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Speciational Evolution or Punctuated Equilibria

by Ernst Mayr

Only recently have we understood how different are the concepts to which the term "evolution" has been attached. With wisdom of hindsight, we can now (250 years after Buffon) distinguish three very different concepts of evolution: saltational evolution, transformational evolution, and variational evolution.

Theories postulating saltational evolution are a necessary consequence of essentialism. If one believes in constant types, only the sudden production of a new type can lead to evolutionary change. That such saltations can occur and indeed that their occurrence is a necessity is an old belief. Almost all of the theories of evolution described by H. F. Osborn (1894) in his *From the Greeks to Darwin* were saltational theories, that is, theories of the sudden origin of new kinds. The Darwinian revolution (Darwin, 1859) did not end this tradition, which continued to flourish in the writings of Thomas H. Huxley, William Bateson, Hugo De Vries, J. C. Willis, Richard Goldschmidt, and Otto Schindewolf. Traces of this idea can even be found in the writings of some of the punctuationists.

According to the concept of transformational evolution, first clearly articulated by Lamarck, evolution consists of the gradual transformation of organisms from one condition of existence to another. Almost invariably, transformation theories assume a progression from "lower to higher" and reflect a belief in cosmic teleology resulting in an inevitable steady movement toward an ultimate goal, an ultimate perfection. In biology all so-called orthogenetic theories, from those of K. E. von Baer to Osborn, L. S. Berg, and Teilhard de Chardin are in this tradition.

As R. C. Lewontin (1983) has correctly pointed out, Darwin introduced an entirely new concept of evolution: variational evolution. New gene pools are generated in every generation, and evolution takes place because the successful individuals produced by these gene pools give rise to the next generation. Evolution thus is merely contingent on certain processes articulated by Darwin: variation and selection. No longer is a fixed object transformed, as in transformational evolution, but an entirely new start is, so to speak, made in every generation. Evolution is no longer necessarily progressive; it no longer strives toward perfection or any other goal. It is opportunistic, hence unpredictable.

What Darwin did not fully realize is that variational evolution takes place at two hierarchical levels, the level of the deme (population) and the level of species. Variational evolution at the level of the deme is what the geneticist deals with. It is effected by individual selection and leads minimally to the maintenance of fitness of the population through stabilizing selection.

The second level of variational evolution is that of the species. Owing to continuing (mostly peripatric) speciation, there is a steady, highly opportunistic production of new species. Most of them are doomed to rapid extinction, but a few may make evolutionary inventions, such as physiological, ecological, or behavioral innovations that give these species improved competitive potential. In that case they may become the starting point of successful new phyletic lineages and adaptive radiations. Such success is nearly always accompanied by the extinction of some competitor. This process of succession of species is often referred to by the term "species selection," but to prevent misunderstandings it may be better to call it "species turnover" (see below).

The transfer from transformational to variational evolution required a conceptual shift that was only imperfectly carried through by most Darwinians. As a consequence, geneticists described evolution simply as a change in gene frequencies in populations, totally ignoring the fact that evolution consists of the two simultaneous but quite separate phenomena of adaptation and diversification. The latter results from a process of multiplication of species, a process almost totally ignored in the writings of R. A. Fisher, J. B. S. Haldane, Sewall Wright, and other leading evolutionary geneticists.

Transformational thinking likewise continued to dominate paleontology, expressed in the concept of phyletic gradualism. Since most paleontologists were typologist (in an almost Platonian sense), they subconsciously assumed that species were everywhere the same and, thus, at any given time essentially uniform. Speciation consisted of the gradual transformation of such species in geological time. Since the gradualness of such phyletic transformation could be documented in the geological record only in the rarest cases, it was postulated that the absence of intermediates was a consequence of the notorious incompleteness of the fossil record. The so-called evolutionary species definition adopted by most paleontologists (Simpson, 1961; Wilimann, 1985) reflects the same focus on the vertical (i.e., time) dimension. If adopted, it leaves only two options: speciation is explained either by gradual phyletic evolution, with the gaps between species being due to the deficiency of the fossil record, or by sympatric saltational speciation. Indeed, most paleontologists adopted both options. Acceptance of phyletic gradualism does not require the acceptance of a constant rate of evolutionary change. The rate may accelerate or slow down, but change leads inexorably to the steady transformation of a lineage.

