

CHAPTER XIII

Evolutionary Trends II: External Morphology

THE PRESENT VOLUME is concerned with the dynamics of plant evolution in general, rather than with the evolutionary origin and phylogenetic history of any particular group or groups, however important they may be. Nevertheless, certain principles and trends of phylogeny are repeated so many times in various groups of plants that some consideration of them is essential to an understanding of the mechanism of evolution. Fortunately, most of these trends can be seen operating to a small extent even within groups of genetically related species, so that to this degree they are open to study by experimental methods.

Since the trends to be considered in this chapter are those characteristic of the vascular plants, the more primitive and generalized structural features of these plants must first be described. These are now well known in the fossil *Psilophytales* (Eames 1936, pp. 309–331), and the vegetative parts are essentially similar in the modern *Psilotum*. The aerial vegetative parts of these primitive rootless plants are simply branch systems which grow at the tips by means of apical meristems and fork repeatedly at regular intervals. This forking or branching is typically dichotomous, that is, the apical meristems of the two branches are of equal size and grow at the same rate. The parts bearing the reproductive structures are also branch systems, which differ principally in bearing sporangia at their apices. Typically, therefore, the primitive vascular plant is characterized by apical, indeterminate growth and the successive differentiation of similar organs, one at a time.

Very early in the evolution of the vascular plants there developed independently in a number of different lines an organization characterized by the presence of a main axis and a number

of appendages. This is found in nearly all the living vascular plants. Evidence both from paleobotany and from comparative morphology strongly supports the telome theory, according to which the appendages of ferns and seed plants (Pteropsida), whether leaves, microsporophylls, or megasporophylls, are derived

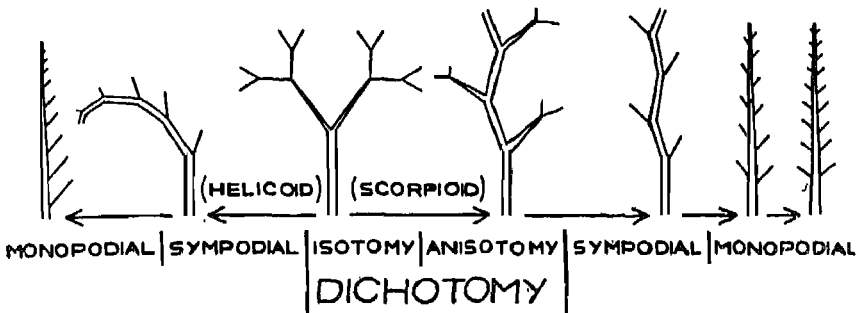


FIG. 45. The main principles of the overtopping process, showing two ways in which a monopodial branch system can evolve from a primitive type of dichotomous branching. From Lam 1948.

from branch systems whose ontogeny has been modified in successive phylogenetic stages by means of reduction of apical growth and fusion of branches (Fig. 46, cf. Zimmermann 1930, p. 67, Bower 1935, Chap. XXX, Eames 1936, p. 348). These three processes of reduction, fusion, and change in symmetry will be discussed in more detail below. In its most generalized form, the shoot-appendage organization of the plant body agrees with the dichotomous branch systems in that organs are differentiated apically and serially, one at a time, but differs in that the meristem undergoes two types of branchings. One of these divides the growing tissue into a portion with finite, determinate growth (appendage) and another with indeterminate growth (continuation of shoot); while the other type, the true branching of the shoot, produces two shoots, each with indeterminate growth (Fig. 45). As Foster and Barkley (1933), as well as Anderson (1937a) have pointed out, the most characteristic feature of plant growth is the constant repetition of similar appendages and similar branches. The spiral arrangement of appendages which is most common in vascular plants is presumably derived originally from a dichotomy in more than one plane (Zimmermann 1930, p. 76).

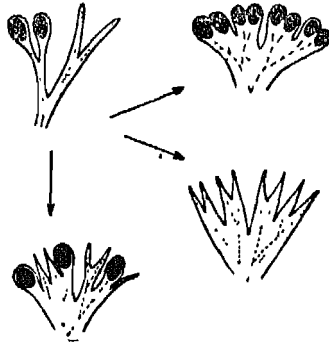


FIG. 46. The main principles of Zimmermann's telome theory, showing the evolution of primitive types of leaves and sporophylls from dichotomous branch systems. From Lam 1948.

SOME COMMON EVOLUTIONARY TRENDS

The great majority of the evolutionary trends toward increased specialization in the vascular plants can be explained as a result of three types of morphological trends, acting either separately or in conjunction with each other. These are *reduction*, *fusion*, and *change in symmetry*.

The most widespread of these trends has been reduction. There is no living species of vascular plant which has not been affected by this trend in one or another of its parts. As mentioned above, the leaves of all ferns and seed plants are reduced from branch systems. In many plants, moreover, reduction has affected the growth of the shoot, reducing in particular the period of growth between the successive differentiation of appendages or the length of the internodes. The limit of this type of reduction is the rosette habit, in which the shoot axis itself is hardly evident and the vegetative part of the plant consists almost entirely of appendages. This has been attained repeatedly in many different phylogenetic lines, such as most ferns, cycads, sedums, dandelions, aloes, yuccas, and a host of others. Another common type of reduction in the vegetative parts of the plants is the conversion of the shoot from an indeterminate one, which produces an indefinite number of appendages and branches, to a determinate one which, after producing a more or less definite number of leaves, either stops growing or starts to differentiate reproductive structures. The best examples of determinate vegetative shoots are the

short shoots of many conifers, in particular the fascicles of needles characteristic of *Pinus*. Determinate vegetative-reproductive shoots are characteristic of many spring-blooming perennial flowering plants, particularly those that grow from rhizomes or corms, like *Trillium*, *Claytonia*, and *Anemone*. They also occur in many annuals, like wheat, oats, barley, and many other crop plants.

Although trends of reduction are common in the vegetative parts of the plant, they are even more characteristic of its reproductive structures. Both the cone or strobilus of gymnosperms and the flower of angiosperms are reduced from shoots or shoot systems. These systems have repeatedly suffered further reduction in both the number and the diversity of their parts and in the structural and anatomical complexity of individual organs. Details of these trends can be found in many books and papers on plant morphology and anatomy (Jeffrey 1916, Goebel 1928, Zimmermann 1930, Eames 1936, Florin 1944a,b). Present knowledge makes possible the generalization that in modern seed plants reproductive organs which are simple in structure and development are many times less likely to be primitively simple than they are to be reduced and simplified from organs which were both structurally and ontogenetically more complex in the phylogenetic ancestors of the modern form. With respect to the angiosperms, we can accept with some assurance the dicta of Bessey (1915), Hutchinson (1926), and others, that apetalous flowers are derived from polypetalous (or sometimes sympetalous) ones; that unisexual flowers are derived from bisexual (perfect) ones; that flowers with few stamens are derived from those with more numerous ones; and that gynaecia with solitary carpels, as well as carpels or ovaries with one ovule, are derived by reduction from more complex structures. The reduced or missing parts are often present as vestigial rudiments or are represented by vascular bundles which pass in the direction of their expected position (Eames 1931).

A noteworthy fact which has not previously been emphasized in discussions of phylogenetic reduction is that reduction in size and complexity of individual structures is often accompanied by an increase in the number of these structures produced, while reduction in number may be balanced by increase in size and complexity of individual structures. The best illustrations of these

480 Evolutionary Trends II: External Morphology

interrelationships are found in the ovules and carpels of the angiosperms. In many groups, such as the genus *Nicotiana* and the family Orchidaceae, the individual ovules are much reduced in size and in the development of their integuments, but their number per carpel is greatly increased over that found in the nearest relatives of these groups. In some genera with much reduced one-seeded carpels that form achenes, the number of carpels is much greater than that found in any of their relatives. This is true in *Fragaria* of the Rosaceae and in *Myosurus*, as well as in some species of *Ranunculus* and *Anemone* in the Ranunculaceae. On the other hand, in such genera as *Quercus*, *Juglans*, and *Prunus*, the single ovule which remains in the ovary has become much enlarged and elaborated in structure. In many families of angiosperms, such as Umbelliferae, Compositae, Gramineae, Cyperaceae and Juncaceae, all of the parts of the flower have become greatly reduced and simplified, but the number of flowers per reproductive shoot or inflorescence has been greatly increased.

These interrelationships between reduction and multiplication deserve attention because they suggest that phylogenetic trends of this nature may in many instances be produced by changes in the timing relationships of growth and differentiation phases in a structure with determinate growth. As stated in Chapter IV, Tedin (1925) found that in *Camelina sativa* the same gene which increases seed size also reduces the number of seeds per pod.

