Evolutionary Theory Under Fire

An historic conference in Chicago challenges the four-decade long dominance of the Modern Synthesis

Overheard at breakfast on the final day of a recent scientific meeting: "Do you believe in macroevolution?" Came the reply: "Well, it depends how you define it."

In many ways this cryptic exchange expressed the prevailing sense of the participants at one of the most important conferences on evolutionary biology for more than 30 years. A wide spectrum of researchers—ranging from geologists and paleontologists, through ecologists and population geneticists, to embryologists and molecular biologists—gathered at Chicago's Field Museum of Natural History under the simple conference title: Macroevolution. Their task was to consider the mechanisms that underlie the origin of species and the evolutionary relationships between species.

It was an extraordinary occasion. "We all went home with our heads spinning," said one participant. "I would have left after the first day," admitted another, "but that would have doubled my excursion air fare, so I stayed. I'm very glad I did." Clashes of personality and academic sniping created palpable tension in an atmosphere that was fraught with genuine intellectual ferment. No book of proceedings will mark the event, but its passage will surely be reflected in the pages of future literature on evolutionary biology as new ideas and approaches generated at the meeting are tested and reported.

For the past 40 years the study of evolutionary biology has been dominated by the Modern Synthesis, a term coined by Julian Huxley in 1942. This theory explained Darwinism in terms of the rapidly maturing sciences of population biology and genetics. Essentially the theory says the following two things. First, that point mutation within structural genes is the source of variability in organisms and that evolutionary change is the result of a shift in the frequency of genes within a population. The origin of species and the development of trends in groups of species are explained as a consequence of the gradual accumulation of these small genetic differences. The pace of evolutionary change, according to the Modern Synthesis, is slow. Second, the direction of evolutionary change is determined by natural selection working on small variations: the variants that survive are those that are best fitted to their environments. The shape of organisms—their morphology—is therefore viewed in the utilitarian light of adaptationism.

The changes within a population have been termed microevolution, and they can indeed be accepted as a consequence of shifting gene frequences. Changes above the species level—involving the origin of new species and the establishment of higher taxonomic patterns—are known as macroevolution. The central question of the Chicago conference was whether the mechanisms underlying microevolution can be extrapolated to explain the phenomena of macroevolution. At the risk of doing violence to the positions of some of the people at the meeting, the answer can be given as a clear, No. What is not so clear, however, is whether microevolution is totally decoupled from macroevolution: the two can more probably be seen as a continuum with a notable overlap.

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The issues with which participants wrestled fell into three major areas: the tempo of evolution, the mode of evolutionary change, and the constraints on the physical form of new organisms.

Evolution, according to the Modern Synthesis, moves at a stately pace, with small changes accumulating over periods of many millions of years yielding a long heritage of steadily advancing lineages as revealed in the fossil record. However, the problem is that according to most paleontologists the principle feature of individual species within the fossil record is stasis, not change.

No one questions that, overall, the record reflects a steady increase in the diversity and complexity of species, with the origin of new species and the extinction of established ones punctuating the passage of time. But the crucial issue is that, for the most part, the fossils do not document a smooth transition from old morphologies to new ones. "For millions of years species remain unchanged in the fossil record," said Stephen Jay Gould, of Harvard, "and they then abruptly disappear, to be replaced by something that is substantially different but clearly related."

The absence of transitional forms between established species has traditionally been explained as a fault of an imperfect record, an argument first advanced by Charles Darwin. The accumulation of sediments and the entrapment and fossilization of animal bones is, at best, a capricious process: as a result, geologists are familiar with the difficulties of reconstructing past events. According to the traditional position, therefore, if sedimentation and fossilization did indeed encapsulate a complete record of prehistory, then it would reveal the postulated transitional organisms. But it isn't and it doesn't.