Even Darwin, for reasons that relate to his struggle against creationism, stressed the transformational aspect of evolution. He was, however, fully aware of highly different rates of evolution, from complete stasis to rates of change so fast that intermediates could not be discovered in the fossil record (Gingerich, 1984; Rhodes, 1983; and others). Owing to his adoption of sympatric speciation, however, Darwin never needed to consider the geographical component in his theorizing. When he said that a new species might originate as a local variety, he did not claim that it was an isolated population. It seems to me that for Darwin the pulsing of evolutionary rates was a strictly vertical phenomenon.

The geneticists, with the exception of a few saltationists such as DeVries and Bateson, usually ignored the problem of speciation altogether. The only geneticists who showed an interest in the multiplication of species were those who had been educated as taxonomists, like Theodosius Dobzhansky and G. L. Stebbins. The problem of relating speciation to macroevolution occupied primarily three zoologists, Julian Huxley (1942), Mayr (1942, 1954), and Bernhard Rensch (1947), who were neither geneticists nor paleontologists. Since these three were among the architects of the evolutionary synthesis, one can state that the problem of the relation between speciation and macroevolution was not entirely ignored by the evolutionary synthesis.

The widespread neglect of the role of speciation in macroevolution continued until Niles Eldredge and Stephen Jay Gould (1972) proposed their theory of punctuated equilibria. Whether one accepts this theory, rejects it, or greatly modifies it, there can be no doubt that it had a major impact on paleontology and evolutionary biology.

The gist of the theory was that "significant evolutionary change arises in coincidence with events of branching speciation, and not primarily through the transformation of lineages" (Gould, 1982a:83, 1983). The contrast between the previously dominant view of evolutionary change was as follows. Traditionally, evolution had been seen as a single-phase phenomenon of gradual change, albeit sometimes more slowly, sometimes more rapidly. Now evolution was seen as an alternation between speciation events during which the major evolutionary (particularly morphological) change occurred and lengthy periods of stasis.

Historical studies have since shown that the term "punctuated equilibrium" was more novel than the concept. A role for peripheral populations in speciation was already postulated by L. v. Buch (1825) and fully substantiated by Darwin for the Galapagos mockingbirds. Unfortunately, by the time Darwin published the *Origin* (1859), he had adopted sympatric speciation (Mayr, 1982a). When he said that a new species might originate as a local variety, he did not necessarily mean an isolated population. Nor are the changes in the rate of evolution to which Darwin refers brought in relation to speciation.

Before going any further in the analysis of the literature, it is important to call attention to a prevailing confusion between two distinct evolutionary phenomena, gradualism and uniformity of evolutionary rate. Darwin emphasized gradualism (Rhodes, 1983), but, as I shall show, even that term is ambiguous, allowing for two very different interpretations. What Darwin did not insist upon was a uniformity of rates (Huxley, 1982; Penny, 1983; Rhodes, 1983). The existence of so-called living fossils was known to paleontologists early in the nineteenth century, and the occurrence of different rates of evolution in different phyletic lines was paleontological dogma already in Darwin's lifetime. George Gaylord Simpson (1953) analyzed this phenomenon in great detail and even introduced a special terminology to characterize lineages with average, very rapid, and extremely slow evolutionary rates. Eldredge and Gould never claimed to have discovered this difference in rates, and the part of the ensuing polemic stressing these differences is therefore irrelevant for the evaluation of the punctuation theory.

It is not always easy to interpret Darwin's statement (Rhodes, 1983) because isolation (at least during the process of speciation) had become unimportant for him owing to his adoption of sympatric speciation. I have been unable to discover in Darwin's writings any connection between allopatric speciation and change of evolutionary rate. Gould and Eldredge correctly state that Simpson likewise failed to make such a connection. His quantum evolution was a vertical (temporal) phenomenon, as it had to be considering his evolutionary species definition (Simpson, 1944:207-217).

