CHAPTER II

Examples of Variation Patterns within Species and Genera

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

THE ECOTYPE CONCEPT

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

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

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

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

ECOTYPIC AND CLINAL VARIATION

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

Among the best examples of clines within plant species are those described by Langlet (1936) in *Pinus sylvestris* for genetic variation in chlorophyll content, length of mature leaves, hardiness, and rapidity of shoot development in the spring. Clausen, Keck, and Hiesey (1948a) found within the ecotypes of *Achillea lanulosa* and *A. borealis* clines for height of plant when grown and compared under uniform cultural conditions. In *A. lanulosa,* the tallest genetic types were from the lowest altitudes, and the decrease in height was more or less continuous with increasing altitude (Fig. 5). Olmstead (1944) found clinal variation in vigor and in reaction to photoperiodism in strains of side-oats grama grass (*Bouteloua curtipendula*) obtained from different latitudes in the Great Plains. Clinal trends were found by Böcher (1943, 1944) in *Plantago lanceolata* and *Veronica officinalis.* It is likely that most species with a continuous range that includes more than one latitudinal or altitudinal climatic belt will be found to possess clines for the "physiological" characteristics
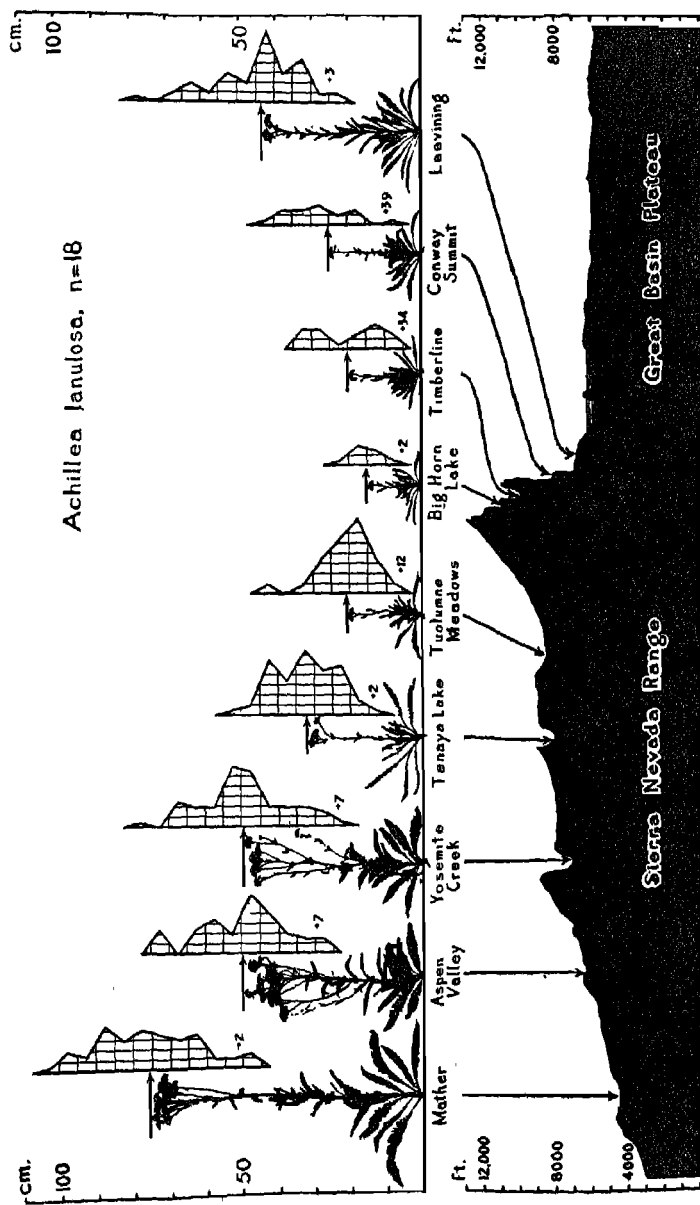
FIG. 5. Representatives of populations of *Achillea lanulosa* as grown in a uniform garden at Stanford. These originated in the localities shown in the profile below of a transect across east central California at approximately 38° N. latitude.

The plants are herbarium specimens, each representing a population of approximately 60 individuals. The frequency diagrams show variation in height within each population: the horizontal lines separate class intervals of 5 cm according to the marginal scale, and the distance between vertical lines represents two individuals. The numbers to the right of some frequency diagrams indicate the *nonflowering* plants. The specimens represent plants of average height, and the arrows point to mean heights. From Clausen, Keck, and Hiesey 1948.

adapting them to the conditions prevailing in the different parts of their range.

Clines have also been reported for the frequency of occurrence in a population of a single qualitative character, such as pubescence. Fassett (1942) found that the pubescent form (var. *hypomalaca*) of *Diervilla lonicera* in the region north of Lake Huron shows a cline ranging from 80 percent frequency at Espanola, Ontario, to 0 percent at Callander, about 100 miles farther east. The data of McClintock and Epling (1946) indicate that in *Teucrium canadense* there is a cline for the frequency of plants with glandular hairs on the calyx ranging from a high of 100 percent in the Rocky Mountains southeast to 0 percent in southern Florida.

Gregor (1939), in his studies of *Plantago maritima*, recognized two types of clines, topoclines and ecoclines. The former are similar to the geographic or regional clines described above for other genera and include variation both in quantitative characters, such as the length/width index of bracts and sepals, and in the frequency of such characters as pubescence and purple spots on the leaves. Ecoclines, on the other hand, are clines related to ecological gradients within a restricted area (see also Gregor 1944). They occur in characteristics such as density of spike, habit of growth, and length of scape, which vary genetically in the same region according to whether the plants are growing under the poor drainage conditions of a salt marsh or waterlogged coastal mud or under the better drainage conditions prevailing higher up and on maritime rocks and cliffs. The extreme forms which are the ends of these ecoclines constitute edaphic ecotypes (see p. 52).

