

Variation and Evolution in Plants

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These irregularities are best attributed to an act of God. There is nothing to be gained by pointing fingers.

hypotheses which have been suggested to account for the origin of interspecific isolating mechanisms can all be supported by some evidence in the case of certain particular groups of animals or plants, we can conclude that the evolutionist must deal, not with a single process, the origin of species, but with several different processes, the origins of species.

CHAPTER VII

Hybridization and Its Effects

THE ROLE of hybridization in evolution has been one of the most controversial topics in the whole field of evolutionary study. Some authors, particularly Lotsy (1916, 1932) and Jeffrey (1915) have assigned a dominant role to this process. Other botanists, particularly systematists occupied chiefly with identification, classification, and the compiling of generic monographs and local floras, have been reluctant to recognize the existence of more than a very small number of hybrids in nature, and have assigned relatively little importance to these. Many zoologists, also, such as Mayr (1942), failing to detect evidence of hybridization in their material, have minimized its evolutionary effects.

The evidence to be presented in this chapter indicates that the true situation, at least as far as the higher plants are concerned, lies somewhere between these extremes. Even if we use the term hybridization in its broadest sense, namely, the crossing of any two genetically unlike individuals, the greatest possible importance we could assign to it would be as a third major evolutionary process, recombination, with an importance not exceeding that of mutation and selection. If we restrict the term to its most commonly accepted usage, namely, crossing between individuals belonging to reproductively isolated species, its importance must be considerably less. On the other hand, careful studies of numerous groups of higher plants from the cytogenetic as well as the systematic point of view have shown definitely that in many of them interspecific hybrids are rather common in nature. Furthermore, these hybrids have frequently given rise to offspring of later generations which have considerably modified the pattern of variation in the groups to which they belong. In fact, the accumulating evidence may make possible the generaliza-

tion that nearly all of the plant genera which are "critical" or intrinsically difficult of classification owe their difficulty largely to either the direct effects of interspecific hybridization or the end results of hybridization accompanied by polyploidy, apomixis, or both, as discussed in Chapters VIII, IX, and X.

THE FREQUENCY OF HYBRIDIZATION IN PLANTS AND ANIMALS

The statement has recently been made (Mayr 1942, p. 122, Turrill 1942a) that interspecific hybrids are much less common in animals than they are in plants. This is undoubtedly true for certain groups of animals. Two reasons may be assigned for this. In the first place, the higher animals, both arthropods and vertebrates, possess a most effective type of isolating mechanism which by its very nature cannot exist in plants. This is sexual isolation, which consists of an instinctive aversion on the part of males for females of another species (Dobzhansky 1941, pp. 261-267). In some groups, such as fishes (Hubbs and Miller 1943), sexual isolation may have its maximum efficiency only when the species are occurring in their natural environment and are represented by a large number of individuals, and it may break down in extreme habitats, where males find available few or no females of their own species. But Levene and Dobzhansky (1945) have shown that males of *Drosophila pseudoobscura* will not mate with females of *D. persimilis* any more frequently when such females are the only ones available to them than they will when they can make the choice between females of *D. persimilis* and those of their own species. Sexual isolation may therefore become developed until it is just as permanent and absolute a barrier as hybrid sterility. Its primary effect will be to lower greatly the frequency with which F_1 interspecific hybrids occur in nature.

The second factor which increases the frequency of hybrids and hybrid derivatives in many groups of plants is the great longevity of their individuals and, more particularly, the efficient methods of sexual reproduction. These points have been discussed in Chapter V, so that here we need only emphasize the fact that in plant groups in which the individual genotypes can be preserved for great numbers of years and can be spread over large areas, the selective disadvantage of a relatively low pollen and seed fertility is much less than in organisms of which the individual genotypes

have a relatively limited life span. In such groups, therefore, the selective advantage of occasional hybridization between species, that is, the ability to produce radically new adaptations to new environmental conditions which may arise, may outweigh the disadvantage incurred by the sterility of such hybrids. On this basis, of course, we should expect to find more examples of natural hybridization in perennial groups than in annual ones, and the latter should be characterized by the presence of sharper species boundaries. Accurate data on this point are not yet available, but it should be noted that of the 16 or more examples of hybridization discussed in this chapter only two, *Helianthus* and *Zea*, involve annual species. The greater frequency of polyploidy, which is often associated with hybridization, in perennial herbs than in annual herbs is discussed in the following chapter.

In spite of these differences, which reduce the frequency of hybrids in animals as compared to plants, interspecific hybridization may not be as uncommon in animals as is usually believed. In plants, every living individual of a species can be observed and its morphological characteristics studied. Although in certain favorable localities natural hybrids occur at a frequency of one to several percent, such localities represent only a small fraction of the total distribution of the parental species. There are probably very few plant groups in which the ratio of natural F_1 hybrids to individuals of the pure species is more than one in ten or one in a hundred thousand. In most animals the critical examination of tens or hundreds of thousands of individuals of a species is so laborious or impractical that it is rarely carried out. Because of this fact, rare hybrid individuals may never be discovered. Furthermore, since relatively few animal species can be bred and hybridized in captivity, the identity of suspected hybrids cannot often be verified experimentally. The experimental work with artificial hybrids and particularly with hybrid derivatives of plants has shown that in their morphological characteristics they often differ considerably from the appearance which one might predict on a priori grounds. It is possible, therefore, that in museum collections there exist a considerable number of specimens of animal species hybrids or hybrid derivatives of which the identity is not recognized. Finally, the processes of meiosis and gamete formation can be much more easily studied in and are

known for a much larger number of species of plants than of animals. If these processes are not intimately known, the existence of barriers of partial hybrid sterility between closely related species may not be detected. In animals, an individual is often considered fertile if it produces any offspring at all, but in plants individuals which produce only 5 to 10 percent of the normal number of seeds and have been found to possess the abnormalities of meiosis usually characterizing interspecific hybrids are judged to be partially sterile hybrids between valid species. It is thus possible that in animals, some of the so-called subspecies which are connected by occasional intermediate forms actually are closely related species, separated by barriers of partial sterility. That this may be true in *Peromyscus maniculatus*, for instance, is shown by the fact that Cross (1938) has found the somatic chromosome number 52 in subsp. *hollisteri* and the number 48 in six other subspecies. In the higher plants, groups having such different chromosome numbers would be judged to constitute different species. Another example is the genus *Platysamia*, in which Sweadner (1937) has shown that the females of hybrids between entities which otherwise would be recognized as subspecies are almost completely sterile.

