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GENETIC NATURE OF SPECIES DIFFERENCES¹

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INTRODUCTION

THE boundless diversity of organic forms is impressive even to a casual observer. Reducing this seemingly chaotic multiformity to some sort of rational system was a prerequisite for a scientific study of living things; hence taxonomy and morphology were in the past the most active branches, description and generalizing induction the main methods of biology. Later the main trend of thought has turned from morphology to physiology, from description to experiment, and from peculiarities of single species to properties common to large groups or to all of them. The problem of organic diversity must now be studied in a new aspect, namely, as a general property of living matter, for such it truly is.

The difference between any two individuals or species may be attributed to the differences between their gene complexes, and in a few cases between their cytoplasm. Assuming this statement to be correct (and it is not universally accepted), one must nevertheless admit that it does not represent an adequate solution of the problem of organic diversity, for it disregards the fundamental fact that the living world is subdivided into discrete groups of forms which we call species. The living world is not an array of individuals embodying all the possible combinations of the existing genes; it is certain that only an infinitesimal fraction of the possible gene combinations has been ever realized. Organisms are more or less adapted to their environment, and the gene patterns each of them carries must represent at least a tolerably harmonious whole. With the sexual process being the predominating mode of reproduction, an unlimited inter-

¹ Lecture delivered before the Genetics Society of America and Marine Biological Laboratory at Woods Hole on September 3, 1936.

breeding of all organisms would result, due to the properties of the Mendelian mechanism of inheritance, in a breakdown of the existing gene patterns and emergence of an almost infinite mass of recombinations. Among these recombinations some would be as harmonious as the existing ones, some might be even more so, but it is at least a fair guess that a vast majority would be discordant. Hence maintenance of life is possible only if the gene patterns whose coherence is tested by natural selection are prevented from disintegration due to unlimited hybridization. It follows that there must exist discrete groups of forms, species, which consist of individuals breeding *inter se*, but prevented from interbreeding with individuals belonging to other groups of similar nature.

On the other hand, evolutionary progress is possible only if new gene patterns are constantly being formed, since only by a process of trial and error can the always precarious balance between an organism and its environment be maintained. Mutation and sexual reproduction are the mechanisms that supply a store of new genic patterns. The process of evolution may then be described in a most general way as a result of the interplay of forces tending toward fixation of the already tested gene patterns, and forces producing new gene patterns some of which may become the forerunners of the world to come. One of the tasks of genetics is to secure an understanding of these forces and their interactions (*cf.* Wright, 1931).

It is a remarkable fact that in different organisms causes preventing free interbreeding of species are frequently different; isolation of species from each other is accomplished in nature by different means. Moreover, taking a given pair of species it is not uncommon to find that their interbreeding is averted not by a single but by several causes reinforcing each other's action. The expression "isolating mechanisms" seems to be a convenient general name for all the mechanisms hindering or preventing the interbreeding of racial complexes or spe-

cies. The present article gives an account of the isolating mechanisms found in three species of *Drosophila*, namely, *D. pseudoobscura* "race" A, *D. pseudoobscura* "race" B and *D. miranda*. The two "races" of *D. pseudoobscura* are very closely related; they seem to be morphologically identical, but can be distinguished because when crossed they produce sterile hybrids, and because they differ in a number of cytological and physiological characteristics (Lancefield, 1929, Dobzhansky, 1935, and others).² *D. miranda* differs from either "race" of *D. pseudoobscura* in a set of slight morphological characters, and also by its cytological and physiological properties (Dobzhansky, 1935). The discrimination of these species must be made through laboratory studies on living materials.

GEOGRAPHICAL ISOLATION

The geographical distribution of the three species under consideration is now known with a fair degree of accuracy (see map in Sturtevant and Dobzhansky, 1936). *Drosophila pseudoobscura* race B inhabits the country from British Columbia to California, and from the Pacific to the eastern slopes of the Sierra Nevada-Cascades mountain range. The distribution of *D. pseudoobscura* race A is much wider: from British Columbia to southern Mexico, and from the Coast Ranges (in the North) and the Pacific (in the South) to the Rocky Mountains and the western edge of the prairies. The coast of British Columbia, Washington, Oregon and northern California is inhabited by race B alone (race A reaches the coast only at Puget Sound, southern California, and possibly at the mouth of Columbia River). East of the Sierra Nevada-Cascades and southward from California race A only is found. The two races occur together in the southern Coast Ranges, in Sierra Nevada, and between the northern

² It is solely because of the lack of externally visible distinctions that these two forms are described as races of the same species. By any other criterion they should be considered distinct species, as the reader can see for himself on the basis of the data presented below.