Treatment of intraspecific variation by clines has advantages as well as disadvantages over the more usual method of dealing in terms of the character combinations which distinguish races or subspecies. One advantage is that it makes possible the analysis of the individual characters of these combinations and is the first step toward the causal analysis of these differences in terms of selection or any other factor. It also focuses attention on the continuous variation in quantitative characteristics which is present in many wide-ranging species and is of great importance in their adaptation to the environment, but which because of its very

continuity is difficult to use as a basis for classification. One disadvantage of the use of clines is that each individual cline can be recognized only after analysis of extensive samples from many localities. This makes it impossible to describe all the clines existing in a species, so that the method of necessity places particular emphasis on certain individual characters, which may or may not be the most important ones from the standpoint of the biology and evolution of the species as a whole. Furthermore, since selection in populations is based on character combinations (see Chapter IV), too much emphasis on gradients in single characters may serve to confuse rather than clarify the whole picture of variation.

The relation of clines to subspecies depends on the character of the clines. If they are continuous over long distances, and if the extreme types are relatively limited in distribution, as with the clines in *Pinus sylvestris*, then they cannot form the basis for classification. But if a number of clines run parallel and are partly discontinuous, with a steep gradient in some regions and a moderate one or a constant level in others, then the different levels of variation in the characters forming the clines may constitute part of the basis of local races or subspecies. These are the intergroup clines of Huxley (1939).

Various species undoubtedly differ from each other in the distinctness of their ecotypes, depending on the regions they occupy and the size of their population units in terms of cross-breeding and seed dispersal. In species occupying an area like the eastern United States, which is comparatively uniform in many climatic characteristics and where a single set of factors, such as temperature and length of growing season, varies gradually and continuously, continuous or clinal ecotypic variation will be particularly prevalent. On the other hand, diversity and discontinuity of the available habitats will promote the differentiation of more distinct, easily recognized groups of biotypes within the species, and therefore of more distinct ecotypes. In addition, as Turesson (1936) has pointed out, species with obligate cross-pollination, particularly those like pines and other wind-pollinated trees of temperate regions, in which the pollen may be carried through the air for many miles, are most likely to show continuous genetic variation. In them the interbreeding

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

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

ECOTYPES AND SUBSPECIES

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

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

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

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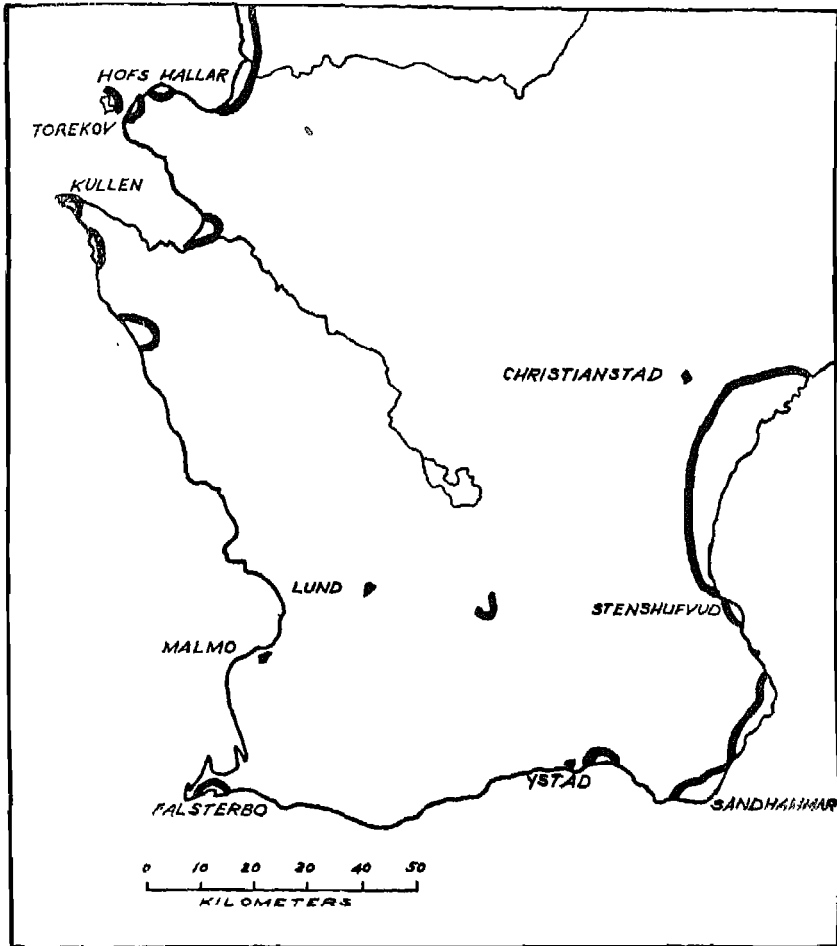
FIG. 6. Map of southern Sweden showing, in heavy lines, the distribution of the maritime ecotype of *Hieracium umbellatum*. Simplified, from Turesson 1922b.

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

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

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

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

VARIATION ON THE LEVEL OF THE SPECIES AND GENUS

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

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

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

majority of plant groups, nevertheless different interrelationships between evolutionary factors have produced in various genera and families a great diversity of variation patterns. These patterns may differ not only between closely related genera but even between different sections of the same genus. Part of this diversity is due to the sporadic or frequent occurrence of such phenomena as self-fertilization, polyploidy, apomixis, and structural hybridity, as is brought out in Chapters V and VIII–XI. Nevertheless, even groups of which all the members are diploid, sexual, and cross-fertilizing may differ greatly from each other in the degree to which isolating barriers are developed and the amount of genetic and ecotypic diversity contained within the species. In some genera, the species are genetically homogeneous, have relatively restricted ranges, and have no close relatives. At the other extreme are genera in which all the species are polytypic in the sense of Mayr (1942, Chaps. V and VI); that is, they consist of a greater or lesser number of partially discontinuous, morphologically recognizable subspecies or ecotypes which replace each other geographically. Most genera have variation patterns somewhere intermediate between these extremes. Camp and Gilly (1943) have attempted a classification of the types of species found in plants, but their terminology has proved cumbersome and not always soundly based on genetic phenomena, so that it has not been generally accepted. Nevertheless, as knowledge of the genetic bases of variation patterns increases, the adoption of a system like that of Camp and Gilly may prove valuable in orienting the thinking of botanists on problems of evolution; their system may be considered premature rather than altogether inappropriate. In the remainder of this chapter, a series of examples will be presented which is intended to give an idea of the diversity of genetic patterns on the diploid level.