This ancient lament was intoned by some at the Chicago meeting: "I take a dim view of the fossil record as a source of data," observed Everett Olson, the paleontologist from UCLA. But such views were challenged as being defeatest. "I'm tired of hearing about the imperfections of the fossil record," said John Sepkoski of the University of Chicago; "I'm more interested in hearing about the imperfections of our questions about the record." "The record is not so woefully incomplete," offered Steven Stanley of Johns Hopkins University; "you can reconstruct long sections by combining data from several areas." Olson confessed himself to be "cheered by such optimism about the fossil record," and he listened receptively to Gould's

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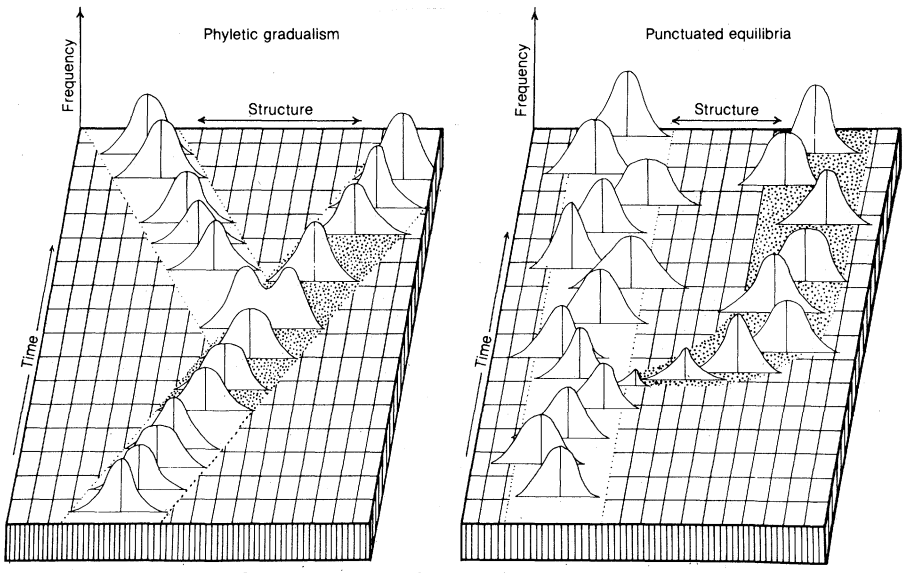


Alternative models of evolutionary change

The classical view is of gradual change (left); more abrupt speciation (right) may instead be the major process. The graphs are drawn as frequency distributions of morphological structure. [*Adapted from* South African Journal of Science **76**, *61 (1980)*]

suggestion that the gaps in the record are more real than apparent. "Certainly the record is poor," admitted Gould, "but the jerkiness you see is not the result of gaps, it is the consequence of the jerky mode of evolutionary change."

To the evident frustration of many people at the meeting, a large proportion of the contributions were characterized more by description and assertion than by the presentation of data. Nowhere was this a greater source of irritation than over the issue of stasis. Not until an unscheduled speaker—Anthony Hallam of Birmingham University, England—came forward with a blackboard sketch of the paleontological history of Jurassic bivalves did many people begin to be convinced of the importance of stasis. Hallam's intervention was much appreciated. However, there were still some reservations: "That's all very well for marine invertebrates," challenged a skeptical voice, "but what about land animals?" "I can show you many good examples of stasis in terrestrial mammals," offered Elizabeth Vrba of the Transvaal Museum, Pretoria.

Thus went the verbal jostling, with the mood swinging perceptibly in favor of recognizing stasis as being a real phenomenon. Gabriel Dover, a geneticist from Cambridge University, England, felt strongly enough to call species stasis "The single most important feature of macroevolution." In a generous admission Francisco Ayala, a major figure in propounding the Modern Synthesis in the United States, said: "We would not have predicted stasis from population genetics, but I am now convinced from what the paleontologists say that small changes do not accumulate."

The emerging picture of evolutionary change, therefore, is one of periods during which individual species remain virtually unchanged, punctuated by abrupt events at which a descendant species arises from the original stock. (This discrete branching of a new species from an established one is known as speciation.) This might be better termed a reemerging picture because the essence of the idea is not new, having at least some roots in the much maligned writings of Richard Goldschmidt in the 1930's. In its modern form, punctuated equilibrium, as it is known, has been crystallized by Gould and Niles Eldredge, of the American Museum of Natural History, New York.

