Evolutionary Feedback: a New Mechanism for Stasis and Punctuated Evolutionary Change Based on Integration of the Organism

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This paper argues that organisms are integrated, holistic systems whose phenotypic traits and genes interact with each other and natural selection. More than this, organisms are feedback systems. I introduce the term integration of the organism to refer to this idea that organisms are such interacting systems. Integration of the organism is a major reason why most mutations are deleterious, and why the larger a mutation's effect, the greater the probability that a mutation will be deleterious. Yet, it is also why macromutations can occasionally be adaptive. Such adaptive mutations of large effect, an example of which is neoteny, must be coordinated with the genetic system and ontogeny of the organism. Integration of the organism and the ability of both the phenotype and genotype to influence and interact with natural selection means a species can undergo sequential evolution, a term I coin in this paper to refer to a change in a trait causing a change in selection on a second trait, which leads to a change in the second trait, which in turn causes a change in selection on a third trait, changing it, and so on. Sequential evolution can sometimes result in closed feedback loops, in which a trait farther down the sequence affects a trait earlier in the sequence of traits. I call this process evolutionary feedback. Both sequential evolution and evolutionary feedback can sometimes cause punctuated evolutionary change. Evolutionary feedback can also act as a mechanism for stasis. Hence, evolutionary feedback is a mechanism for punctuated equilibrium. I propose that species to a large extent influence, even drive, their own evolution. This, of course, is not to suggest they do so willfully or consciously. It is proposed that there are three mechanisms for punctuated evolutionary change; these are described. Examples of and evidence for sequential evolution and punctuated evolution by evolutionary feedback are presented.

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Introduction

I introduce three new terms: *integration of the organism*, *evolutionary feedback*, and *sequential evolution*. *Integration of the organism* refers to the profound interconnectedness of an organism's traits, and may refer to the phenotype or

the genotype. The emphasis in this paper is on the phenotype, because natural selection acts directly on it. Integration of the organism has profound effects on evolutionary rates and the mechanisms causing stasis and punctuated evolutionary change. *Sequential evolution* is evolution in which several phenotypic or genotypic traits of an organism affect each other's evolution in a temporally linear fashion;

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that is, trait A affects the evolution of trait B, B similarly affects C, C affects D, and so on, where the traits are usually previously existing features that are modified. Occasionally, they are entirely novel traits. It may sometimes lead to punctuational change. *Evolutionary feedback* is a special case of sequential evolution in which the sequence of traits has at least one closed feedback loop; that is, in which at least one trait affects the evolution of a trait preceding it in the evolutionary sequence of traits. Positive feedback loops may lead to rapid evolutionary change, especially when these loops sustain directional selection for a sufficiently long time period. Negative feedback loops lead to stasis. Evolutionary feedback and sequential evolution result from integration of the organism. This paper proposes that there are three general mechanisms of punctuated evolutionary change: (1) macromutation, which is rare and requires a mutation whose effect is coordinated with the organism's genetic and developmental systems; (2) directional selection guided by the external environment; and (3) directional selection guided by the interaction of the organism's traits, which is evolutionary feedback or sequential evolution. Two or all three of these mechanisms may act together to cause rapid evolution. The third mechanism is related to integration of the organism and can occur without leading to punctuated evolutionary change. The goal of this paper is to present convincing arguments that integration of the organism, evolutionary feedback, and sequential evolution are valid and important concepts that can act as mechanisms for both aspects of punctuated equilibrium, stasis and rapid change; that evolutionary feedback and sequential evolution act as causative agents of large, rapid phenotypic change with a reasonable frequency; and that the three concepts provide a novel perspective on evolution and have several important implications to evolutionary theory. I will provide examples of punctuated evolutionary change by sequential evolution and evolutionary feedback. Two key points of this paper are: (1) organisms are feedback systems whose genes and phenotypic traits interact with each other and with natural selection, profoundly affecting rates and direction of evolution, and (2) changes in the phenotype, genotype, and gene frequencies can greatly change natural selection, in both intensity and direction.

Some of the key ideas in this paper are not entirely novel, and have been discussed in the literature. The ideas that organisms are integrated systems and influence their evolution have appeared numerous times. For example, Mayr (1963) spoke of the unity of the genotype, and Simpson (1953) and Miller (1949) discussed the concept of key innovations, which represent the first step in sequential evolution and evolutionary feedback step; I will discuss both these ideas. Waddington (1975), in a collection of papers, strongly supports the idea that a change in an organism can lead to further changes by altering natural selection. However, much of the discussion in the literature is the implicit assumption of these ideas or the casual allusion to some of them, without the careful analysis that I think they merit. One purpose of this paper is to make the case that these ideas and views of evolution receive far too little recognition and emphasis. This paper is the first to argue systematically that a significant portion of punctuated events and evolution in general is best explained by the profound integration of organisms and by interactions between their parts, including feedback loops. Secondly, I introduce and define three new terms and make the model and its supporting arguments as well as assumptions more explicit than most previous authors. Thirdly, I will take the arguments further than previous authors in proposing that biological organisms can be viewed as feedback systems with respect to their evolution. Fourthly, I will present diagrams of evolutionary feedback and sequential evolution that represent a powerful, novel way of illustrating and gaining insight into these ideas. Fifthly, I propose that sequential evolution and evolutionary feedback together represent a mechanism for punctuated equilibrium (Eldredge & Gould, 1972). Sixthly, I will present evolutionary scenarios of these processes actually having occurred in nature, with a discussion of the evidence and plausibility of the model. Next, I briefly discuss implications of and areas of research suggested by integration of the organism, sequential evolution, and evolutionary feedback. Finally, I hope to present

a fresh, new way of viewing these ideas and the process of evolution. The purpose of this paper is not a comprehensive historical review of these ideas of organisms affecting how natural selection acts on them; the literature that touches on this is extensive, and starts in a serious way as early as 1896. Therefore, no attempt will be made to cite all previous authors who discussed these ideas. Other than references pertinent to my arguments, previous authors who discussed these ideas only need be and will be cited in a general way. One can obtain a good idea of previous work to compare with my ideas or for general interest in a discussion of these ideas in Simpson (1953) and the references in it, and in Waddington (1975), both mentioned above.

Integration of the Organism

Integration of the organism, although not an entirely novel idea, requires more discussion, since it is the basis for sequential evolution, evolutionary feedback, and two of the three mechanisms proposed in this paper for rapid evolutionary change. It refers to the fact that organisms are holistically interrelated systems, each trait of which is deeply interconnected with several other traits. Thus a change in one character of an organism can change the fitness and evolutionary fate of other characters. This interconnection exists among both phenotypic and genotypic traits. If the traits referred to are phenotypic, the specific organismal integration can be called integration of the phenotype, while if the traits in question are genetic, it can be referred to as integration of the genotype, or by Mayr's (1963) term, "unity of the genotype." Genetic and phenotypic integration can also occur at the population level, so one may speak of integration of the population, in which genotypic and phenotypic traits of different individuals of a population interact with and influence each other's fitness.

Examples of integration of the organism include pleiotropy; polygenic traits; epistasis; epistatic fitness interactions; position effects; hierarchical genetic regulatory systems; induction, repression, and other forms of genetic regulation; correlated characters; and correlated responses to selection. This list, although probably not comprehensive, is quite long, illustrating the large extent of organismal integration.

Integration of the Organism, Stabilizing Selection, and Stasis

Fisher (1958a) argued that organisms are so intricately constructed, complex, and marvelously adapted "both in their internal mechanisms and their relations to external nature," that any major alteration will tend to be deleterious. The rarity of adaptive mutations in a well-adapted, complex organism, *Drosophila melanogaster*, was demonstrated by Roberts & Iredale (1985), and, with a very different method, by Mukai *et al*. (1972). Integration of the organism also predicts this. It is a conservative force, because the strong interrelationship between the parts (traits or genes) of an organism's phenotype or genotype mean a change in any part is likely to destroy the harmonious, coordinated relationship of that part to the rest of the organism. The larger the genetic mutation or phenotypic change, the greater the likelihood of disruption of the integrated system, and hence of deleterious effects. This means most feedback loops in evolutionary feedback will be negative, resisting change. Generic diagrams of hypothetical cases of stabilizing selection causing stasis are illustrated in Fig. 1. Figure 1(a) shows the process when the environment is the selective agent, while Fig. 1(b) illustrates a typical example of negative evolutionary feedback maintaining the status quo and causing stabilizing selection. These diagrams will be discussed in more detail later.

Integration of the organism is, then, an explanation and mechanism for both stabilizing selection and stasis. Alternative explanations for these phenomena are complexity of organisms apart from interconnectedness of their parts, the fact that organisms are well adapted to their environments after a sufficiently long period of evolution, and that stabilizing selection is generally from the external environment. It is likely that a combination of two or more of these explanations for stabilizing selection and stasis applies most of the time, and that the relative

importance of each varies with the species and specific situation. The relative frequency of the predominance of each and the factors influencing that frequency are interesting areas for research. I am suggesting that more emphasis needs to be given to integration of the organism as an explanation for evolutionary homeostasis. It is interesting to ask: what is the relative importance of the external environment as opposed to the internal environment of the organism as an explanation for stabilizing selection and stasis?

Integration of the Organism and Punctuated Evolutionary Change

There are examples of adaptive, successful macromutations, even though they are relatively rare. Several authors, for example, Garstang (1922) and Gould (1977), have suggested that some major animal groups arose from neotenic ancestors. Polyploidy is common in plants (Stebbins, 1950). How can it be that successful, adaptive mutations of large effect occur even occasionally, if organisms are holistic, integrated, interrelated systems?

