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 (May 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.

## 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 allelomorphic 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-

ferred from one subpopulation to another by occasional migration followed by hybridization. This type of crossing, therefore, is an essential part of the "migration pressure," which is responsible for the flexibility of Wright's system of partially isolated subpopulations.

Hybridization between members of different subspecies differs only in degree from that between partly isolated subpopulations of the same subspecies. Such hybridization can be expected on a large scale whenever two subspecies or ecotypes, occupying different ecological niches, are able to come in contact with each other. The genetic consequences of such hybridization in the $F_2$ and later generations will be segregation and recombination of the genetic factors responsible for adaptation to different ecological conditions. Its evolutionary consequences will depend on the conditions under which the hybridization takes place. If the two hybridizing subspecies are old, well-established ones, the chances are that they represent gene combinations so well adapted to the environments they occupy that any new combinations created by hybridization will almost certainly be less favorable and therefore selected against in the original environments. In the absence of new habitats, therefore, hybridization between subspecies will lead to the production of many ill-adapted genotypes, and therefore to evolutionary disintegration rather than to progress.

On the other hand, the situation will be entirely different if the hybridization takes place in an unstable, rapidly changing environment. If enough hybrids are formed, then out of the great array of segregates which they will produce in later generations, some are likely to be better adapted to the new environments than are any individuals of the parental subspecies. Examples of this process going on in nature will be given later in this chapter.

As was pointed out in Chapter VI, species do not necessarily differ more from each other in characteristics of external morphology than do subspecies, although this is usually the case. On this basis, some interspecific hybrids may be no more heterozygous for the genetic factors responsible for such morphological differences than are hybrids between extreme variants belonging to the same species. The really outstanding difference between interspecific hybrids and those within the species is that the former bridge a natural barrier or system of barriers of reproductive

isolation. If these barriers consist entirely of ecological, seasonal, or mechanical isolation, then the $F_1$ hybrid is fully fertile and is in no way different from hybrids between subspecies. Such interspecific hybrids in *Platanus, Ceanothus, Catalpa, Quercus*, and other genera have been mentioned in previous chapters. More often, however, hybrid sterility is present, reducing to a greater or lesser degree the reproductive capacity of the $F_1$ hybrid. Even this, however, is not a unique property of hybrids between species. Semisterile hybrids between individuals of the same species have long been known in *Oenothera, Campanula* (Darlington and Gairdner 1937), *Galeopsis* (Müntzing 1930a, 1938), and many other genera. And in maize, *Crepis* (Gerassimova 1939), and other genera, strains of a species which form almost completely sterile hybrids with other strains of the same species have been produced artificially by subjecting the plants to X rays and then selecting progeny containing appropriate types of structurally altered chromosomes. Usually, the sterility of an interspecific $F_1$ is greater than that of the intraspecific hybrids mentioned above, but this is not necessarily so. The distinguishing feature of interspecific hybrid sterility is that it is always present and differs relatively little depending on which individuals of the parental species are used for crossing. Sterility barriers within species, on the other hand, are relatively local in distribution, so that if two individuals happen to be partially isolated from each other by such a barrier, they can nevertheless exchange genes indirectly through outcrossing with other individuals of the same species. Interspecific hybrids, therefore, are even in their most significant characteristic, sterility, different quantitatively rather than qualitatively from some hybrids within the species. This is to be expected on the basis that, as hypothesized in Chapter VI, species in most instances arise gradually from subspecies.

Sterile interspecific hybrids may be roughly divided into two groups: those which are capable of producing some viable pollen and seed, through selfing, intercrossing between $F_1$ individuals, or backcrossing to the parental species, and those which are completely sterile, except for the occasional production of allopolyploid derivatives. In the terminology of Clausen, Keck, and Hiesey (1939), the first are hybrids between ecospecies, and the second, between cenospecies. The two groups, however, are by

no means sharply separated from each other. Many hybrids exist which are almost completely sterile, but do produce seed at the rate of one in a thousand, one in ten thousand, or one in a million ovules. Such hybrids in the genus *Paeonia* were called to the writer's attention by Dr. A. P. Saunders, after he had observed many of them for periods of several years (Saunders and Stebbins 1938). If hybrid sterility usually has the multifactorial basis postulated for it in the preceding chapter, whether these factors are genes or small chromosomal rearrangements, we should expect to find a larger proportion of species separated by barriers producing a very low degree of fertility, than by those causing partial fertility of intermediate degrees. This point can be illustrated by an oversimplified example. If two species, A and B, are separated by a barrier consisting of several factors, each of which by itself causes the death of one half of the gametes in an $F_1$ hybrid, then the pollen fertility of the $F_1$ will be 50 percent if the parents differ by one such factor, 25 percent if they differ by two, 12.5 percent if they differ by three, and $100/2^n$ percent if they differ by $n$ such factors. With an increasing number of factors, therefore, this ratio forms a logarithmic curve which approaches, but never reaches, zero. In many genera, some modification of this curve, produced by the fact that different factors have different effects on $F_1$ sterility, is the probable distribution of sterility values for $F_1$ hybrids between species separated by barriers of hybrid sterility of increasing intensity.

The evolutionary possibilities of hybrids which can produce even a very few viable offspring on the diploid level are obviously very different from those which are either completely sterile or produce only rare polyploids or apomictic derivatives. The first type of hybrid will therefore be discussed in the remainder of this chapter, and the second type in the two following chapters.

SOME GENERAL PRINCIPLES CONCERNING HYBRIDIZATION

Before the aftereffects of interspecific hybridization are discussed in particular, some important general characteristics about hybridization must be reemphasized. In the first place, although the $F_1$ progeny of an interspecific cross are usually as much like each other as are the different individuals of the parental species, the offspring in the $F_2$ and later generations are extremely vari-

able, due to Mendelian segregation of the genetic factors responsible for the interspecific differences. The extent of this variability cannot be appreciated without first-hand experience of it. If the reader has never seen a large $F_2$ progeny of a hybrid between two widely different subspecies or closely related species, he should study carefully some well-described and illustrated example of one, such as Clausen's (1926) of *Viola arvensis* × *tricolor*, Müntzing's (1930a) of *Galeopsis tetrahit* × *bifida*, or Clausen, Keck, and Hiesey's (1947) of *Layia glandulosa* subsp. *typica* × subsp. *discoidea*. The striking fact about many of these progenies is not only their variability but also the presence of variants which look as if they have entirely "new" characteristics and represent recombination types whose occurrence could never have been predicted from a study of the original parents of the cross. In some of these progenies, such as those of *Apocynum* (Anderson 1936a) and *Quercus* (see Chapter II), types close to the original parents can be recovered in the $F_2$ generation, but in most others this is not possible unless a very large number of individuals is raised.

