

The evidence presented in the two preceding chapters supports the conclusion that speciation in sexually reproducing higher animals normally takes place by way of geographic isolation. Although naturalists had asserted this fact for nearly 100 years, until recently it remained a strictly empirical finding, never receiving a causal explanation, never leading to a genuine theory of speciation. When Moritz Wagner proclaimed in 1868 that geographic isolation was a necessary prerequisite for species formation, he failed to submit any real proof. Worse than that, some of his early explanations were so obviously absurd that they endangered his thesis as a whole and were in part responsible for its cool reception.

Before a theory of geographic speciation could become acceptable, two prerequisites were necessary: (1) a far greater understanding of genetics, particularly of the particulate nature of inheritance, had to be achieved; and (2) population thinking had to become general, replacing the formerly predominant typological thinking. As recently as the 1930's geneticists were still primarily concerned with mutation and selection, that is, with evolutionary change as such. Only after the problems posed by evolutionary change had been essentially solved were population geneticists ready to work out a genetic theory of speciation. Only then was it possible to search for the genetic reasons that necessitate geographic isolation during speciation.

#### THE GENETIC PROBLEM OF SPECIATION

The essence of speciation, as we now realize, is the production of two well-integrated gene complexes from a single parental one. All early attempts to explain the genetics of speciation missed this essential point, since they were concerned entirely with the problem of the origin of difference. To be sure, the differences between species are due to mutation and selection, but demonstrating that does not explain how species split.

Most of the genetic variability produced by mutation is almost immediately removed by normalizing selection. Any mutation that would initiate an incipient difference in reproductive behavior among individuals of a population would be particularly vulnerable to normalizing selection. And yet it is precisely such differences in reproductive behavior and physiology that are needed to build up isolating mechanisms. How can they be accumulated without being at once removed by normalizing selection?

The real problem of speciation is not how differences are produced but rather what enables populations to escape from the cohesion of the gene complex and establish their independent identity. No one will comprehend how formidable this problem is who does not understand the power of the cohesive forces in a coadapted gene pool. It was the object of Chapter 10 to establish this point.

It is now evident that there is only one situation in which a gene pool can be completely reconstituted genetically (with reference to a parental population) while all of its elements remain well integrated and coadapted: spatial isolation. Most students of the speciation of sexual animals from M. Wagner on realized clearly the indispensability of this condition, but they based their conclusion strictly on empirical findings. Why isolation was needed remained a puzzle until the genetics of integrated gene complexes had replaced the old "beanbag" genetics.

#### *Gene Flow and Genetic Cohesion*

To what extent and under what circumstances are the different populations of a species held together by cohesive forces? Conversely, under what conditions can this cohesion be broken? The most important question of all is: What role does gene flow play in the maintenance of genetic cohesion among populations? Is it advisable to classify populations according to the amount of gene flow to which they are exposed?

*Closed and open populations.* All selection experiments, whether on mice, *Drosophila*, or domestic animals, have involved *closed populations* with a negligible genetic input. Population size was far too small in all these cases for mutation to have played a major role unless it was artificially induced. The response of the selected stocks, no matter how spectacular it was, must have been largely due to recombination of the initial gene complement, a source of variation which is bound to dry up eventually. Natural populations (except the most rigidly isolated ones), in contradistinction, are *open populations* with a steady input through gene immigration. This difference in genetic input causes a number of fundamental differences between closed

and open populations (Mayr 1955). In the open system, available genetic variation is not only infinitely greater but also of a different kind. The large and continuous influx of alien genes into every local population, as well as the diversity of the environment in space and time, will never permit the gene complex to reach complete stability. The response to selection in an open system is very different from that in a closed one. It is therefore not admissible to apply automatically the findings made on closed laboratory populations to natural populations. This limitation must be kept in mind when one wants to construct models of species structure.

In all widespread, successful species of relatively mobile sexual organisms, there seems to be sufficient gene flow to maintain great similarity in the gene pools of all local populations. Population geneticists, who work all their lives with closed populations in which all genetic input is due to mutation, tend to underestimate the magnitude of genetic input in open populations. To be sure, it is immaterial for certain aspects of evolution whether mutation or immigration is responsible for new genes in a population. Yet it would be a great mistake to lump these two sources of variation together in calculations of their effect, because they are of totally different orders of magnitude. I estimate that genetic change per generation due to mutation in a local population rarely exceeds  $10^{-5}$  per locus, while the exchange due to normal gene flow is at least as high as  $10^{-3}$  to  $10^{-4}$  for open populations that are normal components of species. With an effective local breeding population often as low as  $2 \times 10^2$  and usually not higher than  $3 \times 10^2$ , this difference in order of magnitude becomes of vital importance. For example, if one assumes a population of 200 individuals, each with 100,000 loci mutating at the rate of 1 in 10,000, a total of 2,000 mutants for the 20 million loci would almost certainly be a maximum figure. Dispersal, however, brings new individuals into the population; they might constitute 40 percent of it, that is, 8 million genes, of which perhaps 200,000 might be new for the population. If one assumes that there will be the same amount of duplication among mutated and immigrant genes, gene replacement by immigration would be 100 times that by mutation in this deme.

The natural landscape is only rarely so uniform that a species (or a part of it) consists of a single contiguous population. Far more frequently, indeed normally, a species is subdivided into numerous partially isolated local populations (Fig. 17.1). Consequently, it is of paramount importance to determine the order of magnitude of the partial isolation. Where the gaps between suitable habitats are smaller than the normal dispersal range of

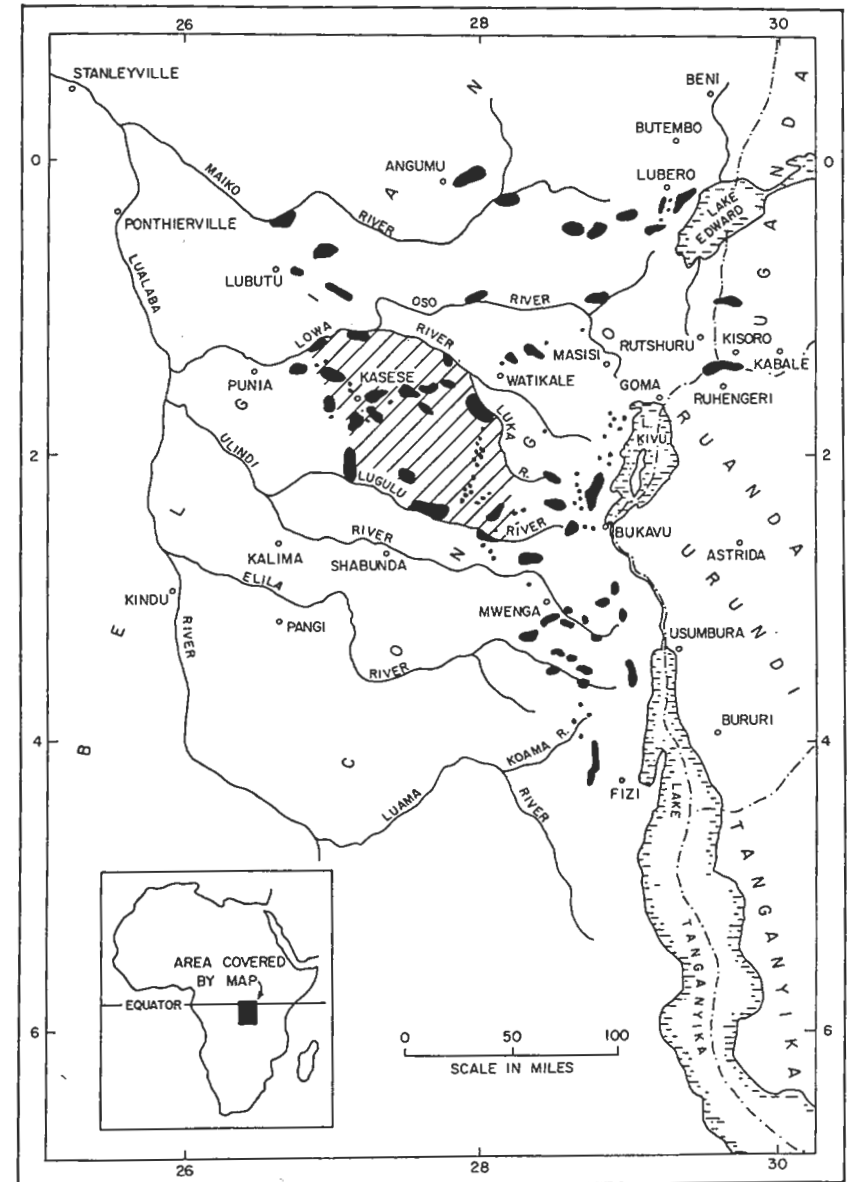


Fig. 17.1. Actual distribution of the Mountain Gorilla in East Africa. Each of the black areas indicates the location and approximate shape of sixty gorilla areas ranging in size from about 10 to about 100 square miles each. The hatching marks a central region of fairly continuous but sparse population. (From Emlen and Schaller 1960.)

individuals, there will be about as much gene flow as if the range were continuous. In view of the steady selection in favor of genes that coadapt easily with immigrant genes, there may well be nearly as much cohesion in this type of a partially isolated system as there is in a panmictic one. The genuinely sharp break is not between the panmictic and the partially isolated system, but between the partially and the virtually fully isolated system. The importance of complete isolation becomes evident as soon as the extensive epistatic effects of genes are properly taken into consideration. As a consequence, a population cannot change drastically so long as it is exposed to the normalizing effects of gene flow.