Coast Ranges and the Cascades. It follows that although the areas inhabited by the two races are clearly different, the geographical isolation is far from complete; they occur together in so broad a zone that if their interbreeding were not prevented by other isolating mechanisms (see below) a large hybrid population would result.

The area inhabited by *Drosophila miranda* is comparatively very small, comprising only the region around Puget Sound. Since both races of *D. pseudoobscura* are found in parts of this region, no geographical isolation between *miranda* and *pseudoobscura* may be said to exist.

ECOLOGICAL ISOLATION

Ecological isolation is a condition in which species or races are restricted to different habitats within the same geographical area. Since occupation of different geographic regions by two species may be due to preferences exhibited by each of them to habitats found only in its own region, there may exist situations which may be classed either as a geographical or as an ecological isolation.

D. pseudoobscura as well as *D. miranda* lives in forests, and is not usually found in treeless or desert localities (although a row of trees along a dry streambed may be sufficient to maintain a small population). In the south the distribution of *D. pseudoobscura* is sharply discontinuous, being restricted mostly to islands of forest growing on sufficiently high mountain ranges. The combined distribution of race A and race B of *D. pseudoobscura* is rather similar to, but wider than, that of the western yellow pine, *Pinus ponderosa*. Yet these flies are not bound to that tree only, and flourishing populations of either race were found in other coniferous (e.g., *Pseudotsuga*) or deciduous (e.g., oak, aspen) forests.

Race A has a higher temperature optimum than race B (Dobzhansky, 1935), and the optimum for *D. miranda* is even lower than for race B. In view of this fact it is not surprising that in mountainous regions where both

races occur together race A occupies predominantly the lower and race B the higher elevations. Thus, a locality in the Kern River valley (California) lying at about 3,500 feet is inhabited by race A only, while on the tops of the surrounding mountains (Greenhorn Mountains, about 7,000 feet) a mixture of race A and race B with a predominance of the latter is found. This suggests a weak ecological isolation between race A and race B. *D. miranda* has been found thus far only in company with *D. pseudoobscura*, and the ecological preferences of the former are unknown.

SEXUAL ISOLATION

Lancefield (1929) observed that males of either race of *D. pseudoobscura* copulate with females of their own race sooner than with those of the opposite race. His results were corroborated by Mr. R. D. Boche working in our laboratory (unpublished). In Mr. Boche's experiments males were offered a choice of females of both races; several freshly hatched males of a given race were placed together with the same number of freshly hatched females of the same race and of females of the other race. At stated intervals of time some females were dissected, and the presence of sperm in their seminal receptacles was determined by microscopic examination. Boche found that at first males pair predominantly with females of their own race, but after the supply of the unfertilized females becomes small some interracial matings also take place. Thus, in one experiment race A males (Texas strain) were kept with race A (Texas) and race B (Seattle-4) females for 72 hours at 25° C.; 93 per cent. of the former and 19 per cent. of the latter females were fertilized. A pronounced sexual isolation between race A and race B is therefore established. On the other hand, no indication of even slight isolation was observed by Boche between strains of the same race coming from different geographic localities.

An aversion to mating with individuals of another species is clearly apparent also in crosses between *D. miranda*

and either race of *D. pseudoobscura*. In a series of experiments conducted by the present writer batches of five females and five males from the same strain of *D. pseudoobscura* and five females of *D. miranda* were kept together in the same vial for approximately 96 hours (at 21–23°). The presence of sperm in the seminal receptacles of these females was subsequently determined by dissection and microscopic examination. Among 376 *D. pseudoobscura* females 351, or 93.4 per cent., were found fertilized, while among 377 *miranda* females only 83, or 22.0 per cent., were fertilized. In another series of experiments five females and five males of *D. miranda* and five females of *D. pseudoobscura* were kept together in vials for 96 hours. The examination showed that 40.0 per cent. of *miranda* and only 13.75 per cent. of *pseudoobscura* females contained sperm (the totals of the flies dissected are 235 *miranda* and 240 *pseudoobscura*). In a third series of experiments *D. pseudoobscura* females were kept for nine days with *D. miranda* males, or *vice versa*. Although in this case the possibility of mating with representatives of their own species was excluded, a large percentage of females remained unfertilized. An interesting detail is that different strains of *D. pseudoobscura* exhibit different degrees of aversion to mating with *D. miranda*. Thus, the Oaxaca-5 strain (from southern Mexico) mates with *D. miranda* rather easily, while the Seattle-4 strain (Washington) refuses to cross in almost 90 per cent. of cases. This result indicates that within the species *D. pseudoobscura* hereditary factors are present which affect the crossability of this species with *D. miranda*. The potential evolutionary importance of such factors is obvious; it is fair to guess that the sexual isolation between two incipient species may be built up as a result of summation of a number of genetic factors of this kind.

