Evolution, 36(3), 1982, pp. 474–498

A NEO-DARWINIAN COMMENTARY ON MACROEVOLUTION

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Received May 19, 1981. Revised October 28, 1981

The neo-Darwinian synthesis that resulted from the integration of Mendelian genetics into evolutionary theory has dominated evolutionary biology for the last 30 to 40 years, due largely to its agreement with a huge body of experimental and observational data. The classic works representative of this school of thought come from the fields of genetics (Fisher, 1930; Wright, 1931; Haldane, 1932; Dobzhansky, 1937; Muller, 1940), development (de Beer, 1940), zoology, (Huxley, 1942; Mayr, 1942; Rensch, 1959), botany (Stebbins, 1950), and paleontology (Simpson, 1944, 1953). These authors broadly agree with Darwin's view that most important evolutionary changes at the level of the visible phenotype, as revealed by paleontological and systematic studies, have resulted from natural selection acting on variation within populations. This variation is ultimately due to mutations that arise at random with respect to the direction of selection. A role for evolutionary forces other than selection and mutation, such as random genetic drift, is of course recognized by neo-Darwinists, but selection is regarded as the main guiding force of phenotypic evolution. Within this general framework, there has been plenty of room for vigorous disagreements about the relative importance of different processes, such as the Wright-Fisher debate on the significance of random genetic drift.

Recently, however, certain elements of neo-Darwinism have been sharply challenged by advocates of the "punctuated equilibria" theory of evolution (Eldredge and Gould, 1972; Gould, 1977, 1980; Stanley, 1975, 1979; Gould and Eldredge, 1977). Indeed, Gould (1980) states:

> "I have been watching it [neo-Darwinism] slowly unravel as a universal description of evolution . . . . I have been reluctant to admit it . . . but . . . that theory, as a general proposition, is effectively dead, despite its persistence as a text-book orthodoxy."

Such a claim calls for serious attention by students of evolution. In this paper, we will discuss the punctuated equilibria theory from the perspective of population genetics and provide evidence to refute the claim that the neo-Darwinian theory is no longer valid.

We start by distinguishing three main elements in the challenge to neo-Darwinism:

(1) Punctuationists assert that the predominant pattern in the fossil record of most groups is the stasis of established species, with most morphological change occuring quickly on a geological time scale during the process of species formation. The pattern of morphological stasis for most lineages and the sudden appearance of new forms is contrasted with the alternative mode of gradual evolution of species. For its most conservative advocates, the punctuational theory is simply a description of the pattern exhibited by the fossil record with no implications about the mechanisms producing the pattern.

(2) Some punctuationists argue that the pattern in the fossil record is not consistent with the predictions of the neo-Darwinian theory. This argument assumes that neo-Darwinian theory predicts only slow and gradual evolution when viewed on a geological time scale.

(3) Those who perceive an incompatibility between the fossil record and neo-Darwinian theory conclude that mechanisms other than microevolutionary processes have been important in producing macroevolutionary patterns. They argue that stasis is due to developmental constraints and to the inability of natural selection to cause significant morphological changes in widespread and abundant species. The association of phenotypic changes with speciation is attributed to events occurring in small populations. It is claimed that the genetic changes occurring during speciation are qualitatively different from those in phyletic evolution. Finally, they argue that the major phenotypic trends within higher taxa are due both to selection among species through differential speciation and extinction rates, and to developmental constraints on the set of possible phenotypes.

We shall defend the neo-Darwinian theory, not primarily by criticizing the punctuational view of the fossil record, but by addressing the question of what genetic theories are needed to explain those patterns where they do exist. There are two parts to our defense. We shall show that the punctuational pattern is entirely consistent with the neo-Darwinian theory that most morphological changes are due to natural selection. And we shall demonstrate that the genetic mechanisms advocated by some punctuationists are either already a part of the neo-Darwinian theory and are simply being described by new terms, or are seriously lacking in empirical and theoretical support. Our conclusion is that there is no reason to discard the neo-Darwinian theory or to regard it as being effectively dead, especially when the proposed alternative is not soundly based.

We shall discuss four patterns in the fossil record that form the main components of the punctuational theory: stasis, the association of morphological change with speciation, evolutionary novelties, and phylogenetic trends. For each pattern we contrast the explanatory power of the neo-Darwinian theory of genetic change with that of the punctuational alternative. Little of what we shall say is new; most of these issues have already been thoroughly discussed in the classic works that constitute the modern evolutionary synthesis. It does not appear to us that any new facts or arguments have been brought forward that require drastic revision of the classical theory. However, it seems appropriate at this time to analyze carefully the ideas that are being presented as a serious challenge to the neo-Darwinian theory, particularly as those ideas have received widespread and uncritical attention.

Stasis

The importance of highly variable rates of evolution, including prolonged stasis and bursts of rapid change, both at the level of species and higher taxa, was clearly recognized by many authors contributing to the modern synthetic theory of evolution. Darwin himself was quite aware of the appearance of sudden change associated with the origin of new species in the fossil record. He stated (1859 p. 464–465) that

> "Local varieties will not spread into other and distant regions until they are considerably modified and improved; and when they do spread, if discovered in a geological formation, they will appear as if suddenly created there, and will simply be classed as new species."

In a later edition (1872 p. 375), he added that

> "Many species when once formed never undergo any further change but become extinct without leaving modified descendants; and the periods, during which species have undergone modification, though long as measured by years, have probably been short in comparison with the periods during which they retain the same form."

Darwin (1859 Ch. 9) stressed the tremendous incompleteness of the fossil record of most taxa, a point that is still worth remembering today, since species usually appear at only one time and place in the fossil record and there are worldwide gaps in the duration of many higher taxa (Simpson, 1953 p. 359–376; Schopf, 1981). Evidently, Darwin did not consider stasis and bursts of evolution to be incompatible with his theory. Neither did H. J. Muller (1949), one of the leading geneticists two generations later, in summarizing the conference on Genetics, Paleontology, and Evolution,

> "it is quite evident that the time-rate of change within individual lines and also the rate of diversification of lines has for some large groups been exceedingly different during some portions of geological history than during others; there have been unquestionable spurts and bursts, and contrasted long periods of relative stasis."

In Darwin's theory, and in its modern successor, stasis is regarded as resulting primarily from stabilizing selection toward an intermediate optimum phenotype. Bursts of change are associated with relatively strong directional selection, usually during adaptive radiation into a set of new ecological niches (Darwin, 1859 p. 303; Simpson, 1944, 1953; Stebbins, 1949; Wright, 1949 p. 387–388, 1978 Chs. 11–13, p. 520). In this section we examine alternative mechanisms which have been proposed to explain observations of prolonged stasis: gene flow, developmental constraints, and stabilizing selection.

Gene flow.—One possible explanation of the stasis of widespread species is gene flow between populations. Following Mayr (1963), Stanley (1979) emphasizes gene flow as a stabilizing mechanism, although Eldredge and Gould (1972) do not. The latter authors accept the evidence presented by Ehrlich and Raven (1969) that, in many species, there is not much migration between local populations and that strong selection due to local conditions can overcome the effects of gene flow. Stanley (1979 p. 48–51) feels that spatial variation in selection combined with local gene flow will largely nullify directional selection in a large population. He ignores the possibility that selective forces may be spatially and temporally sustained in direction, which could produce substantial changes in a widespread species, and parallel evolution in related taxa (Simpson, 1953 Ch. 8).

Mechanisms causing geographic variation have been studied by theoretical population geneticists starting with Haldane (1930) and Wright (1931). These and later studies show that the extent of genetic differentiation between two or more local populations is determined by the balance between the strength of gene flow and natural selection or random genetic drift. For completely neutral genes, Wright (1931) demonstrated that significant differentiation among populations is prevented if on average one migrant individual enters a local population every other generation. This deduction has sometimes been misinterpreted as meaning that such a low level of gene flow will prevent differentiation at all loci. But Haldane (1930) and others (e.g., Slatkin, 1973, 1978; Endler, 1977) have shown that moderate selection in favor of locally adapted genotypes can overcome the effect of gene flow and can maintain substantial geographic variation. This theoretical result has been confirmed numerous times, for example, by the laboratory experiments of Dobzhansky and Spassky (1967) on *Drosophila melanogaster,* and by the field studies of Bradshaw (1960) on the grass *Agrostis tenuis.* Endler (1977 Ch. 1) reviews other examples of empirical studies leading to the same conclusion.