The answer lies in the integration itself and the hierarchical nature of genetic and developmental systems. Regulatory genes that serve as master switches to control other genes are important in development. Mutations in these genes can cause coordinated changes in the entire organism that are adaptive and of very large effect. Such mutations can lead to the appearance of entirely new forms. I will now introduce the term *coordinated macromutations* for these adaptive, successful mutations of large phenotypic effect to emphasize the reason that they are possible in hierarchical, integrated genetic systems; i.e. they alter the different morphological and behavioral characteristics of an organism in a coordinated
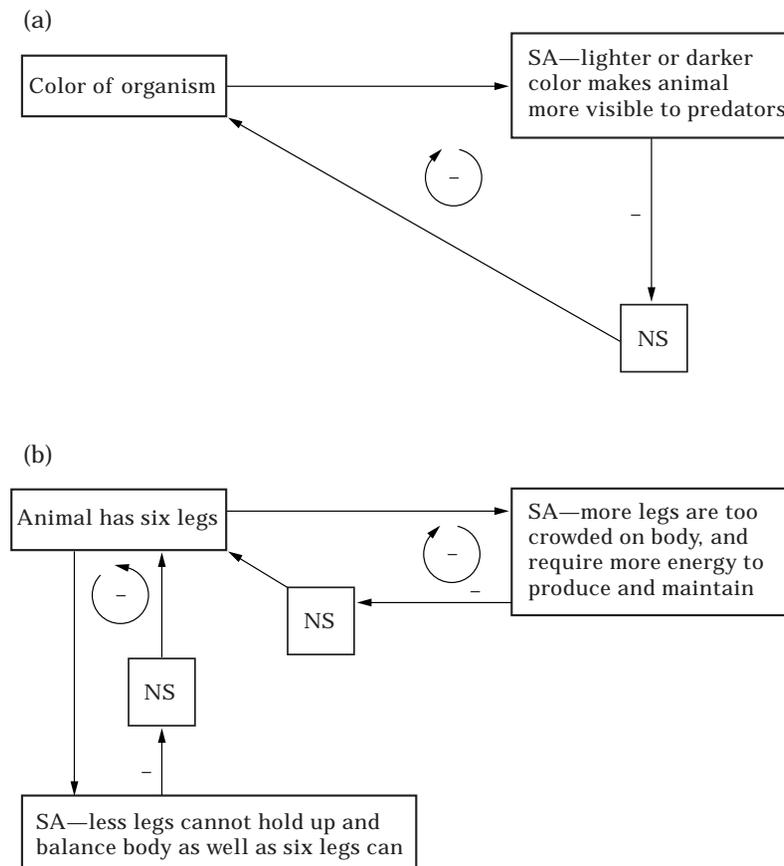

Fig. 1. Generic evolutionary diagrams illustrating the use of such diagrams in stabilizing selection, resulting in stasis. SA = selective agent; NS = natural selection. (a) Selective agent is the external environment; (b) selective agent is the integrated system of the organism. This results in negative evolutionary feedback.

way. In coordinated macromutations, large changes in the phenotype or genotype are coordinated with other characteristics of the organism's phenotype or genotype, resulting in changes that are not developmentally or otherwise disruptive. Coordinated macromutations preclude the need for new developmental patterns to evolve for punctuated evolution to occur. All that is required are very simple shifts in pre-existing patterns that themselves evolved gradually over millions of years. For example, a difference in size between a species and its descendant entails differences in the dimensions of bone, muscles, and nerves, but the two species need not differ in all loci controlling these tissues. Instead, the tissues may be altered in concert by a single control system. A single mutation that increases the level of growth hormone, for example, might result in a large increase in size in one generation, with all tissues responding similarly.

Clear examples of coordinated developmental control and hierarchical genetic regulation acting in integrated genetic systems are found in genes with homeotic effects and the development and genetics of segmentation in *Drosophila*; see, for example, Lewis (1978), Raff & Kaufmann (1983), North (1984), and Slack (1984). An example of an adaptive, coordinated macromutation can also be found in any successful neotenic mutation. For a specific example, Tompkins (1978) found that alternative alleles of a single gene control whether or not an individual axolotl (*Ambystoma mexicanum*) has the capacity for metamorphosis. Thyroxin induces metamorphosis, and a low concentration of it causes failure to undergo metamorphosis. Whether or not most neotenic salamanders arose from a single mutation, it seems likely that they arose from a few macromutations in control genes.

Indeed, Olson & Miller (1958) and Riedl (1977, 1978) claimed that such interrelatedness within developmental systems evolves by natural selection. A large portion of the genome may shape development (Riedl, 1977, 1978). If each gene were expressed independently, then, it is likely one trait or another would suffer a maladaptive developmental accident. Riedl argues that the number of independent traits and hence the opportunities for developmental errors will be lower in an integrated system under hierarchical control.

Therefore, I think that integration of the organism both allows punctuated change by macromutation and insures that it will be a very rare event. Since the interrelatedness of the various aspects of the phenotype and unity of the genotype occur in hierarchical genetic and developmental systems, genetic change in a master control gene can have a large, coordinated, adaptive effect. And since developmental systems are integrated, a key change in early ontogeny can result in a large, non-disruptive, even adaptive change in the phenotype. Yet the cases of this are too few to account for more than a small percentage of the total cases of punctuated change in the history of life. The integration itself assures that only a very small percentage of mutations will be adaptive and even a smaller percentage will be adaptive and with a large phenotypic effect.

Sequential Evolution and Evolutionary Feedback: Two Mechanisms for Punctuated Evolutionary Change

Sequential evolution and evolutionary feedback may act as mechanisms for punctuated evolution. In evolutionary feedback, the interactions link the traits in a closed loop. There may be more than one feedback loop. The feedback loop or loops may be positive, negative, or a combination of the two. Negative feedback loops cause stasis. Positive loops cause evolutionary change, and, in some but not all cases, sustained directional selection and punctuational change. Whether or not a positive feedback loop or set of loops leads to punctuated evolution depends on the amount of change that occurs in the population before the feedback loop or loops change form or cease to exist. Sequential evolution may have less of a chance of leading to punctuated change than evolutionary feedback, because it lacks closed feedback loops. If the traits influence one another in a positive direction, increasing their intensity (e.g. lengthening an appendage or intensifying a color), this maximizes the probability that sequential evolution will act as a mechanism for

large, rapid evolutionary change. One should bear in mind that the interactions and feedback loops are dynamic and interact with changes both in the organism and in the external environment, so how long they remain without changing or ceasing to exist altogether will vary greatly from one loop to another. Forming a predictive theory of their behavior would require a good deal of experimentation and observation, and is a worthy area for study.

An outline of a general scenario by which punctuated change by evolutionary feedback may occur should help clarify the concept. It follows.

1. An adaptive new morphology occurs due to a macromutation, gradual accumulation of many small mutations, genetic recombination, a combination of these, or any other set of genetic changes. This new morphology is often a key innovation. Simpson (1953) suggested that the evolution of a key innovation, or key adaptation, is what allows a group to enter a new adaptive zone, which, once entered, sets the stage for adaptive radiation. Also called key adjustments by Miller (1949), these adaptations may have large phenotypic effects, but may require only small genetic changes, and hence may be rapid and abrupt. They are new, critical adaptations that allow access to resources previously unavailable to the lineage. A key innovation may occur after the accumulation of many small changes suddenly causes a threshold to be crossed.

2. This morphological adaptation spreads throughout the population because of the superior fitness it confers on its bearers.

3. This results in an adaptive advantage among those members of the population who have a behavior that best allows the use of the new morphology. Directional selection for this new behavior and its intensification follows.

4. The behavior selected for increases in frequency in the population. It also increases in intensity in the population; for example, an aggressive behavior becomes more aggressive. At this point, a chain of two traits, in this case one morphological and one behavioral, has occurred. This is the minimum length to qualify for sequential evolution. Of course, sequential evolution may involve chains of much longer length.

5. This may result in the exploitation of a new habitat. This step does not always occur and is not a necessary condition for the process.

6. The new behavior, new habitat, or both confer an adaptive advantage to those organisms in which the morphology that appeared in step 1 is most pronounced or developed. This results in directional selection for the morphology to become more extreme.

7. The morphology therefore becomes more extreme among individuals in the population. For example, a long limb increases in length, or a dark color gets yet darker.

8. For any large genetic changes listed above, especially in step 1, a period of post-adaptive adjustment follows in which the genetic background adjusts to the new adaptive mutations. Because of integration of the organism, even adaptive mutations are likely to have maladaptive pleiotropic effects on one or more aspects of the phenotype, and the larger the mutation, the larger these side effects. Because of these pleiotropic effects, the population may undergo a period of reduced fitness during the process of adaptation, and, in some cases, developmental constraints may limit its ability to evolve (Maynard Smith *et al*., 1985). Fisher (1928a) pointed out that maladaptive pleiotropic effects of adaptive mutations would be followed by selection favoring modifier genes that minimize the harmful effects and maximize those effects that allow adaptation to the environmental challenge that selected for the adaptive mutations. This and similar adaptations by the genetic background to bring it in harmony with the new adaptive mutations is what I mean by post-adaptive adjustment. It may also entail adjustments in the adaptive mutations to better coadapt them to the genetic background.

9. The directional selection fueled by the positive feedback between morphology and behavior continues with the resulting intensification of both until an equilibrium is reached such that the benefits of increasing them equal the costs. When this occurs, one or more negative feedback loops replace the positive one, and directional selection is replaced by stabilizing

selection with respect to the morphology and behavior, which then undergo stasis.

10. The above changes may result in the species entering a new adaptive zone where it is free from interspecific competition. If this is the case, the result could be adaptive radiation, with concomitant speciation. If not, this step does not occur.

Steps 8 and 10, while steps in sequential evolution, do not always involve evolutionary feedback, since closed-loop interactions between phenotypic or genotypic characteristics need not always necessarily occur.

There may be variations in the above scenario. For example, the innovation of step 1 may be a new behavior that causes a morphological change in step 3, or a morphological change may result in directional selection for another morphological change in another structure of the species, and the two morphologies may then become involved in a positive feedback loop. Similarly, two behaviors may interact in a positive feedback loop. Also, the chain of phenotypic changes may be much longer than illustrated here, involving many morphological and/or behavioral changes, and longer feedback loops.

In order for sequential evolution and evolutionary feedback to occur, epistatic fitness interactions must occur. These have been demonstrated. For examples, see Cain & Sheppard (1952, 1954), White (1957, 1958), and Lewontin & White (1959).

Empirical Examples of Some and of All of the Steps of Sequential Evolution Having Occurred Both in the Laboratory and in Nature

Sequential evolution is similar to evolutionary feedback, except that there is no closed loop, hence no feedback. It is a necessary, though not sufficient, prerequisite for evolutionary feedback, and hence for punctuated change by evolutionary feedback. Hence, sequential evolution must be demonstrated to show the feasibility of these two processes, although it does not prove them.

Key innovations are often the first step in sequential evolution (and hence evolutionary feedback), since they tend to lead to subsequent adaptations to utilize the key innovation better,

often result in anagenesis, and lead to adaptive radiation when they precipitate entry into a new adaptive zone.

Examples of key innovations that involve sequential evolution and led to a new adaptive zone, and hence adaptive radiation, include the evolution of flight by archosaurs, and floral components to attract animal pollinators by ancestors of angiosperms. Van Valen (1971) has suggested that about half the orders of mammals arose as the result of special adaptations for feeding or escaping predation. Gest & Favinger (1983) found evidence that the addition of only one oxygen in the side chain of chlorophyll led to photosynthesis.

