



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 Platonic 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). I 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 speciation 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 Collway, 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 is 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 Ricqlès, 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 through 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. This is just one more piece of evidence for the interesting phenomenon that organisms do not evolve as harmonious types but that different characters may evolve at highly different rates. [Archaeopteryx](#), with its incongruous mixture of reptilian and avian characters, illustrates this well, as does the peculiar mixture of similarities and differences revealed by a comparison of human and chimpanzee.

The discovery of highly unequal rates of evolution of different components of the genotype does not, however, eliminate the problem of stasis. Why do certain components of the genotype and phenotype remain so stable for millions or tens of millions of years?

This is a particularly puzzling question because there is an almost inexhaustible source of variation. Not only is there a steady rate of mutation at all gene loci, but various phenomena have been discovered by molecular biology in recent years that would seem to lead almost inevitably to a frequent revamping of the genotype. For instance, merely isolating stocks of *Drosophila* in laboratory populations may lead to

all sorts of mutual incompatibilities. Transposons and other genetic elements may change the mutability of adjacent loci, and a host of other molecular phenomena would seem to encourage genetic changes of evolutionary significance. Furthermore, selection pressures in an incessantly changing physical and biotical environment would seem inductive to continuing evolutionary change. That we encounter the stability found in the living fossils, and to a lesser extent in the majority of species and genera, is very puzzling indeed.

On the whole, three explanations have been advanced to explain stasis. Reductionist geneticists attribute stasis entirely to stabilizing (normalizing) selection. All mutants or recombinants that deviate from the norm are eliminated by natural selection. This is, of course, no explanation because abundant normalizing selection also takes place in rapidly evolving lines. Obviously, all zygotes with lowered viability are apt to be eliminated in any population either before birth or at least before reproduction. Such selection under the name of "elimination of degenerations of the type" was acknowledged by essentialists long before the establishment of evolutionism (Mayr, 1982a:488). The large mortality of zygotes both in static and in rapidly evolving species is evidence for such elimination. The "internal selection" of certain authors is largely such elimination, as pointed out by J. Remane (1983).

This, however, does not explain why, in spite of the universality of such normalizing selection, certain lineages evolve rapidly while others remain in total stasis. Nor does invoking "normalizing selection" make a distinction between the elimination of new deleterious mutations and that of deleterious recombinants, particularly those interfering with developmental constraints. It is misleading to say that stasis is caused either because deviants were weeded out or because the developmental system prevented them from arising. Even in the latter case it is normalizing selection through which the developmental constraints operate.

Another explanation is that species in stasis had reached optimal adaptation and were no longer answering any directional selection. This is improbable for two reasons. First, selection virtually never succeeds in completely optimizing a genotype; hence a change in the degree of optimality should be recognizable during millions of years. Furthermore, the environment is known to have changed considerably in periods during which certain species displayed complete stasis. Why is this environmental change not reflected in an evolutionary response by these species?

Considering that both of these explanations are unsatisfactory, one must ask whether there is any other possible explanation. Yes, provided one gives up the atomistic view that each gene is independent both in its actions and in the effects of selection on it. If one adopts a more holistic (integrative) view of the genotype and assumes that the genes perform as teams and that large numbers of other genes form the "genetic milieu" (Chetverikov, 1926) of any given gene, one can suggest an explanation. It is that epistatic interactions form a powerful constraint on the response of the genotype to selection. Such epistatic interactions were already dimly appreciated by Darwin (1859:11, 146; 1868, vol. 2:319-335) and have since been stressed by S. S. Chetverikov (1926) (genetic milieu), M. Lerner (1954) (genetic homeostasis), K. Mather (1953) (internal balance), and Mayr (1963, 1970, 1975, 1982b) (cohesion of the genotype).

Holists claim therefore that much of macroevolution cannot be explained by atomistic gene replacements or by selection pressures on single genes, but only by a more drastic reorganization, made possible by loosening the tight genetic cohesion of the genotype found throughout widespread populous species. Mayr, H. L. Carson (1975), Eldredge and Gould, and Stanley ascribe the stability of the phenotype, as observed in static species, to such an internal cohesion of the genotype, or parts of it. Significant evolutionary advance can take place only after a breaking up of previously existing epistatic balances.

There is, of course, no conflict whatsoever between this holistic view and Darwinism because the cohesive domains of the genotype must have come into existence through natural selection. Unfortunately, current genetic techniques seem unable to analyze such cases of restructuring. Until such techniques become available—probably in the not too distant future—it is impossible to prove conclusively the

existence of such genotypic domains and a general cohesion of the genotype, or at least of parts of it.