Paleontologists knew that new species may originate in a very circumscribed area and turn up in the fossil record only after having spread more widely (Bernard, 1895). This insight was made use of, however, only in stratigraphic research and not in studies of macroevolution. On the contrary, the importance of peripatric speciation was minimized after Fisher (1930) and Wright (1931, 1932) had asserted, although for different reasons, that evolution was most rapid in populous, widespread species, a conclusion adopted also by Dobzhansky (1937, 1951) and by most evolutionists before the 1970s.

I believe I was the first author to develop a detailed model of the connection between speciation, evolutionary rates, and macroevolution (Mayr, 1954). Although long ignored, my new theory of the importance of peripatric speciation in macroevolution is now widely recognized. "Mayr's hypothesis of peripheral isolates and genetic revolution must of necessity be a centerpiece of the punctuated equilibria theory; it is the theory, for all practical purposes" (Levinton, 1983:113). 1 once more presented my theory in great detail (Mayr, 1963:527-555). Under these circumstances it is most curious that the theory was completely ignored by paleontologists until brought to light by Eldredge and Gould (1972).

The major novelty of my theory was its claim that the most rapid evolutionary change does not occur in widespread, populous species, as claimed by Most geneticists, but in small founder populations. This conclusion was based on empirical observations gathered during my studies of the speciation of island birds in the New Guinea region and the Pacific. I had found again and again that the most aberrant population of a species—often having reached species rank, and occasionally classified even as a separate genus—occurred at a peripheral location, indeed usually at the most isolated peripheral location. Living in an entirely different physical as well as biotic environment, such a population would have unique opportunities to enter new niches and to select novel adaptive pathways.

As I pointed out elsewhere (Mayr, 1982b), my conclusion was that a drastic reorganization of the gene pool is far more easily accomplished in a small founder population than in any other kind of population. Indeed, I was unable to find any evidence whatsoever of the occurrence of a drastic evolutionary acceleration and genetic reconstruction in widespread, populous species.

In view of frequent recent misrepresentations of my 1954 theory I must emphasize also what I did not claim (see also Mayr, 1982b):

1. I did not claim that every founder population speciates. In the vast majority, only minor genetic reorganizations occur, and the majority of such founder populations soon become extinct or merge with the parental species.
2. I did not claim that every genetic change in a founder population is a genetic revolution. Evidently it requires a special constellation for the occurrence of a more drastic genetic reorganization. All I claimed was that when a drastic change occurs, it occurs in a relatively small and isolated population.
3. I did not claim that speciation occurs only in founder populations. Finally, I nowhere claimed that I chose the name "peripatric' (Mayr, 1982c) because the founders came from the periphery of the parental range. I chose that name because the founder populations were at peripheral locations. My interpretation throughout was very pluralistic and was naturally misunderstood in an age when singular, deterministic solutions were strongly preferred.

In 1954 I was already fully aware of the macroevolutionary consequences of my theory, saying that "rapidly evolving peripherally isolated populations may be the place of origin of many evolutionary novelties. Their isolation and comparatively small size may explain phenomena of rapid evolution and lack of documentation in the fossil record, hitherto puzzling to the palaeontologist" (p. 179).

I later supplemented my theory by pointing out (Mayr, 1982c) that peripatric speciation may occur not only in founder populations but also in any population going through a severe bottleneck such as refuge populations during Pleistocene glaciations (Haffer, 1974).

The first to pick up my theory was Eldredge (1971), who found in his study of Paleozoic trilobites that the majority of species showed no change in species-specific characters throughout the interval of their stratigraphic occurrence, whereas new species appear quite suddenly in the strata. He therefore proposed that the allopatric model be substituted in the minds of palaeontologists for phyletic transformation as the dominant mechanism of the origin of new species in the fossil record. This was followed in 1972 by the Eldredge and Gould paper, in which the term "punctuated equilibrium' was proposed. The Eldredge-Gould proposal was essentially my 1954 theory, except for a far stronger emphasis on stasis, indeed a belief that no further evolutionary change would occur after the speciation process was completed.

Questions and Objections

A modest theory of punctuationism is so strongly supported by facts and fits, on the whole, so well into the conceptual framework of Darwinism, that one is rather surprised at the hostility with which it was attacked. The controversy over punctuationism is, by now, more than twenty years old, and it is possible to distinguish different classes of objections. There are questions that deal with the core ideas of the theory: What is stasis? How can one account for it? Do all species experience stasis? Is all evolutionary change restricted to bouts of speciation? If so, why? What are the genetic aspects of speciation? These and other questions will be analyzed in the second part of this essay.