Miller (1949) discussed the evolution of thrashers (genus *Toxostoma*) from the mocking birds (*Mimus*), both of the family Minidae. He proposed that the key adjustment was elongation and curvature of the thrasher's bill, adapting it to digging, to excavate ground-dwelling insects. Heavier legs and wing reduction could only occur in conjunction with or after development of the long, curved bill. Adaptive radiation into several species followed occupation of a new, more terrestrial adaptive zone. Liem (1974) presented strong evidence that the pharyngeal jaw apparatus in the percoid fish family Cichlidae is a specialized, highly integrated key innovation that accounts for this fish family's phenomenal ability to diversify to an extent unmatched by any other vertebrate family.

Larson *et al*. (1981) discussed the evolution of the salamander genus *Aneides* from its ancestral genus *Plethodon*, both of the family Plethodontidae. They suggest *Aneides* evolved from its ancestor and took on an arboreal existence via two key innovations: the rearrangement of carpals and tarsals provided a redistribution of forces to the fingers and toe tips that facilitated climbing, and the fusion of the premaxillary bones provided a foundation for the evolution of a strengthened jaw (Wake, 1966). A strengthened jaw is important for arboreal predators. The authors suggest these two changes were rapid, punctuational events, each possibly resulting from single developmental mutations. This is supported by the lack of intermediate forms for the two key innovations. The authors' sequential morphological analysis of *Aneides* species suggests that the morphological modifications

associated with the two key innovations and an arboreal life occurred gradually by the accumulation of numerous, independent genetic changes, and followed from the key innovations. Therefore, this is a case of key innovations acting as the first steps in sequential evolution.

Post-adaptive adjustment, the adjustment of the genetic background to a large, adaptive evolutionary change, is usually the last step in sequential evolution. Fisher & Holt (1944) demonstrated it in laboratory mice. Lenski (1988) showed that *E. coli* mutants resistant to the bacterial virus T4 had maladaptive pleiotropic side effects that were reduced after 400 generations of evolution. Furthermore, this was not accomplished by the resistant populations reverting to sensitivity, but from changes in the genetic background that compensated for the lack of genetic integration of the mutation for T4 resistance with the genetic background. Post-adaptive adjustment has been shown in the field. In mutants of cultivated plants such as cotton and sweet peas, older varieties have less disadvantageous side effects than do those that have only recently arisen (Fisher, 1928b). McKenzie *et al*. (1982), and again Clarke & McKenzie (1987) showed post-adaptive adjustment of the genetic background to maladaptive side effects of resistance to the pesticide diazinon in the Australian sheep blowfly, *Lucilia cuprina*.

A striking example of a large evolutionary change occurring in nature by sequential evolution involving several steps is found in salamanders of the tribe Bolitoglossini of the family Plethodontidae (Roth & Schmidt, 1993). This group has large amounts of DNA in the nucleus, possibly because of "selfish" DNA (Doolittle & Sapienza, 1980; Orgel & Crick, 1980; Pagel & Johnstone, 1992). Large genome size is correlated with large cell size. This large cell size is correlated with decreased cell metabolism, proliferation, and differentiation. This led to a simpler brain with less photoreceptors and retinal ganglion cells in the brain as a whole. Low cell metabolism also is linked in these salamanders to an inability to walk fast in avoiding predators or pursuing prey (Feder, 1983). This is correlated with, and probably led to the evolution of, an ambush strategy characteristic of bolitoglossines: that is, these

animals sit and wait until a prey animal comes close. The projectile tongue, excellent stereopsis, and fast prey recognition ability of these salamanders had to evolve in parallel with slow movement and an ambush feeding strategy, or the latter two would not have proven successful. This, in turn, required and led to the simultaneous evolution of specific sensory and brain mechanisms, such as a high number of photoreceptors and neurons in the retina and the visual centers, and sophisticated mechanisms for processing visual information.

Behavioral innovation that is probably usually ultimately genetic in origin can lead to further genetic change, which is sequential evolution. This has been discussed by several authors, starting most notably with Baldwin (1896). See Simpson (1953) for a discussion of a good deal of this. I will discuss a more recent example that is actually evolutionary feedback in the next section.

Examples of Punctuated Evolutionary Change Having Occurred by Evolutionary Feedback in Nature with High Probability

Following are plausible scenarios of punctuated evolutionary change actually having occurred in nature by evolutionary feedback. While such examples do not prove that evolutionary feedback is a common cause of punctuated evolution, they suggest it can at least sometimes happen. Some inference is involved in reconstructing evolutionary histories and their mechanisms. However, these scenarios are consistent with and supported by the empirical evidence and what is known about the taxa in question. I believe there is a reasonable probability that the following scenarios actually happened.

Since the examples are for the most part illustrated with figures that are diagrams of the steps in the scenarios, Fig. 2(a) is included to illustrate a hypothetical, generic case of evolutionary feedback by positive feedback [cf. Fig. 1(b), which shows a negative evolutionary feedback loop]. Here, the animal's poison causes selection for bright color that warns potential predators to keep their distance. The bright color then results in selection for greater toxicity, since cryptic coloration is no longer an option, and
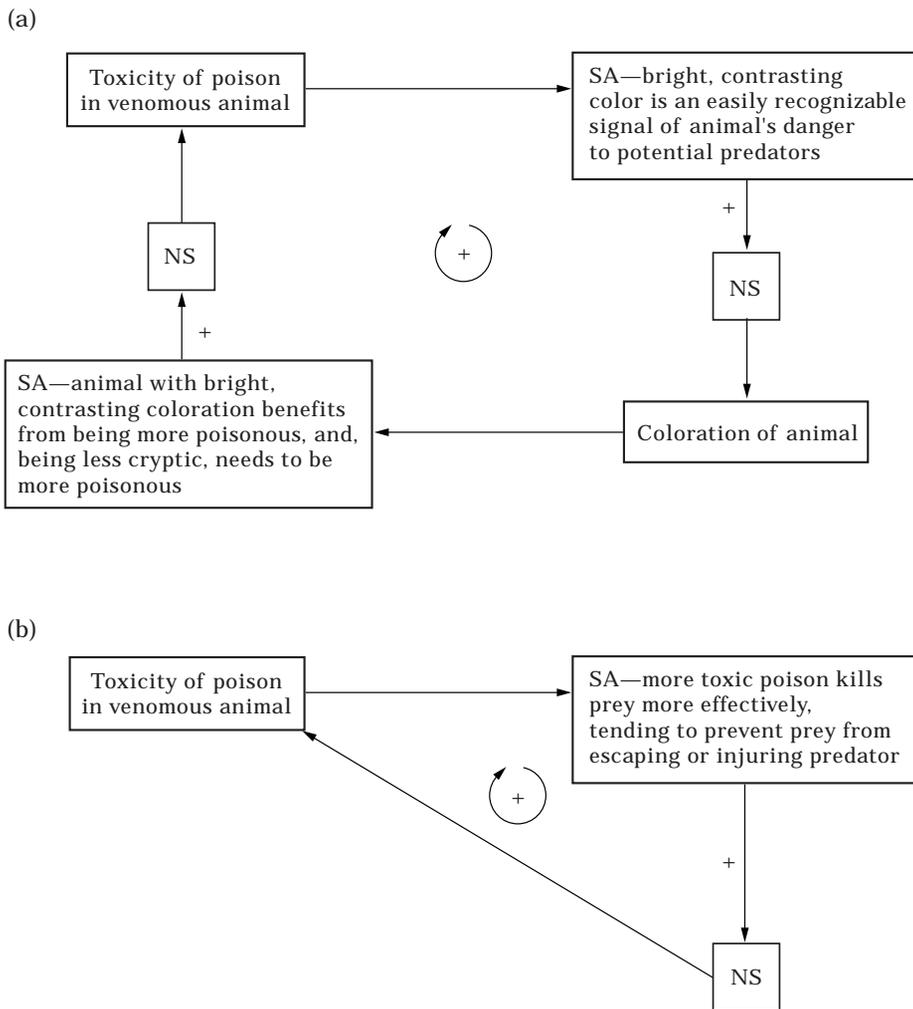
(a)

(b)

FIG. 2. Generic evolutionary diagrams illustrating the use of such diagrams in directional selection. See text for explanation. SA = selective advantage; NS = natural selection. (a) Positive evolutionary feedback loop. This results in directional selection, and hence evolutionary change, which could possibly be large, rapid, or both; (b) environmentally-driven directional selection that is not evolutionary feedback.

since the poison is of more use in a brightly colored animal. This does not necessarily happen in nature; this is a hypothetical example to illustrate the concept diagrammatically. The result is a closed positive feedback loop, in which two phenotypic characteristics re-enforce each other, potentially resulting in large or rapid evolutionary change, or both. The process stops when the brighter coloration and the display have reached an extreme such that their costs equal their benefits. Figure 2(b) is a generic diagram of environmentally-driven directional selection for comparison.

There are some important points to note in Figs 1 and 2. In diagrams with minus signs, illustrating stasis and stabilizing selection, as in

Fig. 1, a loop containing only one characteristic, or three boxes (one for the trait, one for the selective agent, and one for natural selection), which is the smallest loop possible, could designate either negative evolutionary feedback or environmentally-driven stabilizing selection without evolutionary feedback, since no more than one trait is needed for negative evolutionary feedback, with stabilizing selection to occur. Generally, in this case, if negative evolutionary feedback is being illustrated, two loops for the same trait are necessary, one to show negative feedback resisting evolution in one direction, and one showing it resisting change in the other, as shown in Fig. 2(b). This is how one can distinguish negative evolutionary feedback from

environmentally-driven stabilizing selection in these diagrams. Diagrams of the type in Fig. 2 that have plus signs, on the other hand, are different if they have the minimum of only one characteristic. These probably always illustrate environmentally-driven directional selection. It is not reasonable to think that one trait would act on itself, without any influence from other traits or the environment, and increase its own intensity. I can think of no instance of this in nature. Of course, any time two or more traits are in a feedback loop diagram, whether it illustrates positive or negative evolutionary feedback, interaction of the traits is implied, and evolutionary feedback is depicted. Thus, environmentally-driven stabilizing and directional selection show closed loops that are not representative of evolutionary feedback, and hence can be misleading if not scrutinized carefully. Sequential evolution can be illustrated by similar diagrams, but these must be drawn in continuous lines, without closed loops, and would make no sense without at least two traits in the diagram. It is shown, along with feedback loops, in Fig. 5(b), which will be discussed later. Thus, the diagrams have powerful utility, are subject to rules, have limitations, and should be studied with care and caution.

