

Variation
and Evolution
in Plants

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CHAPTER I

Description and Analysis of Variation Patterns

ORGANIC EVOLUTION has through the ages produced a multitude of kinds of living things. Biologists now consider this to be a statement of fact, not a theory. Therefore, our first understanding of evolution must obviously come from an intimate knowledge of the array of diverse living organisms which it has produced. Two cardinal facts stand out about this diversity. First, by and large, no two individuals are exactly alike. Second, organisms can be grouped into "kinds"; races, species, genera, families, and higher categories. These categories can be recognized because groups of individuals resemble each other more than they do members of other groups. The hierarchy of categories is a multidimensional pattern of variation in nature, and the gaps or discontinuities in this pattern give reality to the various categories.

The general outlines of this variation pattern are familiar to everyone. The word "oak" means to us one of a group of trees which have certain characteristics in common: heavy bark; hard wood; wide branching; leaves of various shapes; and acorns in the fall. We distinguish between kinds or species of oaks, such as the red oak, the white oak, the live oak, and the blue oak, by recognizing still other similarities and differences in groups of characteristics: shape of tree; persistence or fall of the leaves in winter; size, shape, and lobing of the leaves; shape and manner of growth of the acorns and acorn cups. When we learn to recognize different kinds of oaks or any other type of plant or animal, we are analyzing nature's pattern of variation in terms of its individual dimensions, that is, the characters by means of which the various categories are distinguished.

EXPLORING AND CHARTING PATTERNS OF VARIATION

The evolutionist, therefore, must be familiar with the science of classification, or systematics. The fund of information built up by systematic botanists and zoologists during the past three hundred years is the first source of his factual data. Nevertheless many systematists, even in modern times, have not adopted a point of view or a method of attack on their problems which is acceptable to the scientist interested primarily in evolution. The reason for this lies partly in the complexity of nature's pattern of variation. Not only are there hundreds of thousands of different kinds or species of plants and animals; in addition the individual differences by which we could recognize and distinguish between them, even if we confined our attention to a small group of related species, are numbered by the score. Our minds are well equipped to compare two or three objects on the basis of a number of characteristics, or several individuals on the basis of one or two characteristics, such as size, color, or general form. But in order to analyze fully nature's pattern of variation we must compare thousands of individuals on the basis of scores of characteristics.

If the reader wishes to grasp the magnitude of this task, let him try to form an accurate mental classification of a roomful of twenty or thirty people on the basis of even five or six individual characteristics, such as sex, height, stoutness, color of hair, color of eyes, and prominence of nose. If he starts by classifying all the individuals in the room on the basis of two characteristics, such as sex and color of hair, he can quickly arrive at a good generalization, such as that the group consists of about one half men and one half women, and two thirds of the men have light hair, while only one fourth of the women are blondes. But as he adds the three or four other characteristics, both the difficulty of his task and the complexity of his generalizations increase manifold. And if he starts his classification by considering all six characteristics, he can quickly single out a few striking individuals, such as the short, stout man with light hair, blue eyes, and a snub nose, or the tall brunette with large brown eyes and delicate pointed nose. But as with the other approach, his difficulties increase out of all proportion to the number of individuals added to the classification. If we classify a group of individuals on the basis of only two

characteristics, we can easily form a diagram on paper or in our mind, representing each individual by a dot with a definite position on a field of variation, so that the clustering of the dots represents the pattern of similarities and differences formed by the group, as in Fig. 38 (p. 410). If we use three characteristics, we can make three-dimensional diagrams, which are relatively easy to picture in our minds, but harder to represent on paper. Kern and Alper (1945) have attempted to express variation in a four-dimensional diagram, with somewhat dubious success. A true diagram of the variation pattern in any group, however, would have to contain as many dimensions as there are character differences in the group. Diagrams in eight, nine, or ten dimensions can neither be imagined nor drawn.

It is obvious, therefore, that the entire pattern of variation is so vast and multidimensional that we could not understand it fully even if all the facts about it were available to us. The great problem involved in learning about the variation pattern is not so much the acquisition of additional factual knowledge, but rather the selection of facts to be emphasized, and their proper organization. Most systematists, so that they may recognize quickly and easily a large number of species, solve this problem by a series of short cuts not very different from those which all of us employ for identifying and classifying the objects about us. They focus their attention on a few easily recognized diagnostic or "key" characteristics. The other similarities and differences between individuals and groups are not ignored, but usually they are not carefully observed and evaluated. The effect of this method on the minds of some systematists is to give them a picture of the variation pattern which is accurate and precise in respect to certain characteristics found in the great majority of the individuals of each group, but which is indefinite in regard to its non-diagnostic characteristics, as well as to the nature, frequency, and distribution of those occasional individuals which deviate from the normal combination of characters.

For those systematists whose principal aim is to identify specimens and to place them into a series of species and genera which can be characterized by a set of keys and descriptions, the recognition and use of a few diagnostic key characters is perhaps the most efficient procedure. But the systematist who wishes to find

in the contemporary pattern of nature a clue to the past must consider such diagnostic characters as only the beginning of his study. He must do three things which systematists interested primarily in identification would consider superfluous. First, he must seek as many additional characters as he can. He must be interested not only in those characteristics which are relatively certain clues to the identity of a species but also in those which are usually but not always different in two or more related species, and even the characteristics which show about the same range of variability in each species or subspecies, but in which this variability possesses certain regularities in relation to geographical or ecological factors. Thus, in his study of variation within *Asclepias tuberosa*, Woodson (1947) made a careful and illuminating analysis of leaf size, even though he was reasonably certain that the three subspecies under investigation did not differ significantly from each other in this respect. Second, the systematist interested in evolution must find ways of estimating variation quantitatively, both in respect to single characters and to the relationship between characters. For this purpose, the accepted methods of statistics and biometry are ideally the best; but, as will be pointed out later in this chapter, the evolutionary systematist cannot always obtain factual data suitable for such statistical treatment. He can, however, resort to a number of relatively crude diagrams and indices which provide a greater degree of precision and communicability than the intuitive judgment relied on by many systematists. Third, he can never obtain a reliable understanding of evolution in his group unless he is able to analyze at least partly the factors responsible for its variation pattern. In particular, he needs to know how much of the variation between individuals is due to environmental causes rather than genetic causes, as well as something of the different cytological and genetic processes which have been operating in the group. As stated clearly by Turrill (1936a, 1938a, 1940), the modern botanist who wishes to employ systematics as a tool for studying evolution must be thoroughly grounded in genetics, cytology, and ecology, and must integrate the evidence from all these fields in approaching his problem.

The need for an amplified taxonomy for dealing with problems of evolution has been recognized by the better systematists ever

since the acceptance of Darwin's theory. But in recent years the rise of genetics, which deals with the relationships between groups of organisms in an entirely different way, has opened up new opportunities to the student of systematics and evolution, and therefore has brought to the fore the need for synthesizing and combining the approach to evolutionary problems from these two disciplines. This has produced discussions of "The New Systematics" (Huxley 1940), of "Alpha and Omega Taxonomy" (Turrill 1938b), and of proposed new disciplines such as "experimental taxonomy" (Clausen, Keck, and Hiesey 1940), "biosystematy" (Camp and Gilly 1943), and "genonomy" (Epling 1943). All these proposals are too new to be properly evaluated at present. With descriptive taxonomy of the traditional sort as his foundation, the evolutionist can explore each of the proposed new methods, both descriptive and analytical, and decide which of them is best suited to the problem which he has at hand. Their ultimate integration and evaluation must be carried out over a period of many years by the cooperation of scientists with different points of view and training who can nevertheless understand each other.

The reader might ask at this point why a book which is intended to discuss the principles and dynamics of plant evolution should devote a major part of its first chapter to a description of methods of investigation. The answer is that our impressions of all scientific phenomena are largely the result of the methods which we use to investigate them, and this is particularly true of such complex phenomena as the variation pattern of living organisms in nature. This book is written chiefly for those who are carrying out or intend to pursue research connected with evolution, a subject which covers a large proportion of the field of biology. For these readers, the writer wishes to repeat a bit of advice which has often been given to scientists. Your understanding of general principles and hypotheses will be sound only if you select the best methods for obtaining facts relating to these hypotheses and are fully aware at all times of the weaknesses as well as the strong points of the methods which you have adopted. This point of view should be held not only in relation to your own research but also in your judgment of the work of others.

OLD AND NEW MORPHOLOGICAL CHARACTERS IN THE HIGHER PLANTS

The classification of the vascular plants has been based traditionally on the characteristics of gross external morphology. Among these characteristics there is usually an ample number which serve the purpose of delimiting species and genera, and in most groups the systematist interested only in identification need not go beyond them. On the other hand, evolutionary studies must make use of all the significant character differences, and these include many features of internal anatomy, as well as of the individual cells. For this reason, one of the chief ways in which systematic studies are being amplified for evolutionary purposes is through the increased use of anatomical, histological, and cytological characteristics.