Developmental constraints.—A second possible explanation for prolonged stasis is that developmental constraints restrict evolutionary changes to only a few directions. Gould (1980) and Alberch (1980) argue that stasis frequently results from the inability of natural selection to overcome developmental constraints and change the phenotypic composition of a population. They ignore, however, the long-established fact that in numerous plant and animal species artificial selection on a tremendous variety of quantitative and meristic characters has generally resulted in a rapid change of the mean phenotype by several phenotypic standard deviations, producing extreme forms not previously present in the population (Falconer, 1960; Lewontin, 1974 p. 86–94; Wright, 1977 Chs. 7, 8). Parameters of allometric growth curves, which are important in determining adult shape (Huxley, 1932; Cock, 1966; Gould, 1966), have been found to be genetically variable and subject to continuous change by selection (Kidwell et al., 1952, 1979; Cock, 1966, 1969; Atchley and Rutledge, 1980). Rapid evolution in natural populations has also been documented for characters including industrial melanism and pesticide resistance in insects, drug resistance in microorganisms causing human diseases, and heavy metal tolerance in plants (Ford, 1975).

Qualitative (threshold) characters also vary in more dimensions within populations than between closely related populations. For example, within various species of turtles Williams (1950) found numerous types of imperfectly formed or poorly articulating neck vertebrae, appearing in low frequencies, which were never established as species specific characteristics. The relative rarity of maladaptive variants within populations probably results from the past action of natural selection in shaping developmental processes leading to patterns of adult variation (Williams, 1950; Grüneberg, 1963). Fisher (1930 Ch. 5) discussed evidence suggesting that variation in meristic and threshold characters is often under polygenic control, as later confirmed by detailed breeding experiments analyzing digit number in guinea pigs and vertebrae number in mice (Wright, 1934*a*, 1934*b*; Green, 1962). The rate of evolution of a threshold character may be very uneven in time, creating a gap in the fossil record, since substantial polymorphism occurs only when the population is evolving past a threshold, and selection cannot act as efficiently on rare variants as on those at substantial (intermediate) frequencies (de Beer, 1958 p. 30–31, 57–58, 123–124; Lande, 1978).

Despite the large number of dimensions in which genetic variation occurs within natural populations of higher organisms, it has long been appreciated that the relative amounts of variation in different characters, as well as correlations between them, place constraints on phenotypic evolution in a population. Thus it is generally observed in artificial selection experiments that strong selection on one character produces correlated responses in other characters. From his familiarity with data on animal and plant breeding, Darwin (1859 p. 11–14, 143–150; 1876 p. 346–347) was well aware of the importance of evolutionary constraints imposed by character correlations due to complex interactions in growth and development.

> "Through the principle of correlated variability, taken in its widest sense, when one part varies other parts vary, either simultaneously, or one after the other. Thus, an organ modified during an early embryonic period affects other parts subsequently developed. When an organ . . . increases or decreases in length, adjoining or correlated parts . . . tend to vary in the same manner. When the whole body increases or decreases in size, various parts become modified . . . . Homologous parts which are identical during their early development and are exposed to similar conditions, tend to vary in the same or in some connected manner . . . ."
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> "Correlation is an important subject; for with species, and in a lesser degree with domestic races, we continually find that certain parts have been greatly modified to serve some useful purpose; but we almost invariably find that other parts have likewise been more or less modified, without our being able to discover any advantage in the change. No doubt great caution is necessary with respect to this latter point, for it is difficult to overrate our ignorance on the use of various parts of the organisation;

> but from what we have seen, we may believe that many modifications are of no direct service, having arisen in correlation with other and useful changes" (1876 p. 346–347).

Of particular importance for evolutionary changes are the genetic correlations between characters due to pleiotropy and linkage disequilibrium which determine the magnitude of correlated responses to selection (Falconer, 1960 Ch. 19). It is a basic postulate of Wright's (1932, 1977 Ch. 13) shifting balance theory of evolution that most genes with phenotypic effects are pleiotropic. In the modern synthetic theory of evolution, the rate and direction of phenotypic change depend crucially on the pattern of genetic variation available for natural selection or random genetic drift to act upon. But to a considerable extent the patterns of genetic and phenotypic variation are themselves shaped by selection.

Stabilizing selection.—It is helpful to distinguish between the immediate effects of selection on the phenotype distribution in a population within a single generation, such as the weeding out of extreme phenotypes by stabilizing selection, and the long-term response to selection over many generations, which may be reflected not only in directional evolution of the mean phenotype, but also in changing patterns of variation (Schmalhausen, 1949; Waddington, 1957). Several experiments have shown that artificial stabilizing or disruptive selection can significantly increase or decrease developmental stability for a variety of characters in *Drosophila,* such as pattern asymmetry, development time, number of abdominal bristles, mutant gene expression, and the expression of threshold characters (Mather, 1953; Thoday, 1958; Rendel, 1959; Waddington, 1960; Prout, 1962; Scharloo, 1964). Fisher (1930 Ch. 5) noted that the developmental mechanisms creating discrete phenotypic classes are themselves molded by selection. He reasoned that in populations polymorphic for meristic characters, the modal (or optimal) phenotypic classes would experience the strongest selection for standardized development, and he cited data on a fish population showing that individuals with the rarer vertebrae numbers have a pronounced tendency for abnormal development. Wright (1968 Ch. 11) presented other examples of meristic characters where the modal number in the population is the most canalized in its development. There is further evidence from natural populations that relaxed selection leads to a breakdown of canalization. Darwin (1859 Ch. 5) and others have observed that vestigial organs tend to be highly variable. Thus, in lizard species with greatly reduced limbs, there is much variation in the skeletal structure of the appendages and limb girdles, with a high frequency of asymmetrical development (Essex, 1927). A similar phenomenon occurs in species of butterflies which are normally polymorphic for highly perfected and uniform mimetic patterns, but in populations which coexist with a low density of models the mimetic morphs show substantial frequencies of imperfect and variable development due to a decay of linkage disequilibrium by recombination between tightly linked genes controlling the polymorphism (Ford, 1975 p. 289–291).

Mimicry studies also shed light on the punctuational theory that developmental constraints restrict the possible evolutionary pathways to a small number of types. Goldschmidt (1945) suggested that the mimetic resemblances between different species are due to such limitations, together with a tendency of related species to evolve similar developmental pathways. This suggestion has been refuted by Ford (1953, 1975 Ch. 13), who pointed out that chemically quite different pigments are frequently used in models and mimics, and that mimicry can occur between members of widely separated taxa such as different orders. The perfection of mimetic resemblances, and the opportunistic fashion in which natural selection has exploited the available genetic variability in order to build them up (Turner, 1977), in itself casts considerable doubt on the idea that developmental constraints restrict the power of selection to accumulate small changes in the phenotype.

Similarly, many cases of convergent evolution, where nearly identical characters have evolved in widely different taxa, also argue against any restriction of developmental pathways to a few possible types. Numerous examples of convergent evolution are discussed by Simpson (1953 Ch. 6) and Rensch (1959 p. 68–72, 191–203).

Direct evidence supporting the neo-Darwinian theory that stabilizing natural selection accounts for morphological stasis has been obtained in studies of quantitative and meristic characters including various measures of body size and shape such as shell shape in snails, bill and body dimensions in birds, and birth weight in humans (reviewed by Haldane, 1954; Johnson, 1976 Ch. 7). It is commonly observed for such characters in longitudinal or cross-sectional studies that cohorts of increasing age show decreasing phenotypic variance, sometimes with little change in the mean phenotype, indicating the immediate action of selection toward an intermediate phenotype, either directly or through correlated characters. Biometrical methods can be used in current or past populations to test whether selection is acting to maintain stasis or to produce change, and quantitative genetics can be applied to determine whether heritable variation exists for selection to act upon. Application of these methods to study the mechanisms producing temporal and geographic variation or stasis in fossil species and their modern relatives would be particularly interesting (e.g., Sambol and Finks, 1977).

