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## Group Report *How Do Complex Organisms Evolve?*

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### INTRODUCTION

"The eye to this day gives me a cold shudder."

— Darwin, 1887

Our group discussed the evolutionary processes that produce complex organisms and phenotypes. We had in mind the evolution of such complex organic structures as the vertebrate eye, the mammalian placenta, and the human cortex, as well as complex developmental phenomena (e.g., morphogenesis of the vertebrate limb) and behavior patterns (e.g., intricate choreography of sexual partners during courtship). In all of these cases, complexity involves numerous heterogeneous, interacting parts with hierarchical structure. In many cases the assembled structure has adaptive consequences, but sometimes it may not (e.g., the complex sutures on the shells of ammonite cephalopods). For further discussion of complexity see Simon (1962), Frazzetta (1975), Dawkins (1976, 1986), and Bonner (1988).

The central evolutionary problem that we discussed is the modification of existing parts and the incorporation of novel parts into a complex, interacting system. Both kinds of change are likely to have repercussions on the operation and performance of the structure. Evolutionary modification of the lens in a vertebrate eye, for example, may require adjustments in many aspects of the visual apparatus. Such cascading effects arise because of changes in developmental processes as well as interactions during function. The lens arises from an induction process during development and cooperates with many other parts of the optic cup to produce vision. The reverberations caused by a modified part are often described as couplings or constraints.



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How do new couplings and constraints arise in development, how can they be detected, how do they affect evolution, and how do constraints themselves evolve?

These questions can be approached from many points of view. Some perspectives from developmental biology, paleontology, evolutionary genetics, functional morphology, and biomechanics are represented in the text that follows. Our discussions often revealed tensions between viewpoints. Some of these tensions evaporated once positions were clarified. Others had deep roots and reflected philosophical differences in outlook (e.g., internalist and externalist perspectives). These deeper conflicts are important and illuminating. We hold them up for scrutiny rather than attempt a superficial, premature reconciliation. We try to avoid an uninteresting consensus. The truth does not necessarily lie midway between two strongly argued alternative positions.

In the following sections we cover an eclectic set of topics that bear on the evolution of complexity. We begin with a discussion of two perspectives on evolution: internalism and externalism. In viewing the evolution of complexity, these two perspectives place different emphasis on the importance of developmental phenomena. We highlight some of those differences and then discuss various evolutionary properties of developmental systems and how they can be studied. Next we discuss the origin of evolutionary novelties. Here we focus on the nature of developmental constraints and their possible role in facilitating the evolution of novelties. We also discuss key evolutionary events that can trigger bursts of cladogenesis and morphological diversification. We then turn to a related topic, levels of selection. We discuss the conflicts between selection that are likely to accompany the origin of new organizational levels, such as multicellular life. We then turn to a general discussion of species or lineage selection. Finally, we discuss two mechanisms that can promote long-term evolutionary trends in complexity: ratchets and arms races.

### THE INTERNALIST-EXTERNALIST DICHOTOMY

Internalism (a variety of structuralism) and externalism (functionalism) are two perspectives on the diversity of life (Chomsky 1957; Lévi-Strauss 1963; Piaget 1971; Gruber and Vonéche 1977; Webster and Goodwin 1982; Hughes and Lambert 1984). Both traditions seek explanations for organic patterns (see Gould 1986; Appel 1987; Wake and Larson 1987; Alberch 1988). Internalism and externalism are not mutually exclusive theories; they are complementary guides to research strategy. Externalism takes selection as the main force producing pattern: hence the central role of the adaptive landscape, the focus on functional design and on the relation of the organism to the environment. Much selection is determined by the environment and

in that sense is external to the organism. On the other hand, "externalism" is a misnomer because the internal environment also exerts selective effects.

Internalism gives form primacy over function. The focus is on the integration and generation of the organism. Hence the response of the organism to perturbation—the production of a finite, biased subset of phenotypes—is taken as evidence for the importance of internal constraints. Historical separation may trace to differences in methodology and outlook. The embryologist's fascination with teratology is matched by the naturalist's admiration for fit to the natural world.

Pure externalist or internalist investigators are rare; mosaics are prevalent. The labels could not easily or infallibly be applied to people at this conference, for example. Most neodarwinists would endorse the internalist's search for generative rules for development. Such rules can give a predictive theory for development (e.g., Oster and Alberch 1982; Oster et al. 1988) as well as an economical parametrization that can facilitate genetic and evolutionary studies (e.g., Raup 1966, 1967). Thus many externalists routinely incorporate aspects of internalism and vice versa. Wake and Larson (1987) discuss and illustrate a melding of the two approaches.

Internalists and externalists differ in their perspectives on the role of constraint in evolution. Internalists consider developmental constraints to be global, i.e., permanent or at least long-lasting, whereas externalists consider constraints to be local, i.e., transitory in evolutionary time (Maynard Smith et al. 1985). Consider how the two schools would approach the problem of evolving an angel:

Darwin's proposal:

"If an angel is all that you lack  
Take a girl with small blips on her back.  
The genes that she brings  
Will soon program for wings.  
So selection's the line of attack."

God's reply:

"If your aim is an angel who sings  
and flies with her elegant wings  
You'll not do it by means  
Of dicing with genes.  
New generative rules are the things."

### DEVELOPMENT AND EVOLUTION

Development is a central issue in the evolution of organismal complexity because all character transformations are modifications of ontogeny. Yet

many developmental biologists are dissatisfied with an evolutionary theory that is grounded in Mendelism and that pays only lip service to developmental issues. We address this dissatisfaction by first discussing developmental and evolutionary perspectives on genes. We then consider some ways in which ontogenetic studies can illuminate evolutionary processes. In particular, we discuss methods for studying the evolutionary properties of developmental systems, the prevalence of heterochronic evolution and, finally, the evolutionary consequences of induction processes.

### The Role of Genes in Development and Phenotypic Evolution

Developmental biologists and geneticists usually focus on different aspects of genes (translation versus transmission). The geneticist uses a particular view of genes as units of heredity (i.e., transmission to the next generation) and may neglect the role of genes in development. Consequently, the developmental biologist may ask whether the distinction between genotype and phenotype advances genetics by leaving out development. Does evolutionary genetics provide a sufficient theory of morphological evolution?

The mapping function from genotype to phenotype is not one-to-one. A gene may affect multiple structures (pleiotropy) and traits are often affected by many genes (polygeny [Wright 1968]). Furthermore, the mapping of gene effects on phenotype may be nonlinear (Rendel 1967; Scharloo 1987). Because gene action during development is a cyclic series of gene-cell interactions (Fig. 1), genes are just one element in the developmental process. Thus the nature of interactions is the primary issue in development.

The two views of genes are sometimes reconciled in genetic studies of developmental processes (e.g., Wright and Wagner 1925; Maynard Smith and Sondhi 1960; Garcia-Bellido 1986). In many other cases, however, extremely simple adult phenotypes are studied in order to score the numerous individuals required for genetic analysis, and issues of development are ignored.