From the developmental point of view, reduction in size and complexity of a mature organ in successive generations of a phylogenetic line must result from the accumulation of mutations which reduce either the rate of growth of that organ or the time during which it grows. And as pointed out above, and illustrated in the example of *Camelina* (page 133), this reduction may be compensated by an increase in the number of parts or in other cases by a corresponding increase in ultimate size, and therefore in speed or length of growth of other parts of the plant. On this basis the phylogenetic trend of reduction may be regarded as one phase of a much more general phenomenon, namely, a change in relative growth rates, or allometry. The great importance of allometry for understanding evolutionary trends in animals has been emphasized by Huxley (1932, 1942, pp. 525-555). In plants,

genetic differences in fruit shape between different lines of various species of Cucurbitaceae and some other families have been explained on this basis by Sinnott (1936, 1937, 1939) and his associates (Sinnott and Kaiser 1934, Houghtaling 1935). Riley (1942, 1943, 1944) has similarly explained differences between species of *Iris* in respect to their ovaries and other floral parts. Foster (1932a, Foster and Barkley 1933) has shown that the difference between leaves and bud scales depends largely on differences in growth rate between different parts of their primordia, while Boke (1940) has demonstrated that the difference between leaves, phylloides, and transitional structures in *Acacia melanoxylon* depends on the relative growth rate of the adaxial part of the foliar or rachis primordium, as compared to the primordia of the leaflets. Nevertheless, so far as this writer is aware, no general evolutionary trends have yet been analyzed on this basis. The phenomena of reduction are so similar in the two kingdoms that their explanation is probably the same.

In particular, allometry explains two generally observed facts about reduced or vestigial structures. As Huxley (1932) has pointed out, we would expect on the basis of allometric growth that the first formed embryonic primordium of a reduced organ would be as large or nearly as large as the corresponding primordium of an organ capable of developing to normal size. If the absence or reduction of the organ were of value to the organism, then selection would establish mutations slowing the growth rate of this primordium up to the point needed to produce the necessary reduction in size at the time of development when the selective factors were operating. The direct action of selection, therefore, would cause an organ to become reduced and vestigial, but not to disappear entirely. On the other hand, if the relative growth rate of one organ in respect to another is a constant function, for instance, if one organ is growing half as fast as another, the relative adult size of the two organs will be determined by the time over which growth is operating, that is, absolute size of the organism as a whole. In other words, given a constant allometric growth rate, reduction of an organ can be produced secondarily by the action of genes increasing absolute size. If the allometric constant is high and the growth persists long enough, this reduction can result in virtual disappearance of the vestigial organ. On

this basis we would expect that direct selection would tend to reduce an organ until it became vestigial, and further reduction, although of no selective value in itself, could come about secondarily through selectively induced changes in absolute size. We can in this way explain on the basis of allometry apparently non-adaptive differences in organs that are themselves of no value to the species. Furthermore, Huxley has pointed out that small differences in growth ratio, if they operate over a wide range of absolute size, can greatly affect the relative size of the organs at maturity. This explains further the variability of vestigial, apparently useless organs.

The second of the three widespread morphological trends, namely, fusion or union of parts, has been nearly as common and important in the evolution of the higher plants as reduction. The term fusion, though it is widely used, is misleading in this connection because of its ontogenetic connotation. The "fused" parts do not usually grow first as separate organs and become united later by growing together. On the other hand, the union is accomplished by a reduction in differentiation of the primordia of the individual organs and the growth of a new, relatively undifferentiated type of tissue. For instance, the growth of a sympetalous corolla with strongly developed lobes, like that of *Lysimachia* (Pfeffer 1872), *Rhododendron*, *Hemerocallis* (personal observation), or the tomato (Cooper 1927), is about as follows. The first parts to appear are the primordia of the apical lobes, which correspond to the separate petals of the ancestral form. Growth is at first most active in separate centers located in each of these primordia, but at some time in ontogeny there appears a new type of growth at the base of the corolla. This has been termed by Coulter, Barnes, and Cowles (1910, p. 254) zonal development, a term which to the present writer seems the most appropriate of those suggested. Goebel (1928, p. 463) has termed the same growth zone a "Ringwall" (circular rampart), while Thompson (1934) uses the term toral growth. Zonal development produces growth as rapidly below the sinuses of the corolla as below the lobes themselves. In all later stages, growth in size of the lobes depends on the activity of the growth centers in their primordia, while elongation of the tube depends on the rapidity of zonal development. Since the lobes have in most corollas a head start

over the tube, they will at certain intermediate stages be relatively large and the tube correspondingly short. But in strongly sympetalous corollas, like that of *Cucurbita* (Goebel 1933, p. 1861), the timing of zonal development is shifted forward so that it coincides with the first initiation of the corolla lobe primordia, and consequently the latter are not distinct from each other at any stage in ontogeny. In various zygomorphic flowers, such as the corolla of various Labiateae and the genus *Veronica*, as well as the calyx of *Utricularia*, some of the perianth lobes may begin their existence as separate primordia, while other lobes of the same perianth may be fused from the start (Goebel 1933, pp. 1859–1860).

It is obvious, therefore, that the eventual degree of "fusion" of the petals will be determined by three factors: first, the relative time of initiation of zonal development as compared to differentiation of the lobe primordia; second, the ratio between the rates of growth of the lobe primordia and the region of zonal development; and, third, the absolute size of the corolla. Thus, while the process of "fusion" is begun by the initiation of a new type of growth center, the degree of union, like that of reduction, is determined chiefly by allometry. On the basis of the conclusions reached in the discussion of reduction, we may expect that the size of the corolla lobes in relation to the tube will be subject to nonadaptive differences which depend on the absolute size of the corolla, or of the entire flower, as well as on slight differences in the degree of allometry.

The description given above holds with slight modifications for most examples of the union of similar parts, such as synsepaly, the uniting of filaments or anthers (Goebel 1933, p. 1860); of carpels to form a syncarpous ovary (cf. the description of *Nigella* by Thompson 1934); of branch systems to form a leaf; of the edges of a leaf to form a sheath, as in many grasses, sedges, rushes, *Allium*, and so forth; or of the edges of a megasporophyll to form a closed carpel (Goebel 1933, p. 1901). On this basis, the contentions of Thompson (1934) and Grégoire (1938), that the closed carpel and the syncarpous ovary are organs *sui generis*, are to a certain extent justified from the ontogenetic viewpoint. The regions of growth which produce the greater part of these structures did not exist in the more primitive ancestral forms. But from the phylogenetic viewpoint, both separate carpels and the

484 Evolutionary Trends II: External Morphology

syncarpous ovary are derived from distinct megasporophylls by means of successive modifications of ontogeny, induced by genes affecting the distribution, timing, and rate of growth.

A second type of union, which has been particularly common in the flower of angiosperms, has a parallel, but somewhat different, explanation. This is adnation, or the union of appendages belonging to different series or whorls. The best-known examples are the adnation of stamens to corolla and of calyx or receptacle to the gynaecium to produce the perigynous and epigynous type of flower. For a complete review of the literature on the latter condition, see Douglas (1944). Adnation agrees with the union of similar parts in that the united portions are produced by the appearance of zonal development. Furthermore, the degree of adnation must likewise be affected mainly by allometric growth. But the zonal development responsible for adnation must originate in a somewhat different manner from that which brings about union of similar parts. There is apparently a condensation of the timing stages of differentiation, so that parts which should normally be differentiated one after the other become differentiated at the same time. In fact, the normal successive differentiation of sepals, petals, stamens, and carpels may actually be partly reversed, as in *Sisyrinchium*, *Helianthus*, *Galium*, and *Valeriana* (Hannah 1916). As Schaffner (1937) has expressed it, "There is, so to speak, a telescoping of the processes of cell development and cell differentiation. . . ." Schaffner has suggested that this tendency is associated with a determinative process, which is responsible for the shortening of the floral axis and for the reduction in number of its parts. This determinative tendency, plus two others, namely, a tendency toward lateral expansion and one toward intercalary growth between stamen and anther primordia, are believed by Schaffner to explain in their interactions all the fundamental modifications of the flower. The tendency toward lateral expansion is simply a type of zonal development involving the entire basal part of the floral primordium (Coulter 1885, Goebel 1933, pp. 1916-1920, Hannah 1916, Thompson 1933, 1934).

The third tendency, change of symmetry, is less common than reduction and fusion and can only occasionally be recognized as a long-continued trend. Probably the most significant example is

that which, according to the telome theory, converted the primitive branch systems into leaves and sporophylls. Most of the other good examples are in the flowers of various angiosperms, converting them from regular types with radial symmetry to various zygomorphic, irregular types. All stages of this change can be observed in different living species of such families as the Leguminosae and the Scrophulariaceae. It is obvious that the change from radial to bilateral symmetry involves the development of unequal rates of growth, affecting either different directions of growth in the same organ or the relative growth of different organs. This third trend, like reduction and fusion, is also associated developmentally with allometry. There is every reason to believe, therefore, that in plants, as in animals, the key to the understanding of the development and genetic basis of the major evolutionary trends in external morphology lies in the study of genetic factors affecting the distribution, timing, and relative as well as absolute rates of growth.

