

CHAPTER XIV

Fossils, Modern Distribution Patterns and Rates of Evolution

THE ULTIMATE problem for students of the dynamics of evolution is to determine how fast evolution progresses and under what influences its speed can be increased or decreased. A complete solution of this problem should make possible the control of evolutionary rates by man and consequently, at least in certain organisms, the artificial acceleration of evolutionary progress to the point where it can be directly observed and analyzed during the span of a human life.

Unfortunately, complete direct evidence relating to this problem is impossible to obtain. In order to have a direct bearing on the causes and dynamics of evolution, these rates must be expressed in terms of numbers of genic changes per unit of chronological time or per generation, and of the corresponding rate at which isolating barriers develop. All these processes occur so slowly under natural conditions that time must be reckoned in geological terms of tens or hundreds or thousands, or even millions of years, so that ideally the perfect evidence for the solution of this problem would be obtained from coordinated paleontological, genetic, and systematic studies on the same group of organisms. Unfortunately, no group of animals or plants is yet known on which all these types of evidence can be obtained. We are thus forced to analyze as best we can the evidence from the fossil record of organisms which have living counterparts and that from historical records of changes in the composition of populations of organisms amenable to genetic studies, and to correlate these two lines of evidence by means of the most plausible inferences we can make. One line of evidence which can help to bridge the gap between genetics and paleontology is that from the geographic distribution of living organisms which are closely enough related so that they can be intercrossed and their genetic relationships determined.

THE NATURE AND VALUE OF PALEOBOTANICAL EVIDENCE

There is no question that the evidence from fossil animals, particularly vertebrates and mollusks, is much more complete and definite than any now available from plants. Simpson (1944) has presented a convincing analysis of evolutionary rates based on the paleozoological evidence, and in general the paleobotanical evidence can do little more than support the principles which he has deduced. The one advantage of fossil plants over fossils of land animals is that, when sufficiently similar to modern types, they indicate much more accurately the nature of the climate at the time and site of deposition. For a student of the dynamics of evolution, therefore, the plant fossils which have the greatest value are those most nearly related to modern species.

As Simpson (1944, Chap. III) has emphasized, the gaps in the fossil record are as important as the fossils themselves. The remains available are not only a minute sample of the plants which existed on the earth; they are far from a random sample. Nearly all of the sites favorable for deposition were moist lowlands; plants adapted to upland areas and to dry climates, although they must have been as abundant in some past epochs as they are now, have only rarely been preserved. Furthermore, only certain types of plants, particularly the large, woody species, have been preserved with any degree of frequency. Fossil evidence in general provides us with a conception of the dominant species of certain sites during past geological ages, but we can expect other habitats and types of plants to be absent from the fossil record.

Another weakness of the fossil record which must be considered in its positive as well as in its negative aspect is the fragmentary nature of nearly all plant fossils. The diffuse structure of the plant body does not lend itself to preservation as a single unit. By far the most common fossils are detached leaves, tree trunks or bits of wood, and spores or pollen, while next in order of frequency are isolated seeds. Fruits and flowers are still less common, and in the case of the angiosperms the flowers are rarely well enough preserved to be identifiable. Now, the botanist judges the systematic position of a species on the basis of the whole plant: arrangement of leaves, character of inflorescence, nature of the floral parts, as well as that of the fruits and seeds. It is a well-known fact that the commonly preserved fossils, particularly the

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leaf impressions of the flowering plants, are the least diagnostic of all plant parts. Leaves of *Cercidiphyllum* (order Ranales) have been mistaken for *Grewia* (Malvales) or *Populus* (Salicales); those of *Arbutus* (Ericales), for *Ficus* (Urticales); and so on. Even a gymnosperm (*Gnetum*) has leaves which to the average observer are strikingly similar to those of some flowering plants (Thymeleaceae).