My first example, the evolution of the insect wing, is an example of rapid evolutionary change by positive evolutionary feedback that will clarify the concept and demonstrate its plausibility. It is illustrated in Fig. 3. There is experimental and fossil evidence for the following scenario. Winged insects first appear in the fossil record from the early to late Devonian, 350–400 Myr (million years) ago. At this time, their wings were too small to support powered flight and lacked hinges and attached muscles. Evidence has recently accumulated favoring a pleural origin of wings, in which wings were derived from pre-existing mobile structures (Wigglesworth, 1976; Kukalova-Peck, 1978; Robertson *et al.*, 1982). Douglas (1981) proposed that these protowings initially served as thermoregulatory structures to absorb heat from sunlight, allowing the insect to be active at lower ambient temperatures. This occurs in many present-day insects (see Heinrich, 1981, for a review). Kingsolver & Koehl (1985) demon-

strated convincingly with epoxy insect models that thermal absorption ability increases as the size of the insect wing increases, up to 1 cm, above which no benefit is realized, because any additional heat absorbed by the wings is lost before it reaches the body. The mere appearance of protowings, therefore, would have precipitated the first step in evolutionary feedback: any protowing under 1 cm long would be subject to selection for greater size because that would confer on it greater thermal absorption ability, until it reached 1 cm. The selection for greater size would then cease. There would be a positive feedback between the protowing, behavior, and wing muscles and hinges. The heat-absorbing ability of the protowing would select for insects that oriented their wings perpendicular to the Sun's rays to maximize the efficiency of thermal absorption, as this angle is optimal for it. In fact, many present-day insects use wing positioning as an important means of thermoregulation (Casey, 1981). This behavior would put a selective premium on better wing muscles and hinges, to better orient the wing. Better orientation would also increase the advantage of increasing wing size up to 1 cm, because it is the orientation that allows optimal thermal absorption. Thus the positive feedback loop is closed. The stronger wing muscles and more effective wing hinges would also preadapt the insect for gliding and, later, powered flight. Notice that this evolutionary process is not precipitated by the external environment, but by a change in the phenotype—the appearance of the small protowing. This positive feedback between morphology, behavior and selection is again changed when the wing reaches 1 cm. At this point, the phenotype affects selection such that it no longer favors longer wings, and directional selection for increased wing length ceases. We cannot be sure from the evidence supplied by epoxy models and present-day insects that insect wings actually initially evolved as a result of selection for thermoregulation, but the evidence seems strong.

Morphological and systematic evidence indicates that winged insects probably arose from ancestors about 2–4 cm in body length (Wooten, 1976; Wigglesworth, 1976). Kingsolver & Koehl also did experiments demonstrating that for insects in this size range, wings more than
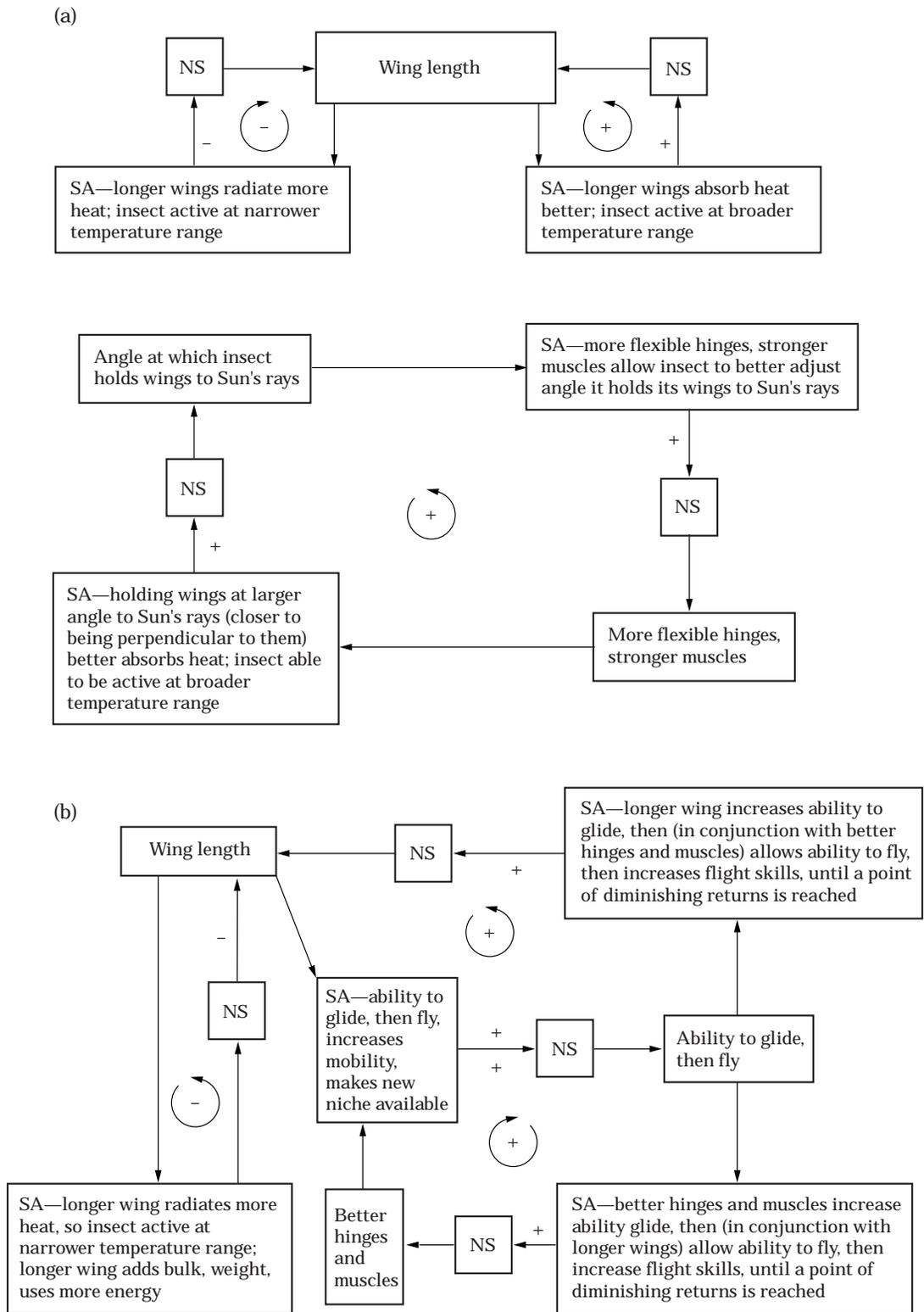
FIG. 3. Punctuated evolution of insect flight by evolutionary feedback. SA = selective advantage; NS = natural selection. (a) Wing length below 1 cm. In top diagram, at wing length below 1 cm, effects of positive feedback loop out-weigh effects of negative feedback loop; above 1 cm, effects of negative feedback loop out-weigh effects of positive feedback loop; thus, wing increases to 1 cm and remains at this length, until part b of this figure occurs. The more wing length increases from above positive feedback loop, the more strongly the feedback loop below applies (until 1 cm is reached); (b) wing length 1 cm and above. Insect increases in size for reasons unrelated to thermoregulation or aerodynamics, increasing wing length by isomorphy, to the point where insect can glide. Wing length increases and function of wing hinges and strength of wing muscles increase, until the magnitude of these positive feedback loops is equaled by that of the negative feedback loop, at which point stabilizing selection occurs and causes stasis with respect to wing length.

30–60% of body length, which is a little over 1 cm, are required before there are any significant aerodynamic effects of wings, and that prothoracic lobes would have no effect on aerodynamic performance. Thus, wings at the 1-cm limit for increasing heat-absorbing ability would be just a little too short to provide aerodynamic lift for gliding. Of course, some insects can fly with wings this short, but they cannot glide, and flight muscles were not yet present at this point. Hence, the authors had to propose a mechanism by which the wings could be enlarged from the 1 cm limit to the minimum size required for gliding. Thus, they pointed out that the minimum wing size required for gliding is constant regardless of body size. Thus, an insect with 1-cm protowings whose body size increased two and a half fold, for reasons unrelated to thermoregulation or flight, with the wings becoming proportionately longer by isomorphy, would be able to glide. Geometrically identical forms may serve different functions at different body sizes. At this point, evolutionary feedback would again be involved, as gliding would change the selective forces experienced by the insect. There would at this point be a premium on better hinges and stronger wing muscles for a second time, as these would increase maneuverability and ability to remain airborne while gliding. This would gradually lead to powered flight, which would select for better hinges and stronger wing muscles. The better hinges and stronger wing muscles would permit yet longer wings, which flight could also select for. The resulting improved hinges and muscles and longer wings would in turn improve flight, causing selection for yet better hinges, stronger muscles, and longer wings. Eventually, the benefits of better hinges, stronger flight muscles, and longer wings would presumably be equaled by the costs. At this point, the positive feedback loop between phenotype and selection and between different traits would be replaced by one or more negative feedback loops, and the directional selection would be replaced by stabilizing selection, with respect to the major aspects of wing structure and function. A new stable evolutionary state would thus be reached, and stasis would replace rapid evolutionary change. Finally, flight is a key

innovation that allowed entry into a new adaptive zone, possibly followed by an adaptive radiation. This last step is not evolutionary feedback, but sequential evolution, since it lacks feedback loops.

For the second example, I have constructed a synthesis of the rapid evolution of sand dollars from their sea urchin ancestors. My scenario is in accord with and is supported by what is known from the fossil record, morphology, ecology, behavior, and natural history of sand dollars. If correct, it is an excellent, detailed example of rapid, large evolutionary change by evolutionary feedback. Since it also involves sequential evolution, it is a case of evolutionary feedback and sequential evolution acting together to cause punctuated evolutionary change.

The phylum Echinodermata includes the class Echinoidea, the sea urchins, which contains the subclass Irregularia, the irregular urchins (sand dollars, keyhole urchins, heart urchins). The phylogeny of the order Clypeasteroidea is shown in Fig. 4. The three forms on the right of the figure are true sand dollars with flat tests. Cassiduloids exist today as high-domed, irregular urchins; oligopygoids are extinct; and *Togocyamis* is an extinct genus, a sister group of the clypeasteroids.