But not all the objections raised against punctuationism deal with these core ideas. Others were raised against rather specific claims made by Eldredge, Gould, or both, or against the way they treated their evidence. It will be helpful to deal with these objections first. They relate largely to claims that are not part of a punctuationist theory of evolution. To deal with them separately and to test them for their validity will clear the field for a subsequent testing of the core ideas of punctuationism.

Four aspects of the treatment of punctuationism by Gould and Eldredge were objected to most frequently. First to receive attention was the seemingly monolithic nature of the claims. Even though Eldredge and Gould (1972) nowhere stated that a neospecies enters a period of total stasis, this is what all their graphic presentations suggested (figs. 5-4, 5-8, 5-10). Furthermore, evolutionary trends are explained by a process of species selection of completely static species (fig. 5-10). Not surprisingly, their opponents assumed that Eldredge and Gould had postulated total stasis for all species after they had completed the process of speciation.

Professor Gould assures me that they had never adopted such an extreme position, and in their next paper they stated emphatically: "We never claimed that gradualism could not occur in theory or did not occur in fact.…The fundamental question is not 'whether at all,' but how often" (Gould and Eldredge, 1977:119). In their abstract, Gould and Eldredge specify: "Most species, during their geological history, either do not change in any appreciable way, or else they fluctuate mildly, with no apparent direction. Phyletic gradualism is very rare" (p. 115).

The second point of contention was the claim of novelty. Nothing incensed some evolutionists more than the claims made by Gould and associates that they had been the first to have discovered, or at least to have for the first time properly emphasized, various evolutionary phenomena already widely accepted in the evolutionary literature. G. L. Stebbins and F. J. Ayala (1981), Verne Grant (1982, 1983), and J. S. Levinton (1983) were fully justified in rejecting these claims of novelty. In particular, they showed that an insistence on gradualism by Darwin and his followers was a denial of saltationism but not a denial of different and changing rates of evolution.

Third, vigorous objection was raised to the claim that punctuationism would require a revision of Darwin's "evolutionary synthesis." "I have been reluctant to admit it, but if Mayr's (1963:586) characterization of the synthetic theory is accurate, then that theory as a general proposition is effectively dead" (Gould, 1980:120). The gist of my statement to which Gould refers was that, contrary to Goldschmidt and Schindewolf, nothing happens in macroevolution that does not happen in populations. What Gould actually attacks, and rightly so, is the completely reductionist characterization of evolution by the mathematical population geneticists. To equate these reductionist views with the theories of the evolutionary synthesis is unjustified, however, as I pointed out in a critical review of similar statements published by M. W. Ho and P. T. Saunders (Mayr, 1984b). A rejection of the axiom of most population geneticists, "Evolution is a change of gene frequencies," is not a rejection of the evolutionary synthesis. The theory of the synthesis is much broader and constitutes in many respects a return to a more genuine Darwinism. The events that take place during peripatric speciation, no matter how rapid they may be, are completely consistent with Darwinism.

Curiously, some authors also mistakenly assume that the occurrence of stasis would refute Darwinism. Teleological thinking requires continuous evolutionary change, but Darwin rejected teleology (Mayr, 1984a) and accepted stasis (Rhodes, 1983). An evolutionary lineage may continue to vary genetically without undergoing any major reconstruction. Alternatively, a stable lineage may continue to send out founder populations, some of which, through peripatric speciation, could become more or less distinct daughter species.

The fourth reason why punctuationism faced so much opposition is that at one stage Gould pleaded for a revival of Goldschmidt's ideas and implied that they were akin to punctuationism. This claim clearly indicated that there was considerable conceptual confusion as to what punctuated equilibria really means. Before the possibility that Goldschmidt was a forerunner of punctuationism can be discussed constructively, it is necessary to discriminate among four interpretations of punctuationism.