MECHANICAL ISOLATION

Discrepancies between the structure of the male genitalia of one species and the female genitalia of another

may render copulation of representatives of these species difficult or impossible. Since in insects the external genitalia are made of inflexible chitin, and since species very similar in appearance are sometimes clearly distinct in genitalic structures, entomologists are prone to ascribe a great significance to the mechanical isolation of species (Jordan, 1905). There is no doubt that the structure of the genitalia may make interspecific crosses difficult; for instance, copulation of *D. melanogaster* male with *D. pseudoobscura* female may result in failure of separation and death of both participants. There is, however, no experimental evidence to show that small differences in the genitalia frequently prevent crossing, and Kerkis (1931) has proved statistically that at least in some Hemiptera the genitalia are as variable within a species as are the external structures. The claims that genitalic differences are of paramount importance in isolating species are greatly exaggerated.

Races A and B of *D. pseudoobscura* have identical genitalia, hence mechanical isolation is out of the question in this case. The genitalia of *D. miranda* are identical in structure with those of *D. pseudoobscura*, but since the former species is generally larger than the latter, the absolute size of the genitalia is correspondingly different. Nevertheless, observations on the copulation of *D. miranda* and *D. pseudoobscura* seem to show that no mechanical difficulty is encountered. Any one having experience with *Drosophila* breeding knows how greatly the dimensions of these flies vary under the influence of culture conditions, but offspring can be obtained from matings in which parents are very different in size.

VIABILITY OF THE F_1 HYBRIDS

The isolating mechanisms reviewed above have the common property of tending to prevent the appearance of hybrid zygotes. The mechanisms that remain to be considered concern the hybrids already produced, and tend to handicap or to eliminate these hybrids from the

breeding populations of the parental species. The simplest mechanism of this class is lowering of the viability of the F_1 hybrids, which in extreme cases results in death of the latter before they reach the stage of sexual maturity (e.g., the fish hybrids described by Moenkhaus, 1910, Newman, 1914, and others).

The F_1 offspring from the race A \times race B crosses in *D. pseudoobscura* seem to be about as vigorous somatically as the non-hybrid individuals of either race, although some observations indicate that the male progeny of the A ♀ \times B ♂ cross consists of individuals that tend to be small in size. The male offspring from the cross *D. pseudoobscura* ♀ \times *D. miranda* ♂ are almost completely inviable, the sex-ratio being about 1 ♂ :200 ♀ . The reciprocal cross produces males that are abnormal in appearance, sluggish and rather short lived. The viability of the hybrid females from either cross is higher than that of their brothers but lower than that of the parental species.

HYBRID STERILITY

When crossed, race A and race B of *D. pseudoobscura* produce in F_1 fertile females and sterile males. The female hybrids can be back-crossed to males of either parental race; their daughters are all more or less fertile, while some of the sons are fertile and others are sterile (Lancefield, 1929). The cytological basis of the sterility of the F_1 males is a disturbance of the spermatogenesis: chromosome pairing is incomplete or absent, the first meiotic division abortive, the second division absent, degenerate polyploid cells are formed instead of spermatozoa. Although these disturbances are greater in crosses between some strains than between others, and although in any given cross the abnormalities are greater at high than at low temperatures, the derangement of the spermatogenesis is under all conditions so profound that the sterility of the F_1 males is complete (Dobzhansky, 1934). Preliminary studies on the spermatogenesis in back-cross males show a whole gamut of conditions, ranging from

normal to even greater disturbance than that observed in F_1 males. The hybrids between *D. miranda* and either race of *D. pseudoobscura* are sterile in both sexes. In the males testes are vestigial, while females deposit eggs which produce no larvae. Several studies of the causes of the sterility of the above hybrids have been made; only a summary of the results obtained may be presented here.

