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CHARACTER CHANGE, SPECIATION, AND THE HIGHER TAXA

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Gould and Eldredge (1977) in their article, "Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered," took issue with the common view of phyletic gradualism. They agreed to a considerable extent with the view of Simpson, to whose book, published 36 years ago, their title referred. Simpson (1944) brought out the enormous differences among rates of evolution indicated by paleontological data: the near stasis (bradytely) of some forms for hundreds of millions of years, typical rates (horotely) (which, however, vary much among phyla) and the enormously rapid rates (tachytely) indicated especially for the periods of origin of many important groups. He used the term "quantum evolution" for evolutionary events of the sort referred to as "punctuational" by Gould and Eldredge. The latter began the abstract of their paper with the statement: "We believe that punctuational change dominates the history of life: evolution is concentrated in very rapid events of speciation (geologically instantaneous even if tolerably continuous in ecological time."

This does not contrast as much as it may seem at first sight with Simpson's assertion (p. 203) that "nine tenths of the pertinent data of paleontology fall into patterns of the phyletic mode," since he held that there might be episodes of tachytely in the phyletic evolution. There is more contrast, however, with respect to mode. Gould (1977) in his paper, "The Return of Hopeful Monsters," wrote: "I do predict that during the next decade, Goldschmidt (1940) will be largely vindicated in the new world of evolutionary biology."

In his paper, "Is a New and General Theory of Evolution Emerging?" (1980), he maintains that "Evolution is a hierarchical process with complementary but different modes of change of its three major levels, variation within populations, speciation and patterns of macroevolution."

Simpson definitely rejected Goldschmidt's (1940) thesis that speciation and the origin of the higher categories depend on types of mutation that have nothing in common with the changes that occur within species.

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

Historical Review

The opposed concepts, gradual and abrupt change, go back to the origins of evolutionary thought. At the beginning of the last century, Lamarck postulated a preordained ladder of life, leading from the simplest forms to man with gradually diverging branches, determined by the inheritance of characters acquired by adaptation to different conditions. E. Geoffroy St. Hilaire, on the contrary, proposed that radically different patterns of life had appeared abruptly from time to time, a view derived from the observed appearance of monstrosities. These speculations came when little was known of the actual course of evolution (cf. Nordenskiöld, 1928).

Darwin (1859), in midnineteenth century, was able to marshall the available data from all fields of biology in such a way as to win almost immediate acceptance by scientists of evolution as a fact. He also presented a theory that was at least in the spirit of physical science. He held that study of the ways in which animal and plant breeders had actually brought about striking changes by artificial selection provided insight into the evolutionary process in nature. After careful consideration (Darwin, 1868 Vol. 2) he concluded that: "Without variability, nothing can be effected: slight individual differences, however, suffice for the work and are probably the chief or sole means in the production of new species."

Thus Darwin came down strongly on the side of gradualness under natural selection though he did not wholly rule out an occasional role of the more striking changes that he called "sports."

The adequacy of Darwin's explanation of evolution was widely questioned, principally for two reasons: (1) the rapid dilution of variation, under the prevailing theory of a blending of the parental heredities, seemed to require an unbelievable efficiency of the selection process, an objection put in mathematical form by Fleeming Jenkin (1867), and (2) the difficulty of accounting for the extraordinary coadaptiveness of all parts of organisms, urged especially by St. George Mivart.

Many biologists continued to accept a perfecting principle as an essential property of life (e.g. Nägeli), a view fervantly advocated as late as 1934 by the leading paleontologist at the time, H. F. Osborn, in his doctrine of aristogenesis.

The majority, however, followed the paleotologist Cope in preferring the inheritance of the effects of use and disuse (cf. Kellogg, 1907).

At the turn of the century, de Vries proposed his mutation theory under which species appear abruptly, natural selection being relegated to the role of guiding the course of evolution beyond the species level. de Vries's theory had the merit of being based on the actual appearance of what seemed new species among plants of the American species, *Oenothera Lamarckiana,* that had escaped from cultivation in the Netherlands. It turned out later, however, that most of his supposed new species were trisomics with merely altered proportions of the elements of heredity of *O. Lamarckiana,* not transmissible, moreover, by pollen, so that the new "species" could exist only as segregants. One mutant form, *O. gigas,* turned out, however, to be a tetraploid, capable of reproducing itself and producing sterile triploid hybrids on backcrossing. It thus really did behave like a new reproductively isolated species, although differing morphologically from the parent species only very slightly. There was thus evidence that a new species might arise abruptly.

The rediscovery of Mendelian heredity in 1900 soon dissipated the first of the objections to Darwin's theory, referred to above. Yule pointed out in 1902 that segregation in the ratio 1:2:1 in F_2 of a cross persisted in randombred F_3 and in later randombred generations. Castle (1903) extended this to ratios based on other gene frequencies and Weinberg (1908) and Hardy (1908) put this in general mathematical form. Under Mendelian heredity there is no such dilution of hereditary elements as implied by the theory of blending heredity.

The study of conspicuous Mendelian difference, led most of the early geneticists to accept an attenuated form of the mutation theory: it was supposed that gene mutations with major effects were occasionally favorable and that these replaced the old type genes, one at a time. This was a form of 'punctuated' evolution but much less drastic than that of de Vries.

A few continued to accept speciation by mutation and some, notably Goldschmidt (1940), went beyond de Vries in holding that the origin of higher categories required mutations of appropriate sorts.

Castle, with an agricultural background, differed from the prevailing Mendelian view in the opposite direction. He challenged the current belief, tracing to de Vries, according to which the selection of quantitative variability could produce no permanent effects. He carried through large scale experiments with a strain of hooded rats in which he attempted to change the pattern of black and white by selection, experiments in which I was his assistant during 1912–1915. He was approaching self-black in 20 generations of plus selection, self-white in the same number of generations of minus selection, when reduced fecundity brought both lines to an end (Castle, 1916). My prior acceptance of Darwin's views on the efficacy of selection of quantitative variability was confirmed though I was somewhat disturbed by the forced termination of the experiments in spite of much heritable variability, which suggested that selection tended to have deleterious pleiotropic consequences.