The fact may seem paradoxical at first sight that increase in complexity of plants results mainly from two processes, reduction and fusion, which would appear to be degenerative. The explanation is, of course, that in a plant, which normally differentiates organs serially one after the other, the way of producing a single complex structure with the least modification of ontogeny is by compressing together and modifying several relatively simple organs. How this has occurred can be best illustrated by describing the known and probable homologies of the various parts of a fruit or "seed" of wild oats (*Avena fatua*), such as one would be likely to pick up in any dry hillside or field in California and many other parts of the world. This structure is definitely a single unit, which with its dorsal, bent awn and stiff, upward-projecting hairs is ideally adapted for transportation by animals and burying in the ground once it has landed, as the rapid spread and common occurrence of the species in favorable climates amply testify.

The derivation of the various parts of this structure is as follows. In the central position is the single ovule, containing the endosperm and the embryo. The latter two parts will be left out of consideration, since they belong to a genetically different individual from the rest of the structure and were differentiated

at a totally different time. The ovule itself, however, is descended from a megasporangium which became surrounded by parts of the reproductive telome system, the latter having become by reduction and fusion the ovule integuments (de Haan 1920, Zimmermann 1930). The ovule is contained within an ovary, which in the oat is merely the thin, hairy outer wall of the caryopsis, but which according to all evidence from the comparative morphology of grasses is derived phylogenetically from a syncarpous ovary with three carpels. Each of these carpels is derived by phylogenetic reduction and fusion from a megasporophyll, which at a much earlier time in the ancestry of the grass was in turn derived in a similar manner from a branch system. The caryopsis of the oat, therefore, contains the homologues of four different branch systems, enormously modified by reduction and fusion. Next outside of the caryopsis, the oat fruit contains the shriveled but persistent filaments of the three stamens. Each of these is a modified microsporophyll and is therefore descended from another branch system. At the base of the caryopsis are found two tiny scales, known as lodicules. These are much reduced petals, which in turn are descended from foliaceous or bractlike appendages, and ultimately from branch systems. Then comes the thin inner husk, or palea. Its homology is somewhat obscure, but it very likely represents two fused sepals, which again are modified from leaf- or bractlike appendages. Finally, enclosing the whole structure, is the firm outer husk or lemma. This is again an appendage, which has acquired its distinctive appearance through allometric reduction and fusion. The main body of the lemma is probably homologous to a leaf sheath (Philipson 1934), while the awn represents a blade which has suffered reduction both in length and in width through negative allometry. The pointed, apical lobes of the lemma are homologous to the ligule, but are relatively enlarged by positive allometry. The dorsal position of the awn on the lemma is due to the fact that the part of that structure above the awn represents the "fused" basal portions of the lobes; that is, it was formed by an area of zonal development which originated between the awn and the lobes. Thus, the entire oat "fruit," or grain with its husks, contains, in addition to the embryo and the endosperm, all or part of eleven different appendages, which were originally modified from as many differ-

ent branch systems. Although this is an extreme case, nearly all the organs of plants have to a certain extent had a similar history. The excellent paleontological evidence of Florin (1944a,b), for instance, would enable one to give a very similar picture of the derivation of the cone of a gymnosperm.

There is no doubt, however, that a fourth trend, namely, differentiation or elaboration, must be added to the three just discussed. But it is a remarkable fact that elaboration has played a relatively minor role in molding the external form of the plant or its organs. We see its effects in such remarkable leaves as those of the pitcher plants (*Sarracenia*, *Darlingtonia*, *Nepenthes*), the Venus' fly trap (*Dionaea*) and other insectivorous plants, and more commonly in various specialized parts of the flower, such as the lip of the orchids, the keel of the Leguminosae, the nectar-bearing spurs on the petals of the columbine (*Aquilegia*), the spurs, nectaries, and pollen clips of the milkweeds (*Asclepias*), and the elaborate nectaries on the petals of the mariposa tulip (*Calochortus*). But all these structures are extreme specializations which have appeared at a relatively late stage of plant evolution and have little to do with the basic evolutionary trends. Some of them, like the petal spurs of *Aquilegia*, are clearly the result of progressively increasing allometric growth (Anderson and Schafer 1931). The most fundamental role of differentiation or elaboration in plant evolution has been in the cellular or histological organization of certain structures, particularly the vascular system. The successive differentiation of various types of tracheids and sieve tubes, and later of vessels, fibers, and wood parenchyma of various types (Jeffrey 1916), is one of the most important trends of morphological plant evolution. We may mention in addition the differentiation and elaboration of epidermal hairs, stomata, and in families like the Gramineae, various other specialized types of epidermal cells (Prat 1932, 1936), of the phenomonal cells known as sclereids which occur in the leaves of certain genera (Foster 1944, 1945, 1946), and of the various fleshy and hard, sclerenchymatous tissues found in many fruits. All of the latter structures, however, are specializations which seem to appear rather suddenly and can only occasionally be followed as evolutionary trends through series of species or genera. Elaboration, therefore, in contrast to reduction and fusion, appears in

488 Evolutionary Trends II: External Morphology

plants most often as short-time tendencies in certain organs of particular, specialized families, genera, or species.

RECAPITULATION AND EMBRYONIC SIMILARITY

The evidence from embryology, which since the time of Darwin has been one of the most important lines of evidence, both for the occurrence of evolution and the course which it has taken, has recently been reviewed for animals by De Beer (1940). He has concluded that the so-called "bio-genetic law" as stated by Haeckel, namely, that ontogeny is a brief recapitulation of phylogeny, is more misleading than helpful, and should be rejected. On the other hand, he finds that the principle of Von Baer, which was also that accepted by Darwin, namely, that the embryos and young of related forms usually resemble each other more than do the adult organisms, is of wide application and has a firm basis in developmental morphology. Judging from the evidence presented below, the same is partly true of plants, though to a considerably lesser extent than it is in animals.

In discussing the ontogeny of plants, we must first remember that because of the presence of an apical meristem and the serial differentiation of organs, a plant has two types of ontogeny. One is that of the embryo and seedling or sporeling and the other is that of the various lateral appendages, starting from the time when they become differentiated from the apical meristem of the shoot. In both of these ontogenies embryonic similarity is evident, but its manifestation might be expected to be different in the two types.

In the sporelings and seedlings of many plants, the appendages first formed often have a more primitive character than those produced by older shoots. In many ferns, the first formed leaf of the sporophyte is often lobed dichotomously, so that it recalls a flattened dichotomous branch system (Fig. 47, Bower 1923, p. 85, Orth 1939). Among seed plants, examples of "recapitulation," that is, seedling similarity, are numerous. Most species of conifers of the family Cupressaceae, such as *Juniperus*, *Thuja*, and *Libocedrus*, have complex, scalelike leaves on their mature branches, but the earliest formed leaves on the seedlings are needles like those found generally in the Coniferales (Goebel 1928, pp. 494-498). Perhaps the most striking examples among

angiosperms are in the species of *Acacia* which at maturity bear only phyllodes, consisting of the expanded, flattened homologues of the leaf petiole and rachis (Boke 1940). As is well known and is illustrated in most textbooks of elementary botany, the seed-

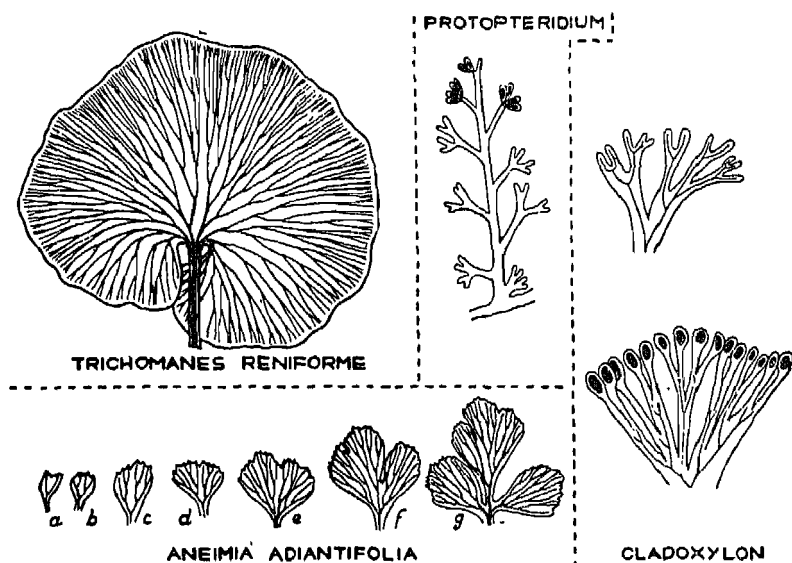


FIG. 47. Similarity in ontogeny and probable organogeny in ferns, showing evidence for the telome theory based on the principle of recapitulation, and from the fossil genera *Protopteridium* and *Cladoxylon*. Partly after Bower, from Lam 1948.

lings of many of these species possess normal, bipinnate leaves. Almost equally striking is the situation in *Eucalyptus*. In contrast to the mature twigs, which bear alternately arranged, pendent, bilaterally symmetrical leaves of a firm, sclerophyllous texture, the seedlings produce opposite, decussately arranged dorsiventral leaves which are broader, thinner, and more herbaceous in texture. Two further remarkable examples are found in species of sclerophyllous shrubs of coastal California. The bush poppy (*Dendromecon rigidum*) bears at maturity narrowly elliptic, entire leaves, quite different from those ordinarily found in the Papaveraceae. The seedlings of this species, however, as observed by Mirov and Kraebel (1939) and by the writer, have relatively broader leaves which are usually three-lobed at the

apex, a common condition in seedlings of species of the family and one which in other genera is followed by the variously lobed, pinnatifid, or pinnate leaves characteristic of the family. The chamise bush (*Adenostoma fasciculatum*) bears at maturity clusters of hard, linear, needlelike leaves with revolute margins, quite unlike those of other genera of Rosaceae, to which the genus belongs. But young seedlings of *Adenostoma* are characterized by relatively large, delicate, finely pinnatifid and dissected leaves, resembling seedling as well as mature leaves of species belonging to the related genera *Alchemilla* and *Acaena*.