Some authors have suggested that these difficulties are so great as to be unsurmountable and that the paleobotanist can never be certain of the identity of the remains which he describes, except in the case of a few angiosperm fruits of a distinctive character and of those parts of gymnosperms and spore-bearing plants which can be sectioned and studied under the microscope. This is, however, an exaggeration. Seward (1931) and Cain (1944, Chap. IV) have given careful, impartial estimates of the accuracy with which fossil leaves can be identified. The method of identification is, of course, simple comparison between the fossil and the leaves of living species, but various approaches which have been adopted by modern paleobotanists have greatly increased its accuracy. In the first place, every observable detail is considered: shape, texture, character of margin and apex; position, distribution, and endings of primary veins; character of secondary venation; and, when possible, the microscopic structure of the epidermis (Bandulska 1924, Edwards 1935, Florin 1931). Secondly, decisions are not made on the basis of one or a few leaves of either the fossil or its possible living relatives, but on the range of variability found among large numbers of leaves of both fossil and living forms. Finally, the identifications are based on the assumption that in the past, as at present, plant associations formed harmonious communities, all of the members of which were adapted to similar environmental conditions. Going on the assumption that in the past, as at present, camphor trees did not grow in or near forests of redwood (*Sequoia*), Chaney (1925a) became doubtful of the reference to the genus *Cinnamomum* of certain leaves found in the mid-Tertiary flora of western America, and he started to compare them with the leaves of various species which now grow in or near forests of *Sequoia*. As a result, the leaves of one of these species of "*Cinnamomum*" were found to be a close match for those of the modern *Philadelphus lewisii* (Hydrangea-

ceae). This species is common in the forests bordering those of the modern *Sequoia sempervirens*, and their similar position in the Tertiary period is entirely to be expected.

The correctness of many of the identifications of angiosperms based on leaf impressions has been verified by the discovery of unmistakable fruits of the postulated species in the same deposits. One of the most striking examples was the discovery by Brown of seeds of the genus *Cercidiphyllum*, of which the only living species is confined to Japan and China, in company with leaves previously assigned by Chaney to that genus and now known to be widespread and abundant in mid-Tertiary deposits of western North America. Other genera which are known from well-preserved leaves and fruits or seeds occurring in the same deposit are *Populus*, *Alnus*, *Quercus*, *Lithocarpus*, *Juglans*, *Carya*, *Engelhardtia*, *Platycarya*, *Chaetoptelea*, *Liquidambar*, *Platanus*, *Cercis*, *Acer*, *Cedrela*, *Koelreuteria*, *Firmania*, *Gordonia*, *Nyssa*, and *Terminalia*. In the famous London Clay Flora of Eocene age, Reid and Chandler (1933) described a whole series of fruits and seeds, many of which were certainly identified as belonging to modern genera. Nearly all the modern counterparts of these early Tertiary species of northwestern Europe are found in the tropics of the Indo-Malayan region, a conclusion which would have been predicted on the basis of other Eocene floras of this region which contained only leaf impressions. There is little reason to doubt, therefore, that the majority of the angiosperm remains which have been assigned by progressive, modern paleobotanists to particular modern genera actually belonged to the genera with which they have been identified. In the case of fossils dating from the latter part of the Tertiary period, the comparison with modern species is usually reliable (cf. Chaney, Condit, and Axelrod 1944, Hu and Chaney 1940).

The positive conclusion which follows directly from the nature of the paleobotanical record of the angiosperms is that forms similar to modern species and genera are recognized with relative ease, while radically different types, including those which might have formed connecting links between existing genera or families, could not be recognized or assigned to their correct phylogenetic position even if they were found. Evolutionary conservatism and stability are much easier to demonstrate by means of fossil evi-

dence than is rapid progress or the differentiation of the modern families and orders.

With this in mind, we can make a brief summary of the fossil record of the modern seed plants and of the forms known to be directly ancestral to them. Among the gymnosperms, the most primitive living order, the Cycadales, are known from scattered remains as old as the beginning of the Mesozoic era (Schuster 1931, Florin 1933), as well as from leaf impressions of Cretaceous and early Tertiary age (Seward 1931, Chaney and Sanborn 1933). The reproductive structures found by Harris (1941) in the lower Jurassic rocks of Yorkshire, England, are very similar to those of modern cycads. This author has concluded that by the beginning of the Jurassic period the Cycadales had evolved to their full extent in respect to the differentiation of genera. The conspicuous, amply preserved, and highly evolved cycadlike plants of the latter part of the Mesozoic era, particularly the Bennetitales, are a line of parallel evolution which is only distantly related to the true cycads and became extinct without giving rise to any modern groups of plants.

The Ginkgoales, represented by the single modern species *Ginkgo biloba*, are known in the fossil record chiefly from leaves, so that their course of evolution is difficult to trace. Forms similar to the modern species are known from the Jurassic period (Shaparenko 1936, Florin 1936). Since this time *Ginkgo* appears to have remained essentially static from the evolutionary point of view, having gradually reduced its area of distribution, until now it is almost extinct except under cultivation.