Gene-Character Relations

Castle originally thought that the quantitative variability was in the piebald factor itself, a view confirmed to some extent by the appearance of a new allele by mutation in the plus series, an allele with effects intermediate between that of the allele in this series and that of the self-colored wild rats. Meanwhile, however, the multiple factor theory of quantitative variation, foreshadowed by Mendel himself and proposed by Yule in 1906, had been exhaustively demonstrated in a case in wheat by Nilsson-Ehle (1909) and more extensively in maize and *Nicotiana* by East (1910, 1916) and his associates. This provided an alternative interpretation of Castle's (1919) results which he accepted after carrying through an extensive test.

The Mendelian interpretation of natural selection requires analyses of the statistical consequences of diverse assumptions on the relations of genes to characters. Figure 1 (Wright, 1980) gives a diagrammatic illustration of a number of different assumptions. Figure 1C applies to cases in which a block of DNA (left) does not code for anything, or anything of significance, and thus has no phenotypic effect (right) that is subject to selection. Kimura (1968) and King and Jukes (1969) suggested that large portions of the protein molecules that are the primary products of DNA activity, may have no functional significance beyond filling space and that this may account for the extensive polymorphism of proteins revealed by electrophoresis in many species. This was obviously, however, not a general theory of gene-character relations.

Figure 1A represents the one-to-one relation of gene and "unit character" postulated in the prevailing Mendelian view of evolution, referred to above. The courses taken under constant selection, but diverse assumptions otherwise, were worked out systematically by Haldane in a series of papers, beginning in 1924 and summarized in 1932, following the working out of special cases by Castle (1903) and H. T. J. Norton (1915).

Such a one-to-one relation could, however, only be assumed for genes with major effects. Haldane also worked out consequences of other assumptions, including multifactorial heredity. Figure 1B represents the latter hypothesis, uncomplicated by gene interaction and pleiotropy. Fisher (1930) presented convincing reasons for holding that only minor factors are likely to be favorably selected. He accepted the occurrence of nonadditive relations between gene and character (dominance, epistacy) but showed that these merely slow down progress by selection under his assumption that species are effectively panmictic. Fisher, in contrast with Haldane, attempted to bring all evolution under a single simple formula, his "fundamental theorem of selection," "the rate of increase in fitness of any organism at any time is equal to its (additive) genetic variances in fitness at that time."

It is not wholly fair to assert that Fisher's conception of the relation of genes to characters was restricted to that of Figure 1B but he clearly tended to think in those terms. Thus his assumption (1929) that "a small selection of intensity, say 1/50,000 the magnitude of a larger one, will produce the same effect in 50,000 times the time," while true of gene character-relations of the sort represented in Figure 1B (and 1A) is not at all true of genes that modify a heterozygote and also have pleiotropic effects on the homozygotes. Fisher (1928) made the above assumption in connection with his theory that the prevailing dominance of wild type over recurrent deleterious mutations is due to specific modifiers of the rare heterozygotes, exerting a selective pressure of the order of the mutation rate, put at 10^{-6} per generation. His principal evidence for his theory was the easy modifiability of intermediate heterozygotes under strong direct selection. The latter well known phenomenon is obviously irrelevant if there are always at least slight pleiotropic effects on homozygous wild type (Wright, 1929*a,* 1977; Charlesworth, 1979).

Figure 1D represents each gene as having multiple pleiotropic effects because of interaction of its products with those of others. It may be assumed, moreover, that the effects of these interactions are not in general additive. These are inevitable consequences of the complex network of biochemical and developmental reactions that intervene between primary gene action and the ultimate effects subject to selection.

The available evidence is in harmony with this concept. My own major experimental project from the time when I was a graduate student (cf. Wright, 1968), has been the study of gene interactions in guinea pigs. Thus I have made many thousand different combinations of the genes at 11 loci that affect coat and eye color and considerable numbers of loci affecting other characters. From the first, I was fascinated by the seeming unpredictability of such combinations and have tried to devise hypothetical interaction patterns to account for them. There were also often surprising pleiotropic effects.

The latter have been even more striking in the studies of the genetics of the mouse by many workers, in which enormously more new mutations, usually deleterious, have been observed. More than 50 loci have been found that affect coat color, of which some 60% also have gross morphological effects (Searle, 1968; Silvers, 1979). On taking account of the pleiotropic effects on eumelanin and phaeomelanin, and the likelihood of other slight morphological and physiological effects, there can be little doubt that pleiotropy is universal. The situation is similar in other organisms.

My own speculations on evolution were dominated from the first by the thought that there must somehow be selection of coadaptive interaction systems as wholes. The difficulty was that under biparental heredity the reduction division breaks up combinations so rapidly in terms of geologic time, that under panmixia natural selection is capable of operating only on the average effects of genes in all combinations. Combinations of unlinked genes go halfway toward randomness per generation; with 10% recombination, half way per 7 generations; and with 1% recombination half way per 69 generations.

The Selective Topography

The nature of the field of variability available for natural selection under the various patterns of gene-character relations requires consideration.

Under the concept of one-to-one relationship (Fig. 1A), it should be possible theoretically to rank the alleles at each locus in the order of their values to the organism. Natural selection would operate under given conditions according to the courses described most systematically by Haldane as already noted.

An organism, however, is very far from being a mosaic of unit characters. The value of any gene depends in general on the array of other genes with which it is associated. This holds even under the pattern of relations of Figure 1B in which the effects of multiple loci are additive with respect to characters but usually there is an intermediate optimum close to the character mean.