The most outstanding example of the use of anatomy and histology in conjunction with gross morphology and distribution to elucidate the evolutionary phylogeny of a group is the long series of cooperative studies which have been carried on at Harvard University on the woody members of the Ranales (Bailey and Nast 1943, 1945, 1948, Nast and Bailey 1945, 1946, Smith 1945, 1946, Swamy 1949; see these for additional references). This study of the most primitive living angiosperms has up to the present brought forth convincing evidence to support the following conclusions. The group includes a high proportion of species which on the basis of all characteristics must be placed not only in monotypic genera but even monogeneric or digeneric families. They are obviously relict types of which the close relatives have long since become extinct. Furthermore these families, as well as the genera within one of the largest of them, the Winteraceae, are not progressive stages in either one or several separate lines of adaptive radiation. Their interrelationships are more nearly reticulate, with most of the species specialized in one or more characteristics, but primitive in others. The significance of this conclusion in relation to the chromosome numbers found in the primitive angiosperms is discussed in Chapter IX (p. 363). Furthermore, both the stamens and the carpels of these primitive groups are clearly seen to be modified sporophylls. Finally, distributional studies show that the genera and species are at present strongly concentrated in eastern Asia and Australasia, and at least one family, the Winteraceae, may have radiated from the

latter center (Smith 1945). This family was dispersed through the Antarctic regions, while others, such as *Cercidiphyllaceae*, the *Trochodendraceae*, and probably the *Magnoliaceae*, were Holarctic in distribution. The Winteraceae do not support Wegener's hypothesis of drifting continents. The concrete results obtained from these studies show that similar investigations will contribute greatly to our knowledge of relationships and evolutionary tendencies in the higher plants. The rapid technique described by Bailey and Nast (1943) of making cleared preparations for anatomical study from herbarium specimens has made such investigations practical on a much larger scale than previously. Stebbins (1940b) and Babcock (1947), using a somewhat cruder method, found that the evidence from comparative anatomy of the flower contributed greatly to an understanding of relationships and phylogeny in *Crepis* and its relatives.

Histological characters have been found useful in determining relationships and probable phylogeny by a number of workers. Stebbins (1940b) found that various species and genera of the tribe *Cichorieae*, family *Compositae*, are characterized by the presence or absence of sclerenchymatous tissue at the summit of the ovary and by the type of crystal, whether simple or aggregate, found in the ovary wall. Avdulov (1931) showed that in the family *Gramineae* the evidence on generic and tribal relationships obtained from cytology is much more in accord with that obtained by Harz from a study of the types of starch grains and by Duval-Jouve and others from the distribution of the chlorophyll-bearing parenchyma of the leaf than it is with the evidence from gross morphology which has traditionally been used to subdivide the family. In addition Prat (1932, 1936) has shown that the histology of the leaf and sheath epidermis of grasses likewise provides evidence which agrees with that from the starch grains, chlorophyll tissue, chromosomes, and geographic distribution, while Reeder (1946) has obtained additional concurrent evidence from a study of the embryos of some genera. In the highly important grass family, therefore, the present evidence indicates that histological and cytological characteristics provide more certain clues to the true affinity of genera than do those of the gross external morphology of the inflorescence (including spikelets and flowering scales) which are the basis for the traditional sys-

tems of classification of the family. The use of epidermal characteristics, particularly trichomes, can undoubtedly be expanded. These have been for many years considered of value by students of the oaks and of the mustard family (Cruciferae), while Rollins (1944) has found that in the genus *Parthenium* of the family Compositae two species, *P. argentatum* and *P. incanum*, differ so strikingly from each other in the shape of their epidermal trichomes that the nature of these structures provides the most reliable clue to the identity of natural hybrids and hybrid derivatives involving them. Finally, Foster (1945, 1946) has shown that the sclereids of the leaf tissue provide a valuable clue to racial differentiation in *Trochodendron aralioides* and are highly characteristic of species and species groups in the genus *Mouriria* of the Melastomaceae.

Pollen grains in many instances provide valuable additional characteristics for determining relationships, as has been shown by a number of investigators, particularly Wodehouse (1935). In some instances they may provide additional evidence for phylogenetic trends, as in certain primitive genera of the Compositae, tribe Cichorieae (Stebbins 1940b). A most ingenious and promising use of pollen grains for investigating phylogeny was worked out by Covas and Schnack (1945). They found that within a group of related species, such as the genus *Glandularia* of the family Verbenaceae, the size of the pollen grain is closely related to the distance which the pollen tube must traverse from the stigma to the ovules. The longer the style, the larger is the pollen grain; which is an obvious adaptation in providing the pollen tube with sufficient food to reach its destination. Nevertheless, although the ratio (size of pollen grain/length of stigma) is constant for the different species of a genus, and sometimes for the genera of a family, it varies greatly from one family to another. Furthermore, those families which on morphological grounds are usually considered primitive most often have a high ratio, indicating unusually large pollen grains, while the more advanced families, such as the Verbenaceae, Labiateae, and Scrophulariaceae, tend to have smaller ones. Covas and Schnack have suggested that this reduction in the relative size of the pollen grains is a phylogenetic tendency associated with the development of more efficient metabolic processes in the more advanced families, which makes

possible the securing of energy for the growth of the pollen tube on the basis of a relatively small amount of stored food. This tendency, if true, is so fundamental that it needs further exploration from the standpoint of comparative physiology as well as of comparative morphology.

CYTOLOGICAL, SEROLOGICAL, AND DISTRIBUTIONAL CHARACTERS

The cytological characteristics which have been most widely used in recent years in connection with systematic studies are those of the chromosomes. A full account of this work is presented in Chapter XII. In the present discussion, however, the fact should be noted that the chromosomes, since they are the bearers of the hereditary factors, are in a class apart from other structures. Some chromosomal studies, particularly those which merely describe the number and external morphology of the somatic chromosomes, do no more than provide the systematist with additional morphological characteristics. But studies of polyploidy in conjunction with external morphology as well as geographical and ecological distribution can be analytical rather than descriptive to the extent that they may make possible the formulation of hypotheses as to the particular evolutionary processes which have been at work in the group concerned. These hypotheses, furthermore, can be tested experimentally, as discussed in Chapter IX. Even more in the nature of analysis are studies of chromosome behavior at meiosis, particularly in artificial and putative natural interspecific hybrids, as discussed in Chapters VI and VII. Chromosomes, therefore, can provide merely additional systematic characters or they may afford the best means which we have of analyzing many of the cytogenetic processes which are going on during the evolution of a group.

An additional characteristic for comparing species and families which is based on biochemistry rather than on morphology or histology, but which nevertheless is descriptive rather than analytical in nature, is provided by serodiagnostic studies of differences in proteins. Such studies were carried out on a large scale by Mez and his associates (Mez and Siegenspeck 1926) and resulted in the formation of an entire phylogenetic tree. Mez's results have been accepted by some, but severely criticized by other botanists. Some attempts to repeat the work have produced

results largely in agreement with those of Mez, but other such attempts have not. The entire subject has been reviewed and discussed in detail by Chester (1937). The technique, which involves the injection of plant proteins into an experimental animal and the detection of the production of antibodies by that animal, is so unfamiliar to most botanists that they cannot evaluate it. According to Chester, the interpretation of the serological results is only partly objective and may in some instances be obscured by precipitation reactions not related to the antigenic properties of the plant sera. The techniques involved can be handled only by experienced biochemists and so are out of the reach of most botanists. Furthermore, the interpretation of the results to determine phylogenetic relationships requires the assumption that changes in protein specificity always proceed at the same rate in relation to other types of evolutionary change, or at least in relation to the amount of genetic and cytological change which is taking place. For such assumptions there is as yet no evidence, either positive or negative.

Since protein specificity is undoubtedly one of the important foundations of the differences between species and other groups of organisms, we can safely assume that studies of this specificity by serodiagnosis or any other method will eventually shed much light on such differences. In animals, the work of Irwin, Cole, and their associates on species and racial crosses in pigeons (see Dobzhansky 1941, pp. 85-87) has shown the value of such studies in analyzing the differences between closely related species. Investigations of this nature on similar groups of plant species would undoubtedly be very rewarding. In the opinion of the present writer, they would be a necessary prelude to the much more difficult task of analyzing the interrelationships between families and orders on this basis.

Finally, descriptive systematics is being amplified by additional data on the distribution and ecological relationships of groups of organisms. Distributional studies have always been an essential part of taxonomy, but in recent years they have become increasingly thorough and illuminating. Modern collectors are paying more attention than ever to careful notes on the environment of the plants which they are gathering, so that many herbarium labels are miniature essays on ecology. The inclusion of distribu-

tional maps of each species discussed is becoming standard practice for monographers, and the correlation of these distributions with the geological history of the regions concerned is an accepted procedure. The importance of such information to students of evolution is obvious. These approaches are discussed further in Chapter XIV, and have been thoroughly reviewed from the evolutionary point of view by Cain (1944).