The most flourishing of the modern orders of gymnosperms, the Coniferales, has also the most completely known fossil history. The thorough and discerning studies of Florin (1944a,b) have produced convincing evidence that, starting with the ancestral order Cordaitales in the upper Carboniferous period, the evolution of the conifers progressed steadily through the latter part of the Paleozoic era and the first half of the Mesozoic era, until forms essentially similar to modern genera appeared in the Jurassic period. Other modern genera of this order are recorded from the Cretaceous period, so that by the end of the Mesozoic era the coniferous flora of the world was not materially different from that of modern times. Fitting this record with the most

widely accepted time scale of the geological periods, we reach the conclusion that for about 100 to 150 million years after the appearance in the fossil record of their earliest recognizable ancestors, the progress of conifer evolution was relatively steady and continuous. There were, however, fluctuations in rate, and a good many side lines were thrown off, which progressed for some time and then became extinct. For the next 40 to 80 million years progress was considerably slower, with many lines ceasing to evolve any new types. During the past 60 to 70 million years, since the beginning of the Tertiary period the conifers have remained remarkably stable. They have produced a good many additional species, but these appear to have been merely variations on a series of complex architectural patterns which were built up as genera during the first 150 to 200 million years of conifer evolution.

The fossil record of the final order of gymnosperms, the Gnetales, is scanty and inconclusive. Nevertheless, analysis of the pattern of distribution of modern representatives of the order, based on principles to be discussed in the next section, suggests that they, too, have evolved very little since the end of the Cretaceous period, 70 million years ago.

In the gymnosperms as a whole, therefore, progressive evolution was confined largely to the end of the Paleozoic era and the major part of the Mesozoic era. Since that time they have remained relatively static, except for the adaptation of old morphological types to new climatic conditions. Nevertheless, they obviously have not become "senescent" or ready to die out. Many species of several genera are still widespread and variable, particularly in *Pinus*, *Abies*, *Picea*, *Juniperus*, and *Podocarpus*. Some of these actually have "weedy" tendencies in land disturbed by man. The gymnosperms, therefore, like many groups of angiosperms, show us that neither chronological age nor evolutionary stability necessarily produces the characteristics attributed by some authors to "senescence."

For the great group of flowering plants, or angiosperms, no series of fossil ancestors exists like those known for the conifers. The Jurassic order Caytoniales (Thomas 1925, Seward 1931, pp. 366-367) and some other Mesozoic groups related to the Pteridosperms or Cycadofilicales may be near to the ancestral angiosperm

stock, but the interrelationships of all of these groups are highly problematical. Except for a few isolated earlier records (Arnold 1947, pp. 336-337), angiosperms enter the fossil record in the lower part of the Cretaceous period, and at that time they already included many surprisingly modern types. Many botanists have argued from this fact that the angiosperms must be vastly older than these records of them, and that they originated in the Triassic or even in the Permian period. But evidence produced by Simpson (1944) and additional facts reviewed in this chapter speak strongly in favor of the assumption that the same evolutionary line can progress very rapidly during some periods of its history and very slowly or not at all during others. If we accept this postulate, we can imagine that the origin of the angiosperms was, geologically speaking, not much before their earliest appearance in the fossil record, but that just before this time they were undergoing a period of particularly rapid evolution. The length of the period of angiosperm evolution prior to their appearance in the fossil record is entirely an open question.

Although the leaves and fruits of some Cretaceous angiosperms are similar enough to modern ones to suggest that they belonged to existing genera, many of them are of doubtful affinity and have been assigned by different authors to various unrelated modern genera (Dorf 1942). Toward the end of the Cretaceous period, however, and particularly during the interval between this period and the Eocene epoch of the Tertiary period, the number of modern types increased rapidly. In the Wilcox flora of the southeastern United States (Berry 1930), the Goshen and Chalk Bluffs floras of the Pacific coast of North America (Chaney and Sanborn 1933, MacGinitie 1941), and several contemporary Eocene floras of Eurasia (Kryshstovovich 1929, 1930, Chaney 1940a,b), the majority of the species belonged to or closely approximated modern genera. These conclusions, based largely on comparisons of leaf impressions, are well supported by the large series of fruits and seeds in the flora of the lower Eocene London Clay, studied intensively by Reid and Chandler (1933). They found that nearly all of the species could be referred to living families, and that most of them were close to or identical with modern genera, although they did not feel justified in using modern generic names, because of the uncertainties of identification.