Assume a group of genes *A, B, C* and *D* that contribute equally and additively to the size of some part, relative to their alleles, *a, b, c* and *d* (Fig. 2) (Wright, 1964*b*). Note that only the positive factors

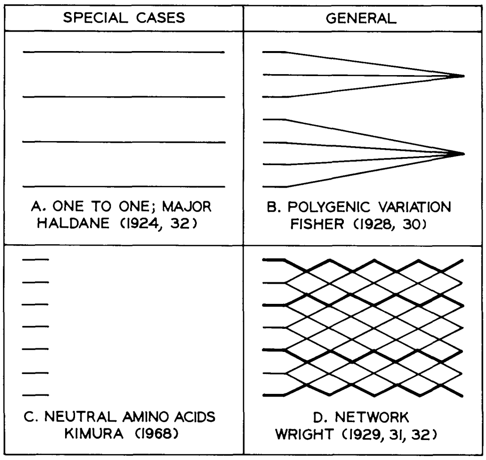


FIG. 1. Four assumptions on the relationship of genotype (left) to phenotype (right).

are shown and these singly in the homozygotes. There is obviously no best allele at any locus. Fixation of any two positive genes and of the negative ones at the other two loci gives the mean and hence the optimum. There are six such optimal combinations (called selective peaks later): *AABBccdd, AAbbCCdd, AAbbccDD, aaBBCCdd, aaBBccDD* and *aabbCCDD*. The mean is also given by many other combinations such as *AaBbCcDd* but these involve heterozygosis and would give some inferior offspring.

In this case, it would make no difference which one of the six optimal types becomes established by selection. In an unfixed population, selection (according to Fisher's fundamental theory) will fix the combination to which the composition of the population is closest.

In actual cases, however, the maxima would not be equally fit, whether because of unequal gene effects or because of different pleiotropic effects. Let us assume that the effects are equal but that *A* and *B* have certain pleiotropic effects that are equal and additive. Figure 3 shows the selective values of the 16 homallelic populations on a vertical scale. With the chosen pleiotropic effect, there is one fittest type *AB*, four at the same lower level (*BC*, *AC*, *BD* and *AD*) and one lowest maximum, *CD*. The four homallelic combinations with only one positive gene and the four with three positive genes are still lower. That with all four positive genes is much lower and that with all four negative genes is the lowest of all.

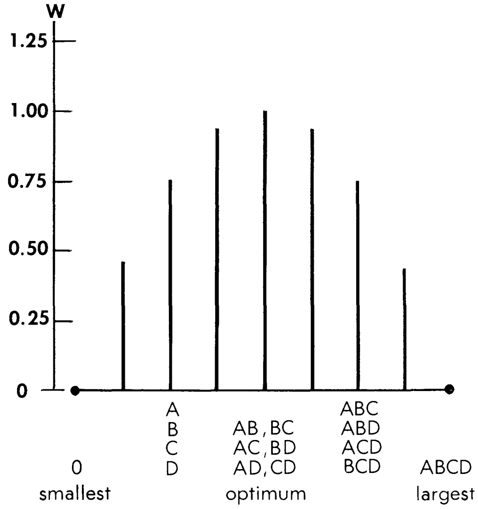


FIG. 2. Contributions to selective value of the combinations of four pairs of alleles to a quantitatively varying character, assuming equality and additivity with optimum in the middle. *AB* represents *AABBccdd*, etc. (from Wright, 1964*b*, Fig. 8).

Imagine now a figure with four orthogenal dimensions, one for each independent gene frequency and imagine a fifth dimension for selective values. Figure 4 shows two of the faces, including the lowest maximum *CD*, one of the four intermediate ones, *BC* and the highest one, *AB*.

The values chosen for the pleiotropic effects determine a saddle between peaks *CD* and *BC* and one between *BC* and *AB*. Arrows indicate the trajectories of populations subject to the assumed selection pressures. If it is assumed that there is recurrent mutation or a small amount of immigration from other demes, this prevents permanent fixation at any peak.

In Figure 5 the selection values of Figure 4 are shown according to a vertical scale. Selective values are also shown along

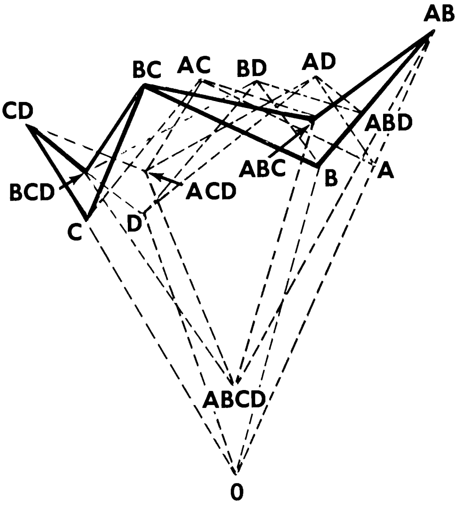


FIG. 3. Total selective values of the 16 homallelic genotypes of Fig. 2 according to the contributions indicated there, supplemented by equal semidominant pleiotropic effects of genes *A* and *B* (from Wright, 1964*b*, Fig. 9).

paths from one peak to a higher one, passing through the saddle: A path directly from lowest to highest peak passes across the 4-dimensional saddle, but this is more depressed and thus presents a greater obstacle to a peak-shift than do the paths passing through the 2-dimensional saddles.

Since quantitative variability with optimum close to the mean is the usual rule for measurable characters in wild species, the foregoing model is practically universal for such characters. It has to do, however, with only small changes.

Of greater importance for major evolutionary changes are probably the unpredictable major interaction effects of genes, referred to earlier, for which Figure 1D with the full complexity expected from the network of biochemical and developmental processes, is intended to be the model. The selective topography would be correspondingly more complex.

Of special importance are interaction systems consisting of a recurrent major mutation and one or more modifiers that neutralize its inevitable deleterious side effects. A shallow saddle may lead to a great step in advance (Fig. 6).

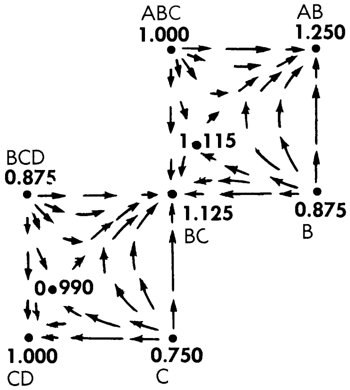


FIG. 4. Two of the surfaces of the 4-dimensional space of frequencies of genes *A*, *B*, *C* and *D* of Fig. 3. Trajectories are indicated by arrows. The selective values at the peaks, pits and saddles are given (from Wright, 1964*b*, Fig. 10).

In my 1932 paper, the first in which the concept of a selective topography was presented graphically, it was stated that "The problem of evolution, as I see it, is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field. In order that this may occur, there must be some trial-and-error mechanism on a grand scale by which the species may explore the region surrounding the small portion of the field which it occupies."

