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Toward a New Evolution

So far from a gradual progress towards perfection forming any necessary part of the Darwinian creed, it appears to us that it is perfectly consistent with indefinite persistence in one state, or with a gradual retrogression.

—Thomas Henry Huxley (1876)

After the Synthesis

Simpson, Haldane, and Wright represented a small group of individuals involved in the formulation of the Evolutionary Synthesis who were not unreserved proponents of some of its basic tenets. Of note was that these evolutionary biologists were not wedded to a picture of constant gradual change.

Haldane appears to have been made most peripheral by those in, as well as off center of, mainstream neo-Darwinism. His proposal that small groups of peripheral isolates should be the stuff of rapid speciation received only cursory mention by his contemporaries. His thoughts on gene-development-environment interaction, with a major component of heterochrony thrown in, also received little notice in the formulation of the Synthesis. And, certainly, his openness to the possibility that reduced selection pressure might be a factor in rapid character change and speciation was not in line with the role other evolutionary biologists assigned to selection. Generally, Haldane was cited for disagreeing with Fisher about whether change could occur within large, freely and randomly mating populations.

Simpson and Wright did not embrace the notion that the major cause of speciation was the imposition of a geographic barrier between a subspecies and the rest of its species. As for the genetic basis of evolutionary change, through his last publication in 1982, Wright steadfastly maintained that it was more than just the accumulation of small mutations and their effects. To the end, he was convinced that shifts in the balance of interactive gene combinations, as well as, for example, chromosome rearrangement, could lead

to evolutionary change, both in transformation within a species lineage and in the divergence of a new species from its parent. Simpson stuck to the more neo-Darwinian geneticist's position that change was a matter of the accumulation of small changes. He did so, it seems, because of his continued rejection of Goldschmidt's and Schindewolf's theories, which invoked a single mutation as the basis of major organismal reorganization.

Although in his book of 1953, *The Major Features of Evolution,* Simpson took a swipe at Wright—in particular, at Wright's model of intergroup competition between subspecies within a large, widespread species as providing the impetus for evolutionary change of significance—the two scholars were, nevertheless, more theoretical bedfellows than archenemies. Both believed that shifts from one environmental situation to another could bring about relatively rapid evolutionary change. This, of course, was the basis of Simpson's theory of quantum evolution: A species that finds itself in a new ecological circumstance quickly adapts to it. Quantum evolution was actually a rewriting of Haldane's theory of peripheral isolates, but without the latter's emphasis on development. Wright's theories of shifting balances and selective topographic landscapes invoked the concept of rapid adaptation to new environmental circumstances as well as the possibility that different interactive gene combinations could be equally workable from an adaptive standpoint.

Simpson and Wright also serve as examples of the inability of the Committee on Common Problems of Genetics, Paleontology, and Systematics to meld these disciplines completely. Simpson worked hard in his writing to invest his paleontologically informed theories with what he thought were the salient aspects of Haldane's, Wright's, and especially Fisher's mathematical modeling of mutation rates and selective forces. But geneticists in general maintained a strong skepticism about the reliability of the fossil record in demonstrating speciation and, consequently, paleontologists' ability to understand how such evolutionary change occurs. A paleontologist could only point to fossils and remark on the fact that change had occurred. Beyond that, and depending on how good the fossil record of a particular group was, paleontologists might at best be able to address rates of evolutionary change and provide a rough picture of the times of origin and extinctions of major groups of fossilizable life.

The persistence of an intellectual hierarchy within evolutionary biology is reflected as recently as 1982, in one of Wright's articles:

> I am not in a position to discuss independently the data of paleontology and recognize that my field, genetics, bears directly only on microevolution, but I feel that we should explain phenomena at the higher levels as far as possible, as flowing from observed phenomena of genetics in the broad sense, including cytogenetics, before postulating wholly unknown processes.