The floras of the middle and latter part of the Tertiary period contain only modern genera, and an increasing number of fossils from deposits of these ages are indistinguishable from living forms. In the Miocene Tehachapi flora of Southern California, which is an association largely of sclerophyllous shrubs indicating a semi-arid climate, most of the species are likewise closely similar to modern ones (Axelrod 1939). By the middle of the Pliocene epoch, as shown by remains from several different localities (Chaney, Condit, and Axelrod 1944), the woody species of the California flora were nearly all similar to modern ones. In fact, a comparison of the extensive table of species published by Chaney, Condit, and Axelrod (1944) with Jepson's manual of the California flora (Jepson 1925) has revealed the fact that all the species of no less than twenty-eight of the woody genera of this flora are represented by identical or nearly identical precursors in the floras of the Miocene and the Pliocene epochs. In many other genera, the species not represented are at present rare and occur in sites unfavorable for preservation. In fact, the abundant fossil evidence suggests that during the past five million years new species of woody plants have been added to the California flora only in such large and complex genera as *Eriogonum*, *Ceanothus*, *Arctostaphylos*, and various Compositae.

Although there is no other region in the world in which the fossil floras of the Tertiary period have been so carefully correlated with each other and with modern floras as they have in the western United States, all the available evidence indicates that the rate of evolution among woody plants since the middle of this period has everywhere been as slow or slower than it has in the western United States. The Miocene Shanwang flora of northern China consists almost entirely of modern species (Hu and Chaney 1940), as do the early Pliocene floras of Japan (Miki 1941), while the essentially modern character of various mid-Tertiary floras from Siberia is reviewed by Kryshstofovich (1929, 1930, 1935). The Miocene and Pliocene floras of Europe are in some respects very different from the modern ones (Seward 1931, pp. 450-453), but this is a result of the great climatic changes which took place on that continent during the glacial epoch of the Pleistocene, causing the extinction of large numbers of species. It is not certain what proportion of the relatively small number of woody species in the

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modern European flora are Tertiary types which survived the ice age in various refugial areas, and how many of them have been newly evolved during that epoch, but the safest inference is that the number of such new species is relatively small.

The reader may justly ask at this point, "How can we be sure that these fossil forms known to have borne leaves or sometimes seeds and fruits similar to those of modern species were actually the genetic equivalents of the modern species which they resemble?" The answer to this question is, of course, that we cannot actually be sure. No conclusions in the field of paleontology can have the degree of certainty and predictability which may be reached in experimental sciences such as physiology or genetics. About all of the events of the remote past we must be content with the inferences which have the greatest degree of probability, based on the widest variety of evidence which can be obtained.

In the present instance, three different lines of evidence point to genetic continuity between most of the woody species of the middle and later part of the Tertiary period and their modern descendants. In the first place, the comparison is usually based on the range of variability within a large series of leaves of the fossil form and its modern equivalent, rather than on a few isolated leaves of each. Secondly, in the more recent and better-known assemblages of fossils, the association of species is similar to that in modern floras.

Finally, the evidence from hybridization experiments between modern subspecies and species of woody plants, as discussed in Chapter VI, indicates that forms which differ greatly in external morphology are often essentially alike in their chromosomes and are not separated from each other by any barriers of hybrid sterility. Species which are closely similar in external morphology, but cannot be crossed or form sterile hybrids, are unknown in woody plants, except for those genera in which polyploidy is present. Hence, the most likely inference on the basis of all available evidence is that most of the woody species of today have existed for five million years or more, and that the evolution of the genetic isolating mechanisms separating them took place largely during the early and middle parts of the Tertiary period.

The most conspicuous feature of the early Tertiary floras is that all of those known consist of types adapted to climates much