In general, hybrid sterility may be due to several causes. Perhaps the most thoroughly studied case of sterility, that of the hybrids between the European and the Japanese races of *Lymantria dispar* (Goldschmidt, 1934), is due to a lack of balance between the sex-determining factors coming from the parental races. The sterile hybrids are here intersexes. That the *D. pseudoobscura* $A \times B$, and the *D. pseudoobscura* \times *D. miranda* hybrids are not intersexes follows from the fact that their secondary sexual characters, as well as their reproductive systems except the gonads, are normal (Dobzhansky and Boche, 1933). The writer has recently found several individuals of race A *D. pseudoobscura* which were probably (and one of them certainly) triploid intersexes. Their reproductive organs were quite different from those of the sterile hybrids.

Another possible cause of hybrid sterility is dissimilarity of the gene arrangement in the chromosomes of the parental forms (chromosomal sterility). In a number of cases, especially among plants, it is now established that races and species may differ in gene arrangement. The first case in which a difference of this sort has been found is that of *D. melanogaster* and *D. simulans* (Sturtevant and Plunkett, 1926, an inverted section in one of the chromosomes). Tan (1935) and Koller (1935) have shown that race A and race B of *D. pseudoobscura* differ in four inverted sections (two in the X-chromosome, one in the second and one in the third chromosomes). The chromosomes of *D. miranda* are built very differently from those of *D. pseudoobscura* (Dobzhansky and Tan, 1936, and a paper in press). In all the chromosomes many genes have

changed their relative locations due to inversions. Some genes located in the same chromosome in one of these two species are located in different chromosomes in the other, indicating that translocations have taken place in the phylogeny. Each species has chromosome sections that can not be identified with certainty in the other; these sections may be accounted for either on the supposition that losses of genic materials have taken place in the phylogeny, or on the supposition that certain parts of the chromosomes were subject to so many reorganizations of the inversion or translocation types that they are no longer identifiable with the aid of the salivary gland chromosome method which was employed in these studies. Dobzhansky and Tan estimate that in order to derive the gene arrangement observed in *D. miranda* from that present in *D. pseudoobscura*, or *vice versa*, at least forty-eight, and probably many more, chromosome breakages and reattachments must take place.

Granting that some, and possibly all, species differ from each other in gene arrangement, one nevertheless must be circumspect in attributing the hybrid sterility to this cause. Cumulative effects of rearrangements of genic materials within the chromosomes may lead to a situation where meiotic pairing between the original and the altered chromosomes will be mechanically difficult or impossible; this, in turn, may result in disturbances at disjunction, and in production of gones containing unbalanced chromosome complements. In plants such gones are frequently inviable, and thus sterility of a hybrid may result. It is, however, not obvious how such a mechanism can produce complete sterility, since even if chromosomes disjoin at meiosis entirely at random a few gones containing balanced chromosome complements should be produced. Hence, accessory hypotheses are needed to explain the complete absence of functional gones in many sterile hybrids. An additional, and even more serious, difficulty is met with if the sterile hybrids in animals are considered. For it is known that, at least in *Drosophila*,

gametes carrying even grossly unbalanced chromosome complements remain functional in fertilization. Translocation heterozygotes and triploids in animals produce functional gametes, some of which may give rise to inviable zygotes. Yet, sterile hybrids in animals, just as in plants, are characterized by non-production of functional gametes rather than by production of inviable zygotes. The writer believes that thus far no case of sterility either in plants or in animals has been conclusively proved to be chromosomal in nature. The main argument that chromosomal sterility exists at all is the occurrence of fertile allopolyploids derived from sterile diploid hybrids, but this argument is not necessarily decisive.