Sand dollars originated from an irregular sea urchin with a spherical, high-domed test (Mooi, 1990), as can be seen in Fig. 4. Echinoids originated 435 Myr ago, and were all spherical in shape until the appearance of sand dollars 60 to 65 Myr ago, at about the Tertiary–Cretaceous boundary (Smith, 1984). Clypeasteroids are not found before the Tertiary–Cretaceous boundary; only high-domed forms appear before this boundary (Mooi, 1992). Thus, a long period of stasis with respect to test shape lasted about 370 Myr during which the only test shape was high-domed. Then a punctuational event occurred during which clypeasteroids became flat, over about a 5 to 10 Myr period, although the exact length of time for this is uncertain (Mooi, 1992). All fossil sand dollars, even the earliest ones, have flat tests; there is no intermediate test shape found in the fossil record (Mooi, 1992). This is truly stasis followed by a punctuated change, since 5 to 10 Myr is a geologically short time for the appearance of a new order. Of
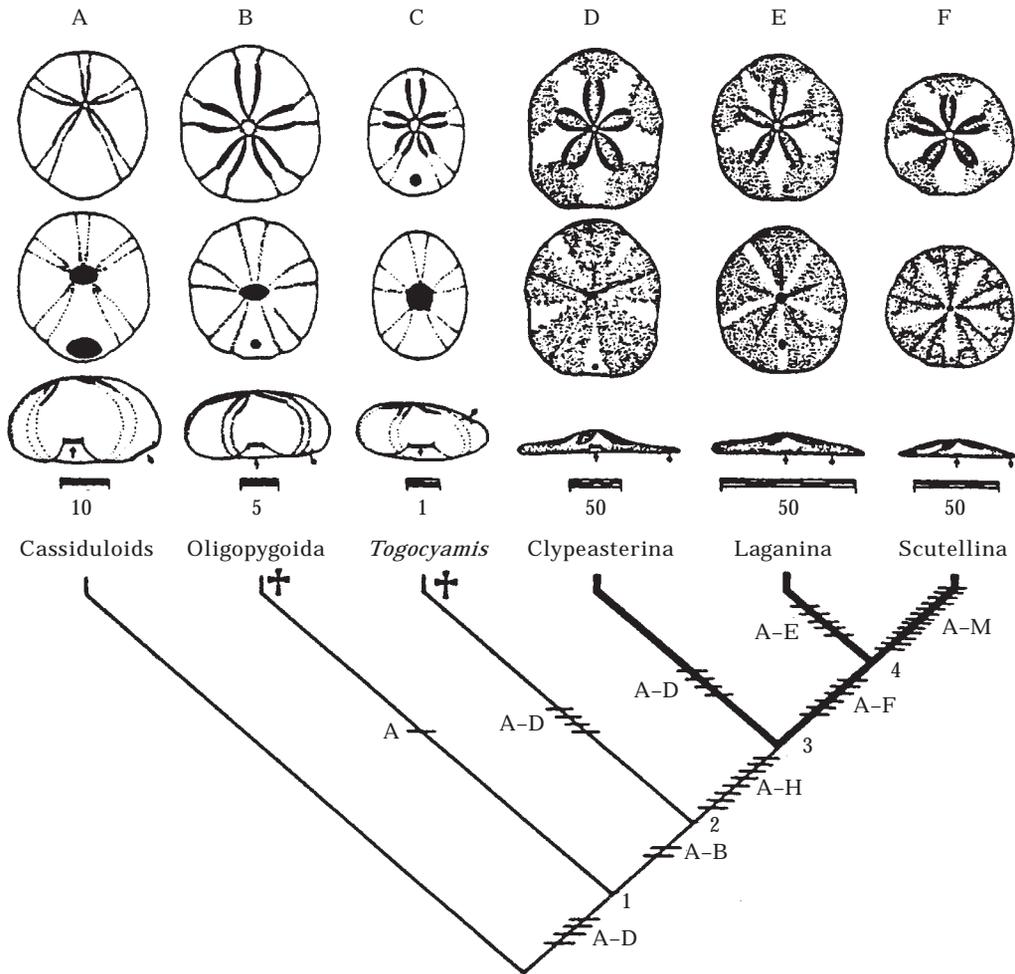
FIG. 4. Phylogeny of the Clypeasteroida (heavy lines in cladogram) and its outgroups. Nodes in cladogram are numbered, characters are lettered, and crosses indicate extinct taxa. For each of A–F in the upper part of the figure, top figure is aboral surface, middle figure is oral surface, and bottom figure is left side of test. Except for side views, anterior is towards the top of the page. Inward arrows indicate peristome; outward arrows indicate periproct. Stippling indicates podia. Petaloids, peristomes, and periprocts in solid black. All scale bars in mm. (From Mooi, 1990).

course, we cannot be sure that there are no undiscovered fossils that would show that the transition took longer, or that there were intermediate test shapes.

Mooi (1990) points out that fossil and other evidence indicates that Aristotle's lantern, the feeding apparatus of echinoids, was present only in the newly settled juvenile and not the adult of a high-domed pre-clypeasteroid. In a case of paedomorphosis, a developmental mutation gave rise to a form in which this juvenile with the lantern became the reproductive adult; it thus became a new clypeasteroid ancestor in which the adult had a lantern. This mutation occurred before the oligopygoids, and after the cassiduloids, branched off the line leading to sand dollars (see Fig. 4). Extant sand dollars have a well-developed lantern adapted to crushing and grinding, as was the case with oligopygoids and the paedomorphic pre-clypeasteroid. Telford *et al*. (1985) (see also Telford & Mooi, 1987) presented evidence that this remarkable set of jaws with five convergent teeth allows sand dollars to process sand by crushing and grinding it. They process sand because, in the upper few millimeters of shallow marine sediment, the surface of each sand grain tends to be coated with a fine film of organic material. About 3% of the surface is encrusted with diatoms and bacteria. Sand dollars eat diatoms, selecting energy-rich individual ones whenever they encounter them. However, they must make do

with the low yield of food on sand grains for the rest of their dietary needs. Oligopygoids fed the same way (Mooi, 1992). Thus, the appearance of the crushing lantern in the adult pre-clypeasteroid allowed exploitation of a new niche not available before the developmental mutation occurred: the ingestion of sand grains to obtain diatoms and other organisms. Clearly, something else occurred to lead to this unique diet, since extant high-domed sea urchins that do not eat sand have lanterns. However, the lantern was necessary and important in the appearance of the new food niche. This new food niche enabled the pre-sand dollar to leave the rocks and live on the sand. Clypeasteroids today live in the sand (Telford & Mooi, 1987), unlike most sea urchins, which wedge in and cling to rocks with their tube feet (although irregular urchins burrow). Living in sand subjected pre-clypeasteroids to the action of waves and currents, as it does to extant clypeasteroids today (Telford & Mooi, 1987). This poses the danger of being swept away. Thus, the new niche caused selection for a flatter test to decrease the probability of being carried away by waves and currents. Also, a flatter test allows easier burrowing, another method sand dollars use today to avoid being swept away by waves or currents.

The flattest members of the population could avoid intraspecific competition by getting into areas of stronger currents or waves, where their less flat conspecifics could not stay anchored. They could also burrow better. So the following positive feedback loop was established. A flattening of the test allowed entry into stronger waves and currents, perhaps to avoid intraspecific competition. It also allowed a better ability to burrow. This entry into the new habitat and burrowing behavior selected for a yet flatter test. This feedback loop continued until the pancake shape seen in sand dollars of today was reached. At this point, selective forces favoring flatness were equaled by the costs of having a flat body, which has less space for internal organs. Therefore, negative feedback loops must have replaced positive ones, stabilizing selection replaced directional selection, and stasis replaced punctuated change, with respect to test shape. In addition, once a critical amount of flatness was reached, it allowed two more adaptations to

hydrodynamic forces. The proximity of the oral and aboral surfaces of the flat test made it easier for pillars of skeletal calcite to connect the two. This adds weight and hence resists lift (Telford & Mooi, 1987). Some sand dollars in environments with waves and currents have shallow depressions along the radii of the undersurface, often leading to indentations on the edge. The depressions form channels that remove water pressure that would cause lift (Telford & Mooi, 1987). Again, the movement of clypeasteroids into a new niche, into a water-swept environment, precipitated selection for these depressions and indentations. In some sand dollars, the indentations have continued along an evolutionary path to become conspicuous notches that further shorten the pathway for the flow of water, dissipating the flow of water even more rapidly, and thus decreasing lift even more. This allowed selection for further refinement by sequential evolution: enclosing the notches to form slits or keyhole structures called "lunules," which have arisen independently in several types of clypeasteroid (Telford & Mooi, 1987). Telford (1981, 1983) has shown lunules are important in preventing moving water from dislodging and carrying sand dollars away.

As all this went on, the ingestion of sand also selected for an increase in the number and specialization of tube feet, allowing them to better pick up sand particles and pass them to the mouth (Mooi, 1986). This also created a positive feedback loop with flattening of the test, which allowed a greater percentage of tube feet to be on the bottom instead of the sides, and hence in a position permitting easier access to sand grains. Thus, three advantages resulted from a flat test: direct avoidance of hydrodynamic forces, better ability to burrow, and placement of more tube feet in contact with the food source.

The lack of a hard substrate, such as rock, meant the non-respiratory tube feet, or podia, had less value as structures to hold onto a substrate to keep the sand dollar in place. The ingestion of sand meant these podia were relatively more important than before in collecting sand grains and associated food particles, and passing them to the mouth. The non-respiratory podia therefore became specialized for this, and not for attaching and anchoring

to rock, evolving from those of the irregular echinoid ancestor. Thus the general shape of the test and feeding behavior helped mold the evolution of the non-respiratory podia.

Any large genetic and phenotypic changes that took place in this scenario would have required and been followed by a period of post-adaptive adjustment, during which the genetic background adjusted to them.

Once a new adaptive zone had been successfully entered, the final step of the process—adaptive radiation—took place. Of course, this took place concurrently with specialization of the podia and perhaps other adaptations. I call it the "final" step because it cannot start until the new adaptive zone has been successfully entered and because it continues until the end of the process. This step is not necessarily part of evolutionary feedback, as it does not require that the sequence of interacting traits result in a closed loop. It is, however, a step in the process of sequential evolution. The entry into a new adaptive zone and access to a new resource with resulting emancipation from interspecific competition allowed a tremendous amount of speciation and diversification. The result was adaptive change in relative numbers of different types of podia, further specialization of the podia, diversification in size, and so on, each species undergoing adaptations specific to its environment. This adaptive radiation led to the many species of extant clypeasteroids.

The following facts support my scenario. Extant clypeasteroids tend to be epifaunal, live in sandy habitats, and ingest sand grains. There are no species of echinoid that are flat and live among rocks, and with one exception, no high-domed echinoids occur in sand, indicating rocks protect these organisms from waves, and flatness serves this function in the absence of rocks. The one high-domed species that does occur in sand is the Sea Biscuit, *Clypeaster rosaceus*, which is secondarily somewhat high-domed, and does live in areas where moderate current can occur, being sympatric with members of the same genus that have a flat test. However, it is very heavy, being doubled-walled, with an inner test, and having a series of pillars that add more weight. It adds yet more weight by

covering itself with seaweed and stones. And it is only moderately high-domed. I cannot prove this scenario. Any reconstruction of an evolutionary history requires some inference because the relevant data are always lacking to at least some degree. However, it is supported by, or at least consistent with, all of the relevant known facts and evidence from the fossil record, systematics, morphology, ecology, behavior, and natural history of the Clypeasteroidea and their relatives. As such, it is feasible and credible.