While recognizing the role of genetic correlations between characters in determining the rate and direction of response of a population to selection, breeders also know that the genetic and phenotypic correlations between characters can be altered by artificial selection (Dickerson, 1955; Falconer, 1960 Chs. 19, 20). This has been confirmed by comparative studies of morphological integration which show that qualitative differences in phenotypic correlation patterns in related populations can be predicted from knowledge of functional specializations (i.e., selective constraints). For example, Kurtén (1953) found that in mammalian species, teeth which are developmentally and/or functionally related tend to be highly correlated in their dimensions, while vestigial teeth show increased variability and decreased correlation with other teeth. These conclusions have been confirmed for other characters of the mammalian skeleton (Olson and Miller, 1958; Bader and Hall, 1960). In plants, Berg (1960) observed that the dimensions of flower parts are more highly correlated in species with specialized insect pollinators than in wind pollinated or selfing species.

A great amount of evidence on patterns of genetic variation and the effectiveness of selection in promoting either prolonged stasis or rapid change was aptly summarized by Muller (1949 p. 426–428),

> "That given phenotypes are maintained over long periods as a result of natural selection . . . is evident from their long continued existence . . . . Were the phenotypes not held in place, so to speak, by a selective process, most of them would be bound to decay into other phenotypes by mere mutation pressure, since enough is known about mutation rates to make it certain that this pressure usually is more than sufficient to change the phenotype over the course of a geological period unless it is counteracted by selection pressure . . . ."
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> "Despite the exactitude with which a given advantageous phenotype can be attained, as shown by such evidence, the organism cannot be considered as infinitely plastic and certainly not as being equally plastic in all directions, since the directions which the effects of mutations can take are, of course, conditioned by the entire developmental and physiological system resulting from the action of all the other genes already present . . . . Nevertheless, . . . there is necessarily a big leeway for selection,

> i.e. a pressure of mutation in many different directions. Thus when it comes to changes in size, proportions and patterns in general . . . the organism may be regarded as exceedingly plastic and correspondingly responsive to selection, and primarily determined by the latter."

Thus the concept of organism, including constraints of history, development and architecture, which Gould (1980) seeks to restore to evolutionary biology, has always been an integral part of the neo-Darwinian theory. The metaphor of the organism as a sphere, equally variable and responsive to selection in all directions, which Gould (1980) uses to describe the modern synthetic theory of evolution, is a severe distortion of that theory.

The assertion, advanced by many punctuationists (e.g., Gould and Eldredge, 1977; Stanley, 1979 Ch. 2), that population genetics does not predict the long-term stasis observed for many species in the fossil record indicates a lack of understanding of the basic nature and purpose of population genetics (cf. Stebbins and Ayala, 1981). (An equally compelling argument could be made that paleontologists could not have "predicted" stasis without first consulting the fossil record.) The main task of population genetics is the description and prediction of changes in the genetic and phenotypic composition of populations responding to the forces of mutation, recombination, selection, migration and systems of mating. With sufficiently detailed knowledge of changes in the genetic and phenotypic structure of populations through time, it is possible to make inferences about the selective forces (if any) which acted to produce those changes. Most frequently, such inferences are restricted to a quantification of the magnitude and direction of the selective forces, because it is not generally possible to identify the factors in a natural environment causing selection. However, some studies of the ecological genetics of populations have identified environmental factors, such as predators, parasites, and chemical or physical stress, that produce a readily observable selective mortality (e.g., Hagen and Gilbertson, 1973; Ford, 1975). Sexual selection can often be observed as differential mating success (e.g., Mason, 1964; Cavalli-Sforza and Bodmer, 1971 p. 614–615). We emphasize that without a detailed knowledge of both the selective forces and the genetic structure of populations, it is not possible to predict the course of evolution. Thus, even if we could infer patterns of genetic variability in past populations (as may sometimes be feasible [Van Valen, 1969; Lande, 1979*a*]), without information on the ecological factors of past environments, and the selective forces they produced, it is impossible for population genetics to predict any pattern at all in the fossil record. But once a pattern of morphological change or stasis is observed, population genetics can be useful in testing alternative hypotheses which might account for it. On the basis of the preceding evidence and lines of reasoning, we conclude that if prolonged morphological stasis exists in fossil populations, it must usually be caused by stabilizing selection, rather than gene flow or developmental constraints. To the extent that morphological stasis can be documented, it is an important problem for paleoecology to explain why selective forces should often be so conservative over long periods of time.

Association of Morphological Change with Speciation

A central part of the theory of punctuated equilibria espoused by Eldredge and Gould (1972), Gould and Eldredge (1977), and Stanley (1979 Ch. 2) is based on the ideas of Mayr (1954, 1963 Ch. 17) who believed that speciation events occur most often in small isolated populations. Random changes in genotypic composition caused by passage through a bottleneck in population size are supposed to induce a "genetic revolution," in which there is a shift in the state of a population from one set of "coadapted" genotypes to another. This idea is, in essence, a special case of Wright's theory of random genetic drift as a mechanism for triggering shifts from one stable equilibrium (adaptive peak) to another, when there are epistatic interactions in fitness effects between loci; such shifts could not occur under natural selection alone (Wright, 1932, 1977 Ch. 3, 1978 Ch. 11). Punctuationists stress the role of chromosome rearrangements in this process. This is partly because certain types of rearrangements cause reductions in fertility when heterozygous, and hence act as partial isolating mechanisms once fixed in a population (Sturtevant, 1938; Wright, 1940). Another reason for stressing rearrangements is the possibility that they may produce changes in the regulation of gene expression; it has been suggested that such regulatory changes may have more significance than structural gene mutations in speciation and morphological evolution (Wilson et al., 1975; Bush et al., 1977). There are thus several interconnected issues which we consider in turn.

Morphological change and speciation.—The lack of resolution in the fossil record, as explained above, makes it unlikely that an association of morphological change with speciation could be proven by paleontological studies. It is also difficult to investigate this problem by means of comparisons of existing species. The occurrence of sibling species in many taxa (Mayr, 1963 Ch. 3) demonstrates that speciation is not necessarily accompanied by morphological change. More relevant to the interpretation of the punctuational pattern in the fossil record are many examples of morphological evolution, manifested as geographic variation, where reproductive isolation has not evolved (Mayr, 1963 Chs. 11–13). The introduction of the concept of polytypic species has provided numerous examples in which taxa previously classified as separate species are now considered conspecific, on the criterion of being potentially interbreeding (Mayr, 1963 Ch. 12). The land snail *Cerion* is an example of a species in which extreme morphological divergence has evolved without reproductive isolation (Mayr and Rosen, 1956; Mayr, 1963 p. 398; Woodruff and Gould, 1980).

There seems to be no way in which systematists can arrive at a certain classification of closely related, allopatric taxa as separate biological species on the basis of purely morphological criteria. Levinton and Simon (1980) remark that the interpretation of punctuated equilibria in the fossil record is practically tautological, since any new forms appearing will automatically be classified as new species or higher taxa. In order to avoid this tautology it seems necessary to study morphological rather than taxonomic rates of evolution (Simpson, 1953 Chs. 1, 2; Maynard Smith, 1981). Lack of a clear definition of stasis has allowed different workers to reach opposite conclusions concerning the pattern of morphological changes in the same set of data (e.g., compare Kellogg, 1975, and Gingerich, 1976, with Gould and Eldredge, 1977). Although the process of speciation cannot be resolved in the fossil record of most organisms, it should still be possible to quantify stasis or change in special cases, as attempted by Bookstein et al. (1978) and Raup and Crick (1981) for morphological measurements on detailed sequences of fossils.