Natural interspecific hybrids have been found relatively frequently in fishes (Hubbs and Hubbs 1932, Hubbs and Kuronuma 1942, Hubbs, Walker, and Johnson 1943), in certain groups of toads (Blair 1941), and in some mollusks, such as the genus *Cerion* (Bartsch 1920). In these groups sexual isolation seems to be relatively poorly developed as compared to the warm-blooded vertebrates and the higher insects, and the individuals are fairly long-lived. We may expect, therefore, that patterns of speciation in marine invertebrates, as well as in many groups of fishes and amphibians, will be more nearly like those in the higher plants than are the patterns found in most warm-blooded vertebrates and insects.

All these considerations suggest that, while hybridization is certainly less common in animals than in plants, and is correspondingly less important as a factor in evolution, its influence in certain groups may be considerable. The points brought up in this chapter cannot be stated categorically to apply to plants alone.

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DEGREES OF HYBRIDITY

Although the terms "hybrid" and "hybridization" are usually applied to crosses between individuals belonging to different species, this is by no means the only usage of the term. As Darlington (1940) has pointed out, there are various types of hybrids and hybridity, some of them within the taxonomic species, and some of them between species. From the genetic viewpoint, interspecific hybridization is only a special case of a much more widespread phenomenon. Moreover, in its effects, as well as its evolutionary importance, it has much in common with other types of hybridization.

The simplest type of hybridity is present in all individuals of a sexually reproducing, cross-fertilized species. It has been pointed out repeatedly earlier in this book that genetic heterozygosity is the normal condition in nature. Individuals are normally heterozygous or "hybrid" for a large number of different allelomorphous gene loci, and they produce variable, segregating offspring, whether through selfing or crossing. The difference in this respect between intersubspecific or interspecific hybrids, on the one hand, and the so-called "pure" individuals characteristic of a subspecies or species, on the other, is entirely quantitative, not qualitative. This fact will become evident to anyone who raises side by side the seedlings of a known or suspected interspecific hybrid and of a plant of its parental species in any cross-fertilized genus, such as *Quercus* or *Ceanothus*.

Hybrids may also be formed between members of different, partially isolated subpopulations having different gene frequencies. Such hybrids will as a rule be more heterozygous than the individuals of a cross-fertilized population and will serve a different purpose in evolution. As Wright (1931, 1940b) has pointed out, the most efficient type of population structure for the promotion of evolutionary diversification consists of the division of a large population into several small subpopulations, partly isolated from each other. Under these conditions, random fixation will tend to establish in each subunit characteristics which may be of no immediate selective value, but may enable the subpopulation to explore new "peaks" of adaptation by developing gene combinations with a new type of adaptive value. These valuable new genes or gene combinations may be trans-

backcross, introgressive types would have been made by the aboriginal cultivators. Hybrid corn is now the most valuable and highly developed form of maize; and hybridization almost certainly played an important role in the evolution of this most interesting crop plant.

From the preceding discussion we may conclude that introgressive hybridization is in many ways similar to evolutionary divergence through mutation, recombination, and selection. One important difference is that the genes which take part in this process enter the germ plasm of the species, not through mutation, but through transfer from another species across a barrier of reproductive isolation. A second is that not single genes, but groups of them, are added to the genetic complement of the species. Nevertheless, the similarities between evolutionary change through introgressive hybridization and that of the more usual type are great enough so that they can be directly compared. A group of closely related, incompletely isolated species, or ecospecies in the sense of Turesson and Clausen, Keck, and Hiesey (1939), can be likened to the type of population structure characterized by Wright (1931, 1940) as that which makes for the most rapid evolutionary progress; that is, a large population subdivided into many, partly isolated smaller ones. In this case, however, the isolation is not spatial, as in Wright's model, but is provided by the reproductive isolating mechanisms which separate the species. The isolation between the subpopulations is in time rather than in space, since F_1 hybrids occur only occasionally. Each species has in its past evolution "climbed" a different "adaptive peak," so that even though these species are closely related and sympatric, they will probably occupy a different ecological niche in their community or exploit their environment in a somewhat different way. This is true of all of the species pairs mentioned above. Therefore, introgressive hybridization between such related species represents the crossing of genes from one "adaptive peak" to another and makes possible the formation of gene combinations capable of climbing new "peaks." In its action it is therefore essentially similar to migration pressure in the partially subdivided population model of Wright. This analogy is entirely in accord with the known conditions under which introgression is most evident, namely, when new "adaptive peaks" in the form of unoccupied environmental niches are available to the population.

HYBRIDIZATION AND THE ORIGIN OF NEW TYPES

Introgressive hybridization, whatever may be its importance in modifying and amplifying the variation pattern of certain individual species, is nevertheless by its very nature not a way of producing new morphological or physiological characteristics, and therefore of progressive evolution. It merely produces convergence between previously more distinct species. There is, however, evidence that in some instances hybridization can result in the appearance of types which are actually new. These may represent various degrees of divergence and distinctness from their parental populations. The least remarkable, but perhaps the most frequent, are new races or subspecies which may arise from hybridization between preexisting subspecies of the same species, provided that a new and intermediate habitat is available to them.

Examples of the origin of such races are not numerous and by their very nature are hard to establish through observation of wild populations. Although the recognition of an F_1 hybrid between members of two adjacent subspecies or species is not a very difficult matter and can be verified experimentally with relative ease in many groups of plants, the identity of segregates in later generations may be much more difficult to recognize and to verify. Furthermore, considerable familiarity with the climatic and physiographic history of a region is needed before a habitat can be recognized as relatively new.

One example which nevertheless seems to be of this nature is *Potentilla glandulosa* subsp. *hanseni* in the Sierra Nevada of California (Clausen, Keck, and Hiesey 1940). As is shown by their chart (Table 1) and as brought out in the text (p. 44), this subspecies is intermediate in a whole series of morphological characteristics between subspp. *reflexa* and *nevadensis*. It also occupies a habitat, the mountain meadows at middle altitudes, which is intermediate between that occupied by the two last-mentioned subspecies. These meadows are moister and cooler than the warm dry slopes which in the same region are the habitat of subsp. *reflexa*, and on the other hand are considerably warmer than the subalpine and alpine habitat of subsp. *nevadensis*. Furthermore, both subsp. *reflexa* and subsp. *nevadensis* range far beyond the area in the central Sierra Nevada occupied by subsp. *hanseni*. Finally, the mountain meadows in which subsp. *hanseni*

is found are new habitats created by the disturbance of topography resulting from the Pleistocene glaciation. They represent either filled-in lake beds or outwash plains which have poor drainage because of their flat surfaces. The most plausible hypothesis, therefore, is that in late glacial or early postglacial times subsp. *hanseni* was produced by hybridization between subspp. *reflexa* and *nevadensis*, and that it then entered the meadow habitat newly available to it. Clausen, Keck, and Hiesey (1947) have shown that a great array of segregates are produced in the F₂ generation of the cross between these two subspecies, and that many of these are very well adapted to conditions in the meadow at Mather, which is occupied by subsp. *hanseni*. Since the authors have not published any comparison between these segregates and subsp. *hanseni* in morphological characteristics, it is not known how nearly this subspecies has been reproduced artificially.