The different perspectives of internalism and externalism on mutation can produce confusion on both sides. The internalist takes bias in the spectrum of phenotypes produced by mutation as evidence for constraints in the developmental system. This claim may not register with externalists or geneticists who see mutation as necessarily being contingent on the existing genetic composition of the population. Genetical parameterizations of mutation often allow for bias or correlation in the distribution of mutant genotypes (e.g., Lande 1980b). The internalist's complaint, however, is that genetics does not supply a theory for bias in the spectrum of mutants. The internalist wishes to know why certain mutants repeatedly arise in different lineages and seeks an explanation in developmental terms. The use of the term "nonrandom" to describe such recurrent themes in mutation, however,

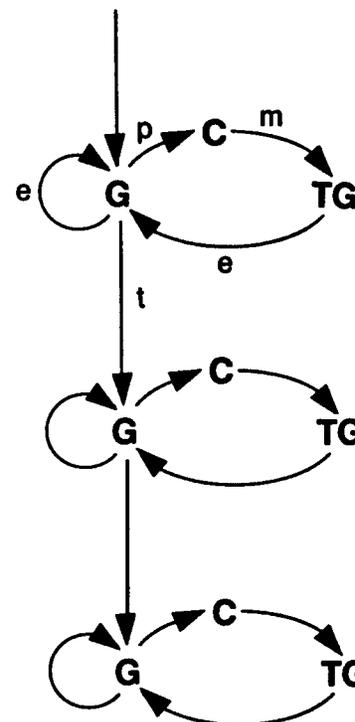


Fig. 1—Genetics has different meanings for developmentalists and geneticists. The developmentalist often focuses on the cyclical processes by which gene expression, *e*, and morphogenesis, *m*, are regulated within a generation. Translation of proteins, *p*, from the genotype, *G*, affects cell properties, *C*, and tissue geometry, *TG*, with subsequent effects on gene expression. The geneticist often focuses on transmission between generations, *t*.

is misleading and should be avoided. Similarly, one can argue that the term "random" mutation has unfortunate connotations (Vrba and Gould 1986). Perhaps no geneticist or neodarwinist would claim that the visible spectrum of mutation is unconstrained or, "random."

Extreme genetic reductionism asserts that evolution is best explained in terms of genes and their frequencies. In quantitative genetics, however, the role of genes is hidden by using the concept of heritability to summarize inheritance. Heritability is only a statistical description of phenotypic resemblance between parents and offspring. Should we instead operate at the gene level? If we do, we will pay a price. When a trait is affected by many genes of small individual effect, each gene may experience a small selective force even though selection on the phenotypic trait is substantial. Consequently, with many genes of small effect, the dynamics of an individual

gene become chaotic and intractable. However, despite the chaotic behavior at the gene level, the evolutionary behavior of the phenotypic trait is predictable from measures of heritability and selection. Consequently, much theoretical progress can be made by using models of phenotypic evolution that employ statistical characterizations of genetics (Lande 1988).

### The Evolutionary Properties of Developmental Systems

*Teratological, experimental and mathematical approaches.* The evolutionary properties of developmental systems can be studied using analysis of mutants, experimental perturbation, and mathematical modeling as well as by comparative studies of ontogeny. The expression of genetic mutations at the phenotypic level is constrained. We find a high degree of specificity in what kinds of variants appear in the population. Alberch (1988) has reviewed the properties of expression of teratological morphologies and used that evidence to study the patterns of internal constraints in the generation of complex morphologies (see also Riedl 1978). For example, certain teratologies, such as bifurcation of the body axis resulting in a two-headed morphology, occur quite commonly throughout the vertebrates. On the other hand, there are very few, if any, reports of three-headed teratologies. This ordered expression of variation can be viewed as a property of the structure of interactions that characterize developmental systems. The fact that the same morphology (in this case, two heads) appears recurrently in distantly related lineages is simply a reflection of the generative properties of a developmental process shared by all vertebrates.

The organizing properties of developmental systems can also be studied by experimental manipulation of development. Since, from the perspective of developmental biology, a mutation is simply a perturbation of developmental parameters—such as diffusion rate, growth rate, etc.—the effects of a genetic mutation can be mimicked by an experimental perturbation of the system that results in the parameter value being changed in a particular direction (Alberch and Gale 1983).

Genetic and epigenetic interactions also can be modeled mathematically as systems of dynamical equations (e.g., Murray 1936; Turing 1952; Meinhardt 1982). Alberch (1982a,b, 1988), Oster and Alberch (1982), and Oster et al. (1988) have specifically explored the properties of dynamical processes of development in an evolutionary context. These authors argue that various evolutionary phenomena—such as stasis, regulation, and biased generation of phenotypic variation, which in turn result in phylogenetic trends and morphological convergence—emerge as an intrinsic property of dynamical systems.

*Comparative studies.* The morphogenetic processes by which complex morphologies such as vertebrate eyes are formed are often highly conserved.

Consequently, ontogenetic studies can offer insight into possible pathways of origin and integration of new features. Embryoclines, however, may not resemble actual evolutionary sequences. A historical analysis is needed to establish the primitive and derived phylogenetic sequences involved in the actual transformation (see Lauder 1981; Lauder and Liem, this volume).

The embryos of related taxa are often more similar than adults. In many cases, embryonic structures play crucial roles in development and so may be retained by stabilizing selection. It may be, however, that only a few critical points (e.g., gastrula, pharyngula) are highly conserved in ontogeny and it is these points that give the appearance of recapitulation (Wake and Roth; Horder, both this volume). These developmental points are characterized by inductive phenomena that produce the characteristic features of major groups (e.g., segments, notochord, etc.).

The existence of a developmental “calendar” makes possible the analysis of morphological transitions in the framework of heterochrony (Gould 1977; Alberch et al. 1979; Fink 1982; Kluge and Strauss 1985). Taking von Baerian recapitulation as the norm, arguments have been made that one can determine the polarity of character state transitions among related taxa using ontogenetic criteria (Wake and Roth, this volume). A recent empirical test of this claim by Mabee (1987) has called this approach into question.

*The importance of heterochrony.* Heterochrony often has been invoked as a major process for producing extensive morphological change (Gould 1977), and also as a means of generating morphological innovation. Shifts in developmental timing can cause a structure to take on a new shape. This alteration in turn may allow for new form-function relationships. Furthermore, when heterochrony occurs in isolated elements, disassociated from general developmental timing of the organism, a shape-structure uncoupling occurs that can lead to new integration and functional capability. Repatterning of ontogeny can then result in novel phenotypes (Wake and Roth, this volume). A good example is presented by the work of Seilacher (Maderson et al. 1982) on the evolution of some bivalve molluscs. A paedomorphic, rock-dwelling species forms a transition between two very different ways of living on soft bottoms. Some authors have claimed that heterochrony is the major process producing morphological change (Gould 1977; Alberch and Alberch 1981; Buss 1987), while others have trivialized the concept by asserting that all change reflects a shift in developmental timing. In fact, many evolutionary innovations do not involve heterochrony (e.g., segmentation). For example, much ontogenetic repatterning can result from change in spatial pattern rather than from change in temporal features.