There are numerous aspects of geographic variation that make sense only if one accepts the notion of a cohesiveness of the genotype. For instance, how else can one explain the pattern of geographic variation of the superspecies *Tanysiptera galatea* (Mayr, 1954)? *T. galatea* is distributed over all of New Guinea, where it is adapted in the northwest of the island to a purely tropical wet climate without any seasons and in the southeast to a trade-wind climate with a nine-month dry season. One would expect that two extremely different phenotypes of this species would have evolved at the two ends of New Guinea in response to two drastically different climatic selection pressures. Actually there is only minimal geographic variation on the mainland in contrast to a series of strikingly different species that have budded off *T. galatea* on nearby islands. What else could have been responsible for the unexpected stasis on the mainland, except some process akin to genetic homeostasis?

It has been claimed that this holistic view of the genotype was not within the spirit of modern Darwinism. This is erroneous. The atomistic viewpoint was defended only by mathematical geneticists from R. A. Fisher to B. Charlesworth and R. Lande. The more holistic viewpoint was promoted by numerous Darwinians from Chetverikov to Mather, Lerner, and Bruce Wallace, and was vigorously promoted by me from 1950 on. It was a strong tradition in evolutionary biology long before the introduction of the theory of punctuated equilibria.

Speciational Evolution

One of the differences between the punctuationists and the defenders of phyletic gradualism is that for the gradualists speciation is the continuing change of a phyletic series until it has become a different species (the total number of species remaining constant), while for the punctuationists speciation means a multiplication of species. If this multiplication is effected by the establishment of a founder population and its rapid genetic reconstruction, then such speciation can occur in a relatively short span of time. It is not sudden like saltational speciation, but it may be "instantaneous" as far as the fossil record is concerned. Even if it takes hundreds or thousands of years, the paleontological analysis would record it as a sudden event.

Many readers of the early punctuationist papers gained the impression that punctuationist speciation was an instantaneous event. Gould (1982a) pointed out, however, that for a geologist "instantaneous" means something very different from what it means to a student of living biota. Instantaneous is to be "defined as one per cent or less of later existence in stasis" (Gould, 1982a:84). Hence one hundred thousand years would be instantaneous for a species experiencing a 10-million-year stasis. The semantic problem is evident when we consider that all population evolution—that is, all evolution we are concerned with—is gradual. It is obvious from the recent controversy that the chronology of speciation events cannot be established by paleontological analysis. Rather, it will have to be inferred from an analysis of currently living speciating species, as I have repeatedly attempted to do (e.g., Mayr, 1963). In freshwater fishes it may take less than four thousand years (Mayr, 1984c).

That peripatric speciation is by far the most common mode of speciation is indicated not only by the pattern of distribution of incipient recent species but also by the frequency by which new species, apparently having originated somewhere else, suddenly appear in the fossil record. Such cases are reported in almost every revision of a fossil genus. For instance, in a Tertiary genus of bryozoans in at least seven cases the ancestral species persisted after having given rise to a descendant species (Cheetham, 1986).

The Genetics of Speciation

The crucial question one must ask is how peripatric speciation differs in its genetic impact from gradual phyletic speciation. Are the genetics of the two processes truly different? Does peripatric speciation speed up evolution? Is the evolutionary pulsing provided by peripatric speciation necessary for the origin of evolutionary innovations? Honesty demands that we admit a lack of concrete knowledge that would permit us to

answer these questions. All that we can do at present is to hypothesize; and in that respect we have not made much progress since 1954.

The genetic interpretation I gave in 1954 (see also Mayr, 1982b) was based on the genetic views of that period. I was much impressed by the findings of Mather, Lerner, and Wallace, largely supported also by Dobzhansky, on the genetic homeostasis of the genotype and the constraints on evolutionary departures imposed by this internal balance. I postulated, therefore, that certain events in the founder population might help loosen this cohesion and liberate the founder population from the straitjacket imposed on it by the epistatic balances of its genotype. I designated such an event a genetic revolution. Curiously, several authors reporting on my papers have claimed that I had postulated macromutations or "thousands of mutations," whereas I had invoked not even a single mutation. Rather, my interpretation was based on a developmental point of view that apparently was incompatible with then current thinking. Developmental considerations were at that time ignored by most evolutionary geneticists. To understand the mechanism I proposed, one must remember that natural selection is a two-step process. My theory dealt exclusively with the first step, the generation of variation. It suggested how additional variation might be made available in a founder population. The only possibility I could see on the basis of then available genetic theory was a change of epistatic balances. Thirty-five years later, such a change is still a conceivable process and is probably involved in some cases of peripatric speciation. Yet, many different kinds of DNA have been discovered which might control a drastically speeded-up genetic reorganization in small populations, also effecting "genetic revolutions." But, these new discoveries do not weaken the basic message of my theory, the role of small founder populations in loosening up genetic cohesion and thus facilitating evolutionary change. A somewhat different version has been suggested by H. L. Carson and A. R. Templeton (1984), likewise based on the concept that recombinational rather than mutational events are the decisive factor in this restructuring and likewise based on a change in epistatic balances.