Another probable example of this nature is *Vaccinium corymbosum*, the common high-bush blueberry of the glaciated regions of northeastern North America (Camp 1945). This polymorphic entity, occupying a habitat known to be relatively recent, is believed on morphological grounds to have resulted from hybridization between four other "species" which occur south of the glaciated territory. The arguments for recognizing these five entities as distinct species, and for the complex phylogeny which Camp postulates, are rather involved and not supported by enough data to be very convincing.

A still more striking example of the origin of a new race through hybridization is that of *Abies borisii-regis*, carefully analyzed by Mattfeld (1930). The common fir of central Europe, *A. alba*, is constant and typical in the northern and western part of the Balkan Peninsula, extending southward to the northern boundary of Greece. In the mountains of central and southern Greece it is replaced by *A. cephalonica*, which is likewise constant and typical throughout the main part of its range. But in northern Greece there occurs a series of intermediate forms, which at their northern limit most resemble *A. alba* and grow with trees typical of that species, and at the southern limit of their distribution resemble and accompany typical *A. cephalonica*. Trees similar to these intermediate forms are the only ones found on the Athos Peninsula, in northeastern Greece, as well as in parts of

Macedonia and in the Rhodope Mountains of Bulgaria. The fir forests of the latter regions are isolated by distances of 60 to 100 miles (100 to 160 km) from those of the Grecian peninsula. The intermediate form from the Rhodope Mountains was named by Mattfeld as a distinct species, *A. borisii-regis*, but the evidence presented by him indicates to the present writer that it, as well as *A. alba* and *A. cephalonica*, should be treated as races of a single polytypic species.

Mattfeld has considered three possibilities regarding the nature of *A. borisii-regis*: first, that it might be considered an intermediate race, corresponding to and of parallel origin with *A. alba* and *A. cephalonica*; second, it might be an original, heterozygous and genotypically rich population from which *A. alba* segregated and migrated northward, and *A. cephalonica* similarly segregated in the south; and, third, that *A. borisii-regis* represents a series of products of ancient hybridization between *A. alba* and *A. cephalonica*, plus derivatives of segregation and backcrossing.

The first possibility is highly improbable because of the nature of the intermediate populations. In no area are they a constant, easily recognizable entity, as are *A. alba* and *A. cephalonica*; rather, each mountain range possesses a different complex of intergrading and recombining forms, which have in common only the characteristic that they show the various diagnostic characters of *A. alba* and *A. cephalonica*, and no others, combined in different ways and with various degrees of intermediacy. The greatest amount of variability is in northern Greece, in the populations which are continuous with those of the other two races; but the isolated populations of Athos and the Rhodope Mountains also show much evidence of segregation and recombination.

The second possibility is rejected by Mattfeld because no characteristics can be seen in these variable, intermediate populations except for those of *A. alba* and *A. cephalonica*. If northern Greece were the original gene center for this complex of *Abies*, it should certainly contain some genes and genotypes which did not become segregated into the populations of *A. alba* and *A. cephalonica*.

This leaves the third possibility, that of ancient hybridization, as the most likely. Its likelihood is strengthened by paleontological, and particularly geological, evidence. *A. alba* and its close

relative of Asia Minor, *A. nordmanniana*, are characteristic elements of the Colchian flora, fossil remains of which indicate that it was widespread throughout central Europe in the latter part of the Tertiary period. *A. cephalonica*, on the other hand, is not only strikingly different morphologically from *A. alba* and *A. nordmanniana* but in addition it occupies a different floristic province, that of the Grecian-Asia Minor Mediterranean flora. This flora appears to have developed in isolation from the Colchian flora during the latter part of the Tertiary period, since the two have very little in common. The most likely hypothesis, advanced by Mattfeld, is that *A. alba* and *A. cephalonica* were well isolated from each other during the Miocene and Pliocene epochs, and that hybridization began with the southward migration of *A. alba* in response to the cooling of the climate at beginning of the Pleistocene glacial, or "diluvial," period. *A. borisii-regis*, therefore, is probably descended from a series of hybrid swarms which have existed for several hundred thousand years. On the Grecian peninsula, their variability is continually being increased by influx of genes from the parental races, but on Athos, the Rhodope Mountains, and probably on the island of Thasos, they are forming intermediate races that are relatively constant and true breeding, although they are still more heterozygous than the parental races.

Other examples will doubtless become available when more groups have been studied critically with this possibility in mind. Further evidence on the ease with which crossing between subspecies can lead to new ecotypes or subspecies could be obtained by experiments on the artificial establishment in new environments of the products of intersubspecific hybridization. The writer is at present conducting such experiments in the genus *Bromus*, but the degree of their success cannot as yet be estimated.

The examples already mentioned are new types only in the sense that they are entities which are recognizably different from their parental populations and occupy new habitats; morphologically they do not contain any new characteristics. But the origin from hybridization of races or species with characteristics that are new, in the sense that they could not have been predicted on the basis of examination of the parental types, has been reported several times. The simplest of such cases are those involv-

ing types of gene recombinations well known to geneticists, that is, the interaction of different allelomorphous series of simple Mendelian factors. A good illustration is found in the work of Brainerd (1924) and Gershoy (1928, 1932, 1934) on the progeny of natural interspecific hybrids between eastern North American species of *Viola*. Although the principal character differences between these species give simple segregations, and many of the F_2 and F_3 individuals show reversion to one or the other of the parental species, nevertheless a considerable proportion of these offspring are considerably modified from the condition found either in the parents or in the F_1 , and some of these modified types will eventually breed true. An illustration of such possible "new" types in respect to leaf shape is given in Fig. 31, showing the leaves of *V. pedatifida*, *V. sagittata*, their F_1 hybrid, and various F_2 segregates. Brainerd's comment on a situation similar to this is as follows (1924, p. 165).