Although Wright did not totally reject other disciplines, it is clear that he was reiterating the common belief that an understanding of evolutionary change at all levels ultimately derives from the studies of the laboratory-based population geneticists, who seemed to be able to demonstrate, and mathematically model, the effects of selection acting on the small mutations that arose. In the face of such assertions, what could the paleontologist do but accede to the majority view?

In the spirit of the Committee on Common Problems, Simpson accepted the premise that "[t]he essential picture of evolution under a Neo-Darwinian concept is that of a slow steady change through the gradual building up of minor modifications; over long periods of time animals become more perfectly adapted to a stable environment or change gently with slowly changing surroundings." This made sense, at least in terms of observations derived from population genetics. But, as a paleontologist, Simpson also saw rapid change recorded in the fossil record. However, because he was unable to embrace saltation of any sort, Simpson modified the typical neo-Darwinian scenario of evolutionary change to the following: "In rapid evolutionary changes in animal lines the process may have been a typically Neo-Darwinian one of the accumulation of numerous small adaptive mutations, but an accumulation at an unusually rapid rate." "Unfortunately," he had to admit, "there is in general little evidence on this point in the fossil record, for intermediate evolutionary forms representative of this phenomenon are extremely rare (a situation bringing smug satisfaction to the anti-evolutionist)." The gaps in the fossil record reared their ugly heads again.

It is to Ernst Mayr that most evolutionary biologists would probably turn as the one person whose notions of evolutionary change most affected the field in general. It was he, it seemed, who could bridge the gaps between the conclusions of geneticists and those of paleontologists. As a systematist trained in the study of living organisms, Mayr had access to an organism's entire biology. Paleontologists had only the typically fragmentary and incomplete bones and teeth of animals whose remains happened to end up in the right circumstances for becoming fossils, and then being discovered. As someone who studied whole, living organisms, Mayr was seemingly in the position of being able to apply the theoretical conclusions of geneticists to real-life, still-ongoing situations. As such, he was also someone who could translate the writings of Fisher and Wright for the vast majority of mathematically naive evolutionary biologists. Although Simpson would be recognized for bringing the rigor of statistical analysis to paleontology and systematics and making its applicability to fossil samples understandable, his discussions of the theoretical population geneticists' mathematical arguments were often beyond the grasp of his fellow systematists.

Mayr seemed to have a gift for explaining even the most complex ideas. He also published his evolutionary ideas through widely differing outlets, from the more rigorously argued *Animal Species and Evolution* to the simpler and more broadly accessible *Populations, Species, and Evolution*. Almost anyone interested in evolution could read the latter book, even if it required a bit more effort than the typical college or trade book. *Populations, Species, and Evolution* and Simpson's *The Meaning of Evolution* were the two major books on evolution that I had to read as a college student in the late sixties.

Mayr's basic message was the same throughout his work, whatever the actual publication: With the exception of chromosome multiplication in various plants and other aberrant phenomena, "[s]peciation proceeds through the gradual genetic modification of spatially segregated populations." The way that species formation most frequently took place was by the introduction of a physical or geographic barrier between a subspecies and the rest of its species. In general outline, Mayr followed Fisher's idea that a large population would be segmented into subsets, which, being separated from one another, would accumulate minute changes over a long period of time until they became reproductively isolated—that is, separate species. But Mayr did not put all his evolutionary eggs into one basket. He also allowed that, at times, rapid change was possible and that species could arise in ways other than those he favored. In spite of his insistence on speciation via gradual transformation, he even approached Haldane's model of species formation in his discussion of peripheral isolates, which, unlike Sewall Wright's peripheral populations, were truly separated from the parent species:

