian sense. We favor not the numerical, or relative abundance, model of fitness, but rather, *persistence*, a conception that is enjoying renewed attention (Slobodkin & Rapoport, 1974; Cooper, 1981; Stearns & Crandall, 1980; Stearns, 1982a; Stearns, Tuomi & Haukioja, 1982). Thus, fit adaptations are those which persist through time. It has been customary to model fitness in either the mechanically quantitative manner of population genetics or the optimality approach of evolutionary ecology, but attention is being directed to a third approach, termed "satisficing" (Stearns, 1982a; Arnold & Fristrop, 1982). As Stearns (1982a) has argued, in a satisficing approach one does not use a conception of numerical superiority or optimality as the end point of a fitness model, but rather the idea of a stopping point, at which the general level of adaptation achieved is sufficient for persistence.

We will examine cases of morphological persistence that transcend species borders and characterize lineages that have lived for millions of years, despite profound environmental changes. We believe that explanations for such stasis may be found in the biology of living species.

Morphological Stasis with Genetic and Environmental Change

A great quantity of morphological and molecular data exist for salamanders of the family Plethodontidae, the largest and apparently most derived group of Urodela (see Wake, 1981, for summary). The genus *Plethodon* is a group of 26 or more North American species that is deeply divided genetically as measured in a variety of ways: allozymic (Larson & Highton, 1978); immunologic (Maxson, Highton & Wake, 1979); nucleic acid sequence homology (Mizuno & Macgregor, 1974; Mizuno, Andrews & Macgregor, 1974, 1977). However, despite minor pigmentation, proportional, and size differences, the species are remarkably uniform morphologically, especially in osteology, the component preserved in the fossil record (Wake, 1963, 1966). Karyotypes of the species are identical with respect to relative lengths, centromere indices and arm ratios (Mizuno and Macgregor, 1974). Genome sizes differ greatly (more than threefold), but have grown in a balanced and uniform manner so as to maintain karyotypic uniformity (Macgregor, 1982).

As currently recognized, the genus is apparently a paraphyletic taxon, in that one section of the genus has given rise to a morphologically differentiated lineage that is placed in a separate genus, *Aneides* (Larson *et al.*, 1981). Using concepts of timing from molecular data, the age of *Plethodon* as a morphological entity is estimated to be over 60 million

years, and possibly older (the date is the estimated divergence of the derived genus *Ensatina* from a *Plethodon*-like ancestor (Maxson *et al.*, 1979; Larson *et al.*, 1981)). Two major sections of *Plethodon*, a more primitive eastern and a more derived western, are estimated to have diverged from one another either about 42 (allozyme data from Highton & Larson, 1979) to form 38 to 48 (immunologic data from Maxson, Highton & Wake, 1979, and Larson, Wake, Maxson & Highton, 1981) million years ago. The only fossil of note, but an important one for establishing a minimum date, is a western *Plethodon* from the lower Miocene, about 20 million years old (Tihen & Wake, 1981).

Species of *Plethodon* from the eastern and western assemblages can be remarkably similar in general morphology (e.g. the eastern, *P. cinereus*, and western, *P. vehiculum*, red-backed salamanders), despite being very different in allozymes (D_{nei} greater than 2·0), albumin (immunological distance approximately 70), and DNA C-value (*P. vehiculum* has approximately twice the C-value of *P. cinereus*). During the 60 million years of existence of this genus, the environment in which these salamanders live has undergone dramatic change. All terrestrial vertebrate genera which co-occurred with *Plethodon* 60 million years ago are extinct, as far as we know. Certainly in terms of competitor species, predator species, and food species (the animals are mainly insectivores), the environmental modifications have been profound. Yet, a standard morphology has persisted (Wake, 1981).

Slatkin (1981) has analyzed allozymic data for *Plethodon* and a related plethodontid salamander, *Batrachoseps*. He concluded that gene flow is very low in these forms, and that natural selection and genetic drift may occur independently in each population of each species. He further stated that "gene flow may not be responsible for genetic or morphological uniformity of such species, and that other causes must be sought". We concur, and suggest one such probable cause below.