*Consequences of processes of induction.* When a crucial element in an inductive process is lost in evolution, a whole, cascading series of developmentally dependent features may be lost as well. Conversely a

change in the key inducing trait may trigger a cascading impact that yields a new trait combination. In the ontogeny of muscle innervation, for example, the number of motor neurons matches the number of muscle fibers because of an interacting developmental process (Betz 1987). The developing motor system shows a mutual dependency of motor neurons with muscle fibers such that motor neurons die if they have no target muscle fibers. This interdependence results in a numerical matching between the initial set of primary muscle fibers and the surviving set of motor neurons. The surviving motor neurons apparently regulate (by an unknown process) the mitotic rate of the developing secondary muscle fibers, leading eventually to the establishment of a set number of motor units. Thus an evolutionary change in number of primary muscle fibers might automatically modify the number of motor neurons. We return to this topic later when we discuss ontogenetic ratchets.

### THE ORIGIN OF EVOLUTIONARY NOVELTIES

An evolutionary novelty is a pronounced and unusual departure in morphology. The panda's thumb, the hinged teeth of sibynophiine snakes, the narwhal's tusk, and the dildo of the salamander *Mertensiella* are good examples of evolutionary novelties (Davis 1964; Gould 1980; Savitzky 1981; Arnold 1987). In each of these cases, a lineage has evolved a radically new morphology. In many cases a special set of selective pressures may push towards novelty: e.g., the bamboo diet of the panda, feeding on hard-bodied lizards by sibynophiine snakes, the female-superior mating posture of *Mertensiella*. While acknowledging the importance of such unusual selection pressures, our group concentrated on the contributing role of decoupling in the origin of novelties. Under the topic of "evolvability" we discuss a special class of novelties, watershed events, that presage a proliferation of lineages and a diversification in morphology.

#### The Role of Coupling

The evolution of novelties might be facilitated by a decoupling of connections between features or because a new, more favorable pattern of coupling has been established (Liem 1973; Maynard Smith 1978; Alberch 1982; Wake et al. 1986; Roth and Wake, this volume). There was general agreement in our group that a change in coupling might often be associated with the origin of novelties, even if the association is not mandatory.

The possible role of coupling in the origin of novelties becomes more concrete if we consider a particular genetical view of coupling. Genetical coupling can arise either from pleiotropy or linkage disequilibrium. Such coupling can be measured as a genetic correlation, estimated within

populations by assessing trait covariance between parents and their offspring (or using other sets of relatives [Falconer 1981]). Such genetic correlation between traits can arise as a natural consequence of development when one trait induces another or when two traits share a developmental precursor or process. The resulting genetic correlation can have the evolutionary effect of constraining the direction of evolution. Selection on one of two coupled traits will evoke evolutionary response in the other trait (Falconer 1981). Consequently, the direction of evolution in multivariate space will reflect both selection pressures and the pattern of coupling between traits (e.g., Lande 1979). While genetic coupling may not affect the equilibrium outcome of evolution (see, however, Slatkin and Kirkpatrick 1987), it may have effects on evolutionary trajectories that last for hundreds of thousands of generations (e.g., Lande 1980a). Consequently, it is conceivable that coupling restricts the spectrum of outcomes and that decoupling or recoupling might sometimes precede the origin of novelties (Wagner 1986).

The association between a change in coupling and subsequent evolutionary diversification can be tested statistically. For example, fusion of two halves of the pectoral girdle has occurred independently on at least eight occasions among 3400 species of frogs (Emerson 1988). Frogs with unfused girdles show a wide range of morphological diversity in shape of the pectoral elements. In contrast, a restricted range of girdle variation prevails in taxa subsequent to the coupling event (fusion of pectoral girdle). Likewise, Schaefer and Lauder (1986) found an association between the degree of coupling of jaw elements (fused vs. unfused mandibles) and trophic diversification in catfish lineages. In both of these cases, a positive genetic correlation between left and right sides seems likely, but lowering of genetic correlation in the unfused state has not been documented (see also Roth and Wake, this volume).

While the role of decoupling in releasing functional constraints is transparent, the role of genetic/epigenetic coupling is more complicated. Mathematical studies of phenotypic evolution have suggested that genetic correlations facilitate evolution by natural selection if and only if there are functional interdependencies among the characters (Wagner 1988).

The resolution of selective compromises (another view of coupling) may also play a role in facilitating the origin of novelties. Consider the air-breathing fish studied by Liem (1987). Because these fish use their buccopharyngeal chambers for breathing and feeding, both functions are compromised. Separation of compartments by fusion of gill valves permitted independent evolution of the two functions and apparently facilitated an enormous morphological diversification.

A special case illustrating the role of decoupling in the evolution of morphological novelties is presented when entire organ systems are lost, such as the electro- and mechanoreceptors of the lateral line system. Because

the lateral line system is derived from placodal material, the central nervous system will be notified of its absence only at the time during development when the central nervous cells receive innervation. If these undifferentiated neurons can derive trophic support (which they would normally receive from the lateral line afferents), they may be incorporated into another functional complex. The evolution of the auditory nuclei in frogs has been suggested as an example in which undifferentiated electroreceptive neurons are captured by the newly evolved afferents of the basilar papilla, trophically maintained, and transformed into auditory neurons (Fritzsch 1988).

Externalists often treat developmental constraints as local rather than as global (Charlesworth et al. 1982; but see Kirkpatrick 1988). The view that at least some constraints are transitory rather than permanent on an evolutionary time scale is supported by selection experiments that have succeeded in altering constraints. Thus, some constraints have a genetic basis that can be altered. For example, vibrissal number in mice is a nearly invariant trait. Nevertheless, Dun and Fraser (1959) and Fraser and Kindred (1960) were able to show that hidden genetic variation for vibrissal number exists in mouse populations. By introducing a mutation that revealed the hidden variation, these workers were able to select for both an increased and a decreased number in different lines (see also Van der Loos et al. 1986). Selection also changed the mapping function between gene effects and phenotype: the system of genetic constraints was altered (see also Maynard Smith and Sondhi 1960; Rendel 1967; Scharloo 1987). Waddington (1942, 1960) accomplished a similar result by using environmental shocks to reveal hidden genetic variation.

Waddington (1942) proposed a mechanism, "genetic assimilation," whereby a new phenotype that appeared in the first instance as a developmental response to an environmental stimulus could become genetically fixed. The proposal is as follows. In the original population, there is genetic variability in the capacity to respond to the novel stimulus. If the response is adaptive, selection will cause the spread of those genes that favor a response. As such genes accumulate, genotypes may arise that produce the response without need of the environmental stimulus. Note that in this process, the environment does not change a gene: it causes phenotypic differences to appear between genotypes that were already present, and so makes selection effective. Although genetic assimilation is plausible under natural circumstances, its prevalence is an open issue. How frequently are novel phenotypes induced by natural fluctuations in environmental conditions?

