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Change of Genetic Environment and Evolution

THAT mutation, recombination, selection and isolation are the four cornerstones of evolution is now generally acknowledged. The way in which these factors interact in the various evolutionary processes and the role played by diverse subsidiary factors are, however, by no means fully clarified. In particular, the role of one factor, a sudden change in the genetic environment, seems never to have been properly considered. That this factor might be exceedingly important in the evolutionary process occurred to me when studying a puzzling phenomenon, frequently encountered by the systematist, the conspicuous difference of most peripherally isolated populations of species.

Let us look, for instance, at the range of the Papuan kingfishers of the *Tanysiptera hydrocharis-galatea* group (Fig. 1). It is typical for

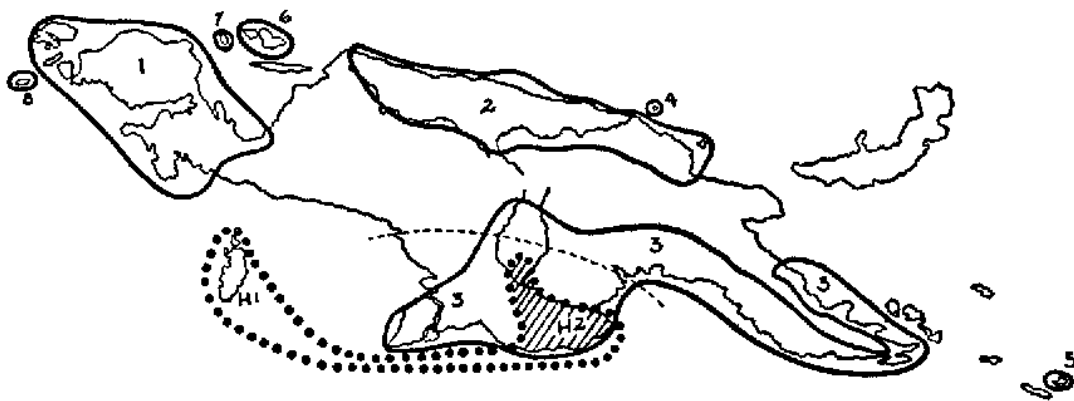


FIG. 1

hundreds of similar cases. On the mainland of New Guinea three subspecies occur which are very similar to each other. But whenever we find a representative of this group on an island, it is so different that five of the six Papuan island forms were described as separate species and four are still so regarded.

EVOLUTIONARY GENE-FLOW

For such a striking dissimilarity of peripherally isolated populations two reasons are usually cited: difference of physical and biotic environment or genetic drift. It seems to me that neither of these factors nor a combination of the two can provide a full explanation, even though both may be involved.

Let us first look at the possible effects of the environment. New Guinea is a tropical continent. If it were projected on the map of Europe, it would reach from England to the Black Sea. In north-western New Guinea (near the Equator) it is exceedingly humid and without pronounced seasons; nearly the same amount of rain falls in every month of the year. In south-east New Guinea (Port Moresby) most of the rainfall is condensed into a short rainy season, while it is dry the rest of the year. The biotic environments in the extreme areas of New Guinea are as drastically different as the physical environments, only heavy rain forest in some areas, much monsoon forest in others. Still, the populations of *T. galatea* which occur at the two ends of New Guinea are hardly distinguishable.

A similar situation is found in numerous other species; if there are subspecific differences within New Guinea they are often merely matters of degree. We can generalize and say that strong environmental differences may not lead to conspicuous morphological differentiation. (This statement does not deny the physiological adaptation of the populations to their respective ranges.)

What is the situation with respect to the islands? Numfor, Biak, Koffiao, and Rossel are less than 100 miles from the New Guinea shelf, and each island is approximately in the same climatic district as the nearest part of the mainland of New Guinea. In spite of this similarity of the environment they are inhabited by populations that are phenotypically strikingly different. Thus, selection alone cannot give the full answer.

Drift—in the ordinary sense—cannot be the complete answer either because in many cases very large islands are involved with populations consisting of tens of thousands, hundreds of thousands, or even millions of individuals (see below).

The phenomenon of conspicuous divergence of peripherally isolated populations, so well illustrated by the *Tanysiptera hydrocharis-galatea* group, is familiar to every taxonomist. Scores, if not hundreds, of examples can be found in every monograph or checklist. We may mention merely a few more:

The kingfisher *Halcyon australasia* is virtually without geographical

variation all over Australia (*sancta*), but has subspecies on New Zealand, New Caledonia, the Loyalty Islands, and very strikingly different subspecies in the Lesser Sunda Islands.

The hawk *Accipiter novaehollandiae* shows little evidence of geographical variation in New Guinea but has endemic subspecies on many islands east and west of New Guinea, five subspecies in the Bismarck Archipelago, and five in the Solomon Islands, in a total land area considerably smaller than the area of New Guinea.

A comparison of the disrupted Mediterranean ranges of many amphibians, insects (e.g. *Bombus*), and lower invertebrates (e.g. *Dugesia gonocephala*) with the contiguous ranges of the same species in the temperate parts of the Palearctic region shows the same. The lizards (*Lacerta*) of the Mediterranean area have only few slight subspecies on the mainland, but scores on islands. The four species of *Peromyscus* most closely related to *P. maniculatus*, are (or have been until recently) peripherally isolated.

It would lead too far to quote here more cases; all would merely be variations on the same theme. I have spoken in earlier publications of the "law of peripheral populations." This is not entirely accurate. Peripheral populations are not outstandingly different if they are part of a continuous series of populations. Only "peripherally isolated" populations show the pronounced deviations from the species "type," illustrated by the above-given examples.

THE STRUCTURE OF SPECIES

It is evident that there are two types of geographical variation.

(1) Ecotypic variation.—This variation adapts to the local environment populations which are members of a continuous series of contiguous populations. Owing to the never-ceasing gene-flow through such a system these populations are merely variations on a single theme, even though they may be sufficiently distinct to have received the attention of the taxonomist and to have been described as subspecies. Goldschmidt (1940: 182) has singled out *such* subspecies to attack the concept of the subspecies as incipient species.

"The differences between two subspecies are usually clinal, merging into each other. . . . While the characters of subspecies are of a gradient type, the species limit is characterized by a gap. . . . The subspecies do not merge into the species either actually or ideally. . . . Subspecies are actually, therefore, neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species."

These statements are correct so long as they are applied only to those

subspecies that are subdivisions of a widespread array of continuous populations. Such subspecies, indeed, are not incipient species. Incipient species require isolation (see under 2).