A notable fact about all these examples of great differences between seedling leaves and those borne by the mature plant is that the species concerned all have at maturity relatively simple, reduced leaves, and are adapted to semiarid climates, particularly to regions with great seasonal differences in precipitation. This suggests that the retention of more complex leaves in the seedling has a selective value in these species. Seed germination and the early growth of the seedlings would naturally occur during the wet season, and the seedlings would be likely to be shaded by their parents and by other plants. For this reason, they would be growing under mesophytic conditions, so that the development of a large leaf surface for promoting rapid growth would have a higher selective value than the conservation of water. But later, with the onset of the dry season, the exposure of the plants to sunlight, as well as with the greater problems of conduction which develop as the plant increases in height, the need for conservation of water would become paramount. Therefore, the highest premium would be placed upon mutations tending to modify the leaves of the adult plant, but not of the young seedling. Evidence for this explanation is provided by the fact that in both *Acacia* and *Eucalyptus*, the cultivated species in which the seedling type of leaves persist the longest (*Acacia melanoxylon* and *Eucalyptus globulus*) are native to regions which are moister than those inhabited by most of the species of these genera, in which the adult, reduced type of leaf appears at a relatively early age.

Nevertheless, many types of seedling resemblances cannot be explained on this basis. For instance, in all the species of oaks (*Quercus*) which at maturity have deeply lobed leaves — both the

white oak (*Q. alba*, *Q. lobata*, *Q. garryana*) and the red or black oak type (*Q. borealis*, *Q. coccinea*, *Q. velutina*, *Q. kelloggii*) — the first leaves of the seedlings are shallowly lobed or merely toothed, as are both the seedling and the adult leaves of oaks like *Q. prinus* and *Q. agrifolia*, whose counterparts are definitely older in the fossil record than are the oaks with lobed leaves (Schwarz 1936b, Arnold 1947, p. 361). In the Gramineae, the typical leaves of mature twigs of the bamboos (tribe Bambuseae) have a complex structure consisting of a broad blade, a constricted, hardened petiole, and a thickened, tough sheath. But the leaves on the young primary shoots have strap- or wedge-shaped blades without petioles and thin sheaths with typical ligules, in all these respects resembling the leaves of ordinary grasses. These and numerous similar examples are difficult to explain on the basis of selection, except to the extent that the more complex type of leaf may have a selective advantage in the mature plant, but not in the seedling or young shoot, a suggestion offered by Massart (1894).

One of the most striking examples of seedling similarity, which is particularly difficult to explain on a selective basis, is that in some groups of Cactaceae. Certain genera of this family have forsaken the xerophytic habitat characteristic of most of its species and have become epiphytes in tropical forests. A notable example is the genus *Phyllocactus* (Massart 1894, Goebel 1928, pp. 511–512). The adult branches in this genus are flattened and nearly or completely spineless, in agreement with the photosynthetic organs of most other mesophytic plants. But the seedlings of *Phyllocactus* are columnar, four- to many-angled, and strongly spiny, as are both the seedlings and the mature plants of the related and more primitive genus *Cereus*.

A partial explanation of these phenomena in terms of developmental genetics is provided by the work of Swingle (1932), Frost (1938), and Hodgson and Cameron (1938) on the genus *Citrus*. These workers have shown that the appearance of the juvenile type of foliage depends not on the incidence of a new sexual generation, but upon the physiological conditions prevailing in the seed and the seedling. In *Citrus* two types of asexual propagation are possible. Mature twigs may be grafted or budded, while in the ovule the embryo often arises asexually as an adventitious bud from the nucellar or integumentary tissue. Trees

492 Evolutionary Trends II: External Morphology

grown from grafts or buds possess from the start foliage resembling that of mature branches, but all seedlings, both those from sexual reproduction and the asexual ones derived from adventitious embryos, are characterized by smaller leaves and a more spiny growth. In this they resemble the seedlings of a number of the more xerophytic genera of the Rutaceae. From this evidence we can surmise that the seedling similarity or pseudo-recapitulation found in many plants is due to the fact that the genetic factors which alter the apical meristem so that it produces appendages of a more specialized type often begin their action relatively late in development. Haldane (1932b) has suggested a similar explanation for the related phenomena in animals, and it was used for plants by Takhtadzhian (1943). They also suggest that if many gene mutations produce their effect by alteration of growth rates, a hypothesis which results directly from applying to developmental studies the principle of allometry, we should on this basis alone expect a certain degree of embryonic similarity.

The probable basis of seedling and embryonic similarity in plants may be summarized as follows. First, mutations which act relatively late in ontogeny are less likely to disorganize the whole process of development and so have a general deleterious effect than those which alter the early stages (Haldane 1932b, Goldschmidt 1940, pp. 389-390). The mutations established will therefore usually be those which affect development at the latest possible stage for the modification of the mature structure in the direction of a selectively advantageous shape. That part of the ontogeny which is less modified by the sum total of these late-acting genes will show embryonic similarity. Second, most mutations which alter the form of the mature organ change the rates of growth processes. Therefore, the longer the genetically different organs grow, the greater is the difference between them at maturity; and, conversely, the younger they are, the more alike they will be. Finally, the fact that seedlings often live under different environments from adult plants, and usually make different demands on their environment, may cause a particular type of structure to retain its selective value in the seedling after this advantage has already been lost in the adult plant.

THE PRINCIPLE OF IRREVERSIBILITY

A concept which figures in all considerations of phylogenetic trends is the principle or "law" of irreversibility, often referred to as Dollo's Law. This generalization states with varying degrees of definiteness that evolutionary trends cannot be reversed. The principle has no genetic basis, as Muller (1939) has pointed out, since reverse mutations occur in nearly all characters. Furthermore, mutations which reverse major phylogenetic trends, that is, atavistic mutations, are also known. Examples are the *radialis* mutation of *Antirrhinum majus*, which converts the corolla from the normal zygomorphic type into one with radial symmetry (Baur 1924, 1930, see Chapter III), and the mutation in *Crepis capillaris* which restores the receptacular paleae, a primitive feature of the family Compositae which is absent in all but one of the species of *Crepis* (Collins 1921, 1924).

As a rule, such atavistic mutations produce a disharmonious combination in association with the other characteristics of the organism, and so are promptly eliminated by selection. This is definitely true in the examples of *Antirrhinum*. But in *Crepis* there is one probable example of the relatively recent establishment in a gene complex restoring the receptacular paleae. The genus *Rodigia* was originally founded to include one species, *R. cummutata*, which is identical with species of *Crepis* except for the presence of paleae on the receptacle. But the experiments of Babcock and Cave (1938) showed that this "species" is interfertile with the common and widespread *Crepis foetida*, and they therefore reduced the "genus" *Rodigia* to the status of a subspecies under *C. foetida*. Furthermore, the presence or absence of paleae is conditioned by only two genetic factors. Now *Crepis foetida*, because of its annual habit, strongly thickened involucre bracts, and long-beaked, dimorphic achenes, is in one of the most advanced and specialized sections of the genus (Babcock 1947), while within *C. foetida*, subsp. *commutata* is more specialized and reduced in habit than subsp. *typica*. Hence, the possibility is very remote that subsp. *commutata* received its gene complex for the presence of paleae from some more primitive ancestors of *Crepis* which regularly had them, and we can assume safely that their existence in this subspecies is due to the establishment of two atavistic mutations.