In these various ways there has arisen in the numerous progeny of the hybrid under discussion a considerable diversity of foliage, such as would present insoluble difficulties to a taxonomic student who did not know that these diverse forms all came from one individual, by close-fertilized reproduction, in the short period of three or four years. The extreme differences are such as would warrant the making of several distinct species, according to the hasty methods of ordinary practice.

In comparing the various segregating types illustrated by Brainerd with the stable and constant species of *Viola* found in the eastern United States, one becomes struck by the possibility that various ones of the unusual leaf forms, such as those found in *V. palmata*, *V. brittoniana*, *V. triloba*, *V. stoneana*, and *V. viarum*, have been derived by the stabilization of hybrid derivatives. There is considerable reason for suggesting that the number of stable, recognizable species in the subsection *Boreali-Americanae* has been considerably increased by hybridization. Brainerd (1924) cites an example of the possible birth of such a new species in the naturally occurring offspring of *V. affinis* \times *sagittata*.

Similar "new" types appear to be segregating from natural hybrids of *Iris* in the Mississippi Delta region of the southern United States (Viosca 1935, Foster 1937, Riley 1938, Anderson 1949). A large number of these have been named as species by

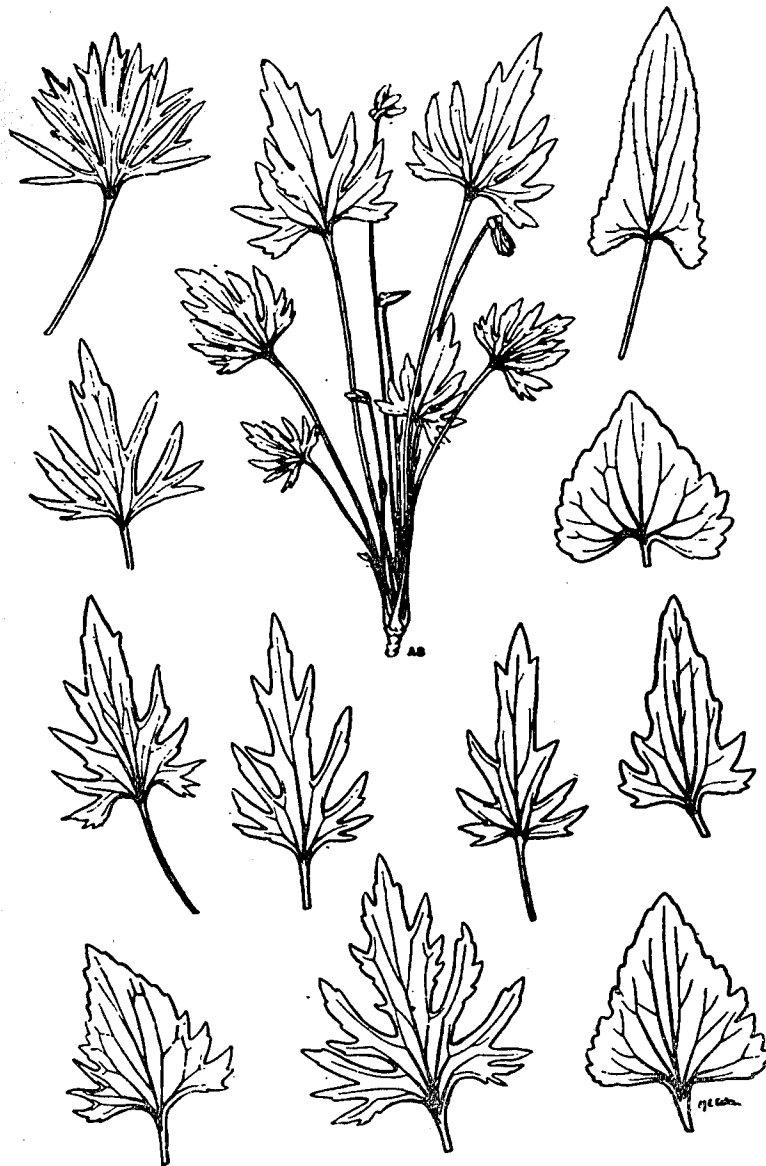


FIG. 31. Leaf of *Viola pedatifida* (upper left), leaf of *V. sagittata* (upper right), plant of the F₁ hybrid *V. pedatifida* × *sagittata* (upper middle), and leaves of nine different F₂ segregates from this hybrid. From Brainerd 1924.

the taxonomic "splitters." In the subgenus *Eubatus* of the genus *Rubus*, there is a diversity of forms in the eastern United States. The data of Brainerd and Peitersen (1920) and Peitersen (1921) on segregation of seedling progenies from putative hybrids found in the wild and corresponding to some of the species recognized by systematists, although far too scanty, suggest that many of these "species" are unstable hybrids or hybrid derivatives. In this subgenus, however, the variation pattern has been greatly complicated by polyploidy and apomixis, as will be discussed in Chapter X.

Some evidence at hand suggests that the recombination of genetic factors in the offspring of interspecific hybrids may sometimes lead to new types radically different from those found in either parent. Lotsy (1915) illustrates some striking examples of this nature in the progeny of *Antirrhinum glutinosum* crossed with a peloric form of *A. majus*. Hagedoorn and Hagedoorn (1921) cite the example of Vilmorin's hybrid between *Argemone mexicana* and *A. platyceras*, from which several strongly aberrant types segregated in the F₂ generation. Some of these were different from either parent in such fundamental characteristics as the number of sepals or of carpels. Similar aberrant types appeared in the F₁ hybrids of *Paeonia lactiflora* ("*P. albiflora*") and various members of the complex of *P. anomala* (Saunders and Stebbins 1938). Less extreme new types are reported by Clausen (1926) as segregates from hybrids between *Viola arvensis* and *V. tricolor*. Griggs (1937) has emphasized the significance of such types in the origin of cultivated plants. Their importance in evolution depends, of course, upon whether they can ever become established in nature. The examples cited above of *Argemone* and *Paeonia* are teratological and not fitted to any environment, while Clausen has remarked that the new types in *Viola* disappear in favor of typical *V. arvensis* when cultivation is abandoned. Nevertheless, the possibility exists that under particular environmental conditions some such new types may become established and may contribute to evolutionary progress. The detection of an existing species or subspecies as a new derivative of past hybridization is well-nigh impossible, since by definition such new types would not be recognizably intermediate between their parental species.