Considering our ignorance of what happens to the genotype during peripatric speciation, it is only natural that models would be proposed by reductionist geneticists that can explain everything in terms of the simplest single-gene assumptions. These models cannot be refuted, but they leave far more natural phenomena unexplained than does the theory of a genetic restructuring of founder populations. Most important, though, is that none of the recent attacks on punctuationism, particularly in its typological quasi-Goldschmidtian version, has affected the recognition of the great potential importance of founder populations. It reveals a complete misunderstanding if any author says of my [1954 theory](#) that it was a "macromutation theory ... an alternative to the selectionist program" (Turner, 1984:351). Nothing was stressed as much in my 1954 theory as selection.

One more point must be emphasized: there is great pluralism in speciation events. Whenever sexual selection in an isolated population leads to the origin of new behavioral isolating mechanisms, new species may evolve that differ by only a few genes (Mayr, 1984c). Such species are usually almost indistinguishable morphologically. They did not experience a genetic revolution.

The punctuationists have rightly criticized the gradualists for using the notorious imperfection of the fossil record to support gradualism. It is ironic that the punctuationists use the same argument when claiming that the populations in which peripatric speciation takes place are too localized and ephemeral to leave a fossil record. The incompleteness of the fossil record is thus as much a part of the argument of the punctuationists as it is of the gradualists.

Species Selection

As I described above, one of Darwin's brilliant insights was that evolution is variational rather than transformational, as was believed by Lamarck and by many anti-Darwinians after 1859. In variational evolution it is the survival of certain favored individuals that leads to evolutionary change; the emphasis is on the individual and the population. But variational evolution also occurs at a higher hierarchical level, that of the species, a fact particularly stressed by punctuationism. Whenever important evolutionary innovations occur, they occur during speciation. Once a species has

become successful and stabilized, it will tend to change very little. The species therefore is considered the unit of evolution.

Recognition of the evolutionary importance of species long antedates punctuationism. I know of no better description of the role of species in evolution than the one I gave in my *Animal Species and Evolution* (Mayr, 1963):

It is the very process of creating [new] species which leads to evolutionary progress. . . . Since each coadapted gene complex has different properties and since these properties are, so to speak, not predictable, it requires the creation of a large number of such gene complexes before one is achieved that will lead to real evolutionary advance. Seen in this light, it appears then that a prodigious multiplication of species is a prerequisite for evolutionary progress.

Each species is a biological experiment. The probability is very high that the new niche into which it shifts is an evolutionary dead-end street. There is no way to predict, as far as the incipient species is concerned, whether the new niche it enters is a dead-end street or the entrance into a large new adaptive zone.

The evolutionary significance of species is now quite clear. Although the evolutionist may speak of broad phenomena, such as trends, adaptations, specializations, and regressions, they are really not separable from the progression of entities that display these trends, the species. The species are the real units of evolution as the temporary incarnation of harmonious, well-integrated gene complexes. And speciation, the production of new gene complexes capable of ecological shifts, is the method by which evolution advances. . . . The species, then, is the keystone of evolution. (P. 621.)

The continuous production of new species inevitably leads to competition among species and to a great deal of extinction. This process has been referred to as species selection (Stanley, 1975, 1979). The term is new, but the concept goes far back in the history of biology. Even in pre-Darwinian days, [Charles Lyell](#) postulated that the introduction of a new and better-adapted species might lead to the extinction of an inferior species, or that the extinction of a species would be followed by the introduction of a better-adapted species. Species extinction by competition was an important process also for Darwin. He illustrated it by the fate of the indigenous New Zealand fauna when it encountered species introduced from the British Isles (Darwin, 1859:201). Extinction of species caused by the appearance of better-adapted species has been frequently discussed in the post-Darwinian evolutionary literature.