The second of these generalizations is that although segregation in the $F_2$ of an intervarietal or interspecific hybrid produces a very large number of recombination types, these are by no means a random sample of the total array of possible recombinations of the phenotypic characteristics of the parents. Correlations between groups of parental characteristics are always evident, so that the recombinations found represent a series of oscillations about a central axis, which is a condition of intermediacy or a greater or lesser approach to one or other of the parental species in all of the interspecific differences simultaneously. This fact has been brought out most strikingly by Anderson (1939) in his analysis of the cross between *Nicotiana alata* and *N. langsdorffii*. These two species are radically different in every visible characteristic, but many of these differences are of a similar nature. For instance, the leaf tips, calyx lobes, and corolla lobes are all relatively elongate and acute in *N. alata*, and short and blunt in *N. langsdorffii*. *N. alata* is larger and coarser in all of its parts; its corollas are not only larger than are those of *N. langsdorffii* but the lobes are still larger in relation to the size of the corolla (Fig. 25). As shown in Fig. 25, the corolla shapes found in the $F_2$ population do not
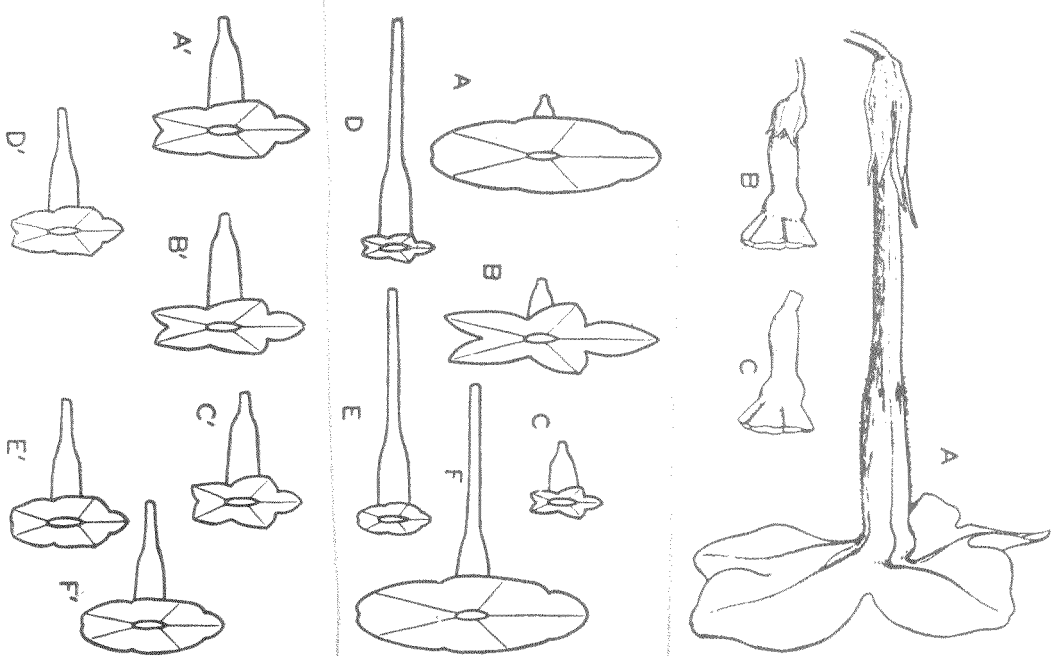
Fig. 25. At top (A), typical flowers of *Nicotiana alata* and (B and C) *N. langsdorffii*. Middle (A–E), extreme recombinations of tube length, limb width, and lobing of *N. alata* and *N. langsdorffii*. Below, actual extremes of recombination found in 147 plants of the $F_2$ generation of *N. alata* × *langsdorffii*. The letters A' to E' correspond to A to E in the middle figure. From Anderson 1939.

include such extreme recombinations as a corolla tube similar to that of *N. langsdorffii* together with lobes like those of *N. alata*. And Fig. 25 shows that when scored in respect to an aggregate of the parental differences, the individuals of the $F_2$ population group themselves for the most part near a line connecting the two parental species.

Two explanations may be given for this situation. In the first place, many of the parallel differences between the parental species are the result of developmental correlation in the action of the genes responsible for these differences, as has been emphasized in Chapters III and IV. In *Nicotiana alata* × *langsdorffii*, Anderson and Ownbey (1939) and Nagel (1939) have produced evidence suggesting that these differences are associated with genically controlled differences in hormone activity. The second explanation, as pointed out by Anderson (1939), is that genetic linkage will be more strongly evident in $F_2$ and $F_3$ populations if the character differences are governed by multiple factors, as is most frequently the case in interspecific hybrids, than if they are controlled by single factors. If, as in the *Nicotiana* hybrid cited, the haploid chromosome number is 9, then some linkage is almost certain to occur between any two characters each of which is governed by nine or more genes. Such linkages will eventually be broken up in later generations, but they will have a great effect on the distribution of variants in the immediate progeny of an intersubspecific or an interspecific hybrid.

The third generalization about the partially sterile offspring of natural interspecific hybrids in the wild is that they have a much greater chance of producing offspring from the abundant viable pollen of the numerous plants of the parental species which surround them than from the scant, poorly viable pollen produced by themselves or by the few other $F_1$ individuals which may be present. For this reason, the offspring of most natural interspecific hybrids are far more likely to represent backcross types than true $F_2$ segregates. This situation can be expected to become accentuated in later generations by natural selection. The combination of characters represented by the parental species have been tried over many hundreds or thousands of generations and have shown themselves to be adaptive; the chances that any new combination will prove equally adaptive are relatively small.

Hence, the nearer a backcross segregate approaches to one or the other of the parental species in characters of adaptive value, the greater its chance of survival. Since selection will have relatively little effect on recessive genes, these might be expected to be transferred relatively easily from one species to another by means of hybridization and backcrossing. In any case, the net effect of interspecific hybridization in nature between partially interfertile species would be expected on a priori grounds to be the reversion of the hybrid offspring toward one or other of the parental species. This effect would be particularly strong in the case of old, well-established species living in a stable habitat, and would be likely to be counteracted only if great disturbance of this habitat caused the original species to be ill-adapted to the new conditions.

The final generalization is the direct outcome of the previous one. In its ultimate evolutionary importance, hybridization depends directly on the environment in which it takes place. Hybridization between well-established and well-adapted species in a stable environment will have no significant outcome or will be detrimental to the species populations. But if the crossing occurs under rapidly changing conditions or in a region which offers new habitats to the segregating offspring, many of these segregates may survive and contribute to a greater or lesser degree to the evolutionary progress of the group concerned. This point has been particularly emphasized by Wiegand (1935) and Anderson (1948, 1949).

INTROGRESSIVE HYBRIDIZATION AND ITS EFFECTS

With these principles in mind, we can now examine some concrete examples of interspecific hybrids and their progenies in nature. According to expectation, we find that the majority of such progenies consist of the products of backcrossing, rather than of true $F_2$ and later generation segregates. An example which has been thoroughly studied is that of *Iris fulva* and *I. hexagona* var. *giganti-caerulea* (Riley 1938, Anderson 1949). These two species occur sympatrically in the Gulf Coast region of the southern United States, particularly in the lower Mississippi Delta. They are very different in external morphology, and *I. hexagona* var. *giganti-caerulea* is more closely related to *I. brevicaulis* of the northern Mississippi Valley than it is to *I. fulva*. The $F_1$ hybrid

between *fulva* and HGC (these two abbreviations were adopted by Anderson for the sake of convenience, and so are used here) is recognizably intermediate and partly fertile. The isolating barrier between the two species consists partly of hybrid sterility, but ecological isolation may play an equal or even more important role. *Fulva* occurs in wet clay soils, mostly along the edges of rivers and drainage ditches, in partial shade, while HGC grows in the mucky soil of tidal marshes, in full sun. Where farming activity has caused the clearing of woodland and the partial drainage and pasturing of swamps, new, intermediate habitats are available; these contain a many-colored array of hybrids and hybrid derivatives of the brick-red flowered *fulva* and the variegated, blue-flowered HGC. Nevertheless, the populations do not contain a complete blend of the two species, but, most commonly, individuals which are more nearly like HGC and contain certain characters or character combinations which suggest *fulva*. Apparently, hybridization followed by backcrossing and selection of backcross types has caused certain genes and gene combinations from *fulva* to pass across the barrier separating the two species and to become incorporated into the genic complement of HGC. This transference of genetic material across an incompletely developed interspecific barrier, usually via a partially sterile $F_1$ hybrid, by means of repeated backcrossing and selection of well-adapted backcross types, has been termed by Anderson and Hubricht (1938a) *introgressive hybridization* or *introgression*. **It has been treated in monographic fashion by Anderson (1949).**

The detection of introgressive hybridization in species populations depends on two characteristics of this process. In the first place, it can occur only in that part of the geographic range of a species which overlaps the distribution of closely related species, and then only when the habitat provides an ecological niche for the establishment of the introgressive types. If, therefore, the variation pattern of a species is being altered by introgressive hybridization, this pattern should contain more variability in regions where the ranges of two related species overlap than where either species is growing by itself. Also, this variability should be greater in newly opened and much-disturbed habitats than in old, stable ones. The second significant characteristic is

that introgression, like all types of intervarietal and interspecific segregation, follows the principle of correlation between different characteristics, as discussed in the previous section. If hybridization and subsequent introgression are taking place between species A and B, then the variation pattern of species A should be increased in the direction of species B in and near the regions where A and B are found together and where their habitats have been disturbed in relatively recent times. Furthermore, the variant, introgressive individuals of species A should not possess different characteristics of species B recombined at random with those of species A. Each individual should vary in the direction of species B in several of the characteristics distinguishing the two species, although obviously any particular characteristic would be expressed to different degrees in different individuals. The manner in which the variation pattern of a species is altered by hybridization and introgression is shown diagrammatically in Fig. 26.
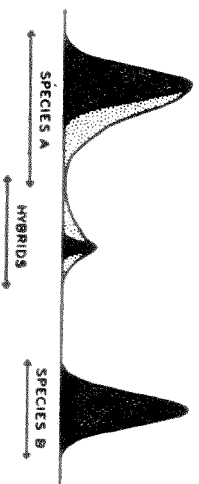


SPECIES A    HYBRIDS    SPECIES B

Fig. 26. Diagram illustrating the application of the terms "species" and "hybrids" to a case of introgressive hybridization. Solid black, original species and first-generation hybrids. Dotted, later hybrid generations and backcrosses. From Anderson and Hubricht 1938.