How efficient is gene flow? One arrives at rather astronomical figures when one tries to calculate the time it would take for a gene to percolate from one end of the range of a widespread species to the other; the figures are especially high if the organisms in question have poor dispersal facilities. It is evident that gene flow alone is not enough to overcome entirely the local effects of mutation and selection. What, then, is responsible for the uniformity of species? I advanced the thesis (1963:523) that—in addition to gene flow—the cohesion of a species is due to the fact that all of its populations share the same homeostatic systems and that this species-wide system of canalization provides great stability: “It is a limited number of highly successful epigenetic systems and homeostatic devices which is responsible for the severe restraints on genetic and phenotypic change” displayed by every species. The total epigenotype governs the range of normalizing selection, which will maintain such epigenetic systems in the face of the centrifugal tendencies of local gene pools. Recent studies (for instance, Lewontin 1967a) have provided evidence for the existence of such genotypic systems.

The adjustment of local populations to the local environment through race or ecotype formation has been stressed so much in previous chapters (Chapters 9, 11, 12), that it would now seem important to stress the basic uniformity of most continuously distributed species. A good example of this is the New Guinea kingfisher *Tanysiptera galatea* (see Fig. 16.4), which displays no significant geographic variation in the vast area of that island, with its strong climatic contrasts. Yet each of the adjacent islands inhabited by this species has a markedly differentiated race even though these islands are in the same climatic zone as the neighboring mainland. Every taxonomist can cite dozens of similar cases. There is, for instance, the butterfly *Maniola jurtina*, which has been studied so intensely by E. B. Ford and his associates:

One of the most striking features of the *M. jurtina* females is their remarkable uniformity across most of southern England [except Cornwall]. This area includes some of the greatest variations in temperature, rainfall, and geology to be found in Britain. Evidence from Cornwall and the Scillies shows that the spotting is capable of marked variation. The fact that it is so stable elsewhere [= across most of southern England] indicates not only that natural selection is holding it at an optimum value but also that the species is in some way insensitive to environmental variation in this part of its range (Dowdeswell 1956).

The fact, taken for granted by every taxonomist, that he can identify individuals of a species (unless its range is dissected by geographical isolation) regardless of where in the range of the species they may come from is further illustration of this phenomenon. Physiologists and embryologists, likewise, have published evidence indicating a remarkable uniformity of physiological constants throughout the ranges of most species. The essential genetic unity of species cannot be doubted.

#### *The Species Border*

The range of a species is delimited by a line beyond which the selective factors of the environment prevent successful reproduction. This line, called the *species border*, is one of the aspects of the population structure of species that can be understood only by taking gene flow into consideration. Single individuals may appear annually in considerable numbers beyond this line, yet fail to establish themselves permanently. Even if they succeed in founding new colonies, these will sooner or later be eliminated in an adverse season. As a result, the species border, though fluctuating back and forth, remains a dynamically stable line. The species border is one of the most interesting phenomena of evolution and ecology, yet as a scientific problem it has been almost totally ignored, except by Finnish authors, who have studied shifts of the species border as correlates of changing climatic conditions (Chapter 18). In the border region there is a never-ending race between reproductive capacity and mortality due to adverse conditions. Population density is far below the saturation point and the border region is a place in the area of a species where density-dependent factors are likely to be of minor, if not negligible, importance.

The essential stability of the species border, on which the annual and long-term fluctuations are superimposed, would seem to contradict our belief in the power of natural selection. One would expect a few individuals to survive in a zone immediately outside the species border and to form a new local population that would gradually become better adapted under

the continuous shaping influence of local selection. One would expect the species range to grow by a process of annual accretion, like the rings of a tree. That this does not happen is particularly astonishing in the frequent cases where conditions beyond the borderline differ only slightly from conditions inside the species border and where no drastic barriers prevent expansion.

The solution to this puzzle is probably that the process of local adaptation by selection is annually disrupted by the immigration of alien genes and gene combinations from the interior of the species range (Mayr 1954). This influx prevents the selection of a new stabilized gene complex adapted to the conditions of the border region. Presumably, the border populations barely maintain themselves, and the new colonists beyond the species border (in mobile species such as birds and insects) come from farther inside the species range, where conditions permit a greater surplus of individuals and the resulting increased population density stimulates emigration of individuals whose gene complex is not adapted for the conditions of the border region.

#### *The Genetic Reconstitution of an Isolated Population*

The argument in the preceding section was essentially negative. It demonstrated that contiguous populations of a species are held together by such close ties of genetic cohesion that one can scarcely conceive of this essentially single gene pool being divided into two. I shall now take up the other half of the argument and show what genetic events take place in spatially isolated populations and how these permit the formation of isolating mechanisms while leaving the genetic integration of the gene pool at all times undisturbed.

*The isolated population.* Let us study the genetic history of a newly founded population that is spatially isolated from the parental population from which it branched off. We shall at first make two simplifying assumptions: (1) that the environments of the two populations are identical, and (2) that the new population is at the beginning completely identical genetically with the parental population. Yet, even so, as soon as they are separated, the two populations will drift apart in their genetic contents, for a number of reasons. The probability is nil that the same mutations will occur in the two populations in the same sequence. Each incorporated mutation changes the genetic background of the population and thus affects the selective value of all subsequent mutations. Furthermore, recombination will produce different genotypes in the two gene pools and thus, since the

same gene may have different selective values in different genotypes, will lead to a gradual shifting of gene frequencies. A third factor leading to the divergence of the gene pools is "genetic indeterminacy" (Chapter 8). If several gene combinations have equal selective values (with respect to a given selection pressure), pure chance or some irrelevant pleiotropic effect may decide which of them becomes established in a given gene pool. The changes in gene frequency due to "genetic indeterminacy" will again not be the same in two independent populations. Each divergence of the two gene pools increases the difference in the genetic background of all the genes of the two populations and will thus tend to set up new selection pressures. The drifting apart is thus evidently an accelerating process.

The rate of divergence, however, is even greater than can be accounted for by the stated factors, owing to the fact that neither of the two simplifying assumptions made above is valid. The selection pressures to which the two separated populations are exposed are not the same, since there are no two places on the face of the earth where even the physical environment is quite identical. Every completely isolated population exists in a biotic environment that is different from any other, and this shift of the biotic environment adds another powerful selection pressure. Competition, predation, and other ecological interactions are apt to be entirely different in the new environment. These local conditions exert selection pressures reinforcing the steady change of gene contents and leading to the development of numerous new adjustments.

*Founder principle.* The second assumption made above, that the new population is at the beginning genetically completely identical with the parental population, is likewise invalid. The founders of a new colony of a species inevitably contain only a small fraction of the total variation of the parental species (the founder principle; see Chapter 8). All subsequent evolution will proceed from this limited original endowment. The importance of this restriction is demonstrated by recent selection experiments in which several parallel lines were exposed to the same selection pressure. Almost invariably the end results were different in the different lines. The smaller the starting populations, the greater the degree of indeterminacy. Ten experimental populations, each descended from only 20 founders, diverged far more from each other than ten other populations founded by 4000 individuals each, all 20 populations having been derived from the same parental population (Fig. 17.2).

The founder principle is an important concept only in the framework of population thinking. For the essentialist any individual of a species has

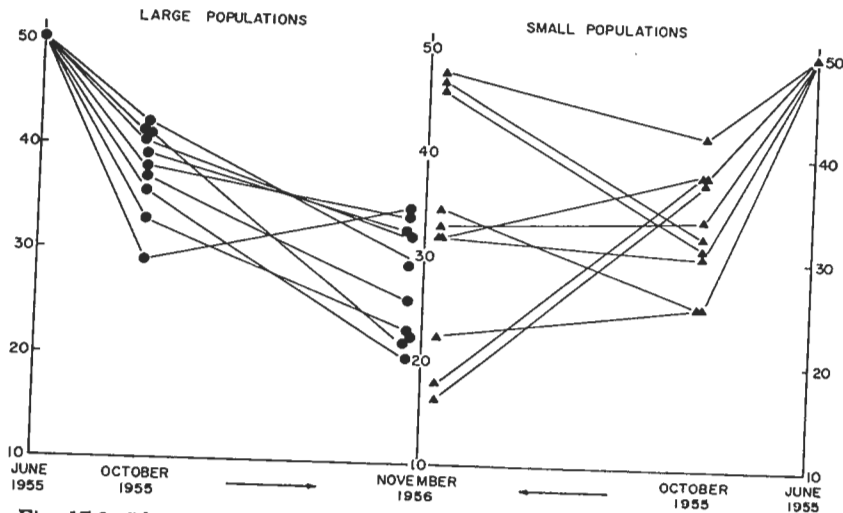


Fig. 17.2. The frequency (percent; vertical scales) of PP chromosomes in 20 replicate experimental populations of mixed geographic origin (Texas by California). The populations that have gone through a bottleneck of small population size show far greater variance after 17 months than the continuously large populations. (From Dobzhansky and Pavlovsky 1957.)

“the essential characters” of the species, and if such an individual establishes a new population by colonizing a previously unoccupied area, its descendants will be typical representatives of the species. For the populationist no two individuals are the same and no individual is ever a typical representative of the species. The particular sample that a founder population represents is inevitably different from the mean values of the parental population. It constitutes a genetically unique population, even though the probability is high that the most common genes of the parental population will be represented.