QUANTITATIVE METHODS IN DESCRIPTIVE SYSTEMATICS

For the systematist interested in evolution, the study of additional morphological characteristics, even such fundamental ones as those of the chromosomes and geographic distribution, is only the beginning of his amplification of taxonomy over the minimal knowledge needed for identification. The next step in descriptive systematics is to obtain as complete a quantitative picture as possible of the variation within species, both in respect to individual characters and to the relationship between different characteristics. Emphasis must be placed not on the similarity between the individuals of a species in respect to certain diagnostic "key characters," but on the fact that in any sexually reproducing, cross-fertilized species no two individuals or populations are exactly alike. Furthermore, we must realize that some of this variation within species is more or less at random, while variation in other characteristics follows regular geographic patterns, which may or may not be associated with the pattern of variation between species.

As was stated at the beginning of this chapter, the pattern of variation which exists in any widespread species is so complex and multidimensional that it cannot be analyzed in its entirety. On the basis of preliminary exploration the investigator must decide what parts of this pattern are likely to provide the most significant information on the evolution of the group concerned, and he must then select the methods which will enable him to obtain this information as efficiently as possible. Three types of approach have been most frequently used for this purpose. One is the intensive study of one or two separate characters, particularly those which show geographic regularities of distribution, or clines (Huxley 1938, 1939, Gregor 1939). The second is the study of the interrelationships of morphological characteristics, through dia-

grams, numerical indices, or statistical methods. The third is the intensive study of the greatest possible number of both morphological and physiological characteristics of a relatively small series of samples of the species population, as is now the standard practice in the field of experimental taxonomy. These methods will be discussed in turn.

The advantage of studying variation in respect to single characteristics is that by this means large numbers of individuals can be examined and the samples treated diagrammatically as well as statistically with relative ease. When we realize that the total population of most species is numbered in hundreds of thousands or more often in millions of individuals, and that consequently a sample consisting even of thousands of specimens can rarely be more than a few percent or even a fraction of a percent of the total, we see that this advantage is not inconsiderable. This type of study, however, requires great care both in selecting characteristics to be studied and in obtaining the sample of the species population or populations to be investigated. The characters should be those which, as a result of previous systematic studies, are known to be significant in separating species or subspecies, or those which are known to have or are suspected of having regularities of geographic distribution which might be connected with the adaptive qualities and the evolutionary history of the species concerned. The selection of characters easy to observe and measure, such as flower color (Epling and Dobzhansky 1942), possesses obvious advantages in respect to efficiency, but is not essential. Woodson (1947) obtained valuable information about variation within *Asclepias tuberosa* by studying two angles of rather complex derivation, one indicating the degree of attenuation of the apex of the leaf blade and the other, the shape of the leaf base.

The sample of any species population most readily available to a systematist is that found in the larger herbaria. Although this will yield valuable information, it rarely is wholly suitable for quantitative studies of variation within species. As Woodson (1947) has pointed out, herbarium specimens are never a random sample of the species population, since they have been collected in great numbers near the centers where universities and botanical gardens are located, as well as in national parks and other points of interest, while many intervening areas have been sampled little

or not at all. Furthermore, most herbarium specimens consist of only one or a few individuals from any locality and therefore cannot give a picture of the range of variation in a population, a type of information which is of the utmost importance in interpreting some of the genetic processes which may be taking place. The investigator will therefore be forced to make for himself additional collections designed to obtain a more even sampling of the range of his species and to show something of the variability at any one locality.

For the latter purpose, Anderson and Turvill (1935) and Anderson (1941, 1943) have advocated making mass collections in which a few critical parts of 25 to 50 or more individuals from each locality are pressed and kept together as a unit. The term local population samples, adopted by Woodson (1947), seems to the present writer more descriptive and appropriate. The statistical work of Gregor, Davey, and Lang (1936) on *Plantago* has served to emphasize the importance of securing a comparable part of each plant. Lewis (1947) has shown that in *Delphinium variegatum* the variation on the same individual plant from year to year in respect to the number of lobes per leaf may be greater than that found in an entire population sample. On this ground, he concluded that data obtained from population samples alone may give a very distorted picture of variation, a picture less accurate than that provided by the average series of herbarium specimens. There is little doubt that studies of a small number of population samples will give an accurate picture of a variation pattern only when combined with parallel studies of a good herbarium collection of the usual type, as well as with observations of the amount of variation induced by the environment, made either on cultivated representatives or on the same wild colony during several successive years.

Once the collections have been made and the individual data recorded, the data must be presented in such a fashion that they may be understood and evaluated as readily as possible, with a minimum amount of personal bias. For simple measurements, the well-known statistical constants, namely, the mean, the standard deviation, the coefficient of variability, and the chi-square test for the significance of differences between groups, should be used whenever appropriate. Erickson (1943, 1945), in his study of

Clematis fremontii var. *richlini*, has shown how the variation pattern of one relatively restricted entity can be recorded almost in its entirety by the use of such statistical methods, and has on this basis been able to demonstrate regularities of geographic distribution of individual characters within an area as small as 400 square miles in habitats which are essentially uniform ecologically. Data like these are essential for an understanding of such evolutionary factors as the rate with which genes may be spread through populations and the effects of isolation on populations of different size. The significance of such problems is discussed by Dobzhansky (1941) and in Chapter IV, below.

Statistics are clearer to most readers when accompanied by diagrams. Simple histograms or curves effectively illustrate the frequency distribution of the variants within one sample with respect to a single character, while two-dimensional "scatter diagrams" like those presented in Fig. 38 (p. 410) are equally effective for showing the relationship between two characteristics in a sample. The geographic variation of a single character, or of the frequency in the populations of one or more distinct morphological types, can be shown on a map in a number of different ways, as has been done by Dobzhansky (1924), Fessett (1941, 1942), Miller (1941), McClintock and Epling (1946), Woodson (1947), and others. None of these methods has been used often enough to permit judgments of which is the most generally effective. At present, the investigator should be aware of their advantages and weaknesses, as well as of the possibility of devising improvements over all of them.

For studying the more complex problem of the interrelationship between characteristics in the variation pattern various methods have been devised, the suitability of which depends upon what the investigator wishes to learn about the populations concerned. Of the numerous problems which center about the interrelationship between characteristics, those most frequently met and most likely to be clarified by quantitative methods are the following. First, within any species population, what characteristics are correlated with each other, either with respect to the variation at any locality or to the geographic distribution of the variants, or both? Second, can two species populations which are known to be separated by barriers of physiological or genetic

isolation (see Chapter VI), but which cannot be absolutely distinguished on the basis of any single characteristic, be distinguished on the basis of a combination of characteristics? Third, how can we estimate the relative amount of difference or similarity between a series of three or more different categories (species, genera, or families) on the basis of several unrelated morphological characteristics? Fourth, how can we estimate the degree of distinctness or the amount of intergradation between two populations on the basis of several characteristics?

The first problem, that of correlation, is relatively simple if only two characteristics are involved. Statistically, it can be solved by the correlation coefficient; and it may be represented diagrammatically by two-dimensional scatter diagrams. When three or more varying characteristics are involved, however, the problem becomes much more complex. Multiple correlations form a difficult statistical problem, and diagrams in three or more dimensions are difficult to construct and even more difficult to interpret. Here the best solution is to use visual methods, in which the particular characteristics to be studied are presented as simply and directly as possible, with the irrelevant characteristics either not illustrated at all or made inconspicuous.

Photographs of a series of leaves or flowers of the different individuals to be compared are often highly successful, particularly if care is taken in the arrangement and lighting of the specimens to be photographed, so that the observer can compare as easily as possible the particular characteristics to which his attention should be drawn. Examples of this technique may be seen in the work of Anderson and Whittaker (1934) on *Urticaria*, of Anderson (1936b) on *Iris*, of Clausen, Keck, and Hiesey (1940) on *Potentilla* and other genera, of Erickson (1945) on *Clematis*, and many others. When the plants or plant parts to be studied differ from each other in a large number of characteristics that are difficult to define or measure, such photographs provide the most satisfactory means of demonstrating with a minimum of personal bias the variation in these characteristics.