Long-term reversals of trend in the structure of single organs also have almost certainly taken place in plant evolution. For instance, the most primitive angiosperms probably had palmately lobed leaves. This assumption is in accordance with the telome theory of the origin of the leaf (p. 477, cf. Zimmermann 1930, p. 343) and is suggested by the fact that the presence of three primary leaf traces is the primitive condition in the class (Sinnett 1914). In the genus *Paeonia*, all the evidence from the comparative morphology of the species indicates that a major trend has been from species with lobed leaflets to those with entire ones (Stebbins 1939). The same trend is suggested by the character of the seedlings in the genus *Dendromecon* of the Papaveraceae, as stated earlier in this chapter. But in the genus *Quercus*, the primitiveness of dentate leaves and the advanced character of lobed leaves is attested by both paleontological and developmental evidence. The evidence from paleontology, from comparative morphology and anatomy, and from development, all combine to suggest that evolutionary trends in the leaves of angiosperms may progress from the lobed to the entire condition and back again toward lobing. Similar reversals of trend have undoubtedly affected the size of parts, both vegetative and floral. Anatomical and developmental evidence indicates that the leaves of the original monocotyledons were relatively small, simple structures, which had suffered considerable reduction in the differentiation of this subclass from their less specialized ancestors (Arber 1924, Chap. V). In such groups as the asparagus tribe of the Liliaceae this reductional trend has continued. On the other hand, reversals in the direction of increasing leaf size have undoubtedly taken place rather frequently, as in bananas, palms, and aroids. In the case of the flower, the general trend has been toward reduction in size, particularly in stamens and carpels, which are almost certainly smaller than were the micro- and megasporophylls of the ancestors of the angiosperms. But this trend seems to have been reversed not infrequently. Probable examples are *Lilium*, *Tulipa*, *Godetia*, and many genera of the Cucurbitaceae. An example of reversals of trend within a group of closely related, specialized genera is provided by the tribe Cichorieae of the family Compositae. As Babcock (1942, 1947) has shown for *Crepis* and the writer for the more primitive genus *Dubyaea* and its relatives

(Stebbins 1940b), the general trend in this tribe has been toward reduction in size of involucre, flowers, and achenes. However, the largest floral parts known in the tribe are found, not in a primitive genus, but in *Tragopogon*, which in its vegetative characters, involucre, and achenes is one of the most specialized genera of the tribe. It is related to and probably descended from the larger genus *Scorzonera*, which also has large heads, though not so large as those of *Tragopogon*. In *Scorzonera* the species least specialized in vegetative habit, involucre, and achenes have the smallest heads, indicating that in these two genera the evolutionary trend has been toward increase in head size, or the reverse of that in most genera of the tribe. A similar trend toward increase is found in the American genera *Lygodesmia* and *Agoseris*. It is a noteworthy fact that the large florets of these specialized genera have a simplified, reduced vascular anatomy similar to that in specialized types with small florets, and quite different from the complex vascular anatomy found in the large-headed species of *Dubyaea* (Stebbins 1940b).

Reversals in habitat preferences and mode of life have also occurred frequently. Like the higher animals, all the higher land plants are descended from aquatic ancestors. And as in animals, examples of reversions to aquatic life are well known. The Salviniaceae and the Marsileaceae among ferns and the Najadaceae (pondweeds), the Lemnaceae (duckweeds), and the Nymphaeaceae (water lilies) among seed plants are good examples. The trend from mesophytic to xerophytic adaptation has also been reversed in a number of different lines. One example is the genus *Tragopogon* of the Compositae, tribe Cichorieae, mentioned above. Its probable ancestors in the genus *Scorzonera* are nearly all more or less xerophytic, but *Tragopogon* itself lives in relatively moist climates. Another rather frequent reversal is in the type of pollination. It is most probable that the ancestors of the flowering plants were wind-pollinated, but the earliest angiosperms themselves, on the other hand, were in all likelihood pollinated by insects. Nevertheless, a large number of families of angiosperms — Fagaceae, Betulaceae, Chenopodiaceae, Gramineae, Cyperaceae, and many others — have reverted to wind pollination. But in at least one case this trend has been reversed again. It is most probable that the flowers of the Euphorbiaceae became apetalous and

496 Evolutionary Trends II: External Morphology

unisexual as an adaptation to wind pollination, and that the ancestors of this family were insect-pollinated relatives of the order Geraniales. But in the most advanced genus of its family, *Euphorbia*, the presence of nectaries and brightly colored bracts surrounding the still monoecious and apetalous flowers indicates that the species of this genus have reverted to insect pollination.

We thus have evidence of reversibility in single mutations or gene complexes, in the size and morphology of individual organs, and in the general habit and functions of the plant. There are, nevertheless, certain ways in which reversal of trends occurs little or not at all. In particular, lost parts are seldom regained. This is apparently not because reverse mutations restoring these parts cannot occur — the example of receptacular paleae in *Crepis* is evidence of that — but because mutations altering the growth rates and the final shapes of existing parts probably occur with greater frequency and in any case can become established more easily because they cause less disturbance of the growth pattern of the plant as a whole. Thus, when the primitive xerophytic pines became adapted to more mesic conditions, the greater leaf surface necessary for this adaptation was more easily accomplished by the establishment of mutations increasing the length of the leaves and the number of short shoots per branch than by the restoration of the long leafy shoots which probably existed in the remote ancestors of the pine. In the asparagus tribe of the Liliaceae, in which the leaves have been reduced to small, colorless scales, probably as an adaptation to aridity, the reversion to more mesic habitats could occur more easily through factors increasing the number of minute branchlets, or causing a broadening and flattening of individual branchlets, as in various species of *Asparagus*, than by factors causing the reappearance of chlorophyll-bearing parenchyma in the original leaves. In the example mentioned above of the reversion to a tendency toward increasing size in the florets of the genus *Tragopogon*, the vascular supply needed for these larger parts is obtained more easily through genetic factors increasing the size of the bundles already present than it would be through the restoration of bundles lost through reduction. Bailey (1944) has made similar observations regarding the recovery of xylem vessels, once these structures have been lost during the evolution of a group. Thus, that part of the "law" or

principle of irreversibility which states that lost parts cannot be regained is the only one which has even partial validity in plants. In fact, most of the trends of plant evolution are best expressed by disregarding this law entirely and by substituting for it the fourth and fifth of the "cardinal principles of morphology" suggested by Ganong (1901). One of these, which is perhaps stated too strongly, is

the principle of indeterminate anatomical plasticity, that is, in all anatomical characters (size, shape, number, position, color, cellular texture) plant-organs, or, if one pleases, plant-members, are not limited by anything in their morphological nature, but under proper influence, may be led to wax and wane indefinitely in any of these respects.

The other is the

principle of *metamorphosis along the lines of least resistance*. . . . This means that when, through a change in some condition of the environment, the necessity arises for the performance of a new function, it will be assumed by that part which happens at the moment to be most available for that purpose, regardless of its morphological nature, either because that part happens to have already a structure most nearly answering to the demands of the new function, or because it happens to be set free from its former function by change of habit, or for some other non-morphological reason.

As a matter of fact, recent work on comparative morphology and phylogenetic trends has emphasized more and more the validity of the realistic point of view toward morphology advocated by Ganong and has suggested a broadening of this viewpoint to encompass all evidence on phylogeny. According to Ganong, this realistic point of view constitutes a synthesis of evidence both from comparative anatomy and from embryology, in which the changes in the mature structures are visualized as the outcome of alterations in ontogeny. Some recent authors, however, have merely substituted for the idealistic morphology, based entirely on comparative anatomy, an idealistic embryology. This is based on the assumption, first, that in all the higher plants serially homologous organs would have to be formed according to a fixed sequence and, second, that the ontogenetic development of homologous organs is always similar, so that the phylogenetic origin of a structure can always be reconstructed on the basis of its ontogeny. The fallacies inherent in these assumptions have been

498 Evolutionary Trends II: External Morphology

pointed out by Clapham (1934), by Kozo-Poljansky (1936), and by Arber (1937), in their criticisms of the work of Grégoire and Thompson. They fall down completely when tested by examining the ontogeny of any series of organs which are becoming progressively more different from each other, and they are not in accord with the realistic modern concepts of genetics. In particular, we should emphasize here the principle brought out in Chapter III, that genes affect primarily not the adult characters, but developmental processes. Hence, gene mutations, which are the building stones of phylogenetic changes, alter various developmental processes, some occurring early and some late in ontogeny. Similarity in ontogeny between organs which are descended one from the other will be found only if the evolution of the organs concerned has taken place by means of mutations which have affected chiefly the later stages of development.