Modes of Evolution

At this point I will go back to a group of six diagrams (Fig. 7) that I used in 1932, and often later, for consideration of possible modes of evolution under Mendelian heredity. In these diagrams the multiple dimensions of gene frequency change, provided by thousands of heterallelic loci, are flattened out into two dimensions on which all genotypes are supposed to be located and the dimension of selective value is represented by contours. The innumerable selective peaks are given token representation in only two.

The three upper diagrams represent cases in which the number of individuals in an effectively random breeding population is so great that accidents of sampling can play no significant role. In Figure 7A it is assumed that recurrent

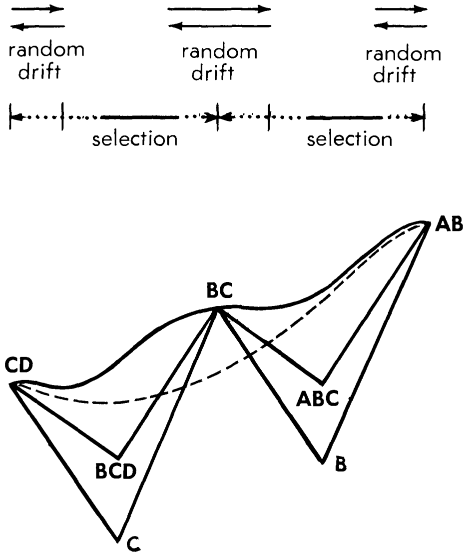


FIG. 5. Profile of trajectories from peak to peak (*CD* to *BC* to *AB*) through 2-dimensional saddles and from *CD* to *AB* through a 4-dimensional saddle and from pits to peaks (straight lines) (from Wright, 1964*b*, Fig. 11).

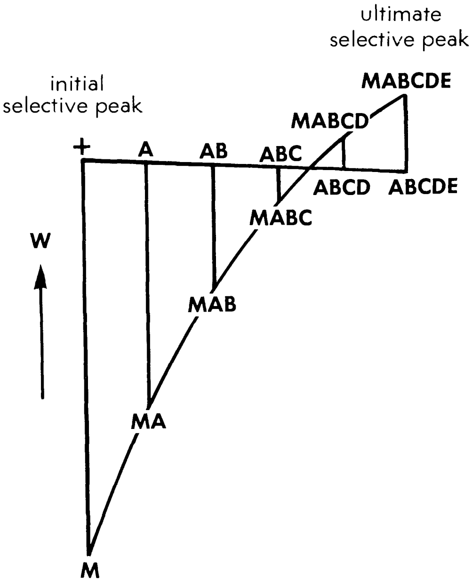


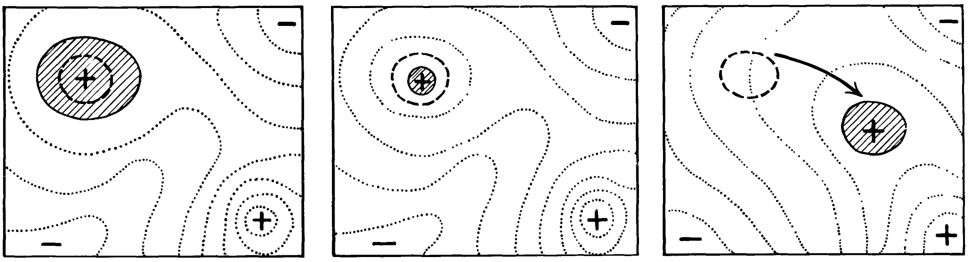
FIG. 6. Combinations of an initially deleterious, but potentially favorable, major mutation, with favorable modifiers (from Wright, 1964*b*, Fig. 13).

mutation is balanced by feeble selection. The population occupies a small portion of the field (indicated by a broken circle) about the joint equilibrium point. An increase in mutation rate would bring about an increase in the portion of the field occupied (indicated by a solid line). There is no appreciable chance, however, that this will come under control of a higher peak. A decrease in selection, such as occurs when a particular character ceases to be of value, has a similar effect. The character may wholly disappear under the mutation pressure but selection for pleiotropic effects of the genes is likely to be much more important beyond the point of selective advantage from degeneration of the character as an encumbrance (Wright, 1929*a*, 1964*a*). Mutation pressure by itself is probably of little importance for characters though it probably is for useless genes.

Figure 7B represents the case of mass selection in an effectively panmictic population, living for a long time under the same conditions. The population moves toward the selective peak, the slope of which it has reached for historic reasons, comes to occupy a region of the field about this peak and stays there without further change except in so far as novel favorable mutations create a change in the topography, an exceedingly slow process. With increased selection, the region occupied decreases.

If, however, conditions change qualitatively (Fig. 7C), the topography changes. The species tends to move with movement of the peak that it has occupied. As I noted in 1932: "Here we undoubtedly have an important evolutionary process and one which has been generally recognized. It consists largely of change without advance in adaptation. The mechanism is, however, one which shuffles the species about in the general field. Since species will be shuffled out of low peaks more easily than high ones, it should gradually find its way to the higher general regions of the field as a whole."

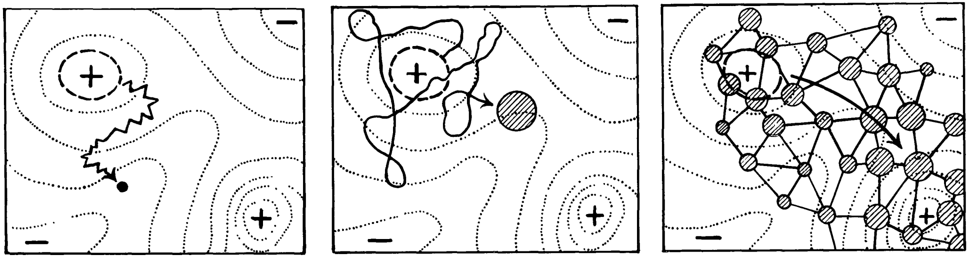
The process of change without advance is what Van Valen has called "the Red Queen Process." The process as a whole is that under which selection according to Fisher's fundamental theorem is most ef-