Another way of representing several different characteristics so as to permit easy comparison is the use of simple line diagrams, or ideographs. The floral diagrams of classical taxonomy are good examples of these, since they illustrate simply and effectively the number of sepals, petals, stamens, and carpels possessed by a

family or genus, as well as whether these parts are free or united, and similar traits. As Anderson and others have shown in a number of studies, such diagrams may be adapted in an endless number of different ways, depending on the ingenuity of the investigator. They may represent the shape of a tree (Fassett 1943), the branching and internode pattern of an herb (Anderson and Whitaker 1934), the shapes and relative sizes of the sepals and petals of a flower (Anderson 1936b), or even a complex of characters taken from the leaves, inflorescence, calyx, corolla, and seeds (Epling 1944; see Fig. 1). Anderson (1946) has shown that the

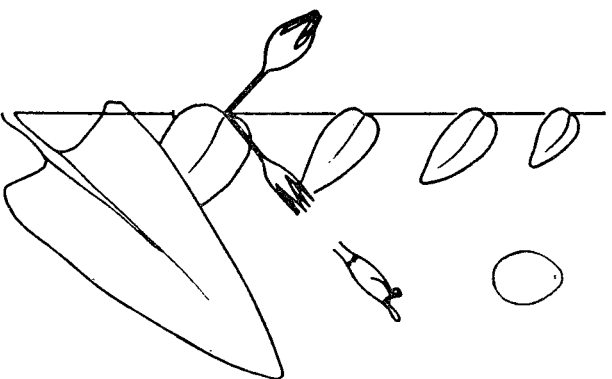


FIG. 1. Ideograph showing the average measurements of the important diagnostic characteristics of a subspecies of the genus *Lepechinia* (Labiateae), constructed from a series of measurements of the various parts. From Epling 1944, by permission of the University of California Press.

correlation between the shape and size of various structures among the variant individuals of a population can be shown by superimposing ideographs representing the shape upon a graph in which the ordinates and abscissae represent certain size measurements (Fig. 2). Diagrams of this type are termed pictorialized scatter diagrams (Anderson 1949).

The second question—that of distinguishing entities on the basis of a combination of characters—was answered in the affirmative by Anderson and Whitaker (1934) in their study of *Urtularia grandiflora* and *U. perfoliata*. These two closely related species, which both occur together in the forests of the eastern

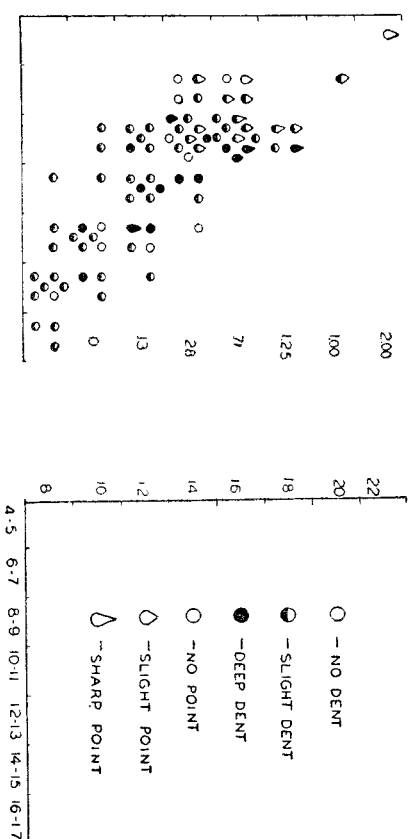


FIG. 2. At left, diagram showing the mean values in respect to four different characteristics of a series of collections of maize from Mexico. The position of each symbol on the vertical scale represents the mean number of rows of kernels per ear for that collection; its position on the horizontal scale represents the mean width of the kernel. At right, explanation of the symbols. From Anderson 1946.

United States, cannot be absolutely distinguished from each other on the basis of any single diagnostic characteristic. There are, however, at least 14 characteristics of the stems, leaves, and flowers by which a large proportion of the plants of one species can be distinguished from those of the other, and if a particular individual is examined for all of these, it can be placed in one or the other species with a reasonable degree of certainty. The reason for this is that the characters under consideration vary independently within each species, so that any individual of *U. grandiflora* which resembles *U. perfoliata* in a character such as the number of nodes below the lowest branch of the stem is typical of its own species in all or nearly all of the other characteristics, such as number of flowers, leaf shape, flower size, the character of the perianth segments, and the length of the style.

Anderson and Whitaker devised a crude numerical index by which each individual could be rated according to several characteristics with less danger of personal bias than that resulting from purely subjective judgments. This index can be used only if all the characteristics selected have about the same range of variation in the two species and if they all vary in the same direction. Nevertheless, they obtained by this method a series of values for *U. grandiflora* which was entirely distinct from the range of values for the same index in *U. perfoliata*, although in every single

character from which the index was compounded the ranges of values for the two species were found to overlap. Fisher (1936) demonstrated statistically the soundness of the postulate that two entities can be separated on the basis of a combination of characteristics even when no single characteristic entering into this combination is sufficient, and he devised a more precise, but statistically much more complex, index. This is termed the linear discriminant function, and is discussed further by Hoel (1947).

The third problem, that of deciding which of several entities are more similar to and which are more remote from each other, is basic to the task of grouping species into genera, as well as to the delimitation of higher categories. The most common procedure of systematists when faced with this problem is either to use an intuitive judgment based on long experience with the group concerned or else to follow a few well-marked and presumably fundamental diagnostic or "key" characteristics. The first method has the disadvantage of being almost impossible for other systematists to interpret or to repeat, while the latter inevitably leads to a certain amount of artificiality. Anderson and Abbe (1934) have devised a method of estimating the "aggregate difference" for this purpose, which serves to systematize and standardize the subjective judgments of the monographer. The same purpose is served by representing the values for each of the groups concerned on a polygonal graph, as recommended by Hutchinson (1936) and Davidson (1947). This method has the advantage of showing not only which entities are the most similar and which the most different but also the particular characters which are most alike, and to a certain degree the amount of correlation between characteristics.

The fourth problem, that of obtaining and systematizing evidence on intergradation between subspecies or, more usually, species, was attacked by Clausen (1922) on *Viola arvensis* and *V. tricolor* and by Raunkiaer (1925) on *Cynoglossus monogyna* and *C. oxyacantha* by tabulating the characteristics of a number of individuals in various natural populations. This method is long, cumbersome, and difficult to follow. Anderson (1936c) has devised a much simpler and neater method of systematizing judgments on possible natural hybridization. This he has called the hybrid index. It is discussed with illustrations in Chapter VII. The third type of quantitative approach to the study of the

variation pattern is well exemplified by the monographs of Clausen, Keck, and Hiesey (1940, 1945a) on experimental studies of the nature of species. These combine quantitative descriptive accounts of both external morphology and physiology with analysis of the environmental and genetic basis of the variation observed. They are therefore discussed in the next section, under analytical methods for studying variation.

The fact is obvious that each of these three approaches has its advantages and limitations. The first permits a relatively complete degree of sampling, but is obviously inadequate to explain the nature of variation in the organism as a whole. The study of the interrelationship between characteristics is more satisfactory in this respect, but it still provides only a part of the information needed for an interpretation of variation in terms of evolution, and it involves highly complex problems of methodology, which at present can be solved only on the basis of subjective judgments, however systematized. Furthermore, no descriptive study of variation in phenotypes is satisfactory unless something is known about how much the environment contributes to this phenotypic variation and how much of it is actually due to genotypic variation. This point will be discussed more fully in the next section and in Chapter III. On the other hand, complete descriptive and experimental studies of variation are so laborious and time-consuming that they can never be carried out on more than a small sample of the species population and therefore cannot be relied on as the only source, or even the principal source, of our knowledge about variation. Ideally, all three of these approaches should be made on the same groups, and the results should be integrated and compared before evolutionary interpretations are made.

ANALYZING THE VARIATION PATTERN

The final and most essential stage in the study of variation, that of analysis, should be begun while observational, descriptive studies are still in progress. Four different methods of analysis are commonly used in the higher plants. The first of these methods is transplantation of different genetic types into a uniform habitat, so that the effects of differences in the environment on the phenotype are eliminated, and the genotypes of different individuals, varieties, and species may be compared directly. The earliest experiments of this sort were the classic ones of Gaston

Bonnier, but they were carried out under such poor conditions of cultivation that their results and the inferences drawn from them are completely unreliable (Hiesey 1940). On the other hand, Turesson (1922a,b), Gregor (1938a, 1939), Gregor, Davey, and Lang (1936), Clausen, Keck, and Hiesey (1940), Turrill (1940), and others have shown by careful transplant experiments that in all the species studied plants adapted to different habitats are usually different genetically, so that they remain different in appearance even when grown side by side. This is the basis of the ecotype concept of differentiation within species, which will be discussed in the next chapter. Constant-environment gardens are now standard procedure in the experimental analysis of species, as well as in the application of this work to the practical task of reforestation, soil conservation, and revegetation of depleted stock ranges.

A refinement of the transplant technique has been developed with great success by Clausen, Keck, and Hiesey (1940), as well as by Turrill (1940) and his associates. This consists of dividing a single large perennial plant into several parts and growing these clonal divisions under different environmental conditions. By this method important physiological differences between closely related types have been discovered. Some genotypes have a constitution which renders them very plastic, so that their phenotype may be greatly altered by the environment, while others are much more rigid and can be modified little or not at all. These authors, as well as Anderson (1929), working with *Aster anomalus*, and Brainerd and Peitersen (1920), working with *Rubus*, showed that the vegetative parts of the plant can be modified much more by the environment than the flowers and fruits, thus confirming experimentally the common belief of taxonomists that the latter organs are generally more reliable as diagnostic criteria to separate species and other categories. Turrill (1936a) and his coworkers, using similar methods, have also shown that some species, like *Centaurea nemoralis*, are relatively little modified by the environment, while others, like *Plantago major*, are extremely plastic.