An interesting attempt to test directly for an association between speciation and morphological evolution has been made by Douglas (1980) and Douglas and Avise (1982). They performed multivariate analyses on morphometric data on species of North American sunfishes and minnows. These two groups are roughly the same geological age, as far as can be determined from the fossil record, and the latter has apparently undergone more rapid speciation than the former. It has already been shown (Avise and Ayala, 1976) that the mean genetic distance between species pairs, as determined from studies of electrophoretic alleles, is similar in the sunfishes and minnows, suggesting that on average the amount of evolutionary time separating a pair of species is similar in the two groups. Douglas' analysis indicates that the same is true for distances calculated from the morphometric data. This suggests that morphological divergence between species is due to phyletic evolution and is not causally related to speciation. More studies of this kind are desirable.

Thus there is little evidence directly supporting the idea that morphological changes are usually coincident with speciation. On the classical view that morphological evolution is largely guided by natural selection, and that reproductive isolation is a by-product of genetic differences accumulated between (allopatric) populations, no such coincidence is necessary. Of course, ecological opportunities offered by the opening of new niches, either by changes in the environment or by the evolution of a key adaptation will, on this classical view, generate an association between rapid morphological evolution and the proliferation of species, as seen in adaptive radiations (Wright, 1949; Simpson, 1953 Ch. 7).

Population bottlenecks and genetic revolutions.—If genetic revolutions were important in speciation, and if changes in the genetic systems controlling morphology were similarly accelerated by stochastic changes in gene frequencies, then a strong association between morphological evolution and speciation could be generated (Gould and Eldredge, 1977; Stanley, 1979 Ch. 2). Before discussing the extent to which this concept of speciation is supported by the data, we may note that there is no question that epistasis in fitness, which is an essential condition for the existence of multiple adaptive peaks, has been observed in many instances. A series of classic experiments by Dobzhansky and his school have documented this in *Drosophila,* for example (Dobzhansky, 1946, 1955; Spiess, 1959). Another important condition for the operation of Wright's shifting balance process, a strongly subdivided population structure, is met in many species (Wright, 1978 Ch. 2). But without detailed knowledge of the population structure, and the linkage relations and fitness interactions of the genes involved, it is impossible to assess theoretically the probability of a genetic revolution in a given case. We must therefore have recourse to laboratory experiments and comparisons of existing species to test these concepts.

Laboratory experiments on genetic revolutions.—Dobzhansky and Pavlovsky (1957) and Dobzhansky and Spassky (1962) showed that replicate laboratory populations of *D. pseudoobscura* which were passed through bottlenecks of small population size attained more widely divergent, apparently stable, equilibrium frequencies with respect to a chromosome inversion polymorphism than did populations maintained without such bottlenecks. At first sight, this supports the model of a genetic revolution. But the stocks used were derived from interpopulation crosses, and there is good evidence that the natural populations used to construct the stocks differed with respect to background genes that interacted in fitness with genes contained in the inversions (Dobzhansky and Pavlovsky, 1957). It is therefore difficult to judge the relevance of these experiments to the consequences of founder events in populations derived from a single ancestral locality, which seems to be the most likely situation in natural populations. A similar criticism applies to the experiments of Powell (1978), who obtained evidence for partial sexual isolation between lines of *D. pseudoobscura* that had been passed through bottlenecks. Ahearn (1980) reported asymmetrical sexual isolation between a strain of *D. silvestris* that had undergone a bottleneck, and a stock recently derived from the wild. Inspection of her data suggests that the males from the bottleneck stock had a lower mating success than males from the outbred stock. This may simply reflect the effects of inbreeding depression caused by homozygosity of partially recessive, deleterious genes (cf. Maynard Smith, 1956).

Templeton et al. (1976) and Templeton (1979) have shown that different parthenogenetic strains of *D. mercatorum* contain different sets of epistatically interacting genes affecting fitness. Templeton

(1979, 1980) suggests that this provides a model of genetic revolution. But the relevance of observations on totally homozygous lines to speciation in relatively outbred, sexual populations is obscure. These data simply provide more evidence for epistasis at some loci affecting fitness.

In the phenomenon of hybrid dysgenesis in *D. melanogaster,* crosses involving certain laboratory strains as maternal parents display a syndrome of abnormal traits in F_1 hybrids, including male and female sterility (Kidwell et al., 1977; Bregliano et al., 1980; Engels, 1980). Engels has shown that one form of hybrid dysgenesis occurs when a set of transposable genes is absent in the mother of F_1 individuals, but present in the father, and has suggested that these genes may be subject to stochastic loss in small, laboratory populations. The relevance of this phenomenon to speciation in nature is not clear, since it is uncertain whether hybrid dysgenesis ever occurs in natural populations.

Strong evidence against the concept that genetic revolutions are often induced by population bottlenecks comes from the usual lack of any indication of incipient speciation in domestic and laboratory plants and animals, despite the intense artificial selection and inbreeding to which many have been subjected. A few exceptions are known, however (e.g., Dobzhansky and Pavlovsky, 1967). Wright (1980) remarks that laboratory populations are commonly started from a single wild-caught individual without causing appreciable morphological changes or reproductive isolation.

Species comparisons bearing on genetic revolutions.—One line of evidence that seems to have inspired Mayr's ideas on genetic revolutions is provided by an association between peripheral isolation and divergence from the species type (Mayr, 1954, 1963 p. 541). If valid, such an association would not in itself indicate a causal role of population bottlenecks in speciation. However, it has recently been questioned as a general rule (Endler, 1977 Ch. 1), as has the theoretical basis for Mayr's belief in the need for almost complete geographic isolation for the evolution of species barriers (Endler, 1977; White, 1978). It seems clear that Fisher's (1930, 1958 Ch. 6) model of semigeographic speciation, based on selection for habitat preferences or for sexual isolation between neighboring populations in a cline, provides an adequate basis for species formation in some cases. The classical examples of Rassenkreise and of hybrid zones do not demand interpretations in terms of past episodes of complete geographic isolation, as has been proposed (Mayr, 1963 p. 542), and certainly do not constitute evidence for bottleneck effects.

One of the most frequently cited examples of an association between geographic isolation, founder events and rapid speciation is the Hawaiian Drosophilidae (Carson, 1970, 1975; Carson et al., 1970; Carson and Kaneshiro, 1976). Repeated colonizations of new islands have taken place, and different populations of the same species on one island often show asymmetrical sexual isolation in laboratory tests. Again this may simply reflect inbreeding depression, which may diminish female mate discrimination as well as male attractiveness. An important feature of the genetic data on this group, remarked on by Templeton (1980), is that there seems to be no indication of unusually low heterozygosity at enzyme loci within populations. This is clearly shown in the data of Johnson et al. (1975) on the *D. planitibia* subgroup, where species at the ends of chromosome phylogenies do not have lower heterozygosities than their presumed ancestors. There are also cases of highly heterozygous species pairs that are almost identical electrophoretically, although distinct morphologically, such as *D. heteroneura* and *D. silvestris* (Craddock and Johnson, 1979). (Avise [1977] has also demonstrated a lack of correlation between low heterozygosity and rapid speciation in fishes.) As shown by Nei et al. (1975) and Chakraborty and Nei (1977), the heterozygosity at enzyme loci is sensitive to depletion during population bottlenecks (if prolonged over several generations) and takes a long time to be restored by mutation once a large population size has again been attained. The low genetic distance between *D. heteroneura* and *D. silvestris* suggests that they have been isolated only comparatively recently. This seems to be inconsistent with their high heterozygosities if they had gone through severe bottlenecks. However, Templeton (1980) asserts that the conditions for a shift between adaptive peaks are most favorable when population bottlenecks are not severe, and do not cause large reductions in heterozygosity, so that the high heterozygosities of the Hawaiian *Drosophila* are consistent with very brief bottlenecks followed by a population flush. Therefore, although bottlenecks may have occurred in the founding of new populations, there is little direct evidence that genetic revolutions have happened in this group. It is nevertheless possible that even brief periods of random genetic drift in small populations could interact with sexual selection to produce rapid nonadaptive evolution of mating preferences and secondary sexual characters (as opposed to a shift between adaptive peaks), leading to speciation (Carson, 1978; Lande, 1981*a*). Other criticisms of the founder effect-genetic revolution model of speciation have been advanced by Wright (1978 p. 474, 1980) and Lande (1980).