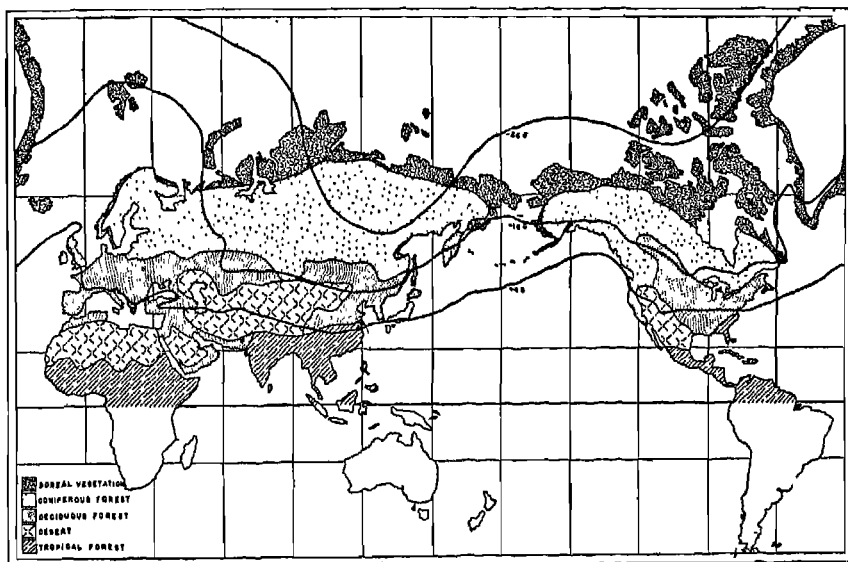
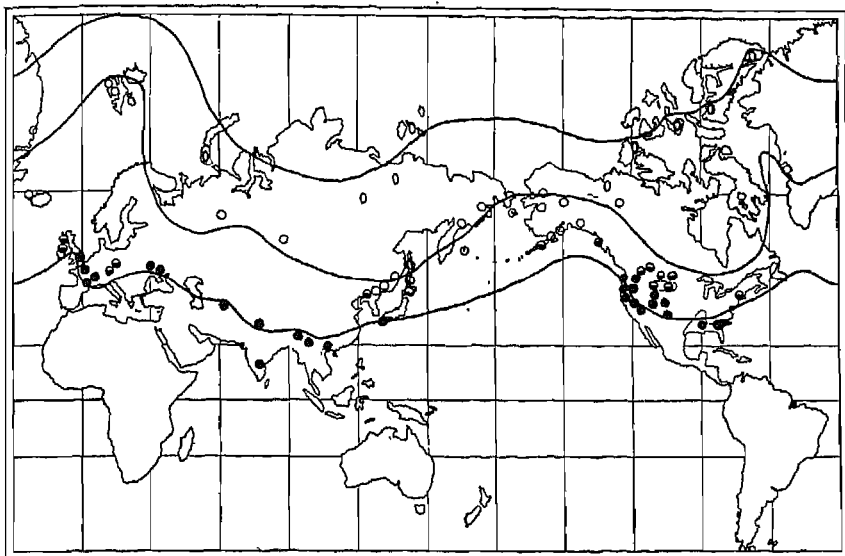


FIG. 48. Top, distribution in the Northern Hemisphere of Eocene fossil floras of tropical character (solid circles), of warm temperate character (open circles), and of cool temperate character (open ellipses), and the Eocene "isoflora" constructed from these distributions. Below, distribution in the Northern Hemisphere of modern vegetation and January isotherms. From Chaney 1940.

milder than that which now prevails at the sites of deposition. Reid and Chandler (1933) found that the large assemblage of fruits and seeds in the early Eocene London Clay flora resembles most closely the modern flora of the tropical Indo-Malayan region, with the *Nipa* palm as the dominant species. The numerous Eocene floras of the United States, such as the Wilcox (Berry 1930), the Goshen (Chaney and Sanborn 1933), and the Chalk Bluffs (MacGinitie 1941), likewise have tropical or subtropical affinities, particularly with the modern floras of Mexico, Central America, and the West Indies (Chaney 1947). Certain subtropical species, such as palms and cycads, extended even to southern Alaska (Hollick 1936), although most of the Alaskan floras of this epoch were temperate, containing *Metasequoia* in great abundance (Chaney 1948), accompanied by deciduous angiosperms like *Acer*, *Betula*, *Fagus*, *Liquidambar*, *Platanus*, *Populus*, and *Ulmus*. Similar temperate floras are known from Eocene deposits of central and eastern Asia, Greenland, and Spitzbergen, while the floras of arctic Siberia, Novaya Zemlya, Ellesmere, and Grinnell Land, the latter at 82° North Latitude, were cool temperate, containing chiefly *Picea*, *Salix*, *Populus*, and *Betula* (Chaney 1940a,b). The Southern Hemisphere is less well known paleobotanically, but subtropical early Tertiary floras are known from relatively high latitudes both in South America and in Australasia (Ettingshausen 1887a,b, Berry 1922, Florin 1940), while the Tertiary floras of the far southern island of Kerguelen, as well as of Graham Land, near Antarctica, are at least temperate in character (Dusén 1908, Hill 1929, Seward 1934). The evidence for this relatively warm, mild climate in the Eocene epoch is not confined to plant fossils, but is supported by the vertebrate and even the marine invertebrate fauna (Smith 1919). When jungles containing palms, figs, and lianas grew along the shores of California, Oregon, and Washington, the warm waters of the adjoining oceans were populated with corals and large clams (*Venericardia planicosta*) closely related to species now living in the Gulf of Panama. Evidence for similar warm climates near the poles in earlier geological periods is abundant and is well reviewed both by Seward (1931) and by Arnold (1947).