The realistic point of view toward phylogeny may be summarized as follows. As stated by De Beer, phylogeny consists of a succession of modified ontogenies. The geneticist can add that these modifications have been induced by gene mutations altering the nature or timing of various growth processes. Furthermore, the overwhelming body of evidence from genetic analysis of hybrids between species and subspecies indicates that for the most part alterations have been produced through a long succession of small mutational steps, rather than through the sudden action of a few mutations, each with a radical effect on development. Hence, Ganong's principle of continuity of origin is upheld. This means that we must also uphold Ganong's seventh principle, that "in the progressive development of metamorphoses, difference of degree passes over gradually into difference of kind." As Ganong has pointed out, and Goebel (1933, p. 1862) has also made clear, the full acceptance of this principle renders futile any arguments about such points as whether the inferior ovary is axial or appendicular in nature. It is both in the phylogenetic sense, since both the floral axis and the bases of the various appendages were greatly modified during its formation; and it is neither, in the sense that no part of the ontogeny, histology, or anatomy of any inferior ovary resembles closely that of any particular structure or series of structures in a plant with a superior ovary. Finally, we must state that such regularities of phylogenetic pro-

gression which may be observed are based, not on any predetermined laws or principles, but on regularities in the selection and establishment of certain types of mutations and in the rejection of others. These regularities, and therefore the phylogenetic principles, can have numerous exceptions and so must be applied cautiously and critically, in correlation with all other available evidence on the group of organisms concerned. The great frequency of reduction sequences, in which mutations curtailing growth after the formation of vascular tissue seem to be established more often than those which reduce vasculature, gives value to evidence on phylogeny from comparative anatomy, which makes use of vestigial vascular bundles. Similarly, the greater alteration of the later processes of ontogeny renders qualified validity to evidence from comparative embryology, as based on similarities both in seedlings and in the primordia of the foliar and reproductive appendages of the mature plant. But, since these anatomical and embryological regularities are based on the establishment, in most instances by natural selection, of certain types of mutations, they can be greatly modified or even obliterated by the selective action of unusual environmental factors, as well as by the occasional random establishment of mutations without selective value. Each proposed phylogenetic sequence must be approached with all these considerations in mind, and the most probable course of evolution must be determined by weighing all the lines of evidence against each other. As Bailey (1949) has pointed out, this is the approach which should characterize the "new morphology."

ORTHOGENESIS, SPECIALIZATION, AND THE DIFFERENTIATION OF PLANT FAMILIES

The causal explanation of any evolutionary trend must have two parts. The first part is the developmental explanation. We must explain how the altered genotype acts to produce the visible changes seen in the phenotype. This can be done largely in terms of time action of genes, growth substances, allometric growth, and the influence of the environment, as indicated earlier in this chapter. But more fundamental from the standpoint of evolution in general is the second part, namely, an explanation of how the mutations originate which produce the altered genotype and,

500 Evolutionary Trends II: External Morphology

more particularly, how they become established in natural populations. The origin and establishment of mutations was discussed in Chapters III and IV, in which the points emphasized were the random nature of individual mutations, the fact that most mutations which become established in populations are those which have a relatively slight effect on the phenotype, and the fact that most of the qualities which give a selective advantage to individuals or populations are produced by combinations of different, genetically independent, morphological and physiological characteristics. In addition, the process of establishment itself was described as one which cannot be accomplished by chance alone, and for which some positive force is necessary in order to change the frequency of genes in populations. When these points are kept in mind, the conclusion becomes inevitable that all long-continued evolutionary trends must be governed by some guiding force.

Only two such guiding forces have ever been postulated, and it is unlikely that any others could be imagined. One of these is natural selection, and the other is some unexplained force which, presumably by causing the more frequent or predominant occurrence of mutations which are genetically unconnected, but have a similar morphological and physiological effect on the phenotype, directs or canalizes the course of evolution. The latter force is specifically designated or at least implied in explanations of evolutionary trends on the basis of orthogenesis.

The explanation of evolutionary trends on this strict orthogenetic basis has been done chiefly by animal paleontologists. The fallacies in their reasoning have already been pointed out by Goldschmidt (1940, pp. 321-322), by Mayr (1942, pp. 291-294), and particularly by Simpson (1944, Chap. V). The only serious attempt known to the writer to interpret evolutionary trends in plants on the basis of orthogenesis is the work of Schaffner (1929, 1930, 1932). In the examples which he cites, as in the zoological ones reviewed by Simpson, explanations on the basis of selection are in no case impossible or even improbable.

In the first place, the "series" described by Schaffner are all based on different living forms, which may have been derived from a common ancestor, but are certainly not derived one from another. In fact, Florin (1944b) has shown by fossil evidence that

some of the "series" described by Schaffner (1932) in the conifers are actually different end points of a number of adaptively radiating lines, of which the common ancestor was much more primitive than, and in some ways intermediate between, the modern extremes. Furthermore, the "series" of Schaffner are not cited for the organism as a whole, but for certain structures. In some of the "series" cited, like the fruits of various species of *Stipa* (Schaffner 1930), only certain features, like awn length, are progressive. The other characteristics of the species concerned vary in many different directions. Finally, nearly all of the structures described are highly adaptive, and it is only through a peculiar type of logic, the fallacy of which was pointed out in Chapter IV, that this adaptiveness is dismissed by Schaffner as not significant.

The conclusion is inevitable, therefore, that all long-continued evolutionary trends in plants, as well as in animals, are guided by natural selection. This means that the differences between families and orders of flowering plants must originally have had a selective basis, at least in part. Nevertheless, an explanation of the nature of this basis is admittedly one of the most difficult problems in plant evolution. The difficulty lies in the fact that not only are plants now living which appear to represent the earliest, most primitive stages of these evolutionary trends, as well as their highly specialized end products, but in addition there is surprisingly little difference between some primitive types and many advanced types, either in their abundance of individuals or in geographic distribution and the habitats they occupy. The differentiation of orders and families of flowering plants through the action of natural selection under present conditions is well-nigh impossible to imagine.

The solution to this difficulty probably lies in the following facts. First, all the trends leading to the differentiation of families of flowering plants probably took place simultaneously and at a relatively early stage in angiosperm evolution. For instance, both distributional and paleontological evidence indicates that the Compositae, the most highly specialized family of dicotyledons, already existed in the latter part of the Cretaceous period (Stebbins 1941c), and distributional evidence indicates a similar age for the most advanced families of monocotyledons, the

502 Evolutionary Trends II: External Morphology

Orchidaceae and the Gramineae. It is likely, therefore, that the major part of angiosperm evolution, involving the principal trends in the modification of the flower, took place during the Mesozoic era. The environmental conditions prevailing during that time were quite different from those now operating. In the first place, during at least half of this era angiosperms were in the minority, at least in those regions, now rather numerous, from which fossil records have been obtained. They were competing less with each other than with various types of gymnosperms, many of which were less efficient in their reproductive mechanisms. Second, the climate prevailing throughout the earth was at that time more uniform than at present, so that selective pressures favoring the differentiation of the vegetative parts of the plant in adaptation to new climatic and edaphic conditions were relatively low. Finally, the various types of flower-pollinating insects, as well as seed- and fruit-eating birds, were also probably undergoing relatively rapid evolutionary differentiation at that time. One would expect, therefore, that gene combinations adapting plants in new ways to pollination or seed dispersal by insects and birds would have had a particularly high selective value during the Jurassic and the Cretaceous periods.

The next set of facts to be remembered is that the flower is not just a collection of structures which have convenient diagnostic characters, but a harmonious unit which performs more or less efficiently the two vital functions of cross-fertilization and the maturation and dissemination of seed. Therefore, an alteration of one of its parts will immediately change the selective value of modifications in all the others, as well as the value of such general characteristics as the size, number, and arrangement of the flowers produced.

Furthermore, the nature of the functions performed by the flower is obviously related to the economy of the plant as a whole. It was pointed out in Chapter V that the value of self-pollination as against cross-pollination is different in plants with different types of life cycle and with populations of different size and structure. The nature of the pollinating agents available will likewise differ, depending on whether the plant is terrestrial or aquatic, mesophytic or xerophytic, temperate or tropical, and so forth. Also, the selective value of various types of seed dispersal will vary

similarly with the structure and habitat of the plant as a whole.

To illustrate this situation, the writer has made a tabulation of the families of flowering plants according to their primitiveness or advancement in respect to the eight diagnostic characteristics used most commonly and prominently in keys to plant families. These are: apetalous vs. presence of sepals and petals; choripetalous vs. sympetalous; actinomorphic (regular) vs. zygomorphic (irregular) flowers; many vs. few stamens; apocarpous vs. syncarpous; many vs. few ovules; axial vs. parietal placentation; and superior vs. inferior ovary. One can see that a family, or part of one, can be classified as primitive in all eight characteristics (corolla present, choripetalous, regular; stamens numerous; apocarpous; ovules several to many; placentation axial; ovary superior), as advanced in all eight, or as advanced in any one of a number of different combinations of two to seven characteristics.

The details of this study will be published elsewhere, but its principal results can be summarized as follows. In the first place, the total number of combinations realized is only 86, or 34 percent of the 256 possible, and 37 of these are represented by only one or two groups. Of the 438 groups (families or part families) which are classified, 200 are contained in only 12 combinations, or less than 5 percent of the total number possible. On the other hand, certain combinations are represented by a large number of groups, the largest numbers of groups per combination being 36, 24, and 20. Thus, the eight characters studied are far from being combined at random in the different families and genera of angiosperms.