The issue of punctuated equilibrium highlighted the particular problems of drawing together such a disparate array of scientific disciplines. The main point of entanglement was one of scale. Ecologists spend much of their lives being impressed by the subtle ways in which populations of organisms can adapt morphologically or physiologically to local conditions. And the population geneticists' view of the world through a *Drosophila* bottle teaches them how readily fruit flies (and presumably other organisms) can be modified by changes in selection pressure. So how can paleontologists suggest that species remain the same through most of their existence? And who in their right mind would contemplate speciation occurring in an instant? The resolution of this apparent conflict is this. Species do indeed have a capacity to undergo minor modifications in their physical and other characteristics, but this is limited and with a longer perspective it is reflected in an oscillation about a mean: to a paleontologist looking at the fossil record, this shows up as stasis.

The troubling specter of "instant" speciation is again a product of misunderstandings over scale. What is an instant to a paleontologist is an unimaginable tract of time to either an ecologist or a population geneticist. "I'd be happy to see speciation taking place over, say, 50,000 years," said Gould, "but that is an instant compared with the 5 or 10 million years that most species exist."

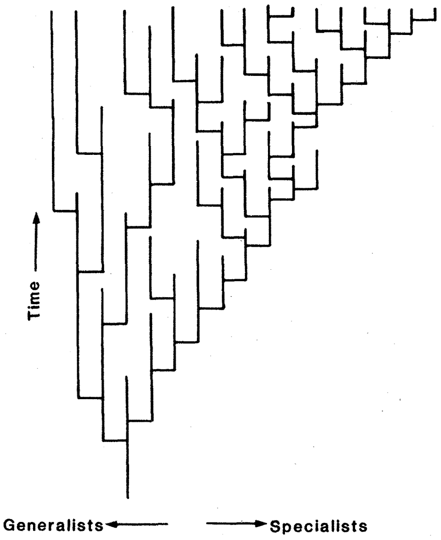
However, even the most ardent punctuationists do not dismiss gradual change as a force in evolution. "We are not saying that population genetics is irrelevant," said Eldredge, countering accusations of monotheism; "The question is over what process is most important in bringing about the major changes we see in evolution. And the answer is punctuated equilibrium." Gould also sees gradual change as an important influence in evolutionary history: "The point is one of the relative frequency of one process as against the other," he explained with deliberate emphasis, betraying some frustration at having been repeatedly misunderstood on this particular issue.

If it is true that most evolutionary change follows the model of punctuated equilibrium, then there is the immediate problem of how to explain morphological trends that are frequently seen in the fossil record. A classic example of such a trend is the evolution of the modern horse, whose distant ancestor *Hydracotherium* was a three-toed creature no bigger than a dog. The fossil record shows an apparently steady "progress" through time, with gradual changes in body size and form leading eventually to the familiar *Equus*. Classical gradualism would explain such a trend in terms of a progressive expression of the forces of natural selection within a single lineage: a continuous evolutionary ladder would connect the ancestor *Hydracotherium* with the modern animal, *Equus*.

By contrast, punctuated equilibrium would explain the morphological trends in horse evolution (and other such trends) as the result of a differentially pruned bush rather than a directed ladder. Think of the evolutionary history of the horse sketched out as a multiply speciating lineage, with some new species projecting in the direction of bigger bodies and fewer toes and others displaying smaller bodies and more toes. Now, if the species with the bigger bodies and fewer toes (the more "advanced" features) thrived more successfully than those with "primitive" features, then this would produce an asymmetric bush. The center of gravity of morphological change through time would lean steadily toward the bigger species equipped with the single toe. The same principle would apply to any characteristics in a group of related species in which natural selection favors one form against another. Known as species selection, the theory was first proposed by Eldredge and Gould and later elaborated by Steven Stanley.