How far a founder population may diverge genetically is well illustrated by the isolated Bogotá (Colombia) population of *Drosophila pseudoobscura*. All over Central America (south to Guatemala) and North America (north to British Columbia) this species shows only modest geographic variation in a set of investigated enzyme genes. The Bogotá population, however, has a strikingly different composition in the frequency of the enzyme alleles (Table 17.1).

It must be remembered that each genotype is a discrete genetic system, constituting an experiment in coadaptation. Occasionally such a genotype is uniquely adapted to be successful in its evolutionary experiment. If this exceptional genotype is a member of a large population, it is bound to

be broken up (in the next generation) by recombination. In a small founder population, however, this coadapted system has a good chance of being perpetuated in its descendants and of giving rise to an evolutionary novelty (Chapter 19).

*The Chances of Success of a Founder Population*

The founders carry such a small reservoir of genetic diversity with them that the population founded by them is highly vulnerable to the dangers of inbreeding (homozygosity). The situation is aggravated in most cases by the ecological uniformity of the insular environment and the resulting one-sidedness of selection. These phenomena are principally responsible for the frequent extinction of island populations. Indeed, extinction under adverse conditions is the fate of most peripheral isolates. The smaller a population the more vulnerable to extinction it seems to be (Fig. 17.3; Mayr 1965a).

Awareness of the frequency of extinction among island species and of the severe inbreeding depression observed by animal breeders might induce one to take a dim view of the prospects of founder populations. However, one must be cautious when generalizing from highly artificial selection experiments. Selection in nature, even in the smallest population, is primarily for overall fitness. The same is true of so-called “unselected” inbred lines in the laboratory. On the whole, loss of genetic variance through inbreeding occurs far more slowly than one might expect.

Table 17.1. Geographic variation of two enzyme genes (*Pterine-8* and *Xanthine dehydrogenase*) on chromosome II of *Drosophila pseudoobscura*. The difference in the frequency of the alleles between the three North American and the isolated South American locality is striking (from Prakash et al. 1969).

Allele	California	Mesa Verde	Texas	Bogotá
<i>Pterine-8</i>				
.80	.014	.009	.011	.870
.81	.472	.410	.441	.100
.83	.514	.576	.512	.030
.85	—	.005	.035	—
<i>Xanthine dehydrogenase</i>				
.90	.053	.016	.018	—
.92	.074	.073	.036	—
.99	.263	.300	.232	—
1.00	.600	.580	.661	1.00
1.02	.010	.032	.053	—

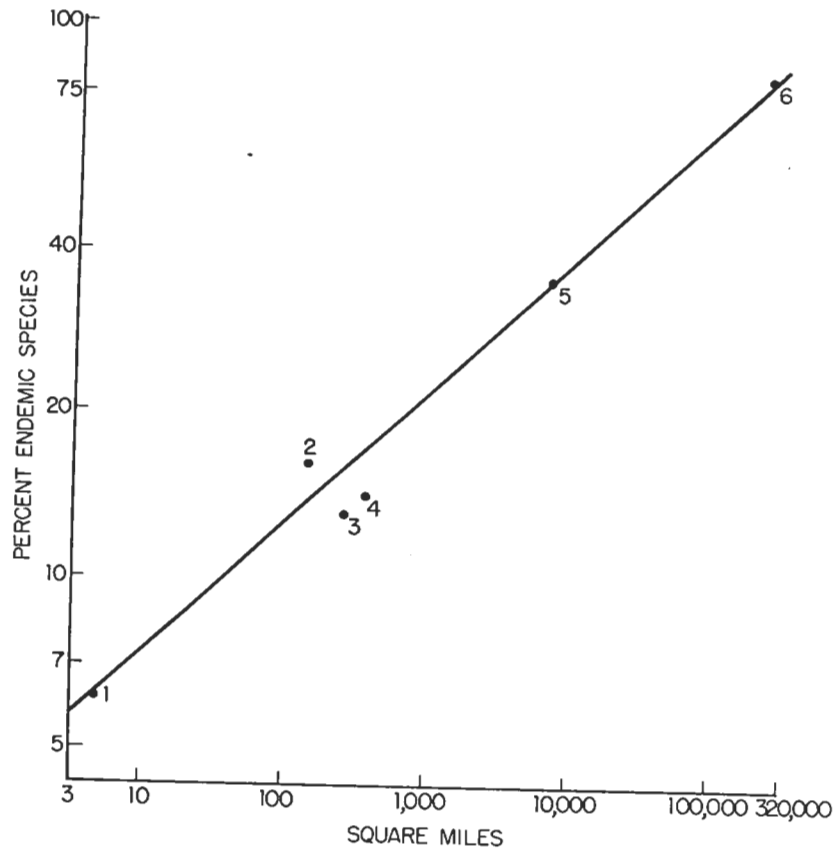


Fig. 17.3. Double logarithmic plotting of area against percentage of endemic species of birds on single well-isolated islands. The smaller the island the more frequently the endemic species become extinct, the more rapid the faunal turnover. 1 = Lord Howe, 2 = Ponape, 3 = Rennell, 4 = Chatham, 5 = New Caledonia, 6 = Madagascar.

There is abundant evidence in the literature for an occasional phenomenally successful founder population (Mayr 1963:530). Most of the mammals and birds successfully introduced into North America, Australia, and New Zealand, and nearly all accidentally introduced insects, were the offspring of a handful of individuals (Elton 1958). Inbreeders are, of course, vastly more successful colonizers than outbreeders.

Sometimes an exceedingly small population maintains itself successfully over a long series of generations. Examples are fish in desert springs and a number of protected mammals and birds that, like the American bison

and the European ibex, successfully overcame an extreme reduction in numbers. The millions of golden hamsters (*Mesocricetus auratus*) in the laboratories around the world are supposedly all descendants of a single pregnant female. The establishment of highly successful colonies by single founders is not only feasible, but quite likely; it seems to be the normal method of spreading in many species of animals and plants (Baker and Stebbins 1965).

These observations also have a bearing on the problem of the genetic composition of rare and localized species. One would expect great homozygosity owing to inbreeding. The available information is slight, but indicates that this assumption is not necessarily true. In *Keyacris scurra*, an Australian grasshopper reduced to isolated populations in cemeteries, many of them quite small, White (1957b) found that only a few of the usually polymorphic karyotypes of this species had become homozygous. Clearly, drift had been unable to override an obvious but not yet analyzed selective advantage of the heterozygous condition. There are numerous records in the genetic literature of the tenacity with which genetic variability is maintained in small laboratory populations through scores of generations of inbreeding (Chapter 9).

#### *The Genetic and Biotic Environment of the Founder Population*

The founder population is differentiated from the parental population not only by the drastic reduction of the diversity of its gene pool, but also by its exposure to a totally new constellation of environmental factors, biotic as well as genetic. The most important of these is the sudden conversion from an open to a closed—and at that to a *small closed*—population. It is the suddenness and completeness of this shift that is decisive. The new population is at once completely emancipated from the parental population. In an open population there is a steady and rather high input of alien genes. “Little or no thought [has been given in the past] to the effect 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 alien genes into a gene pool will lead to the selection of such ‘native’ genes as are tolerant to combination with these alien genes, that is, which produce viable heterozygotes with a great assortment of alien genes or gene combinations” (Mayr 1954:162) (Fig. 17.4). I have referred to such genes as “jack-of-all-trades” genes or “good mixers.” The less inflow of alien genes in a population, the lower the special selective advantage of the good mixers.

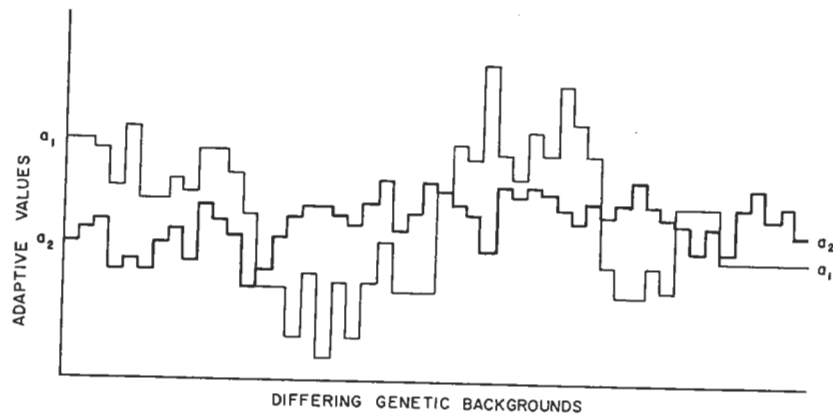


Fig. 17.4. Diagrammatic representation of the changing adaptive value of genes  $a_1$  and  $a_2$  on different genetic backgrounds. Gene  $a_1$  is very good on some backgrounds and very poor on others; gene  $a_2$  fluctuates only slightly around the mean. (From Mayr 1954.)

The effect of the increased homozygosity at some loci on other loci of the founder population is, perhaps, more important.

As a consequence of their increased frequency in the founder population, homozygotes will be much more exposed to selection and those genes will be favored which are specially viable in homozygous condition. Thus, the "soloist" is now the favorite, rather than the "good mixer." We come thus to the important conclusion that *the mere change of the genetic environment [and particularly the change from an open to a closed population] may change the selective value of a gene very considerably.* This change . . . 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 of many other loci, until finally the system has reached a new state of equilibrium (Mayr 1954:169).