Emphasis must be placed upon the evidence that the Eocene climate, although certainly milder than that of the present, was

nevertheless zonal, with warmer temperatures near the equator and cooler ones near the poles. Furthermore, Chaney (1940a,b) has shown that the position of Eocene floras was about the same distance north of their present counterparts at all longitudes (Fig. 48). The available data suggest a similar southward displacement of the floras of the Southern Hemisphere. This evidence is best explained on the assumption that the amelioration of the climate was world-wide and that the continents occupied approximately the same positions that they do now. The various climatic changes which may have been responsible for these alterations in the environmental conditions of the earth's biota have been discussed by Brooks (1926) and Simpson (1940), while Mason (1947) has raised the problem of the availability of sufficient light for the growth of shrubs or trees at high latitudes. The explanation of the climatic and edaphic conditions which permitted the existence of the Eocene floras and faunas in their present position undoubtedly raises many difficult and as yet unsolved problems. But, as Reid and Chandler (1933), as well as Chaney (1940b), have pointed out, problems of equal or even greater magnitude arise when attempts are made to explain all the available evidence by assuming extensive shifts in the position of the continents or poles, at least during the time since the advent of the flowering plants. There is not time in this chapter to discuss the much-debated hypotheses concerning the migration of continents; Just (1947) has presented a fine review of this subject, with full literature citations.

From the beginning to the end of the Tertiary period, the habitats available to subtropical and tropical species were contracting, while temperate and arctic species were finding larger and larger areas open to them. Furthermore, the latter part of this period, particularly the Pliocene epoch, saw the rise of great mountain chains in many parts of the world, including the Alps, Himalaya, the western Cordillera of North America, and the Andes. The appearance of semiarid steppes and deserts in the rain shadows of these mountain systems restricted greatly the areas occupied by mesophytic plants of both tropical and temperate climates, while the opportunities for expansion afforded to xerophytes, as well as to alpine types adapted to life on the crests of the mountains, were greatly increased. This progressive cooling

and diversification of the Tertiary climate, with consequent segregation and diversification of floras, is well described by Chaney (1936, 1947), by Cain (1944, Chap. IX), and by Axelrod (1941, 1948). The latter author has pointed out that the origin of most of the modern ecotypes and ecospecies of woody plants must have taken place during the Pliocene and the Pleistocene epochs.

The fossil record of the woody angiosperms may therefore be summarized as follows. They first appear in great abundance in the early part of the Cretaceous, about 100 million years ago, with many families and genera already represented, some of them modern. For the next 40 to 50 million years, until the beginning or middle of the Eocene epoch, the differentiation of modern genera occurred at a gradually decreasing rate. During this time, the climates of the world were milder than they are at present, although there was alternation of cooler and warmer periods. The culmination of this period of warm climate came in the Eocene epoch, when plants now typical of subtropical floras reached latitudes of 55 to 60 degrees north, while woody plants now characteristic of cool temperate regions grew within ten degrees of the north pole, and forests covered at least part of the Antarctic continent. Since the Eocene epoch, in accompaniment with the cooling and diversification of the climate, the evolution of woody plants has consisted chiefly of the differentiation of new species and ecotypes, and at least in temperate regions few if any new genera have appeared. Most modern species of woody plants date back at least to the middle of the Pliocene epoch, about five million years ago, while several (*Liriodendron tulipifera*, *Populus trichocarpa*, *Castanopsis sempervirens*, *Quercus engelmannii*, *tomentella*, *chrysolepis*, and *palmeri*, *Cellis reticulata*, *Umbellularia californica*, *Lyonothamnus floribundus*, *Rhus integrifolia*, *Fremontia californica*, *Arbutus menziesii*, and so forth) have been practically unchanged since the beginning to the middle of the Miocene epoch, 20 to 30 million years ago, and some species (*Chaetopteleu mexicana*, *Cercidiphyllum japonicum*) have existed in essentially their present form since the Eocene epoch, 40 to 50 million years ago.

The evidence from fossils of herbaceous angiosperms, although it consists of only a few isolated examples, nevertheless suggests that evolution in herbs has not always progressed at the same rate

as it has in the woody plants associated with them. The best preserved fossils of herbaceous species are usually fruits and seeds, and so do not give a record which is strictly comparable to the bulk of the record from woody angiosperms. The three best examples known to the writer are, fortunately, representatives of entirely different types of plants.