The variation in such a system of contiguous populations is characteristically "ecotypical," that is, adaptive within the established "type." It is characterized by clines, and most variation within such a system obeys the various ecological rules. That the evolutionary changes due to this type of variation do not necessarily lead to species formation has been long recognized by systematists.

"Clines indicate continuities, but since species formation requires discontinuities, we might formulate a rule: *The more clines are found in a region, the less active is species formation.* We can prove this if we compare regions in which clines are frequent with those in which they are rare" (Mayr, 1942: 97).

Nevertheless there may be an accumulation of considerable genetic differences at the opposite ends of a cline. Nothing illustrates this better than the well-known overlapping circles of races as well as reduced fertility among geographical races. A secondary isolation of such populations may quickly lead to completion of species formation (see below).

(2) "Typrostrophic"* variation.—Isolated populations, such as the ones illustrated above, show a type of variation so different from that of contiguous populations that we may be dealing with something entirely new. These peripheral populations often have not only the characteristic features of incipient species, but what is more important they often are species or incipient species of an entirely new type. That is, they may have morphological or ecological features which deviate quite strikingly and unexpectedly from the "parental" pattern.

A comparison of the two kinds of geographical variation, as well as of the populations produced by them, leads inevitably to the question: What is the factor that distinguishes the isolated population from the population which is part of a large group of populations? We shall attempt to answer this in the next section.

THE EFFECT OF GENE-FLOW

Of the many factors that are of importance to the evolutionist, gene-flow is perhaps the most neglected one. In a given wild population genetic novelties may occur through mutation or through immigration from outside populations (with recombination making available an unlimited assortment of these factors). While there are numerous studies on all aspects of mutation, virtually nothing is known on the genetics

* A term used by the paleontologist Schindewolf to denote the origin of a real evolutionary novelty, a new "type."

of gene-flow. In fact, the technique of the geneticist is built on the avoidance of gene-flow or of immigration, hence the stoppers on *Drosophila* bottles and the wire netting of mouse cages. Whenever gene-flow occurs in spite of all precautions it is called "contamination," and the contaminated cultures are carefully destroyed. Since the genetics of gene-flow has not yet been studied in the laboratory, a determination of its importance depends either on field work, such as done by Timofeeff-Ressovsky, Dobzhansky, and Ford, or on guesses. In orthodox genetics the effects of gene-flow are usually presented as the addition of the immigrated genes to the gene pool of the local population and their subsequent gradual elimination in so far as they are inferior to the other genes of the gene pool. Such a purely additive treatment of gene-flow is not correct, as we shall presently discuss, since it neglects the fact that a gene pool is not an unconnected "pile of genes," but a well-integrated, balanced system.

For a further analysis of this problem it is of vital importance to determine how great the amount of gene-flow is as compared with mutation. I venture the guess that the total amount of genetic change contributed by immigration to a given local breeding population of a prosperous widespread species is many times that contributed by mutation occurring among the members of this population.*

Since gene-flow is due to the movement of individuals which are the carriers of genes, the phenomenon of dispersal becomes of interest to the geneticist. This was clearly realized by Timofeeff-Ressovsky, Dobzhansky, Ford, and other population geneticists. To measure the amount of gene-flow through a study of dispersal, as was attempted by naturalists and geneticists, encounters various difficulties.

The chief difficulty is that at best one can determine only what percentage of individuals in a population are immigrants, but not how genetically similar or different these immigrants are as compared with the members of the "native" population. The amount of genetic difference depends largely on the distance (within the species range) from which these immigrants have come. The usual assumption is that individuals settle within a predictable and rather narrow circle around their place of birth. In studies of non-colonial bird populations it is usually found that 30-40 per cent of the individuals that newly settle in a study area are born within the study area, the remainder being new arrivals. It is usually assumed that most of these come from the immediately adjacent area. This assumption is based on the further assumption that the dispersal curve is essentially a normal curve. Bateman

* It has no bearing on the present argument that the genetic differences of the immigrants are ultimately also due to mutation.

(1950), however, has summarized numerous data, including his own and those of Dobzhansky and Wright, which indicate that the dispersal curve is not normal but leptocurtic and probably not even symmetrical but strongly skewed. In fact, so far as birds are concerned, there are some indications that the populations in many species are composed of two kinds of individuals, those with a strong locality sense and those with little or none. It is possible that the latter, perhaps up to 10–30 per cent of the population (differing from species to species) may settle in any suitable spot up to 100 kilometres or more of the place of birth. Dobzhansky and Wright (1947) likewise suggest for *D. pseudoobscura* the possibility of a composite dispersal curve. Previous calculations of the amount of gene-flow have tended to ignore this minority of long-distance colonists, which are nevertheless of considerable importance in counteracting the effects of local selection-pressures. Such long-distance dispersal has been established not only by bird banders, but is very characteristic for the spreading of expanding species like the Serin Finch (*Serinus serinus*) or the Ring Dove (*Streptopelia decaocto*). Individuals from far distant populations, even though few in number, are apt to contribute many new genetic factors to a population.

In previous discussions of the genetic effects of long-range dispersal attention was focused almost entirely on the fate of the alien genes in the new gene-complexes. Since they are usually from regions with rather different selective factors, such alien genes are apt to be of inferior viability in the new environment and will be eliminated sooner or later. Little or no thought, however, was given to the effects of these alien genes on the relative viability of the genes of the gene-complex into which they were introduced. It appears probable that the frequent introduction of such alien genes into a gene pool will lead to selection of such "native" genes as are tolerant to combination with such alien genes, that is, which produce viable heterozygotes with a great assortment of alien alleles or gene combinations.

A further effect of such gene-flow is that it disturbs the integration of local gene-complexes in response to local selection-pressures. Although all populations are somewhat ecotypical, such infiltration of alien genes may prevent a complete response of the gene-complex to the local selection-pressure and may therefore act as a conservative ("stabilizing") element in the whole evolutionary picture.

Several proofs can be cited for the reality of this effect of gene-flow. Dr. R. A. Fisher kindly called my attention to a case described by Turesson where in a specialized habitat no specific ecotype developed because the location was too small and therefore too much exposed to gene-flow from adjacent localities. But, even where a local ecological

race develops, its great variability is evidence for the continued inflow of genes from adjacent populations (see the cases described by Clausen, Hiesey and Keck and those summarized by Stebbins, 1950).