Another way in which hybridization may result in evolutionary

progress is through its stimulation of the mutation rate. In Chapter III the example was cited of the increased mutability of the petal spot gene of *Gossypium hirsutum* when transferred by means of interspecific hybridization to the genetic background of *G. barbadense* (Harland 1937). Furthermore, if Sturtevant's and Shapiro's hypothesis of the gradual reduction of mutation rates through selection of mutation suppressors is correct (see page 99), then interspecific hybridization followed by segregation and recombination would be a way of eliminating these suppressors and of enabling a previously stable evolutionary line to progress rapidly in response to a newly changing environment. Unfortunately, evidence for increased mutation rates following hybridization is difficult to obtain because new mutations occurring in the strongly segregating progeny of an interspecific hybrid are in most cases impossible to detect. Such evidence will be obtained most easily in genera like *Gossypium*, which contains several species that can be crossed and produce partially fertile hybrids, and in which a number of different gene loci have been identified. Giles (1940) has produced evidence that gross structural changes in the chromosomes occur three times as frequently in the hybrid *Tradescantia canaliculata* \times *humilis* than in its parents. He suggested that this difference might be due to disturbance of the normal coiling cycle of the chromosome threads or chromonemata in the chromosomes of the hybrid.

THE EFFECT OF HYBRIDIZATION ON INTERSPECIFIC ISOLATING MECHANISMS

Offspring produced from partly sterile interspecific hybrids often retain the sterility of their F_1 progenitors, but in many instances have been known to become more fertile. The most spectacular and widely known of such examples of recovery of fertility are those in which the chromosome number of the hybrid has been doubled, and a constant, fertile, allopolyploid species has been produced. These will be discussed in the following chapter. Less widely known and studied, but of equal or greater evolutionary importance, are examples of the recovery of fertility and the establishment of constant, true-breeding lines from highly sterile interspecific hybrids without doubling of the chromosome number. Such increase in fertility has been reported by Brainerd

(1924) and Clausen (1926, 1931) in *Viola*, by Ostenfeld (1929) in *Polemonium mexicanum* \times *pauciflorum*, by Müntzing (1930a) in *Galeopsis tetrahit* \times *bifida*, by Anderson (1936a) in *Apocynum androsaemifolium* \times *cannabinum* and (unpublished) in *Nicotiana alata* \times *landsdorffii*, by Winge (1938) in *Tragopogon pratensis* \times *porrifolius*, by Lamprecht (1941) in *Phaseolus vulgaris* \times *coccineus*, by Zakhharjevsky (1941) in *Triticum durum* \times *timopheevi*, by Hiorth (1942) and Håkansson (1946a, 1947) in *Godetia amoena* \times *whitneyi*, and has been found by the writer in the progeny of several hybridizations in the genera *Bromus* and *Elymus*. Constant, true-breeding lines have been extracted from such fertile segregates in *Galeopsis*, *Tragopogon*, *Phaseolus*, *Triticum*, *Viola*, and *Godetia*.

The evolutionary importance of such fertile hybrid derivatives depends both on their morphological characteristics and on the degree of fertility or sterility which is found when they are crossed back to their original parents. Three situations can exist with respect to these fertility relationships. First, the fertile hybrid derivative may form fertile hybrids with one of its parental species, and sterile ones with the other. In this case it represents either the complete recovery of the genic complement of one parent or the establishment of an introgressive type. This is true of the lines established in *Tragopogon* and some of those in *Phaseolus*. Second, the line might conceivably form fertile hybrids with both of the parental species, and so represent the obliteration of the isolating barrier between them. This situation, however, has never been reported so far as the writer is aware, and on the basis of our knowledge of genetic isolating mechanisms would not be expected unless the fertility of the F_1 hybrid were itself relatively high. The third possibility, and the one which is by far the most important from the evolutionary point of view, is that the new stabilized, fertile line would form partly sterile F_1 hybrids in crosses with either of its parental species. This is apparently true of some of Lamprecht's derivative lines in *Phaseolus*, although his data are not as complete as might be desired. It may also be true in *Viola*, *Nicotiana*, *Godetia*, and *Triticum*, but the appropriate hybridizations have not been made, or at least have not been reported. In an earlier paper (Stebbins 1942a) the writer suggested that if, as now seems even more evident, barriers

CHAPTER II

Examples of Variation Patterns within Species and Genera

BEFORE discussing the individual factors responsible for evolution, it seems desirable to describe some of the patterns of variation which are the outcome of these processes. These exist on two different levels; first, that within the species and, second, that involving the different species of a genus or larger grouping. As is discussed in greater detail in Chapter VI, the distinction between these two levels is that of whether the pattern is essentially continuous or only partly discontinuous, owing to the more or less free interchange of genes between the various individuals or populations constituting the pattern, or whether the presence of isolating mechanisms preventing or greatly restricting mating and gene interchange has produced a number of sharply discontinuous and distinct populations or population systems.

THE ECOTYPE CONCEPT

The type of variation within species which is most important in evolution is that showing certain regularities, particularly in connection with adaptation to ecological conditions. For this reason, major emphasis has been placed in recent years on the concept of the *ecotype*. This term was originally defined by Turesson (1922a) as "the product arising as a result of the genotypical response of an ecospecies or species to a particular habitat." Turesson, in a long series of publications (1922a, 1922b, 1925, 1927, 1931a, 1936, etc.; see Clausen, Keck, and Hiesey 1940 or Hiesey 1940 for complete list), has described ecotypes in a large number of wide-ranging Eurasian species, mostly perennial herbs. He has emphasized (1936) the fact that differentiation into ecotypes is much more likely to be found in common, widespread species

than in rare, local, or endemic ones. In this country, the studies of Clausen, Keck, and Hiesey (1940, 1947) have shown a similar condition in several species of western North America, while various other workers have demonstrated intraspecific genetic variation correlated with habitat differences. Groups of biotypes like those which Turesson has recognized as ecotypes undoubtedly exist in most wide-ranging plant species. Two questions arise in connection with the ecotype concept. First, to what extent are the different biotypes of a species grouped into partly discontinuous aggregates which may be recognized as distinct ecotypes, and to what extent do they form a continuous series? Second, what is the relation between the ecotype concept in plants and the concept of *polytypic species*, or *Rassenkreise*, as it has been developed by modern zoological systematists like Rensch (1939), Mayr (1942), and Miller (1941)? These two questions will be considered in turn.