There is some experimental evidence which supports these conclusions. In several recent selection experiments, it was found—contrary to classical assumptions—that more homozygous stocks sometimes respond phenotypically more strongly to selection pressures (for example, for more bristles in *Drosophila*) than genetically more variable stocks. The genetically more variable populations seem to be richer in balanced systems of regulating genes and epistatic balances and thus better equipped to resist one-sided selection pressures. The depletion of such balancing systems in founder

populations may facilitate their phenotypic response to new selection pressures.

There are other factors that may favor a rapid genetic turnover in populations which pass through the bottleneck of reduced population size. One is that the rate at which a gene is replaced by its allele depends on its initial frequency. In large populations the frequency of a new favorable gene will be very low, by definition, and the rate of substitution correspondingly slow (Haldane 1957). In a founder population, however, a gene that is elsewhere rare may start with a relatively high frequency and thus be able to replace its allele very quickly. This may be the most important reason for rapid evolution in small speciating populations.

Haldane (1956) has called attention to an important difference between central and peripherally isolated populations: the role of density-independent mortality. In the central populations of a species, the physical as well as the biotic environment is optimal, and much, if not most, of the mortality is somehow connected with the high population density. In peripheral and peripherally isolated populations, conditions are usually near the minimum for the species. In bad years the populations will be wiped out, or nearly wiped out; in good years they may build up to large numbers (because of the scarcity of species-specific predators and pathogens). There will thus be strong population fluctuations and these will favor genetic turnover. The strength of density-dependent factors in the central part of the species range damps such fluctuations (see Chapter 13).

#### *Consequences of the Genetic Revolution*

During a genetic revolution, the speciating population passes from one well-integrated and stable condition through a highly unstable period to another period of balanced integration. Various genetic phenomena characterize the passing through the bottleneck. Most conspicuous among these is a great loss of genetic variability (Fig. 17.5). For this loss there are a number of reasons: (1) the founders represent only a fraction of the variability of the species; (2) owing to inbreeding, more recessives will become homozygous and thus be exposed to selection; (3) owing to the reduced population size, there will be changes in the selective value of alleles and certain alleles will be eliminated (loss of "good mixers"); (4) during the reconstitution of the epigenotypes, many genes will lose the advantage of being part of a balanced system and will be selected against; (5) as long as the new population is small it may lose additional genes through errors of sampling.

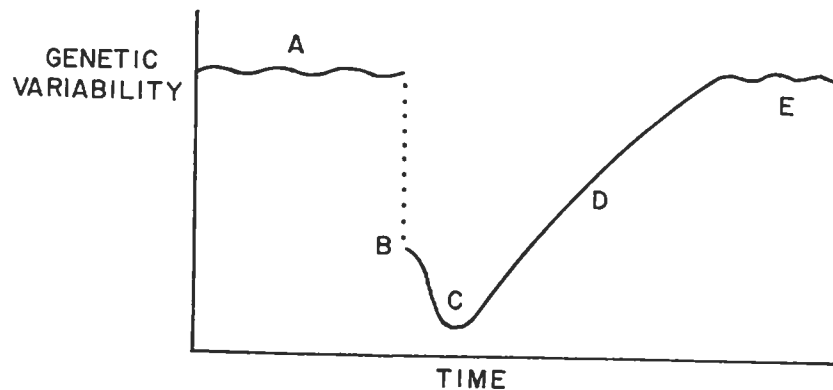


Fig. 17.5. Loss and gradual recovery of genetic variation in a founder population. The founders (*B*) have only a fraction of the genetic variation of the parental population (*A*) and further genes are lost during the ensuing genetic revolution (*B* to *C*). Variation is gradually recovered (*D*) if the population can find a suitable niche, until a new level (*E*) is reached. (From Mayr 1954.)

Not all of this loss of genetic variability is deleterious. It reduces the genetic load quite drastically and gives the surviving population a “clean start.” It has been found in natural as well as experimental populations of *Drosophila* (several species) that small populations carry far fewer genes that are deleterious in homozygous condition than large ones. Furthermore, the loss of balancing systems often permits a stronger response to selection pressure.

A genuine genetic revolution is characterized by a breakdown of genetic homeostasis through a loss or a reconstitution of previously existing balancing systems. The population will go through a labile state. The situation is made still more acute by the fact (discussed below) that the population has to cope with new selection pressures owing to the changed physical and biotic environment in the isolate. Those populations that succeed in surviving the genetic revolution, presumably very few, will enter a new state, one characterized by the renewed accumulation of genetic variability and the acquisition of new and usually very different balancing systems.

#### Chromosomal Rearrangements and Speciation

Closely related species often differ more conspicuously in their karyotype than in their morphology. Among aspects of the karyotype that differ are chromosome number; the number of metacentric or acrocentric chromosomes; the presence and kind of paracentric or pericentric inversions, or

of supernumerary chromosomes; and just about every other aspect of chromosomal evolution. It has, therefore, been held by most cytogeneticists that chromosomal reconstruction (“chromosomal mutation”) is an important and indeed indispensable component of the speciation process. This belief is based on two assumptions: (1) that the degree of difference displayed by two species requires a speciation process of such drastic dimensions that only chromosomal mutation can qualify, and (2) that reproductive isolation between two species cannot be achieved without chromosomal reorganization. Although it is now known that both of these assumptions are invalid, there is still need for explaining the frequency with which speciation seems to be accompanied by chromosomal rearrangements. The analysis may be facilitated by showing in a diagram (Fig. 17.6) the three possible relationships between the occurrence of new chromosomal rearrangements and the acquisition of reproductive isolation.

(1) *Speciation without chromosomal rearrangement.* Numerous cases in various groups of organisms are now known of well-defined and reproductively isolated species that agree completely in their chromosome structure and differ only in their gene contents. Such cases show that speciation can be completed by genic differentiation without a structural repatterning of the chromosomes. To prove this conclusively is difficult in the case of ordinary chromosomes, such as those of vertebrates. The evidence supplied by the giant salivary gland chromosomes of certain Diptera with highly specific banding patterns is, however, irrefutable. In a study of 69 related Hawaiian species of *Drosophila*, Carson and his coworkers (1967, 1970) found 10 groups of species in each of which several related species had the identical highly complex banding pattern in their salivary chromosomes.

		Chromosomal Mutation	
		No	Yes
Reproductive Isolation	No	<del>X</del>	2
	Yes	1	3

Fig. 17.6. The three possible relationships between chromosomal rearrangements and the acquisition of reproductive isolation.

In one case three species with structurally identical chromosomes coexist in the same habitat without interbreeding. Clearly in these cases the isolating mechanisms were built up without the help of chromosomal mutations. Carson refers to species with an identical sequence of bands on the chromosomes as *homosequential* species. The extreme similarity of the karyotype in various groups of animals, for instance, in certain families of artiodactyls among the mammals and in certain groups of insects, indicates that much speciation and adaptive radiation without restructuring of the chromosomes may also occur in cytologically less favorable groups.

(2) *Chromosomal rearrangement without speciation*. Much, if not most, chromosomal rearrangement, unless deleterious, leads to chromosomal polymorphism rather than to the development of isolating mechanisms. The paracentric inversions of *Drosophila* (Chapter 9) are a well-known example; for others see White (1954, 1969) and other textbooks of cytology. Yet, each species has its own species-specific polymorphism, and only very rarely do even the most closely related species share the same chromosomal polymorphism. This fact underlines the drastic nature of the chromosomal reconstruction during much of speciation.

These two classes of phenomena (1 and 2) prove that there is no necessary correlation between chromosome mutations and speciation, since either can occur without the other. Yet, closely related species are far too often differentiated by a major chromosomal rearrangement to permit considering this fact a pure coincidence.

(3) *Speciation coinciding with a chromosome mutation*. It is obvious that a reconstruction of the karyotype during speciation would not occur so frequently if it did not have a selective advantage. What could this advantage be? It is now becoming evident that there are two advantages, two separate phenomena contributing to the success of chromosomal speciation: (a) chromosomal mutations have the potential to serve as (or contribute to) isolating mechanisms, and (b) the locking up and protection of a particularly favorable gene complement through a chromosomal mutation may create a new supergene, as Wallace (1959a) was perhaps the first to see clearly. Both of these components of chromosomal speciation can subsequently be improved by natural selection, either during a period of segregation in a geographic isolate or during subsequent parapatric speciation (see below) or by both processes.

(a) *Chromosomal mutations as potential new isolating mechanisms*. Any change in the structure of the chromosomes is called a chromosome mutation, whether it is an inversion, translocation, duplication, or any other

change in the linear sequence of the genes or in the mechanics of the chromosomes (for instance, spindle attachment). For details see textbooks of cytology or recent reviews (for example, White 1969; Benirschke 1969).

Chromosomal mutations (mostly inversions) are estimated to occur at a rate of 1 in 1000. Most of these are sufficiently deleterious to be eliminated at once, that is, before the mutation's carrier can reach reproductive age. Others are capable of giving rise to a system of balanced polymorphism and they will be retained in the population. In addition, there is a third class of rearrangements that appears to reduce the fecundity of the heterozygotes to some extent. It is the incorporation of these chromosome mutations into the gene pool of species and the role they play in speciation that remains a controversial issue to this day. Heterozygotes for the kind of chromosome mutations that seem important in speciation usually encounter the following difficulties during meiosis: (1) meiotic asynapsis (partial failure of chromosome pairing), or (2) malorientation of multivalents at the first metaphase, or both. Both of these difficulties may lead to production of gametes carrying chromosomal deletions or duplications or broken or acentric chromosomes and thus lead to a significant reduction in the fecundity of male hybrids.