> Peripheral isolates, no matter how close to the main range of the species, almost always are noticeably different, in contrast to the essential uniformity in the contiguous range of the species. . . . The rapidity with which morphological changes take place in peripheral isolates confirms our conclusion that the genetic reconstitution permits or induces shifts in the previously existing developmental homeostasis. . . .
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> The environment in the peripheral isolate is almost always rather unlike the optimal environment of the species in the center of its range. The biotic environment, in particular, is usually somewhat unbalanced at isolated locations. The new isolate will thus be exposed to a considerably changed selection pressure. . . . [T]he response of the isolated population to this selection pressure will be quite different from that of a population which is part of a contiguous array of populations held together by gene flow and [other] cohesive devices. . . . [T]he isolated population can respond to its local adaptive needs without having to compromise with the solutions found by other populations.
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> The only answer that is possible in many cases is a shift into a new niche. Such a shift is greatly facilitated by a genetic revolution and the special properties of isolated populations. In particular, the genetic liability of such populations and the pronounced population fluctuations (in the absence of strong density-dependent factors) facilitate such shifts. In no other situation in evolution is there a greater opportunity for adaptive shifts or evolutionary novelties.

Mayr's concept of the role of peripheral isolates differed from Haldane's in that he did not specify rapid change as part of the process of species formation. Mayr also emphasized the importance of the environment much more than Haldane did, and he did not consider developmental processes at all. In fact, Mayr envisioned speciation as being possible and successful only when there were vacant ecological niches to be filled: "Most habitats are saturated with species at any given time, and there is room only for so many new species as are needed to fill newly opened niches." Without citing Haldane, Mayr concluded that, since "[m]ost species bud off peripheral isolates at regular intervals," their "continued presence . . . is a guarantee of the occurrence of speciation whenever the ecological situation is opportune." What is confusing at times when one reads Mayr's work is that he often used the more generic phrase "geographic isolate." Since he was a proponent first of geographic isolation as the key to the process of species formation, one cannot equate peripheral isolate with geographic isolate. Peripheral isolate is only one example of geographic isolate.

As for the process of evolution in general, Mayr reiterated the neo-Darwinian position that "evolution is a two-stage phenomenon: the production of variation and the sorting of the variants by natural selection." Following the lead of the population geneticists, Mayr accepted that variation was produced by small-scale random mutation. He also embraced Darwin's utilitarian argument for the selection of advantageous traits, as well as the latter notion that the advantageous traits selected in some way constituted an improvement over what had been the previous state. This is evident, for instance, in his response to those in the field who objected to the neo-Darwinian view of evolution:

> Whether function precedes a structure, or vice versa, gives rise to eternal argument. Did finches develop heavy bills because they ate seeds, or are finches able to eat hard-shelled seeds because they had developed heavy bills? The answer is, of course, that neither is correct. . . . The development of the heavy bill was a slow process, probably involving dozens of small mutational steps, each one surviving only if proving its usefulness in the actual test of selection. It must be admitted, however, that it is a considerable strain on one's credulity to assume that finely balanced systems such as certain sense organs (the eye of vertebrates, or the bird's feather) could be improved by random mutations. . . . However, the objectors to random mutations have so far been unable to advance any alternative explanation that was supported by substantial evidence.

Whenever Mayr spoke, evolutionary biologists, whether student or seasoned professional, listened. The weight of his pronouncements—such as the last sentence in the quote immediately above—was not inconsequential. However, proclamation and reality are two different matters. There was no substantial evidence to support the scenario of gradual finch-bill evolution. Nevertheless, Mayr's particular presentation of the evolutionary process is consistent with the uniformitarian approach of extrapolating from the laboratory experiments of population geneticists to the time-depth evidence required. But there is an underlying contradiction in Mayr's assertion, for as he discussed elsewhere, there was a significant difference between the

"closed" populations that population geneticists studied and the "open" populations that existed in nature:

> Population geneticists, who have worked all their lives with closed populations in which all genetic input is due to mutation, tend to underestimate the magnitude of genetic input in open populations. To be sure, it is immaterial for certain aspects of evolution whether mutation or immigration is responsible for new genes in a population. Yet it would be a great mistake to lump these two sources of variation in calculations of their effect, because they are of totally different orders of magnitude.