Although both Turesson (1936) and to a lesser extent Clausen, Keck, and Hiesey (1940) have tended to emphasize the distinctness of ecotypes, other authors have found difficulty in recognizing well-marked groups of genetic variants because of the presence of a more or less continuous series of morphologically and ecologically intermediate populations. Engler (1913), Burger (1941), and Langlet (1936) showed the presence of much variation of a continuous type within *Pinus sylvestris* of Europe, although a slight discontinuity in the variation pattern in northern Scandinavia permits the recognition of a separate ecotype or subspecies for the pines of Lapland, as suggested by Turesson (1936) on the basis of Langlet's preliminary and incomplete data. Gregor, Davey, and Lang (1936) found that in *Plantago maritima* "there are . . . many quantitative characters which vary continuously within populations. The ranges of these in different populations nearly always overlap, and even if they do not, a series could be arranged so that there could be continuous variation throughout." Faegri (1937) has pointed out that the apparent distinctness of ecotypes in many of the species studied by Turesson results from comparison of biotypes taken from a relatively small number of widely separated localities. The same comment may be made about many of the examples given by Clausen, Keck, and Hiesey

(1940), as was suggested by Turrill (1942b). The validity of Turrill's criticism is evident from a comparison of the discussion of *Achillea* given in the above-mentioned work with the later, more complete study by the authors of the same group (Clausen, Keck, and Hiesey 1948). There is no doubt that in plants, as in animals, many species may be divided into races or groups of genetic types which are adapted to the different ecological conditions found in different parts of their ranges, and that these subdivisions are separated from each other by partial discontinuities in the variation pattern. But in addition, many widespread species possess a considerable amount of ecotypic, that is, directly adaptive, genetic variation which because of its continuous nature does not permit the recognition of distinct ecotypes.

ECOTYPIC AND CLINAL VARIATION

For this reason, much of the variation within certain species is best portrayed by the use of the "auxiliary taxonomic principle" defined by Huxley (1938, 1939) as the *cline*, or character gradient. Clines are probably common in plant species, but the ordinary methods of systematics, which deal with combinations of characters and are aimed at detecting character correlations and discontinuities, are not likely to reveal them.

Among the best examples of clines within plant species are those described by Langlet (1936) in *Pinus sylvestris* for genetic variation in chlorophyll content, length of mature leaves, hardness, and rapidity of shoot development in the spring. Clausen, Keck, and Hiesey (1948a) found within the ecotypes of *Achillea lanulosa* and *A. borealis* clines for height of plant when grown and compared under uniform cultural conditions. In *A. lanulosa*, the tallest genetic types were from the lowest altitudes, and the decrease in height was more or less continuous with increasing altitude (Fig. 5). Olmstead (1944) found clinal variation in vigor and in reaction to photoperiodism in strains of side-oats grama grass (*Bouteloua curtipendula*) obtained from different latitudes in the Great Plains. Clinal trends were found by Böcher (1943, 1944) in *Plantago lanceolata* and *Veronica officinalis*. It is likely that most species with a continuous range that includes more than one latitudinal or altitudinal climatic belt will be found to possess clines for the "physiological" characteristics

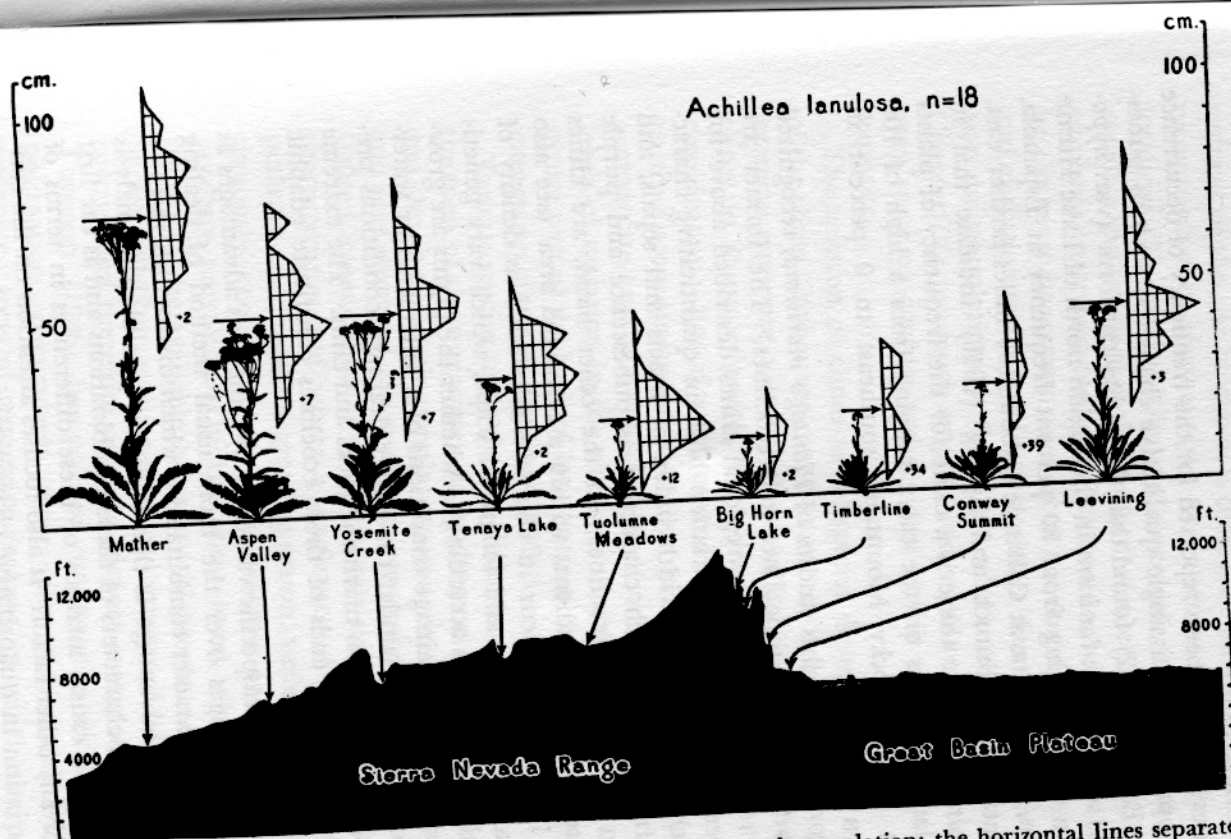


FIG. 5. Representatives of populations of *Achillea lanulosa* as grown in a uniform garden at Stanford. These originated in the localities shown in the profile below of a transect across east central California at approximately 38° N. latitude.