Severe problems exist with the concept of stasis in respect to evolution, not the least of which is the fact that paleontological species are recognized on the basis of absence of change over a given interval of time. "In the fossil record, rapid morphological change *is* speciation" (Levinton & Simon, 1980). As originally conceived, stasis was associated with species and punctuated equilibria with speciation. With such a concept, morphological evolution is reduced to a problem of speciation (Gould, 1982).

Our concept of stasis separates it sharply from any tie with speciation. Indeed, the highly static *Plethodon* has at least 26 living species, while its morphologically diverse, specialized derivative *Aneides* has but five. We envisage a range of rates of morphological evolution, from slow to rapid. There is no dichotomy. What we term relative stasis, Simpson (1943) would have called bradytely (but his rates were based largely on taxa turnover,

and thus species and morphology were necessarily confounded). We believe that relative stasis is common. A relatively static morphology nevertheless displays variation. There are large and small species of *Plethodon*, and an eastern assemblage differs from a western one in subtleties of vertebral proportions that can be detected in the fossil record (Wake, 1981; Tihen & Wake, 1981; Highton, 1962). However, relative to other plethodontids, *Plethodon* is morphologically monotonous, and this monotony has apparently prevailed for vast periods of time.

The static morphology of *Plethodon* may be even older than we have indicated. In almost all respects, *Plethodon* is a generalized, plesiomorphic group. While *Plethodon* cannot be the stock from which all other plethodontids are derived because it lacks an aquatic larval stage, which some other genera have, in nearly every other respect it is primitive (Wake, 1966). Its tongue and method of feeding are especially generalized (Lombard & Wake, 1977), and we believe that the biology of feeding offers an important clue to understanding the morphological stasis of *Plethodon*.

Behavioral Plasticity and Generality of Function

We believe that feeding biology offers insight into an important component of stasis—behavioral plasticity combined with morphological and functional generality. A variety of behavioral studies (e.g., Himstedt, 1967; Roth, 1976, 1978; Luthardt & Roth, 1979a) have shown that most salamanders have a broad range of acceptance of prey stimuli within their feeding repertoires. Within a considerable range of size, velocity of movement, shape (from compact to elongated), and odor of prey, feeding responses will be elicited. Response to such moving stimuli is inborn (Himstedt, Freidank & Singer, 1976; Roth & Luthardt, 1980); however, the response is highly modifiable by experience immediately following metamorphosis (or hatching). The response pattern can be changed dramatically during the first months after metamorphosis by feeding the salamanders a single kind of prey, which represents only one category of shape, velocity, pattern of movement, and odor of prey objects (Luthardt & Roth, 1979b). Furthermore, salamanders can be brought to feed consistently on non-moving prey if they have appropriate early experience (Roth, 1976; Himstedt, Tempel & Weiler, 1978). Willingness to feed on stationary prey contradicts the widespread assumption that amphibians feed only on moving prey (Autrum, 1959; Lettvin *et al.*, 1960). The modifiability of the olfactory guidance system seems to exceed even that of the visual system: animals which were raised with only one prey odor did not accept the odor of the other prey.

The above facts indicate that salamanders possess a semi-conservative system of sensory guidance of feeding behavior. They have a rather general prey stimulus pattern (inborn) which can, however, change greatly as a result of early experience. Accordingly, salamanders readily "adapt" (in a physiological sense, or adjust in an evolutionary sense) to specific environmental conditions (availability of prey objects). The special plasticity of the olfactory system is of great importance, for most salamanders feed mainly under conditions of dim lighting or even of total darkness. Doubtless behavioral plasticity is a major factor in the inability of workers to find evidence of strong preference for any particular prey in the feeding ecology of salamanders.