PATTERNS IN THE FAMILY RANUNCULACEAE

In the Ranales, the most primitive order of angiosperms, three genera have been studied by experimental as well as by descriptive systematic methods. These are *Paeonia, Delphinium,* and *Aquilegia.* In *Paeonia* the two New World species are complicated by structural hybridity and are discussed in Chapter XI. In the Old World there are ten to twelve diploid species plus a

number of polyploids which will not be discussed here (Stebbins 1939, Stern 1946). Four of these diploid species, *P. suffruticosa, P. emodi, P. tenuifolia,* and *P. cretica,* are fairly certainly homogeneous in nature, and two others, *P. albiflora* and *P. intermedia,* are probably so. *P. delavayi* is very polymorphic in nature, but the evidence from herbarium specimens does not indicate any geographic segregation of its variants. Careful field study may nevertheless reveal that it is a polytypic species. The three remaining species groups, *P. anomala* (including *P. veitchi, P. woodwardii,* and *P. beresowskii*), *P. obovata* (including *P. japonica*), and the *P. daurica-mlokosewitschii-broteri-cambessedesii* series, are characteristic polytypic species or species groups. Experimental evidence on most of these has shown that they are separated from each other by strongly developed genetic barriers (Saunders and Stebbins 1938, Stebbins 1938a). It is possible that some of the units of the last-mentioned complex are also genetically isolated from each other. In *Paeonia,* therefore, homogeneous and polytypic species occur with about equal frequency.

The genus *Delphinium* has been treated in two monographs, one of which (Ewan 1945) explored thoroughly the North American species. In addition, the chromosomes are known of all the species native to California, and many of these have been further analyzed by means of transplants, progeny tests, and interspecific hybridization (Epling and Lewis 1946 and unpublished). These are all diploid, except that three, *D. hanseni, D. variegatum,* and *D. gypsophilum,* contain related tetraploid forms. Ewan described subspecies in 23 of the 79 species recognized by him, and further field studies, as well as genetic analyses, may show that some of the species which he recognizes are no more than subspecies. A group of "species" which probably form a single polytypic species (Epling, oral communication) is that consisting of *D. decorum, D. patens, D. menziesii, D. nuttallianum,* and their relatives, including 13 species placed by Ewan in his "tuberiform series." These forms replace each other geographically, and Ewan cites examples of intermediate and intergrading populations.

In another species group are found seven species which have been extensively observed in the field and intercrossed, namely, *D. variegatum, D. hesperium, D. hanseni, D. gypsophilum, D. parryi,* and *D. amabile.* These simulate the subspecies of a poly-

typic species in that they in general replace each other geographically or ecologically, and they are obviously closely interrelated. But they all overlap with one or more of their relatives in a considerable proportion of their ranges, and in these regions Drs. Mehlquist, Epling, Ewan, Lewis, and the writer have repeatedly and independently seen two or three species growing side by side with no signs of intergradation. The isolating mechanisms are, however, of a somewhat puzzling nature, and they will be discussed further in Chapter VI. Five of these species are themselves polytypic, with two to four subspecies each. Two California species, *D. uliginosum* and *D. purpusii*, are sharply distinct relict endemics. In *Delphinium*, as in *Paeonia*, the pattern is that of closely related homogeneous species more or less sharply isolated from each other, as well as of polytypic species, the two types occurring with about equal frequency.

Aquilegia has become a classic example of a genus in which isolating barriers between species are weak or absent. The latest monograph of the genus, that of Munz (1946), lists 67 species, distributed through temperate Eurasia and North America. They are almost entirely allopatric; in a few places two species grow in the same region, but rarely, if ever, more than two, if we except regions which because of their great topographic relief include more than one climatic zone. All the species have the same vegetative habit and essentially similar leaves, and the differences between them in stamens and seed follicles are relatively slight. The species are based almost entirely on differences in the size, shape, proportions, and color of the sepals and petals. It has long been known among gardeners that they hybridize freely and that a large proportion of F_1 hybrids, even between species that are relatively remotely related to each other, are highly fertile. Natural hybridization between two such species, *A. formosa* and *A. flavescens*, has been recorded by Anderson (1931) and apparently is not uncommon.

The genetic barriers between some of the species have been studied by Skalinska (1928a,b). She found that the F_1 hybrid between the European *A. vulgaris* and the rather remotely related *A. chrysantha* of western North America has about 50 percent normal pollen and 20 percent normal seed setting, regardless of which way the cross is made. On the other hand, if the Japanese

species, *A. flabellata nana*, a close relative of *A. vulgaris*, is crossed with *A. chrysantha*, the F_1 is highly sterile and resembles the mother when *A. flabellata nana* is the pistillate parent, and furthermore it tends to produce matroclinous segregates in the F_2 generation. But the reciprocal hybrid, with *A. chrysantha* as the pistillate parent, is normal and rather highly fertile (Skalinska 1929, 1935). On the other hand, if *A. flabellata nana* is crossed with another North American species, *A. californica*, the F_1 hybrid is normal and has almost normal fertility no matter in which direction the cross is made (Skalinska 1929). In a later paper (Skalinska 1931) the author reported matroclinous behavior and high sterility in *A. flabellata nana* $\times$ *A. truncata*. Since according to Munz (1946) *A. californica* is merely a synonym of *A. truncata*, the evidence of Skalinska would suggest that in this group of *Aquilegia* species the sterility and the genetic behavior of the F_1 hybrid differs according to the strain of the parental species used in the cross. At any rate, there are no strong genetic barriers to gene exchange between the Old World species centering about *A. vulgaris* and their morphologically very different relatives in North America.