The plants are herbarium specimens, each representing a population of approximately 60 individuals. The frequency diagrams show variation in height

within each population: the horizontal lines separate class intervals of 5 cm according to the marginal scale, and the distance between vertical lines represents two individuals. The numbers to the right of some frequency diagrams indicate the nonflowering plants. The specimens represent plants of average height, and the arrows point to mean heights. From Clausen, Keck, and Hiesey 1948.

population is relatively large, and the seedlings which survive are selected from a great store of genetic variants. The chances are therefore particularly favorable that the survivors will be closely adapted to their environment and will reflect more or less exactly the continuity or discontinuity of the environmental gradient. On the other hand, species in which pollination is nearly always between neighboring individuals, and particularly those with a relatively high proportion of self-pollination, will tend to be more uniform within colonies of closely adjacent plants and to show more differences between colonies. In them, therefore, distinct ecotypes are likely to be recognized with greater ease. Although much more experimental work is needed before any really conclusive generalizations can be made, the present evidence justifies the following tentative answer to the first question posed above. Intraspecific variation of an ecotypic (that is, strictly adaptive) nature is found in nearly all species with a wide ecological distribution; but the ease with which distinct ecotypes can be recognized probably varies greatly from one species to another and depends on various factors, both external and internal, which promote continuity or partial discontinuity in the variation pattern.

From the foregoing discussion, the fact should be clear that clines and ecotypes are not mutually exclusive concepts, but merely express different ways of approaching the same problem. Clinal variation may occur in the characters which determine the nature of adaptation, and therefore form the basis of the ecotypes, or it can also be found in characters of no apparent adaptive value. Correspondingly, ecotypic variation may consist of a series of clines, running either parallel to each other or in opposite directions, or it may have such well-marked discontinuities or be of such an irregular type that constant gradients are not apparent. As Gregor (1939) has emphasized, both these approaches are valuable aids to an understanding of the variation within species.

ECOTYPES AND SUBSPECIES

There are two differences between the ecotype concept and that of the polytypic species, or *Rassenkreise*. In the first place, subspecies are based primarily on recognizable differences, while ecotypes are distinguished primarily by their reaction to the

environment, and may or may not possess well-marked morphological differences which enable them to be recognized in the field. Clausen, Keck, and Hiesey consider that (1939, p. 106) "limits of subspecies (a morphologic term) correspond to the limits of one or a group of several ecotypes (an experimental term)." And on the same page they state specifically that "it is sometimes necessary to include more than one ecotype in a subspecies." The relation between ecotypes and subspecies is expressed briefly as follows (Clausen, Keck, and Hiesey 1940, p. 33), "we consider a morphologically distinguishable ecotype the basis of a subspecies." A specific example of this relationship may be cited in their discussion of *Potentilla glandulosa* subsp. *nevadensis*, as follows (1940, p. 43): "It consists of two ecotypes: one is a dwarf, early-flowering alpine that occurs above 2600 m., while the other is subalpine and may be distinguished in garden cultures by its taller stature and later flowering. Since the differences between the two are not sufficiently distinct to be recognized in the field or in the herbarium with certainty, the two ecotypes are here included in one subspecies." In this example the genetic differences between the two ecotypes of this subspecies, stature and time of flowering, are clearly among the characteristics most strongly affected by the environment, so that the inability to recognize ecotypes in the field or the herbarium is due to the masking of genetic differences by environmental modification. This effect can be eliminated only by growing the two ecotypes under uniform conditions. This example is probably typical of those in which a single subspecies contains more than one ecotype. It permits the generalization that the frequency of such situations in plants probably results from the fact that the most important genetic adaptive characteristics are often paralleled by environmental modifications. Since environmental modification in animals is much less frequent than in plants, and only rarely masks racial differences, zoologists do not need a purely genetic-ecological term in addition to a primarily systematic one.

The second difference between the concept of ecotypes and that of subspecies is that the ecotype is primarily an ecological and adaptational concept, while the subspecies is primarily a morphological, geographical, and historical one. Gregor (1944) graphically describes the origin of ecotypes as follows, "The

habitat environment is likened to a sieve which sorts out from among the constituents of a population those genotypes which are best fitted to survive." Ecotypes correspond with subspecies in so far as different geographical regions possess different ecological conditions. But the presence of two or more ecotypes of the same species is expected in a single geographic region wherever several ecological habitats available to the species occur. Thus, within a relatively small section of southern Sweden, Turesson (1922b) described four ecotypes of *Hieracium umbellatum*; one typical of shifting sand dunes, one of arenaceous fields, one of sea cliffs, and one of interior woodlands. Furthermore, since the ecotype is produced by the direct selective action of the environment on a heterozygous population, the same ecotype may originate independently in different localities. This is also shown by Turesson's studies of *Hieracium umbellatum*. Figure 6 shows the distribution of the different coast types of this species in the province of Scania, in southern Sweden. Turesson points out that the dune ecotype found at Torekov (upper left of map) has leaves which in many respects resemble those of the cliff and inland types occurring in the same region and are very different from those of the dune ecotype found at Sandhammar (lower right). The same is true of the cliff types found respectively at Stenshufvud on the east coast and at Kullen or Hofs Hallar on the west coast. Each of these cliff and dune races seems to have originated independently from the more widespread inland ecotype of *H. umbellatum*. The "cliff ecotype" and the "dune ecotype" are therefore aggregates of races which have originated independently in response to the same selective forces. The cliff ecotype and the salt marsh ecotype described by Gregor (1939) in *Plantago maritima* have undoubtedly arisen repeatedly. The subspecies, on the other hand, is usually conceived of as a group of populations with a common origin and a more or less integral geographic distribution, which has acquired its distinctive morphological characteristics partly through the influence of similar environmental factors, but also to a large extent through partial isolation from other subspecies. Lawrence (1945) found that in *Deschampsia caespitosa* "the evolution and distribution of its taxonomic variants appear to be entirely independent of any ecotypic adaptation." In this species, different subspecies possess similar ecotypes.