The long-standing recognition of species selection refutes the claim that the recognition of the hierarchical level of species selection invalidated Darwinism. Gould (1982b:386) claims that a "hierarchical based theory [of evolution] would not be Darwinism as traditionally conceived." This view restricts the term "Darwinism" to the most reductionist concept of the mathematical population geneticists. I agree with the nonreductionist Darwinians who believe in a hierarchical order of the evolutionary process and who have never seen species selection as conflicting in any way with Darwinism.

The recent arguments indicate that the answer to two important questions about species selection remain controversial: (1) Is species selection in conflict with (and/or independent of) individual selection? (2) Are there different kinds of species selection, with different authors defining species selection differently, or even in a contradictory manner?

Several authors have rejected species selection by considering it a strict alternative to individual selection (e.g., Hoffman and Hecht, 1986). Indeed, if one asks the uncompromising question, Is the individual or the species the target of selection?, one is forced to reject species selection. One can express this even more unequivocally by asking whether there are properties of species that are not properties of the individuals of which the species is composed. Most authors have conceded that such situations indeed occur, even Maynard Smith (1983:280), who on the whole is hostile to the concept of species selection. By contrast, I must state I do not know of a single

species character that is not also part of the genotype of every individual. Furthermore, it had become a species character because it had been favored by individual selection.

In the classical situation, one species is superior to another because its individuals are better adapted and better able to utilize the resources of the environment. Even though competition between two species is seemingly involved, analysis establishes that the superiority is due to the greater success of the individuals of the "superior" species and that individual selection is involved. Whenever two species are competing with each other, the individuals of both species are, so to speak, merged into a single ecological population, and selection deals with the total of these individuals. The individuals of the superior species have a higher expectation of survival and successful reproduction than those of the inferior species, so that eventually only individuals of the superior species will survive. The traditional process of individual selection has thus led to the extinction of one species, that is, to species selection. In such a case there is no conflict between individual selection and species selection. This will be the case whenever the "characters in common" of the individuals of the one species provide competitive superiority over the individual of another species.

It has, however, also been argued that one species may be superior to another not because of any superiority of the composing individuals but because the species as a whole has characteristics that give superiority to its members. For instance, it has been argued that forms of reproduction or of dispersal and colonization that favor speciation, being species-specific, would give such species greater competitive superiority and thus constitute species selection. I am not persuaded by this argument. All the stated characteristics are also the characteristics of individuals and, when first appearing in evolution, entered populations in a polymorphic condition. It was the selective advantage of the individuals with the new characteristics (and of their offspring) that led to the spread and eventual universal incorporation of these new characteristics. In other words, these species characters were established by individual selection. I have failed to find in the literature a single good example of a species characteristic that is not also a selectable characteristic of individuals.

It has become evident in recent years that the term "species selection" has been applied to diverse phenomena. I have distinguished three kinds of species selection (Mayr, 1986), while Maynard Smith (1983) recognizes four kinds. It would seem irrelevant how many kinds one recognizes as long as one accepts the conclusion that species selection is not in opposition to individual selection but is an additional process at a higher hierarchical level.

The term "species selection" is somewhat unfortunate for several reasons. The first is the stated misconception that there is a conflict between individual selection and species selection, a conflict that I have shown does not exist. A second reason is that in the case of individual selection one can rightly say that a property or behavior is for the good of the individual. There is, however, no property that is, strictly speaking, for the good of the species. A favored property is always for the good of the individuals of which the species is composed. It is for this reason that I prefer the term "species turnover" for what others call species selection. We can conclude this discussion by stating that there is no conflict between individual selection and species turnover. Individual selection is usually involved in species turnover, but the loss of species from a biota may also be caused by cosmic and climatic catastrophes or other stochastic processes. Yet the effects of any restructuring of the biota relate to a different hierarchical level from individual selection.

Pluralism and Simultaneity

My 1954 proposal of genetic revolutions during peripatric speciation was pluralistic. I emphasized that no major evolutionary innovations occurred in the origins of most new species. By contrast, the first statements of the punctuationalists sounded quite categorical, and this led to polarization and resistance. Their more recent statements have been formulated in a more pluralistic manner: "gradual phyletic transformation can and does occur" (Gould, 1982a:84) and "the relative frequency of punctuated equilibrium differs across taxa and environments" (Gould 1986:439). This renunciation

of absolute, all-or-nothing statements has greatly contributed to reducing the opposition.