#### The Evolution of Evolvability

Just as some kinds of animals are good at flying or swimming, so may some kinds of animals be good at *evolving* (Dawkins 1988). In particular, certain

kinds of embryology may be predisposed to spawn rich evolutionary radiations. At first this sounds like a heretical idea. Superficially, it sounds like the heresy of ascribing evolutionary foresight to a lineage. However, there seems to be no objection to our recognizing, with hindsight, that certain key innovations in embryology ("watershed events") have been the forerunners of massive evolutionary flowerings. A possible example of a watershed event is the invention of segmentation in the ancestors of vertebrates and, independently, in the ancestors of annelids/arthropod. The first segmented individual may or may not have been particularly good at surviving as an individual. However, it can still be true that lineages with segmented bodies are good at *evolving*. Other possible watersheds include the evolution of tooth replacement in placental mammals (Werdelin 1987; discussed by Vrba, this volume), the invention of multicellularity, the sequestration of the germ line, and "bottlenecking" of the life history. The invention of sexual reproduction is frequently mentioned in this kind of context.

The evolution of evolvability may be a cumulative, progressive process, not just a single-step event. This is because lineages that become good at evolving thereby place themselves in a good position to accumulate further changes in their embryology that make them become even better at evolving.

The idea of evolvability is one that has occurred to many people (e.g., Liem 1973; Lombard and Wake 1977; Raup 1985). It is vividly illustrated by Dawkin's (1986) "biomorph" computer program. The original version of the program produced a rich flowering of pseudo-evolution on the computer screen, but nevertheless limits began to appear. It took a few major innovations in the writing of the embryology procedure in the program (the equivalent of watershed events) to unleash a new spectrum of evolutionary possibility (Fig. 2).

Some watershed events are unique. In such cases, diagnosis of a key innovation may be viewed with skepticism for causation is a risky inference. In other cases, the watershed event may have occurred repeatedly in different lineages. This situation may permit statistical treatment of the association between the candidate watershed event and subsequent radiation. Schaefer and Lauder (1986) proposed multiple comparisons between sister taxa that possess and lack the key innovation. Causation remains an inference, but at least the statistical reality of the association between a particular innovation and subsequent lineage proliferation or rapid morphological diversification can be tested.

The causes of lineage persistence and proliferation can also be considered from the perspective of selection theory. Thus a recurrent pattern of association between a particular watershed event and subsequent lineage proliferation can be further investigated as a sign of lineage selection.

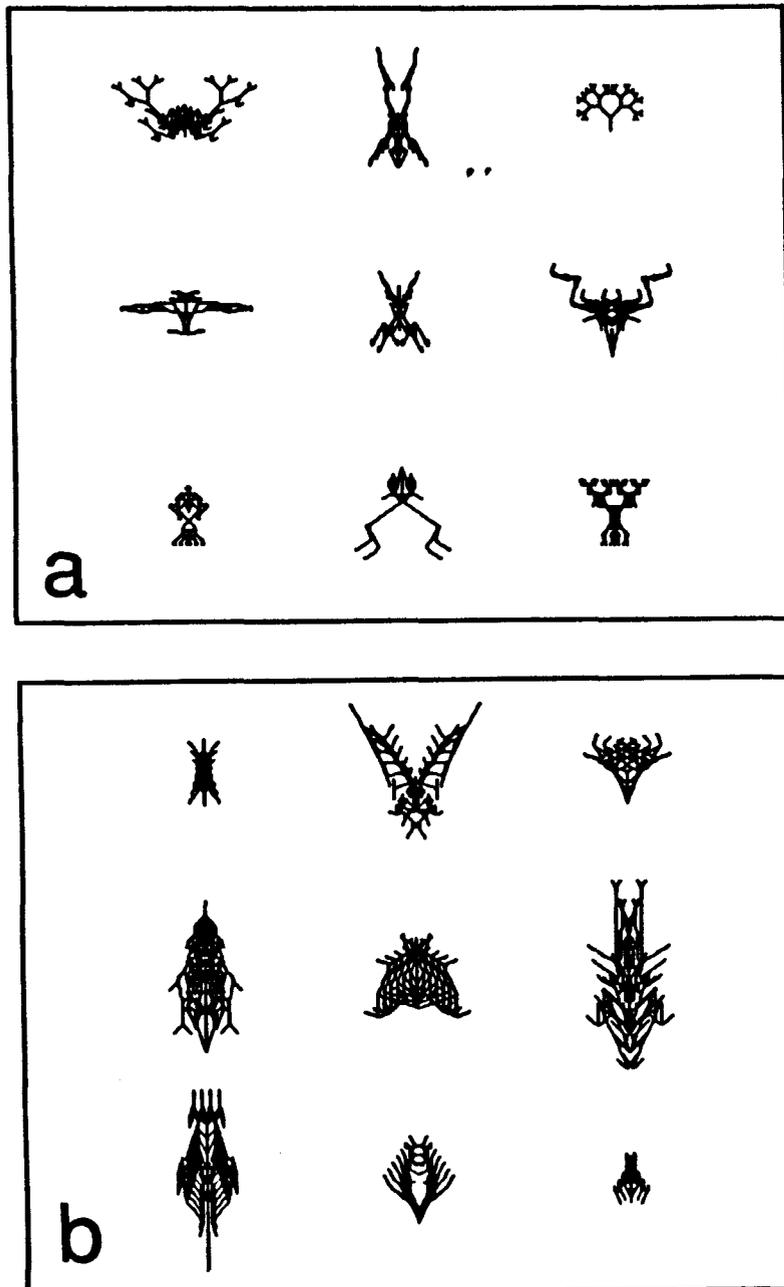


Fig. 2—Diversity of artificial organisms (biomorphs) produced in a computer simulation of evolution before (a) and after (b) the introduction of “genes” that yielded segmental gradients (from Dawkins 1988).

### LEVELS OF SELECTION

The emergence of new levels in the hierarchy of life is a fundamental issue in the evolution of complexity. Analysis of this phenomenon includes consideration of the synergistic and antagonistic interactions between selection at the existing lower level and selection at the emerging higher level. Thus, genes and cells could evolve to cooperate in producing integrated organisms only through suppression of selection among genes and cells within organisms (Weismann 1904; Dawkins 1982; Buss 1987; Csányi, this volume). Once a new level has become established, such selective interactions can continue. For instance, cancer is a grim reminder of the ongoing, potential antagonism between the selective interests of the organism and those of entities included in its body. Similarly, the maintenance of sex, and its dominance in contrast to the thin representation of asexual reproduction, has been ascribed (at least in some major phylogenies) to selective antagonisms between the level of asexual organisms and that of sexual lineages (Williams 1975; Maynard Smith 1978; Bell 1982; Michod and Levin 1988). In considering such issues, we first discuss the evolution of multicellular life (under the topics of sequestration of the germ line and bottleneck life cycles; see also Csányi, this volume). Then we turn to the problem of selection at levels higher than that of the multicellular organism.