Another convincing example of punctuated change by evolutionary feedback is provided by A. C. Wilson (1991) concerning the evolution of vertebrate intelligence as indicated by brain size relative to body size for modern humans and four vertebrate ancestors of humans. The times when the four ancestors lived is known from a combination of fossil and molecular evidence. Figure 5(a) shows that the brain has grown in relative size by 100-fold on the lineage leading from the early amphibian ancestor to modern humans, a rate of increase that is actually greater than exponential! This hyperexponential function has also been demonstrated for the brain of song birds (Wilson, 1991), and the arguments and model that follow apply to them as well. Wilson points out that on the lineage leading from early amphibians to humans, the brain has driven its own evolution in an autocatalytic process.

The following qualitative model is what Wilson proposed, with some modifications made by me where indicated:

1. an adaptively superior behavior that is based on intelligence arises non-genetically in an individual in the population. Wilson says this happens by chance, but I think it is fair to say that it appears because of the individual organism's superior intelligence, so is not really occurring by chance;

2. there is genetic variation in the population in the ability to detect, evaluate, and copy the new behavior. Therefore, the new behavior spreads unevenly through the population by learning, non-genetically. To this I add to Wilson's thesis that individuals also vary in their ability to adaptively respond to the new behavior, without copying it;
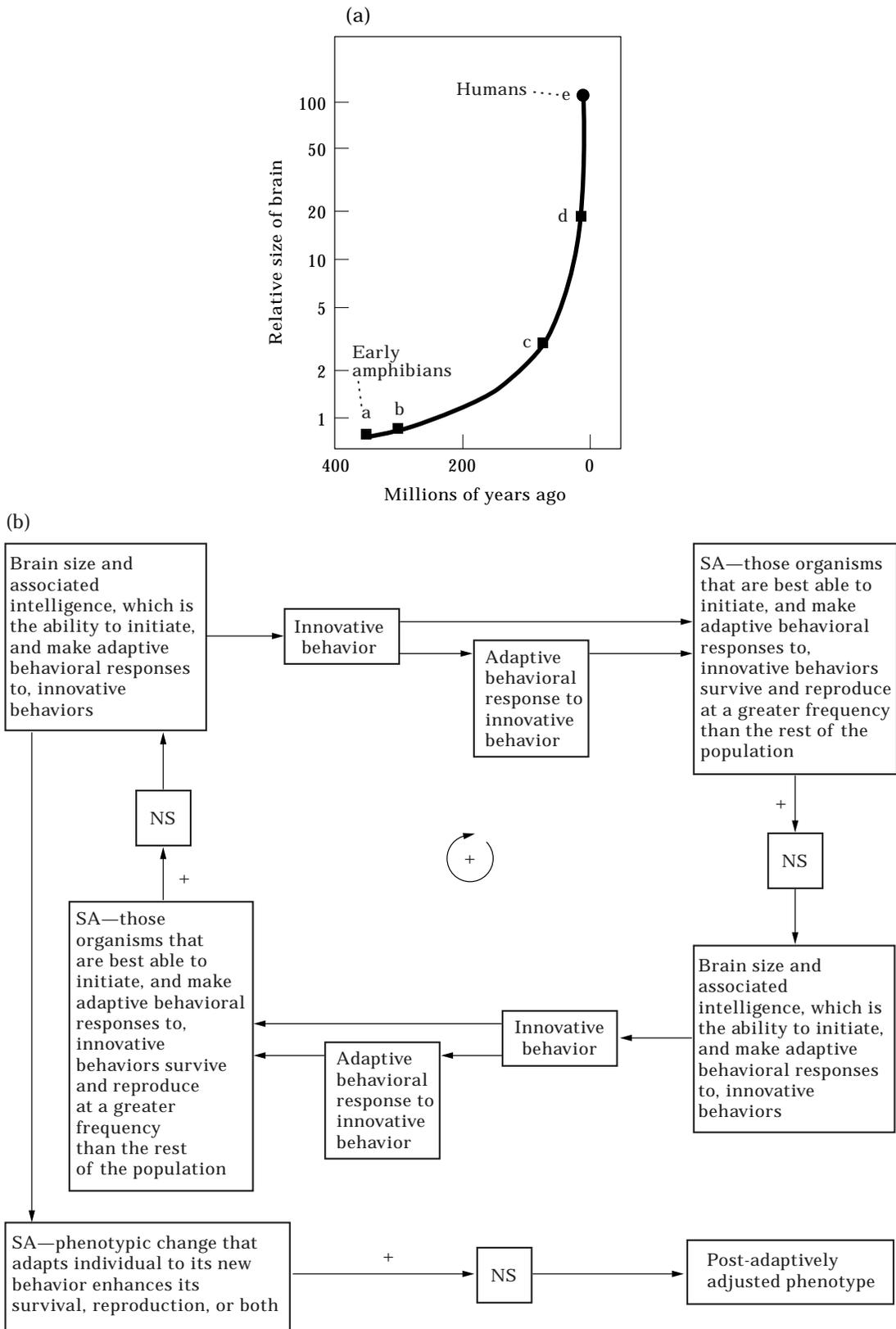
FIG. 5. (a) Relative brain size at various times on the lineage from early amphibians to modern people: a—amphibians, b—reptiles, c—mammals, d—apes, e—modern *Homo sapiens*. (From Wilson, 1991). (b) Punctuated evolution of the vertebrate brain by evolutionary feedback, and post-adaptive adjustment of organism to increased intelligence and behavioral plasticity by sequential evolution. See text for explanation. SA = selective advantage; NS = natural selection.

3. selection favors those individuals with the best genetic predisposition to learn and imitate the new behavior; i.e. the most intelligent ones. I add that selection also favors those who adaptively respond to the behavior with a creative new behavior; they need not imitate the behavior;

4. this results in a more intelligent population, genetically different than the original one. Because the individuals are more intelligent, more new, adaptive, innovative behaviors appear non-genetically, by use of this intelligence;

5. the process repeats itself several times in a positive feedback loop.

Populations of more intelligent individuals have a greater rate of new innovative behavior per unit time, and the behaviors spread more quickly, because the more intelligent individuals are better able to invent, imitate, and respond to new behaviors. Therefore, the rate of the process increases over time. This is probably the major reason why it is hyperexponential. It should be a fair assumption that brain size is correlated with intelligence over vertebrates as a whole. Figure 5(b) illustrates the rapid evolution of the vertebrate brain by evolutionary feedback. This figure differs from the others that illustrate feedback in that I added boxes labeled "innovative behavior" and "adaptive behavioral response to innovative behavior," to emphasize that these processes are in the loop and affect natural selection. Hence, their placement is before, with arrows pointing to, the "selective agent" box. The process is truly different than the others discussed in this paper in that innovative behavior and the response to it arise as a result of intelligence, non-genetically and affect the further evolution of intelligence. Secondly, since the adaptive response to the innovative behavior entails innovation as well as imitation, initiation of a novel behavior and an adaptive behavioral response to it are similar phenomena, and so are included together in the same boxes each time they appear in the diagram. Of course, in the first box in the diagram (in the upper left), on the first time around the feedback loop, only initiation and not adaptive response applies, even though they both appear in the box, which is appropriate for all subsequent times around the loop.

Wilson also suggests the brain played a role in adaptive evolution of other aspects of the phenotype, which would be at least sequential evolution if not evolutionary feedback. He cites as an example human populations whose ancestors tamed cattle and became dependent on dairy farming. This subjected them to lactose in the diet as adults. Within only 5000 years, the northern European population, which was especially dependent on dairy products, underwent virtual fixation for a regulatory mutation that causes β-galactosidase to be expressed permanently in the small intestine, allowing the adult population to digest milk. In human populations that did not depend heavily on dairy products as adults, the galactosidase gene is usually expressed in the small intestine only during infancy, as in the case with most mammals.

Wilson's ideas on the influence of behavior on evolution are somewhat similar, although certainly not identical, to the Baldwin effect (1896).

Another example comes from the fact that deductive arguments suggest that the joint evolution of female mating preferences and male secondary sexual characteristics provide a very general example of rapid evolution by evolutionary feedback, implying it happens commonly in the evolution of these features, during the process that Darwin (1871) called sexual selection. Fisher (1958b) suggested that if a male secondary sexual characteristic confers even a small advantage, it will be to the advantage of females to choose males with this characteristic. The advantage to the male may be that such a characteristic is intimidating to rival males. Female preference for the character will select for even greater intensity of the character. The increased advantage of the character due to female preference for it will in turn select even more strongly for female preference for it. Fisher saw the period of directional selection during which the character and preference for it increased as happening rapidly and over a short time period. Lande (1981) showed the validity of Fisher's reasoning through population genetic modeling. He showed that even with stabilizing selection on males, certain female mating preferences can create a runaway process where the outcome of phenotypic evolution depends
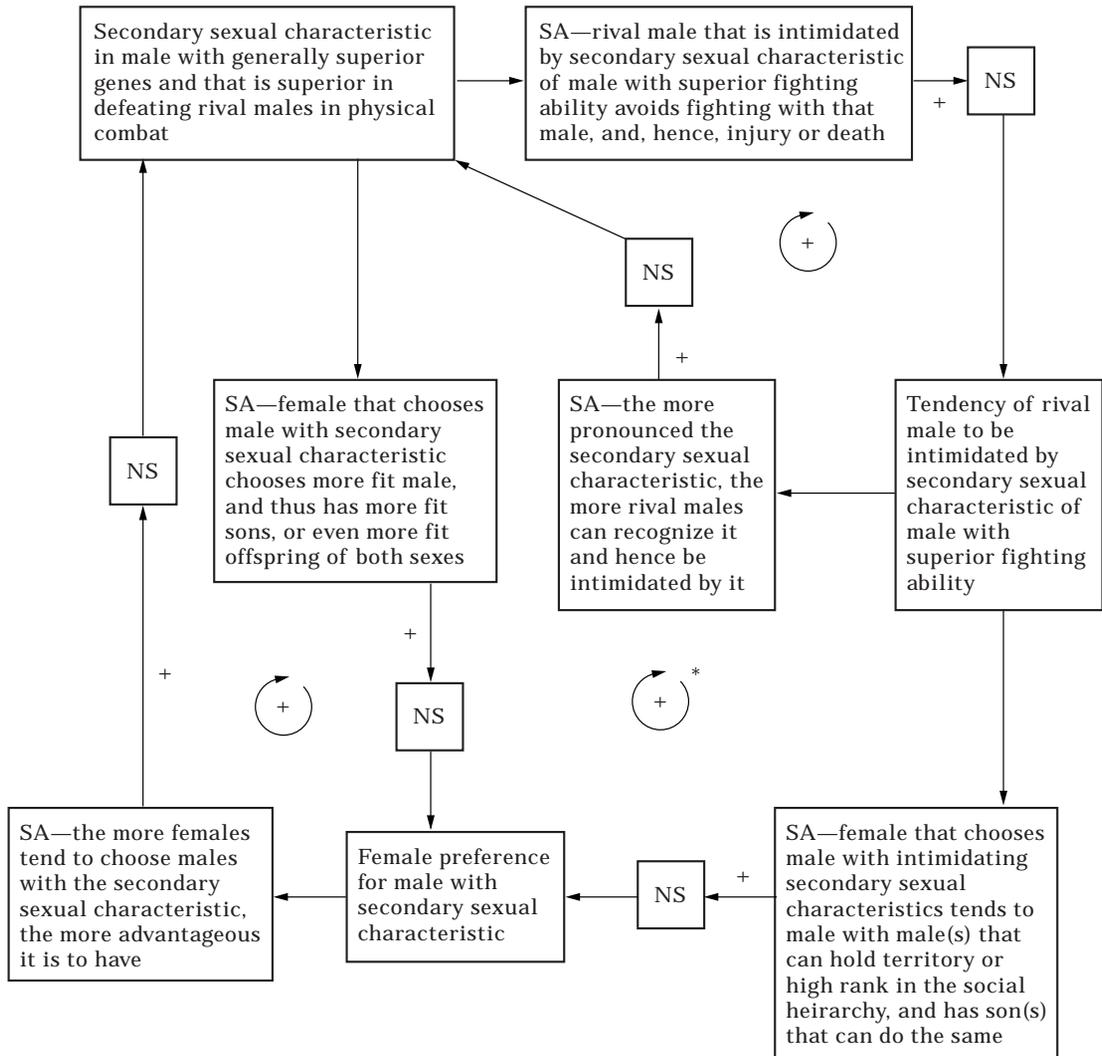
FIG. 6. Punctuated evolution of male secondary characteristics by evolutionary feedback. SA = selective advantage; NS = natural selection. *Designates three-step positive feedback loop involving the nine boxes on the outer portion of the figure only (i.e. boxes on the inside are not involved in this feedback loop).