Chromosome rearrangements and speciation.—There is no doubt that related species very frequently differ with respect to gross chromosomal rearrangements (Muller, 1940; Stebbins, 1950; Dobzhansky, 1951; White, 1978). Such rearrangements often contribute to sterility of F_1 hybrids because of the formation of unbalanced gametes at meiosis in rearrangement heterozygotes (e.g., Dobzhansky, 1951 Ch. 7). White (1978 Ch. 6) has argued for an important causal role of chromosome rearrangements in speciation, by their fixation in a local population and its consequent reproductive isolation from neighboring populations. Lewis (1962, 1973) has put forward a similar model of speciation, based on his studies of the annual plant *Clarkia*. Such ideas are by no means new. Wright (1940, 1941) calculated approximate probabilities of fixation of chromosomal rearrangements with reduced heterozygous fertility, when introduced by mutation into small, geographically isolated populations, and proposed that such fixation events could sometimes promote speciation in a taxon with suitable breeding structure. His calculations have since been extended by Bengtsson and Bodmer (1976), Lande (1979*b*), Hedrick (1981) and Slatkin (1981*a*).

It is clear that rearrangements with a substantial detrimental effect on fertility when heterozygous are rather unlikely to be fixed, except in very small, isolated populations if these are mating randomly. (Self-fertilization or other types of extreme inbreeding will help to overcome the fertility handicaps of structural heterozygotes. This may explain the unusually frequent fixation of reciprocal translocations in *Clarkia* species, many of which are highly self-fertilizing.) Thus, the greater the chance of fixation of a rearrangement, the less effectively it will act as a reproductive isolating barrier, as noted by Sturtevant (1938). This prediction accords well with the data from comparative cytology in many taxa, which show a preponderance of types of rearrangements that involve the least disturbance of segregation. For example, in *Drosophila,* paracentric inversions distinguish species far more frequently than pericentric ones, and centric fusions are much more commonly fixed than reciprocal translocations (Muller, 1940; Spieth and Heed, 1972). Even if a rearrangement with a substantial fitness deficit to heterozygotes is fixed in a local population, it is likely to be ineffective in preventing gene flow at loci which are not tightly linked to it (Bazykin, 1969; Barton, 1979).

Therefore it appears extremely improbable that speciation could result from the fixation of a single chromosomal rearrangement. The successive fixation of different rearrangements could, however, produce an effective reproductive isolating barrier, and there are examples where this may have occurred, such as the Swiss tobacco mouse *Mus poschiavinus,* which differs from *M. musculus* by seven centric fusions that together cause semisterility in F_1 hybrids (Ford and Evans, 1973; White, 1978 p. 208–211). But caution should be exercised in interpreting chromosomal differences as primary agents in causing hybrid sterility, in the absence of detailed genetic investigations. Although there are relatively few cases in which such analyses have been carried out, it is evident that hybrid sterility may often be genic rather than chromosomal in origin (Dobzhansky, 1951 Ch. 8). This is necessarily true for homosequential species, which are common in the rapidly speciating Hawaiian *Drosophila* (Carson, 1970). The extremely low rate at which new rearrangements are fixed in evolutionary time (on the order of one per lineage per million years in karyotypically rapidly evolving groups [Bush et al., 1977; Lande, 1979*b*]), also appears inconsistent with a role in promoting rapid proliferation of species.

We now turn to an examination of the notion that chromosomal rearrangements may be responsible for morphological evolution, due to selection for associated changes in the expression of genes transposed near to new controlling elements (Wilson et al., 1974; Wilson et al., 1975; Bush et al., 1977; Gould and Eldredge, 1977; Stanley, 1979 Ch. 6). The main empirical basis for this idea is the work of Wilson's group, who have shown that rates of speciation or morphological evolution tend to be correlated with rates of chromosomal evolution when different taxa are compared, whereas rates of protein evolution are fairly constant. Mammals, for example, have apparently evolved karyotypically and phenotypically faster than cold-blooded vertebrates. Wilson and his colleagues suggest that the morphologically and karyotypically more rapidly evolving taxa have more subdivided population structures that are favorable for the fixation of chromosomal rearrangements which produce advantageous morphological changes when homozygous, but which have impaired fertility when heterozygous.

However, widely disparate taxa such as mammals and cold-blooded vertebrates, or even different orders of eutherian mammals, differ in many characteristics which may affect evolutionary rates. It is therefore invalid to conclude that a correlation of rapid karyotypic evolution with rapid speciation and morphological evolution implies that chromosome rearrangements are a direct cause of either reproductive isolation or morphological evolution. It might well be that certain mammalian characteristics, such as homeothermy or behavioral plasticity, give them a much greater evolutionary potential than say frogs. Lande (1979*b*) and Bengtsson (1980) have suggested that vivipary, with the accompanying intra-uterine competition between young, may result in a lower fertility loss to rearrangement heterozygotes. (This is because early death of zygotes carrying unbalanced chromosome complements will not be reflected in a proportionate reduction in the number of young at birth; such reproductive compensation has been demonstrated in the mouse for recessive lethals [Grüneberg, 1952].) The population structure effects advocated by Wilson and coworkers may also play a role, but there seems to be little ground for accepting the high levels of inbreeding to which they appeal in order to explain rapid karyotypic evolution in groups such as horses and primates. Mechanisms such as inter-troup transfer of males in baboons (Packer, 1979), and abduction of young mares by stallions from different herds in equids (Klingel, 1975), may usually prevent close inbreeding. (The literature on dispersal in higher vertebrates is reviewed by Greenwood, 1980.)

If causal relationships between karyotypic evolution and other evolutionary changes are to be detected, it is clear from the above that comparisons must be made between taxa that are rather closely related and share many important characteristics. Such a study has been made by Gold (1980), who found no correlation between rapid speciation and rate of karyotypic evolution in cyprinid fishes. Similarly, there seems to be no association of karyotypic and morphological changes among closely related species of bats (Baker and Bickham, 1980) or among lizard species of the genus *Anolis* (G. C. Mayer, pers. comm.). White (1973) documented the fact that in various taxa, pairs of sibling species differ by chromosomal rearrangements.

Furthermore, there is no evidence from genetics that major chromosomal rearrangements are more important than cytologically undetectable mutations (i.e., DNA base substitution, unequal crossing over, and small insertions and deletions) in producing morphological effects. It is certainly true that newly-arisen rearrangements in *Drosophila* often have phenotypic effects, usually because of transposition of genes located in euchromatin into heterochromatic regions (Lewis, 1950). But apart from the phenomenon of variegated position effect, which has no obvious evolutionary significance, just the same types of phenotypic effects can be produced by mutations with no detectable karyotypic change as by mutations associated with rearrangements (Lindsley and Grell, 1968). In many species of higher plants and animals, spontaneous and induced chromosomal rearrangements usually have no noticeable morphological effects (Burnham, 1956; Muller, 1956). In natural populations of *Drosophila,* the most abundant rearrangements are paracentric inversions, which have no detectable morphological effects, and are probably maintained as polymorphisms within populations by selection for reduction of recombination between genes having epistatic fitness interactions (Dobzhansky, 1951 Ch. 5; Charlesworth, 1974).

Regulatory versus structural genes.—The suggestion that morphological evolution depends on changes in gene regulation rather than in structural genes (Wilson et al., 1975; Bush et al., 1977; Gould, 1977 p. 405–409; Stanley, 1979 Ch. 6) lacks strong empirical support. This claim may well be true, but the fact that species can differ in many morphological characters but be very similar at the structural loci detected by protein sequencing and electrophoresis (such as *D. heteroneura* and *D. silvestris*) indicates only that the loci coding for soluble enzymes and proteins (chosen purely for ease of study) are not involved in the morphological differences observed. The latter could well be controlled by structural genes, if these are defined as DNA sequences that are transcribed into RNA and translated into proteins. In fact there may be no sharp distinction between regulatory and structural genes, since genetic regulation of developmental processes can occur at many levels. In the absence of detailed molecular and developmental studies, any interpretations of interspecific differences invoking gene regulation are strictly hypothetical. An example of this sort of speculation is Stanley's (1979 p. 185) claim that the peculiarities of the giant panda are due to mutations at a small number of regulatory loci, in the complete absence of any genetic information.