These characteristics permit the use of two different methods for detecting introgression. One is the scoring of herbarium specimens of a species with respect to certain individual characteristics which might be expected to be altered by introgression. If introgression is present, the character selected should be more variable in that part of the range of a species which coincides with the range of its relatives and should vary in the direction of the species with which introgression is suspected. This method was used by Anderson and Hubricht (1938a) for *Tradescantia occidentalis* in relation to *T. canaliculata*, for *T. canaliculata* in relation to *T. subaspera*, and for *T. bracteata* in relation to *T.*

canaliculata. The data, although admittedly very scanty, suggest that the variation patterns of *T. occidentalis* and *T. bracteata* have been modified by introgression from *T. canaliculata* (see Table 6). The latter species, on the other hand, has been unaltered by hybridization with *T. subaspera*. Another study of introgressive hybridization on the basis of individual characteristics as found in herbarium specimens is that of Epling (1947b) on *Salvia apiana* and *S. mellifera*. In the latter work, statistical comparison of population means in respect to two characteristics, one of the inflorescence and one of the corollas, failed to show any significant difference between colonies of *S. mellifera* close to known occurrences of the $F_1$ hybrid between *S. mellifera* and *S. apiana*, and other colonies of *S. mellifera* far outside of the range of *S. apiana*. In this instance, therefore, frequent interspecific hybridization is not accompanied by introgression of genes across the barrier formed by partial sterility of the $F_1$ hybrid.

The second method of detecting and estimating the extent of introgressive hybridization is through the use of the *hybrid index* (Anderson 1936c). As stated in Chapter I, this index is a modification of the statistical principle of discriminant functions. It makes use of the principle that, in contrast to the variability produced by the occurrence and segregation of individual mutations, variation caused by hybridization and introgression is characterized by correlations between characteristics which otherwise are genetically independent of each other.

The procedure is as follows. To each characteristic an index number is assigned, which is always 0 for the condition typical of one species, and may vary from 1 to 6, depending on the character, for the condition typical of the other. Thus, the characters are weighted according to their importance as diagnostic characteristics of the species concerned. This weighting is, of course, subjective, but must be based on the worker's intimate knowledge of the species concerned. Greater weight is attached to characteristics which are known to be relatively constant in regions where each of the parental species occurs by itself. If artificial hybrids and $F_2$ offspring have already been produced between the two species concerned, the weighting can take into account the probable number of genes which differentiate the two parental species with respect to each character. It is obvious that since the effectiveness

## TABLE 6

COMPARISONS OF HERBARIUM MATERIAL OF *Tradescantia canaliculata*, MARKED "CAN.," *T. bracteata* OUTSIDE THE RANGE OF *T. canaliculata*, MARKED "BRACT.," AND *T. bracteata* WITHIN THE RANGE OF *T. canaliculata*, MARKED "BRACT. (CAN.)" [a]

| | NODE NUMBER | | | | | | | | LEAF NUMBER | | | | | | | | | | INTER-NODE | | TUFT | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | Increase | Decrease | None | Weak | Strong |
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | | | | | |
| Bract. | | 11 | 1 | | | | | | 1 | 7 | 3 | 1 | | | | | | | 6 | 6 | 4 | 7 | 1 |
| Bract. (Can.) | 2 | 9 | 9 | 2 | | | | | 1 | 8 | 8 | 4 | 1 | | | | | | 12 | 10 | 1 | 3 | 19 |
| Can. | 2 | 12 | 18 | 19 | 14 | 5 | 3 | 1 | | 3 | 10 | 22 | 12 | 10 | 2 | | 2 | 3 | 56 | 18 | | 26 | 42 |

[a] From Anderson and Hubricht 1938.

of the hybrid index depends largely on correlation due to genetic linkage, greater weight should be attached to those characteristics which are controlled by multiple factors than to those which are governed by a single gene.

A typical example of this assignment of index values is given in Table 7. From this table it is evident that individuals typical of *Iris fulva* will receive the total index of 0, those typical of *I. hexagona* var. *giganti-caerulea*, that of 17, and the hybrids and their segregating and backcross derivatives, various intermediate scores. The larger the number of characters used, the larger is the number of genetic correlations reflected in the index values; and in the case of characters governed by multiple factors, the index values usually reflect the true genetic situation most closely when the largest possible number of intermediate conditions is recognized for each character and a maximal range is assigned to each index value. On the other hand, care should be taken to avoid including two different characteristics, such as the size and propor-

## TABLE 7

CHARACTERS AND INDEX VALUES OF *Iris fulva* AND *I. hexagona* VAR. *giganti-caerulea* [a]

| | *I. fulva* | Index value | *I. hexagona* var. *giganti-caerulea* | Index value |
| --- | --- | --- | --- | --- |
| 1. | Tube of perianth (hypanthium) yellow | 0 | Hypanthium green | 2 |
| 2. | Sepals orange-red | 0 | Sepals blue-violet | 4 |
| 3. | Sepal length 5.1–6.4 cm | 0 | Sepal length 8.6–11.0 cm | 3 |
| 4. | Petals narrowly obovate | 0 | Petals cuneate-spatulate | 2 |
| 5. | Anthers extruded beyond limbs of styles | 0 | Ends of anthers about 1 cm below ends of style limbs | 2 |
| 6. | Appendages of style branches small, barely toothed | 0 | Appendages of style branches large, deeply lacerate-toothed | 2 |
| 7. | Crest of sepals absent or very small | 0 | Crest of sepals present | 2 |
| | Total index value | 0 | | 17 |

[a] Data from Riley 1938.

tions of the leaves and the same characters of the sepals and petals, which might be governed partly or wholly by the same genetic factors and therefore show developmental correlation.

Fig. 27 shows the distributions of total index values in a colony of typical *Iris fulva*, one of typical *I. hexagona* var. *giganti-caerulea*, and two which contain plants typical of HGC plus
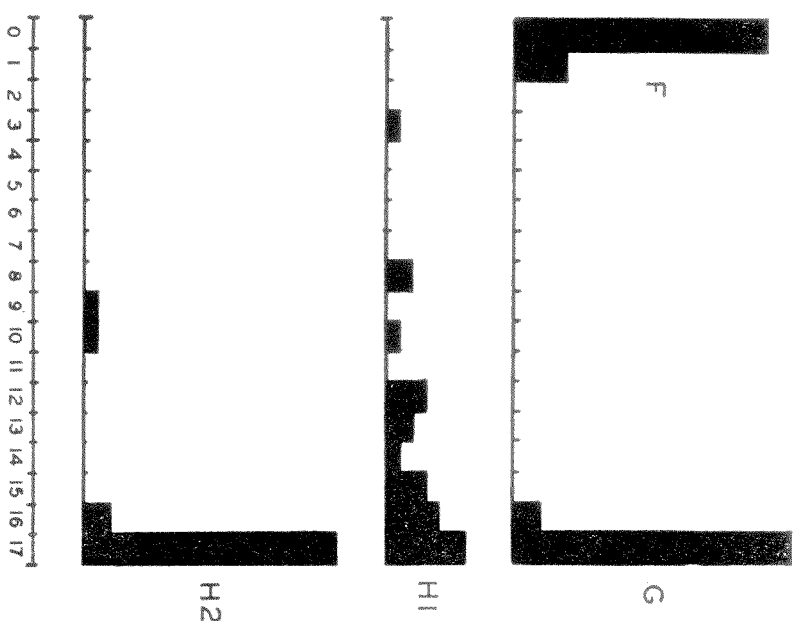


Fig. 27. Frequency distributions of total index values of 23 individuals in a typical colony of *Iris fulva* (F), one typical of *I. hexagona* var. *giganti-caerulea* (G), and two containing hybrid types (H1 and H2). From Riley 1938.

hybrids and their derivatives. In each colony, 23 plants were scored. Although the four colonies were only 500 feet or less from each other, the typical colonies grew in habitats characteristic of their respective species, while those containing hybrid types grew in an old stream bed, now heavily pastured.