Evidence of a different type of genetic isolating mechanism between species of *Aquilegia* was found by Anderson and Schafer (1933). They grew a plant of *A. vulgaris* which was homozygous for two recessive genetic factors in a garden beside plants of the same species which had the corresponding dominants, and in addition plants of three other rather distantly related species, *A. pyrenaica*, *A. skinneri*, and *A. caerulea*. Seed harvested from open pollination gave 16 percent of offspring which were the result of outcrossing to other plants of *A. vulgaris*, but no interspecific hybrids were found.

It is evident, therefore, that while many of the described species of *Aquilegia* are only subspecies from the standpoint of their genetic isolation from each other, nevertheless the whole genus cannot be viewed as one large polytypic species. Munz, however, was unable to divide the genus into natural species groups even on the basis of the most careful study of herbarium specimens and living plants in the garden, and he pointed out great divergences between previous groupings of the species. The true boundaries of the species, therefore, cannot be determined

by a study of the specimens alone, but will become apparent only after a careful and systematic series of hybridizations. However, we may now safely accept the statement of Clausen, Keck, and Hiesey (1945a) that *"Aquilegia* is one huge ccnospecies composed of only a few ecospecies. Probably most of the recognized 'species' are merely morphologically distinguishable ecotypes or subspecies." The largest of these ecospecies is undoubtedly the European *A. vulgaris.* Twenty-nine of the 67 species recognized by Munz have been recognized by at least one other botanist as varieties or subspecies of *A. vulgaris,* and 12 more are obviously closely related to these. *A. vulgaris,* therefore, is probably a polytypic species which in its complexity rivals *Peromyscus manicu-latus* among the vertebrates. Among the North American Aquilegias, the red-flowered series, consisting of the eastern *Aquilegia canadensis* and the western *A. formosa* and their relatives, is probably another rather complex polytypic species. The suggestion of Clausen, Keck, and Hiesey, that *Aquilegia* "possibly represents a youthful stage experienced by many other, now mature genera" is reasonable if the reference is confined to the evolution of the interspecific barriers themselves. But *Aquilegia* is probably not a youthful genus in terms of chronological time. It is distributed chiefly in the old floristic communities of the mesophytic forests of the north temperate regions (see Chapter X). Furthermore, it belongs to the primitive family Ranunculaceae and in some respects is primitive even for that family. In *Aquilegia,* therefore, the development of complex polytypic species has been accompanied by much geographic isolation of segments of its populations, along with great variability of certain organs of the flower. On the other hand, the rest of the plant, as well as the chromosomal apparatus, has remained comparatively stable.

VARIATION PATTERNS IN THE GENUS *Potentilla*

The second family of angiosperms to be considered, the Rosaceae, is noted for the frequency of polyploidy, both within and between genera, as will be discussed in Chapter VIII. Phylogenetically it is usually placed in an intermediate position. The genus that will be considered here, *Potentilla,* contains at least three different types of variation pattern. Most of the genus consists of one or a few large polyploid or agamic complexes and will be

discussed in Chapters VIII–X. The subgenus *Drymocallis,* how-
ever, consists entirely of diploid species, with the somatic number
of 14 chromosomes. Its most widespread and complex species is
P. glandulosa, which contains at least 11 subspecies (Clausen,
Keck, and Hiesey 1940). These are adapted to regions as widely
diverse as the warm-temperate, semiarid coast of Southern Cali-
fornia and the arctic-alpine meadows of the high Sierra Nevada.
Diagnostic characters for distinguishing the subspecies are found
in the stolons, leaves, stems, inflorescences, sepals, petals, and
seeds, and 16 such characters are tabulated for the 11 subspecies
by Clausen, Keck, and Hiesey. In addition, transplant experiments
revealed great physiological differences in rhythm of growth and
other characteristics, and an important biological distinction is
that some of the subspecies are self-incompatible and normally
cross-pollinated, while others are self-compatible and largely self-
fertilized.

Within *P. glandulosa,* therefore, we find all the types of mor-
phological and physiological differences that often separate good,
distinct species. If the extreme forms, such as subspp. *typica* and
nevadensis, should become completely isolated from each other
geographically and should develop genetic sterility barriers, they
would become amply distinct species even without any further
divergence in morphological and physiological characteristics.
What keeps the species a single unit is the fact that every sub-
species is at some locality or localities in contact with at least one
other subspecies, and where these contacts occur, hybrid swarms
are regularly found.

Two other species of the subgenus *Drymocallis* occur in the
United States, *P. arguta,* which has two subspecies, and *P. fissa,*
which is confined to high altitudes in the central Rocky Moun-
tains and is homogeneous. Intermediates between these two and
P. glandulosa are reported from herbarium specimens, but ap-
parently have not been observed in the field. In the Medicine
Bow Mountains *P. fissa* and *P. glandulosa* subsp. *glabrata* occur
sympatrically, but no information is available on the extent and
manner of their isolation from each other in that region. The
uncertainty in regard to these species, which belong to one of the
groups best known from the experimental point of view, is clear
evidence of how much work is necessary before the true nature of
species even in a relatively simple group can be made clear.

Since *Potentilla glandulosa* is one of the best-known species of flowering plants in North America from the standpoint of experimental taxonomy, a further examination of the variation pattern within this species is desirable. Its four best-known subspecies are *typica,* most characteristic of coastal California, and subspp. *reflexa, hanseni,* and *nevadensis,* all best known from the Sierra Nevada. Subspecies *hanseni,* when compared with subspecies as they are usually understood in animals, has two unusual characteristics. In the first place, it is included entirely within the geographic range of subsp. *reflexa.* The two subspecies are, however, ecologically isolated from each other, subsp. *hanseni* occurring in moist meadows and subsp. *reflexa* on dry slopes. Where these two habitats come together, as at Aspen Valley in Yosemite National Park, hybrid swarms are found, but elsewhere the subspecies maintain themselves as fairly distinct. This separation is aided by the fact that subsp. *reflexa* is self-pollinating and therefore has a relatively small chance of receiving pollen from subsp. *hanseni.* These two subspecies, therefore, represent edaphic ecotypes and differ from the strictly geographic subspecies commonly recognized in animals.