Particularly instructive are the races of small mammals in the southwestern United States that live on lava flows. Endemic blackish races develop on small lava-flows only if they are completely surrounded by sandy desert. If they are in contact (on more than $\frac{1}{10}$ of their circumference) with areas of desert rocks there will be too much gene-flow to permit the development of endemic black races (Dice and Blossom, 1937; Hooper, 1941). When two soils of different colours come in contact, the effects of gene-flow will be noticeable for many miles on either or, at least, on one side of the zone of contact as shown by Sumner, Dice, Blair, Hayne, and others. It is evident in all these cases that local selection-pressure is partially neutralized by the effects of gene-flow.

Selection will be able to work unimpeded only if the selective agent simultaneously eliminates dispersal. Contact poisons for insects, as for instance, DDT are indeed such an agent. In a population, which is being selected for DDT resistance, all non-resistant flies that enter the population are eliminated before they can counteract through their genes the genetic process of the continued improvement of the DDT resistance.

These considerations finally elucidate a problem which has been a great puzzle to all naturalists and zoogeographers, namely, the problem of the borderline of species. The species-border is the line beyond which the selective factors of the environment prevent the successful reproduction of the species. However, it is well known to naturalists that through dispersal from the species range a considerable number of individuals settle down annually beyond the normal species-border where they attempt to reproduce. Some even succeed in establishing new colonies, but these are sooner or later eliminated in an adverse season. This has the result that the species border, though fluctuating, remains at a dynamic, stable line. What has been puzzling is the fact that the natural selection in the belt immediately beyond the previously existing borderline has not been able to produce a population adapted to the local conditions, in the same way as the application of DDT produces a DDT-resistant strain of flies. This is particularly puzzling since conditions beyond the borderline differ from conditions within the species border usually only slightly and in degree. This puzzle can be considered solved if we assume that this process of adaptation by selection is annually disrupted by the infiltration of alien genes and gene-combinations from the interior of the species range which prevents the selection of a stabilized gene-complex adapted to the conditions of the border region.

THE GENETIC ENVIRONMENT

The reason for the importance of gene-flow and of isolation is implied in much of the recent genetic work but has never been fully stated. Classical genetics studied the genetic changes at a given gene locus as well as the physiological and selective effects of such changes. Since—for the sake of simplifying the analysis—each locus was studied separately, the genetic factors of an organism were treated as so many beans in a large bag. That this is not so is now known to every geneticist, but “bean-bag” thinking is still widespread. The fact is, of course, that genes do not exist in “splendid isolation,” but are parts of an integrated system. In order to appreciate the complexity of this system it is necessary to recall some of the recent studies.

The normal model of genetic change, presented in most evolutionary studies, is that of a gene p , originally in homozygous condition, on which mutation pressure (or immigration pressure) is exerted by an allele q . A maximum of 50 per cent heterozygotes may occur under these conditions (if both alleles are of equal frequency). Numerous studies indicate, however, that such a situation in which there are only two competing alleles may be the exception rather than the rule. At many loci there are simultaneously three, four, five, or more alleles available.

Two alleles produce one kind of heterozygote, 3 alleles 3 (ab, ac, bc), 4 alleles 6, 5 alleles 10, and 6 alleles 15 kinds of heterozygotes. The series expands very rapidly: 15, 21, 28, 36, 45, 55, etc. The number of homozygotes (under the simplified assumption of equal frequency of the various alleles) is $\frac{1}{n}$, so that with 5 alleles present, only $\frac{1}{5} = 20$ per cent of the genotypes might be homozygotes. It is quite evident from these considerations that the heterozygotes are of much greater importance in such a system than the homozygotes, and the more so, the greater the number of alleles.

In view of the considerable morphological uniformity of samples from most natural species, it may be denied that multiple alleles are frequent in nature. This may be true for some loci, but it is certainly not true for others. Even alleles that produce lethal homozygotes may be indistinguishable as heterozygotes, and it is known that lethals are frequent in many wild populations. A consideration of the so-called *isoalleles* (Stern) is important in this connection. Isoalleles are alleles that are phenotypically indistinguishable in homozygous condition from the “normal” wild-type allele but have different expression when placed in heterozygous combination with tester alleles. Only few studies have been made so far to determine the frequency of isoalleles (Stern, Timofeeff,

Spencer), but, as Spencer's summary indicates (Spencer, 1944), isoalleles appear to be amazingly common at some loci. The fact that there are different frequencies of hereditary diseases in different human races may in part also be due to different mutation-rates in different isoalleles.

Still more important than are the multiple alleles is the fact that during development all genes are members of a team. Not only has every gene that has been thoroughly studied been found to have pleiotropic effects, but it has also been found that every character is produced by the joint action of many genes. It is immaterial in this connection what particular genetic theory one adheres to: major genes and modifiers, genes and polygenes, switch genes and gene complexes, position effects, and non-localized genes. They all agree in the essential point which is that the action of a given gene is strongly influenced by its genetic background, its genetic "co-actors." And what is true for the function of a gene is true also for its selective value. A gene which is of high selective advantage on one genetic background may be selected against on another genetic background. *The selective value or viability of a gene is thus not an intrinsic property but is the sum-total of the viabilities on all the genetic backgrounds that occur in a population.*

THE COADAPTED SYSTEM

The concept that the viability of a given allele depends on its genetic background is not new. It has been emphasized by several students of this problem. Sewall Wright (1931:155), for instance, stated: "The selection coefficient of a particular gene is really a function not only of the relative frequencies and momentary selection coefficients of its different allelomorphs, but also of the entire system of frequencies and selection coefficients of non-allelomorphs." Recently Dobzhansky has supplied experimental proof for coadapted selective changes in chromosomes or gene-arrangements (Dobzhansky, 1950; Dobzhansky and Levene, 1951). The relativity of such viabilities is most convincingly illustrated by the findings of Wallace and King (1951) in irradiated *Drosophila* populations. They find "that while an examination of the individual chromosomes of a population may reveal that these are generally "deleterious" when homozygous, an examination of pairs of unrelated chromosomes from the same population may reveal that these pairs are distinctly superior." Muller's (1948) work on dosage effects and much other genetic work points in the same direction.

Such a well-integrated, coadapted gene-complex constitutes an evolutionary unit in spite of its intrinsic variability. Any disharmonious gene or gene-combination which attempts to become incorporated in such a gene-complex will be discriminated against by selection. There is much

evidence for this, partly from experiments and partly from a study of natural populations. That the offspring of crosses among species or other only distantly related populations produce inferior gene-combinations has long been known to students of hybridization. This is often true even in cases where there is superficial heterosis. In the cases of back-crosses of F_1 hybrids with one of the parents, it is often found that only those back-crosses are viable that are close to the parental type.