1. An evolutionary novelty originates by a systemic mutation: the individual produced by such a mutation is the representation of a new species or higher taxon.
2. Evolutionary change is populational, but all substantial evolutionary changes takes place during bouts of speciation. As soon as the process of speciation is completed, the new species stagnates ("stasis") and is unable to change in any significant way. Early statements by Eldredge and Gould (1972) and Gould and Eldredge (1977) gave the impression that this was their interpretation.
3. Phyletic lineages ("evolutionary species") can evolve

slowly and gradually into different species and even genera, but the more pronounced evolutionary changes and adaptive shifts take place during speciational bouts in isolated populations. This has been all along my own interpretation (Mayr, 1954, 1982b) and is presumably that of many evolutionists familiar with geographic speciation.

4. A multiplication of species (the branching of lineages) occurs but is of no greater evolutionary importance than changes within lineages. In fact, phyletic gradualism is responsible for most evolutionary change. It was this view, held by the majority of paleontologists, that induced Eldredge and Gould (1972) to propose their theory of punctuated equilibria

Only the first one of these four theories conflicts with Darwinism. It was Goldschmidt's theory, and because Goldschmidt has often been cited in connection with punctuationism, it is necessary to discuss his ideas in more detail.

To strengthen the punctuationism case, Gould cited Goldschmidt's views on macroevolution, indicating that "during this decade Goldschmidt will be largely vindicated in the world of evolutionary biology" (Gould, 1980:186). Goldschmidt had claimed that the differences among subspecies, and more broadly all geographic variation, was caused by minimal genetic changes, mutations of alleles, mostly being selected merely for climatic adaptation. Such changes would not permit any transgression of the ancestral type. Any genuine evolutionary novelty was due to the origin of a "hopeful monster," caused by a systemic mutation. This thesis followed from Goldschmidt's rather eccentric conception of nature of chromosomes and the genotype. According to him, a systemic mutation is a complete change of the primary pattern or reaction system into a new one and has the capacity to produce a strikingly different new individual that could serve as the founding ancestor of a new type of organism. As J. Maynard Smith (1983:276) pointed out, hopeful monsters, by contrasts, are drastically altered phenotypes. They are possible, at least in theory, and it should be possible to discover empirically how often they occur and how often (if ever) they are selectively superior.

It entirely misrepresents Goldschmidt's theory to claim that Goldschmidt "argued that speciation is a rapid event produced by large genetic changes (systemic mutations) in small populations" (Gould and Colloway, 1980:394). The whole concept of populations was alien to his thinking. According to him, a new type is produced by a single systemic mutation producing a unique individual. Gould (1982) is also wrong in claiming that Goldschmidt never had the view "that new species arise all at once, fully formed, by a fortunate macromutation." Actually , this is what Goldschmidt repeatedly claimed. For instance, he cited with approval Schindewolf's suggestion that the first bird hatched out of a reptilian egg, and he was even clearer on this point in a later paper (1952:91-92) than in his 1940 book.

In refutation of Goldschmidt's claims I demonstrated (Mayr, 1942) that geographic variation in isolated populations could indeed account for evolutionary innovations. Such populations have a very different evolutionary potential than contiguously distributed, clinally varying populations in a continental species. As I stated (Mayr, 1954), and have reiterated (Mayr, 1963 1982b), one can defend a moderate form of punctuationism, based on strictly empirical evidence, without having to adopt Goldschmidt's theory of systemic mutations.

Some Basic Questions About Punctuationism

The theory of punctuationism, to repeat, consists of two basic claims: that most or all evolutionary change occurs during speciation events, and that most species usually enter a phase of total stasis after the end of the speciation process. The two claims are to some extent two separate theories.

The controversy that followed the proposal of this theory revealed that there are considerable conceptual and evidential difficulties in either substantiating or refuting this theory. First, the nature of the fossil record makes it exceedingly difficult, if not impossible, to obtain irrefutable evidence either for stasis or for a very short time span speciation. Second, throughout the controversy one encounters considerable terminological vagueness and equivocation, as for instance concerning the meaning of such words as "gradual," "stasis," "speciation," and "species selection." A careful analysis of the terms most frequently used in the punctuationism controversy is therefore indispensable.