The following evidence indicates that this nonrandom distribution of character combinations is connected with adaptation, so that the combinations realized by very few or no genera can be considered as adaptive "valleys" and those characteristic of many genera and families as adaptive "peaks." In the first place, most of these "valleys" represent combinations of which the inadaptable character can be clearly recognized. Many of the combinations not represented are impossible or nearly so from the structural point of view. These are all of the combinations which include epigyny or parietal placentation without union of carpels. Another series consists of those combinations which include sympetalous or zygomorphy together with a large number of stamens.

504 Evolutionary Trends II: External Morphology

The poorly adaptive nature of most combinations of this type probably results from the fact that sympetalous and zygomorphic corollas are usually highly adapted for insect pollination and function best in this respect if the stamens are definite in both number and position. Another combination, absence of petals with zygomorphy, is rare because the former characteristic is usually associated with wind pollination, the latter with pollination by insects. The majority of the "valleys" can be explained on the basis of these five impossible or poorly adaptive combinations.

Among those character combinations which represent "peaks," some are found in a relatively large number of unrelated groups, none of which contains many genera and species. For instance, the combination of polypetal, regular corollas, few stamens, hypogyny or perigyny, syncarpy, few ovules, and axial placentation is found in 34 different groups of various relationships. The largest of these are the Anacardiaceae, the Rutaceae (except the Aurantoideae), and the Celastraceae, but some Liliaceae and Commelinaceae are also found here. Combinations of characters such as this may be considered high peaks that are relatively easy to climb, that is, they may be reached by relatively little modification from a number of different floral types with more primitive combinations. Other combinations are represented by only a few groups, but one of these constitutes all or the major part of one of the very large plant families, and therefore is represented by a larger number of genera than all but a few of the other peaks. For instance, the combination of polypetal, zygomorphic corollas, stamens of a definite number, and apocarpous, hypogynous gynaecium with several ovules is the exclusive property of the Leguminosae (*sens. lat.*) and therefore is represented by 400 genera. Similarly, the combinations found in the large families Orchidaceae, Gramineae, Cruciferae, Malvaceae, Scrophulariaceae, Rubiaceae subfamily Coffeoidae, and Compositae are shared by relatively few other groups. These can be considered as peaks which are difficult to climb, but have plenty of room on top; that is, they permit a wide range of variation in the adaptive types of floral structure based on the combination of fundamental characters which forms the general plan.

The next fact which has become evident is that certain combinations of two or three characters are particularly prevalent.

For instance, apetaly is usually accompanied by reduction in ovule number. Furthermore, certain tendencies in the flower are correlated with characteristics of the inflorescence. Zygomorphic flowers are correlated with racemose, spicate, or axillary inflorescences, while actinomorphy is most commonly associated with cymose, corymbose, umbellate, paniculate, or capitate inflorescences. Reduction in number of ovules or seeds per flower is usually correlated with increase in the number of flowers per inflorescence. Many other similar correlations can be cited. All have their exceptions, but the correlations are close enough so that their origin by chance is highly improbable.

In addition, most of the different families occupying certain of the higher peaks are similar in general habit and in habitat preferences. For instance, the high peak mentioned above as occupied by the Anacardiaceae and other families contains mostly woody families of primarily tropical and subtropical distribution. Another high peak, characterized by sympetalous, actinomorphic corollas, stamens definite in number, and hypogynous, syncarpous ovaries with many ovules and axial placentation, is occupied chiefly by mesophytic herbs, of both temperate and tropical distribution (Polemoniaceae, Solanaceae, Plantaginaceae, some Bromeliaceae, some Liliaceae, and so on).

Finally, the characters chosen, though diagnostic of families more often than any other characters, break down in many cases, so that different parts of the same family have different combinations of the eight character pairs and therefore are placed in different groups. The significance of this in connection with the nature of families and other higher categories will be discussed later in this chapter. The noteworthy fact relevant to the present discussion is that groups consisting of part of a family are in a considerably higher percentage in the combinations with a low degree of specialization than they are in those which are more highly specialized. In other words, evolutionary experiments with single ones of these fundamental characters on the level of the genus or the species are more likely to be successful when the flower as a whole is more generalized than when it has reached a high degree of specialization. Primitive groups have more diversity in the "fundamental" characteristics than advanced ones.

When all these facts and interrelationships are considered, the

506 Evolutionary Trends II: External Morphology

hypothesis becomes most probable that the differentiation of families and genera of flowering plants is an example of adaptive radiation, which nevertheless differs quantitatively from the ones well known in animals. These quantitative differences are as follows. First, the number of possible adaptive combinations, which solve adequately the problems of cross-pollination and seed dispersal, is relatively large, so that many more different lines of radiation exist in the higher plants than in the higher vertebrate animals. Second, the relative simplicity of plant structure restricts the distance to which specialization can be carried, so that each line of adaptive radiation must be relatively short. At the same time, this simplicity makes possible an exceptionally large amount of parallel variation, so that morphological similarity is much less indicative of phylogenetic relationship in plants than it is in animals. Finally, this adaptive radiation affects only the reproductive characteristics of the plant. Since the importance to the plant of an efficient reproductive mechanism varies greatly with its habitat and vegetative life cycle, the selective pressure in favor of specialization along some line of adaptive radiation is much greater in some groups of plants than in others. This makes possible the existence side by side of relatively generalized and highly specialized types to a much greater degree than in most groups of animals.

As emphasized in Chapter IV, recent studies of natural selection have shown that the existence of a selective basis for an evolutionary change is relatively easy to demonstrate, while the actual selective agent responsible is much more difficult to identify. This generalization holds with particular force in respect to the differentiation of the families of flowering plants, since this differentiation took place many millions of years ago, when both the climate and the biota of the world were entirely different from what they are now. We can, therefore, do little more than speculate on the probable nature of these selective agents. The three particular agents which probably played the largest role were insect pollinators, the wind as a pollinating agent, and the needs of the seedling, as they affected ovule and seed size.

The fact is well known that many flowers are adapted in size, color, and form to the needs of insect pollination. Nevertheless, these adaptations have appeared independently within many

different families, and there is little evidence that they affected materially the differentiation of the families themselves. Zygomorphy is perhaps the principal tendency which is based on adaptation to insect pollination. It is rare or absent in wind-pollinated flowers, and among entomophilous types it is closely correlated with the racemose or spicate character of the inflorescence, which causes the flower to be borne horizontally rather than vertically. When the horizontal position is adopted, differentiation of the corolla into an upper and lower lip, as well as the grouping of the stamens on the roof or the floor of the corolla, greatly increases the efficiency of insect pollination. Wind pollination, on the other hand, often brings about a reduction or disappearance of the perianth, as well as the loss of stamens and the evolution of unisexual (monoecious or dioecious) flowers.

The selective significance of seed size and its relation to alterations in the structure of the gynaecium were fully discussed in Chapter IV. On the basis of that discussion, we should expect to find a relatively high proportion of small-seeded types, which very often have capsules with parietal, axial, or free central placentation, among mesophytic herbs, particularly those of meadows and among plants like the Ericaceae and the Orchidaceae, of which the roots possess symbiosis with mycorrhizal fungi. On the other hand, large-seeded types, with reduction of the number of ovules per gynaecium, might be expected most frequently among herbs, shrubs, and trees of forest areas and among xerophytes. These conditions were observed to be true to a considerable extent in the survey of families and genera of angiosperms on which the present discussion is based.

It is possible, however, that one general selective agent has been operating in different ways in the differentiation of many if not most of the families of angiosperms. This is the value to the plant of increasing rapidity in the cycle of flowering and fruiting, and of economy in the use of available food for the manufacture of reproductive structures, particularly seeds. This value would be especially great in plants of desert areas and of the cool temperate zone, in which the growing season has been much reduced in length. Mutations tending to speed up the development of flowers would almost automatically cause a reduction in the size and number of their parts. Furthermore, the generalized growth

508 Evolutionary Trends II: External Morphology

region responsible for zonal development, and therefore for "fusion" and "adnation," might be expected to originate and develop more rapidly than the series of separate growth centers in each primordium.

If such a generalized selective agent were operating, we should expect to find a great amount of parallel evolution in the fundamental organization of the flower, and this appears to have taken place. Divergence, on the other hand, could be produced by special environmental agents acting concurrently with this general tendency, as well as by isolation and chance reassortment of different combinations of genetic factors promoting increased rapidity in development.