### Sequestration of the Germ Line

Buss (1987) has argued that the sequestration of the germ line and maternal control of development evolved because they suppress competition between somatic cells for opportunity to be represented among germ cells. He has also suggested that, once these two mechanisms have evolved, this reduces the “window” on further major morphological evolution. The first part of this argument can be supported by more formal models. Thus, if there is genetic variation between the cells of an organism (which must in general have arisen by mutation since the zygote stage) which causes some cells to migrate to the gonads, and by so doing to lower the fitness of the organism, then it can be shown that a “suppressive” allele, *S*, which prevented such migration, could be established by natural selection. A natural way for *S* to act would be by germ line sequestration. For example, allele *S* might prevent meiosis in any cell that did not contain a particular class of molecule: if the molecule were confined to a particular region of the egg cytoplasm, then both maternal control and germ line sequestration would be achieved.

Concerning Buss’s second argument, members of our group differed in their impressions of what Buss had actually argued. Some of us interpreted him to say that a new mutation, altering morphology, must act “synergistically”: that is, it must increase fitness at the cell level (i.e., it must increase the probability that the cell in which it first occurs will become a germ cell),

and at the organism level (by generating an improved morphology). Those with this interpretation found this argument difficult to sustain. With rigid germ line sequestration, the first type fitness increment is impossible, and so, Buss argues, evolutionary novelty is less likely to arise. But it is hard to see why there must be synergism of this kind. A mutant that has no effect on selection between cells within an organism can still be established by natural selection if it occurs in the germ line. Morphological novelty may be rare or absent in particular taxa because changes that increase fitness are rare or absent, but it is not clear that germ line sequestration can itself be a cause of evolutionary conservatism.

### Bottleneck Life Cycles

The organism, as a level of organization, is possible only if genes are prevented from indulging in independent "selfish" expression. In eukaryotes this is achieved by the discipline of meiosis, which means that each allele of a diploid pair has a "fair" 50% chance of ending up in each gamete produced. If organisms did not channel all their efforts into a final common pathway—reproduction of all the genes of the organism impartially—organisms would not hang together as organized wholes: in effect, there would not be any organisms, because they would be torn apart by selfish "rebels" within themselves. The importance of "bottlenecked" life histories, life histories that restart with a single cell in every generation and then grow through a fixed cycle of events before returning to the single-celled starting point, has been stressed by Dawkins (1982). The consequences of bottlenecking can most easily be understood by contrast with an imaginary nonbottlenecking species of plant that grows in a straggling manner without releasing unicellular propagules. If it reproduces at all, it does so by giving off multicellular fragments of indeterminate size. Bottlenecking means that evolution can be seen as a succession of life cycles, each of which may be an improvement on its predecessor.

Bottlenecking has three important consequences:

1. It allows innovations to be restructured from scratch rather than as remouldings of existing organs. Remoulding—beating swords into ploughshares—has grave limitations. Returning to a single-celled beginning allows the equivalent of going "back to the drawing board."
2. It provides a calendar with reference to which embryological events may be timed. For instance genes may be turned on or off at particular moments during the growth cycle. The hypothetical straggling species does not have a recognizable timetable to govern such regular switching on and switching off.

3. It tames the menace of somatic mutation. The hypothetical straggling plant may undergo somatic mutation at any time, in which case clones of mutant cells will crop up heterogeneously in parts of the plant. If new "individuals" form by fragmentation, most individuals will eventually end up being genetically heterogeneous. If the life cycle is bottlenecked, on the other hand, most individuals will be genetically homogeneous. This is because somatic mutations that occurred in previous generations will not contribute toward individuals being genetically heterogeneous: every individual begins from a single-celled zygote and its cells will share the genotype of that zygote unless there are somatic mutations within this particular individual's lifetime. Only very recent somatic mutations, therefore, will contribute to making organisms genetically heterogeneous. Selection between rival individual organisms, as opposed to between rival cells, therefore is made possible, together with all that follows from it in the way of intra-organismal cooperation, by the bottlenecking of the life history. Note that this argument works independently of whether reproduction is sexual or asexual, and independently of whether the germ line is "sequestered."

### The Relevance of Species Sorting and Species Selection

Genealogical entities (individuals *sensu* Ghiselin 1974 and Hull 1980) at different hierarchical levels, from genomic elements to species, undergo processes of "sorting." That is, there are differential "birth" and "death" rates that correlate with variation among entities at each level. A more contentious question, which we address in the next section, concerns the conditions under which one can ascribe such sorting at levels higher than that of organisms to group or species selection.

Using a restricted concept of species selection, as outlined below, all of us agree that species selection is unlikely to produce complex organismal characters. Yet species selection, and other causes of heritably based sorting among species, can shape macroevolutionary patterns. Hypotheses of this kind can feature in the explanations of questions such as: Why has the bauplan of beetles diversified into hundreds of thousands of species and complex organismal characters, while other lineages, such as those of pogonophorans and horseshoe crabs, contain a mere handful? Why did some lineages become hugely dominant during past time periods, such as trilobites and ammonites in the marine realm, only to be totally replaced later? Why is organismal complexity today vastly more diversified in the tropics than in temperate regions? Why has sex not only maintained itself in the face of the cost of meiosis, but also immeasurably increased the range of organismal complexity that is there for us to see? Related questions, to which hypotheses

of species sorting are equally relevant, concern analysis of "key characters," constraints (Lauder and Liem, this volume) and "evolvability."

While our group agreed on all these issues, divergent opinions became apparent when we explored the implications of punctuated equilibria (Eldredge and Gould 1972). Group members had different views on the prevalence of punctuated equilibria in evolution. Yet all granted that, to the extent that it obtains, it is relevant to the evolution of organismal complexity: Under this model most net, long-term phenotypic change, and especially the evolution of phenotypic complexity, is causally associated with lineage splitting. Punctuationists and others all recognize that lineage splitting does not necessitate notable phenotypic divergence (as is obvious from the existence of sibling species), and that a measure of phenotypic divergence may obtain within polytypic species. But take the case in which a more pronounced long-term trend does occur in one cladistic branch A than in a related one B. Then the hypothesis of punctuated equilibria (together with the assumptions that biases in the directions and magnitudes of "punctuations" do not account for the trend) predicts that the larger trend in clade A should be associated with a higher lineage splitting rate for A, and vice versa for clade B (Gould and Eldredge 1977; Stanley 1979; Vrba 1980). Some long-term patterns in the fossil record are consistent with this proposal (Vrba, this volume). However, in counterargument some members of our group cited findings that significant morphological transitions can occur within species (Gould and Johnston 1971; Kaufman and Liem 1984; West-Eberhard 1986). How such "intraspecific macroevolution" may relate to long-term trends is not clear.