Feeding mechanisms of plethodontid salamanders have been studied in some detail (Wake, 1966; Roth, 1976; Lombard & Wake, 1976, 1977; Thexton, Wake & Wake, 1977; Wake 1982a) and a broad range of degrees of morphological specialization and specific function are found. *Plethodon* has one of the most generalized (relatively unmodified in structure from postulated ancestral forms, and utilitarian in function) tongues—a large, semiprotrusible tongue pad with long, free posterior flaps. Its jaws and teeth, too, are relatively generalized in size and shape. Most plethodontids are not so generalized. For example, the bolitoglossine plethodontids (supergenera *Bolitoglossa, Hydromantes* and *Batrachoseps*) all have highly protrusible tongues with small pads, and some have the most highly specialized tongues in the order Urodela. The bolitoglossines include nearly one-half of living urodele species and they are highly diversified and widespread. They range from Europe and North America through Central America and into South America, and include the only truly tropical salamanders. Many genera and species of bolitoglossines have specialized behavior, ecology and morphology (Wake, 1966; Wake & Lynch, 1976). Prey recognition in the bolitoglossines is restricted (Roth, 1982a). All large and elongated prey objects are typically excluded. The small dimensions of the tongue tip and its specific biomechanics render bolitoglossine tongues effective primarily for small, compact prey. The combined morphological and sensory physiological (behavioral) adaptations considerably restrict the range of acceptability of prey object characteristics. These specializations of bolitoglossines have constrained the capacity for behavioral interaction with the environment, and have led to a channeling of further evolution. Feeding biology, an important component of many adaptive radiations of vertebrates, shows little variation in the vast radiation of the tropical bolitoglossines.

Plethodon has had the capacity to compensate environmental change, and has remained relatively unchanged in morphology. Bolitoglossines, in

contrast, have lost some of this compensatory capacity, as a result of specialization; in the course of their substantial adaptive radiation they have become sorted ecologically into distinct structural niches, largely as a result of modifications of the locomotor apparatus (structure of hands, feet and tail) in relation to patterns of habitat and microhabitat utilization (Wake & Lynch, 1976).

Morphological Evolution Within a Framework of Stability

Morphological, physiological, and behavioral plasticity, as well as the complementary aspect, rigidity, are consequences of the internal dynamics of organisms. In order to understand how organisms evolve, a concept of the way in which living systems are dynamically organized is essential. Organisms are entities which have the capacity of self-maintenance and self-stabilization. In the sense that very specific thermodynamic and biochemical processes are required for their maintenance, living systems—organisms—are highly improbable. The specific conditions governing each internal process are provided by preceding processes within the system. Consequently a network of interaction exists which constitutes a circularly closed system. This circular interaction of the elements of the system guarantees the continued existence of each element, or process, through its necessary participation in the production and maintenance of all other elements. Such a system has been termed *autopoietic* (Varela, Maturana & Uribe, 1974; Varela, 1979; Roth, 1982*b*).

Due to the circular organization of living systems, the activity of one element (organ, tissue, cell) affects the activity of all other elements, though not necessarily in the same way and with the same intensity. The range of ontogenetic and phylogenetic change of one element is, therefore, determined by the structural and functional properties of all other elements. Each ontogenetic or phylogenetic change of the system must remain within the functional limits of the process of circular production and maintenance of the elements, or the system itself will decompose. To rephrase the proposition positively, the system can undergo any change, provided the circular organization is not interrupted.

The environment acts upon the system as a *whole*. No element can interact with the environment independently from the other elements, and no independent change (evolution) of single elements can take place. This means that the "response" of a system to the environment is never linear, but a complex event. The same is true for the "activity" of the genes: they never "express" themselves in a direct, linear way. Both environment and genome act as "perturbations" upon the internal dynamics of the system.

Where a change will take place and how intensive it will be is determined by the internal dynamics of the system; it may totally supress or strongly amplify those perturbations.

Living systems are informationally closed: the environment has no direct control concerning how the system behaves. The autopoietic organization of a living system specifies the set of possible developmental pathways. The perturbation from the environment induces a rearrangement of the internal dynamics of the system. Which of the possible developmental pathways is chosen is determined both by the actual state of the system and the perturbation from the environment. Therefore, what we as observers call adaptation of a system (represented by a sequence in time of populations of organisms) to a specific environment, is for the system itself a sequence of bifurcations (by developing individual organisms) between possible internal states (or developmental pathways) (see Waddington, 1975; Alberch, 1981a; Oster & Alberch, 1982), provided stability is maintained.