We may now construct a tentative picture of how the families and orders of flowering plants became differentiated. Let us imagine the existence at an early geological period, perhaps the Jurassic, of an original stock of angiosperms, all of which are relatively similar to each other and possess the generalized characteristics associated with the order Ranales. They are scattered throughout the earth, but being still relatively inefficient competitors against long-established, abundant gymnosperms, like Bennettitales, cycads, conifers, Ginkgoales, and Gnetales, they are not present, except locally, in large numbers of either individuals or species. Spatial and ecological isolating mechanisms are therefore rather well developed. Under these conditions, mutations toward one or more of the various fundamental specializations, such as zygomorphy, syncarpy, or reduction of ovules or stamens, may have arisen in one or more localities and may have become established, either through accidental association with some highly adaptive vegetative characteristic or because of some local adaptive value in connection with the mode of life of the species in which the specialization arose. Even when such a mutation or series of mutations became fully established, the population bearing it would by no means have been a newly evolved family or even a new genus, any more than is a saxifrage with a zygomorphic corolla, a *Hypericum* with a one-celled ovary and parietal rather than axial placentation, or an *Oxalis* with the petals united at the base. But the establishment in a population of one such morphological change, or even of the beginnings of one, would increase the selective value of mutations in the direction of any one of

several other specializations, so that the population might soon come to possess a combination of characteristics quite different from the original, undifferentiated populations. Once this was achieved, the individuals with an intermediate condition would tend to be eliminated by competition, and the population would be separated by a morphological gap from its altered relatives. Now, the high adaptive value of this new combination would enable the population bearing it to spread rapidly, particularly in areas opened up by climatic or edaphic changes. It would therefore become geographically diverse rather quickly. At the same time, it would meet primitive, unchanged relatives of its ancestral population. If these relatives were separated from the changed population by genetic isolation barriers, they would either be eliminated by the latter or they would stop its advance, depending on the relative efficiency of the two species in both vegetative and reproductive characteristics. But if reproductive isolating mechanisms were absent or weakly developed, hybridization would occur, and from segregation of these hybrids there would arise new types, possessing the selectively advantageous combination of new floral characteristics associated with factors for vegetative characteristics, and perhaps also for size and arrangement of flowers, quite different from those present in the first altered population. This might increase the selective value of still further specializations in floral structure, and thus continue the adaptive trend, in addition to increasing diversity in other respects. By repetition of this process, a series of populations or species could arise, all possessing the same selectively advantageous and diagnostic modifications of the flower which arose monophyletically, but different from each other in various characteristics acquired both through independent variation under isolation and through hybridization. Such a series would constitute a new genus. Its further expansion and diversification, along with more complete extinction of its ancestors and more primitive relatives, would elevate it to the status of a family. If this hypothesis is a fair approximation of what actually happened in the early history of angiosperm evolution, we can assume that the earliest appearance, on the species level, of individual characteristics now considered to be diagnostic of families and orders was largely associated with chance, but that the molding of the higher categories themselves

510 Evolutionary Trends II: External Morphology

through the assembling of successful combinations of characteristics was guided mainly by natural selection. In the adaptive radiation of both plants and animals, the higher the level of specialization reached, the less is the possibility of chance variation in fundamental characteristics, and the more powerful is the guiding influence of natural selection in a particular direction.

The hypothesis presented, therefore, suggests that natural selection has played a large role in directing evolutionary specialization during the differentiation of the families of flowering plants, but that this role has been much obscured by the effects of chance in the first establishment of individual characters, by parallel evolution, and by hybridization. The first stages of adaptive radiation were mega-evolution in the sense of Simpson (1944, p. 123), and probably took place rather rapidly.

The same course of evolution was probably followed by other highly differentiated groups of plants. Heitz (1944) has suggested that the great diversity of structure in the peristome of the capsule of mosses, which has provided the best characters for dividing the class into orders, families, and genera, is mainly the result of random diversification in evolution. He bases his conclusions on the fact that the different types of peristome, as well as capsules devoid of any peristome, are found in different species living apparently the same type of life in the same habitat. The condition is precisely what one would find if he studied the distribution of a single important diagnostic character in angiosperms. But, as Heitz recognizes, the peristome certainly has a function, namely, to sift the spores and prevent their too rapid dissemination. The selective value of this function would depend greatly upon such matters as the size and shape of the capsule, the length and flexibility of its stalk, the precise habitat and length of fruiting season of the maternal gametophyte, and many other factors. Furthermore, the mosses are an ancient group, and some families may have originated under rather different conditions from those in which most of their representatives are found today. One would expect, therefore, that the guiding action of selection would have been obscured in mosses just as it has been in flowering plants and would become more evident only after a detailed ecological as well as systematic study of the group.

THE NATURE OF THE HIGHER CATEGORIES

No discussion of evolutionary trends is complete without a consideration of the nature of genera, families, and still larger subdivisions, all of which are, at least ideally, the nomenclatorial framework supporting our concepts of lines of evolution. The opinions of botanists as to the nature of these categories have differed as widely as their opinions about species. But in contrast to the recent history of the species problem, which has been one of increasing agreement as our knowledge of the biology of species formation has increased, opinions about the higher categories have if anything become more diverse, and the tendency has increased to regard genera, families, and orders as partly or wholly subjective groupings for convenience in classification.

Yet there is no doubt that many genera and families are as real as the species which compose them. Some genera, like *Pinus*, *Picea*, *Abies*, *Salix*, *Populus*, *Betula*, and *Alnus*, have been far more stable and uniformly delimited in the history of classification than their component species. If that group is the most natural which is the most easily recognized and has been the most consistently delimited by one careful observer after another, then the conclusion is inevitable that in some families of plants (Pinaceae, Salicaceae, Betulaceae) the genus is more natural than the species, while in others (Leguminosae, Cruciferae, Asclepiadaceae, Orchidaceae) the species is more natural than the genus.

The difficulty of recognizing genera and other higher categories as natural units lies partly in the fact that they cannot be defined on an experimental basis, as can most species (see Chapter VI). As a rule, members of different genera cannot be hybridized, and if they can, the resulting F_1 hybrid is completely sterile, barring the rare occurrence of allopolyploidy. If two species supposed to belong to different genera do form partly fertile hybrids, as with maize \times teosinte (*Zea* \times *Tripsacum*), the two "genera" are probably artificial groups which should be merged.

Anderson (1937a) has suggested a fundamental difference between generic and specific characters. He found that the species of such genera as *Aquilegia* and *Narcissus* differ from each other chiefly in "change of emphasis," that is, in the shapes and relative proportions of their different parts. When genera were compared, however, their differences appeared to represent "actual differ-

512 Evolutionary Trends II: External Morphology

ences in the pattern [of variation] itself." For instance, species of *Narcissus* differ from each other largely in the size of the flower and the proportion of its parts, but the chief difference between *Narcissus* and the related genus *Cooperia* is that the former possesses and the latter lacks a crown or corona at the apex of its corolla tube.

Epling (1938, 1939) attempted to apply this criterion to generic distinctions in the large family Labiatae, but he found that obvious differences in the pattern were not usually evident. On the other hand, species groups in this family are usually separated by "an accumulation of changes in emphasis," affecting many different parts of the flower. They are thus quantitatively, but not qualitatively, different from the differences between related species. The same may be said about the differences between species groups or sections of *Crepis*, as recognized by Babcock (1947).

As a matter of fact, most systematists recognize genera on the basis of morphological similarities between groups of species and of actual or presumed gaps in the variation patterns separating the different genera. In general, these gaps may be presumed to have resulted from the extinction of ancestral connecting links between the various groups of species, so that the greater the amount of extinction a family or order has suffered in its evolutionary history, the more easily recognizable are its genera. If a particular type of structural pattern has a specific selective advantage, various modifications of this pattern in its more perfect form have a better chance of survival than conditions intermediate between this and some other adaptive combination of structures. When this is true, generic boundaries coincide with changes in pattern, as in *Narcissus*. But in many instances, the species groups do not possess structures with distinctive adaptational features, and the gaps have resulted at least partly from accidental extinction of species. This is true in the case of many groups of genera in large families such as the Gramineae and the Compositae. In them there is no easy way of defining genera, and many of these groupings must be frankly subjective. Although they are based on discontinuities between groups of species, the particular discontinuities which are recognized as of generic value, as compared to those which have been used to separate sections or subgenera,

are based largely on tradition and convenience. Mayr (1942, Chap. X) has discussed the great divergences of opinion among ornithologists as to the delimitation of genera and the difficulty of reaching an agreement about situations in which the probable phylogeny of the group is generally accepted. Similar disagreements have arisen among botanists, particularly in regard to such genera as *Saxifraga* and *Astragalus*, and there has been the same difficulty in finding an objective basis on which to found a generally acceptable opinion. In general, the genera of the higher plants are much larger than those of vertebrate animals. This may be partly the result of tradition, but it is to a greater extent the result of such processes as hybridization and allopolyploidy, which have woven together networks of species. In genera such as *Stipa* and *Carex*, clusters of twenty or thirty species exist which cannot be subdivided on any basis except for artificial key characters. Splitting of genera in such groups would be more confusing than helpful.

In the opinion of the writer, there are no characteristics of genera, families, or any other higher categories of plants which would suggest that the mechanism of their evolution was anything more than a continuation of the processes which give rise to subspecies and species. Mutation, recombination, and selection, as well as isolation and extinction, are responsible for groups and categories of organisms at all levels. As we go higher up the scale, reproductive isolation becomes less important as the basis for the delimitation of categories, and extinction more so, but this is a quantitative rather than a qualitative change. Once species have appeared, the origin of genera and families, as well as orders, classes, and phyla, is largely a matter of time and further genetic plus environmental change.