There seems to be a widespread impression that the genetic variation revealed by classical and quantitative genetics is restricted to structural genes. This view is quite erroneous. All classes of mutations affecting the visible phenotype are material for conventional genetic studies. The results of such studies when applied to the genetics of race and species differences show that morphological differences are nearly always controlled by multiple genetic factors. Evidence for this in plants is reviewed by Stebbins (1950 Ch. 2). The evidence for *Drosophila* is reviewed by Muller (1940 p. 191–205); a particularly striking recent example is the very large difference in head shape between *D. silvestris* and *D. heteroneura* (Templeton, 1977; Val, 1977). Similarly, reduction of eyes in a cave fish was demonstrated by breeding experiments to involve several genes (Wilkens, 1971; Lande, 1981*b*). Data on other animals can be found in Wright (1978 Ch. 8). There are, of course, characters such as color differences that may be controlled mainly by one or a few loci, as in Goldschmidt's (1940) data on *Lymantria,* but even in such cases the segregation of the major locus is blurred by modifiers. Similar remarks apply to the genetics of sterility of interspecific crosses, which have been extensively investigated in *Drosophila* (Dobzhansky, 1951 Ch. 8; Patterson and Stone, 1952). There is simply no evidence to support the claim that the genetic basis of variation between species differs qualitatively from that of variation between populations of the same species, or that between individuals of the same population. The rejection of Goldschmidt's claim that there is such a difference was based on the same type of evidence that is available today (e.g., Wright, 1940; Mayr, 1942 Ch. 7), and it is difficult to understand why such a claim should be resurrected except in support of preconceived notions about evolutionary mechanisms (see Stanley, 1979 Ch. 6; Gould, 1980).

Evolutionary Novelties

A central problem for evolutionary theory has always been to account for complex adaptations (Darwin, 1859 Ch. 6). Furthermore, because most of the features distinguishing higher taxonomic categories are recognizable as adaptations to different modes of life (Simpson, 1953 p. 171–181), the problem of explaining the origin of higher categories can largely be reduced to that of explaining the emergence of a new adaptation or set of adaptations. As Simpson (1953 Chs. 6, 7, 11) has thoroughly documented, the evolution of a higher category often seems to involve a comparatively rapid shift from one adaptive zone to another, with a corresponding shift in basic design. Once this design has become established, variations on it are evolved as adaptations to different ecological niches, leading to the phenomenon of adaptive radiation. The transition from reptiles to birds, for example, involves skeletal characteristics which are virtually all adaptations to flight: e.g., the fusion and reduction of many bones, hollow bones, the keeled sternum to which the massive flight muscles are attached, and the elongated bones of the wing. The subsequent adaptive radiation of the birds has not involved any great modifications of their basic design, except when the evolution of flightlessness has led to a loss of some of the original distinguishing features (Feduccia, 1980 Ch. 6). The relative suddenness with which such major changes in design often occur can be accounted for in terms of the comparatively strong selection likely to be acting on characters poised on the threshold between an old and a new adaptive zone (Simpson, 1953 p. 198). But it is important to note that the speed of adaptive transitions is only relative. Although geologically rapid, from a genetic or ecological point of view, major adaptive transitions are probably slow and gradual, involving many thousands of generations (Simpson, 1953 p. 350–353), and there is nothing in the fossil record that compels one to adopt a saltational interpretation of such events (Simpson, 1953 p. 359–376).

Mechanisms for the origin of novelties.—Nevertheless, the question may legitimately be asked as to whether microevolutionary theory is adequate to account for the evolution of major new adaptations. The important feature of such adaptations, emphasized by Darwin (1859 Ch. 6) is that they involve a set of mutual adjustments of the parts of a complex structure (the vertebrate eye is the classic example). It is thus almost inconceivable that such an adaptation could arise as a result of a single mutational change, as was advocated by Goldschmidt (1940) and Schindewolf (1950), and appears to be advocated at present by Gould (1977 p. 405–409, 1980) and Stanley (1979 Ch. 6). Darwin's solution to the problem was to use the analogy of artificial selection in animal and plant breeding, by which complexes of characteristics are gradually built up by selection of the best individuals in each generation with respect to some criterion (e.g., speed of running in racehorses and greyhounds). He suggested that a complex adaptation was similarly evolved as a result of a step-by-step accumulation of numerous, individually advantageous phenotypic changes. Alterations that may have been neutral or even harmful originally would become advantageous once earlier changes had taken place. In this way, he was able to picture the evolution of as complex a structure as the vertebrate eye by means of a series of gradual elaborations of an initial, rudimentary, light-sensitive structure (see Salvini-Plawen and Mayr [1977] for a thorough documentation of the gradation of different types of eye structures in animals). Fisher (1930 Ch. 2) argued that small, successive steps are required, since a small random change in a complex structure has a reasonable chance of being in the direction of increased adaptation, whereas a large change is almost certain to be out of adjustment in some respects (see also Muller, 1949 p. 423–429). The fact that mutations with major effects on morphology tend to have deleterious pleiotropic side-effects also means that large changes in morphology are unlikely to occur in one step. The argument of Gould (1977, 1980) and Stanley (1979 Ch. 6) that mutations can produce striking phenotypic effects, as a result of small changes in the timing of developmental events etc., is not at issue; the relevant question is whether or not such mutations are likely to provide the basis for evolutionary novelties.

The only genetically credible alternative theory to the Darwinian process of step-by-step evolution under the guidance of individual selection is Wright's (1932, 1977, 1978) shifting balance theory that was discussed earlier in connection with speciation. On this theory, favorable combinations of genes are produced by random genetic drift in small populations, and then spread through part or all of a species range by a combination of group and individual selection. It is thus possible for an evolutionary transition to occur between two states of a population which are separated by selectively disadvantageous intermediate states (adaptive valleys, in Wright's metaphor), since the transition is initiated by random genetic drift rather than selection. This theory has the merit that it can account for the evolution of character complexes that could not be produced by selection alone. It thus avoids some of the difficulties of conventional selection theory in explaining adaptive transitions. Its weakness, as pointed out by Simpson (1953 p. 123), is that it is critically dependent on a favorable population structure: a large population subdivided into numerous, partially isolated local populations in which many different gene combinations can be generated by random genetic drift, until a selectively advantageous one arises and diffuses throughout a larger region. (Note that numerous small local populations are required in Wright's model, since the probability of producing a selectively useful combination of genes by chance is rather small.) It is quite uncertain at present whether the values of the relevant parameters such as selection intensities, local effective population sizes and migration rates are often such as to permit Wright's theory to be a general model for the evolution of adaptation.

In contrast to this model, and to saltational models for the evolution of adaptations, Darwinian natural selection is an almost inevitable process that requires only a supply of genetic variability to work in virtually any type of population structure. Its operation in present-day populations has repeatedly been demonstrated (Dobzhansky, 1970; Ford, 1975; Sheppard, 1975). Since plausible scenarios can be constructed to account for the step-by-step evolution of even the most complex structures (Darwin, 1859; Mayr, 1959), there is no a priori reason to deny individual selection a major role in such evolutionary events. There is, nevertheless, considerable difficulty in discriminating between alternative models of any but the simplest examples of adaptations, suitable for studies by ecological methods, such as industrial melanism in moths and heavy metal tolerance in plants. We are usually ignorant of the strength and direction of the selection pressures operating on the individual characters concerned, and of the sequence of genetic changes that have taken place. It is thus rarely possible to do more than make guesses about the events underlying the emergence of a particular adaptation.