Elizabeth Vrba sought to develop the notion further by letting the driving force of change relate to internal rather than external factors. Consider, she suggested, two groups of antelope: the Alcelaphini (blesbok, hartebeests, wildebeests) and the Aepycerotini (impala). The former can be described as specialists, both in the food they eat and in the habitats they can occupy. The latter, by contrast, are generalists: they can consume a wide range of food types and can survive under a broad range of environments. "If you look in the fossil record," Vrba told *Science*, "you will count just two or three species of Aepycerotini (the generalists) over a period of 6 million years, whereas there are at least 27 species of Alcelaphini (the specialists)." The reason, it seems, is simple. Specialists occupy narrow biological ruts. They can therefore tolerate many related species in similar but different narrow ruts. In other words, specialists can successfully speciate frequently. The obverse, however, is that even small shifts in prevailing environment can readily knock them out of their ruts. Simply, specialists are particularly vulnerable to extinction. By contrast, species that can exploit many different types of food resources and can cope with a spectrum of environments are to some degree resistant to ready extinction. The obverse of this, of course, is that a generalist species is especially intolerant of related species occupying its territory. In other words, generalists do not speciate frequently.

In sum, specialists both speciate and become extinct frequently whereas generalists speciate and become extinct infrequently. The upshot of this is that the evolutionary history of a group of related species (such as the antelopes) that display a spectrum of life-styles from specialist to generalist can be sketched as a skewed branching bush leaning heavily toward the rapid speciators. And whatever morphological features characterize the rapid speciators will appear to represent a morphological trend in the fossil record. Vrba calls this the Effect Hypothesis. So, whereas species selection puts the focus of change on environmental conditions, the Effect Hypothesis looks to internal parameters that affect the rates of speciation and extinction.



The Effect Hypothesis

A phylogenetic tree is skewed in the direction of species with higher rates of speciation and extinction. [Adapted from South African Journal of Science ***76**, 61 (1980)*]

Eldredge was delighted with the conceptual development encapsulated by the Effect Hypothesis; John Maynard Smith (Britain's foremost evolutionary biologist) considers that the hairs are too thin to split between this and species selection; and Ledyard Stebbins (one of the architects of the Modern Synthesis) feels there is little to be explained at all by species selection or the Effect Hypothesis, adhering as he does to the gradualist position. "You don't have to invoke anything except the natural selection of small differences," Stebbins told *Science* shortly after the Chicago meeting. "Pretty well everyone agreed on that," he said, giving what surely must be a polarized view of what actually transpired.

If theories on the tempo of evolution are contentious, then the question of mode is certainly no less so. Pedro Alberch, a developmental biologist from Harvard, explained the problem in the following terms: "Even if we knew every detail of genetic change through time, we would still have no idea about how the phenotype [the physical form] would alter." In other words, what genetic changes underlie the appearance of evolutionary novelties and the origin of new species?

The revolution in molecular biology during the past several years, which has revealed an extraordinary promiscuity of genetic elements within the genome, must eventually have a substantial impact on evolutionary theories. It is now clear that many possibilities of genetic change exist, ranging from simple point mutations, through jumping genes and transposable elements, to major chromosomal rearrangements. It is also clear, mainly from experimental work, that all permutations of genetically determined morphological shifts are possible: small genetic changes can give rise to either minor or major morphological modifications; and the same holds for large genetic changes. The issue, as Maynard Smith stated, is which of these possibilities is most important in speciation events in nature. The data are not yet available to provide an answer to this question.

Russell Lande, from the University of Chicago, tried to persuade his audience of the more traditional view, that substantial morphological changes were usually a consequence of many genetic mutations. Stuart Kaufman of the University of Pennsylvania, countered this by saying that, in *Drosophila* at least, one did not see intermediate changes between major mutants, implying single gene switches. Where might such switches be located? Kaufman suggests that hierarchically organized developmental control systems could be a prime "target" for minimal genetic changes that could effect major morphological modification. A fruit fly mutant having no thorax, for instance, looks as if it is the victim of a confined but dramatic misreading of developmental instructions.