We also considered whether under certain conditions it might be appropriate to view high speciation rate itself as a proximal cause of trends—as a "motor" that accelerates the evolution of organismal complexity (see discussion and Fig. 1 in Vrba, this volume). A positive reaction to this possibility turned out to be very much a minority view in our group.

Nevertheless, all of us agreed that in principle species selection and other forms of heritably based sorting among species can be causally associated with trends toward increasing phenotypic complexity, and that the possible rules of species sorting must be considered in addressing how complex organismal characters are distributed among phylogenies, through time and over geography.

#### Species Effect Sorting in Distinction to Species Selection

As Williams (1966) pointed out, many claims of group selection are actually instances of group sorting as an incidental effect of lower level selection. Similarly, species in clades may undergo effect sorting, in distinction to species selection (the effect hypothesis [Vrba 1980, 1984]). Evidence from

African mammals provides an example (Vrba, this volume). Clades of organisms, whose resources have tended to persist through environmental extremes during their histories (including generalists and specialists on resources that range across environments), had a low incidence of vicariance and low speciation and extinction rates. This is interpreted to indicate that they experience relatively little directional selection pressure. In contrast, clades of specialists, whose necessary resources have tended to disappear during recurrent environmental extremes, seem to have had a higher incidence of strong, directional selection pressures, vicariance, speciation, and extinction. Where differential species diversification results as an effect of organismal selection regimes that differ among clades, as in the African mammal example, the process is not species selection but species effect sorting.

What, then, are the characteristics of group and species selection? The discussion of species selection that follows applies analogously to group selection. Species in clades must vary in heritable characters, and this variation must interact with the environment to result in sorting. But these conditions are not sufficient. In order for a sorting process to be labeled species selection it must at least in principle be able to oppose selection at lower levels (Vrba 1983, 1984; Maynard Smith 1983). Selection regimes at different levels need not have synergistic outcomes. Rather, such selection regimes are independent of each other, and this aspect is most apparent in the case of antagonism between them. Species selection has been said to require "species structure"—emergent characters of species which vary heritably among species and lineages, and which arise from the interactions among organisms (Maynard Smith 1983; Vrba 1984; Vrba and Gould 1986). Such species structure may be manifest in the form of characteristic composition (age and sex), size, and geographic separation of component populations. This is analogous to emergent organismal traits that arise from cellular interactions and are manifest by the relative abundances and spatial distributions of different cell types, namely morphology. A hypothetical example is given by Vrba (this volume).

The invocation of selection at levels higher than that of the individual organism is fraught with controversy of several kinds. Some authors use group selection in a broad sense to include all processes arising from differences in the fitness or success of groups (Wright 1977; Wade 1985). Many other authors use group selection in a narrower sense. They do not see variation in group fitness as a sufficient condition for group selection (Williams 1966; Arnold and Fristrup 1982; Sober 1984; Vrba 1984; Heisler and Damuth 1987; see rebuttal by Griesemer and Wade 1988). Within this second position, various criteria have been proposed: (a) group membership must account for some of the covariance between fitness and phenotypic traits (Arnold and Fristrup 1982), (b) group attributes must account for

some of the covariance between fitness and phenotypic traits, in other words selection is dependent upon the group context in which it occurs (Wimsatt 1981; Heisler and Damuth 1987), (c) heritable emergent characters must vary among groups or species and interact with the environment such that there is differential birth and death of groups or species (Vrba 1983; Vrba and Eldredge 1984; Vrba and Gould 1986), (d) group or species selection must in principle be able to oppose selection at lower levels (Vrba 1984; Maynard Smith 1983).

The covariance approach, initially championed by Price (1972) and later by Arnold and Fristrup (1982), Wade (1985), and Heisler and Damuth (1987), has some problems as a diagnostic tool (Sober 1984; Vrba and Eldredge 1984). Some see these problems as fatal to the approach, while others see them as solved or solvable by extensions of the statistical framework. For example, selection at the individual level can cause sorting at the group level, manifest as an among group covariance between fitness and traits (Vrba 1984; Vrba and Gould 1986; Heisler and Damuth 1987). In addition, frequency-dependent selection at the individual level can masquerade as group selection (Sober 1984). Even where group selection is occurring it may be masked by a variety of processes at lower levels such that covariance between trait and fitness at the group level is negligible (Sober 1984). Furthermore, within any level, selection on a trait can induce a covariance between an unselected, correlated trait and fitness (Pearson 1903). Lande and Arnold (1983) refer to the induced covariance as an indirect effect of selection, whereas Sober (1984) refers to it as selection of the trait, in contrast to selection for the trait (the direct effect). Fitness currency is an additional challenge facing the development of hierarchical theories of selection. When we move up the hierarchy to the level of species or lineages, we need a new fitness currency which measures the differential proliferation and extinction of species and lineages (Eldredge and Gould 1972; Stanley 1975; Vrba 1980, 1984; Slatkin 1981). What is the connection between emergent properties and fitnesses at the organismal and species levels?

#### Phylogenetic Indicators of Lineage Selection

In some cases it may be possible to identify traits that are individually advantageous, but which are selected against at the level of species or lineages by making use of phylogenetic information, as in the following cases.

Maynard Smith (1978) compared the taxonomic distribution of parthenogens with that of haplo-diploids. The former characteristic is widely distributed in some taxa, but is usually found in single "species" within a

genus, or in varieties within species. It is rare to find a larger taxonomic group (genus or above) composed only of parthenogens, or to find a parthenogen with no close sexual relatives. This is the taxonomic distribution to be expected of traits selected against at a higher level. The proposition is that individual selection favors parthenogenesis but opposes sexual reproduction because of the cost of meiosis (Williams 1975; Maynard Smith 1978). However, in the long term, as a consequence of meiosis and recombination, sexual lineages are able to prosper, survive, and diversify in spite of environmental change. In contrast, haplo-diploidy has arisen rather seldom, but has given rise to whole orders or suborders (e.g., hymenoptera, monogonont rotifers), and monospecific genera. In principle, a search for "spotty" taxonomic distributions could identify other traits whose distribution may have been influenced by selection at higher levels, although it will be necessary to test the statistical significance of any conclusions drawn.