A number of examples are now available of the use of this index to detect hybridization and introgression. That of Riley (1939), on *Tradescantia* demonstrates the passage of genes across a sterility barrier formed by the difference in chromosome number between a diploid species (*T. palustosa*) and two tetraploid species (*T. canaliculata* and *T. hirsutiflora*). Goodwin (1937a) on *Solidago rugosa* × *sempervirens*, Wetmore and Delisle (1939) on *Aster multiflorus* × *novae-angliae*, and Heiser (1947, 1948) on *Helianthus annuus* × *bolanderi* and *H. annuus* × *petiolaris* have supported their studies of natural populations with parallel analyses of artificial hybrids and their derivatives. In *Helianthus* the introgressive types have spread as weeds over a considerable area in California and are beginning to assume the character of newly formed subspecies, or ecotypes. Other population studies which have demonstrated the occurrence of hybridization and introgression are those of Dansereau (1941b, 1943) on *Cistus*, of Dansereau and Lafond (1941) and Dansereau and Desmarais (1947) on *Acer nigrum* × *saccharophorum*, and of Stebbins, Matzke, and Epling (1947) on *Quercus ilicifolia* × *marilandica*. Heiser (1949) has made a thorough review of the literature in this field.

In nearly all of the examples cited in this section, the species concerned are to a certain extent "weedy" in character and the introgressive types have become established in habitats much disturbed by the activity of man. On the other hand, the two examples cited by Epling (1947a,b) of hybridization in nature without subsequent introgression, namely, *Salvia apiana* × *mellifera* and *Arctostaphylos mariposa* × *patula*, involve nonweedy species occurring in undisturbed habitats. A similar example is that of *Pinus brutia* and *P. halepensis* in Greece (Papajoannon 1936). These two strictly indigenous species hybridize extensively in two small districts, but populations only a few miles away and elsewhere show no evidence of the effects of hybridization or back-crossing. In a totally different environment, namely, the tropical rain forest of Brazil, Seibert (1947) and Baldwin (1947) have noted that the species of *Hevea* occurring in undisturbed virgin forests are relatively constant and distinct from each other, while in the vicinity of towns there are hybrid swarms involving various ones of the species usually recognized by systematists. Darrow and

Camp (1945) have also emphasized the importance of man's activity in increasing the number of hybrids and hybrid derivatives in the genus *Vaccinium*, while great emphasis has often been given to this factor in the origin of the highly complex situations which exist in genera such as *Crataegus* (Wiegand 1935), *Rubus* (Brainerd and Peitersen 1920), and *Amelanchier* (Wiegand 1935).

There is little doubt, therefore, that the majority of the examples of hybridization and introgression which can be found in plant populations at the present time are associated with the disturbance of old habitats and the opening up of new ones through human activity.

Indirect evidence of a different type for the importance of disturbance of the habitat in permitting the establishment of introgressive types is provided by Dansereau's study of × *Cistus florentinus* (C. *monspeliensis* × *salviifolius*). This hybrid has been produced artificially by Bornet (Gard 1912) and has 90 percent of obviously abortive pollen. It is a very common hybrid, reaching a frequency of 10 percent in the large stands of *Cistus* found in parts of Italy, and it has crossed back to both parents. The data of Dansereau, although based on only three characters — form of leaves, texture of leaves, and number of flowers per inflorescence — suggest that C. *salviifolius* is everywhere more variable than C. *monspeliensis*, and that much of this variation is in the direction of the hybrid with C. *monspeliensis*. It is likely, therefore, that the products of backcrossing from the F₁ to C. *salviifolius* have more often been successful than have backcross types involving C. *monspeliensis*. In other words, hybridization and introgression have promoted a flow of genes from C. *monspeliensis* to C. *salviifolius*, but not in the reverse direction. Although the ranges of these two species coincide for the most part, C. *monspeliensis* prefers relatively dry, sunny sites, while C. *salviifolius* usually occurs in more mesic habitats, particularly in the shade of oaks and pines. The disturbance of the Mediterranean regions by human activity during the past centuries has consistently and progressively destroyed the forested areas containing habitats of the latter type and has opened up sites suitable for C. *monspeliensis*. Typical plants of the latter species, therefore, have been as well adapted to these newly opened habitats as are genotypes modified by introgression. But C. *salviifolius* has constantly found

itself exposed to habitats drier than those to which it is best adapted, and in the colonization of these new sites it has profited by the acquisition from C. *monspeliensis* of genes for greater resistance to drought.

Baker (1948) has studied a somewhat different type of example in *Melandrium dioicum* (*Lychnis dioica*) and *M. album*. The former species is indigenous in the forested areas of Europe, including Great Britain; *M. album* is a field weed, indigenous in the Near East, which has been spreading with human cultivation ever since the Neolithic Age. They hybridize easily, and the F₁ hybrids are rather fertile, although some sterility is present in both F₁ and F₂ generations. Baker was able to distinguish between ecologically neutral characters, such as length of calyx teeth, color of petals, and fertility of pollen, and those of adaptive significance. Depending on the degree to which the original forests are intact or cut down and replaced by plowed fields, a region contains pure *M. dioicum*, pure *M. album*, or populations of various hybrid and introgressive types. Baker recognized three stages of invasion and replacement of *M. dioicum* by *M. album*: first, the introduction into each species of ecologically neutral characters possessed by the other; second, the establishment in ecologically modified areas of various intermediate types; and, third, the disappearance of *M. dioicum* except for ecologically neutral characters which have become incorporated into the germ plasm of *M. album*. The strains of this weed introduced into North America all appear to be introgressive forms of *M. album*, containing some genes from *M. dioicum*.

In view of the complexity of adaptation, as discussed in Chapter IV, the present writer is somewhat doubtful of the ability of an observer to distinguish between adaptive and nonadaptive characteristics in hybrid derivatives. This somewhat reduces the general applicability of Baker's scheme of stages. In his example, the plants considered by him to be "pure" *M. album* may themselves differ from the indigenous eastern Mediterranean form of the species in possessing genes of *M. dioicum* acquired through hybridization and introgression in the remote past. Physiological characteristics acquired in this manner may have aided in adapting them to the climate of northern Europe.

Valentine (1948) has described a situation involving *Primula*

*vulgaris* and *P. elatior* in Britain, in which hybrids and hybrid derivatives appear to have persisted in about the same proportion in a population for many years, although they may have been produced originally by disturbance of a natural area. This suggests that hybridization and introgression can reach a stable equilibrium, if ecological conditions originally disturbed later become relatively constant.

We cannot conclude, however, that hybridization and introgression are geologically recent phenomena in the history of plant populations. Throughout the history of the world there have been great environmental disturbances, caused by natural fires, landslides, volcanic eruptions, floods, the rise and fall of inland seas, glaciations, and similar agencies. Each of these has given opportunities for the occurrence and spread of hybrids and their derivatives among some plant groups. The detection of introgression resulting from these past disturbances is, however, beset with considerable difficulties. The $F_1$ hybrids from which the introgressive types arose have in most cases disappeared completely, and in many cases the parental species are likely to have altered the geographic distribution which they possessed at the time of the disturbance. The best evidence for hybridization in the remote past can be obtained from a study of naturally occurring allopolyploids of hybrid origin, as discussed in the next two chapters.

The best example known to the writer providing evidence of the occurrence of interspecific hybridization and introgression in
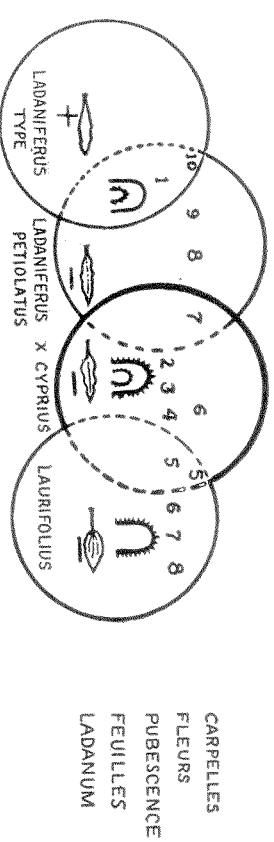


Fig. 28. Ideographs showing the number of carpels (upper row of figures), number of flowers per inflorescence (lower row of figures), pubescence of leaves and sepals, shape and margin of leaves, and presence or absence of ladanum in *Cistus ladaniferus, C. laurifolius,* and their $F_1$ hybrid. From Dansereau 1941.