The second peculiarity about subsp. *hanseni* is that in morphological characteristics and ecological preferences it is intermediate between subsp. *reflexa* and subsp. *nevadensis.* Furthermore, all the moist meadows which it occupies have resulted from the filling up of postglacial lakes and are therefore one of the most recent habitats in the region. The suggestion of Clausen, Keck, and Hiesey (1940, p. 44) that subsp. *hanseni* has resulted from hybridization between subspp. *nevadensis* and *reflexa,* with subsequent stabilization of a group of segregates adapted to meadow conditions, is very plausible. It may be true that this type of origin of new subspecies in plants is not infrequent.

The other seven subspecies of *Potentilla glandulosa* are much less well known, but the fact that four subspecies occur together in another region, namely, the Siskiyou mountain area of northwestern California, suggests that here also edaphic factors rather than climatic or geographic factors are maintaining the isolation between subspecies. The subgenus *Drymocallis* contains, in addition to the three American species mentioned, six in Eurasia. One of these, *P. rupestris,* is widespread, while the other five are

endemic to mountain areas in southwestern Asia, from Asia Minor and the Crimea to the Himalaya. The interrelationships between these species are relatively poorly known, but available evidence indicates that some of them may be subspecies of *P. rupestris*. Attempts to produce hybrids between *P. rupestris* and *P. arguta* have failed, suggesting that the American and the Eurasian species of the subgenus *Drymocallis* are well isolated from each other and may represent different cenospecies.

The subgenus *Drymocallis* of *Potentilla,* therefore, contains two widespread, polytypic species, one in each hemisphere of the Holarctic region, and several less complex species about equally distributed in each hemisphere.

THE GENUS *Quercus*

The next variation pattern to be considered is that of the oaks, a typical genus of angiospermous trees of the north temperate regions. According to present systematic treatments the genus *Quercus,* of the family Fagaceae, contains between 250 and 300 species, but it is very likely that many of these actually are subspecies of a smaller number of polytypic species. Cytologically all species of *Quercus* investigated, as well as all other genera of the Fagaceae, have the same chromosome number, $n = 12$, and only slight differences exist between them in size and in morphology of the chromosomes (Hoeg 1929, Ghimpu 1929, 1930, Jaretzky 1930, H. J. Sax 1930, Natividade 1937a,b, Duffield 1940). Natural hybrids between generally recognized species are not uncommon, and both cytological and genetic studies indicate that most are fertile (Sax 1930, Yarnell 1933, Wolf 1938, 1944).

The usual treatments in the various regional floras do not describe geographic varieties or subspecies within most of the oak species, although *Q. borealis,* the common red oak of the eastern United States, and three species of live oaks of California, *Q. wislizenii, Q. agrifolia,* and *Q. dumosa,* are commonly recognized to be polytypic. Nevertheless, the experience of the writer and of most other observers with whom he has spoken indicates that a much larger number of species will be found to possess geographic variation when their intraspecific variation patterns are studied more carefully. Furthermore, hybrid swarms are often found in regions where the ranges of markedly different allo-

patric species overlap. A conspicuous example of this is *Quercus garryana* and *Q. douglasii*, mentioned in Chapter I. Furthermore, similar hybridization apparently occurs at the southern end of the range of *Q. douglasii*, where it overlaps with *Q. dumosa* and its var., *turbinella*. There is thus good evidence of gene interchange between a chain of forms ranging from a large tree with broad, deciduous, lobed leaves to a shrub with very small, coriaceous, evergreen, unlobed leaves; and the range of differences in acorn cups and other reproductive structures within this series of forms is equally great. This situation is further complicated by the fact that the valley oak of California, *Q. lobata*, which is the counterpart of *Q. garryana* both in habitat and in the character of the tree, shows relatively little evidence of hybridization in localities occupied by these two species. Furthermore, *Q. lobata* and *Q. douglasii*, although they occur sympatrically and often in mixed stands throughout most of their ranges, also show little evidence of intergradation with each other. In the oaks of California, therefore, the magnitude of the visible differences between species seems to bear no direct relationship to the amount of intergradation that can occur between them.

A relationship of a somewhat different type is shown by *Q. marilandica* and *Q. ilicifolia*, two species of the subgenus *Erythrobalanus* (black oak) in the eastern United States. These species occur together chiefly on the coastal plain of New Jersey, Long Island, and Staten Island, New York, but elsewhere are usually well separated from each other geographically or ecologically. Both species are relatively uniform throughout their ranges, as is evidenced from the fact that a single population sample of *Q. marilandica* from Cliffwood, New Jersey, showed a range of variation in six important diagnostic characteristics equal to that found in a series of specimens representing the entire geographic range of the species from Pennsylvania to Kansas and Arkansas (Stebbins, Matzke, and Epling 1947). In New Jersey, the two species occur sympatrically over a large part of the pine-barren area and in general remain quite distinct from each other. But shrubs intermediate between them do occur and were described as natural hybrids more than fifty years ago (Davis 1892). Study of a population sample from one of these localities by Stebbins, Matzke, and Epling (1947), with the aid of Ander-

son's hybrid index method (see Chapter VII), revealed that eight out of the sample of 86 specimens were sufficiently intermediate between the two species so that they could be considered F_1 hybrids or their derivatives, while about 35 percent of the specimens showed some evidence of admixture of genes derived from the two species. Most of them were introgressive types of Q. marilandica, containing a few genes from Q. ilicifolia.