Stasis is but the most rigid form of the stability that pervades living systems. Thus organisms have evolved as systems resistant to change, even genetic change. While changing environmental conditions may ultimately necessitate change in the system, until some critical point the system remains stable and compensating. The living system is sometimes envisioned metaphorically as a kind of puppet, with enormous numbers of strings, each controlled genetically, or as a blob of putty that can flow in any direction given sufficient force (selection). Our metaphor is the living system as a balloon, with the environment impinging as countless blunt probes. The system compensates environmental and genetic changes, and persists by evolving minimally. If the compensation mechanisms are well developed, as we postulated for *Plethodon*, the system remains relatively stable in outward appearance for millions of years, despite environmental and genetic changes including even speciation.

However, when change is required one would predict that it, too, occurs within a framework of stability. Perhaps this is why directions of change within a lineage seem limited, and why we see so much parallelism in evolution. Elongation of the body, apparently associated with the use of underground retreats, has occurred in several well separated groups of species of *Plethodon* primarily by increases in the numbers of trunk vertebrae (Highton, 1962). Elongation is encountered in remotely related genera of plethodontids (e.g. *Phaeognathus, Batrachoseps, Oedipina*) and is accomplished in the same manner. Only one novel pathway to body elongation has evolved—*Lineatriton* has become elongated primarily by increase in the length of individual vertebrae.

Sometimes change that is apparently minimal in terms of functioning can have immediate major consequences and result in dramatic morphological change. We refer to modifications of developmental patterns such as progenesis and neoteny. In the most extreme cases reproductive maturity is achieved while the organism is still in a larval or partially embryonic state, with consequent enormous morphological change when the condition evolves to genetic fixation in a population. Such phenomena are well documented in plethodontids, in which paedomorphosis was the initial step in the evolution of such organisms as the blind, permanently gilled, largely depigmented cave salamanders (*Typhlomolge, Haideotriton,* and species of *Eurycea*) (Wake, 1966). In the evolution of these strongly paedomorphic forms, selection has been directed to the entire life history of the organism, not to any particular trait or set of traits (for elaboration of this point see Gould, 1977).

Modifications of developmental patterns apparently have been responsible for the extensive parallelism evident in the evolution of complete webbing of the hands and feet of lowland tropical species of the large (about 70 species) genus *Bolitoglossa* (Wake, 1966; Wake & Brame, 1969; Alberch & Alberch, 1981). In some species the fully webbed hands and feet are strongly adaptive structures capable of generating suction in order to cling to smooth, moist, arboreal surfaces, but in others the fully webbed hands and feet are only manifestations of a general developmental syndrome that simultaneously affects many parts of the organism (Alberch, 1981*b*; Alberch & Alberch, 1981). On the basis of a detailed electrophoretic analysis, Larson (1983) has recently concluded that complete webbing has evolved from three to five times in one segment of the genus alone, *Bolitoglossa* beta. Larson also argued that the morphological transitions were concentrated in relatively short periods of time, and that even in such a morphologically diversified genus as *Bolitoglossa* periods of relative morphological stasis comprise the majority of the evolutionary history.

The morphologies we have discussed result from internal characteristics of the organism, which on the one hand only tolerate certain kinds of change, and on the other are capable of producing only a limited array of new morphologies. The resultant morphologies that appear in a population may enable selection to operate, but it also is possible that most alternative morphological states might be selectively equivalent. Selection may frequently act only as a "coarse filter" (Stearns *et al.*, 1982). If so, increased morphological variability would result that would be a further manifestation of organismal plasticity. When morphological change is "noticed" by selection, the focus of selection is not the trait *per se* but the whole organism, ultimately via its life history (see also Stearns *et al.*, 1982).

Internal Dynamics and Evolutionary Change

It is the internal dynamics of organisms which ultimately determines whether and what kind of evolutionary change will occur. The environment and the genes act as triggers for change. The system may be plastic, and respond to environmental or genetic "messages" by compensating via rearrangement of the internal dynamics of the system. Or, the internal dynamics of the system may be rigid, in which case the system *must evolve* in order to respond to the environmental or genetic triggers, for it cannot compensate via change in internal dynamics. Not to respond for a non-compensating organism leads to extinction. Similarly, neither gene nor environment play any dogmatic role in evolution. Genes are not a master control. There is no genetic "program" (see Stent in Bonner, 1981). The stability of genes is not a property of the genes, but the organism (e.g. the role of enzymes in gene repair). Genes are not autonomous, but a part of a genetic *system*, which in turn is part of the general system—the organism.