LADANIFERUS TYPE　　LADANIFERUS PETIOLATUS　　× CYPRIUS　　LAURIFOLIUS

CARPELLES
FLEURS
PUBESCENCE
FEUILLES
LADANUM

the remote past and the subsequent establishment of the introgressive types as a new variety with a wide geographic range, is the work of Dansereau (1941) on *Cistus ladaniferus* and *C. laurifolius*. These two species, the only members of the section
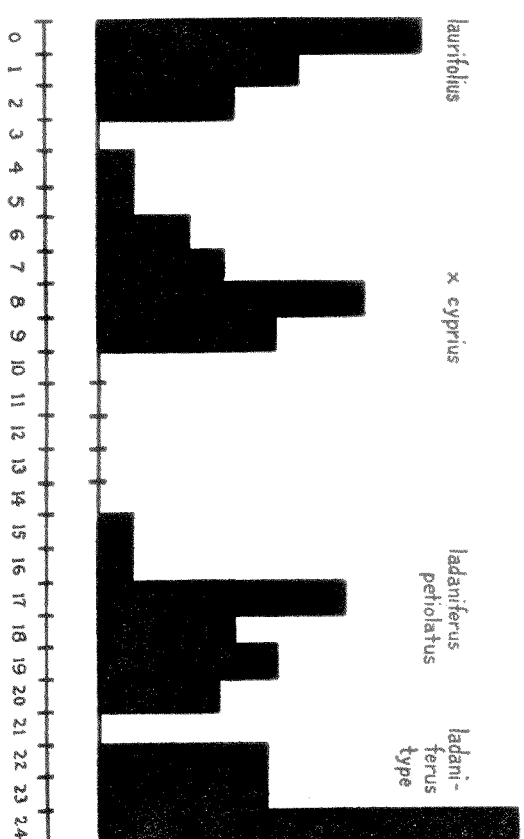


laurifolius　　× cyprius　　ladaniferus petiolatus　　ladaniferus type

0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24

Fig. 29. Diagram showing index values and their frequencies obtained from the five characters shown in Figure 28. From Dansereau 1941.

*Ladanium*, occur together over most of Spain, Portugal, and southern France, and occasional $F_1$ hybrids are found throughout this region. This hybrid also was produced artificially by Bornet (Gard 1912), and has 80 percent of sterile pollen. Figure 29 shows that in respect to index values compounded from the seven characters illustrated in Fig. 28, namely, number of carpels, number of flowers, pubescence of sepals, length of petioles, margin of leaves, width of leaves, and presence or absence of ladanum, the variation patterns of the two species are completely discontinuous with each other and with the intermediate one formed by the $F_1$ hybrids (× *C. cyprius*).

Typical *C. laurifolius* occurs in central Italy and western Asia Minor without *C. ladaniferus* (Fig. 30), while in Corsica and North Africa is found its subspecies *atlantica*, which differs in being smaller in certain of its parts (Fig. 28). The range of typical *C. ladaniferus* does not extend beyond that of *C. laurifolius*, but its variety *petiolatus* is abundant along the coast of North Africa,

in Morocco and in Algeria. All the differences which distinguish this variety from typical *C. ladaniferus* are in the direction of *C. laurifolius*. This is good evidence in favor of the hypothesis of Dansereau, that var. *petiolatus* originated from past hybridization



○ C. LAURIFOLIUS TYPIQUE
◔ C. LAURIFOLIUS VAR. ATLANTICUS
◒ C. LADANIFERUS TYPIQUE
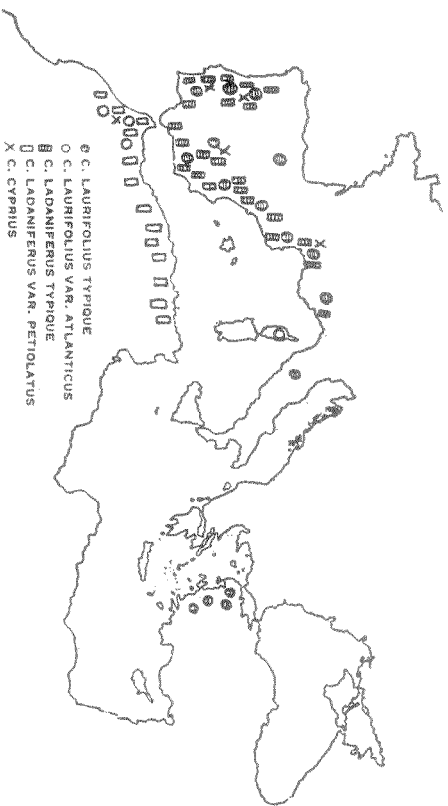□ C. LADANIFERUS VAR. PETIOLATUS
× C. CYPRIUS

FIG. 30. Map of the geographical distribution of *Cistus ladaniferus*, *C. laurifolius*, their hybrids, and the hybrid derivative *C. ladaniferus* var. *petiolatus*. From Dansereau 1941.

between typical *C. ladaniferus* and *C. laurifolius*. One might suggest an alternative hypothesis, namely, that var. *petiolatus* is the primitive ancestor from which the two other types diverged, but this hypothesis seems less likely in view of the present geographic distribution of the three entities. The present center of distribution and variability of the genus *Cistus* as a whole is the Iberian Peninsula (Dansereau 1939), which is the home of *C. ladaniferus typicus* rather than of var. *petiolatus*.

Another example which suggests the occurrence of hybridization in the remote past is that of the sugar maples, *Acer saccharophorum* and *A. nigrum* (Dansereau and Lafond 1941, Dansereau and Desmarais 1947). The degree of intermediacy described in this example, however, suggests that the two "species" concerned are merely subspecies or ecotypes, which coincide to a large extent in their geographic distribution, but are separated by ecological barriers. Anderson and Hubricht (1938b) found them to be distinct in southern Michigan, while the greatest assortment of

"pure" and "hybrid" colonies located near each other was found by Dansereau in the glaciated region of southern Quebec.

The studies made by Fassett (1944a,b, 1945a,b,c) on three closely related North American species of *Juniperus* show how the effects of contact between related types may be entirely different depending on the environmental conditions at the point of contact. *J. virginiana*, of the eastern United States, *J. horizontalis*, of the northeastern United States and Canada, and *J. scopulorum*, of the Rocky Mountains, are in general allopatric, and might well be considered well-marked subspecies rather than species, all of them being perhaps subspecies of the Old World *J. sabina*. Where two of these three forms come together at the margins of their ranges, the following different phenomena are found. *J. virginiana* and *J. scopulorum* intergrade like typical subspecies. They form hybrid swarms in southwestern North Dakota, and "introgressive" types of *J. virginiana*, containing some characteristics of *J. scopulorum*, are found hundreds of miles to the southward and eastward, in Nebraska and Kansas. These two forms have obviously been in contact for a long time, and in their region of contact, intermediate types of habitat are widespread. *J. scopulorum* and *J. horizontalis* occur together in northeastern Wyoming, and each can be found in its purest form a short distance from the other. In one locality, the east side of the Big Horn Mountains, however, a stand of *J. scopulorum* growing across the road from typical *J. horizontalis* contained many introgressive individuals. On the western side of these mountains a large stand of pure *J. scopulorum* is accompanied by smaller groups of semiprostrate individuals which in other respects correspond to that species, but may have originated through backcrossing from ancient hybrids with *J. horizontalis*, which is absent from the vicinity.

*J. virginiana* and *J. horizontalis* meet in several regions, two of which Fassett has carefully studied: the driftless area of Wisconsin and the coast of southern Maine. In the former area he found one locality containing only pure *J. virginiana* and *J. horizontalis* growing side by side, another in which pure *J. virginiana* was accompanied by a semiprostrate form of possible hybrid derivation, and still another occupied by both species plus a hybrid swarm of intermediate types. The latter condition was the usual one in

southern Maine. These diverse situations prevailing at different localities of contact of these three entities might be due to the fact that they themselves are sufficiently diverse genetically so that the forms growing in one region cross easily with members of another "species," while those found in another region do not; or the abundance or paucity of hybrids and their derivatives in any particular region may be due to the particular selective forces at work in that environment. Additional more detailed analyses of situations such as this, supplemented by experimental work, should contribute greatly to our understanding of the nature of species barriers and the significance of hybridization.