Gradualness

Whether evolution is gradual became the focus of a heated controversy in the punctuationist argument. Darwin (1859), as everyone knew, had frequently emphasized the gradual nature of evolutionary change (pp. 71, 189, 480), largely because of his opposition to two ideologies dominant in his time, creationism and essentialism. After these ideologies lost their power, it was no longer necessary to be so single-mindedly opposed to the occurrence of discontinuities. Yet the recent controversy concerning the saltational versus gradual origin of evolutionary novelty revealed an equivocation.

Most modern authors failed to distinguish between two very different phenomena: the production of a new taxon, and the production of a new phenotype. If the production of a new taxon is gradual, it is taxic gradualism; if it is instantaneous, it is taxic saltation. Likewise, one can distinguish phenotypic gradualness and phenotypic saltation. What Darwin mostly argued against was the thesis that evolutionary novelties could originate through taxic saltation, that is, through the production of a single individual representing a new type, a new taxon. Instead, he proposed that all evolutionary innovation is effected through the gradual transformation of populations.

This distinction became important after Goldschmidt revived the essentialistic idea that a new higher taxon could be established as the product of a single systemic mutation. Even though the success of such a taxic saltation is too improbable to be endorsed by a contemporary evolutionist, it still leaves the possibility of the occurrence of phenotypic saltations. If a mutation with a drastic phenotypic change could be incorporated in a population and become part of a viable phenotypic polymorphism, it could lead to a seemingly saltational evolutionary change. Gould (1980:127) indeed envisages a "potential saltational origin for the essential features of key adaptations. Why may we not imagine that gill arch bones of an ancestral agnathan moved forward in one step to surround the mouth and form proto-jaws?" Maynard Smith (1983:276) points out that the occurrence of "genetic mutations of large phenotypic effect is not incompatible with Darwinism." Steven M. Stanley (1982) has argued quite persuasively that gastropod torsion might have originated through a single mutation. It would have had to pass through a stage of polymorphism until the new gene had reached fixation. Evidently such a process is feasible, but its importance in evolution is contradicted by the fact that, among the millions of existing populations and species, mutations with large phenotypic effects would have to be exceedingly frequent to permit the survival of the occasional hopeful monster among the thousands of hopeless ones. But this in not found.

Furthermore, enough mechanisms for the gradual acquisition of evolutionary novelties are known (Mayr, 1960) to make the occurrence of drastic mutations dispensable, at least as a normal evolutionary process.

The argument, thus, is not whether phenotypic saltations are possible, but rather whether evolution advances through the production of individuals representing new types or through the rapid transformation of populations. No matter how rapid, such a populational "saltation" is nevertheless Darwinian gradualism.

Stasis

Of all the claims made in the punctuationist theory of Eldredge and Gould, the one that encountered the greatest opposition was that of "pronounced stasis as the usual fate of most species," after having completed the phase of origination (Gould, 1982a:86). Yet it was this very claim which the authors designated as their most important contribution.

The extraordinary longevity of the so-called living fossils had, of course, been known since the early days of paleontology (Eldredge and Stanley, 1984; de Ricqles, 1983). But is such stasis the usual fate of most species? Evidence supporting this claim can be found in Stanley's book (1979), some review papers (e.g., Levinton, 1983; Gould, 1982b), and recent volumes of *Paleobiology*, *Systematic Zoology*, and other journals. Yet the literature also reports numerous cases of seeming speciation by phyletic gradualism (e.g., Van Valen, 1982:99-112). Perhaps most convincing are the cases of significant evolutionary transformation in continuous phyletic lineages reported by K. D. Rose and T. M. Brown (1984) for Eocene primates and by J. Chaline and B. Laurin (1986) for Pliocene rodents. Such phyletic speciation seems to be more frequent in terrestrial than in marine organisms.

Two objections have been raised against the seeming cases of phyletic speciation. First, hiatuses and depositional breaks seem to occur even in the most complete sequences; second, the so-called species of these sequences may not be valid species because they usually differ only in minor characters of size and proportions. Be that as it may, Gould has recently seemed to concede that speciation by phyletic gradualism does occur.

I agree with Gould that the frequency of stasis in fossil species revealed by the recent analysis was unexpected by most evolutionary biologists. Admittedly, stasis is measured in terms of morphological difference, and the possibility cannot be excluded that biological sibling species evolved without this being reflected in the morphotype. Let us tentatively assume that some species enter complete stasis while others evolve by phyletic gradualism.