critically on the genetic variation parameters and initial conditions of a population, and that genetic mechanisms can initiate or contribute to rapid speciation by sexual selection and divergence of secondary sexual characters.

I would like to propose that the process is even more complex than this. I suggest a feedback system involving three sets of organisms, each with different interests, in a population, as illustrated in Fig. 6. The first set of organisms is the males that are superior competitors to other males in conflicts for females, the second is males that are not as skilled at such competition, and the third is the females. If any secondary sexual characteristic that is easily recognizable, such as

a colorful spot on the wing (if the species in question is a bird), appears by a random mutation that is selectively neutral, in one of the superior male competitors, selection will favor those rival males that are intimidated by this secondary sexual characteristic. This is because avoiding conflict with an adept combatant avoids injury or death. Most rival males would be defeated by the superior competitor with the secondary sexual characteristic at any rate. Those few that could defeat it would likely do better to be intimidated by the secondary sexual characteristic and avoid combat with its possessor, and hence possible injury, limiting their combat to less effective competitors that they

could defeat with a minimal risk of injury. Thus, the secondary sexual characteristic will become intimidating to rival males through evolution of their nervous systems, conferring to it an advantage, and causing selection for increasing the intensity of the characteristic in the superior males. Simultaneously, there should be selection for female preference for the characteristic because of its association with the superior males, and because it intimidates rival males. The intensity of this selection will increase as the characteristic becomes increasingly intimidating to other males. Females that choose males with the characteristic will be choosing males that are better competitors for mates and that carry genes for this ability. Therefore, female preference for the characteristic increases, and this selects for increasing the intensity of the characteristic. These positive feedback loops continue until all the males in the population have the secondary sexual characteristic, strongly developed. The characteristic may start as a small, brownish spot on the wing, and end up as a large, bright red patch. Eventually, the positive feedback loops are replaced by negative feedback loops, as the advantages of increasing the characteristic's intensity, female preference for it, and response of other males to it become equaled or surpassed by the disadvantages of each, and stabilizing selection replaces directional selection, and stasis replaces punctuated evolution. This process can cause speciation if, at the beginning of the process, different colors for the intimidating secondary sexual characteristic in the superior male competitors appear in allopatric populations, due to random mutations and genetic drift.

I have been oversimplifying when I spoke only of "the organism" undergoing evolutionary feedback. Of course, as in all evolutionary processes, evolutionary feedback and sequential evolution happen at the level of the population as well as the individual. However, this case of sexual selection differs from most cases in that individuals with different phenotypes and interests undergo a process of feedback on each other. This puts more emphasis on evolutionary feedback happening at the level of the population than in other examples I have discussed.

An example that appears to involve several feedback loops is found in pitvipers. Greene (1992, 1997) provided evidence that the heat-sensing pits of these snakes did not evolve primarily for killing prey, but for defense. He compared pitvipers with their pitless relatives, which are more primitive. He found no difference in their hunting or eating habits. Both types of vipers eat rodents and other small mammals, which they largely catch by sitting still and ambushing. However, the snakes differ in their means of defense. Pitvipers tend to stand their ground when predators appear, and many pitviper females defend their eggs and/or young, rattling the rattles on their tails or thumping the ground noisily with a nubby precursor to a rattle, depending on the species. Pitless vipers do not defend their eggs or young, and flee predators. They tend to be striped, making an optical illusion that makes it hard for the eye to follow when they move. Pitvipers have an incentive to attempt to frighten potential predators of their eggs or young away. That attempt only makes sense if the mother snake can detect an oncoming threat and appraise its dimensions. The pit organs allow them to make just such an assessment. The pits are used for detecting prey as well, but Greene thinks this is a secondary function. Further evidence that the pits are primarily defensive in pitvipers comes from the fact that in antipredatory behavior, pitvipers that gape open the mouth and show the white of it as a threat display do so with their fangs retracted, while their pitless relatives gape with their fangs fully extended. If pits function only in feeding, this difference would make no sense. However, it makes a good deal of sense in an evaluate-and-engage defensive strategy, because a pitviper that gaped like a pitless viper would not be able to "see" with its pits. This is because when rising maxillary bones erect the fangs, the sides of a viper's snout are folded up.

Note these feedback loops. Venom developed before the other traits that I will discuss, since it is found in the larger taxonomic group containing pit vipers, whereas the derived features of defending eggs and young, making a warning noise with the tail, and the pit organ are not. When digestive enzymes evolved into venom as a device to better kill prey, there was selection for fangs to deliver the venom efficiently. Fangs in turn favored venom, so they likely evolved in

conjunction with each other, in a positive feedback loop, although one cannot be certain that venom did not fully precede fangs, in a process of sequential evolution. The poison makes it feasible to defend the eggs and/or young and stand one's ground against predators. But defense of eggs/young causes strong selection for an effective way to warn predators in order to keep them at a distance; hence the evolution of the behavior of tail rattling to make an aposematic sound. This would certainly favor the evolution on the tail of nubby precursors of rattles to thump on the ground, amplifying the sound. As pointed out in the previous paragraph, this suite of characters and behaviors selects for a device to detect incoming predators, and the heat-sensing pit is ideal for this. The rattles on the tail are known to have evolved last, since the Rattlesnakes are a derived group. These would have been favored to increase the signal, given the adaptive suite of characteristics. Any structure on the tail that made the rattling louder would favor the behavior of tail rattling, so we may have a short feedback loop between this behavior and the structure on the tail. The pit organs select for care of the eggs and/or young and the warning rattling of the tail, closing two more feedback loops. Parental care re-enforces the need for poison, closing another. The rattling of the tail might re-enforce parental care, venom, and the pit, forming three additional possible evolutionary feedback loops. Standing one's ground and having an auditory warning means striped coloration makes no sense; hence the splotches for a cryptic coloration to avoid detection, using the rattling of the tail should this fail. Thus, the cryptic coloration came about by sequential evolution.

Greene thinks the defense of eggs and/or young, pits, nub or rattles on the tail and tail rattling are an adaptive suite of characters that evolved simultaneously. This is in accord with evolutionary feedback as the mechanism for their evolution, with the loops being travelled over a number of times, until a stable state is reached. Although my scenario of evolutionary feedback is in good agreement with the empirical data and what is known about pitvipers, it is possible that an alternative scenario of evolution of this suite of characters occurred.

There is no longer any doubt that mitochondria and chloroplasts originated from free-living procaryotes (Margulis, 1970, 1981; Gray & Doolittle, 1982; Gray, 1989). This is a wonderful example of evolutionary feedback between species. First, a bacterium ingested a bacterium of another species. The ingested bacterium became a parasite of the bacterium that had ingested it. In the case of the one that became the mitochondrion, the parasite was better at cellular respiration than the host, and supplied the host with some of this function. This resulted in the host losing this ability, and selected for the host to provide services and proteins to the parasite, since those hosts that had healthy providers of cellular respiration survived better. This led to a loss of non-respiratory functions in the parasite, which was at this point becoming mutualistic with its host. The feedback loop continued until an obligate mutualism and then finally an organelle evolved. Then a stable state with stasis replaced the feedback loop, and a new adaptive zone was entered as a result of the efficient mutualistic system, and adaptive radiation was possible. A similar scenario of evolutionary feedback occurred in the evolution of the chloroplast.

There are Three Mechanisms for Punctuated Evolutionary Change

I propose, and it follows from the above discussion, that there are three general mechanisms for punctuated evolutionary change: macromutation, directional selection driven primarily by the external environment, and directional selection driven primarily by the organisms of the population and their phenotypes and genotypes and the interactions of these with natural selection. The latter of these three is sequential evolution, and, if a closed loop exists in the sequential chain of interacting traits, that special case of sequential evolution that I call evolutionary feedback. Of course, punctuated evolution may occur by a combination of any two or all three of these mechanisms.

I think mechanisms proposed by other authors tend to be invalid, limited in the amount of change they permit, or they can be placed in one

or more of the three categories I listed. For example, West-Eberhard's (1986) hypothesis of the origin of evolutionary novelties by alternative adaptations within a species is limited in the amount of evolutionary change it can provide. The ideas proposed by Simpson (1959) rely on directional selection, both driven by the environment and the mechanisms I am proposing in this paper. The mechanisms proposed by Eldredge & Gould (1972) and Stanley (1975) fail to effectively oppose the idea of the above three basic mechanisms for punctuated evolutionary change, and this is explained in the following section.