#### A Possible Example of Levels of Selection Acting in Opposition

One of the crucial conclusions of population genetics is that the direction of evolution is determined by selection rather than by directional mutation (Haldane 1927; Fisher 1958; Wright 1977). Evolution in a given direction may be slowed down, or prevented altogether, by developmental constraints, but evolution will not be driven in a given direction by mutation. An apparent exception to this conclusion can arise if selection between genes operates within the individual. A possible example is afforded by plethodontid salamanders (Sessions and Larson 1987). In this group, there has been a dramatic increase in the DNA content of the genome, accompanied by a corresponding increase in cell size. In those lineages in which body size has decreased, and in which feeding depends on efficient vision, this increase in cell size has caused serious difficulties, because an efficient visual system requires many neurons, e.g., in the context of visual acuity and stereopsis (Roth et al. 1988). These difficulties have been overcome by a slight reduction in genome and cell size, by a large increase in the relative size of the brain, and by devoting a large proportion of the brain cells to the visual function. But why did genome size increase in the first place? The most plausible answer (but one that has not as yet been investigated at the molecular level) is that there are repeated DNA elements in plethodontids capable of replicative transposition. Frequent transpositions to random sites in the genome would be favored by gene-level selection and would lead to an increase in genome size without change in chromosome morphology, which is what is observed. If this interpretation is correct, it is an interesting example of a conflict between selection at different levels (see Vrba and Gould 1986 for further examples and Vrba, this volume).

## LONG-TERM TRENDS IN THE EVOLUTION OF COMPLEXITY

The existence of a complex structure implies a long history of elaboration, a long-term trend in increasing complexity. In discussing the evolution of "organs of extreme perfection," such as the vertebrate eye, Darwin (1859) stressed the importance of heritable variations of slight selective advantage at each stage in the elaboration of the organ. Our group discussed two other aspects of long-term evolutionary trends in complexity of structure: arms races or coevolutionary spirals and ratchets that facilitate evolution in one direction while inhibiting evolutionary reversals.

### Arms Races

Animals must become adapted to prevailing weather conditions, but weather does not progressively and systematically work to counteract those adaptations. Enemies such as predators and parasites do. Each adaptation against a particular predator or parasite calls forth a counteradaptation, which necessitates a counter-counter, and so on. The weather (standing for the whole of the nonbiotic environment) may be unpleasant but it does not systematically work at becoming progressively more unpleasant in the way that the biotic environment does (Van Valen 1973). Arms races provide pressure for sustained evolution of a kind that may not be provided by the selection pressures from the inanimate environment (Dawkins and Krebs 1979; Stenseth and Maynard Smith 1984; Vermeij 1987). Interspecific arms races, such as those between predators and prey, are familiar and straightforward. Intraspecific arms races could also have powerful evolutionary consequences. Male adaptations, for instance, may sometimes be seen as counteradaptations to female reluctance to mate, and vice versa (Lloyd 1979). Models of sexual selection, especially runaway models of escalating male ornamentation coevolving with escalating female choice, have been suggested in this context (Bradbury and Andersson 1987). The very existence of sexual reproduction itself, according to one school of thought (Hamilton 1980), depends upon a ceaseless cyclical arms race between hosts and parasites. In general, it is possible that some, if not most, complex and elegantly designed organ systems of the kind that this conference has discussed are the endproducts of prolonged arms races.

The role of arms races in generating complexity and novelty was hotly debated in our group. Enthusiasm for arms races was countered by the response that arms races would merely add spangles and sequins. Most agreed that sexual selection arms races could produce important innovations with pervasive effects on many aspects of both sexes.

### Ratchets as Possible Causes of Trends

Trends are well known in the fossil record. In many cases one might plausibly argue that net directional environmental change accounted for them by conventional natural selection. But some trends are difficult to explain that way, such as the following case (Vrba, this volume). It is known that, at least since the Pliocene, global climate was cycling about a mean that was constant for long periods of time (the astronomical or Milankovitch cycles). In tropical Africa this resulted in alternation between vegetationally open and more wooded environments. Some clades of browsing and grazing antelopes responded to these cycles by species diversification and trends. But, curiously, these clades seem to have remained "faithful" either to grassland habitats and grazing specialization, or to browsing in more densely vegetated habitats. The pattern suggests a possible directional bias—an apparent inability to switch to an alternative ecological mode in spite of the fact that alternative vegetational habitats were being presented recurrently. How could such trends evolve? One process which we discussed in this connection is the selective ratchet illustrated below. Another possibility is some form of ontogenetic ratchet. For instance, during one phase of the climatic cycles, selection together with ontogenetic processes may result in new ontogenetic couplings that constrain reversal during the alternative climatic phase. We know of no example in relation to climatic oscillations. But we illustrate below how interactions between genetic loci, together with different phenotypic expression depending on environment, could facilitate evolution in one direction and preclude reversals.

### Selective Ratchets

If there are epistatic fitness interactions, then it is possible for there to be a "selective ratchet." The simplest possible model is shown in Fig. 2. In this figure, *a*, *A* and *b*, *B* represent alternative states of two characters, or the genotypes that determine them. The epistasis arises because the selective advantage of state *a* or *A* depends on whether *b* or *B* is present, and vice versa. In environment 1, a population would evolve from *ab* to *AB* under natural selection. However, in environment 2, the reverse change from *AB* to *ab* would not take place, even if it would be advantageous if it did. It is not clear, however, how such selective ratchets could account for a consistent, long-term phenotypic bias in a clade. For further discussion of selective ratchets see Wagner (1982) and Levinton (1986).

### Ontogenetic Ratchets

Can developmental interactions cause irreversibility of transformation, just as functional interactions can cause selective ratchets? As a possible example,

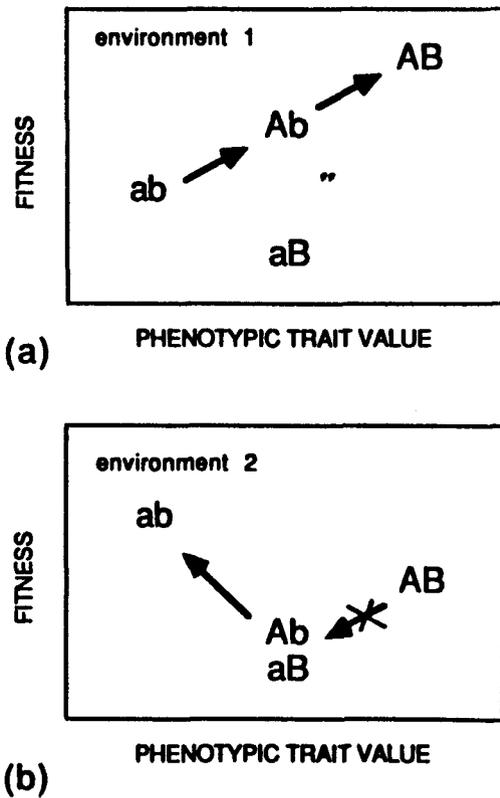


Fig. 3—A selective ratchet arising from epistatic gene interactions that vary with environment. Four genotypes are denoted ( $ab$ ,  $Ab$ ,  $aB$ , and  $AB$ ) and their effects on a phenotypic trait and on fitness are indicated by their positions in fitness-phenotype space. (a) In environment 1 selection favors the transition from  $ab$  to  $Ab$  and from  $Ab$  to  $AB$ . The ratchet rolls, resulting in an evolutionary trend. (b) In environment 2, selection acts against the transition from  $AB$  to  $Ab$  or  $aB$ , even though the transition from either  $Ab$  or  $aB$  to  $ab$  would be favored. Once the population becomes fixed for  $AB$ , the ratchet locks.

consider the development and evolution of the vertebrate eye. The various components of the vertebrate eye were acquired in a gradual fashion (Horder 1983). Photoreceptive elements evolved first as part of the diencephalon, and then became located directly under the body surface. Finally, the elements of the image projecting apparatus were added, e.g., the lens and the cornea. However, in evolutionary studies of eye reduction, no such piece-by-piece deletion of elements is evident. Genetic analysis of hybrids derived from crosses between cave populations and surface populations of the fish *Astyanax mexicanus* revealed no genes that affect only one of the

major structural elements of the eye (Wilkens 1971, 1987). Instead individual genes had effects on the size of all components. This is surprising in the light of the plausible step-by-step evolutionary origin of the eye. Why is it not possible to go back step-by-step?