That gene-complexes are well integrated units is the explanation of a phenomenon that has long been a puzzle to naturalists. There are many cases known where two incipient species come together in an allopatric zone of hybridization after a previous extrinsic barrier has been removed. Sometimes this zone is wide, but more often it is very narrow, even though all the available evidence indicates that the zone has existed for thousands of years. The border between the carrion crow and the hooded crow (*Corvus corone* and *cornix*) is an excellent example. Peus (1950) discusses such a case in a flea. In these and many similar cases it appears that the gene-complexes which come together are so well balanced within themselves that combinations with alien genes lead to combinations of inferior viability and are eliminated by selection. This counter-selection reduces introgressive gene-flow drastically.

Even a gene-mutation which leads to an improvement in the phenotype may have difficulties in such a system because it will take a long period before it is fully fitted into the total pleiotropic-buffered gene-complex. Simpson's findings that the tooth elongation in fossil horses was of the order of only one millimetre per one million years is a suitable illustration of this process. To be of real value such an improvement in the teeth has to be correlated with a strengthening of the upper and lower jaw and with numerous other readjustments of the skeleton, the muscles, and presumably even the viscera and the nervous system. All these changes require a rather thorough overhauling of the total gene-complex. It is not often that selection permits a single structure to rush far ahead of the other parts of the system to which it belongs.

The better integrated such a gene-complex is, the smaller the chance that a novel mutation will lead to an improvement. As Schmalhausen, Heuts, and others have pointed out, much of selection is stabilizing. A widespread species, with many local populations among which there is active gene exchange, tends to be very conservative.

Even though a species may have many local races (ecotypes), it arrives sooner or later at a geographical line, its species border, beyond which it cannot expand. As stated above, and other things being equal, this appears to be due to the fact that even the border populations are tied by gene-flow to the integrated gene-complex of the main body of the

species. This applies to horizontal as well as to vertical (altitudinal) distributions. In most species there is a limit to ecotypic adaptation. It has long been known, for instance, that the validity of the so-called ecological rules (Bergmann's rule, Allen's rule, etc.), so far as it exists at all, is restricted to intraspecific variation. Subspecies of birds living in a cool climate tend to be of larger body size than subspecies living in the warmer parts of the range of the same species. However, a more northerly *species* is by no means always larger than its nearest more southern relative. The same is true for altitudinal variation. As Rand and others have shown, there is a steady increase of size with altitude within most sedentary species of birds with a wide altitudinal range. However, again, this does not necessarily apply to full species which replace each other altitudinally, as Dr. Rand pointed out to me. In 15 such pairs of bird species from New Guinea, the higher species was larger in 5 cases, of equal size in 3 cases, and smaller in 7 cases. It appears as if in these latter cases expansion into the higher altitudes was made possible on an altogether different physiological (and hence genetic) basis. The gene-flow through the lower altitude species was too stabilizing to permit range expansion into the higher altitude. (There is enough altitudinal overlap between the members of nearly all of these pairs to permit neglect of Gause's rule in this particular problem.)

CHANGES OF THE GENETIC ENVIRONMENT

The make-up of the well-integrated gene-complex, discussed in the previous section, as well as the continuous immigration of alien genes from adjacent or far distant populations, makes it evident that genes with either or both of the following two properties will be specially favoured by selection.

(1) Genes which produce heterozygotes of high viability, preferably viability superior to the homozygotes.

(2) Genes which produce viable combinations on the greatest number of different genetic backgrounds.

The former phenomenon leads to balanced polymorphism, first postulated by R. A. Fisher, the widespread occurrence of which has been abundantly confirmed in recent years. Dobzhansky and Levene (1951) have shown how quickly natural selection can produce such heterosis in cases where it was previously absent.

The selective advantage of genes that do well on a great variety of genetic backgrounds, "jack-of-all-trades" genes, does not seem to have received much attention in the genetic literature. The richer a population is in genetic factors (multiple allelic heterozygosity on many loci), the

more important such genes are. A "good mixer," rather than a good "soloist," has a tremendous advantage in such a system.

This all may change dramatically when a few individuals are taken out of the stream of genes and placed in isolation. Let us illustrate this again with reference to the kingfishers of the *Tanysiptera galatea* complex. Let us assume, for instance, that Numfor Island, previously without *Tanysiptera*, was colonized by a couple of pairs of New Guinea birds. What changed in the conditions? The climate of Numfor is much like that of the opposite coast of New Guinea, thus the selection-pressure by the physical environment will remain much as it was in the previous range. The flora is somewhat different and the fauna is somewhat impoverished but the only potentially serious predator, *Accipiter novaehollandiae*, occurs both on Numfor and New Guinea. The physical and biotic environments are thus rather similar in both places. A third environment, however, the genetic environment, is strikingly different. The Numfor population is geographically and hence also genetically completely isolated from all other populations of the species (perhaps a few New Guinea individuals may get there every ten years), while every New Guinea population is in the midst of a continuous stream of genes flowing back and forth across the entire island continent. While the number of possible contacts of a given gene with other genes is exceedingly high in New Guinea, it is drastically reduced among the founders of the Numfor population.

The total sum of the relative selective values of each allele may be changed because the number of possible genetic interactions of this allele is much reduced. To illustrate the situation diagrammatically we might group the total number of possible genetic backgrounds of the parental populations in ten classes, x_1 to x_{10} . Let us further assume that in the population there are two alleles, of which one (a_1) is of broad, general efficiency on many genetic backgrounds, while the other allele (a_2) is very superior on some genetic backgrounds but inferior or even lethal on others. We are assuming arbitrarily for the sake of illustration an extreme situation. Most genes would presumably be ranged somewhere between the extremes of a_1 and a_2 . The selective values of the two alleles a_1 and a_2 on the 10 backgrounds might be as in Table 1 on p. 169.