A probable solution to a problem which has puzzled systematists for some time is provided by Goodwin's (1941, 1944) uniform garden studies of *Solidago sempervirens*. This species of goldenrod, which is found along the seashore of the Atlantic

coast from Newfoundland south to Florida, flowers in August in the northern end of its range and progressively later as one goes southward, so that in Florida it flowers in November. This situation is typical of wide-ranging, fall-blooming plants and is at least in part adaptive, since if the plants bloomed late in the northern regions they would be killed back by frosts before maturing their seeds. Early blooming in the south is a probable disadvantage also, because of the hot weather prevailing in the summer months. Goodwin found that when plants collected respectively at Ipswich, Massachusetts, Ocean City and Point Lookout, Maryland, and Fort Myers, Florida, were grown under uniform conditions at Rochester, New York, those from Massachusetts flowered earliest, those from Maryland next, and the Florida plants latest. The Florida plants could, however, be made to flower relatively early by covering them with hoods of heavy black cloth from late afternoon until early morning, thereby subjecting them artificially to day lengths of nine to ten hours, according to the well-known method of Garner and Allard. It is evident, therefore, that the three races studied differ genetically in physiological factors affecting their reaction to photoperiodism, or day length. This leads to the hypothesis that *S. sempervirens* and other fall-blooming species consist of a large number of different genetic types, each with a photoperiodic reaction which adjusts it to a time of blooming most favorable for its particular habitat.

A second and related method of analysis is the progeny test. For this purpose, seed of single representative individuals of a natural population are gathered and planted under uniform conditions. This provides valuable evidence on the degree of homozygosity or heterozygosity of the plants in question, and therefore of the amount of variation which they can produce by segregation and recombination, without the occurrence of new mutations. If the species is predominantly self-pollinated, the progeny grown under uniform, optimum conditions will be very much alike. The progeny of a single plant of a cross-pollinated species will, on the other hand, be very variable, but this variability will be limited by the size of the population and the conditions under which it is growing. For instance, Hiesey, Clausen, and Keck (1942) found that plants of *Achillea borealis* from a large colony (San Gregorio, California) growing under favor-

able conditions produced very variable offspring and were apparently highly heterozygous. On the other hand, progeny from individuals growing in a small population on an exposed coastal bluff (Bodega, California) were much more nearly uniform. This indicates a much more severe action of selection in the latter locality (Fig. 3).

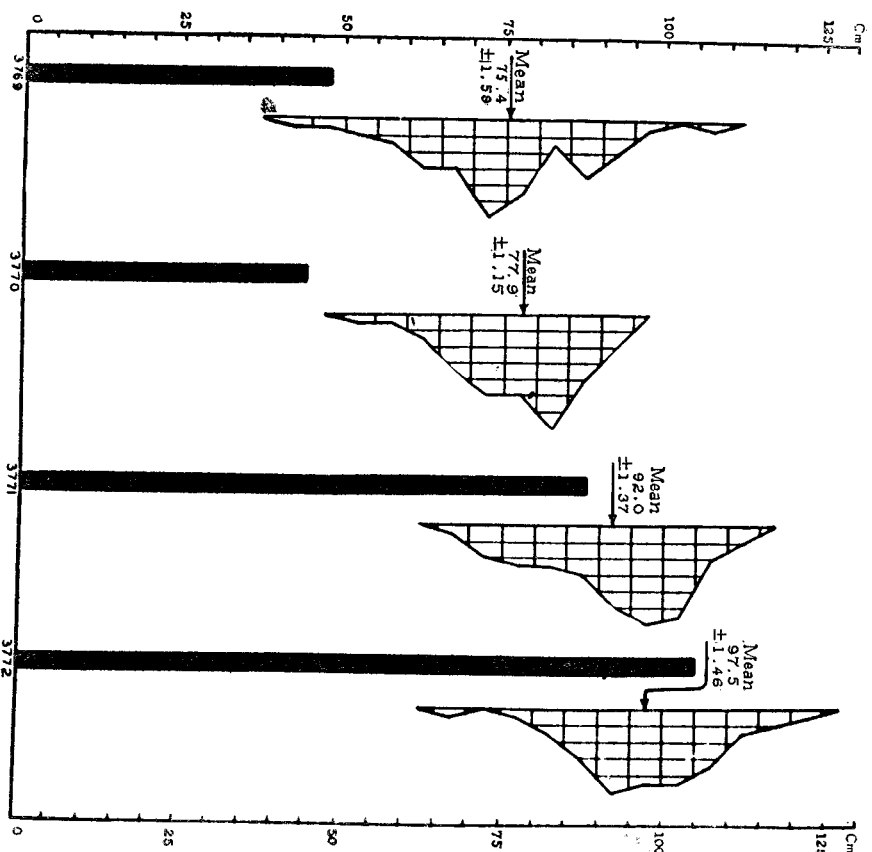


FIG. 3. Diagram showing the variability in the progeny of four different plants of *Achillea borealis* from central California. Black columns show the height of the parent plants in their native habitat; frequency curves, the variation in height of their offspring at Stanford. From Hiesey, Clausen, and Keck 1942.

The progeny test is particularly useful in testing the hybrid nature of individuals which appear to be intermediate between two species or subspecies. A well-known example of the use of

this method is the work of Anderson (1936a) on *Abocynum*. In this case a taxonomist, Dr. R. E. Woodson, separated a series of specimens into three groups, identified respectively as *A. androsæmifolium*, *A. canabinum*, and *A. medium*, the latter of which he suspected of being a collection of F_1 hybrids between the two former, or of F_2 and backcross types derived from them. The geneticist Anderson then grew progeny from each of these plants and sent flowering and fruiting specimens to Woodson for identification, but did not reveal their parentage. All the progeny of typical *A. androsæmifolium* and *A. canabinum* were identified as belonging to their own species, but among those of *A. medium* were individuals identified as *A. androsæmifolium* and *A. canabinum*, as well as those referable to *A. medium*. There is no doubt, therefore, that in respect to the characters considered diagnostic by taxonomists, *A. medium* segregates in the direction of one or both of its putative parents, and its hybrid nature is very likely.

In long-lived woody plants, in which testing putative hybrids by artificial crossing of the supposed parents is particularly difficult because of the long time involved, progeny tests of seedlings are often of great value. In the genus *Quercus*, for instance, the hybrid nature of *Q. heterophylla*, which is intermediate between the very distinct species *Q. phellos* and *Q. borealis maxima*, was verified by this method (MacDougal 1907). The writer has used it successfully to verify the occurrence of hybridization between the California blue oak (*Q. douglasii*) and the Oregon oak (*Q. garryana*) first noted by Epling (Dobzhansky 1941, p. 259). Seedlings of intermediate trees collected with their parents in a grove west of Kenwood, Sonoma County, California, were grown beside progenies of typical *Q. douglasii* and *Q. garryana*. The latter are relatively uniform and quite distinct from each other, but the seedlings from intermediate trees included segregates strongly resembling both parents, giving good evidence of their hybrid nature. In a similar experiment designed to test the hybrid nature of a population of aberrant trees resembling the black oak, *Q. kelloggii*, the seedlings closely resembled those from a typical representative of that species, so that the aberrant character of the parental trees must be ascribed to causes other than hybridization. Other examples of the use

of the progeny test for demonstrating segregation in hybrid trees are those of Henry (1910), Allard (1932), and Yarnell (1933).

The ultimate analysis of both species differences and species barriers is obtained by artificial hybridization, accompanied by careful cytological and genetical studies of the F_1 hybrids and their progeny, if any are produced. Unfortunately, this method is possible in only a limited number of groups which are easily raised and in which the plants are not too large or the generations too long. Furthermore, as should become evident from material to be presented in later chapters, the relation between visible, external differences between species and the extent and nature of their genetic and cytological differences varies so greatly from one group to another that one rarely can make inferences about those groups which are impossible to grow in cultivation on the basis of results obtained with those which can be cultivated.

We should be forced to conclude, therefore, that in a large majority of plant genera a clear picture of species interrelationships can never be obtained, were it not for the fact that nature often makes experiments for us. Spontaneous hybrids between plant species are by no means uncommon, and in just those types in which they are most needed, namely, shrubs and trees, they are particularly large, long-lived, and easy to recognize. Nevertheless, no plant can be considered a hybrid after mere casual inspection. Hybrids must be distinguished from plants representing a primitive, intermediate species or subspecies, from aberrant types which may segregate from a population near the periphery of its geographic range, and from members of different species which have converged because of recent mutation. This requires careful analysis, of which the most important steps are as follows. Whenever two related species occur in the same territory, this region should be carefully searched for intermediate individuals. If none are found, this is in itself evidence that the two species are separated by some efficient isolating mechanism, or a system of them. As described in Chapter VI, many types of isolating mechanisms exist, and while some of them, like seasonal isolation, are easy to detect in the field, most of them are not. Plants appearing at first glance to be intermediate between two species should be carefully compared, character by character, with both parents. Since most morphological differences between species of plants

depend on multiple factors rather than single genes and show relatively little dominance, the hybrid can be expected to be intermediate between its parents in nearly every character. Consequently, the larger the number of characters in which a particular plant can be found to be intermediate between its putative parents, the greater is the probability of its hybrid origin. Often the microscopic appearance of certain specialized cells is particularly diagnostic, as in the leaf trichomes of *Parthenium argentinum* and *P. incanum* (Rollins 1944). For evaluating systematically a large number of such differences the numerical hybrid index (described in Chapter VII) is of great value.