The question of what percentage of new species adopts one or the other of these two options cannot be resolved either by genetic theory or through the study of living species. It can be decided only though an analysis of the paleontological evidence, and this poses great methodological difficulties (Levinton and Simon, 1980; Schopf, 1982). For instance, in the analysis of the benthic foraminifers, the calculated average age of 20 million years was based on only 15 percent of the recent species. For all the others the fossil record was too spotty to permit any determinations. In other words, the proof of stasis was based on a highly biased sample, consisting of common widespread species, which one could expect to have longevity and which comprised a small minority of the entire fauna. It is conceivable that a considerable fraction of the remaining 85 percent underwent rapid phyletic speciation and thus became unavailable for analysis. The indications are that the vast majority of the so-called rare species are short-lived, probably not for reasons of rapid phyletic change but rather owing to extinction. The best one can do under the circumstances is to adopt an intermediate position by admitting the occurrence of some gradual phyletic speciation but pointing also to the unexpectedly large number of cases in which fossil species showed no morphological change over many millions of years.

Recent discoveries in molecular biology have raised questions about the meaning of stasis. The stasis found in morphological characters in such old genera as *Rana*, *Bufo*, *Plethodon*, or even *Drosophila* is not at all owing to the retention of an entirely unchanged genotype. Through the electrophoresis method, countless changes in quasi-neutral enzyme genes have been discovered, but numerous other nonmorphological changes have also taken place in these genera, such as the acquisition of new isolating mechanisms, as well as of numerous adaptations to changing environments. What has remained stable, however, is the morphotype, the basic *Bauplan*. The species in some lineages that can be inferred to have separated 30 to 60 million years ago are morphologically still almost indistinguishable except in size, coloration, and minor differences in skeletal dimensions. […]

The Contributions of Punctuationism to Evolutionary Theory

Even some of its opponents admit that punctuationism has had an enormously stimulating effect on evolutionary biology (Rhodes, 1984; Maynard Smith, 1984b; Gould, 1985). The controversy has brought to light numerous equivocations and has helped to clarify distinctions between alternatives, such as between phyletic and allopatric speciation, between phenotypic and taxic saltations, between various types of group selection, between the evolutionary potential of small and large populations, between an uncompromisingly reductionist and a more holistic concept of the genotype, between various concepts of species selection, and still others. To eliminate these equivocations it was not only necessary to clarify concepts but also to show that we needed a broader factual foundation. As Gould has correctly emphasized, one of the most important contributions of punctuationism has been its stimulation of fruitful empirical research, much of it still ongoing.

To be sure, the claims of some punctuationists, such as the prevalence of total stasis and the impossibility of evolutionary change without speciation, are clearly invalid. Furthermore, it has been shown that "speciational evolution" (perhaps a better term than "punctuationism") is fully consistent with Darwinism; and finally, that seeming evolutionary saltations, as indicated by the fossil record, can be explained without invoking systemic mutations or other mechanisms in conflict with molecular genetics. It is irrelevant for the theory of speciational evolution how relatively frequent evolutionary stasis is or how frequent the occasional occurrence of drastic reorganization during peripatric speciation.

Most of all, punctuationism has shown how one-sided has been the myopic focusing of paleontologists and population geneticists on the one-dimensional, transformational, upward movement of evolution. It finally brought general recognition to the insight of those who had come from taxonomy (E. Poulton, Rensch, Mayr) and had consistently stressed that the lavish production of diversity is the most important component of evolution.

What had not been realized before is how truly Darwinian speciational evolution is. It was generally recognized that regular variational evolution in the Darwinian sense takes place at the level of the individual and population, but that a similar variational evolution occurs at the level of species was generally ignored. Transformational evolution of species (phyletic gradualism) is not nearly as important in evolution as the production of a rich diversity of species and the establishment of evolutionary advance by selection among these species. In other words, speciational evolution is Darwinian evolution at a higher hierarchical level. The importance of this insight can hardly be exaggerated.

[Ernst Mayr, "Speciational Evolution or Punctuated Equilibria," from Albert Somit and Steven Peterson's *The Dynamics of Evolution*, New York: Cornell University Press, 1992, pp. 21-48.]