The sterility of the hybrids between race A and race B of *D. pseudoobscura* is certainly not chromosomal, as shown by the following evidence. (1) The inverted sections found in the chromosomes of these hybrids are too few to produce sterility; fertile individuals heterozygous for a larger number of inversions can be obtained artificially in *D. melanogaster*. (2) The hybrids between some strains of *D. pseudoobscura* show complete chromosome pairing at meiosis and yet they are sterile. (3) In the hybrids abnormalities in spermatogenesis are observed at stages preceding as well as following meiosis. (4) Reduplication of the chromosome complement (allotetraploidy) in a section of the testis in the F_1 males does not alter the course of the spermatogenesis (Dobzhansky, 1933, 1934). On the other hand, it has been shown that the sterility of the hybrids under consideration is genic in nature, that is dependent upon interactions of complementary genes contributed by both parents (Dobzhansky, 1936). Such "sterility genes" are present in all the chromosomes of each race studied, and in the parts of the chromosomes having different gene arrangement in the two races, as well as in the parts in which the gene arrangement is similar. The back-cross males are sterile or fertile, depending upon which combination of the chromosomes of the ancestral races they carry. The precise mechanism through

which the sterility genes exert their action leading to the disturbance of the spermatogenesis in the hybrids is unknown, but this mechanism is probably intracellular in nature. This is suggested by the experiments of Dobzhansky and Beadle (in press), who transplanted testes of the hybrid males into males of the pure races and *vice versa*, observing that in all cases the development of the implants as well as of the host's testes proceeds autonomously, *i.e.*, in accordance with their own genetic constitution.

The cause of the sterility of the *D. miranda* \times *D. pseudoobscura* hybrids is unknown at present. The profound differences in gene arrangement observed between these species warrant a suspicion that in these hybrids chromosomal sterility, or a combination of chromosomal and genic sterility, may be involved, but further studies are needed to elucidate this point (*cf.* Dobzhansky and Tan, 1936).

VIABILITY IN THE F_2 AND IN FURTHER GENERATIONS OF HYBRIDS

As stated above, the F_1 hybrids from the cross *D. miranda* \times *D. pseudoobscura* are completely sterile, and no F_2 generation can be obtained. The F_1 hybrid females from $A \times B$ crosses in *D. pseudoobscura* are, however, fertile, and back-cross progenies can be produced. Lancefield (1929) has noticed that in these back-cross progenies the sex-ratio is distorted in favor of females. Dobzhansky and Sturtevant (1935) have confirmed this observation, and pointed out that the general viability of the back-cross products is very low in comparison both with the pure races and with the F_1 hybrids. Some flies of either sex are visibly weak and show various somatic abnormalities, many of the females are either completely sterile or produce very few offspring, the longevity of the flies is generally low. This weakness is more pronounced among males than among females, which fact accounts for the modification of the sex-ratio.

Some of the individuals obtained from the back-crosses must have all the chromosomes, and hence all the genes,

of the race to which the father of the back-cross belongs; other individuals are identical in chromosomal constitution with the F_1 hybrids; but the majority of individuals carry various combinations of the chromosomes of race A and race B. It was tempting to suppose that the low viability of the back-cross products is due to unfavorable effects of mixtures of chromosomes of the two races, that is to say, that individuals carrying some chromosomes of one race and other chromosomes of the other race have an inferior viability. A closer study has shown, however, that this guess is not true, or at any rate not adequate to account for the whole complex of facts (Dobzhansky and Sturtevant, 1935, and unpublished data).

Experiments were so arranged that it was possible to determine the racial origin of all the chromosomes (except the very small fifth chromosome) present in a given back-cross individual by inspection of its phenotype. For this purpose strains of race A and race B having the chromosomes marked by appropriate mutant genes were intercrossed, and the resulting F_1 females were back-crossed to males of both parental races. The startling result of these experiments was the fact that those individuals in the back-cross progenies that are identical in their chromosomal constitution with individuals of pure races or with the F_1 hybrids proved to have a low viability, just as low as the individuals carrying various mixtures of the chromosomes of both races. In other words, the low viability observed in the back-crosses between race A and race B is general, and not restricted to some classes carrying particular combinations of chromosomes. The only way to account for this situation is to suppose that the low viability of the back-cross products is due to a maternal effect, that is, to an influence exerted by the chromosomal constitution of the mother on the development of her eggs. The F_1 females from the interracial crosses carry half of the chromosomes of race A and another half of race B; it appears that the presence of this hybrid chromosome complement in the developing oocyte (or in

the surrounding tissues) influences the constitution of the resulting egg in such a way that the viability of a zygote coming from this egg is decreased. Furthermore, this decrease of viability is independent of the chromosomal constitution which the eggs possess after reduction and fertilization, in the sense that individuals having the same chromosomal constitution are less viable if they come from eggs deposited by an F_1 female than if they develop from eggs of a pure race mother. Thus, an individual carrying all race A chromosomes obtained in a back-cross of an F_1 hybrid female to a race A male is greatly inferior in viability to an individual of pure race A parentage.