A second source of opposition to punctuationism is more difficult to overcome. It is the tendency of many authors to present two simultaneously occurring processes as a choice between one or the other. This is what Maynard Smith (1983) does when he asks whether the increased rate of evolutionary change in small populations is due to Mayr's genetic revolutions or to natural selection. This is curious considering how strongly I stressed the role of natural selection in the reorganization of the genotype of founder populations. Maynard Smith apparently failed to realize that genetic revolutions deal with the first step of the selection process while selection proper is the second step. He does not accept the possibility that a thawing out of the congealed part of the genotype, possible in founder populations, might make it easier for natural selection to achieve a stable new balance. Too often (Mayr, 1982a), evolutionary factors or processes are presented as alternatives when in reality they occur simultaneously.

Speciation and Macroevolution

The great importance of the speciation event is that it links macroevolution with microevolution. The facts that the individual is the target of selection and that the population and the species are the locale of evolutionary change automatically reduce all macroevolutionary processes to the microevolutionary level. The actors in this process, however, are not genes but genotypes and gene pools, entire cohesive systems of genes. The important insight is that whatever happens either in microevolution or in macroevolution, and whatever genetic phenomena are involved, proceeds through the selection of individuals: "All the processes and phenomena of macroevolution and of the origin of higher categories can be traced back to intraspecific variation, even though the first steps of such processes are usually very minute" (Mayr, 1942:298) Admittedly, genetics has so far been unable to analyze that part of the genotype that does not ordinarily vary in a local population but is so tightly integrated that it gives the genus, the family, the order, or the phylum its particular character (Carson, 1975). But even this part of the genotype, when it varies, varies in individuals and is subject to the recombination-selection cycle of ordinary allelic variation.

For the extreme reductionists among the geneticists who look at evolution, even macroevolution, as a process of changing frequencies of genes, there is a complete continuity among all phenomena of evolution. But those who think of evolution also as a change of species and higher taxa, including Darwin, have always considered evolution as hierarchical in structure. No other component of Darwin's thinking was as readily and widely adopted as his theory of common descent, a strictly hierarchical theory. And most of the paleontological literature, largely devoted to an elucidation of common descent, was hierarchical in approach. The term "hierarchical approach" introduces perhaps a new terminology but not a new concept. I agree with Grant (1983) that "adherents of the synthetic theory have in fact [consistently] employed a hierarchical approach to problems of macroevolution" (p. 153).

Remaining Problems

The controversies about punctuationism have clearly revealed that there remain major gaps in our knowledge. Several of these have been mentioned above, but I will single out two of them for more detailed discussion.

Population Size and Rate of Evolution

For the past sixty years, biologists have debated whether evolution advances more rapidly in large populations (species) or in small ones. Beginning with R. A. Fisher and Sewall Wright, geneticists favored the large population as the locale of the most rapid evolutionary change. Under the assumptions that the gene is the target of selection and that one can calculate the rate of evolution of a population or species by combining the rates of change of various independent genes, they concluded that the larger the population, the faster evolution will occur. As recently as 1977, Wright made this claim for widespread species consisting of many populations, a claim not based on observed facts but on theoretical considerations. This theory includes the

acceptance of group selection among local demes, a type selection questioned by nearly all those who have thoroughly studied the problem (Sober, 1984).

Wright's scenario also assumed that the amount of gene flow among the postulated semi-isolated populations is very low, an assumption which has fared poorly in recent research. To be sure, there are species with low gene flow, but these are species with spotty, isolated distributions. In all widespread populous species there seems to be far more unobserved gene flow than is usually believed (Slatkin, 1985). Here the gene flow is often restricted to certain years in which the species has been particularly successful and the population has reached high densities. There is little evidence in most species for the semi-isolated demes postulated by Wright.

The evolutionary stability of large, widespread species is supported by the observation that most of the species in the fossil record that display stasis are large, widespread species with the samples taken from central populations. The claim of rapid evolutionary advance in large, widespread, populous species was questioned, on a theoretical basis, as far back as 1957 by Haldane and more recently by some mathematical population geneticists (Newman, Cohen, and Kipnis, 1985; Lande, 1985).

By contrast, I (1942, 1954) and my followers were impressed by the striking difference between the parental population and many peripherally isolated founder populations and species. This evidence was enriched by the findings of Carson and associates on incipient species and neospecies of *Drosophila* in Hawaii. The relative rapidity with which new and often drastically different species of *Drosophila* originate through founder events suggests an enormously accelerated rate of evolution, as compared to the widespread and relatively uniform sibling species complexes of *Drosophila* with continental distributions (e.g., *D. affinis*, *D. obscura*). The theory that evolution in small founder populations is more rapid than in large continental populations is based on solid observational evidence in contrast to the theorizing of reductionist genetics. We have yet to find a situation in which the isolated peripheral allospecies essentially retain their ancestral condition, while the large central population has seemingly greatly diverged.