The morphological examination of the putative hybrid must be followed by as thorough a cytological and genetic analysis of it as is possible. A study of chromosome behavior at meiosis will be decisive if the parents differ in the number and structure of their chromosomes. But even if meiosis is normal, the fertility of both pollen and seed should be studied. If the plant is completely healthy and growing in company with its putative parents, then the discovery of a high proportion of well-filled pollen grains in the latter and 50 percent or more of empty ones in the suspected plant is strong evidence that this plant is a hybrid between two forms that are partly isolated from each other genetically. Low seed set is a much more hazardous criterion, since seed sterility can be caused by self-incompatibility or "self-sterility" and is much more subject to environmental influences than is abortion of the pollen. Finally, if morphological evidence suggests intermediacy in all or a majority of characters and the plant is fertile enough to produce seed, then a progeny test will give the crucial criterion of genetic heterozygosity for the characters which separate the species. If one or two hybrids of a particular combination have been subjected to such a careful analysis, then others of this combination can be detected with relative ease, and the collective hybrid indices of populations expressed graphically gives a rough but reasonably reliable estimate of the amount of gene interchange taking place between the two parental species populations. This is valuable both in determining the systematic position of the populations concerned and in leading toward an analysis of the isolating mechanisms which have promoted their divergence.

This completes our brief survey of the combined use of descriptive and analytical methods in studying the interrelationships of a group of species. It must be clearly understood not only that both these approaches are essential to an understanding of the evolutionary processes at work within a group of organisms but that they also require diligent, careful work and a meticulous attention to accuracy of detail which can never be overlooked. It is just as misleading and reprehensible to speculate on the degree of relationship between species or on their phylogeny on the basis of subjective examination of a series of herbarium specimens as it is to speculate on chromosome numbers and polyploidy when no counts have been obtained or to revise generic, species, or varietal names on the basis of cytological data alone, without careful studies of the traditional systematic nature. Combined attacks of this sort are often most successful when carried out by a group of cooperators, but in this case it is essential that the systematists, the cytologists, and the geneticists be not only sympathetic with the aims and methods of their coworkers in the other fields, but in addition it is necessary for them to have a good understanding of the scope and the limitations of these methods. Too often the cytologist looks to the systematist merely to give him a reliable, unchanging name for the form on which he is working; while the systematist in turn hopes that the cytologist will give him a precise tag, which he can add to his list of diagnostic key characters, thereby enabling him to make infallible diagnoses of his species. Unfortunately, however, the more thorough study of nature's variation pattern reveals that fickle Dame Nature has very different ends in view from that of making neat hierarchies of species and genera which naturalists can file away tidily in cabinets with the least possible trouble.

The relation between the various approaches to the study of variation may be illustrated by the following analogy. The pattern of variation among organisms may be likened to the topography of the earth's surface. The races, species, and genera are the various eminences, mountain peaks, and mountain ranges, while the gaps between them are the canyons, the gorges, and the valleys. The study of any part of the earth's surface has three stages. First come the explorers, who in a general way and with the crude methods at their disposal find the approximate location,

height, and breadth of the mountain peaks, the depth and direction of the major valleys, and the trend of the mountain ranges. When the mountains of the region are similar in height, are separated by broad valleys, and are grouped into ranges that run straight and parallel to each other, the job of the explorers is easy. But if the topography is very rough and irregular, they must leave many purely geographical problems unsolved. The next step is the surveying of this partly known region. Exact distances and heights are obtained by triangulation, meridians and bench marks are established, and contours expressing the exact steepness and direction of the slopes of each mountain are established by means of careful observation with appropriate instruments. The third stage, that of geological study, must either follow or partly accompany the surveying process. Not until the geology is known can anything be really understood about the past history of the region in question.

The descriptive phases of systematics and cytology are analogous to exploration and surveying. They are essential preliminaries to all further study of evolution, but in themselves can never do more than suggest lines of attack and provide tentative working hypotheses for analytical studies. The simpler its evolutionary history, the more easily can the "topography" of a genus (that is, its species and subspecies) be recognized by descriptive methods. But even in these simple groups, the degree to which we can consider that we understand the evolution of a group depends to a large extent upon how many of our hypotheses and predictions are verified by experimental analysis.

Moreover, in difficult groups having a confused "topography" resulting from a complex evolutionary history, descriptive methods alone are never sufficient, even to provide a basis for recognizing biologically valid species or subspecies. Some descriptive systematists, dealing with the flora of a well-known region, often turn to the difficult or critical groups, such as *Rubus*, *Rosa*, *Lupinus*, *Antennaria*, *Hieracium*, and *Poa*, hoping that their intuition, insight, and creative ability will enable them to improve on their predecessors who have studied the same or similar series of herbarium specimens. In this they are wrong. For various reasons, which will be discussed in detail in Chapters VIII-XI, these groups are intrinsically complex in their variation patterns,

and repeated studies by the traditional descriptive methods can scarcely serve to lessen the confusion in our knowledge about them. Such genera can be understood only with the aid of analytical techniques, supplemented by quantitative descriptive studies.

On the other hand, the student of evolution must not place undue emphasis on the problems presented by these critical groups. Most of them are difficult because of the presence of polyploidy, apomixis, structural hybridity, or some other complicating factor. From the broader viewpoint of the evolution of all living organisms, these are not generally distributed and significant evolutionary processes, but are more like excrescences or rococo decorations on the fundamental framework of the variation pattern. It is a basic principle of science that we can learn much about normal phenomena from studies of the abnormal, but it is equally true that we must know thoroughly the familiar, everyday situations. The basic facts about variation and evolution are most likely to be learned from studies of simple, diploid species, like the studies of Gregor (1938a, 1939) on *Plantago maritima*, of Clausen, Keck, and Hiesey (1940) on *Potentilla glandulosa*, of Epling (1944) on the genus *Lepechinia*, of Erickson (1943, 1945) on *Clematis fremontii* var. *richlii*, and of Woodson (1947) on *Asclepias tuberosa*.

SOME PRINCIPLES OF VARIATION

Before systematic units or their patterns of variation can be studied intelligently, certain basic principles about their nature must be clearly understood. These are as follows.

First, all taxonomic entities, including varieties or subspecies and species as well as genera and higher categories, are not simple units, but complex systems of populations. This fact, though obvious to anyone who really knows species as they grow in nature, is often overlooked both by systematists and geneticists whose experience has been confined to herbarium specimens or garden cultures. Some systematists have based their philosophy on the superficially simple statement, "if two things are different, they should be described as different species." The fatal weakness of this philosophy is that these workers never form, even in their own minds, a clear conception of what they mean by the "things"

or by "different." Usually the "thing" is conceived as a carefully selected type specimen plus a series of other specimens or vaguely remembered living plants which share with the type a series of easily recognized diagnostic characters. And the "different thing" is another group of specimens which for one reason or another do not fit the key characters established for the first "thing." Once the variation pattern in almost any group of species is understood, the fact becomes clear that any two individuals, populations, or series of populations of a sexually reproducing, cross-fertilized organism are somewhat different from each other, and that if the systematist is to produce a classification which will help him understand the evolution of his group, he must find out as nearly as possible which differences are biologically significant and what is the nature of the groups which they separate.

Second, any population will be constant for some characters and highly variable for others. In genetic terms, this means that in any population some genetic factors are present in 100 percent of the individuals, while the gene frequency for other factors may have any value down to a fraction of a percent. Conversely, any character or group of characters may be constant in one population and variable in other populations of the same species or subspecies.

From these two principles follows the corollary that populations must be compared in terms of differences in the frequency of qualitative, "presence or absence," characters and in the modal or mean values of quantitative characters. A second corollary is that all differences between populations are multidimensional; that is, they exist in several different characters, and the degree of difference is never the same in any two characters. Populations, therefore, should be compared in respect to an aggregate of differences, and it is for this reason that the graphs and indices described earlier in this chapter are valuable.