The total selective value of both alleles is identical, allowing for the relative frequencies (q) of the carriers of the genetic backgrounds x_1 - x_{10} in the population. If the founding of the Numfor population was made by individuals with only the genetic backgrounds x_1 - x_4 , each being present with equal frequency ($q = 0.25$), the total viability of the alleles a_1 and a_2 suddenly changes to 1.075 for a_1 , and to 2.5075 for a_2 . Instead of retaining equal viability, the viability of a_2 is now $2\frac{1}{2}$ times

TABLE I

Arbitrary values of the frequencies (q) of ten classes of genetic backgrounds (x_1-x_{10}) in a population and of the viabilities (w) of alleles a_1 and a_2 on these ten backgrounds. The total viabilities of a_1 and a_2 are about equal in this population (1.102).

	x_1		x_2		x_3		x_4		x_5	
a_1	q	w	q	w	q	w	q	w	q	w
	0.1	1.1	0.05	1.2	0.02	0.9	0.17	1.1	0.12	1.3
	0.110		0.06		0.018		0.187		0.156	
a_2	0.1	1.33	0.05	3.4	0.02	2.8	0.17	2.5	0.12	0.4
	0.133		0.17		0.056		0.425		0.048	

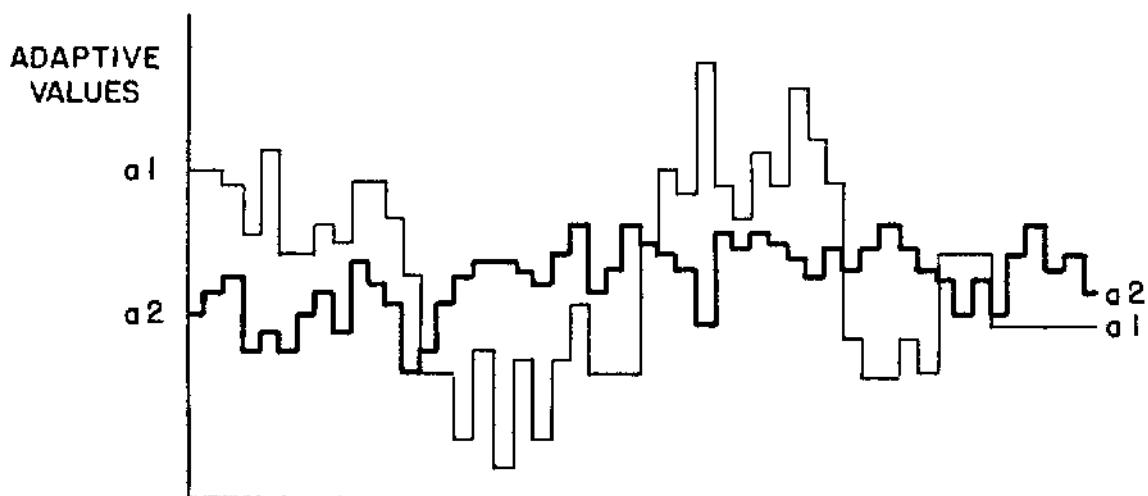
	x_6		x_7		x_8		x_9		x_{10}	
a_1	q	w	q	w	q	w	q	w	q	w
	0.09	0.4	0.07	1.4	0.06	1.8	0.19	1.2	0.13	0.08
	0.036		0.098		0.108		0.228		0.101	
a_2	0.09	0.1	0.07	1.0	0.06	0.5	0.19	0.3	0.13	0.8
	0.009		0.07		0.03		0.057		0.104	

that of a_1 . It is evident that a formidable selection-pressure will be exerted against a_1 which presumably will soon lead to its elimination from the new population. Even if the two alleles in question are less different in kind than a_1 and a_2 , it is very unlikely that their selective values will remain unchanged (Fig. 2).

One of the obvious effects of the sudden reduction of population size in the founder population will be a strong increase in the frequency of homozygotes. As a consequence, homozygotes will be much more exposed to selection and those genes will be favoured which are specially viable in homozygous condition. Thus, the "soloist" is now the favourite rather than the "good mixer."

We come thus to the important conclusion that *the mere change of the genetic environment may change the selective value of a gene very considerably.*

Isolating a few individuals (the "founders") from a variable population which is situated in the midst of the stream of genes which flows ceaselessly through every widespread species will produce a sudden change



DIFFERING GENETIC BACKGROUNDS

FIG. 2

of the genetic environment of most loci. This change, in fact, is the most drastic genetic change (except for polyploidy and hybridization) which may occur in a natural population, since it may affect all loci at once. Indeed, it may have the character of a veritable "genetic revolution." Furthermore, this "genetic revolution," released by the isolation of the founder population, may well have the character of a chain reaction. Changes in any locus will in turn affect the selective values at many other loci, until finally the system has reached a new state of equilibrium.

THE ROLE OF THE PHYSICAL AND BIOTIC ENVIRONMENT

Focusing our attention on the decisive effects of interrupted gene-flow should not make us forget the important synergistic role of selection by the new physical and biotic environment. Selection on an island differs in two ways from selection on the mainland. The selection-pressure itself is different, since the environment (particularly the biotic one!) is inevitably somewhat different. Secondly, this selection can express itself more directly because its effects are not continuously disturbed by the inflow of alien genes. Selection, then, on an island will, if anything, produce even more conspicuous results than on a mainland.

The amazingly great differences among populations of adjacent islands, e.g. *Tanysepta carolinae* (Numfor) and *riedelii* (Biak), indicate that the accidents of gene assortment during the "genetic revolution" of the isolated population may be more important than the "directive" force of the similar environment of adjacent islands.

It should be emphasized that such a "genetic revolution" in the founder population is only a potentiality but does not need to happen every time a population is isolated, if the genetic constitution of the founders does not favour it. The amount of the genetic revolution is unpredictable since it depends on many factors. It proceeds at the most rapid rate,

(1) if the parental population was particularly variable and subject to much gene-flow,

(2) if the founder population contained genes of very uneven selective values in different genetic environments and particularly genes that contribute high viability in homozygous condition,

(3) if the founders happened to have many genes of particularly high selective value in the new environment, and

(4) if the new physical and biotic environment is capable of setting up and maintaining divergence producing selective pressures and, in particular, if it permits a shift into a vacant ecological niche somewhat different from the parental one!

The fact that neither the Starling (*Sturnus vulgaris*) nor the House Sparrow (*Passer domesticus*) after their introduction in North America, nor many of the introduced agricultural pests have shown indications of a drastic evolutionary change confirms that the isolation of a population is not by itself a guarantee for a drastic change. Perhaps these colonies regained large population size too quickly. As has been shown by Ford and others (Ford and Ford, 1930), there is an increase in variability and a relaxation of selection in a rapidly expanding population. This relaxation of selection may mitigate or even counteract at first some of the effects of the sudden isolation. Perhaps this explains why there is apparently a lag between isolation and the differentiation of the isolated populations. One might expect the isolated populations to change conspicuously within the first two or three generations, but this is usually not the case. The fact that the gene-complex as a whole has to remain well integrated at all times (cf. tooth elongation in fossil horses) is another retarding factor.