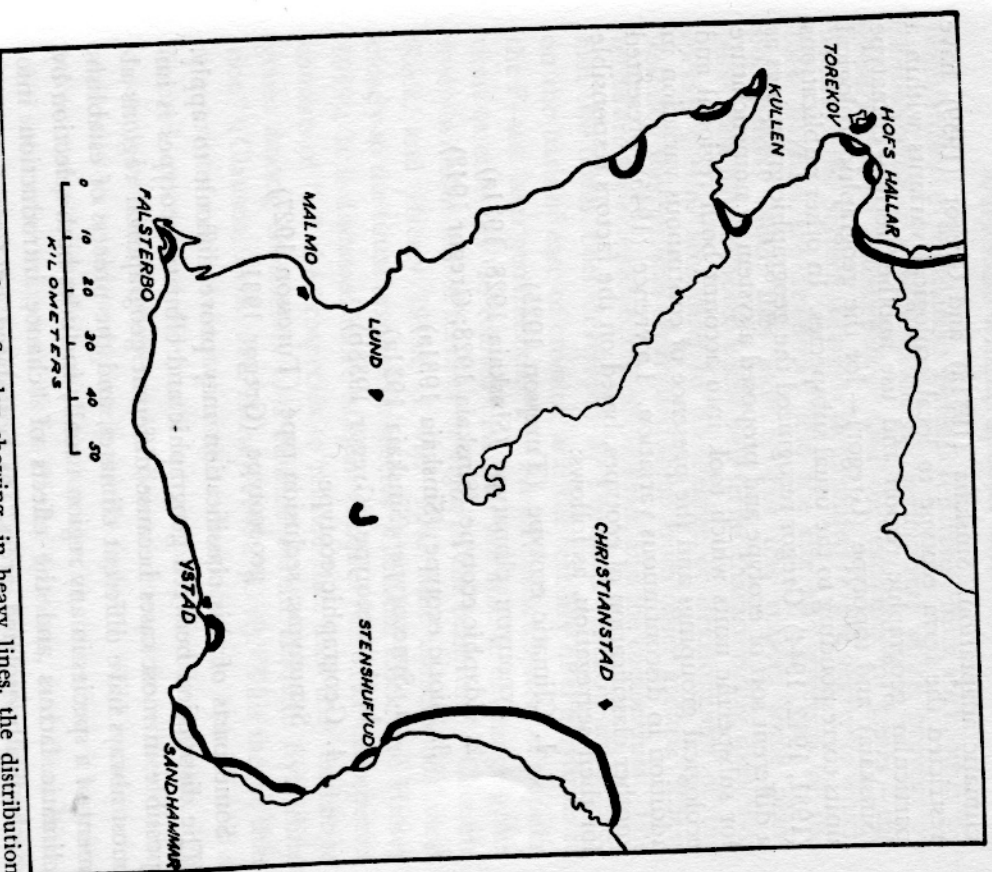


FIG. 6. Map of southern Sweden showing, in heavy lines, the distribution of the maritime ecotype of *Hieracium umbellatum*. Simplified, from Turesson 1922b.

The ecotype and subspecies have been interpreted by some authors in a relatively broad sense and by others in a relatively narrow one, but this has been true to a considerably greater degree in regard to the ecotype. This is because the concept of what constitutes an ecological difference is largely relative. As Turrill (1946) points out, the ecotypes of Turesson include both regional groupings and small local groupings of biotypes, while in the work of Clausen, Keck, and Hiesey emphasis is placed on regional or

climatic adaptation. Sinskaia (1931a) and Gregor (1939) have restricted the term ecotype to local ecological variants within a particular geographic region and use another term — climatype (Sinskaia) and topotype (Gregor) — for the geographic-ecological units corresponding to the usual subspecies. In other publications (1931, 1942, 1944), Gregor recognized the geographic groupings as a different sort of ecotype and proposed a system of nomenclature for subspecific units which took into account both regional and ecological groupings and the presence of continuous variation in addition to discontinuous variation. Lawrence (1945) presented another classification of ecotypes, based on the factors responsible for their segregation, as follows:

1. Climatic ecotype (Turesson 1925)
Synonym: climatype (Sinskaia 1928, 1931a)
2. Edaphic ecotype (Sinskaia 1928; Gregor 1942)
3. Biotic ecotype (Sinskaia 1931a)
 - a. Synecotype (Sinskaia 1931a)
 - b. Agroecotype (Gregor 1938b)
4. Geographic ecotype
Synonyms: seclusion type (Turesson 1927)
geocotype (Gregor 1931)

Some parts of this classification may prove difficult to apply. The distinction between geographic and climatic ecotypes is impossible in most cases because different geographical regions almost always have different climates, and the process of establishment of a species in any region usually includes both selection by climatic factors and the effects of "chance introduction into mechanically isolated areas," as postulated by Gregor for the origin of geocotypes. As recognized by Sinskaia, the biotic ecotype may be considered a special type of edaphic ecotype adapted to the type of plant competition existing under human cultivation. Like all other problems of classification, that of the infra-specific categories will be solved only by impartial discussion among all scientists interested in the subject and by mutual agreement as to what constitutes the most convenient and efficient method of expressing the actual biological situation.

VARIATION ON THE LEVEL OF THE SPECIES AND GENUS

In the case of variation patterns involving species — that is,

populations or population systems separated from each other by physiological or genetic isolating mechanisms which prevent or greatly restrict interbreeding and the exchange of genes — the nature of the pattern is largely determined by the degree to which these barriers are developed and the size and diversity of the populations which they isolate. For this reason, some plant geneticists have adopted a series of terms characterizing species or species groups according to the degree of development of the isolating mechanisms separating them from other groups. These terms are the *ecospecies*, the *cenospecies*, and the *comparium*. The first two terms, both developed by Turesson (1922b), are defined on the basis of ease of crossing and the fertility of the hybrids of the F_1 and later generations. The *ecospecies* is a system of populations or ecotypes "so related that they are able to exchange genes freely without loss of fertility or vigor in the offspring" (Clausen, Keck, and Hiesey 1945a, p. vi). This unit corresponds most closely to the usual taxonomic species (Clausen, Keck, and Hiesey 1939). It is discussed more fully in Chapter VI. The *cenospecies* consists of "all the *ecospecies* so related that they may exchange genes among themselves to a limited extent through hybridization" (Clausen, Keck, and Hiesey 1945a, p. vi). This means that the various *ecospecies* composing a *cenospecies* can hybridize to a limited extent and form at least partially fertile hybrids, but crossing between members of different *cenospecies* either is unsuccessful or yields completely sterile hybrids. The *cenospecies* may correspond exactly with the *ecospecies*, but often it consists of a section or subgenus, as in *Pinus*, *Quercus*, and *Ceanothus*, or it may comprise a whole genus, as in *Aquilegia*. The *comparium* (Danser 1929) is a more inclusive and strictly genetical term and includes (Clausen, Keck, and Hiesey 1945a, p. vi) "all the *cenospecies* between which hybridization is possible, either directly or through intermediaries." Like the *cenospecies*, it may in isolated instances consist of only one *ecospecies*, but usually it approaches the size of a genus, and in some plant groups, such as the grasses and the orchids, it may include a whole series of recognized genera.

Although the terms and concepts which have already been discussed and the factors of evolution which will be reviewed in the remaining chapters of the present volume all apply to the great