The variation pattern in Quercus is further complicated by the fact that species may occur together in many regions without showing any signs of intergradation, but in other areas these same species may be connected by both first-generation hybrids and other intergrading types which are the result of segregation or backcrossing. Q. douglasii and Q. lobata, mentioned above, are an example of this. Although they are distinct nearly everywhere, a series of hybrid types under the name × Q. jolonensis has been described from a small area in central California. In the eastern United States, where in many regions as many as ten or eleven species of oaks may occur sympatrically, examples of this type are more numerous. Two very distinct species of this region are Q. imbricaria, the shingle oak, which has elliptic entire-margined leaves, and Q. velutina, the black oak, which has much broader, deeply lobed leaves and differs greatly in acorn cups, bark, and other characteristics. The easily recognizable hybrid, which bears the name × Q. leana, has often been noted as an occasional isolated tree, and in some regions considerable numbers of hybrid and hybrid derivative trees have been seen (W. H. Camp, oral communication). Quercus coccinea, the scarlet oak, resembles Q. velutina more closely than does Q. imbricaria, and although the two species are sufficiently distinct over much of their range, in some areas, such as the Atlantic coastal plain of Long Island and southeastern Massachusetts, intermediate types are almost as frequent as trees typical of one or the other species. Furthermore, in the coastal plain of New Jersey and probably elsewhere the populations of Q. velutina contain genes from Q. marilandica, the blackjack oak. It is likely, therefore, that most of the geographic and other variability of Q. velutina has resulted from hybridization and introgression of genes from other species, as is discussed in Chapter VII. Turning to the white oaks, an even more marked degree of intergradation has been noted by

Hampton (Trelease 1924) and by E. Anderson (oral communi‑cation) between *Q. bicolor,* the swamp white oak, and *Q. macro‑carpa,* the bur oak, both of the central United States. It is re‑markable that these two species, although they occur sympatri‑cally over most of their geographic ranges and inhabit rather similar ecological sites, should be able to intergrade so freely and nevertheless retain their identity.

In Europe, the species of *Quercus,* though extremely variable, cannot be segregated into well-marked geographical races or sub‑species (Ascherson and Graebner 1913, pp. 445–544). Of the 15 species recognized by Ascherson and Graebner, at least 12 occur sympatrically in parts of the Balkan Peninsula. The three most variable species are the closely interrelated group, *Q. robur, Q. sessilis (Q. sessiliflora),* and *Q. lanuginosa.* Hybrids between all three of these species have been reported as frequent by numerous botanists from many parts of Europe, and there is some evidence that triple hybrids occur, involving all three species. Further‑more, forms intermediate between the hybrids and their parental species are frequent in many places, so that many forms have been considered by some specialists to be of hybrid derivation and by others as merely aberrant forms of the parental species. Salisbury (1940) has given an account of the ecological relation‑ships between *Q. robur* and *Q. sessiliflora* in Hertfordshire, England. In this region, the soil preferences of the two species are different, and hybrid trees are frequent along the zone where two types of soil meet. The same hybrid was studied in Denmark by Hoeg (1929), who noted also trees intermediate between the hybrid and its parents. Studies of chromosome behavior in meiosis showed perfectly regular, normal conditions in the par‑ental species, but in several trees of an intermediate type Hoeg found irregularities typical of interspecific hybrids, such as lag‑ging univalent chromosomes and tetrads with extra nuclei.

One interesting feature of the progeny of both artificial and natural oak hybrids is that in respect to vegetative characteristics they usually segregate so sharply that even among a relatively small number of individuals the parental types can be recovered (MacDougal 1907, Ness 1927, Coker and Totten 1934, Allard 1942, Wolf 1938, 1944, Yarnell 1933, and Stebbins, unpublished). This is in striking contrast to the behavior of interracial and inter‑

specific hybrids in most other plant groups, in which the number of genetic factors controlling the differences between them is so large that it is relatively difficult to recover the parental types (Müntzing 1930a, Goodwin 1937, Winge 1938, Jenkins 1939, etc.). The evidence available suggests that the number of genes by which species of oaks differ from each other is considerably smaller than it is in the case of most other plant groups.

Palmer (1948) has presented a complete list of the hybrid oaks of the United States, compiled from the extensive references in the literature, but based also on his own experience with them in nature over a period of many years. He has pointed out that although hybrids may be expected between almost any two species belonging to the same section, nevertheless they always form a very small percentage of the total population. They are most often found near the edge of the geographic range of a species, where it is rare and related species are more common. He has concluded that this rarity is due, not to the difficulty of producing interspecific hybrids, but to the small chance which the hybrids have of becoming established. This conclusion is borne out by the results of Pjatnitzky (1946a,b) from experiments on artificial cross-pollination of several different species. He obtained in every case a rather low percentage of acorns set, but this was also true in pollinations between members of the same species. A noteworthy fact is that some intersectional crosses, such as *Q. macranthera × robur* and *Q. macranthera × alba*, gave higher yields of acorns and seedlings than did the maternal parents when pollinated with their own species. Pjatnitzky was even able to obtain a type of hybrid not known at all in nature, namely, one between the subgenera *Lepidobalanus* and *Erythrobalanus* (*Q. robur × borealis maxima* and *Q. macranthera × borealis maxima*). These seedlings, though vigorous, have apparently not yet reached maturity, and no data are available on their fertility.

In *Quercus*, therefore, we have a rather large number of species, many of them polytypic, which are often capable of exchanging genes with other, morphologically distinct populations occurring in the same region and in similar habitats. These sympatric populations have always been kept apart as distinct species, but some of them, such as *Q. bicolor* and *Q. macrocarpa*, behave genetically more like subspecies. The correct systematic treat-

ment of such a variation pattern is a difficult problem, and it may be remarked that other genera, for instance, *Ceanothus* (McMinn 1944), and probably *Vitis,* are essentially similar to *Quercus.* The great evolutionary possibilities of such situations will be discussed in Chapter VII.