The first is the series of seeds assembled by Chandler (1923) of the aquatic genus *Stratiotes*. The oldest seeds in this series, of Eocene age, are small, broad, and heavily sculptured, while those of younger strata are progressively longer, narrower, and smoother, until in the uppermost Pliocene there occur seeds which are indistinguishable from the modern European *S. aloides*. The significance of this extensive evolution is difficult to estimate. *Stratiotes* is today a monotypic genus of the small, aquatic, or subaquatic family Hydrocharitaceae, in which it occupies a rather isolated position. Most members of this family multiply vegetatively to such an extent that plants with seeds are rarely collected, and the seeds of most species are not available for study, description, or comparison with those of *Stratiotes*. There is no way of deciding, therefore, whether the recorded changes in the seeds are on the species level, or whether the Eocene seeds belonged to plants of a different genus. *Stratiotes*, therefore, represents an isolated case of undoubted progressive evolution of which the causes and significance are obscure.

The second and most significant series is that of the grass seeds of the tribe Stipeae described by Elias (1942). This shows an undoubted progression from the beginning of the record in the lower Miocene epoch to its end in the middle of the Pliocene, a period of about 18 million years (Fig. 49). The fruits found in all the earlier deposits are different from any known in modern species of Stipeae, but many of those from the mid-Pliocene beds resemble modern species of the genus *Piptochaetium*, subg. *Podopogon*, nearly all of which are now confined to South America. Since the modern species of Stipeae of the North American Great Plains are fewer in number than the known Pliocene fossils, their history since the Pliocene has been mainly one of extinction. The four remaining species related to the fossil group are all polyploid with respect to the South American species of *Piptochaetium*, and presumably also with respect to the extinct

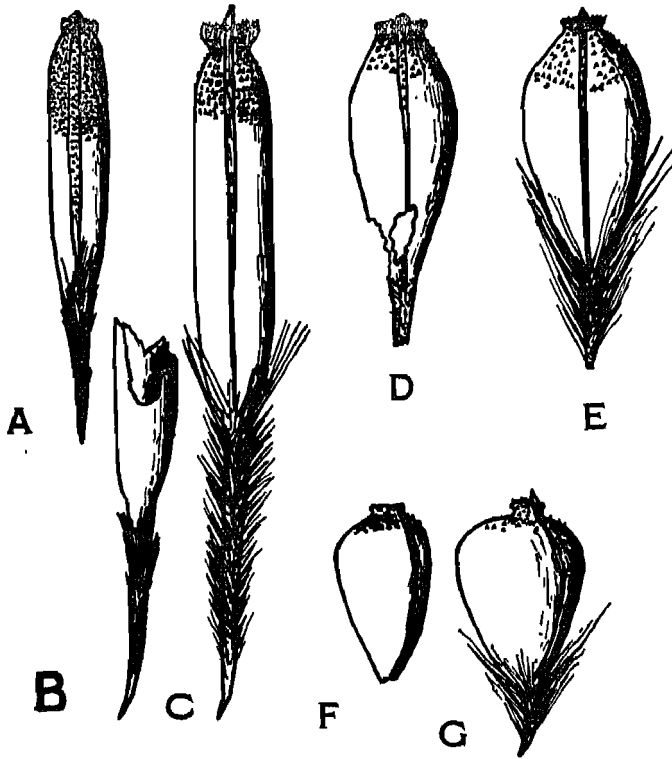


FIG. 49. Fruits of fossil *Stipidium* and *Berriochloa* and of living *Piptochaetium*. A and B, *Stipidium commune* Elias, redrawn from Elias 1942; C, *Piptochaetium napostaense*, drawn from herbarium specimen from Argentina; D, *Stipidium intermedium*, redrawn from Elias 1942; E, *Piptochaetium ruprechtianum*, drawn from herbarium specimen from Argentina; F, *Berriochloa amphoralis*, redrawn from Elias 1942; G, *Piptochaetium bicolor*, drawn from herbarium specimen from Argentina. From Stebbins 1947b.

North American ones, and they are probably allopolyploids. The period of extinction of Stipeae species, therefore, was apparently accompanied by hybridization and polyploidy. Moreover, Elias has noted that the only seeds of woody plants found in these deposits are identical with those of the modern *Celtis reticulata* and show no change from the oldest to the youngest deposits. In the Great Plains, therefore, the herbaceous species seem to have evolved rather rapidly during the latter part of the Tertiary period, while the woody ones, like the trees and shrubs of the forest belt, may have remained more constant.