It is important to distinguish between the observational evidence and the genetic interpretation. I believe that the observational evidence for greatly increased rate of evolution in small populations is far better established than the reverse. Whether this increased rate is due to the breaking up of previously existing balances and the formation of new ones, as postulated by Mayr (1954), or simply to stochastic processes (or that both are involved), is still an open question. By merely invoking stochastic processes, however, Newman and his associates (1985) and Lande (1985) demonstrated that passage from one to another adaptive peak had a much better chance of success in a small population. By contrast, the chance of success can be vanishingly small in large populations. Hence, say Newman and his colleagues, their model "predicts stasis and punctuation for a small to moderate population but only stasis for a large population" (p. 401). This is consistent with the observations of the naturalists. The breaking up of epistatic balances in founder populations has now also been demonstrated experimentally (Goodnight, 1987; Bryant et al., 1986).

There is one argument, seemingly based on observational evidence, that would seem to refute the thesis that large, widespread species are uniform at a given time level, a uniformity continuing as stasis. It is the argument that geographic variation is prevalent in all widespread species, a notion that conflicts with the postulated temporal uniformity of such species. If this claim were substantiated, it would be a valid objection to punctuationism. The factual evidence is limited, however. On the basis of my own analysis of the bird fauna of North America (Mayr and Short, 1970) and of the New Guinea area (Mayr and Diamond, 1992) three counterarguments can be made against this thesis.

First, most widespread species are remarkably uniform. This is particularly true for planktrophic marine invertebrates.

Second, most species displaying geographic variation vary clinically only in ecotypic characters affecting primarily size, proportions, and coloration, but show no significant evolutionary departures. This is true for virtually all the illustrations of phyletic

gradualism discovered by P. D. Gingerich (1977) in early tertiary mammals. Nor is the thesis of the evolutionary uniformity of widespread species refuted by the discovery of the localized selection of a few genes controlling mimicry in the genus *Heliconius* (Turner, 1984). Such selection for local mimicry is the exact equivalent to substrate protective coloration in rodents and other animals selected for crypsis. Species with oligogenic geographic variation in crypsis may be exceedingly widespread, but the genes involved in this adaptation do not seem a suitable basis for speciation. Interestingly, such genes are rarely combined into domains. The fourteen or so variable characters of *Heliconius melpomene* that permit the mimicry of coexisting species are scattered over nine chromosomes, and in the case of *Heliconius erato* some seventeen or eighteen variable characters are dispersed on ten chromosomes (Turner, 1984). Such independence of the gene loci greatly facilitates a shift to new patterns, but it does not encourage the evolution of a new stable evolutionary type.

Finally, polytypic species with striking variation are invariably secondarily fused mosaics of former founder populations. Their variation cannot be used to argue against the evolutionary role of founder populations.

Structure of the Genotype

Another unresolved argument concerns the structure of the genotype. Mathematical geneticists base their calculations on the assumptions that all genes are more or less independent of each other and that recombination following crossing over can produce a virtually unlimited assortment of genotypes. Other evolutionists, including such geneticists as Mather, Dobzhansky, Lerner, Wallace, and Carson, believe that there are cohesive domains in the genotype maintained by epistatic balances and that many evolutionary phenomena are best explained by such an assumption. Reductionist geneticists believe that they can explain all phenomena of seeming cohesion (domains of the genotype) in terms of single genes. Their opponents are yet unconvinced. Considering the rapid progress of molecular genetics and the ongoing discovery of new molecular structures and interactions of the genotype, there is every reason to believe that this argument will soon be resolved.

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.

The replacement of transformational evolution (including Lamarck) in 1859 by Darwin's variational evolution necessitated a complete rethinking of the old question of gradual versus saltational. The adoption of any kind of saltational evolution before 1859 documented essentialism. Now we can have quasi-saltational evolution (on the geological time scale) by gradual population change. Consequently, all the arguments against saltational evolution made against the pre-1859 paradigm are irrelevant when applied to rapid variational evolution. I suspect that some of the non biologists contributing to this book have failed to see that after 1859 we have been in a different ballpark and must use different arguments.

[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.]

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