Although this statement was part of a criticism that Mayr levied at Wright's model of speciation via partially isolated peripheral subspecies—because he was critical of Wright's belief that partial rather than complete isolation can lead to species formation—it is not dissimilar in content to the latter scholar's insistence that interactive gene combinations play a major role in evolutionary change: That is, in addition to mutation (which population geneticists studied), new gene combinations also produced variation, if not also evolutionary change. And, as Wright envisioned it, one way in which new gene combinations could arise was for one subspecies to migrate into an area occupied by another subspecies of the same species. This, of course, would not lead to the emergence of a new species through a process of divergence. Rather, it would return an incipient species to the fold of the parent species. But it could, theoretically, lead to the generation of different gene combinations from the already existing gene pools of the subspecies.

The topic of human origins was not exempt from Mayr's evolutionary speculations. In 1950, he made the case that, of the many genera that had by then been proposed for various hominid fossils, only two were theoretically viable and taxonomically necessary. As a result, *Homo* and *Australopithecus* became the hominid genera of record, even though, Mayr admitted, he had his doubts about giving genus status to *Australopithecus*. By 1963, however, he was able to state: "I now agree with those authors who have since pointed out not only that upright locomotion was still imperfect but also that the tremendous evolution of the brain since *Australopithecus* permitted man to enter so completely different a niche that generic separation is definitely justified." The importance of the ecological niche in providing a space into which the first species of *Homo* could invade and become differentiated is evident in Mayr's thinking. As for not recognizing Robert Broom's *Paranthropus* as a distinct taxonomic entity above the species level, Mayr simply stated that this hominid "hardly shows the degree of difference from *Australopithecus* necessary to justify generic status." In 1963, and from their respective genetic and paleontological perspectives, Dobzhansky and Simpson also came to agree with Mayr's restriction of hominids to only two genera.

Not surprisingly, Mayr was convinced that the general course of human evolution had been a gradual one. In its details, bipedalism and the freeing of the hands evolved first. Then there was the reorganization of the pelvic girdle and the limbs. Toward the end of this phase came an increase in brain size and changes in the architecture of the skull.

As for the species of hominid at each of these perceived phases of human evolutionary change, Mayr was a bit ambiguous about the number of species that he thought represented *Australopithecus,* but the sense he gave was that it was probably two and, at most, three. Mayr mentioned by name no species other than Raymond Dart's *africanus,* which he suggested "might well have been one of the more extreme and aberrant races of the species." His taxonomic minimalism extended to the species of the genus *Homo* as well. He mentioned only in passing the new species that Louis Leakey and his colleagues had discovered at Olduvai Gorge and that they placed in the species *Homo habilis.* Although Mayr did not cite *H. habilis* by name, he accepted it as representing early *Homo.* From there, human evolution flowed directly into *Homo erectus* and then *Homo sapiens.*

The rationale for Mayr's view of human evolution lay in his belief that "since Recent Man is a polytypic species [a species of many varieties, or races] and since most species of mammals are polytypic, it can be assumed that the species of fossil hominids likewise were polytypic." Because, in Mayr's theoretical framework, the success of speciation depends on invading a vacant econiche, and hominids, in his view, had always been both widespread geographically and diversely adapted ecologically, there had been little opportunity for speciation. In addition, according to Mayr, "isolating mechanisms in hominids apparently develop only slowly." Consequently, although there may have been potential isolates, "isolation never lasted sufficiently long for isolating mechanisms to become perfected."

Clearly, these are not morphologically based conclusions about the taxonomy and evolutionary history of hominids. Rather, Mayr's theoretical constraints as to how he thought about evolution and speciation drove his interpretation of the morphology. Consequently, a diversity of often markedly morphologically dissimilar fossils were committed to the same species. Of course, this then created the impression that the degree of variation within a particular hominid species was so extraordinary that it surpassed the norm for all other mammals. But, as Mayr remarked, since present-day *Homo sapiens* is such a highly variable, or polytypic, species, "as concerns the fossil hominids, the simplest assumption would be that at any given time only a single polytypic species of hominid existed, and that the variety of observed types is merely a manifestation of individual and geographic variation." This particular scheme of human taxonomy and evolution came to dominate the field of paleoanthropology, and of anthropology in general.