A. Increased Mutation or reduced selection 4Nu, 4Ns very large

B. Increased Selection or reduced mutation 4Nu, 4Ns very large

C. Qualitative Change of environment 4Nu, 4Ns very large



D. Close Inbreeding 4Nu, 4Ns very small

E. Slight Inbreeding 4Nu, 4Ns medium

F. Division into local Races 4nm medium

FIG. 7. Token representation of a portion of the multidimensional array of genotypes of a population with fitness contours. Field initially occupied indicated by heavy broken contour. Field occupied later indicated by crosshatched area (multiple subpopulations in F). Courses indicated in C, D, E and F by arrows. Effective population numbers, N (total), n (local); v (mutation), s (selection), m (migration) (from Wright, 1932, Fig. 4).

fective (more effective than under the unchanging conditions of Fig. 7B). It is the process which such recent authors as Maynard Smith (1975), Williams (1966) and Dawkins (1976) consider all-important.

Figure 7D refers to populations that have become so small that accidents of sampling overwhelm all but the strongest selective differences. The population wanders from the selective peak that it has occupied, moves about irregularly, decreases in variability. As I noted in 1929, (as essentially in 1931 and later): "In too small a population, there is nearly complete random fixation, little variation, little effect of selection and thus a static condition, modified occasionally by chance fixation of a new mutation, leading to degeneration and extinction."

In spite of this, most authors including Huxley (1942) and Fisher and Ford (1947) followed by many others (including textbooks published in 1979 and 1980), have attributed to me the view that fixation of nonadaptive characters by random drift was the essence of my theory.

It should be noted that I was considering the evolution of ordinary characters, not completely neutral primary gene effects such as Kimura (1968) and King and Jukes (1969) have discussed in recent years.

Figure 7E represents the case of loci with respect to which the effects of accidents of sampling and of selection are about equal within a rather small isolated population. I noted of this in 1932: "The species moves down from the extreme peak but continually wanders in the vicinity. There is some chance that it may encounter a gradient leading to another peak, shift its allegiance to this. Since it will escape relatively easily from low peaks—there is here a trial-and-error mechanism by which in time the species may work its way to the highest peak in the general field. The rate of progress is extremely slow, however, since change of gene frequency is of the order of the reciprocal of the effective population size and this reciprocal must be of the order of the mutation rate in order to meet the conditions of this case."

Finally, Figure 7F represents a species that is subdivided into local populations (demes), sufficiently small and isolated that accidents of sampling may overwhelm many weak selection pressures. There must, however, be enough diffusion that a deme that happens to acquire a favorable interaction system may transform its neighbors to the point of autonomous establishment of the same peak, and thus ultimately transform the whole species or at least that portion of it in which the new system actually is favorable. The field of variability of the species is here amplified by local differentiation, and natural selection is amplified by the selective diffusion from the superior demes.

The process within each of the demes is somewhat similar to that in Figure 7E, but is limited here only by the immigration rate which may be thousands of times the mutation rate. If there are thousands of sufficiently independent demes, the process in the species as a whole may be millions of times as effective as in Figure 7E. This is the process that I later called the shifting balance process.

I have devoted many papers (with conclusions summarized in Wright, 1969 Chapter 12) to the conditions under diverse population structures (continuous, clustered, 'island,' multiple colonies subject to frequent extinction and refounding from the superior ones) under which the process may be effective.

Going back to the model with factors *A, B, C* and *D,* the operation of the shifting balance process within the range of the species is represented in Figure 8. It is assumed that the species has been under control of the lowest of the six selective peaks (*CD*). Shifts to control by certain higher peaks, *BC, AC* and *AD* have occurred and are spreading by selective diffusion, according to their times of origin. The highest peak, *AB,* has been arrived at both within that characterization by *BC* and by overlapping of the regions controlled by *BC* and *AC.*

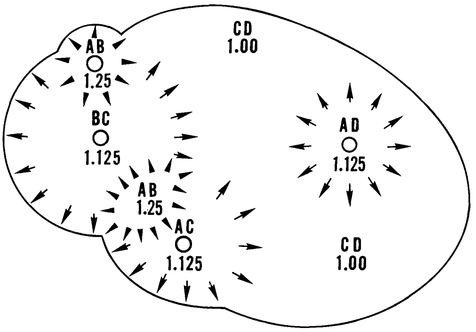


FIG. 8. Diagram of a population range, characterized initially by the lowest peak, *CD* of Fig. 4 in which intermediate peaks, *BC, AC* and *AD* have been arrived at locally and the highest peak *AB* has been arrived at from *BC* and from overlap of *BC* and *AC* (from Wright, 1964, Fig. 12).

It should be added that I suggested in 1931 and demonstrated later (Wright, 1948) that random differentiation of local populations may be due to fluctuations in the systematic pressures of selection and of amount and kind of immigration without there being small size populations. Random drift from accidents of sampling, however, affects all of the thousands of loci not subject to strong selection while fluctuations in selection would affect a more limited number.

Selection by Man in Relation to Evolutionary Theory

Darwin in "The Variation of Animals and Plants under Domestication" organized his discussion of "selection by man" under three heads: methodical, unconscious and natural, all concerned with direct selection among individuals. He did not discuss the sort of selection practiced by breeders in purchasing breeding stock from superior strains. The only references to this are in quotations. Thus in a section on "selection in ancient and semicivilized people" he quotes Virgil "as giving as strong advice as any modern agriculturist could do, carefully to select the breeding stock 'to note the tribe, the lineage, and the sire, whom to reserve for husband of the herd.'" He also quotes verses from ninth century Ireland describing a ransom demanded by Cormac:

> Two pigs of the pigs of MacLir
> A ram and ewe both round and red,
> I brought with me from Aengus,
> I brought with me a stallion, and a mare
> From the beautiful stud of Manannan,
> A bull and a white cow from Druim Cain.

There is clear recognition of selective diffusion from superior herds in a quotation from a Mr. Wilson to the effect that in certain districts of the Scottish Highlands: "The breeding of bulls is confined to a very limited number of persons, who by devoting their whole attention to this department are able from year to year to furnish a class of bulls which are steadily improving the general breed of the district." Darwin presented this quotation to illustrate "the great principle of division of labor" rather than that of selective diffusion from superior herds.