One of the boldest hypotheses, involving extensive introgression, is that of Mangelsdorf (Mangelsdorf and Reeves 1939, Mangelsdorf and Cameron 1942, Mangelsdorf 1947) regarding the origin of certain varietal characters in maize. These characters, particularly cylindrical ears; grains in few, straight rows; hard, stiff cobs; and small, flat kernels, are believed to have entered the germ plasm of maize through introgression from hybrids with species of the related grass genus *Tripsacum*. This hybridization is believed to have yielded as a by-product another more or less constant species, *Zea (Euchlaena) mexicana*, or teosinte. Evidence in favor of this hypothesis is the concentration of "tripsacoid" characteristics in the numerous varieties of maize found in the lowlands of southern Mexico and Guatemala, which is the center of variability of the genus *Tripsacum*, and the correlation of these morphological characteristics with a cytological peculiarity most strongly developed in the species of *Tripsacum*, namely, the presence of heavily staining knobs on the ends of several of the chromosomes at mid-prophase. The evidence provided by artificial hybridization is in some ways favorable and in others unfavorable to the hypothesis. Mangelsdorf could produce the $F_1$ hybrid only by a special technique which involves shortening the styles or silks of maize. There is considerable doubt that it occurs naturally at present. The hybrid is highly sterile, but does set some seed with maize pollen. Fertile types extracted in later generations are mostly plants with 20 chromosomes and morphologically typical of maize, but since maize and *Tripsacum* chromosomes can occasionally pair and exchange segments, transfer of *Tripsacum* genes into the maize germ plasm is possible and occurred in Mangels-

dorf's experiments. Nevertheless, this occurrence is so rare that in order to produce the "explosive" increase in variability which Mangelsdorf attributes to introgression from *Tripsacum* into the maize of Guatemala and Mexico, the occurrence of a large number of spontaneous hybrids would have been necessary. Such hybridization would be a very unlikely occurrence with maize and *Tripsacum* as strongly cross-incompatible as they are now. On the other hand, the data carefully gathered and critically evaluated by Mangelsdorf (1947) show that teosinte differs from maize genetically in a peculiar way. The genetic differences are confined to certain chromosomal segments with definite locations; but each segment, rather than containing its own particular complement of genes, contains and shares with the other segments some genes which influence each of the diverse and unrelated morphological characteristics differentiating teosinte from maize. It is difficult to see how such a situation could have arisen except through hybridization.

A possible solution to this dilemma might consist in alternatives to the Mangelsdorf hypothesis which do not involve recent hybridization between modern maize and any contemporary species of *Tripsacum*. The basic haploid chromosome number of *Tripsacum*, $x = 18$, is almost certainly a polyploid one, and the whole genus may well have an allopolyploid origin. The nine- or ten-paired ancestors of modern *Tripsacum* are very likely now extinct, but they may have existed in Mexico or Guatemala before these countries were as extensively disturbed by human cultivation as they now are. They may have included forms which could hybridize more readily with primitive maize than can any modern species of *Tripsacum*.

Even if the hypothesis of the hybrid origin of teosinte is rejected as too improbable, there remains a strong possibility that the characteristics peculiar to the "tripsacoid" maize varieties of Guatemala and Mexico arose through hybridization and introgression. If, as seems likely from the evidence of Mangelsdorf and his associates, as well as of Brieger (1944a,b), maize originated in South America, and if teosinte existed as a wild species before the introduction of cultivated maize into Guatemala and Mexico, then this introduction must have been accompanied by extensive hybridization between the two species, and selection of valuable

backcross, introgressive types would have been made by the ab-original 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 subsp. *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 subsp. *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 $F_2$ 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 and migrated . . . 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 such 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 allelomorphic 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* × *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
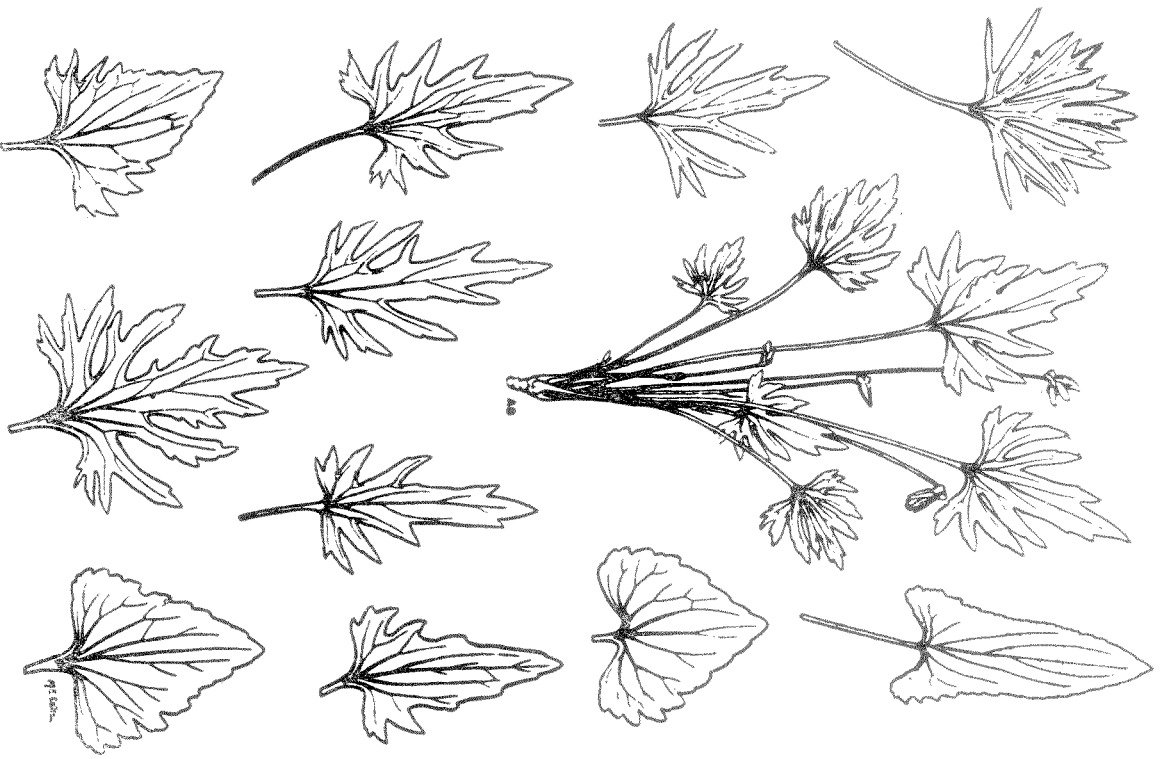
Fig. 31. Leaf of *Viola pedatifida* (upper left), leaf of *V. sagittata* (upper right), plant of the F₁ hybrid *V. pedatifida* × *sagittata* (upper middle), and leaves of nine different F₂ segregates from this hybrid. From Brainerd 1924.

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* × *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* × *pauciflorum*, by Müntzing (1930a) in *Galeopsis tetrahit* × *bifida*, by Anderson (1936a) in *Apocynum androsaemifolium* × *cannabinum* and (unpublished) in *Nicotiana alata* × *landsdorffii*, by Winge (1938) in *Tragopogon pratensis* × *porrifolius*, by Lamprecht (1941) in *Phaseolus vulgaris* × *coccineus*, by Zakharjevsky (1941) in *Triticum durum* × *timopheevi*, by Hiorth (1942) and Håkansson (1946a, 1947) in *Godetia amoena* × *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