Chromosome mutation is an entirely different phenomenon from gene mutation. First of all, it almost always has no effect on the visible phenotype, and is therefore difficult to detect. Second, heterozygotes are not shielded by dominance; indeed the heterozygotes with their meiotic difficulties are the prime target of selection (John and Lewis 1969). Finally, chromosome mutation is not (or at least not primarily) a change in the DNA program, but in the linear sequence (or duplications or deletions).

Breakage and fusion of chromosomes are prominent in chromosomal mutation, but there is still considerable disagreement among experts about the cytological details of these processes. One's interpretation of certain sequences in chromosome phylogeny will depend on whether one assumes that a metacentric chromosome can simply divide by "fission" into two acrocentric ones or one demands that a new centromere has to be acquired by translocation, whether one feels that broken chromosomes can simply "heal" their open ends or one demands that they must acquire a new "telomere" (end piece), also by translocation or inversion. See White (1969) and John and Lewis (1969) for a discussion of some of the opposing views.

The most frequent or at least most conspicuous chromosomal change is the *fusion* of two acrocentric chromosomes into a single metacentric chromosome. The result is a reduction in chromosome number. A trend

toward such a reduction is widespread among animal taxa. For instance, the most primitive isopods have 28 haploid chromosomes and this number is independently reduced through fusion to the lower number of 8 in several unconnected lines. It is now clear that most differences in chromosome numbers between closely related species of animals is the result of such fusions.

If only fusions occurred during evolution, soon all species would have only a single pair of chromosomes. Obviously some opposing process must also occur that leads to an increase in chromosome number. The seemingly simplest such process would be the exact reverse of fusion, that is a *fission* (or disassociation) of a metacentric chromosome into two acrocentrics. That such simple fissions can occur is, however, doubted by most cytologists. Yet increases in the chromosome number (not due to polyploidy), whatever the mechanism, are frequent in animal evolution and may well play an important role in speciation.

There seem to be considerable differences in the mechanical aspects (for example, spindle attachment, spindle orientation) of the chromosomes among different groups of animals. Centric fusion, for instance, permits in some organisms the development of perfectly viable polymorphisms, as in the mollusk *Thais*, the shrew *Sorex*, and certain beetles and mantids. On the other hand, no species of *Drosophila* or morabine grasshopper is polymorphic for a fusion. In these groups fusion occurs only in association with speciation.

(b) *Chromosomal mutation and the production of new supergenes.* The cyto-mechanic aspects of chromosome mutation have perhaps been over-emphasized in the past. If mechanical difficulties during chromosome pairing were the major selection pressure against chromosome mutations, one would expect such mutations to accumulate in species without meiosis. This inference, however, is not substantiated by a study of parthenogenetic species. They do not seem to have a larger number of chromosomal rearrangements than sexual species. Furthermore, the mere fact that so many populations pass successfully through the heterozygous bottleneck of a "deleterious" chromosomal mutation likewise militates against too exclusive a stress of the mechanical aspects. It now appears that gene contents rather than mechanical qualities determine in many cases whether or not a new gene arrangement can establish itself in a population.

Most structural rearrangements of chromosomes inhibit or prevent crossing over in heterozygotes. A new gene arrangement may "lock up" a coadapted gene sequence and, by protecting it from crossing over, create

a new supergene (Mayr 1963:536). This eventuality is particularly important in peripheral populations where only an unusual constellation of genes can expect to be successful. Wallace (1959a) pointed out that bearers of such protected chromosomes or chromosome segments, being members of peripheral populations, are better adapted for the marginal environment of the species border than are genotypes from the center of the species range. To him, the most important aspect of the chromosomal reorganization is the protection from disruptive recombination that it affords certain new supergenes. Chromosomal mutation, thus, is an instrument of ecotypic adaptation.

It is evident that these two aspects of chromosomal mutation—production of mechanical incompatibilities and development of new supergenes—reinforce each other. There will be a steady selection for an improvement of the adaptation of the supergene and this will tend to produce an increase in genic heterozygote inferiority. This, in turn, will strengthen the effectiveness of the cyto-mechanic isolating mechanisms.

The reason chromosomal speciation is so controversial is the temporary nature of the transition stage. The duration of the stage in which the original chromosome arrangement and the new rearrangement coexist in the population is too short to be directly observed (except in rare cases). It is so short because the coexistence of both chromosomal types is discriminated against by the lowered fitness of the heterozygous combinations, in contrast to a balanced polymorphism maintained by heterozygote superiority. Interpretation must rely on inference, the best clues being furnished by the distribution pattern of species and incipient species that differ from each other in chromosomal mutations. These patterns suggest that such speciation must occur somewhere at the periphery of the range of the parental species. A study of the chromosomal situation in peripheral populations is, therefore, a prerequisite for a full understanding of chromosomal speciation.

#### *Chromosomal Variation in Peripheral Populations*

In all species with polymorphism for chromosome arrangements there is a tendency toward a reduction of this polymorphism in the peripheral populations, some of which may be entirely monomorphic. This chromosomal and genetic uniformity is selected for primarily because only a very small assortment of genotypes is able to cope with the marginal conditions of the species border (see above). As White (1959) has pointed out, however, reduction in the number of heterozygous balances yields a further advan-

tage: it reduces genetic homeostasis and evolutionary inertia in these peripheral populations. They are far better capable of responding to new selection pressures, and consequently, to new evolutionary opportunities than populations from the "dead heart" of the species. They are better situated to utilize new gene combinations that are generated during the genetic revolution than are populations in which the genes are tightly knitted together by numerous balancing mechanisms. Finally, being essentially monomorphic, they are in a better position to incorporate new chromosomal arrangements.

That speciating populations pass through a stage of drastically reduced polymorphism is also supported by the observation that closely related, chromosomally polymorphic species, have only little of this polymorphism in common. For example, the two sibling species *Drosophila pseudoobscura* and *D. persimilis*, both of which are highly polymorphic for inversions of the third chromosome, have only a single inversion in common. The same has been found for many other closely related species of *Drosophila*, for instance, those in the *virilis*, *repleta*, and *willistoni* (except *paulistorum*) species groups. A karyotypic homozygosity of incipient species of *Drosophila* is further substantiated by the relative chromosomal uniformity of many of the most successful and widespread species of *Drosophila* (Carson 1965). It is apparently this chromosomal monomorphism that has permitted them to acquire a genetic constitution of such flexibility and adaptability that they can feed and breed in the most diverse sites in many climatic zones and geographic regions. *Drosophila simulans*, *D. melanogaster*, *D. immigrans*, and *D. m. mercatorum* fit into this category.

#### *The Population Aspects of Chromosomal Speciation*

Two kinds of karyotype changes can be distinguished (John and Lewis 1966) that—from the point of view of chromosomal variability of populations—have quite different rates of occurrence and evolutionary potential (neglecting in this context all strictly deleterious chromosome mutations): (1) chromosome mutations, such as paracentric inversions in *Drosophila*, that give rise to polymorphism, thereby demonstrating that they are compatible and perhaps even heterotic with the parent arrangement; and (2) more drastic chromosomal mutations, such as translocations, fusions, fissions, and the like, which usually occur (or at least are successful) only during speciation.

Chromosomal speciation, mediated by the second of these kinds of karyotype changes, apparently occurs only under special circumstances.

This conclusion is indicated by the following facts: most chromosomal sibling species are parapatric; a definite inferiority of heterozygotes is found in zones of secondary hybridization between such species; and intermediate populations (except those produced by secondary hybridization) are absent. The special circumstances required for chromosomal speciation are provided in peripherally isolated populations. Whether established as founder populations or consisting of relict populations isolated owing to climatic fluctuations, such populations can undergo drastic chromosomal reorganization for several reasons: (1) their small population size, which favors errors of sampling; (2) the environmental pressures, which favor unusual genotypes in these populations; and (3) the reduction or cessation of gene flow, which permits an undisturbed reorganization of the isolated gene pool. All these conditions favor the "locking up" of new gene constellations—new supergenes—which are especially favorable in the marginal environment.

It is thus an unusual combination of factors—chromosomal monomorphism, small population size, a rigorous environment, and temporary shielding from gene flow, possibly accompanied by a genetic revolution—that permits a population to pass through a temporary stage of heterozygosity for two somewhat incompatible gene arrangements. The amount of potential incompatibility between the two chromosomal conditions is usually sufficiently great to require a very rapid transition. Therefore, it would seem altogether improbable that this could happen in a large continuous population. Possibly another factor favors the occurrence of chromosomal speciation in marginal populations. Mortality produced by the adversity of the marginal environment takes a very high toll. Should a new rearrangement produce a large number of deleterious segregation products, they may not be fatal for its establishment if the deleterious zygotes can be "charged" to this inevitable high mortality. If a new gene arrangement in homozygous condition is of high selective value, it has a good chance of becoming established (helped by errors of sampling), even if only 2 among 100 or 1000 offspring survive. Such a low survival rate is common among animal and plant species.

As soon as the new gene arrangement is established in homozygous condition and its new supergene (or genes) has become coadapted with the residual genotype, in other words, as soon as the incipient new species has consolidated its new genotype, it can take advantage of its special adaptive potential and begin to expand into unoccupied territory until a new species border is established along the line where its adaptive potential and the resistance of the environment are in equilibrium. Where it comes

parapatrically in contact with the parental species, it will establish a narrow secondary hybrid zone (reproductive isolation will rarely be complete at the beginning). If the genotype of the new species is superior to that of the parental species, it will "roll back" the hybrid zone at the expense of the parental species.