The Post–Neo-Darwinian World

Although the paleontologists and systematists who contributed to the Evolutionary Synthesis were greatly influenced by the work of population

geneticists, their concerns with evolutionary change were directed primarily at the level of the species. True, there was an awareness of processes within a species. But the focus was on the formation of species in terms of the questions "how come, and how fast?" The words *mutation, selection,* and *adaptation* were used, but usually in the context of "the organism versus the environment."

In 1966, George Christopher Williams, a professor of biology at the State University of New York at Stony Brook, published *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought.* According to Williams, he began writing the book in 1963, which happened to be the year Mayr's *Animal Species and Evolution* appeared in print. As the title of his book suggests, Williams planned to address those aspects of Darwinian theory that had been omitted from the Synthesis. Clearly, while the leaders of the Synthesis were pursuing a solidification of their evolutionary positions, Williams and others like him were attempting to fill in the still-vacant lacunae in evolutionary theory. Although Williams's monograph was also written in part as a response to various evolutionary biologists who were not content to explain everything evolutionary in terms of selection arguments, it became the centerpiece of a new neo-Darwinian effort, which would become known as sociobiology.

The essence of Williams's thesis was that the organic world can be reduced to the level of genes alone, and that natural selection, pretty much as conceived by Darwin, operates in the realm of the available alternative alleles, or genetic character states. Williams's reason for focusing on genes rather than on the entire organism, or some subset of its anatomy or behavior, was that while organic bodies come and go, genes are essentially immortal. Genes are self-replicating and have the potential to be passed on through an endless number of generations of offspring. Admitting that "the gene" was still an abstract concept in population genetics, Williams conceived of it as the indivisible, or ultimately unfragmentable, unit of inheritance. As for chromosomal rearrangement, he argued that the rearranged chromosome fragment "behaves in a way that approximates the population genetics of a single gene." Putting this all together, Williams defined the gene as "that which segregates and recombines with appreciable frequency." He also reminded his audience that, as pre-Synthesis geneticists had learned, a gene could produce more than one effect. The sum total of the genes of an individual—its genotype—could be expressed differently in different individuals because, according to Williams, the genotype is interpreted by the "soma" of the individual.

Williams also reduced the concept of natural selection to the level of the gene. He did so through the simple mechanism of Mendelian inheritance. In sexually reproducing organisms, with each parent contributing half of its offspring's genes, natural selection would be faced with a choice between two different alleles of the same gene. By choosing from among the available, alternative alleles, there would be differential survival and, consequently, selective accumulation of genes. Ultimately, this selection of genes could have quite an impact on organisms. Although it is never stated fully, the implication throughout Williams's book is that even if the pace of accumulation were rapid, each allele so accumulated would have only a small effect. In this sense, the shift in gene frequencies would be a slow and gradual process. As for adaptation, Williams felt that "[N]atural selection would produce or maintain adaptation as a matter of definition. Whatever gene is favorably selected is better adapted than its unfavored alternatives. This is the reliable outcome of such selection, the prevalence of well-adapted genes."

Since a gene is ultimately expressed through the physical being, or phenotype, of the organism, in order for it to be selected it must be responsible for something that enhances the reproductive success of the organism. In other words—recasting concepts as they had first been proposed by Darwin in the light of population genetics—a well-adapted gene is one that contributes to the individual's reproductive success.

In dealing with Darwin's notion of competition, Williams admitted that while "natural selection works only among competing entities . . . it is not necessary for the individuals of a species to be engaged in ecological competition for some limited resource." In fact, he argued, selection could be most intense during the early phases of a population's expansion, when available resources might not be scarce. What is at stake, ultimately, is mean phenotypic fitness, which boils down to how many offspring an individual can produce and, consequently, how successful an individual will be in spreading its genes throughout subsequent generations. But it is not the absolute number of offspring an individual sires that is important. Fitness is judged on the basis of how many offspring an individual produces relative to the average number of offspring produced by the individual's population or species. An individual that sires more offspring than the average for its population would be doing well within this view of selection and adaptation. If, then, adaptation is thought of in terms of reproductive success, with genes being the ultimate focus of selection, the phenotypic traits of importance would be those that enhanced the gene's chances of being transmitted to as many offspring as possible. Although physical characteristics can be accommodated in this model, so, too, can behavioral, including social, attributes.