PATTERNS IN THE FAMILY COMPOSITAE

In the great family of Compositae, three genera will be discussed, all of which have recently been studied with the use of quantitative and analytical methods. The first is the genus *Wyethia,* monographed by Weber (1946). This consists of 14 species, all deep-rooted and large-flowered perennials, native to the arid and semiarid regions of the western United States. The four species counted have the basic haploid chromosome number $x = 19$. Only one, *W. scabra,* is recognized as polytypic, but in three others, *W. angustifolia, W. ovata,* and *W. arizonica,* the presence of variant forms is noted. In the most primitive of the three subgenera, subg. *Agnorhiza,* the six species are allopatric and markedly different, as well as distinct from each other. In the other two subgenera, *Alarçonia* and *Euwyethia,* each species is wholly or partly sympatric with at least one other of the same subgenus. When two such species occur together, occasional hybrids between them are found. Although these are fertile, they rarely produce enough offspring in nature to form extensive hybrid swarms, and even when two species are completely sympatric, like *W. helianthoides* and *W. amplexicaulis,* they completely retain their identity. Such small groups of hybrids as are found have probably resulted from recent spreading of the species in range lands overgrazed by cattle. *Wyethia,* therefore, presents a pattern of mostly homogeneous, sharply differentiated species which form occasional hybrids when they come in contact with each other. This situation is not uncommon in the higher plants.

The next genus to be discussed, *Layia,* is one of the most thoroughly investigated cytologically and genetically, as well as systematically, of any of the plant kingdom, but only part of these investigations have been published (Clausen, Keck, and Hiesey 1941, 1945a, 1947). It contains 13 diploid and one tetraploid species. Of the diploids five — *L. platyglossa, L. chrysanthemoides, L. gaillardioides, L. pentachaeta,* and *L. glandulosa* — are

polytypic, while the others are genetically rather homogeneous and of limited geographic distribution. Interspecific hybridization, which has been attempted in nearly every possible combination, has in many cases been completely unsuccessful and in others has yielded hybrids of various degrees of sterility and reduction in chromosome pairing. The results of these hybridizations are summarized in Fig. 7.

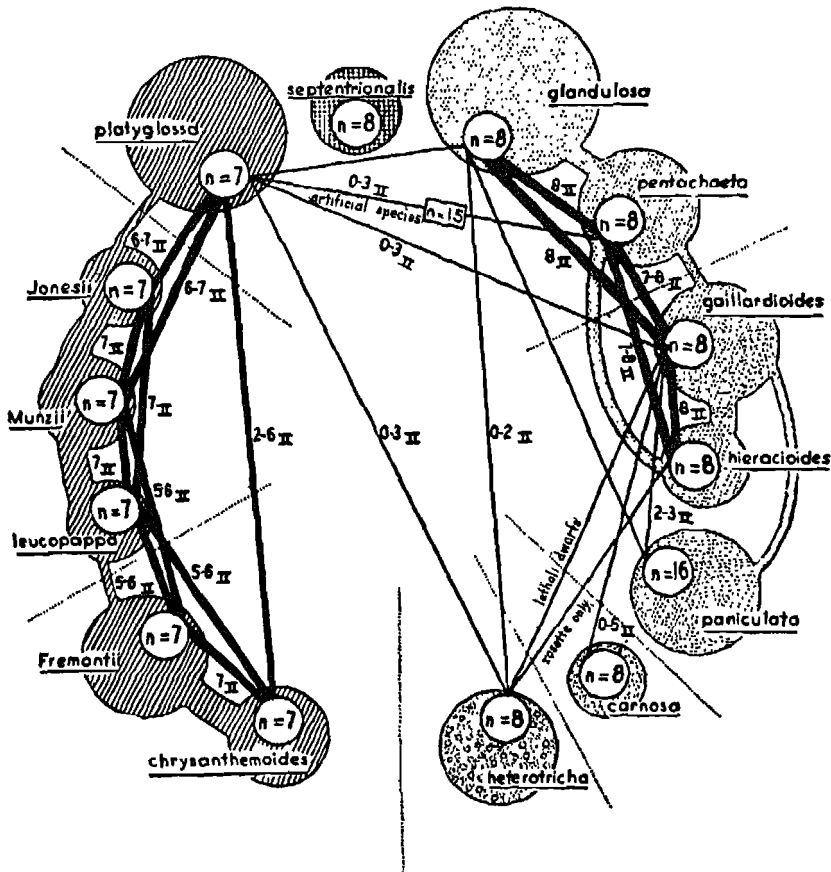The pattern of species relationships in *Layia* is in some respects

FIG. 7. Relationships in the genus *Layia*. The circles represent species, with chromosome numbers indicated; shaded connections show degrees of genetic affinity, and width of solid black lines represents degree of chromosome pairing in interspecific hybrids. The dotted lines indicate major morphological breaks in the genus. From Clausen, Keck, and Hiesey 1941.

different from that found by Clausen, Keck, and Hiesey (unpublished) in other genera of Madinae, but it is probably similar to that in other genera of annuals which make up a large proportion of the California flora. The presence of closely related species in adjacent areas and occupying habitats known to be geologically recent, along with genetic barriers in various stages of development, suggests that *Layia* is in an active state of relatively rapid evolution.

The genus *Crepis* is the most thoroughly studied of the larger genera of angiosperms. The monumental work of Babcock (1947) on this genus shows a remarkable insight into the genetic evolutionary processes that have been operating in it. With the exception of the polyploid, apomictic species of North America, the bulk of the species are diploid and form an aneuploid series with the numbers $x = 7, 6, 5, 4$, and 3. Of the 196 species recognized by Babcock, 97 are known to be diploid, and 78 are probably so. Of these 175 diploid species, only 18 are recognizably polytypic. The best known of these is *C. foetida* (Babcock and Cave 1938), which has three subspecies, within some of which local varieties and forms have been recognized.