On the basis of his studies of morabine grasshoppers in Australia, White (1968) has advanced a slightly different interpretation of chromosomal speciation, at least for that group of organisms. He envisages the chromosomal mutation as "arising at a single point in the area of occupation of a species and spreading out from there on an advancing frontier," forming a narrow zone of polymorphism. He designates this process *stasipatric speciation*. Key (1968) considers such a process improbable. If the heterozygotes are inferior, as White himself infers, it would seem rather unlikely that the new arrangement would advance, considering that it occurs in the frontier zone primarily in heterozygous condition. Instead of interpreting the belt of polymorphism (which is usually only a couple of hundred meters wide) as an advancing frontier of heterozygosity it would seem simpler to consider it a zone of secondary hybridization. In most mammalian genera in which parapatric chromosomal species occur, such belts of secondary hybridization are even narrower, if not altogether absent. In the case of the morabine grasshoppers, an interpretation of past speciation is facilitated if one assumes that the size of the populations pulsed with the fluctuations of the climate. Much remains to be done to answer the many unsolved problems raised by chromosomal speciation. With the steady refinement of the techniques of chromosomal analysis and with the growing interest in the study of the geographic variation of the karyotype, there is every reason to hope that such answers will soon be forthcoming.

*Semigeographic speciation.* It has often been postulated by evolutionists that genetic differences and eventually isolating mechanisms can be built up in an ecological "tension zone." The occurrence of such *semigeographic speciation* seems unlikely. There is no evidence that reproductive isolation can be acquired in a zone of primary intergradation as long as the two adjacent populations are in broad contact with each other. Gene flow and the cohesion of the gene pool of the species prevent semigeographic speciation, regardless of diversifying selection. The minor ecotypic adaptations on either side of a habitat border can be acquired and strengthened without a disturbance of the basic epigenotype of the species. For a discussion of the feasibility of such speciation see Clarke and Murray (1969).

There is, however, the possibility that speciation can be completed in

belts of secondary contact. If hybrids are of sufficiently lowered fitness, there will be a steady elimination of those genes and chromosome arrangements that permit the interbreeding of the two incipient species. Concurrently there will be a steady accumulation of those components of the genotype (previously acquired in geographic isolation) that discourage interbreeding. This process of improving allopatrically acquired isolating mechanisms in a contact zone (a process corresponding to character displacement) can be called *parapatric speciation*. Key (1968) considers that the "tension zones" of morabine grasshoppers illustrate this type of speciation in its nearly final stages.

Obviously not all populations involved in secondary intergradation are in the process of completing speciation. The *Corvus corone-cornix* case (p. 221) proves this conclusively. If the compatibility of the two incipient species is high, that is, if the hybrids are only slightly inferior, there is nothing to stop the continuing process of interbreeding.

Populations with conspicuously different phenotypes meet in many species along a sharp border. Such meetings occur most often in slow-moving organisms like snails. It is still uncertain in all of these cases whether these sharp borders are zones of primary or secondary intergradation (Chapter 13). Even less certain is whether such a phenotypic escarpment can ever evolve into a species border (through semigeographic speciation). The absence of species swarms related to species (like *Cepaea nemoralis*) that are rich in phenotypic escarpments, and everything we know about the cohesion of genetic systems, argues against the possibility of semigeographic speciation with the help of purely genic differentiation.

Speciation in plants is often very similar to that in animals, likewise involving "a rapid process of speciation at the diploid level in peripheral populations" and "catastrophic selection in ecologically marginal populations" (Lewis 1962). A repatterning of the chromosomes is frequent in the founder population that gives rise to a new species.

#### *Speciation and Continuous Ranges*

Not all isolates are established by founders. Sometimes they arise through the contraction of a previously continuous species range into isolated pockets. Mutation, recombination, and selection will henceforth be different and independent in the two areas and an increasing genetic divergence is inevitable. How rapidly this will proceed and whether or not it will result in speciation are largely determined by population size. It occurs not infrequently in plants and in highly sedentary animals that the population

cf  
Ende

Parapatric

in such an isolated pocket is drastically decimated by an environmental adversity. Such catastrophic selection (Lewis 1966) may produce the same results as a genetic revolution in a founder population. If aided by chromosomal mutations, it may lead to an almost instantaneous origin of a new species.

Yet, if two separated populations remain large throughout, they will not pass through a genetic revolution and will continue to share the same balancing systems, the same epigenotype. Normalizing selection will tend to eliminate the same deviants in both daughter gene pools, which, although now independent, will continue to act as if they were parts of a single cohesive system. No one knows how long such a "parallel cohesion" can be maintained. The case of the American and Asiatic sycamores (*Platanus*), which have failed to acquire reproductive isolation after millions of years of separation (Stebbins 1950), gives one pause. It appears that the basic epigenotype of a species, its system of developmental canalizations and feedbacks, is often so well integrated that it resists change with remarkable tenacity (Chapter 10). Isolated populations sometimes remain amazingly similar to the parental populations during long periods of complete isolation. In a large population the genetic change toward species level will progress only slowly, unless speciation is favored by environmental conditions and the genetic structure of the isolated population.

*Speciation by distance.* Speciation by distance is a process that seems far less well established now than it did 20 years ago. It would seem reasonable to assume that gene flow is so slow in highly sedentary organisms that it cannot compensate for the centrifugal forces of genetic changes in all populations. As a consequence one should find abundant evidence for speciation by distance in all widespread, sedentary organisms. However, such evidence is singularly missing in all species with a contiguous distribution of populations. Not even the cases of circular overlap (Chapter 16), often cited as evidence, are conclusive. There are major gaps in nearly all of these chains of populations or at least evidence for the former existence of such gaps. Circular overlaps, therefore, are the product of orthodox geographic speciation.

The rarity of speciation by distance and the slowness of gene flow in most species are two phenomena seemingly in conflict with each other. How can this conflict be resolved? Perhaps, it might be suggested, gene flow is not quite so slow as it appears. Even highly sedentary species have a dispersal stage during which a few individuals scatter unexpectedly far. But this occurrence of long-distance dispersal cannot by itself compensate

for the overall slowness of gene flow. Yet gene flow alone cannot prevent abundant speciation by distance. However, it is strongly reenforced by the epistatic systems that the members of a species share (see p. 170), and it is presumably these shared homeostatic mechanisms that ordinarily prevent speciation by distance.

### *The Genetics of Species Differences*

Recent studies on the integration of species-specific gene complexes have considerably changed our ideas on the nature of species differences. After the claims of the early Mendelians that one or a few mutations "made" species had been refuted, we had come to think of the genetic difference between species as a matter of quantity: if enough gene substitutions were piled on top of each other, there would eventually be a different species. Early authors spoke of dozens or scores of gene differences between species, but when it was realized that even individuals within a single population (including the human species) may differ by hundreds of genes, one began to talk in bigger numbers. Haldane (1957) said recently, "Good species, even when closely related, may differ at several thousand loci," and this order of magnitude would probably be supported by most current investigators. Actually such figures tell us relatively little. Indeed, it is becoming increasingly evident that an approach that merely counts the number of gene differences is meaningless, if not misleading.

The genetic analysis of species hybrids has shown that few species differences appear to be controlled by single genes or by a few genes with large phenotypic effects. Where single gene differences do distinguish species, the very same genes may be polymorphic in related species, for instance, black versus yellow wing color in *Papilio*. Most species differences, however, seem to be controlled by a large number of genetic factors with small individual effects. The genetic basis of isolating mechanisms, in particular, seems to consist largely of such genes.

Each isolated gene pool is a different biological system, and the organization that is the result of the coadaptation of the genes may add a new dimension to the difference that cannot be stated as the arithmetic sum of the individual gene differences. It is easy to imagine two conspecific populations that share the same species-specific isolating mechanisms and essential chromosome structure, and yet differ from each other by more individual gene substitutions than some good species. It is evident that a purely quantitative approach may well be misleading. Nor can species difference be expressed in terms of the genetic bits of information, the

nucleotide pairs of the DNA. That would be quite as absurd as trying to express the difference between the Bible and Dante's *Divina Commedia* in terms of the difference in the frequency of the letters of the alphabet used in the two works. The meaningful level of integration is well above that of the basic code of information, the nucleotide pairs.

What, then, makes a species different from an intraspecific variant? I believe that Harland hit the nail on the head when he said many years ago that species are characterized by their modifiers. Today we would perhaps use a slightly different terminology for what Harland had in mind. We might say that it is the total system of developmental interactions, the totality of feedbacks and canalizations, that makes a species. Two individuals of *Drosophila melanogaster* that differ in five conspicuous mutations affecting eye color, pigmentation, wing shape, bristle structure, and haltere formation may look strikingly different from each other, yet they still share their "modifiers," their total developmental system, and are thus still *Drosophila melanogaster*. Two wild-type individuals of *D. melanogaster* and *D. simulans*, which are hardly distinct visibly, nevertheless differ from each other by hundreds, if not thousands, of genes and are the possessors of totally different developmental systems. The important point is that *different species are different systems of gene interaction, that is, different epigenetic systems.*

*Morphological consequences.* That the genetic reconstitution of isolated populations is often rather drastic and affects major homeostatic systems is supported by studies of morphological and physiological characters. Peripheral isolates, no matter how close to the main range of the parental species, almost always exhibit noticeable differences, in contrast to the essential uniformity of the contiguous populations in the main range of the species. Such differences are well illustrated by *Tanyiptera galathea* (Fig. 16.4), *Dicrurus hottentottus* (Fig. 16.2), and other species cited in Chapter 13. An independent evolution of isolates characterizes geographical variation in all regions with insular distribution. The rapidity with which morphological changes take place in such peripheral isolates confirms our conclusion that shifts in the previously existing developmental homeostasis are permitted or induced by the genetic reconstitution of these populations.