FRACTIONING OF A CONTINUOUS SPECIES RANGE

Not all population discontinuities in nature originate by the colonization of islands. Sometimes they arise by the contraction of a species range and the separation of a previously continuous area into separate ranges. If a continuous large species range is split, let us say, into two wide ranges, A and B, both will contain a similar rich mixture of isoalleles, polymorph genes, pleiotropic factors, and polygenes. It will take some time before the interruption of gene-flow between the two

population groups will make itself felt. But eventually some of the genes in A will disappear that had continuously drifted in from B (where they are superior) and vice versa. Also in view of the randomness of mutation, it is unlikely that the same mutations will occur in the two areas with identical frequencies. The result will be an increasing genetic divergence, accelerated by the different selection factors (of the external and genetic environment) in the two areas until the two population groups have again reached equilibrium.

If the respective environments remain rather similar and if the gene-complexes that were fractioned by a secondary discontinuity were particularly well balanced, they may diverge only very slowly after separation. There are many cases known, particularly among plants, where striking geographical discontinuities have not led to much of an evolutionary change in the separated populations. Stebbins (1950) has called attention to many such cases as, for instance, to that of the American and Asiatic *Platanus* which have not even reached reproductive isolation in spite of many millions of years of geographic isolation. It is evident from such cases that the length of the period of separation and the amount of genetic divergence are not always very closely correlated. Why some gene-complexes are so stable, while others evolve rapidly is still an unsolved problem. It appears very probable that differences in selection-pressures are not the complete answer.

It is possible that the difference in the mode of speciation (founder population versus fractioned species range) contributes to the differences in species patterns found in nature. It is well known among systematists that in some taxonomic groups there are many very similar species (including sibling species), while in certain other groups (e.g. Cerambycidae) most species are so different from each other that many of them are placed in monotypic genera. It would be interesting to determine whether most speciation in the former cases had proceeded via fractioning of initially large populations, while founders gave rise to many of the monotypic genera. Too many additional factors enter the picture to permit any generalization, but the possibility that the mode of speciation is one of these factors should not be entirely ignored.

GENETIC VARIABILITY

During a genetic revolution the population will pass from one well integrated and rather conservative condition through a highly unstable period to another new period of balanced integration. The new balance will be reached after a great loss of genetic variability. There are several sources of loss:

- (1) The founders represent only a segment of the variability of the

parental population. (2) During the period of rapid readjustment, alleles that had been previously of equal viability will change their relative viability, like a_1 and a_2 discussed above, and the inferior ones will become eliminated. (3) Recessives will have a much greater chance to become homozygous in the reduced population and thus become more exposed to selection. As a consequence of these gene-loss inducing factors, a population may result which is not only very different genetically from the parental population but also genetically comparatively invariable. Much that is known about island populations supports the validity of this conclusion.

The evolutionist takes, on the whole, a dim view of the future prospects of populations with depleted genetic variability. Such populations are not very plastic. If they live on an island (in the broad sense of the word), they will probably be successful as long as conditions remain stationary. However, such populations rarely have the capacity to adapt themselves to severe environmental shocks. The arrival of a new competitor or of a new enemy or a drastic change of vegetation or of the physical environment is apt to lead to extinction. It is no coincidence that even though less than 20 per cent of all species of birds are island birds, more than 90 per cent of all bird species that have become extinct in historical times are island species. An island bird thus has at least fifty times as great a chance to become extinct as a mainland bird. Only part of this extinction can be attributed to the small size of the range of these island species.

Permanent genetic depauperization and eventual extinction are, however, not the inevitable fate of island populations. An occasional population succeeds in making an ecological shift during the "genetic revolution" and during the period of relaxed selection accompanying the phase of rapid expansion. It may become adapted to a new ecological niche or even to a major new ecological zone. If such a population can colonize the nearest adjacent "mainland," it may find this ecological niche or zone unoccupied and be able to invade it. Once it starts spreading over wide areas it can again start accumulating additional genetic variability so that in due time it may be as full of heterozygosity and concealed variability as the ancestral species with which it may now be sympatric.

We may illustrate this diagrammatically (Fig. 3).

Genetically depauperized populations have the best chance of survival in an unsaturated environment, an environment relatively free of competitors and enemies. This is the reason why speciation of this type has played such an important role on "vacant" archipelagos, such as the Galapagos or the Hawaiian Islands, or in "empty" lakes. Similar considerations may apply to the apparent bursts of speciation encountered

by the paleontologist whenever a new major "type" appeared on the scene and entered a "vacant" ecological zone.

It has been questioned whether any natural population can pass through a genetic bottleneck of reduced variability (Fig. 3, B or C).