The basis of speciation theory is that a new species should arise from parental stock, probably delimited as a small isolated population. The notion of small populations is important in the gradualist model too, where speciation is allowed for through the steady accumulation of genetic change within a limited number of organisms that are geographically separated from the stabilizing gene flow of the main population. Eventually the isolated group might attain sufficient genetic distance from the parental stock as to be reproductively isolated: hence the establishment of a new species.

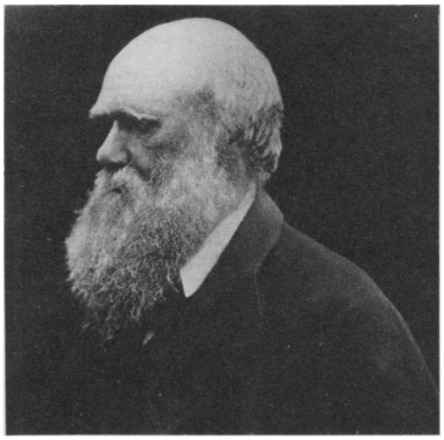
Recently, geneticists Guy Bush at the University of Texas, Allan Wilson at Berkeley, and others, have proposed what might be termed chromosomal speciation. A single chromosomal rearrangement in an individual, it is argued, might be sufficient to begin driving a wedge of evolutionary distance between itself and its parent stock. Such an aberration could survive only under certain conditions of social organization involving substantial inbreeding possibilities. For instance, if such a chromosomal modification were to arise in a male that became the controller of a harem, then the genetic novelty would become distributed among a large number of offspring, some of whom might eventually mate with each other. In this way the new genetic configuration would become "fixed" in a small population and begin to be transferred through further generations. Here one would have an instance of reproductive isolation in a limited number of individuals established through a combination of significant chromosomal reorganization and a particular social system. "Such favorable social organizations are relatively common," claims Bush, "in horses, many primates, and rodents, for instance."

Clearly, the chromosomal alteration must be substantial enough to constitute the tip of an evolutionary wedge, but not so extensive as to isolate the bearer instantly from all possible mates. In this model reproductive isolation of a small group is the primary event in speciation, and this might be accompanied by morphological change. The system does not depend on geographical isolation.

As with other issues in evolutionary biology, no one should be dogmatic about the mechanisms of speciation. Elizabeth Vrba put it this way: "Speciation has to do with isolation, and there are probably many ways by which this can come about."

The scientific argument over the third major area of discussion—that of constraints on evolutionary expression—was edged with tinges of sociological conflict too. At their most extreme, the two opposing technical positions are these. According to the Modern Synthesis, species look the way they do as a consequence of utilitarian adaptation to their environments. This theory also implies that organisms of all sizes, shapes, and forms are possible, and it explains the fact that life is actually restricted to a few very limited basic patterns by saying that there exists only a limited variety of ecological opportunities. Why does there not exist a species of cow with a head at either end of its body? Because, according to this line of argument, no adaptational niche is available for such a creature.

The opposing view is that adaptation, though important, is a secondary factor in shaping species morphology. There are, it argues, fundamental constraints in morphological possibilities imposed by mechanical properties of the building materials, basic forms embodied in the building blueprint that underlie many related species, and conservative rules that govern embryological development. In other words, organisms of all sizes, shapes, and forms are not possible.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Charles Darwin

The emphasis of gradual change of species began with the great man. A shift in emphasis is now due.

Why do most land vertebrates have four legs? The seemingly obvious answer is that this arrangement is the optimal design. This response would ignore, however, the fact that the fish that were ancestral to terrestrial animals also had four limbs, or fins. Four limbs may be very suitable for locomotion on dry land, but the real reason that terrestrial animals have this arrangement is because their evolutionary predecessors possessed the same pattern. If four limbs on dry land had proved to be highly unsuitable, then no doubt adaptation would have eventually modified the pattern. In general, however, evolution is a very conservative affair.