I do not mean to imply that Virgil, the ancient Irish author and Mr. Wilson recognized an important aspect of selection overlooked by Darwin. He undoubtedly recognized this aspect but the grading up of inferior stock by sires drawn from superior herds had no such clear analogy to anything happening in nature as did selection among individuals. It was moreover, impossible to grasp fully the qualitative difference between the merely *genic* consequences of selection among individuals and the *organismic* consequences of selection among differentiated herds, before the mechanism of heredity had come to be understood. This is still not grasped by those who urge strongly the importance of selection for coadaptation but reject the only process, interdeme selection, by which this can occur in nature under biparental reproduction.

Studies of the breeding history of the Shorthorn breed of cattle by means of a previously devised inbreeding coefficient (Wright, 1923; McPhee and Wright, 1925) led directly in 1925 to the two level shifting balance theory of evolution in nature, though publication was delayed in 1931 (abstract 1929). The general conclusions were somewhat revised in 1932 on the basis of the concept of a selective topography along the line brought out in the preceding section. The mathematical treatment in the 1931 paper dealt only with certain aspects of the simplest model. This was remedied and conclusions on various special aspects arrived at in papers in the next two decades but the general conclusions still held (cf. Wright, 1977).

These conclusions had to do with character change within species (microevolution). I had, however, accepted from the first the concept of speciation as reproductive isolation. I suggested in papers in 1940 (abstract 1938) and 1941*a* that incipient speciation from chromosomal rearrangement depends on an extreme pattern of population structure that is also very favorable for character changes by means of peak-shifts.

I tacitly treated macroevolution as merely an extension of evolution within species in my early papers but in reviews of books by Willis (Wright, 1941*b*), Goldschmidt (Wright, 1941*c*) and Simpson (Wright, 1945), all concerned especially with macroevolution, I held that the determining factor was in general an unusual ecological opportunity, not any sort of unusual mutation, an opportunity consisting of the occurrence for one reason or other, of vacant ecological niches, more or less related to that occupied by the species in question. The occupation of these in a rapid adaptive radiation constituted the origin of a new higher taxon. These concepts will be elaborated in the following sections.

Speciation

Discussion of speciation had best begin with the recognition that the term "species" has come to mean something very different, at least in principle, to neontologists from what it is possible for it to mean in practice to paleontologists. Before the beginning of the present century, there was no such divergence. The species were the kinds of organisms, distinguishable by clear-cut differences in morphology (excluding "varieties" known to occur within progenies).

It came to be recognized by such systematists as Osgood (1909) that reproductive isolation and thus incipient evolutionary branching, constituted a criterion of more significance biologically. A species came to refer to a population or group of intergrading populations, reproductively isolated from all other such populations.

Intergrading populations might differ greatly at their centers, but should be designated as merely subspecies, while ones that could be demonstrated to be reproductively isolated, even though showing no consistent morphological difference, should be considered separate species.

There are, of course, many intermediate cases, difficult to classify, but the identification of the branching points of the evolutionary process as accurately as possible came to be considered the primary objective.

This concept necessarily breaks down in the attempt to name successive species in a chain along which the morphological differences ultimately become so great that recognition of speciation becomes imperative. If change has occurred at a uniform rate, the boundaries between species are necessarily arbitrary. If, on the other hand, there have been periods of apparent stasis, separated by apparently abrupt, or at least very rapid, change, the boundaries are made most conveniently at the latter times.

Reproductive isolation may be brought about in several different ways (cf. Dobzhansky, 1970): (1) union of egg and sperm from the two populations may be prevented in various ways; (2) if fertilization occurs, normal development may fail because of imperfect cooperation of the two heredities; (3) chromosome rearrangements may interfere with normal meiosis, leading to more or less aneuploidy and thus incipient separation; and (4) there may be nucleo-cytoplasmic incompatibility which I will not discuss further.

Under the first head, mating may be prevented by geographic isolation, by difference in the breeding seasons, by difference in ethological patterns such as courtship, by ecological difference within the same region or by anatomical incompatability. Finally there may be biochemical bars to fertilization.

Under the second head, faulty development or low fecundity may occur in F_1 but if F_1 is normal, the irregular proportions of the components of the two heredities in F_2 and later may lead to enough faulty development or low fecundity to bring about at least incipient speciation.

Under both of these heads, the difference may be due either to a single locus or may require passage of a threshold after accumulation of slight effects at many loci. There is no essential difference from microevolutionary changes except in that there is some contribution to reproductive isolation.

Chromosomal differences are conveniently divided into balanced and unbalanced. The latter includes duplications and losses either of whole chromosomes or of portions down to single loci. The unlikelihood of speciation involving whole chromosomes has already been touched on in connection with de Vries' *Oenothera* mutations.

Deficiencies of any extent are usually lethal when homozygous and thus also have little or no significance for evolution. Small duplications on the other hand, are usually viable even as homozygotes. Typically they have effects similar to those of gene mutations and are transmitted as if Mendelian genes. Many of them probably become inactivated ultimately. Those that persist tend to become differentiated and increase the stock of loci. They are undoubtedly important in evolution but not with respect to speciation.

This brings us to the balanced chromosome changes. Here, as noted earlier, we encounter a real abrupt species-forming mechanism, the duplication of the entire genome. If occurring in a hybrid between species whose chromosomes have become so differentiated that none of them pair in meiosis, amphidiploids are formed, capable of breeding true to the hybrid phenotype and reproductively isolated from both parent species because of the sterility of the triploids resulting from backcrosses. There is no doubt that a great many species of plants, though few of animals, had this origin. On the other hand, the autotetraploids formed from doubling the genome of a single species differ little from the parent in phenotype. They can reproduce their type and produce sterile triploids in backcrosses but the sets of four chromosomes cause irregularities in meiosis. They are, no doubt, responsible for many new species but not as many as amphidiploids. Allotetraploids with pairing of some but not all chromosomes resemble full amphidiploids in originating a morphologically new species but resemble autotetraploids in having some irregularity in meiosis.