A remarkable test case is, however,

provided by the ecological genetic studies of Clarke, Sheppard, Turner and colleagues on Batesian and Müllerian mimicry in butterflies (reviewed by Turner, 1977, 1981). These have led to convincing reconstructions of the sequences of genetic events involved in the evolution of complex mimetic phenotypes built up of numerous distinct elements. Despite the fact that Batesian mimicry is often associated with polymorphisms for different mimetic forms, apparently controlled by alternative alleles at a single locus, it has been possible to exclude the saltatory interpretations of Punnett (1915) and Goldschmidt (1945). It is now clear that the polymorphic mimicry loci in species of *Papilio* are actually complexes of closely-linked loci (supergenes), each controlling different elements of the mimetic character complex. The evolution of this close linkage has been discussed by Sheppard (1959), Charlesworth and Charlesworth (1975*b*) and Turner (1977), and fits in well with the concept of stepwise incorporation of mutations at separate loci, each of which has a net selective advantage on the background established by previous evolution. Furthermore, it is certain that the effects of the major mutations incorporated into the supergenes have been considerably enhanced by the selection of minor modifiers that interact with them in very specific ways to perfect the mimetic patterns (Clarke and Sheppard, 1960*a*, 1960*b*, 1962). This is in accord with the theoretical predictions of Fisher (1927, 1930 Ch. 7) and Nicholson (1927), made long before the genetic studies were carried out.

Macromutations.—The possible role of mutations with relatively large phenotypic effects in initiating new adaptations, by permitting a population to cross a selective threshold from one adaptive peak to another, has been discussed by Muller (1949 p. 434), Simpson (1953 p. 105–112), Turner (1977, 1981) and many others. The evidence from mimicry suggests that this possibility may sometimes be realized. It is important to note, however, that the initial mutations in both Batesian and Müllerian mimicry seem to have produced only very crude mimetic resemblances, and that their incorporation was followed by numerous subsequent steps. In addition, the elements involved in creating mimetic resemblances are structurally superficial characteristics such as pigmentation, where genes with large effects may be much less likely to have deleterious side-effects than mutations with major morphological effects. Finally, there are strong theoretical reasons, based on the detailed dynamics of selection for mimicry, to expect a selective premium on initial mutations with substantial phenotypic effects, both in Batesian (Charlesworth and Charlesworth, 1975*a*) and Müllerian (Turner, 1977) mimicry. Caution should therefore be exercised in generalizing this aspect of mimicry to more complex adaptations, particularly as the evidence from species crosses discussed above suggests that morphological differences between species generally have a polygenic basis.

The high rate of mutations with small effects, compounded with their much larger probability of improving adaptation in comparison with macromutations (discussed above), explains why morphological evolution should generally be polygenic. Studies of spontaneous mutations affecting quantitative characters have shown that mutation rates are typically in excess of 10^{-2} per gamete per character per generation (Russell et al., 1963; Hoi-Sen, 1972; Mukai et al., 1972). This is orders of magnitude higher than conventional mutation rates for genes with major effects (about 10^{-6} per locus per generation). In units of additive genetic variance, spontaneous mutation typically produces in each generation about 10^{-3} times the environmental variance of a character (that which would be expressed in a genetically homogeneous population [Lande, 1975]). The implication of these findings is that spontaneous mutation can maintain high levels of heritable variation in natural populations, and that even a small isolated population can generate sufficient genetic variation for a geologically rapid shift into a new adaptive zone (Lande, 1980).

According to Muller (1949 p. 432),

> "In the great majority of cases in which large gene mutations of a given sort are found, others deviating in the same direction but to a lesser degree are more frequent, and various grades of intermediates usually coexist. In other words, the more extreme mutants simply form one end of a curve."

Thus there is usually no reason to appeal to macromutations to explain the production of a given phenotype. Consider, for example, genetic assimilation experiments in which the phenotype produced by a gene with major effects, such as the bithorax mutation in *Drosophila,* can be built up by selection of polygenic modifiers (Waddington, 1956; Bateman, 1959*a,* 1959*b*).

The evolution of certain types of characters may occur (or begin) with a gene having major effects, if minor modifiers are selected to remove deleterious pleiotropic effects of the major gene during its evolution (Wright, 1977 p. 463), or if selection on the main effect is strong enough to overcome deleterious side-effects. For example, the ability to detoxify a specific chemical may require a specific form of enzyme, as in the case of resistance to DDT by *Drosophila* larvae, and resistance to the poison Warfarin by rats (Ford, 1975 p. 378–379). But the response to such specific selection is often polygenic, as for resistance to DDT in adult *Drosophila* and heavy metal tolerance in plants (Crow, 1957; Ford, 1975 p. 386–387). Adaptations based on single gene mutations with large effects are occasionally found segregating as balanced polymorphisms within a population, such as sickle cell anemia in humans and Warfarin resistance in rats, because the heterozygotes have a selective advantage over the normal homozygote, whereas the mutant homozygote is effectively lethal (Cavalli-Sforza and Bodmer, 1971 Ch. 4; Ford, 1975 p. 378–379).

Phylogenetic Trends

Three phylogenetic patterns have been extensively discussed by punctuationists: morphological trends, parallel evolution, and divergence. The trends of greatest interest to punctuationists are those in characters, such as body size in mammals, that have no globally adaptive value. Punctuationists do not claim to be the first to notice these patterns, but they contend that, in view of the other parts of the theory of punctuated equilibria, these patterns are not consistent with the neo-Darwinian theory and new mechanisms are required to explain them. The basis for their argument is that the stasis of established species and the large, stochastic changes associated with speciation will not lead to the observed phylogenetic patterns without the additional mechanism of species selection.

The term "species selection" was coined by Stanley (1975), although the concept was discussed by Fisher (1930, 1958 Ch. 2), Lewontin (1970) and Eldredge and Gould (1972). Most punctuationists hold that differences among species of a higher taxon in some character or set of characters are created by the speciation process, which produces changes that are random with respect to the direction of long-term evolutionary trends. Any characters associated with higher speciation rates or lower extinction rates will tend to increase in frequency in the group, leading to a trend; and as discussed by Vrba (1980), lower extinction rates and higher speciation rates will be selected by this mechanism. Raup et al. (1973) and subsequent workers, using computer simulation, have tried to show that completely random events alone can produce phylogenetic patterns similar to those in the fossil record.

Phylogenetic patterns.—In the neo-Darwinian theory, phylogenetic patterns are supposed to be predominantly due to natural selection acting in each species. As discussed above, natural selection on one character will produce changes in that character and also in characters genetically correlated with it. Correlated evolution of a set of characters in parallel in different lineages may arise either through functional interactions between the characters (i.e., selective constraints) or through genetic and developmental constraints reflected in the pattern of genetic variation and correlations among characters. Both types of factors have long been discussed as an explanation for trends and parallel evolution. The nature of developmental constraints on evolutionary trends, acting through the pattern of variation and correlations among characters in a population, was clearly expressed by Darwin (1876 p. 346–347, quoted above).

Representing the neo-Darwinian view, Rensch (1959 p. 191–192) stated,

> "Although some parallelisms involve surprisingly large numbers of morphological and anatomical characters . . . one can well interpret such phenomena by the principles of mutation and natural selection, provided that one takes into account the correlations referred to in the preceding chapter (i.e. allometric growth, compensatory processes, pleiotropic gene effects, etc.)."

It is revealing to contrast this statement of the neo-Darwinian theory with its characterization by Alberch (1980 p. 653–654),

> "To explain this [parallel evolution] from a neo-Darwinian perspective amounts to assuming an unlimited source of variation with an omnipotent selective force, and that selection optimally solves the functional problem in every case. This, I believe, is an unrealistic view of evolution . . . ."

The view of evolution that Alberch describes is indeed unrealistic, but it is not the neo-Darwinian theory.

The neo-Darwinian explanation for large-scale trends in monophyletic taxa is that natural selection tends to produce similar changes in ecologically similar species. Since most conspicuous trends, such as those of increased body size, are known to be trends in averages of species in a higher taxon (Stanley, 1973), it is not necessary to assume that each species is affected by selection in the same way or to the same degree. Furthermore, for different higher taxa, it is not necessary to assume that the same ecological factors are acting even though the same phenotypic trend is observed. Rensch (1959 p. 211–218) lists several reasons why increased body size might be favored by natural selection. It is notable that Stanley (1979 p. 98) says that body size is one character which may have a substantial phyletic component in evolution. Some of the most conspicuous phylogenetic trends are those for increasing body size, or decreasing it, the latter particularly in parasitic species (Rensch, 1959 p. 70–71). Trends in many other characters, such as those in tooth size and shape in horses, carnivores and cetaceans, have a clear adaptive basis (see Simpson, 1953 Ch. 8; Rensch, 1959 Chs. 4, 6).