The third principle, and the most important one for the systematist, is that when series of populations are compared, they may often be separated into two or more groups on the basis of discontinuities in certain characters. In terms of "presence or absence" characters, this means that the frequency of the character is very low in some populations and very high in others, and that intermediate frequencies do not exist. For instance, in one group

of populations the percentage of individuals with hairy sepals may vary from 0 to 20 percent, while in another, 80 to 100 percent of the individuals may have hairy sepals, and populations containing intermediate percentages of hairy-sepaled individuals may be rare or absent. In quantitative characters, a discontinuity between two groups of populations will consist of the absence or scarcity of certain intermediate values between the contrasting series of mean or modal values found in the two groups. Taxonomic categories are based on these discontinuities between series of populations. No matter how great and numerous are the differences between certain individual plants, they cannot be segregated into biologically significant subspecies, species, or other categories unless the populations to which they belong are separated as wholes by at least partial discontinuities in several characters.

TAXONOMIC CATEGORIES AND THEIR GENETIC SIGNIFICANCE

The integration of systematics and genetics, which is essential for a true understanding of the variation pattern in nature, is possible only if workers in both fields have a full understanding of and a reasonable amount of agreement on the terms used by both themselves and their colleagues to describe the phenomena of variation. This cannot be accomplished by discarding or redefining the terms now used in either discipline or by inventing new terms. The terminology of both disciplines has grown up in response to the need for describing phenomena in a certain way, and therefore both sets of terms have their own value. They should be retained as parallel series, each fitted for describing certain natural phenomena on the basis of a particular type of evidence. The following discussion will attempt to give as nearly as possible the genetic significance of the most useful taxonomic terms, and vice versa.

The fact that no two populations are exactly alike would make possible the recognition of a limitless number of categories below the rank of species. Practically, the number and nature of the categories which are to be recognized depends largely on convenience, that is, how many such categories give us a clear picture of the variation in the group concerned. The experience of most plant systematists, as well as their zoological colleagues, has been

that the recognition of intraspecific units of several degrees of rank, such as subspecies, variety, subvariety, and form, produces more confusion than order. Units of one rank, termed subspecies by all zoologists and many contemporary botanists, are enough to express the great majority of the biologically significant intraspecific variation that can be comprehended by anyone not a specialist in the group. The English term variety, as well as its Latin equivalent *varietas*, is often used in nearly the same sense. But these terms have been used in a number of different ways by systematists, horticulturists, and others, so that they lack the precise connotation that is usually attached to the term subspecies. The subspecies or geographic variety is a series of populations having certain morphological and physiological characteristics in common, inhabiting a geographic subdivision of the range of the species or a series of similar ecological habitats, and differing in several characteristics from typical members of other subspecies, although connected with one or more of them by a series of intergrading forms. The only difference between this definition and that accepted by most zoologists is that in plants, which are more closely tied to their habitats than animals, two subspecies of the same species are more likely to coexist over the same territory, but are likely to be at least partly isolated from each other by habitat preferences. This is well illustrated by *Potentilla glandulosa*, which is discussed in Chapter II.

In applying the subspecies concept, the systematist cannot adhere too rigidly to certain diagnostic "key characters." After all, the characteristics which enable a plant to grow in a particular region or habitat are chiefly intangible ones, such as root growth, seasonal rhythm, transpiration rate, photosynthesizing ability, preference for certain soil types, and so forth. Some of the diagnostic characters, such as leaf size, height, and pubescence, contribute to this adaptation, but others do not, and are merely associated with the adaptive complex for one reason or another, as discussed in Chapter IV. Moreover, since different subspecies may interbreed and exchange genes, and since mutants simulating a distantly related subspecies may occasionally become established, individuals may occur which have all or nearly all of the adaptive characteristics of one subspecies, but certain diagnostic characteristics of another. Goldschmidt (1940, pp. 54-55) has given

a graphic account, based on actual experience, of the errors which a systematist made when confronted with such individuals. For this reason, the assigning of individuals to a subspecies should always be done on the basis of as broad a knowledge as possible, and the locality and habitat in which the plant grew should be given as much if not more consideration than any particular morphological characteristic which the plant might possess.

In addition to the subspecies, another infraspecific unit, the form or forma, is used by some plant systematists. As a category, this has no genetic or evolutionary significance, since it consists of all of those individuals which possess in common some conspicuous aberration from the norm of the species or subspecies. Typical examples are white-flowered forms of a species which normally has colored flowers, and lacinate-leaved forms of a species with entire-margined leaves. The recognition and listing of such artificial categories in manuals and local floras is useful to botanists working in a limited area and with limited facilities, as it points out to them the relatively minor significance of plants which might otherwise be given undue attention because of their conspicuousness. Furthermore, the population geneticist may find in such conspicuous forms, many of which differ from their normal relatives by a single genetic factor, valuable material for a study of gene frequency or even of mutation rates in nature.

The *species*, the fundamental unit of the systematist, has been subjected to more arguments over its proper definition than has any other biological term. In the opinion of the writer, however, the concepts held by those systematists and other biologists concerning the nature of this entity which are expressed by Dobzhansky (1941), Mayr (1942), and Huxley (1940) and his collaborators in the same volume are notable, not for their divergence, but for their essential similarity. All agree that species must consist of systems of populations that are separated from each other by complete or at least sharp discontinuities in the variation pattern, and that these discontinuities must have a genetic basis. That is, they must reflect the existence of isolating mechanisms which greatly hinder or completely prevent the transfer of genes from one system of populations to another. Further consideration of these mechanisms and of the nature of species will be left to Chapter VI, in which the species problem will be taken up in detail.

In discussions of species and infraspecific units, reference must often be made to the fact that they occur in different geographic regions or in the same one. For this reason, Mayr (1942) has established the term *sympatric* for systematic units of which the geographic ranges coincide or overlap, and *allopatric* for those which do not occur together. More recently Mayr (1947) has recognized the difficulties of applying these terms to sedentary species and to those which occupy radically different but adjacent habitats. Nevertheless, they are very useful in general discussions of the relationship between geographic distribution and species formation and so will be employed for this purpose in the present volume.

The categories higher than the species, that is, genus, family, order, class, and phylum, are impossible to describe or to define except in highly subjective terms. This does not mean that they are purely artificial aggregates without biological meaning. On the other hand, the systematist sometimes finds that species fall naturally into clusters which have many characteristics in common and share only a few of these with the most nearly related cluster. In the conifers, for example, most botanists are in agreement over the boundaries of such genera as *Pinus*, *Picea*, *Abies*, *Tsuga*, and most of the others. This is because any species of *Pinus* resembles all other pines much more closely than it resembles any species of spruce, fir, or hemlock, and the same is true for the other genera mentioned. This situation has undoubtedly resulted from the fact that the conifers are a very ancient group and that forms which previously connected the genera have become extinct long ago. In fact, it is likely that most families in which the genera are well defined have suffered the extinction of many species, and further that most boundaries between neighboring genera represent gaps left by species which have perished. If this fact is kept in mind, then the search for natural boundaries to genera has some meaning to the evolutionist and is not entirely a matter of convenience. The recognition of partial discontinuities between genera and of a small number of species frankly transitional between two genera is probably necessary in complex families like the Gramineae and the Compositae. But in any case the boundaries between genera must be drawn on the basis of the largest possible number of

characters rather than one or two conspicuous "key characters," as is now the case in several groups. From the genetic point of view, the separation into different genera of species which intercross and form partially fertile hybrids is particularly unnatural, so that genera like *Festuca* and *Lolium*, *Aegilops* and *Triticum*, *Elymus* and *Sitamon*, and *Zea* and *Euchlaena* in the Gramineae, as well as *Laelia* *Cattleya*, and their relatives in the Orchidaceae, should certainly be united. But this does not mean that species which cannot be intercrossed necessarily belong in different genera. If hybrids can be obtained it is possible to determine the degree of relationship of the parental species. But failure to obtain hybrids may be due to any one of a number of causes, as discussed in Chapter VI, and may have no connection with the degree of genetic relationship between the parental species.

SOME GENETIC TERMS AND THEIR TAXONOMIC SIGNIFICANCE

On the genetic side, the terminology begins with individuals and other units within a population, and on this level was first codified by Johannsen (1926).¹ In the first place, each individual organism has a genotype and a phenotype. The genotype is the sum total of all the genes present in the individual. For any particular locus on a chromosome, the genotype may be homozygous, that is, it may possess identical genes or alleles on the two homologous chromosomes, which are the corresponding chromosomes derived from opposite parents. Or if the two allelic genes at a locus are different, then the individual is heterozygous for that gene pair. The number of genes for which an individual is heterozygous determines the degree of its homo- or heterozygosity.

The most important genetic factor affecting the dynamics of evolution in populations is the degree of homo- or heterozygosity of the individuals composing them. Evidence for this statement is discussed fully in Chapters IV and V. In preparation for this discussion, however, the reader should remind himself of these elementary genetic principles. All the first-generation progeny of a cross between two completely homozygous individuals have

exactly similar genotypes, no matter how different are the two parents. But depending on the degree of heterozygosity of one or both parents of any mating, whether within a population, between varieties, or between species, the genotypes of the offspring will differ from each other to a greater or lesser degree. Homozygous parents produce uniform progeny; heterozygous parents, diverse progeny. Over a period of generations, the maintenance of genetic variability within a population depends either on the constant existence of heterozygosity or on the occasional crossing between homozygotes bearing different genotypes.