It is so obvious as to be overlooked, but the ultimate measure of adaptation can be nothing but persistence. Organisms, especially multicellular ones, are special systems—dynamic networks of components. The components must persist if the system is to persist. Organisms arc minimal networks of components that are necessary and sufficient for survival. All components which are not necessary have a higher probability of becoming eliminated. But such systems deteriorate with time. Thus the only way to assure persistence is reproduction. There is no pre-fixed way to reproduce, but there are vast numbers alternative modes which are effective because they persist. To say that a population increases in density because it is better adapted seems quite illogical. In fact, one cannot predict that because a population is well adapted it will increase in numbers. It only will persist.

Persistence, Plasticity and Stasis

If the internal dynamics of organisms sets the limits of evolution, then the degree of tolerance of the system becomes of great interest. The plasticity of the system will determine what changes do or do not occur in response to environmental perturbations. Plasticity has long been of interest to evolutionary biologists (for a recent review of some aspects of plasticity, see Stearns, 1981). Wright (1931) argued that phenotypic plasticity might be the chief object of selection, but his suggestion has not attracted great attention. If a system is very plastic, it is effectively buffered from the environment and even from many genetic changes, for the internal system can compensate. While plasticity is not adaptation, it may indeed relate directly to persistence without change, or stasis. Stearns (1981) has clearly

stated this view in relation to one class of plasticity—developmental plasticity (but see also Stearns, 1982*b*). We see canalization (see Waddington, 1975, for a general review) during development as an example of a combination of plasticity and autopoiesis that has been an element of great conservatism in phyletic evolution (see also Rachootin & Thomson, 1981). We here extend the concept of the relationship of plasticity to stasis to include other forms of plasticity as well, and have illustrated our approach with an example of behavioral plasticity (see above).

However, Stearns (1981) explicitly stated that to the extent that plasticity and canalization lead to an uncoupling of the gene pool from the selective impact of the environment, they promote genetic stasis. We would argue that the stasis is more likely to be organismal, not genetic. Certainly at the level of allozymes and DNA the genome continues to change. These changes simply are not expressed, or expressed so subtly that they do not have major impact on behavior and morphology. Stearns postulated that breakdown of plasticity and canalization may be a necessary spur to a speciation event, which might appear as a punctuation in the fossil record of organisms. We simply would modify this view by generalizing it. No speciation event is necessary. These changes could take place in a lineage of organisms in which the system has incorporated changes triggered by environmental and genetic stimuli, by passing beyond thresholds, for example, which lead to new states of autopoietic organization. Dover *et al* (1982) have recently offered a third process whereby systems might be reorganized (concerted evolution, in addition to gene substitution by natural selection and genetic drift), and there may be more. What is important is that some systems have great stability and plasticity—they are often characterized as "constrained" (Gould & Lewontin, 1979; Hickman, 1981; Gould, 1980; Wake, 1982*a*, *b*; Bonner, 1981). *Plethodon* may be one such system—a system that transcends species borders and has a life of its own as a supraspecific adaptation.

Doubtless many systems such as we have described exist in nature. A striking example has recently been provided by Nanney (1982). The protozoan genus *Tetrahymena* includes a number of morphologically similar species, so similar as to be judged nearly equivalent, and formerly thought to be young. There are "enormous molecular chasms among the species" (Nanney, 1982), implying great age. Rates of morphological evolution vary greatly among taxa (Wilson, Carlson & White, 1977), and the number of speciose lineages that are essentially identical in morphology has yet to be determined. Surely any theory of morphological evolution that has speciation as the engine of change is suspect.

Systems such as we have described are not necessarily limited in space or in time. The system reproduces in varied ways, and if it has variants

(species), perhaps this is little more than perfection of adaptation, in terms of great certainty of persistence.

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