of hybrid sterility are made up of many different genetic factors, either genes or small chromosomal segments, a considerable proportion of those fertile types which have been extracted by segregation, without doubling of the chromosome number, from partly sterile interspecific hybrids should form partly sterile hybrids with both of their parental species. Furthermore, the larger the number of genetic factors which contribute to the original sterility, the smaller is the number of fertile lines which can be extracted in a given number of generations, but the larger is the proportion of these fertile types which will be thus isolated from both of their original parents. If we use a simplified model of complementary sterility factors, we can make the following calculations by the use of the expansion of binomials as required for genetic experiments of this nature. If the parents differ by one pair of complementary sterility factors producing 50 percent genetic sterility in the $F_1$, then 50 percent of the $F_2$ offspring will be fully fertile and will form fertile hybrids with one or the other of the original parents. If the parents differ by two such factor pairs, and the $F_1$ is 25 percent fertile, then 25 percent of the $F_2$ offspring will be fully fertile, but only half of them will form fully fertile hybrids with one or other of the original parents. The other half of these fertile $F_2$ derivatives will consist of two types, each of which will form partly sterile hybrids with both of the original parents, and in addition will be partly intersterile with each other. The general formula may be expressed as follows. If $n$ is the number of independently segregating factor pairs which separates the parental species, and each factor pair causes when heterozygous the death of 50 percent of the gametes, then the percent of individuals in the $F_2$ generation which will be fully fertile is $100 \times 1/2^n$. But the percentage of these fertile types which will be partly intersterile with their parents and therefore a potential new species is $100 \times (1 - 1/2^{n-1})$. With a difference between the parents of four factor pairs, this last figure is 87.5 percent, and if the number of factors is six and the gametic fertility of the $F_1$ hybrid is reduced to 1.56 percent, then the percent of fully fertile types in $F_2$ is also 1.56 percent, and nearly 97 percent of these will be partly intersterile with their parents. Even though, as stated earlier, this simple accumulation of similar sterility factors is probably never actually followed in the evolu-

tion of sterility barriers in nature, nevertheless it is probably approached nearly enough so that the results calculated on this basis will be approximated to a considerable degree in the progeny of many interspecific hybrids.

The testing of this hypothesis in any group of plants obviously requires a long series of experiments extending over a considerable period of time. Even more work would be required to prove conclusively that any particular wild species has originated in this fashion, since one would first have to identify its parental species by means of morphological studies and would then have to obtain $F_1$ hybrids and later-generation progenies on a large scale in order to obtain a sufficiently large proportion of the multitude of segregant types so that some of them could be expected to be similar to or at least approximating the particular segregants which had become selected out of the progeny of the natural hybrid leading to the species in question. Nevertheless, strong circumstantial evidence has been produced by Epling (1947a) that the Californian species Delphinium gypsophilum arose in this fashion. It is intermediate morphologically between D. recurvatum and D. hesperium and occupies a natural range in the inner coast ranges of central California which is climatically and edaphically intermediate between that of the two other species. All three species are diploids, with eight pairs of chromosomes, except that D. gypsophilum also has a tetraploid race. The F₁ hybrid between D. hesperium and D. recurvatum resembles D. gypsophilum morphologically, but differs from it in having a large amount of aborted pollen and a very low seed set under open pollination, while D. gypsophilum grown under the same conditions is fully fertile as to both pollen and seed. More important, the progeny obtained from crossing this F₁ with wild D. gypsophilum have a higher fertility than those derived from backcrossing the same F₁ to its immediate parents. Apparently, therefore, the artificial F₁ hybrid between D. hesperium and D. recurvatum resembles the naturally growing species D. gypsophilum in its fertility relationships, as well as external morphology, and the most likely hypothesis is that the latter species has been produced by segregation from such a hybrid. The fact that it retains its intermediate character would be explained on the assumption that the morphological differences between D. hesperium and D. recurvatum are governed by multiple factors.

## THE SIGNIFICANCE OF HYBRIDS IN AGRICULTURE AND FORESTRY

From the evidence presented in this chapter, it is apparent that under favorable environmental conditions some phases of evolution can be greatly speeded up by interspecific hybridization. The parallel between organic evolution in nature and the improvement of cultivated plants through artificial breeding and selection on the part of man is close enough so that we might expect such hybridization to be important in plant breeding as well. Furthermore, the value of this procedure should vary depending on the character of the plant under cultivation, the use to which it was put, and the environmental conditions under which it was grown. This is just what we find. Interspecific hybridization has been carried out by plant breeders on an empirical basis for centuries, and in some groups, such as roses and tulips, it has played a major role in the origin of the types now being cultivated. And in recent years some of these plant hybridizers, like the Vilmorins in France, Burbank in the United States, and Michurin in Russia, have achieved spectacular results and wide popular acclaim through the use of this method. Furthermore, the usefulness of hybridization has proved great in some crops and relatively slight in others, depending on various factors. This fact can be brought out by a brief comparison of the amount of hybridization which has figured in the ancestry of modern varieties of field and forage crops, orchard crops, truck crops, and horticultural ornamentals.

In these four classes of cultivated plants, hybridization has been most important in garden and greenhouse ornamentals. The majority of the widely grown varieties of perennial herbs and shrubs, such as roses, tulips, hyacinths, narcissus, pansies, orchids, primroses, chrysanthemums, irises, delphiniums, and rhododendrons, are of hybrid origin, and during the past hundred years plant hunters have been exploring every corner of the globe for new species of these genera which might be combined with the well-known ones to produce an ever-increasing array of novelties. It is in this field that the daring, imagination, and keen eye of the professional hybridizer are most richly rewarded.

Next in importance are the orchard crops, both fruits and berries. Many of these, such as apples, cherries, plums, peaches, grapes, various types of berries, citrus fruits, and bananas, have been much hybridized, while in others, such as pears, walnuts,

olives, avocados, and papayas, all the numerous varieties now being grown have probably originated by selection from a single original species. Except in the genus *Rubus*, the hybridization has been restricted for the most part to crosses between closely related species belonging to the same section or subgenus, while in ornamentals hybrids between members of different subgenera or even genera have been more frequent.

In the field and forage crops, such as cereal grains, fiber crops like cotton and flax, tobacco, and forage crops like alfalfa and the clovers, hybridization between reproductively isolated species has been still less frequent. Several of them, such as wheat, cotton, and tobacco, are allopolyploids and therefore are derived originally from hybrids between widely different species, as will be discussed in the following chapter. But this hybridization, even if it took place after the parental species had been brought into cultivation, was spontaneous, not guided by the hand of man. The recent improvement of these crops by breeding has mainly been through intervarietal crossing and selection within the genetic species. Interspecific hybridization has in many instances contributed much to this improvement, but usually the crosses have been between closely related species, like the emmer and the *vulgare* or *aestivum* species of wheat, and the sea island and the upland cotton. Wider crosses, such as wheat with rye or quack grass (*Agropyron*), figure prominently in recent literature, but the polyploid derivatives of such crosses are all still in the experimental stage. Furthermore, the greatest use of interspecific hybridization in these crops in recent years has been not through the selection of new types from their segregating progeny, but through the transfer of individual characters from one species to another through a careful combination of hybridization, backcrossing, and selection. The majority of the characteristics of the more desirable parental variety is combined with one particular character, such as resistance to disease, insect pests, drought, or early maturing, derived from the other (Briggs 1938, Hayes and Immer 1942). In both purpose and method, this technique appears like a highly refined version of the introgressive hybridization which occurs so frequently in nature.

Finally, hybridization between distinct species has been least important in the truck crops or vegetables. In nearly all of the

most important ones — carrots, beets, turnips, radishes, asparagus, celery, spinach, lettuce, peas, snap beans, lima beans, and tomatoes — the cultivated varieties have all been derived by selection from a single diploid species or from a complex of interfertile taxonomic "species." In some of them, like the cultivated *Brassica oleracea*, including cabbage, cauliflower, broccoli, and Brussels sprouts, and *Cucurbita pepo*, including most types of garden squashes and pumpkins, the varieties which have been selected from a single species may be so widely different that their specific identity would hardly be suspected without careful study. In these crops, even hybridization and backcrossing for the purpose of transferring single characters has not been widely used, and the results of such hybridization are still largely in the experimental stage. The vegetables which form an exception to this rule are the tubers, like the potato and the sweet potato.

These differences between the classes of crops in respect to the importance of hybridization can be explained on the basis of two assumptions: first, that hybridization is of much greater value in plants which are usually propagated by vegetative means and less valuable in those reproduced primarily by seed: and, second, that the value of hybridization between widely different species is comparatively high in crops in which quantity of yield is the principal objective of breeding and falls lower as the demands for quality of the crop become more and more exacting.

The first assumption would explain the greater importance of hybridization in ornamentals and orchard crops as compared to field and truck crops. In these first two categories a large proportion of the most important varieties, even those of nonhybrid origin like the seedless table grapes and the double varieties of the common Chinese peony, produce no viable seeds and are propagated exclusively by vegetative means, via grafts, root divisions, or cuttings. Others which do produce seeds, like apples, pears, and peaches, are so heterozygous because of previous intervarietal or interspecific hybridization that seedling progeny are for the most part segregates with undesirable characteristics of yield or quality. Hybridization is more valuable in such crops because a long and expensive program of selection and genetic purification is not needed in them. Any single valuable hybrid individual, once obtained, can immediately become the progenitor of a new variety and can be perpetuated indefinitely.