One reason for this conservatism is the apparently extreme resistance to change of the embryological process. Why otherwise would the embryos of land vertebrates pass through morphological stages reminiscent of their biological ancestors, developing evanescent gills and associated circulation? Evolutionary history is clearly a potent force in determining evolutionary future.

The detailed regulation of embryological development still remains elusive from scientific investigation, but at one level at least it does appear to involve series of binary "decisions," the outcome of each decision determining the possibilities available in future decisions. Whole sets of possibilities are therefore shut off as each bifurcation is passed. George Oster, from Berkeley, described his computer model of the morphological development of the skin which illustrates this principle very neatly.

Essentially, the model contains a small set of rules governing the mechanical properties of the cells that make up the skin. Given a simple initiation signal, the group of cells progresses through a series of developmental stages in a manner very reminiscent of what occurs in nature. Folds in certain layers of the cells lead on the one hand to the potential development of scales and feathers (evagination) and on the other to glands, teeth, and hairs (invagination). "This indicates," suggested Oster, "that there cannot be a smooth evolutionary transition between, say, feathers and hair because they are on two separate arms of a binary decision." Such elucidation of which morphological transitions are developmentally possible and which are not will undoubtedly illuminate the boundaries within which evolutionary change can take place.

The outcome of all this was the proposal of a hierarchy of processes and constraints linking possible genotypes with actual phenotypes: instructions encoded in the genetic library are filtered through a net of developmental constraints, giving rise to a set of possible phenotypes; it is at this stage that natural selection works, limiting the surviving phenotypes to those with suitable adaptive features. The omnipotent position of adaptationism embodied in the Modern Synthesis is overturned.

At this point in the discussion Maynard Smith felt moved to protest: "These structuralist ideas are presented as if they are antagonistic to the Modern Synthesis. In fact, you will find the major ideas here in a book I wrote 25 years ago and in the writing of many others in the tradition of the Modern Synthesis," he said, adding with obvious concern, "You are in danger of preventing understanding by suggesting that there is intellectual antagonism where none exists."

"You may have had the wheel, John, but you didn't ride away on it," Oster quipped with a telling metaphor. Gould added in more serious vein: "It is not so much what is said that counts, but what is done. These phenomena we talk about may have been acknowledged in the Modern Synthesis, but the principle guiding all the work of the past few decades has been adaptationism."

David Raup, of the Field Museum, described the meeting aptly when he said that it had been "easier to identify the issues than to draw conclusions." The atmosphere of questioning, probing, and seeking common ground was perceived by all present. Although the proceedings were at times unruly and even acrimonious, Maynard Smith's postmeeting comment to *Science* would certainly meet with broad agreement: "I thought the meeting was very positive. This was the first time for more than 25 years that there has been serious discussion between paleontologists, geneticists, and the like. This can't be anything but good."

Many people suggested that the meeting was a turning point in the history of evolutionary theory. "I know it sounds a little pompous," Hallam told *Science*, "but I think this conference will eventually be acknowledged as an historic event." Will it prove to be the current equivalent to the 1946 Princeton meeting at which the capstone of the Modern Synthesis was laid? Will a new synthesis emerge, signaling a true paradigm shift in the Kuhnian sense?

Perhaps. Gould expressed his expectations in more modest terms: "I hope that this meeting will lead to a rapprochement. I hope it will set the basis for a reconstruction of ideas."

—ROGER LEWIN

The 1980 Nobel Prize in Chemistry

Three molecular biologists win the prize for discoveries that can be used to study gene structure and control

The current Nobel Prize in Chemistry spotlights contributions to the methodological revolution that is allowing researchers to examine the structure and control of genes of higher organisms in a detail previously unimagined. Half of the prize was awarded to Paul Berg of Stanford University; the other half was awarded jointly to Frederick Sanger of Cambridge University and Walter Gilbert of Harvard. This is Sanger's second Nobel Prize.