The degree of morphological distinctness acquired during the period of isolation is not necessarily an accurate measure of the degree of general genetic difference or, more specifically, of the degree of reproductive isolation. This is true both where, as with the snails of the genus *Cerion* (Fig. 2.1), a high degree of morphological difference is associated with lack

of reproductive isolation and where, as is the case in sibling species, the situation is reversed (Chapter 3).

*Ecological consequences.* The marginal environment of the geographical isolate and the unfavorable properties of the "normal" niche of the species under these marginal conditions often reinforce the genetic revolution. The genetic changes, in turn, may profoundly affect the ecological preferences and adaptations of a population.

The environment in the peripheral isolate is always to some degree unlike the optimal environment of the species in the center of its range. The biotic environment, in particular, is unbalanced at isolated locations. The new isolate will thus be exposed to a considerably changed selection pressure. Even where the physical environment in the peripheral isolate is not very different from the environment in nearby peripheral areas of the species, the response of the isolated population to selection pressure will be quite different from that of a population which is part of a contiguous array of populations held together by gene flow and by all the cohesive devices discussed in Chapter 10. A population that is part of a continuum of populations is forced to compromise between becoming adapted to local conditions and remaining coadapted with the gene pool of the species as a whole. The more distant a population is from the optimal center of the species range, the less suitable its genetic equipment will be to cope with the optimal species-specific niche. The species border represents the stalemate between local ecotypic adaptation and coadaptation with the gene pool of the species as a whole. In contrast to the population that is part of a continuum, the isolated population can respond to its local adaptive needs without having to compromise with the solutions found by other populations.

The best answer to the challenge of an unusual peripheral environment is in many cases a shift into a new niche. Such a shift is greatly facilitated by a genetic revolution and the special properties of isolated populations. In particular, the genetic lability of such populations and the pronounced population fluctuations (in the absence of strong density-dependent factors) facilitate such shifts. In no other situation in evolution is there a greater opportunity for adaptive shifts or evolutionary novelties. That this is not merely a hypothesis is documented by the many ecological shifts in peripherally isolated populations that have been observed (Chapters 11, 13, and 19). Indeed, nearly all aberrant populations of species are peripherally isolated. The ecological shifts on oceanic archipelagos illustrate this phenomenon dramatically.

### Requirements for Successful Speciation

A species is an independent genetic system that has the properties of being reproductively isolated from and ecologically compatible with other sympatric species. Speciation means the acquisition of these properties. It may take place almost instantaneously, as in the case of polyploidy, or gradually, as in the case of geographic speciation. The process by which reproductive isolation and ecological compatibility are acquired is sufficiently important to deserve detailed analysis.

The term isolation has been used in evolutionary biology for two very different kinds of phenomena: geographic isolation and reproductive isolation (Mayr 1959a). Some authors have confounded these two phenomena and have thereby been led to erroneous theories of speciation. *Geographic isolation* refers to the division of a single gene pool into two by strictly extrinsic factors. It is a reversible phenomenon that in itself has no effect whatsoever on the two separated gene pools. What it does is to guarantee their independent development and to permit the accumulation of genetic differences. *Reproductive isolation* refers to the devices that guard a harmoniously coadapted gene pool against destruction by genotypes from other gene pools. These protective devices are called isolating mechanisms (Chapter 5). Speciation is characterized by the acquisition of these devices.

*Ecological compatibility.* An incipient species, in order to complete the process of speciation, must acquire sufficient differences in niche utilization to be able to exist sympatrically with sister species without fatal competition (see Chapter 4). Such differences are due to ecological shifts in the isolate. The longer the populations have been isolated, the more drastic the genetic revolution; and the greater the ecological differences between the areas, the greater is the probability of ecological differences. Ecological compatibility ("exclusion") need be only initiated during geographic isolation. Even if the ecological divergence is only slight when the species begin to overlap, selection can continue to widen the gap. Such selection will be strongly centrifugal (Fig. 17.7), since it will be directed against the individuals in the zone of ecological overlap. That such selection actually takes place is substantiated both by observation (Chapter 4) and by experiment. When *Drosophila melanogaster* and *D. simulans* are put together in the same culture at 25°C, *D. melanogaster* always eliminates the competing species sooner or later. If, after 10 or 15 generations of competition, some of the experimental *simulans* flies are placed in competition with a new (unselected) batch of *D. melanogaster*, they prove to be con-

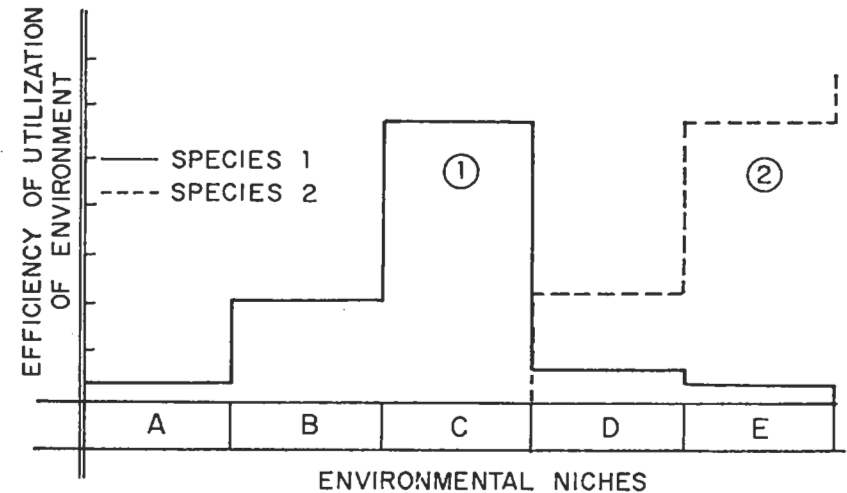


Fig. 17.7. Niche utilization by two different species. Species 1 finds optimal conditions in environmental niche C; it utilizes niche B inefficiently and niches A, D, and E very poorly. Species 2 cannot utilize niches A, B, and C at all, but finds optimal conditions in niches E and F. The absence of competition in niche A will invite the evolution of a species adapted for this niche. (From Mayr 1949.)

siderably improved as competitors (Moore 1952a,b). This indicates that genes had accumulated in the experimental *D. simulans* population that enhanced their status as competitors.

### The Origin of Isolating Mechanisms

The most indispensable step in speciation is the acquisition of isolating mechanisms. Isolating mechanisms have no selective value as such until they are reasonably efficient and can prevent the breaking up of gene complexes. They are ad hoc mechanisms. It is therefore somewhat difficult to comprehend how isolating mechanisms can evolve in isolated populations. This problem has been the subject of considerable discussion during recent years, and scientists are only now approaching agreement.

There are two major theories of the origin of isolating mechanisms. According to the *sympatric theory*, isolating mechanisms are built up through natural selection when two incipient species begin to become sympatric, that is, when their geographic ranges begin to overlap. This hypothesis is based on the observation that hybrids between two species are usually of lowered fitness. It argues that individuals with inefficient isolating mechanisms will be susceptible to hybridization in areas of contact

between the parental and the incipient new species. These genotypes will be eliminated from both populations as a consequence of selection against the hybrids that they produce. Genotypes with better-developed isolating mechanisms are not apt to hybridize and will not be eliminated by selection. Their frequency will increase in the population. This process, it is postulated, will in due time lead to an improvement and final perfection of the isolating mechanisms.

Cases in which reproductive isolation between sympatric species was found to be greater than that between allopatric species are usually cited as evidence supporting the theory of the sympatric origin of isolating mechanisms. For instance, Dobzhansky and Koller (1938) found that *Drosophila miranda* was more strongly reproductively isolated from the populations of the two related species *D. persimilis* and *D. pseudoobscura* that occurred in the zone of overlap with *miranda* than from those populations that came from outside the range of *miranda*. Other similar cases have been reported in the literature. Singling out such instances is, however, biased sampling. If isolating mechanisms are simply a by-product of genetic divergence, and if—as is well established—different populations of a species differ in the level of divergence, one might expect, in comparing pairs of closely related species, to find some cases where the degree of reproductive isolation is higher between sympatric populations and other cases where it is higher between allopatric populations. This, indeed, is exactly what Patterson and Stone (1952) have found. Even more frequently, however, no differences exist between sympatric and allopatric populations of two species with respect to the degree of reproductive isolation.

A similar objection may be raised against the citation of evidence that two species are more different in coloration or in call notes in areas of sympatry than where they are allopatric. These instances can easily be matched by cases where the reverse is true. The best evidence for the sympatric theory would be cases where incipient species began to overlap in historical times, hybridized at first quite freely, but at present hybridize much less freely or not at all. Several cases that might qualify are recorded in the literature, but they are susceptible also to a very different interpretation. When the titmouse *Parus cyanus* invaded the range of *P. caeruleus* in western Russia or the woodpecker *Picoides syriacus* that of *P. major* in southeastern Europe, quite a few hybrids were reported during the first invasion but only a few later, except at the front line of expansion. It is quite likely that the first flush of hybridization was due to the fact that the sparse early invaders failed to find conspecific mates and hybridized

only after their threshold had lowered. Hybridization decreased or disappeared after the population density of the invading species had risen (Short 1969). Where the Mallard (*Anas platyrhynchos*) and the Black Duck (*A. rubripes*) have been overlapping in the eastern United States, no change in the frequency of hybridization has been noticed in the last 75 years. Hybridization is most frequent (about 4 percent) where both species are almost equally abundant, there being no indication of a reinforcement of isolating mechanisms in the primary zone of contact.