The *biotype* consists of all the individuals having the same genotype. Since even a small amount of cross-fertilization will produce heterozygosity and differences between genotypes for at least a few of the hundreds of genes present in any organism, the biotype in cross-fertilized organisms usually consists of a single individual. But in self-fertilizing plants, the individuals may become completely homozygous and produce by selfing a progeny of individuals all with the same genotype, and therefore belonging to the same biotype. The offspring of a single homozygous individual is called a *pure line*, which therefore represents the appearance of the same biotype in successive generations. Pure lines can exist only in self-fertilizing organisms, and they are maintained in nature only if natural selection constantly purifies the line of all new mutations.

When asexual reproduction occurs, either through vegetative means or through seed produced by apomixis, as discussed in Chapter X, several individuals of the same biotype may be produced even if the parent is heterozygous. All asexually produced offspring of an original individual are collectively termed a *clone*. Members of a clone and individuals of a biotype resemble each other in that both consist of many individuals, perhaps hundreds or thousands, having the same genotype and therefore appearing identically with each other when grown under the same conditions. Both clones and biotypes have been classified by some systematists and geneticists as Jordanons, isoreagents, micro-species, or even species. But such terms are more misleading than helpful if they are used for both asexual clones and sexual biotypes, since the genetic behavior of these two entities is entirely different. All the individuals of the same homozygous biotype

¹ The reference is to the third and final edition of Johannsen's well-known text, since here the final word on the terms is given. The original use of most of them, however, dates from the first edition of this text, published in 1909.

produce genetically uniform progenies, unless crossing occurs with individuals of another line. But most clones are heterozygous, because asexual reproduction is most common in groups where cross-fertilization prevails. Hence, when members of a clone do occasionally produce offspring through the sexual process, these are usually very diverse and different from the progeny of any other member of the same clone.

A practical illustration of this point is familiar to gardeners and farmers. If one sows the seed of any plant of a well-selected, purified variety of wheat, barley, tomato, or snapdragon, the seedlings are alike and resemble the offspring of any other plant belonging to that variety. But cultivated varieties of apples, peaches, potatoes, dahlias, or lilies never come true from seed. The latter varieties are heterozygous clones and therefore produce very diverse offspring by the sexual process. Their constancy is maintained entirely by asexual reproduction. Further discussion of these points, with specific examples, is presented in Chapters V and X.

The collective term most widely used in evolutionary genetics is the *population*. This term has no single precise meaning and never denotes a unit which is analogous to any of the systematic categories. That is, whatever the scope of a population, the individuals composing it are grouped together not because they look alike or because they have any characteristics in common, but because they bear a certain temporal and spatial relationship to each other. In sexual organisms, this permits them to intercross. It is true that the members of the same population often resemble each other more than they resemble members of different populations, but this is because they constantly exchange genes and are subjected to similar selective agencies and is not implicit in the concept of the population. In sexually reproducing organisms, therefore, a population may be defined as a group of individuals among which a larger or smaller amount of interbreeding and gene exchange can occur.

This admittedly elastic definition obviously can include groups of individuals of almost any size. Furthermore, Wright (1940a,b, 1943) has emphasized the fact that the effective size of the population, which determines the degree to which its members can interbreed and share each other's genes, is much less than its apparent

size. There are two reasons for this. In the first place, organisms are most likely to mate with, or to receive pollen from, individuals adjacent to them in the population, so that individuals occurring at opposite ends of a large population may be isolated from each other nearly as effectively as if they occurred in separate populations. Secondly, many populations fluctuate greatly in size from generation to generation, and in such populations the effective breeding size is, according to Wright's mathematical calculations, near the minimum size reached.

In large populations divergent evolution of segments of the same population, due to isolation by distance, has been shown by Wright to be at least a theoretical possibility. Wright has, furthermore, attempted to define subdivisions of the population of such a size that this isolation by distance does not occur or is at least a negligible factor. The numerous variables involved here require complex mathematical treatment which cannot be effectively summarized; for further details the reader is referred to the original papers of Wright (1943, 1946).

A series of population units which can be plotted and visualized is illustrated by Erickson's (1945) analysis of the distribution of *Clematis fremontii* var. *riehlii* in the limestone glades of Missouri (Fig. 4). He found that within the local populations or colonies of this species occupying a single glade, groups of plants numbering up to several hundred, which he termed aggregates, were the smallest ones that could be demonstrated to be homogenous within themselves in respect to leaf shape, and possibly differentiated from other such groups. On the other hand, his calculations suggested that differentiation might be effective only between groups of plants numbering about two thousand.

Further discussion of the problem of population size in relation to gene exchange and divergent evolution will be deferred to Chapter IV, after the discussion of selection. The present account, however, should serve to emphasize the difficulties involved in determining the size of the constant N, or effective population size, in any natural population (cf. Dobzhansky 1941, pp. 164 ff.). These difficulties indicate that we must know much more about the actual rate at which genes can spread through populations before we can apply the mathematical models constructed by the theoretical evolutionists like Wright and Fisher to many actual situations in nature.

The concepts embraced by the terms ecotype, ecospecies, and cenospecies (Turesson 1922a, Clausen, Keck, and Hiesey 1939, 1940) are both systematic and ecological, as well as genetic. They can be best defined and characterized in connection with accounts either of the nature of variation within species or of the species problem. Discussion of them is therefore deferred until following chapters.

The methods and concepts discussed in this chapter are the principal tools with which the evolutionist can work at present. The aim of the subsequent chapters will be to describe and to interpret as far as possible the results which up to this time have been obtained by these methods and to suggest further avenues of approach to problems of evolution.

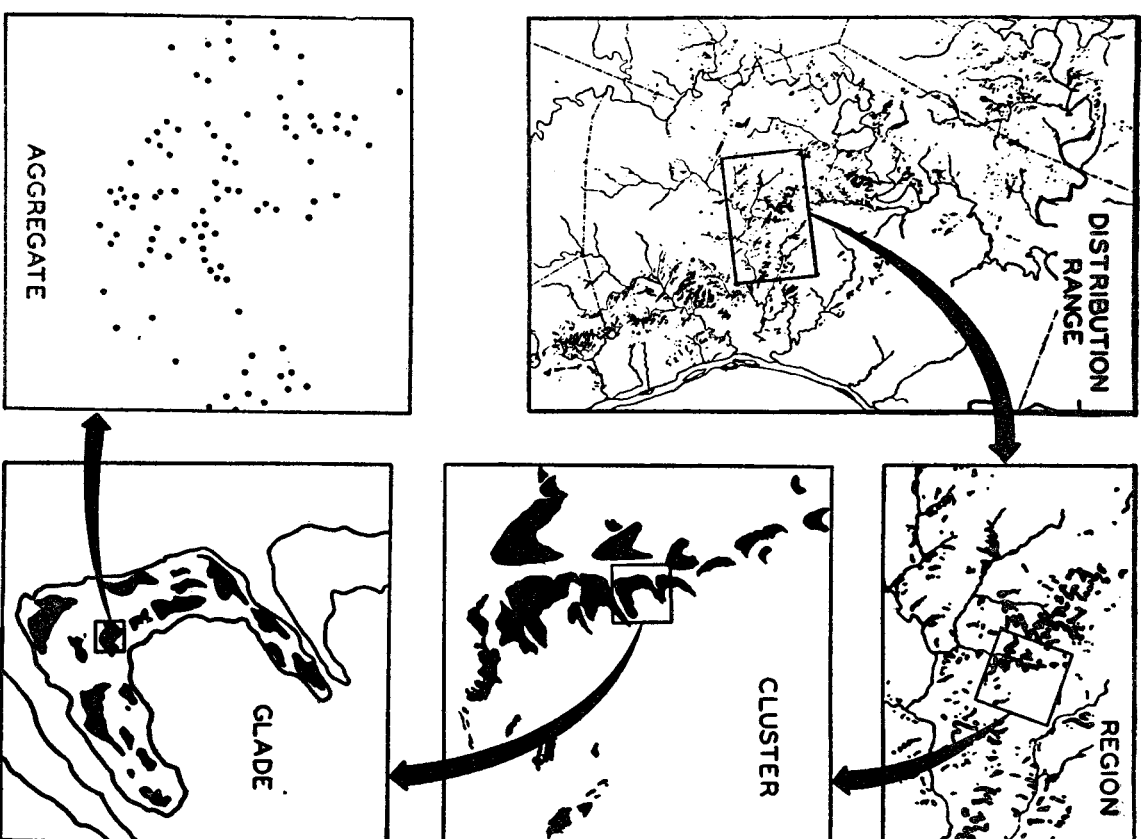


FIG. 4. Diagram illustrating the organization of the distribution range of *Clematis fremontii* var. *ritchii* into a series of subdivisions. From Erickson 1945.