Balanced chromosome rearrangements include inversions and translocations of various sorts. Paracentric inversions, at least in *Drosophila* and some grasshoppers, suffer very little reduction in fecundity. They are important in evolution by permitting segregation of chromosomes, or at least large blocks, as wholes. They permit adaptation to different ecological niches and thus increase the adaptability of the species, but are not involved in speciation.

Pericentric inversions and translocations typically lead to significant reduction of the fecundity of heterokaryons, 50% in the case of a typical reciprocal translocation, and thus to incipient speciation. They may be important in speciation for this reason even though the character changes (from position effects) are slight or absent.

According to M. J. D. White (1978): "Over 90 percent (and perhaps over 98 percent) of all speciation events are accompanied by karyotypic changes and—in the majority of these cases, the structural chromosomal rearrangements have played a primary role in initiating divergence."

On the other hand, there are many cases in which a chain of intergrading subspecies has returned on itself in a circle and it is found that the overlapping populations coexist without interbreeding as if distinct species (Osgood, 1909; Mayr, 1963). Extinction of the intermediates would elevate them to this rank without any change whatever in themselves. These cases indicate that not all speciation depends on chromosomal rearrangement.

Returning to the latter, there is a problem as to how a new chromosomal rearrangement can pass the barrier imposed by strong selection against the heterokaryons. White (1978) and Hedrick (1981) lean to meiotic drive from asymmetrical segregation, as the explanation.

Fixation by accidents of sampling is, however, another possibility. It can occur only in extremely small colonies (Wright, 1940, 1941*a*). The most favorable situation is that in a region in which there are numerous colonies, subject to frequent extinction and refounding by stray fertilized females from the more successful ones. Since this is also a situation especially favorable to peak-shifts, there should be a strong correlation between speciation by the above process and favorable character changes.

Studies of the differences between closely related species have made it clear that reproductive isolation usually involves several processes (review by Dobzhansky, 1970). It is clear that incipient reproductive isolation, whatever its cause, tends to be made complete, in one way or other, by natural selection against individuals involved in hybridization.

The general conclusion of this section is that speciation may take place in a great many different ways that have nothing in common except the promotion of reproductive isolation and hence branching of the evolutionary process. The effects of speciating events on other characters range from zero where the event is merely the extinction of intermediates in a chain of subspecies, to abrupt and great in the case of amphidiploidy, but in general the effects on characters are at the microevolutionary level.

The Higher Categories

The only aspect of the evolution of the higher categories of which the actual genetics is fairly clear, is the course of substitution in the amino acid sequences of several proteins over long periods of geologic time (Zuckerkandl and Pauling, 1965). The rates of substitution separating hemoglobin β of man from the globin of the lamprey (1.3 per site per billion years), hemoglobins α or β of several mammals from α of a bony fish (carp), and either α or β of several mammals with each other, are surprisingly uniform (grand average 1.1 per site per billion years) (Kimura, 1969).

This is largely true of substitutions in the amino acid sequences of cytochrome-c throughout eukaryotic evolution since the separation of the higher plants, insects, lower chordates, reptiles, birds, and mammals from the fungi some 1.3 billion years ago and the separation of the higher groups from each other (Fitch and Markowitz, 1970).

The rates in the nonessential portions of any given protein have been so uniform that Kimura has held that natural selection must be ruled out and has proposed that the substitutions are the cumulative consequences of accidents of sampling. While most others advocate mass selection (e.g., Ayala, 1975) and I have proposed the shifting balance process (Wright, 1978), the near uniformity of rate over a period encompassing the origins of kingdoms and phyla implies continuity of the evolutionary process.

The evolutionary potentialities of most species are probably restricted to very slow, gradual progress in adaptation to the single ecological niche which they occupy, by the occupancy of all related niches by other species. From time to time, however, an opportunity is presented for adaptive radiation into other niches. Such ecological opportunities are, it has seemed to me, much the most important cause of the origin of higher categories (Wright, 1941*a*, 1941*b*, 1945, 1949). The occurrence of any particular kind of mutation (usually recurrent) is of little significance in the absence of such an opportunity.

Such an opportunity arises on entry of the species into a region in which niches, related to its own, are unoccupied. The remarkable adaptive radiation of families of marsupials in Australia and of families of several primitive orders of mammals in South America, both in the early Cenozoic, are examples. At a lower level is the adaptive radiation of the Geospizidae from a species of ground finch that reached the Galapagos Islands (that attracted Darwin's attention) and that of the Drepanididae from a species of bird (honeycreeper) that reached the Hawaiian Islands.

A similar opportunity is presented to the survivors of a catastrophe that has caused extensive extinction of species. The extraordinary adaptive radiation of the orders and families of mammals in the Paleocene and Eocene following the worldwide extinction of the dinosaurs and many other forms at the end of the Mesozoic is an example. The mammals had existed as a small group for some hundred million years without much differentiation before this opportunity occurred.

Of special importance, however, are the cases in which evolution along a restricted line happens to lead to an adaptation that turns out to open up an extensive new way of life. The evolution of a motile, tadpole-like larva of a certain type of sessile echinoderm seems to have opened the way, by means of neoteny, to the active life of the chordates other than tunicates. Later modification of the first gill arch made possible an effective jaw, leading to the adaptive radiation of the fishes. Modification of the ventral fins to permit locomotion on land and of the swim bladder for respiration in the air, enabled crossopterygian fishes to move from one drying pool to another, a peripheral niche for a fish, but this opened up life on land and the adaptive radiation of the amphibia. Similarly certain specializing adaptations later led to the adaptive radiations of the reptiles and birds.

A species presented with an opportunity to invade an unoccupied niche would be able to use mutations with more drastic effects than the quantitative variants used before and to do so sometimes in spite of rather unfavorable side effects because of the absence of competition. These may in a sense be considered to be the species mutations postulated by Goldschmidt but it is the ecological opportunity, not mere occurrence of this sort of mutation, that leads the way.

It should be added that much more drastic mutations may be utilized and fixation may be much more rapid if the mutation is recurrent and comes to be associated with otherwise neutral modifiers that remove its inevitable deleterious side effects. In all three of the book reviews referred to earlier (Wright 1941*b*, 1941*c*, 1945), it was noted that the origin of a higher taxon is expected to be an "explosively" rapid process under the shifting balance theory. This has been reiterated in many later papers.