A possible answer may be found in the properties of systems which arise from networks of interdependencies among components of the vertebrate eye during development. Figure 3 gives a simplified outline of how such a network may cause an ontogenetic ratchet.

Often one organ, such as the vertebrate eye, originates from an organizing center which forms first, and subsequently triggers the differentiation of the other parts of the organ such as the lens. However, the reacting tissue often affects the further development and/or maintenance of the inductive tissue. In this way developmental interactions can feedback to the subsequent development of the inductive tissue. As soon as such a cyclical network of developmental interactions has evolved, the phenotypic effects of further gene substitutions must deal with an ensemble of features that constitutes a semiautonomous unit of the phenotype. A gene that causes deterioration of one character will also affect inductive interactions with other characters. Its effects will reverberate through the whole system. Thus, in cyclically coupled suites of characters, a mutation that affects mutual developmental interdependencies has phenotypic effects that are no longer localized to the

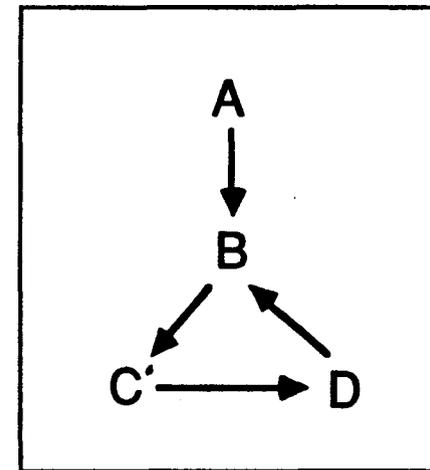


Fig. 4—An ontogenetic ratchet resulting from a cyclic induction process during development. Inductions of one part by another are indicated by arrows. B helps induce D via induction of C, but D induces the further differentiation of B. A gene with a specific effect on any one part will also reduce all the other parts. Once the inductive interactions evolve, regressive evolution of the structure formed by the four parts will be a cascading process.

tissue in which the gene is expressed. All genes are then effectively eye genes, and mutations knocking out one character are no longer possible. This example illustrates how ontogenetic ratchets are mechanistically realized, because in networks of this kind the deletion of one of the characters participating in the developmental feedback appears to be impossible. There are only two choices left: either mutations do not interfere with the inductive feedback or they simultaneously reduce the whole ensemble of characters as is the case in eye reduction. Some caution should be exercised in applying this model. There is interspecific variation in the inductive pathways for homologous characters. For example, multiple inductive pathways for the same character may explain the maintenance of photoreceptive cells despite the absence of lens development in at least one species of caecilians (Wake 1985).

## CONCLUSIONS

Two contrasting views were emphasized during our discussions. On the one hand is the view that complex structures appear during development as the outcome of generative processes involving interactions between many components. Genes are only one among many components, with no privileged position. Although selection can eliminate structures incompatible with survival and reproduction, it can only select within the realm of potential structures that the generative processes produce. On the other hand is the view that all novelty in evolution depends on mutations that are nondirected at their origin, and that the direction of evolution is determined by selection.

Are these two views merely different perspectives, determined by differences of interest, or is it possible, at least in principle, to decide between them by experiment and observation? Even this question is hard to answer. On the one hand, there was much agreement among us. Geneticists agreed that pattern-formation in development is important, and that an understanding of generative rules in any taxon can help to explain why morphological evolution is easy in some directions, and difficult or impossible in others. Internalists agreed that differences are transmitted between generations by changes in genes, so that evolutionary change requires genetic change. But some differences seemed irreconcilable. At the very least, there were deep disagreements about what is the most fruitful way of studying evolutionary change: should we try to understand inheritance, function, and selection or pattern formation and morphogenetic processes? At times, it seemed that the disagreement was profound. The controversy, however, was partly a matter of emphasis. A structuralist is interested in order, integration, and invariant organization among interacting elements. The emphasis is on the limits of variation and consequently directional

selection is given a limited role in evolution (no one disputed the evolutionary importance of stabilizing selection). Therefore, there is a difference in opinion about how to interpret trends, convergence, and parallelism. Selectionists, interested in variation and organism-environment interactions, prefer to invoke selection as the initial hypothesis to explain such order in nature. Internalists, on the other hand, would frame their working hypothesis around rules of development and the issue of constraint.

Some other points of disagreement were more fundamental. In particular, developmentalists complained that the existing body of genetic theory cannot explain system-level properties such as regulation, integration, and constraint. Instead they saw these attributes as properties of the dynamics of interacting systems. In contrast, geneticists viewed constraints as amenable to both genetic and developmental analyses.

## RESEARCH QUESTIONS

1. Genetic studies of important generative rules of development are needed. Could Raup's (1966) model of shell coiling, for example, be used to inspire genetical studies of mollusc shells?
2. How do generative rules vary across species?
3. Can generative rules successfully predict parallel evolution?
4. Do changes in patterns of genetic correlation characterize the evolution of functional novelties?
5. Developmental studies of genetic correlations are needed. Often constraints are described merely in bald statistical terms.
6. What is the time scale for the evolution of developmental constraints? Is there a continuum between local and global constraints? Comparative studies of genetic correlations offer one possible approach.
7. Can we produce a developmental theory of genetic correlation and test it?
8. How prevalent are ontogenetic and selective ratchets?
9. Can we produce a statistical theory that distinguishes between species selection and species effect sorting?
10. What sorts of traits evolve by lineage selection? Statistical tests using multiple lineages appear feasible but are rare.
11. We need a mathematical formulation of how properties and fitnesses at the level of organisms and species relate to each other during the processes of species selection and effect sorting.
12. Did lineage selection contribute to the evolution of viviparity in nonmammalian vertebrates or dioecy in higher plants?
13. How do networks of inductive interaction for homologous organs vary across species? How prevalent are inductive cycles (cf. Fig. 4)? Are there trends in the evolution of inductive networks?

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