In the neo-Darwinian theory, divergent evolution could be caused by ecological interactions among related species. The pattern of body size distributions of anoline lizards in the Greater Antilles is one example in which competition for food is the principal mechanism producing the size differences among species (Williams, 1972). Ecological interactions cannot be invoked to explain patterns of divergence among allopatric species unless the allopatry was secondary. However, non-directional changes could still occur in allopatric species in the process of ecological specialization during adaptive radiation, if each responds independently to different selective forces in the different environments. Then in considering a sufficiently large collection of lineages, the overall pattern could be the same as that produced by a purely random process acting independently in each species. This is recognized by Stanley (1979 p. 189), ". . . I stress that *it is quite possible for directions of speciation within a clade to be randomly determined even if evolution is guided solely by natural selection.*"

The appearance of randomness when considering all the changes together does not imply that each change is due to a random process; it is due only to the independence of changes in allopatric species. The simulation results of Raup et al. (1973), Raup and Gould (1974) and later authors confirm that independent random processes can produce patterns similar to those found in real phylogenies, as is expected on theoretical grounds, but they do not imply that changes in real phylogenies must be attributed to random processes (cf. Stanley et al., 1981). Of course it is possible that random genetic drift may contribute significantly to diversification, as in Wright's shifting balance theory. Rapid nonadaptive speciation in some taxa might lead to overpacking of communities with ecologically similar species that can not coexist in a stable equilibrium, producing a susceptibility to extinction by "stochastic" environmental fluctuations (Van Valen, 1973). But as Levinton and Simon (1980) note, the frequent occurrence of similar branching patterns in the phylogenies of widely different taxa inhabiting the same area, revealed in vicariant biogeography, strongly argues against the predominance of truly random branching in most phylogenies, at least for taxonomic categories above the species level.

Species selection.—Punctuationists regard species selection as a mechanism for producing phylogenetic trends in characters associated with high speciation rates and low extinction rates. However, there is as yet no evidence that species selection has been effective in producing major morphological trends. The data reviewed above do not suggest a strong association of morphological change with speciation, and as Darwin (1859 p. 432) observed, "Extinction has only separated groups: it has by no means created them . . . ." Stanley (1979) and Gould and Eldredge (1977) claim that natural selection cannot account for phylogenetic trends, major morphological changes in widespread species, and that some other mechanism is required. If, as we have argued, natural selection can largely account for major changes, then species selection does not necessarily play a dominant role in the production of trends.

A serious problem with species selection is that the number of species and their turnover rate by speciation and extinction is far less than that of individuals within species. This greatly limits the potential importance of species selection in comparison with individual selection (Fisher, 1958 p. 50; Lewontin, 1970; Slatkin, 1981*b*). In this context there is a further difficulty with species selection, which has been pointed out by Maynard Smith (1981). Because morphological evolution can occur in many directions (as discussed above), if the changes during speciation are random for each genetically independent combination of characters, then the time scale for species selection seems too slow to explain the rapid origin of complex adaptations which require mutual adjustments of numerous parts that vary in many independent dimensions.

It has nevertheless been widely recognized that the vast majority of species that ever existed are now extinct; this evidently provides a large opportunity for stochastic events or selection between species and higher taxa (Simpson, 1953 Ch. 9; Wright, 1978 Ch. 12). For example, the initial theories of island biogeography were based on the assumption that the expected species diversity on an island is achieved by a balance between random extinction and colonization from an outside source. MacArthur and Wilson (1967) and Leigh (1981) point out, however, that stochastic events in the demography of a single population can cause extinction at an appreciable rate (even on a geological time scale of millions of years) only in rather small populations. This implies that changes in the physical and biotic environment which produce a definite effect on population density must be largely responsible for the extinction of species that were abundant enough to be preserved in the fossil record (Leigh, 1981). Van Valen's (1973) law of a nearly constant rate of extinction within a given taxonomic level (except during mass extinctions) may seem to be consistent with predominantly random extinctions; but it should be realized that if extinction rates are actually constant at any one taxonomic level, say for species, then they cannot generally be constant at any other level, for example because genera containing many species would be expected to persist longer than those with few species, without differential speciation (Van Valen, 1973). The nearly constant rates of extinction at various taxonomic levels thus imply that subtaxa of a particular taxon tend to respond numerically in a similar (nonrandom) fashion to environmental fluctuations occurring on a large geographical scale. Mass extinctions are also known to be nonrandom to a large extent (Simpson, 1953 Ch. 9).

Based on the assumed randomness of morphological changes during speciation, and the guidance of trends by species selection, punctuationists claim that macroevolution is "decoupled" from microevolution, and deny that gene frequency changes within populations are the foundation of major morphological changes (Stanley, 1975, 1979; Gould and Eldredge, 1977). This argument seems to neglect the fact that every living or fossil organism owes its existence to a continuous line of descent going back generation by generation into the remote past. Although apparently random (or directed) changes during speciation, and subsequent species selection, may provide a convenient description of macroevolutionary patterns, these terms should not be identified with the genetic and ecological mechanisms causing the changes. Even if it can be established in some cases that morphological changes during speciation are uncorrelated with the direction of trends, macroevolution can be decoupled from microevolution only at a gross descriptive level. Different terms may be used to describe the same processes, but there is no evidence suggesting the need for qualitatively new mechanisms to account for macroevolutionary patterns (cf. Stebbins and Ayala, 1981).

CONCLUSION

The original paper on punctuated equilibria by Eldredge and Gould (1972) espouses a philosophy of science inspired by Kuhn's (1962) description of scientific revolutions. "Science progresses more by introduction of new world-views or 'pictures' than by the steady accumulation of information" (Eldredge and Gould, 1972 p. 86). Although recognizing the role of theory in guiding observation and experiment, and that, like evolution, science proceeds at variable rates, philosophers have criticized Kuhn's conception of scientific revolutions (see Lakatos, 1970; Shapere, 1971; Suppe, 1977). But regardless of how such events are defined, it does not appear to us that the theory of punctuated equilibria should be accepted as a major revolution in evolutionary biology. With reference to empirical findings from many areas of biology, particularly population genetics, we have shown that the neo-Darwinian theory is strongly supported by the available evidence, and is consistent with paleontological observations of the sudden appearance and prolonged morphological stasis of many species. We have also demonstrated, as has Orzack (1981), that punctuationists have often severely distorted the neo-Darwinian theory of evolution. Punctuationists are mainly criticizing oversimplified versions of neo-Darwinism (which are currently popular in some fields) rather than the original statements of this theory and the evidence which has been used to support it. Furthermore, some of the genetic mechanisms that have been proposed to explain the abrupt appearance and prolonged stasis of many fossil species are conspicuously lacking in empirical support. Thus, we do not feel logically compelled to abandon neo-Darwinism in favor of the theory of punctuated equilibria.

ACKNOWLEDGMENTS

We thank J. Damuth, J. Felsenstein, A. R. Kiester and R. C. Lewontin for helpful discussions. D. Charlesworth, J. Coyne, W. Engels, J. Griesemer, M. Kirkpatrick, E. G. Leigh, G. Mayer, E. Mayr, J. Maynard Smith, S. M. Stanley, S. Orzack, G. Paulay, A. Templeton, E. Vrba and A. C. Wilson read the manuscript and provided valuable criticisms. This work was supported by NIH grant GM27120 and NSF grant DEB7827045.

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ANNOUNCEMENT

The *International Organization of Plant Biosystematists* will hold a Symposium entitled *Cytology and Hybridization: 40 Years Later* at McGill University, Montreal, Canada, July 17–21, 1983. Attendance will be limited to 150. The program is presently being arranged. It is planned to have the proceedings published. For information on attendance or participation write to Dr. William F. Grant, Genetics Laboratory, Box 282, Macdonald Campus of McGill University, Ste. Anne de Bellevue, Quebec, Canada H9X 1C0.