Berg is cited for "his fundamental studies of the biochemistry of nucleic acids, with particular regard to recombinant DNA." According to a press release from the Swedish Royal Academy, "Berg was the first investigator to construct a recombinant DNA molecule, i.e., a molecule containing parts of DNA from different species. His pioneering experiment has resulted in the development of a new technology, often called genetic engineering." Berg does not know whether the Nobel committee had a particular experiment in mind but, he says, "I would like to think it [the prize] was for a body of work and not for a single experiment." Arthur Kornberg, also of Stanford, thinks the only way to interpret the Nobel committee's "carefully worded citation" is as recognition for Berg's 20 years of leadership in the molecular biology of nucleic acids.

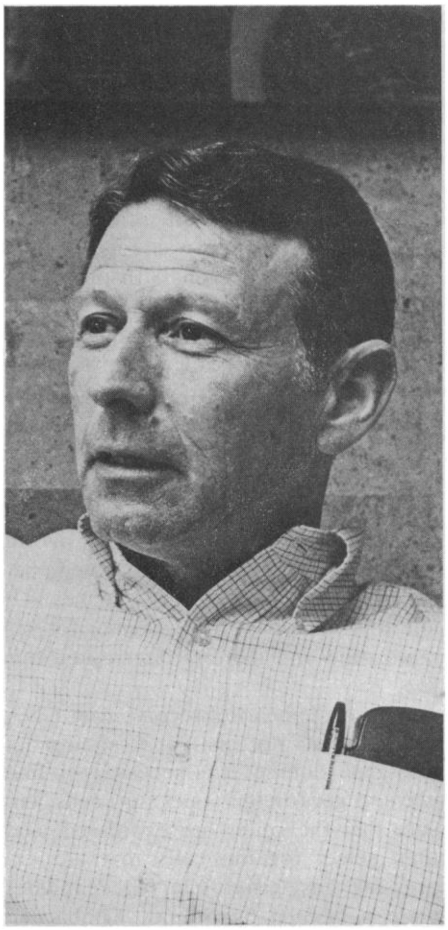
In the 1960's, Berg did a great deal of innovative work on bacterial protein synthesis, particularly the interaction of amino acids with transfer RNA's. His work helped explain how these RNA's are used as adapters in decoding. His group and several others also discovered one of the enzymes that copies DNA into RNA.

Then, about 10 years ago, Berg and many other molecular biologists became interested in applying what is known about bacterial gene expression to the study of gene expression in higher organisms. "We began to think of using SV40 [an animal tumor virus] to carry genes into mammalian cells," Berg says. The foreign genes could then be studied and manipulated to see what controls their expression.

In 1971, Berg and his colleagues David Jackson and Robert Symons opened the circular SV40 molecule with a restriction enzyme, Eco R1. This enzyme, which was discovered in Herbert Boyer's laboratory at the University of California at San Francisco, cleaves DNA at specific base sequences. In the case of SV40 DNA, it cleaves it in exactly one spot. Berg's group then spliced the linear SV40 DNA to the DNA of the bacterial virus λ. The λ DNA also is circular and Berg's group cleaved it too with Eco R1.

Although this was the first time that DNA's from two different species were joined, it was not the first time that any DNA's were joined. H. Gobind Khorana, of the Massachusetts Institute of Technology, discovered in the 1960's that an enzyme produced by the bacterial virus T4 can catalyze the linking together of DNA molecules. Berg, Jackson, and Symons enzymatically constructed complementary or "sticky" ends on the two DNA segments to be joined and then used the T4 enzyme to do the joining. The method they used was developed and tested independently by Berg's group and by Peter Lobban and Dale Kaiser of Stanford. Although no one knew it at the time, it was unnecessary to construct sticky ends, since they are automatically produced when Eco R1 cleaves DNA. This fact was discovered in 1972 by Janet Mertz and Ronald Davis and independently by Vittorio Sgaramella, all of Stanford University.

It had been Berg's intention to introduce the SV40-λ hybrid molecule into the bacterium *Escherichia coli*, which λ can infect. In that way, he could get many copies of the molecule to be used for future experiments in gene expression in



Paul Berg

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