In Williams's formulation, natural selection serves to maintain stability. This would make sense in a context in which natural selection chooses among alleles that are already present within the species and available to selection through the phenotypes of individuals. On the other hand, mutation, according Williams's theory, acts to disrupt this stability. This suggestion seems to imply that a mutation is expressed via the phenotype shortly after it has arisen. Nevertheless, Williams had to admit, "[m]utation is . . . a necessary precondition to evolutionary change," which "takes place, not so much because of natural selection, but to a large degree in spite of it."

Williams's speculations about how evolution would be enacted over a period of a million years is exemplified in the following passage:

> The important process in each such period was the maintenance of adaptation in every population. This required constant rectification of the damage caused by mutation, and occasionally involved gene substitutions, usually in response to environmental change. Evolution, with whatever trends it may have entailed, was a by-product of the maintenance of adaptation. At the end of a million years an organism would almost always be somewhat different in appearance from what it was at the beginning, but in the important respect it would still be exactly the same; it would still show the uniquely biological property of adaptation, and it would still be precisely adjusted to its particular circumstances. I regard it as unfortunate that the theory of natural selection was first developed as an explanation for evolutionary change. It is much more important as an explanation for the maintenance of adaptation.

Williams was very clear about how he read the work of paleontologists and systematists, and even population geneticists who were interested in processes that went beyond the level of the individual. As he saw the situation, these evolutionists were discussing only speciation, long-term morphological change, and environmental or ecological adaptation. Williams believed that these evolutionary biologists were not using "[t]he principle of natural selection . . . in an adequately disciplined fashion." As far as he was concerned, "[m]ost of the conclusions on patterns of speciation would be much the same whether based on Lamarckian, nineteenth-century Darwinian, or modern genetic concepts." Just because a publication on speciation contained the words *selection, mutation,* or *gene flow* did not mean that it was "conceptually much advanced beyond what Lamarck or Darwin might have written." In fact, Williams continued; "Darwin's or even Lamarck's concepts form a perfectly adequate basis for explaining most of the phenomena of systematics."

Williams adopted the term *teleonomy* for the discipline he was developing: the study of adaptation as informed by a particular theory of gene selection. Although *teleonomy* was later replaced by *sociobiology,* the focus remained the same: "Its first concern with a biological phenomenon would be to answer the question: 'What is its function?' " The answer to this question came by defining natural selection as "the differential survival of alleles." The simpler the explanation to the question, the stronger, Williams argued, would be the strength of this theory of natural selection.

Although the goal of simplicity may lead to a better, or at least a clearer, explanation, it does not constitute a test of the theory of natural selection itself. Nonetheless, it is important to realize that if, according to Williams, natural selection strives to maintain stability, then the picture of evolution that emerges is one in which nothing of significance happens until it is disrupted by mutation. Natural selection may be accommodating individuals to the vicissitudes of daily existence by choosing among the already available alleles, but it is not creating anything new. This does indeed appear to be what Williams meant when he so clearly distinguished between individual adaptation and the processes of evolutionary change that lead to speciation. In fact, he was even clearer on this point in a more recent book:

> The microevolutionary process that adequately describes evolution in a population is an utterly inadequate account of the evolution of the Earth's biota. It is inadequate because the evolution of the biota is more than the mutational origin and subsequent survival or extinction of genes in gene pools. Biotic evolution is also the cladogenetic [branching] origin and subsequent survival and extinction of gene pools in the biota.