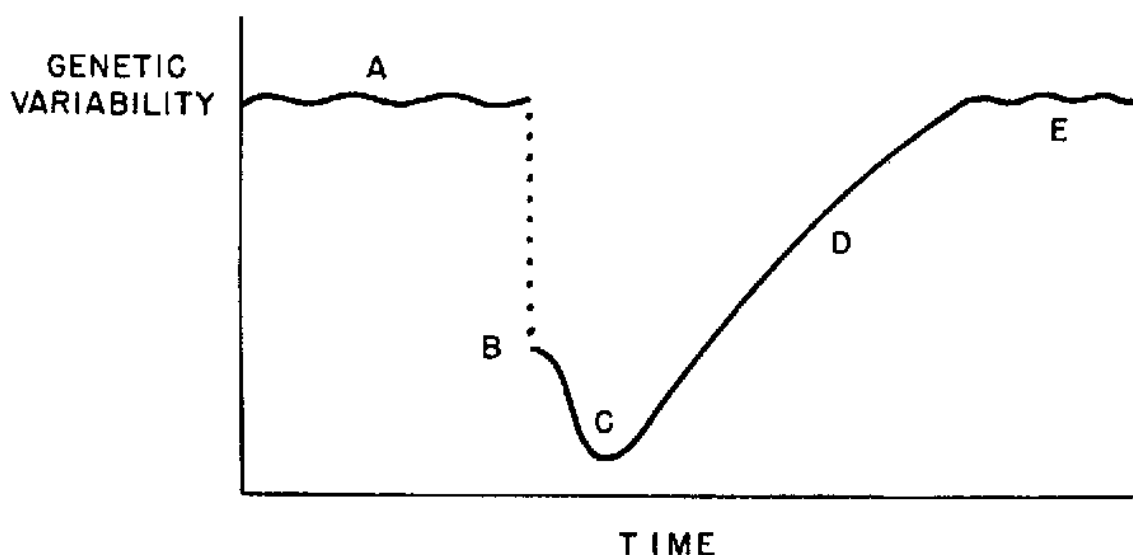


FIG. 3

However, there is abundant evidence that this *is* possible. Less than twenty pairs of the European Starling were introduced to the United States in 1890; and only a fraction of them bred successfully. It took more than fifteen years before they began to increase materially, but now (only forty years after they really started to spread) they are one of the most common birds of North America having increased to an estimated number of over fifty million individuals. The story of the House Sparrow (*Passer domesticus*), the Japanese beetle, the potato beetle, or of any other kind of successful introduction is the same. But there are also many cases of spontaneous founding of new species ranges. The Australian White-eyes (*Zosterops lateralis*), a small flock of which found its way in 1856 from Australia to New Zealand, is now the most common land bird in New Zealand, having settled the outlying islands as well. Finally, it is now well established that most, if not all, the birds of the Australian region got there island-hopping across the Malay Archipelago. The result has been a rich fauna of successful species, genera, and even families. All of them must have gone at one stage or repeatedly through a genetically extremely depauperized condition. The adaptive radiation of birds, insects, and other animals on isolated archipelagos, like the Galapagos Islands or Hawaii, is further proof. It is thus evident that populations can get through such a bottleneck and still become the progenitors of successful stocks.

Not enough quantitative analyses of species structure have been made to determine the average number of peripherally isolated incipient species

in various groups of animals. Many species have none; others have five or six. Since most of the parental species have—speaking in terms of geological time—a long life-expectancy, there is only little opportunity for replacement, unless a population succeeds in entering a novel ecological niche. Thus, in spite of the continuous budding off of peripheral populations undergoing major or minor “genetic revolutions” as described above, only few will play a role in long-term evolution, perhaps one in fifty. The odds are very much against a successful passing through the bottleneck of reduced variability (Fig. 3) as well as the reaching of a new level of high variability and of an unoccupied ecological niche.

PERIPHERAL POPULATIONS AND MACROEVOLUTION

The peripherally isolated population has various attributes that are of great interest not only to the student of speciation but also to those who study major evolutionary changes. It seems to me that many puzzling phenomena, particularly those that concern paleontologists, are elucidated by a consideration of these populations. This concerns primarily the phenomena of unequal (and particularly very rapid) evolutionary rates, breaks in evolutionary sequences and apparent saltations, and finally the origin of new “types.”

Evolutionary rates. It is now realized that the rate of evolutionary change is closely correlated with population structure. Evolutionary transformation would tend to be very slow in large panmictic populations, if such should exist in nature. A more rapid rate of evolutionary change will be induced by a different population structure. “A fine-scaled structure of partial isolation without marked environmental differences presents the most favourable condition for transformation as a single species” (Sewall Wright, 1951, summarizing earlier work). It seems to me, however, that even such a system is comparatively slow and conservative because it is rich in diverse genetic factors, including multiple alleles and, as Heuts (1951) points out, there will be a premium for constancy in such a system. Genetic factors will be selected for their ability to form viable combinations with the greatest number of other genetic factors.

It is very doubtful whether the population structure cited by Sewall Wright is favourable enough to explain the sudden, sometimes almost precipitous, changes of evolutionary rates which have been so puzzling to paleontologists. The (relative!) suddenness of these changes is unquestionable and even Simpson, who on the whole is successful in explaining evolution within the framework of the current genetic theory, found it necessary to coin a special term, quantum evolution, for this type of rapid evolutionary change.

Two kinds of explanations for rapid evolution have most often been given previously, a genetic and an ecological one, but both are unconvincing. Previous genetic interpretations are based on the occurrence of macromutations ("systemic mutations") or on mutational avalanches. Either type of event would have exceedingly slim chances of success in a population which is part of a connected system of populations with undiminished gene-flow. Equally unlikely is an ecological explanation based exclusively on a cataclysmic change of selective factors. Mountain building, shifts of climatic belts and similar events are by far too slow to account for "quantum evolution."

The genetic reorganization of peripherally isolated populations, on the other hand, does permit evolutionary changes that are many times more rapid than the changes within populations that are part of a continuous system. Here then is a mechanism which would permit the rapid emergence of macroevolutionary novelties without any conflict with the observed facts of genetics.

Phylogenetic saltations. Many paleontologists have postulated various kinds of typrostrophic "saltations" in order to explain the absence of crucial steps from the fossil record. If these changes have taken place in small peripherally isolated populations, it would explain why they are not found by paleontologists. In fact, peripheral populations are neglected even by the taxonomists of most living faunas because they are comparatively small, isolated, and often in far distant or inaccessible places. In birds, however where they have been well studied, it is quite evident that they are not only incipient species but in many instances also incipient genera and higher categories. It has been pointed out earlier (Mayr, 1942; Rensch, 1947) that the problem of the origin of higher categories is inseparable from the problem of the origin of new species. Those who have denied this seem to be unfamiliar with the facts. It is, of course, inadmissible to apply the term speciation to subspeciation within continuously ranging populations and use this as evidence for denying that speciation could have anything to do with the origin of the higher categories. As stated above, the clinal variation within continuous populations is not of the type that normally leads to the origin of major evolutionary novelties. Such are found only in isolated allopatric peripheral populations.

As an example may serve the drongo species *Dicrurus hottentottus*. Though we are dealing here merely with inconsequential plumage features (Fig. 4), it is noteworthy not only that every aberrant population is peripheral but also that several of these populations have been considered by avian taxonomists to be generically distinct.

As stated above, most of these populations will eventually die out

without playing a major role in the evolutionary picture. Only a very occasional one will be able to reach a vacant ecological zone. This agrees with the observed evidence, since the number of real evolutionary inventions ("new types") in the history of the earth is quite small in comparison with the total number of forms occurring at any one time.