On the other hand, the offspring of a given F_1 hybrid female may be more or less viable, depending upon the male to which she is mated. Thus, in one experiment made by the present writer race A females carrying the genes beaded, yellow, vermilion, singed and short were crossed to race B males carrying the genes scutellar and prune. The resulting F_1 females were back-crossed to race A beaded yellow vermilion singed short males. About one hundred culture bottles of this back-cross have produced not a single adult offspring; an inspection of the bottles has shown, however, that many eggs were deposited in them, but that the larvae coming from these eggs have died in very early stages. The decrease of the viability observed here is, consequently, so great that all the back-cross zygotes die before reaching maturity. Nevertheless, the same F_1 females proved capable of producing relatively more viable offspring. They were separated from their mates and re-crossed to wild-type race A males (the Texas strain); larvae soon appeared in the cultures, and at least some of them grew to maturity and produced adults. This experiment has been repeated twice with identical results, and moreover some other experiments involving different strains of A and B races have behaved similarly.

The phenomena of maternal effects have considerable interest intrinsically, and further experiments in this field

are in progress. At present we are interested in this subject only in so far as it has a bearing on the problem of isolating mechanisms. The good viability of the F_1 generation of the interracial hybrids stands in sharp contrast to the low viability of the offspring of the F_1 hybrid females. It is safe to assume that under the conditions of competition in nature this deterioration of viability will tend to eliminate the interracial hybrids from the breeding populations of the ancestral races.

SUMMARY AND CONCLUSIONS

The interbreeding of race A and race B of *Drosophila pseudoobscura* is impeded by (1) a pronounced, though incomplete, geographical isolation, (2) a weak ecological isolation, (3) a marked sexual isolation, (4) a complete sterility of the F_1 hybrid males and of a part of the back-cross males, and (5) a low viability of the offspring of the back-crosses of the F_1 hybrid females to males of the parental races. None of these isolating mechanisms is in itself sufficient to achieve a complete separation of the breeding populations of the two "races," but taken together they probably accomplish this task with a margin of safety.

The interbreeding of *D. miranda* with either race of *D. pseudoobscura* is precluded by (1) a strong sexual isolation, (2) a decrease of the viability and (3) complete sterility of the F_1 hybrids of both sexes. The last of these isolating mechanisms is sufficient for a total separation of the two species, the others increasing the margin of safety.

The great variety and the apparent high efficiency of the mechanisms isolating the two "races" of *D. pseudoobscura* from each other is rather surprising, since these "races" seem to be, at least judging by their external similarity, very closely related. No indication that interracial hybrids occur in nature has been found. In other groups of organisms, notably in some families of plants, the isolation of species is by no means so secure, and hy-

bridization of species in nature is frequently reported in literature. The significance of such differences in the behavior of different groups of organisms is unknown at present, but it seems certain that they must exert a profound influence on the evolutionary pattern of a given group.

The mechanisms isolating species from each other must be considered the only true specific characters, if the expression "specific character" is to have any real meaning. The genetics of species differences is therefore a study of the hereditary nature of the isolating mechanisms, and of their rôle in the dynamics of Mendelian populations.

It has been contended by many authors that the grouping of individuals into species is merely a matter of convenience, since species have no existence apart from the mind of investigator. As a proof of this contention, it has been pointed out that such criteria of species distinction as the production of sterile hybrids sometimes break down because some forms which are classed as species can be crossed experimentally and can produce semi-fertile or fertile hybrids. This point of view is fallacious, and is based on a failure to understand that the fact that some species can be crossed and can produce fertile hybrids does not prove that these species cross regularly in nature. Species is a dynamic rather than a static entity, and the essential feature of the process of species differentiation is the formation of discrete groups of individuals which are prevented from interbreeding with other similar groups by one or more isolating mechanisms. Isolating mechanisms seem to be a rather haphazard collection of phenomena, and yet their genetic effects are alike in kind, namely, the formation and maintenance of discrete groups of organisms. The degree of isolation of these groups from each other is of necessity variable; presumably increasing with time, but in some cases perhaps also receding and disappearing. A thorough understanding of the nature and the functioning of isolating mechanisms is essential, because without it no trustworthy picture of the mechanism of evolution can be drawn.

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