Here we find an analogy to the significance of hybridization in organic evolution. Earlier in this chapter the greater importance was indicated of hybridization in plants with efficient means of vegetative reproduction. This is because the hybrid product, even though highly sterile, can persist for a long time if it is well adapted to its environment, and it may eventually yield more fertile derivatives.

The differences in the demands for quality would explain most of the differences in the importance of hybridization in ornamentals as compared to orchard crops, and in field crops as compared to vegetables. In garden flowers and shrubs, quality is very important, but the demand is not so much for a particular quality as for an aesthetic value which can be achieved in a number of different ways. In fact, novelty is of itself often desirable, and this is, of course, the one characteristic of quality which is obtained more easily by hybridization than by any other method. On the other hand, the demands for quality in fruits and fruit products are exacting and conservative, in that the traditional flavors are those usually desired. Furthermore, certain additional characteristics of quality are essential in those fruits which are regularly shipped long distances, dried, or canned. To obtain as a result of wide interspecific crossing even individual genotypes which will meet all these demands on quality is no easy task, and the breeder cannot rely on luck to nearly as great an extent as he can with many types of ornamentals.

Similar considerations hold in a comparison between field and truck crops. In certain of the former, such as wheat, cotton, and flax, the demands on quality are exacting; but in others, particularly those like field corn, barley, oats, and alfalfa, which are used principally as feed for animals, they are much less so. Most of the vegetable crops, on the other hand, have originally been selected out of a large number of potentially edible types of roots, leaves, or stems because they possess certain qualities of flavor, tenderness, or succulence, and the first consideration of the breeder dealing with such crops is to maintain these qualities. In addition, vegetables, like fruits, must under modern conditions possess shipping or canning qualities to be widely useful. If such qualities are to be maintained in a crop reproduced entirely or largely by seed, the breeder cannot afford to break them down

completely by introducing into the stock a whole complement of widely different genes obtained from a distantly related species.

Here again we have an analogy to organic evolution. If the adaptation of the species to its environment is of such a broad, general type that many different gene combinations are equally adaptive, then the chances are very good that some of the segregates from interspecific hybridization will have a selective value, and this process may figure prominently in evolution. But if certain of the adaptations possessed by the species are very exact and specific, like the elaborate flower structure of orchids and milkweeds, then the products of hybridization will almost certainly be nonadaptive, and this process will take a relatively small part in evolution.

In recent years, a type of plant breeding has been undertaken which differs radically from the breeding of typical cultivated plants and more nearly approaches the conditions found in organic evolution. This is the breeding of trees for reforestation and of forage grasses and other plants for the revegetation of uncultivated pastures and range lands. This differs from the breeding of cultivated crops chiefly in the fact that the finished product cannot be provided by man with the optimum conditions for growth, but must be able to compete successfully under more or less natural conditions. In forest trees, three additional characteristics affect the breeding process. In the first place, the amount of time and space needed for growing to maturity a single crop is much greater than that needed for annual seed crops, but, like the latter, only one harvest is possible for each planting. This puts a relatively high premium on the quality of the seed and should make it economically profitable to spend large amounts of time and money in securing the best possible seed. Second, the length of generations in forest trees makes impossible the establishment and maintenance of genetically pure stocks after hybridization. Finally, as Righter (1946) has pointed out, genetic uniformity is not necessarily a desirable quality in stands of forest trees, which occupy a relatively heterogeneous environment, and in which the destruction through natural causes of 90 percent of the original stand of seedlings is actually beneficial.

All of these differences favor the use of interspecific hybrids in forest-tree breeding. The same amount of time and money used

in securing a large amount of hybrid seed would be a relatively high proportion of the total cost of raising the crop in an annual plant and a much lower one in forest trees. And the heterozygosity or partial sterility of $F_1$ hybrids is a relatively slight disadvantage, since breeding and artificial selection from such hybrids is impractical, and genetic uniformity is not necessarily a desirable characteristic. Additional characteristics which increase the value of interspecific hybridization in forest-tree breeding are that the demands on quality in a lumber- or pulp-producing tree are relatively general and not very exacting, and, finally, that in most genera of trees, as pointed out in the preceding chapter, hybridization between widely different species often yields vigorous and partly or wholly fertile offspring.

As a result, interspecific hybridization has played a prominent role in the breeding of forest trees. This will be evident from a study of the reviews of this subject by Syrach-Larsen (1937), Johnson (1939), Smith and Nichols (1941), and Richens (1945), in which many examples are cited. A short description of the principal work in two of the most important genera, *Populus* and *Pinus*, will serve to illustrate the nature of this work. In poplars, the experiments of several workers (Stout, McKee, and Schreiner 1927, Wettstein 1933, 1937, Johnson 1942) have shown that the $F_1$ progeny of some hybrid combinations, both between and within species, may be more vigorous under conditions of cultivation than either parent. This hybrid vigor, however, is by no means universal. It is not found in some hybrids between species belonging to different sections, such as *P. tremula* × *grandidentata* (Wettstein 1933) and *P. balsamifera virginiana* × *grandidentata* (Stout and Schreiner 1934). In other hybrids its manifestation may be very irregular. Johnson (1942) found that the average vigor of hybrid progenies between *P. alba* and either *P. grandidentata* or *P. tremuloides* was greater than that of their parents, but the variability of the seedling lots was in every case very large, and there was much overlapping. He found that there was in general no inverse correlation between vigor of the seedlings and pulping quality of the wood, so that hybrid vigor, when obtained, carries a practical advantage in this genus. Furthermore, since vegetative propagation through slips or cuttings is practicable in poplars, the best method of increasing yield in this genus may be to select

particular parental trees which give exceptionally vigorous hybrids, to obtain a large number of $F_1$ seedlings, perhaps over a period of years, and to reforest with series of cuttings from several different vigorous $F_1$ genotypes.

In pines, as in poplars, many interspecific crosses yield hybrids more vigorous than their parents (Righter 1946). Vegetative reproduction is impracticable in this genus, but Righter has shown that large quantities of $F_1$ seed can be produced relatively economically. In pines, therefore, reforestation with hybrids will in every case make use of the seedlings obtained directly from crossing. The mean vigor of the progeny will be relatively important, and the occurrence of particularly vigorous individual genotypes will be less important than it is in poplars. Righter has suggested that in some instances, in which previous progeny tests have shown that many vigorous trees can be obtained from the $F_2$ generation, reforestation of an area planted previously to an $F_1$ population of an interspecific hybrid or a series of different hybrids can be secured by leaving a few vigorous seed trees. The high quality of the strongly segregating $F_2$ progenies might be maintained by natural selection plus artificial culling of undesirable segregates. If such reforestation practices are carried out, botanists of the future should be able to follow spectacular experiments on speeding up the rate of evolution on a stupendous scale.

In the revegetation of uncultivated pasture or range lands, the nearest possible approach is made to the conditions of organic evolution in nature, since natural selection can here be only modified by controlling the amount and time of grazing and by other management practices, while frequent artificial reseeding is often so impracticable that successful natural reseeding is a particularly desirable characteristic of the forage crop to be sown. Since livestock will eat and thrive on forage plants of a great variety of types, the principal characteristics which the desirable strains should have are vigor, competitive ability, and resistance to drought, cold, and other extreme conditions. Such characteristics can often be found in interspecific hybrids.

The use of wide crosses in this manner is discussed by Love (1946). He found that when sample plots were seeded to a mixture of three species of *Stipa* and the plants allowed to mature, a number of natural interspecific hybrids were found after the first

season in which the species were able to cross-pollinate. These hybrids were more vigorous than their parents, and under the dry conditions prevailing at Davis, California, had the additional advantage of remaining green later in the spring and becoming green earlier in the fall. Although sterile, they are very long-lived, and as long as the parental species were present in sufficient number, might be expected to be replaced periodically. Their presence, therefore, might be a permanent asset to a pasture seeded originally to a mixture of these or any other groups of related species capable of forming vigorous $F_1$ hybrids. Interspecific hybridization followed by polyploidy may have an even wider application in the revegetating of uncultivated pasture and range lands, as will be discussed in the following chapter.