Integration of the Organism, Sequential Evolution, and Evolutionary Feedback are Mechanisms for the Pattern Seen in Punctuated Equilibrium

Eldredge & Gould (1972) proposed the hypothesis of punctuated equilibrium, which postulates both a pattern of evolution and a mechanism to explain it. The pattern is that most of evolution is characterized by stasis, punctuated occasionally by episodes of rapid evolutionary change. The mechanism they proposed to explain this pattern consisted of two parts. First, they followed the lead of Mayr (1963) in arguing that coadapted gene pools resist genetic change and that a shift from one adaptive peak (Wright, 1932) to another is facilitated by the destabilizing effect of the increased importance of random factors in small populations (the founder effect). However, Lande (1980) and Barton & Charlesworth (1984) argued effectively that population genetics shows the founder effect is usually ineffective in shifting a population to a new adaptive peak. Also, small populations have a lower probability of large evolutionary change from the standpoint that they are more likely to go extinct. Second, they argued that most large evolutionary change is associated with and contingent on speciation. Yet speciation, although it may permit the retention of new characters, is not necessary for their evolution (Futuyma, 1986a), nor do the theory and data of population genetics support this idea (Futuyma, 1986b). I suggest that selection is the common driving force of both most speciation and most

anagenetic change, rather than speciation being a force that mysteriously drives anagenetic change. Eldredge & Gould (1972) and Stanley (1975) went on to argue that long-term morphological trends are not the result of anagenetic change within single lineages, but of selection among species. They argued that differential speciation and differential extinction can result in the prevalence of character states within a clade, and establish a long-term trend, even if the direction of morphological change during the speciation process varies at random with respect to the trend. Although this could be true, for a clade to undergo diversification into many species with different characters and thus be capable of undergoing species selection, it would first have to undergo directional selection in at least one direction. Just as genetic variability must be present for natural selection to operate on a population, species must undergo enough adaptive radiation to provide the raw material for species selection. Although disruptive selection could provide some of this, logic dictates that directional selection in one direction or in two opposing directions would generally be required to achieve this. Hence, it is likely that directional selection is an important cause of the punctuated change aspect (as opposed to the stasis aspect) of punctuated equilibrium. Coordinated mutations of large effect could play an occasional role. When the directional selection is driven by the integration of the organism, the punctuated change is the result of sequential evolution or evolutionary feedback. I hope I have demonstrated that this is sometimes the case, in the previous sections of this paper.

The assertion that coadapted gene pools resist genetic change is a form of the idea that integration of the organism generally results in stabilizing selection and stasis for the population. Coadapted gene pools are a form of integration of the organism and integration of the population. I have already presented arguments that integration of the organism is a mechanism for stasis. Thus, although not the sole mechanism for the pattern seen in punctuated equilibrium, integration of the organism, sequential evolution and evolutionary feedback represent an important mechanism for it.

How Often does Punctuated Evolutionary Change Occur by Evolutionary Feedback?

I have already pointed out that the hierarchical nature of the genome and integration of the organism together assure that macromutation can successfully cause rapid evolution, but only on rare occasions. The great majority of rapid evolutionary change is probably driven by directional selection. Of interest is the relative importance of the two sources of directional selection driving rapid evolution. How much of it is driven primarily by the external environment, and how much is driven primarily by the organism itself and evolutionary feedback? It is probable that both play some role in all or nearly all cases of large evolutionary change, regardless of which one predominates. The question is thus ultimately quantitative: what percentage of evolution is due to the external environment vs. the organism driving its own evolution? What percentage of the time did the latter predominate in punctuated events in the history of life? Though this question can only be adequately answered empirically, a beginning at understanding can be attempted here.

One line of evidence that indicates the organism influences its own evolution at least some of the time involves cases in which parallel evolutionary transitions of large effect occur in different taxa, with a change in one phenotypic trait consistently being correlated with another, regardless of the environment. For example, Lande (1978) analysed limb loss in two lizard families, Scincidae and Teidae. He found a consistent pattern of elongation of the body preceding structural limb reduction accompanied by loss of limb elements, always beginning distally. Three years previous to this, Gans (1975) had also emphasized that in lizards, body elongation and streamlining precede structural reduction of the limbs, which begins by the loss of distal elements. This consistent pattern of correlated morphological changes in diverse species and in diverse environments, indicates the environment is not the sole cause of the pattern. Rather, elongation of the body may cause a selective advantage to limb reduction and loss in several environments, since it consistently precedes it. The consistent pattern of loss of the distal elements first also seems to be at least partially due to the phenotype providing selective pressure for this. These kinds of correlations constitute examples of sequential evolution, and of natural selection acting as a dependent variable, with the phenotype affecting its direction and intensity. It would be instructive to look for further examples of this nature.

Secondly, correlated phenotypic characters may often indicate a selective connection between different aspects of the phenotype, and thus sequential evolution or evolutionary feedback. For example, species of snake that are sit-and-wait predators tend to have cryptic coloration and lack longitudinal stripes. Snakes that spend a good deal of time moving and hunting prey are often longitudinally striped, which gives the illusion that the animal is moving more slowly than it is. In this example, it is the behavior that acts as a selective agent on color pattern.

Another potentially fruitful area to investigate is forms that underwent parallel or convergent evolution in similar environments, then solved the same problem by different means because of phenotypic differences. For example, the Sidewinder Rattlesnake (*Crotalus cerastes*) of southwestern U.S. and northern Mexican deserts, warns potential enemies of its venom by rattling its tail. Its ecological equivalent that occurs in the deserts of northern Africa and southwestern Asia, the Desert Horned Viper (*Cerastes cerastes*), loops its body around and rubs its scales together to make a similar aposematic sound when alarmed. It lacks the rattles on the tail possessed by the Sidewinder. Perhaps pre-existing morphology affected the evolution of the behavior and morphology of each species, resulting in different mechanisms to achieve the same solution. Presumably evolution followed the path of least resistance, and something in the morphology of each species made it easier to solve the problem in its particular way. Study of the frequency of examples such as this one could throw light on how often evolution is influenced by the phenotype.

Large evolutionary change driven exclusively by the external environment requires a constant selective pressure sustained over many generations, such as a cooling or drying of the climate

or a predator that selects prey of a certain phenotype. This pressure must not be so great as to drive the population to extinction. Although not proof that organism-directed evolution occurs frequently, this indicates it could play an important role.

Punctuated change due to evolutionary feedback and sequential evolution are plausible, because of the scenarios of them happening that I listed. But how does one test these ideas? The best way to determine the percentage of time that they are predominant is to reconstruct many scenarios of rapid evolutionary change based on the best available evidence, and compare the frequency that they occur by sequential evolution and evolutionary feedback with the frequency that they occur by the alternative of environmentally-driven change. A testable prediction of my hypothesis is that a significantly large percentage of the scenarios will be driven by the interaction of the organism with natural selection.

There are other testable predictions of my hypothesis. One test of my model is that an adaptive change in the phenotype will be followed by further change with higher probability than no change, because it leads to a new selective regime, and because it requires post-adaptive adjustment. This is testable in the laboratory, with, for example, bacteria or *Drosophila*. Does an artificially induced adaptive mutation result in further change with greater probability than if no mutation were induced? For the same reasons as those I just listed in this paragraph, my hypothesis also predicts that the larger the adaptive mutation, the greater the subsequent change or changes.

The hypothesis also predicts many cases of correlated characters, and, in the fossil record, many cases of correlated sequential changes. Furthermore my model predicts that cases of correlated characters independent of the environment, such as the example of striped snakes being active and fast and cryptic snakes being more sedentary will be relatively common. Another prediction is that any mutation with a net adaptive effect and a large effect on the phenotype will be deleterious in the absence of the selective agent that gives it the net advantage. For example, resistant individuals should be less fit than sensitive individuals in the absence of the selective agent, such as a pesticide or bacteriophage. This is because integration of the organism has the result that new mutations will not fit the genetic background. A further prediction is that a period of post-adaptive adjustment will be required, in which modifier genes integrate the new mutation to the rest of the genome. Another prediction is that large, rapid change could occur in species without the requirement of any significant change in the environment. Admittedly, measuring environmental change and deciding how often such evolution must occur to support the hypothesis are difficult questions. Finally, if stasis is the result of integration of the organism, rather than stabilizing selection from the external environment, we would expect stasis could occur with respect to major phenotypic traits, even in changing environments. Combining these last two predictions, my hypothesis predicts that phenotypic change will be significantly less correlated with environmental change than would be the case if the alternative hypothesis of environmentally-driven change were the predominant one. I have presented evidence that many of these predictions hold true in this paper, but more research needs to be done to test them.

I now want to make the assumptions of my thesis explicit. They are: natural selection can act as a dependent variable; the organism and selection can influence each other; organisms are holistic, integrated systems; organisms and changes in them affect their evolution and can lead to further changes; and organisms are feedback systems that can be involved in both positive and negative feedback loops in their evolution. These assumptions are fulfilled in the evolutionary scenarios I provided. How often they will be fulfilled in other evolutionary scenarios is necessary to discover for further testing of the hypothesis. They must hold up for my model to be correct. It is incorrect if they consistently fail to do so. It is important to note that, in spite of the arguments I presented, it is not sufficiently clear how often punctuated change by evolutionary feedback occurs in nature; further research is needed to determine this.

Implications of and Areas of Research Suggested by Integration of the Organism, Sequential Evolution, and Evolutionary Feedback

The model I have presented has some interesting implications. The first is that natural selection can act as a dependent variable as well as an independent one. Although population genetic models often treat natural selection as a dependent variable, I suggest that there needs to be more emphasis on this and the fact that a change in the organism or one of its traits can affect the coefficient of selection on that trait or other traits. Genotypes, phenotypes, and gene frequencies in populations can affect natural selection, perhaps even as much as it affects them. Related to this is the idea that organisms, through their behavior and morphology, influence and, to some extent, even direct their own evolution (although of course not consciously).

Another implication of the model is that parallel and convergent evolution are not due solely to similar environments in all cases. If the phenotype and genotype have a profound influence on evolution, similar morphology and/or behavior can work in conjunction with similar environments to shape the evolution of similar forms. In fact, the environments need not always be similar. I have already cited Lande's and Gans' work on the recurring pattern of limb loss in different lizard groups, which happens in different environments. I suggest more research into this area, with a search for further examples and a deeper look at parallel and convergent evolution.

Evolutionary feedback also provides a novel way of viewing coevolution. Even though for brevity I spoke of evolutionary feedback happening to "the organism," this is a somewhat misleading oversimplification. It also occurs between individual organisms in the population. It can happen between species as well. Whether coevolution is adversarial or mutualistic, the feedback loops can cross species boundaries. This "interspecific evolutionary feedback" occurs, for example, in predator–prey, host–parasite, and pollinator and flower interactions. Thus, integration of the organism, sequential evolution, and evolutionary feedback suggest exciting areas for further research.

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