This is certainly a different approach to neo-Darwinism than the one the predecessors and founders of the Evolutionary Synthesis propounded. They—from Morgan to Dobzhansky and Mayr—were invested in the applicability of observations on laboratory population genetics to microevolutionary processes and the expandability of microevolutionary processes to explain all aspects of evolution, from the individual to the largest of evolutionary groups. Following Fisher, in particular, the mottoes of the neo-Darwinism of the Synthesis was "variation furnished by random micromutation," and "change enacted by natural selection on this low-level variation." Because microevolution was slow and gradual, so, too, must be macroevolution.

But then came Williams, a neo-Darwinian who suggested that microevolution and macroevolution should be decoupled. Granted, Williams was no Bateson or early Morgan, or a Goldschmidt or Schindewolf. But he was not a promoter of the kind of neo-Darwinism that became incorporated into the Synthesis. Nonetheless, the intellectual offspring Williams sired often cite him as suggesting that his adaptationist program is explanatory of all levels of evolution. Perhaps this overgeneralization of Williams's intent is due to a confusion that arises when the word *evolution* is used to discuss two very different phenomena: the maintenance of adaptation versus the introduction of change. But, clearly, as the quotes above demonstrate, Williams was not promoting the kind of uniformitarianism that was followed by the neo-Darwinians who preceded him; namely, that of expecting the processes of micromutation within species to be of equal validity for understanding the origin of species.

Back to the Fossil Record

In 1972, a different approach to distinguishing between processes that are relevant at the within-species level and those that result in the origin of species came from two graduate students in invertebrate paleontology at Columbia University, Niles Eldredge and Stephen Jay Gould. The impetus for this particular joint effort came from the studies on a group of fossil invertebrates—the primitive, shrimplike trilobites—that Eldredge had been conducting.

A marine environment provides a better setting for a more reliable picture of what happened over a period of geologic time than does a terrestrial environment. Being in water facilitates fossilization. A dead body will probably sink to the bottom, and become covered by sediment, which will protect it. And small marine organisms tend toward large populations, so there will be a greater number of individuals contributing to the potential population of fossils. Consequently, marine invertebrates, such as trilobites, would have a much better chance of demonstrating the details, over geologic time, of their comings and goings geographically, and of their evolutionary changes, than, for example, would elephants or even most insects.

By following the representative fossils of different groups of trilobites over time, Eldredge was struck by how stable a particular group remained in its morphology. Moreover, it appeared that one population of trilobites with, typically, fewer lenses quickly replaced another population that, typically, had a greater number of lenses. The fossil history of trilobites did not conform to a model of gradual evolutionary change, with transformation via all possible permutations from one lens count to another. Rather, these fossils presented a totally different picture: long periods of relatively no change, and occasional rapid episodes of morphological change. To Eldredge, this paleontological observation suggested a particular mode of allopatric speciation, or speciation by way of geographic separation: allopatric speciation via peripheral isolates. It turned out that Gould, too, had been impressed by a similar picture of the fossil record of the fossil Bermuda snails he had been studying.

In their joint article, Eldredge and Gould introduced the concepts of phyletic gradualism, stasis, and punctuated equilibria. They used the phrase "phyletic gradualism" to encompass the kind of slow change via a succession of intermediates that, especially in paleontology, had become the image of how evolutionary change actually occurs—in spite of the frequent gaps in the fossil record that intrude upon this ideal. In this framework, gradually accumulating change can produce a continuum of transformation that does not increase species diversity, but it can also be involved in the origin of a species. In contrast, the picture of evolution that derived from the study of trilobites and Bermuda snails was that of long periods of stasis—no morphological change beyond minor individual variation—that were infrequently punctuated by abrupt or rapid episodes of population replacement. In addition to summarizing their work on trilobites and snails, Eldredge and Gould cited the fossil record of the horse, the extinct oyster *Gryphaea,* and another extinct invertebrate, the echinoid *Micraster,* as other examples of rapid, or punctuated, evolution.

By rapid evolution, Eldredge and Gould were not suggesting that a new species arises instantaneously, or even within a matter of generations. Rather, in everyday life—that is, in terms of ecological time—the process of speciation might not appear excessively rapid, even if one knew that it was taking place. However, in terms of evolutionary or geologic time, a new