The possibility is remote that any appreciable number of the species of *Crepis* are actually allopatric subspecies of more comprehensive species, as Mayr (1942, p. 122) has suggested may be true of plant genera. In 22 of the 27 sections into which Babcock has divided the genus, the majority of the species are either sympatric or with overlapping distributions, and natural hybrids between them are rare or unknown. Of the five sections with predominantly allopatric species, the one which has been investigated genetically possesses complete barriers of genetic isolation separating its species. The species of the four other sections are morphologically at least as sharply distinct from each other as are species of *Crepis* known to be separated by reproductive isolating mechanisms; hence, it is unlikely that they represent subspecies under any criterion.

Jenkins (1939) has described an example of four allopatric, insular endemic species of *Crepis* which are separated by imperfectly developed barriers of hybrid sterility and might therefore be considered to be species in the making. It is very likely that there are other similar examples in the genus, but both mor-

phological and genetical evidence indicates that these are un-
common. In another example, *C. pulchra, C. palaestina,* and *C. pterothecoides,* all of which occur sympatrically in Palestine and Lebanon, were found to form fertile or only partly sterile hybrids (Babcock 1947, p. 150). These are apparently separated from each other by barriers of ecological or seasonal isolation (see Chapter V). •

In *Crepis,* therefore, the great majority of the diploid species, though somewhat variable, are not polytypic in the sense that they consist of well-marked subspecies which replace each other geographically or ecologically. And when studied, they have been found to be separated from each other by more or less well-developed barriers of reproductive isolation, which differ in character according to the group investigated. The processes which have given rise to these barriers, and to the alteration in chromosome number and morphology which is one of the most distinctive features of the genus, will be discussed in later chapters.

THE FAMILY GRAMINEAE

The fifth family to be discussed here, the Gramineae, probably has the highest proportion of polyploid species of any family of angiosperms. The only genus containing more than a few species which is strictly diploid is *Melica.* This genus was studied cytologically and systematically by Boyle (1945), while Joranson (1944) has investigated representative hybrids between closely related species. Of the 18 North American species, all of which have the somatic chromosome number $2n = 18$, only two are polytypic, and these contain only two subspecies each. Three very closely related species, *M. imperfecta, M. torreyana,* and *M. californica,* have been artificially crossed. They form almost completely sterile hybrids, so that gene exchange between them is impossible or nearly so. The systematic treatments of the Eurasian species in such standard floras as those of Hegi, Ascherson and Graebner, and Komarov indicate that the variation pattern in them is similar to that in North America, except that *M. ciliata* and its relatives apparently form a polytypic species with more subspecies than are found in any North American species. The South American Melicas are less well known, but apparently similar. *M. papilionacea* is probably polytypic, but few, if any, of

the others are. *Melica,* therefore, in contrast with most other genera of grasses, consists mostly of homogeneous or only slightly variable species which are sharply separated by barriers of genetic isolation.

In another genus, *Bromus,* the subgenus *Bromopsis* consists in western North America mostly of diploid species. Two of these, *B. ciliatus* and *B. orcuttianus,* have at least two subspecies, but the others — *B. kalmii, B. porteri, B. laevipes, B. grandis, B. vulgaris,* and *B. suksdorfii* — appear to be homogeneous. Morphologically these species are rather similar, and for the most part they replace each other geographically except for smaller or larger regions of overlap. They might be taken for well-marked subspecies were it not for the fact that hybrids have been made connecting the majority of them, and all these hybrids are completely or almost completely sterile (Stebbins, unpublished). The variation pattern in this section of *Bromus,* therefore, is similar to that in *Melica,* except that the species are less sharply defined in characteristics of external morphology.

GENERAL CONCLUSIONS

This survey of ten genera of seed plants belonging to five families scattered throughout the system of classification and phylogeny may be summarized as follows. Four of them — *Wyethia, Crepis, Melica,* and *Bromus* subg. *Bromopsis* — contain a majority of homogeneous or variable, but not polytypic, species, but in every case a larger or smaller minority of the species consists of two or more geographically separated subspecies. In *Crepis, Melica, Bromus,* and probably *Wyethia,* genetic diversity exists in the form of variants distinguishable when grown side by side under uniform conditions and occupying somewhat different habitats. These are ecotypes in the original sense of Turesson, but they cannot be recognized as subspecies because they are not distinguished by morphological differences recognizable over a geographic range of any extent. The recognized species, whenever investigated, have been found to be separated by well-marked barriers of reproductive isolation. These barriers are of a diverse nature, but the partial or complete sterility of pollen or seed in F_1 hybrids is the most common type.

Of the remaining six genera three, *Paeonia, Delphinium,* and

Layia, contain polytypic and homogeneous species in about equal proportions. In *Paeonia,* barriers of hybrid sterility between the species are very well developed, but in *Delphinium* they are rather weak. In only three of the ten genera, *Quercus, Aquilegia,* and *Potentilla* subg. *Drymocallis,* are the majority of the species polytypic. But it is noteworthy that the woody genus discussed is of this type. What is known of the woody genera of temperate regions, such as *Acer, Fraxinus, Populus, Vaccinium, Ceanothus,* and *Diplacus,* indicates that the pattern found in *Quercus* is typical of such genera (see Chapter VI). A notable feature of this pattern is not only the fact that the species are mostly wide ranging and polytypic; in addition the good species, even those having ranges that coincide almost completely, often form fertile F_1 hybrids. The isolating mechanisms best developed are of an ecological nature and operate through the failure of most hybrid derivatives to become established.

The generalization emerging from these examples, as well as from the additional ones given in Chapters V to XI, is that we cannot apply uncritically the criteria of species which have been developed in one group to the situations existing in another, particularly if the groups are distantly related to each other and have very different modes of life. This generalization applies with particular force to attempts of zoologists to reinterpret the species which have been recognized by botanists, or of the latter to use their yardsticks of species on animal material. General principles of systematics, as well as of evolution, must be based on as broad a knowledge as possible of different groups of plants and animals.