The reorganization required for the origin of the highest categories may seem so great that only "hopeful monsters" will do. Here, however, we must consider the size and complexity of the organisms. Such changes would probably have been impossible except in an organism of very small size and simple anatomy. I have recorded more than 100,000 newborn guinea pigs and have seen many hundreds of monsters of diverse sorts (Wright, 1960) but none were remotely "hopeful," all having died shortly after birth if not earlier. Yet among nine specimens of a small trematode (*Microphallus opacus*) about 1.5 mm long, of which I made serial sections in my first research project (Wright, 1912), one was highly abnormal in form and had two large ovaries instead of only one. It would probably have been considered a monster if it had been a large complicated organism, but it was apparently flourishing as well as the others before it was fixed.

It would hardly be possible for a typical clam to be derived from a typical snail by mutation or a succession of mutations but it is not unreasonable to suppose that a small protomollusk with a single simple shell, produced a mutant in which this was divided laterally into two and that the pelecypods evolved from this mutant type. All of the classes of mollusks could reasonably have arisen in somewhat this way. All of the phyla of multicellular invertebrates and most of their classes probably arose from small rather simple forms, most of them not long, in geologic terms, after the origin of the eukaryotic cell.

The pattern of evolution thereafter was probably one of very gradual orthogenetic progress along many lines with occasional appearance of ecological opportunities of the sorts discussed above, followed by explosively rapid divergence of species in exploiting these. The group could be considered to constitute a new genus unless secondary divergencies raised the level of the group to the family and tertiary divergencies, perhaps, raised it to the level of a new order, all within no more than a moment in geologic time. At some level, major divergence ceases, and the species settle down with only minor differentiation of new species to slow orthogenetic progress (Wright, 1949).

SUMMARY

The implications of the shifting balance theory with respect to the course of evolution agree in the main with the pattern indicated by the fossil record, according to Simpson in 1944 (cf. Wright, 1945), reiterated by Gould and Eldredge (1977) in their statement quoted in our introduction: "Punctuated change dominates the history of life: evolution is concentrated in very rapid events of speciation (geologically instantaneous even if tolerably continuous in ecological time." I would, however, substitute the phrase "of character change" for "of speciation." Character change and speciation (in the sense of reproductive isolation) are wholly different

phenomena genetically, even though closely correlated in occurrence.

There is agreement only with the first but not the last part of the sentence also quoted in our introduction, from Gould (1980): "Evolution is a hierarchic process with complementary but different modes of change of its three leading varieties: within species, speciation and patterns of macroevolution." The shifting balance process is a two-level one (selection among individuals and among differentiated local populations), but no difference is assumed in the rates of minor and major mutation during the phases of near-stasis and rapid change. The interpretation of these phases under the shifting balance theory is in terms of differences in ecological opportunity. Speciation tends to accompany rapid change both because each of these processes tends to bring about the other and because speciation from chromosome rearrangement and peak-shifts is favored by the same population structure (numerous small colonies subject to frequent extinction and refounding by stray individuals from the more flourishing colonies).

According to the shifting balance theory the determining factor for rapid change, and the origin of a new higher taxon that usually accompanies such change, is the presence of one or more vacant ecological niches, whether from entrance of the species into relatively unexploited territory or from its survival after a catastrophe has eliminated other species occupying related niches, or from gradual attainment of an adaptation that opens up a new way of life.

We consider first the course of evolution of a species restricted to a single niche (because of occupancy of all related niches by other species) and living for a long time under relatively unchanging conditions. If its population density is great or there is a wide dispersion of offspring, a state of near-stasis should soon be reached as it comes to occupy the most available selective peak. It cannot move down from this against natural selection to reach a saddle leading to a higher selective peak.

If on the other hand, the species occupies a wide range but in part at least only sparsely and with restricted dispersion, the operation of the shifting balance process leads to gradually improving adaptation of the species as a whole, by means of successive minor peak-shifts and selective diffusion from them.

Still with only a single niche but under continuously changing conditions, there is continual readaptation largely of the treadmill sort, change without progress. A very gradual improvement is, however, to be expected as the species is shuffled into the higher general regions of the selective topography. This occurs even in populations that are effectively panmictic. In such a population, the rate of change is approximately according to Fisher's fundamental theorem except as qualified by frequency dependent selection or linkage disequilibrium. If, however, population structure permits significant operation of the shifting balance process, readaptation is facilitated by minor peak-shifts, not allowed for in Fisher's theory.

In cases in which new ecological niches become available in any of the ways referred to, their occupation may require allelic substitutions with major effects. Such substitution may occur in spite of imperfect adaptation and the inevitable deleterious effects of any major change, because of the absence of competition, but is greatly facilitated if population structure is favorable to peak-shifts, involving the gene in question and one or more nearly neutral modifiers that tend to eliminate the more deleterious of the side effects. Such major peak-shifts are most likely if the major mutation is recurrent and thus becomes available, sooner or later, wherever a favorable modifier or a pair of such modifiers, reaches sufficiently high frequencies for crossing of a saddle that pulls the major mutation to occupancy of the higher peak.

Such occupancy tends to give incipient reproductive isolation, followed by full speciation under selection against hybridization. On the other hand, speciation may come first, because of geographical isolation of a portion of the species or local establishment of a chromosome rearrangement or other cause, and be followed by occupancy of the new niche by means of a major peak-shift. In either case, the decisive peak-shift occurs within a species and is likely to be accompanied by minor peak-shifts that improve adaptation.

The occupancy of new niches, accompanied by speciation, constitutes the origin of a new higher taxon. This may merely be a new genus but if there is extensive adaptive radiation into new niches, the array may constitute a new family, new order, or very rarely a new class or phylum.

It may seem that mutations with impossibly drastic effects would be required for the origins of the higher of the taxa. Such origins, however, probably all occurred from species, the individuals of which were so small and simple in their anatomies that mutational changes, that would be complex in a large form, were not actually very complex.

The final conclusion is that the evolutionary processes indicated by the fossil record can be interpreted by the shifting balance theory without invoking any causes unknown to genetics or ecology.

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