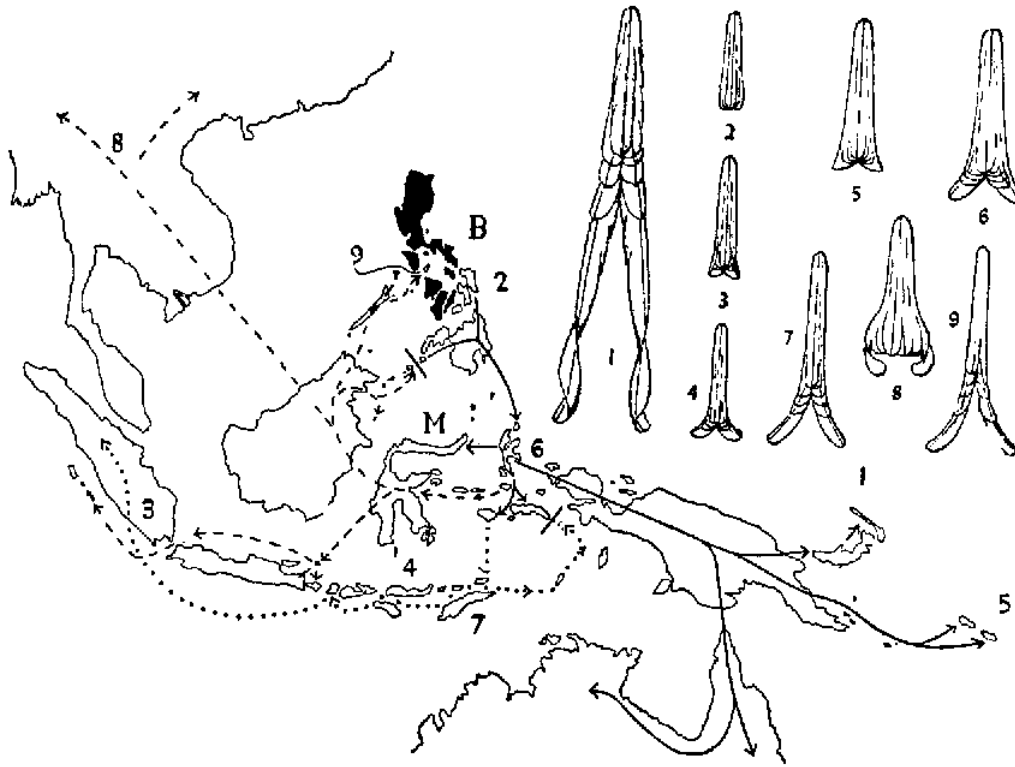


FIG. 4

As soon as such a population has completed its genetic reconstruction and ecological transformation, it is ready to break out of its isolation and invade new areas. Only then will it become widespread and is likely to be found in the fossil record. But then it is already too late to record the evolutionary change through which it has gone. All the paleontologist finds is the fact that one widespread numerous species was replaced or succeeded by a rather different species which is again widespread and numerous. Contrary to the belief of many paleontologists, such an apparent "jump" is consistent with the accepted genetic theory, as detailed above.

Ecological shifts.—Oceanic archipelagos are the best place to observe the results of sudden ecological shifts of populations in living faunas. A particularly convincing case has been described by Amadon (1947) in a Hawaiian honeycreeper. Here is an allopatric population which has not only undergone a change in bill structure but also in feeding habits. It has truly switched into an entirely new ecological niche. I visualize

all major evolutionary novelties to occur in a similar manner. E. Zimmerman has described the case of a species of dragonflies, isolated on the Hawaiian Islands, in which the larva has entered into a totally new niche. It no longer lives in water like the larvae of all other dragonflies, but in the moist humus and plant debris on the forest floor. It could well become the progenitor of an entirely new type of insect.

POSTSCRIPT

Much of the above discussion is frankly speculative. It was prepared in order to call attention to previously neglected aspects of the evolutionary process. May it stimulate further research in this field.

The above concepts were discussed by me with E. Caspari, Th. Dobzhansky, E. B. Ford, M. J. Heuts, Julian S. Huxley, J. King, and B. Wallace, all of whom have helped me to clarify my ideas, much as they themselves may disagree with some of my conclusions.

SUMMARY

Successful species are usually widespread and rich in genetic variability, but they tend to be rather conservative from the evolutionary point of view. Populations within such species display much ecotypic adaptation and clinal variation.

Along the periphery of the geographical range of such species there is frequent budding off of geographically isolated populations.

The genetic composition of a population which is one of a large series of contiguous populations of a widespread species is continuously affected by the immigration of genes derived from adjacent or far distant populations.

In such a population there will be a selective premium on genes which do well on a great variety of genetic backgrounds and which are thus adapted to cope with the continuous influx of alien genes.

The selective value of many genes will change drastically on the altered genetic background ("genetic environment") of a newly founded peripherally isolated population. This will lead to a rapid change of gene-frequencies simultaneously at many loci ("genetic revolution"), assisted by the selective effects of the change in the physical and biotic environment of the isolated area.

Furthermore, a different set of genes is apt to be superior in such an area in which gene-flow does not interfere with selection by the local environment.

Isolated populations are relatively invariable genetically for various reasons, and appear to become vulnerable to extinction, particularly if they live for long periods in a very uniform environment.

An occasional one of such populations may succeed during the period of genetic reorganization to enter a previously unoccupied ecological niche and to expand into this niche. As such a population becomes more and more numerous, it builds up again its previously depleted genetic variability.

The period of genetic reorganization and relaxed selection-pressure is not only a period permitting rapid evolutionary change, but also offers an otherwise unavailable opportunity for a drastic ecological change of a somewhat unbalanced genetic system.

Rapidly evolving peripherally isolated populations may be the place of origin of many evolutionary novelties. Their isolation and comparatively small size may explain phenomena of rapid evolution and lack of documentation in the fossil record, hitherto puzzling to the paleontologist.

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LIST OF ILLUSTRATIONS

FIG. 1. Species and subspecies of the *Tanysiptera hydrocharis-galatea*-group. The subspecies 1, 2, and 3 of *galatea* on the mainland of New Guinea are exceedingly similar to each other. The subspecies *vulcani* (4) and *rosseliana* (5) are much more distinct. The populations on Biak (6), Numfor (7), and Koffiao (8) have reached species level. The form of Aru Island, *hydrocharis* (H_1), has also reached species rank and now coexists in South New Guinea (H_2) (shaded area) with a subspecies of *galatea* (3). (From Mayr, 1942.)

FIG. 2. Diagrammatic presentation of the relative selective value of alleles a_1 and a_2 on many different genetic backgrounds. On some a_1 is superior, on others a_2 ; a_1 has a more even viability on many backgrounds; a_2 is very superior on some and very inferior on others.

FIG. 3. Levels of genetic variability. A, in parental species, B, in founder population, C, after "genetic revolution," D, during recovery period, E, after a new level is reached.

FIG. 4. Geographic variation of the form of the tail in the polytypic drongo species *Dicrurus hottentottus*. The central populations, such as those on Sumbawa (4) and Halmahera (6), have a normal drongo tail. Nearly all peripherally isolated populations have a more or less aberrant tail, as those on Samar (2), Sumatra (3), San Cristobal (5), the Asiatic mainland (8), Timor (7), Tablas, Philippines (9), and New Ireland (1). The populations of Asia (8), New Ireland (1), Tablas (9), and Kei, near Timor (7) were once considered generically distinct. (From Mayr and Vaurie, 1948.)