The various objections against the theory of the sympatric origin of isolating mechanisms have been ably stated by Moore (1957). Perhaps the most convincing argument against the power of natural selection is supplied by the "old" hybrid belts (Chapter 13). These have existed in many cases for thousands of years, and the narrowness of the belts proves that the hybrids are indeed being selected against. Yet there is no indication that this selection has led to a strengthening of the isolation in any of the cases. Proponents of the hypothesis that isolating mechanisms originate or are markedly improved by natural selection have not been able to solve the difficulties raised by introgression. If the hybrids are not sterile, some of them will backcross with the parental species, a process that will lead to a further weakening of isolation rather than to its strengthening (but see p. 326).

Another objection to the sympatric theory emerges from a comparison of the strength of isolating mechanisms within zones of overlap with the strength of those outside such zones. The genetic factors responsible for reproductive isolation should, according to the sympatric theory, be restricted to zones of overlap between the related species, since there would be no selective advantage in having these ad hoc mechanisms spread beyond the area where they are favored by selection. However, there is no evidence that isolating mechanisms are geographically thus confined. That selection is not necessary for the perfecting of isolating mechanisms is demonstrated by the numerous cases in which efficiently functioning isolating mechanisms have undoubtedly evolved in geographic isolation without any possibility of their improvement by subsequent selection.

These facts are taken into account in the *allopatric theory of the origin of isolating mechanisms*, according to which they arise as an incidental by-product of genetic divergence in isolated populations. This was the thesis of Darwin (see Mayr 1959a), who could not see how natural selection could produce interspecific sterility. Since Darwin's time many evolutionists have defended this thesis.

According to this theory any drastic genetic reconstitution, such as may take place in isolated populations, particularly if they are subject to a pronounced ecological shift, may simultaneously affect the genetic basis of isolating mechanisms. Since most genes are pleiotropic, selection pressures against one portion of the phenotype very often affect also the genetic basis of an entirely different component of the phenotype. A genetic restructuring of an incipient species, in response to an adaptive shift, may concurrently produce new isolating mechanisms.

This hypothesis is supported by three sets of observations. First, there is much evidence for the geographic variation of isolating mechanisms (Chapter 16), including incipient sterility and ethological isolation. The beginnings of such isolation have been observed even in separate cultures of laboratory stocks, for instance in *Drosophila*. Second, in view of the highly composite and polygenic character of the isolating mechanisms (Chapter 5), it would be unlikely for them not to be affected by genetic reconstitution. Third, many isolating mechanisms have ecological components. The ecological shifts in incipient species are bound to have an effect on their isolating mechanisms. The thesis that reproductive isolation arises as a by-product of the total genetic reconstitution of the speciating population is consistent with all the known facts.

The theory of allopatric origin does not conflict with the fact that natural selection plays a role in the subsequent improvement of subsidiary isolating mechanisms. One primary mechanism, however, or a combination of several, must be fully efficient before contact is first established. Otherwise, a zone of secondary hybridization is inevitable.

Much of the apparent conflict between the opposing theories disappears when the large category "isolating mechanisms" is subdivided. It is quite evident that one primary isolating mechanism, or several, must be acquired in geographical isolation before contact is established. Depending on the group of animals in question, this may be a behavior barrier or cross-sterility (Chapter 5). This single mechanism will prevent hybridization in most cases, and where it does not do so, inferior hybrids will be produced, owing to behavioral, ecological, or cytological incompatibilities. Such hybrids will reproduce poorly, if at all, and there is, thus, no danger of a breakdown of the species barrier. And there will be strong selection in favor of the acquisition of additional isolating mechanisms to prevent such wastage of gametes. Many such cases have been described in the literature (Mayr 1963; Blair 1964). The selection theory is, thus, valid as far as the strengthening of secondary isolating mechanisms is concerned.

It is not certain for most groups of animals whether the behavior barrier

or the sterility barrier is the first isolating mechanism to be perfected. In many families of birds, the duck family (Anatidae) for instance, sympatric species may still be quite fertile with each other and yet not hybridize in nature, because of the efficiency of the ethological barriers. Occasional hybrids occur, but at such a low rate that the elimination of the introgressing genes is not too severe a burden on the parental species. Most of the hybrids are in any case excluded from further reproduction owing to behavioral incompatibility. Such "behavioral sterility" of hybrids has also been observed in *Drosophila*. Ever more exceptions are found to the traditional view that the sterility barrier is the first one to be perfected.

Perdeck (1957) shows that reproductive isolation between *Chortippus brunneus* and *C. biguttulus*, two sibling species of grasshoppers, is maintained exclusively by the difference in display song. No other isolating mechanism can be detected.  $F_1$  and backcross hybrids seem to have the same fertility as intraspecific crosses (although the material is limited). The only handicap of the hybrid males is that they are discriminated against by females. The functioning of this ethological isolating mechanism must have been virtually perfect before contact was established, because otherwise the essentially fully viable hybrids would have served as a channel of gene flow between the two species. A number of additional cases among amphibians and insects have been described in which the vocalization of the males seems to be the primary and by far the most important isolating barrier.

Gradual speciation, then, proceeds as follows: an isolated population acquires, during its isolation, the primary isolating mechanisms that guarantee its integrity after establishment of contact with a sister or parent species. It also acquires a minimal amount of that "adaptive property" which permits the two species to be ecologically compatible. Selection pressures, after the establishment of sympatry, will help to improve the isolating mechanisms to such an extent that no more wastage of gametes (at least not of female gametes) occurs, and ecological exclusion will be steadily improved at the same time.

## CONCLUSIONS

Geographic isolation is a purely extrinsic and completely reversible factor that does not by itself lead to the formation of species. Its role is simply to permit the undisturbed genetic reconstruction of populations that is the prerequisite for the building up of isolating mechanisms.

The need for coadaptation and for the harmonious integration of genes

sets severe upper limits to the number of genes that can be accommodated in a gene pool, since many genetic combinations are incompatible. The rapid elimination of disharmonious combinations after hybridization is proof of this conclusion. There is a tendency in the integrated gene complex to establish an ever-greater cohesion, to achieve a steady improvement of developmental and of genetic homeostasis. Numerous feedbacks permit the individual as well as the population to compensate for the unsettling impact of the environment. Heterosis, in particular, tends to diminish the effectiveness of selection for specific effects by raising viability and by decreasing dependence on the environment. A well-integrated genetic system may come into perfect balance with its environment and become so well stabilized that evolutionary change will no longer occur. Such a system will be able to cope with the regular input of mutations and the normal environmental fluctuations without having to undergo any change. Its future is at best *evolutionary inertia* and, more likely, eventual extinction when there is a drastic change of the environment.

Speciation is potentially a process of evolutionary rejuvenation, an escape from too rigid a system of genetic homeostasis. Speciation disrupts the cohesion of the gene pool by temporarily depleting its gene contents and by inevitably forcing the population into a slightly or drastically different environment. If the genetic shake-up is sufficiently severe, it may start a chain reaction, a genetic revolution. The greater the genetic change, the greater the probability that the daughter species can enter a new ecological niche and be successful in it. The genetic chain reaction may thus start an evolutionary chain reaction. This process is most likely to occur in its purest form in peripherally isolated populations.

Speciation is a risky process. The impoverishment of the gene pool and the genetic instability that accompanies it are far more likely to lead to disaster than to success. Even though most incipient species will die out, an occasional one not only completes the process, but also succeeds in entering a new niche or adaptive zone.

The importance of speciation is that it invites evolutionary experimentation. It creates new units of evolution, particularly those that are important for potential macroevolution. Speciation is a progressive, not a retrogressive, process.

## 18 • The Ecology of Speciation

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Geographic speciation means the genetic reconstruction of a population during a period of geographic (spatial) isolation. The genetic factors involved in this reconstruction were discussed in the last chapter. In the present chapter I will attempt to analyze the role of the environmental factors that influence the origin and maintenance of discontinuities between populations. Four sets of factors that have an effect on the rate of speciation will be singled out for special discussion: (1) factors determining the effectiveness of geographical isolation; (2) factors affecting shifts into new ecological niches; (3) factors affecting the frequency with which geographic isolates are established, and (4) factors favoring genetic turnover within isolates.

### THE EFFECTIVENESS OF GEOGRAPHICAL ISOLATION

One of the basic properties of species, and of the individuals of which species are composed, is the capacity to spread. Every species has at least one dispersal stage in its life cycle. A study of the geographical barriers that surround every species and every geographical isolate must take this ability for dispersal into consideration. To be sure, "geographical isolation" means the interruption of gene flow by external barriers. But we must realize that the physical nature of these barriers (extrinsic factors) is only one aspect of this isolation. The numerous physiological and psychological characteristics of the individuals that encounter these barriers during their dispersal stage are of crucial importance. Indeed, to a large extent, these intrinsic factors determine the effectiveness of barriers.

#### *The Role of Extrinsic Factors*

An understanding of the functioning of the natural barriers that are responsible for the discontinuities between geographical isolates is an indispensable prerequisite for an understanding of speciation. The study