The third group of fossils of herbaceous angiosperms is the extensive series of seeds known from the Pliocene deposits of northwestern Europe (Reid and Reid 1915, Reid 1920a,b, Mädler 1939). As was shown by Reid and Reid, many of these can be compared directly with the seeds of modern species now living in the mountains of China, and they thus represent species which have become extinct in part of their range, but remain unchanged in another part. Other seeds were identified as belonging to a modern genus, but they did not seem to represent any living species, while a small percentage were unidentifiable as to genus or even to family. It is, of course, possible that these seeds belong to some as yet unrecognized modern species, and there is no way of saying how many of them, instead of becoming extinct, gave rise to divergent modern European species of their genera. Nevertheless, the proportion of unidentifiable seeds to those resembling modern species should provide a rough estimate of the amount of evolution which has taken place in western Europe since the Pliocene. In particular, the fact that these floras contain seeds of herbaceous and woody species in about equal proportions should provide a basis for comparing the rate of evolution in the two types. The results of such a comparison, compiled from Reid and Reid's (1915) data on the early Pliocene Reuverian flora, are given in Table 9.

From these figures it seems likely that the herbs associated with

TABLE 9
COMPARISON BETWEEN RATE OF EXTINCTION IN WOODY AND HERBACEOUS SPECIES OF THE EARLY PLIOCENE REUVERIAN FLORA

	Woody		Herbaceous	
	Number of species	Percent	Number of species	Percent
Fossil seeds referred to modern species, either European or exotic	25	27	31	25
Fossils referred to modern genus, but not species	56	59	70	57
Fossils not identified	<u>13</u>	14	<u>22</u>	18
Total	94		123	

the forest existing in western Europe in early Pliocene times have not evolved any more rapidly than the woody species of this flora.

Thus, the scanty fossil evidence available suggests that under some conditions the herbaceous elements of the flora may have evolved at about the same rate as the woody species, but that at other times their evolution was considerably faster. Many more examples must be available before this evidence can be of major service in determining the rates of evolution of herbaceous groups.

MODERN PATTERNS OF DISTRIBUTION AND THEIR INTERPRETATION

Evidence on rates of evolution may be obtained from one direction by means of fossils, which tell more or less directly how fast certain particular groups of animals and plants have evolved under environmental conditions which may be elucidated, at least in part. And from another direction, the evidence from genetics, by explaining the mechanism and the dynamics of evolution, makes possible the formulation of hypotheses concerning the rates of evolution in entirely different organisms. Barring the unlikely discovery of an organism which is well represented in the fossil record and at the same time is favorable genetic material, the gap between these lines of evidence can be filled only to a limited extent. But the best means of filling this gap are provided by an entirely different discipline, namely, the study of the contemporary distribution patterns of modern animals and plants of all types. These patterns, like the external appearance and genetic constitution of the organisms themselves, are the end result of the interaction of various evolutionary processes and of changes in the earth's surface and climate over long periods of time. If, therefore, two or more unrelated groups of organisms have identical or similar modern patterns of distribution, one can reasonably infer that their evolutionary histories have been similar, at least in certain respects, and during the more recent periods of geological time. Furthermore, if a large enough number of such distribution patterns is known, comparisons can be made between those exhibited by organisms well represented in the fossil record, but unknown genetically, and those of other organisms of which the genetics and cytology are known, but which do not occur as fossils. But in all such studies of distribution, evidence from every possible direction must be considered, and the most probable

hypothesis must be developed separately for each group of organisms, after the different lines of evidence have been compared. There is probably no field of biology in which broad generalizations are more dangerous than in plant or animal geography.

Two generalizations which must be greatly qualified or entirely discarded on the basis of modern knowledge are, first, that the age of a group of organisms may be determined by counting the number of members of that group now living and comparing its size with that of related groups and, second, that the age of a species or of any other systematic category is directly related to the size of its distributional area. These generalizations are the basis of the Age and Area hypothesis advanced by Willis (1922, 1940). The numerous criticisms of this hypothesis have been discussed by Wulff (1943) and by Cain (1944), and are ably summed up in the words of the latter author (1944, p. 230):

According to Willis' age-and-area hypothesis, most endemic species are considered to be youthful. It is a truism of biology that populations tend to expand their areas in ever-increasing concentric circles, other things being equal. This ideal is seldom realized, for other things are seldom equal. Nevertheless, it is not possible to accept the fact, for an endemic species of narrow range, either that it is young or that it is old from a knowledge of its area alone. It is necessary to inquire into its other characteristics.

Babcock (1947) has inquired very thoroughly into other characteristics of the genus *Crepis*. As a result, he has been able to classify the species of this genus in respect to age and degree of advancement with greater probable accuracy than has been possible in any other genus not well represented in the fossil record. He has found (p. 129) that among the narrowly restricted endemic species of these genus there are two primitive, three intermediate, and five advanced types. Obviously, neither the age and area nor the relict hypothesis are valid as generalizations to explain the narrow endemics of *Crepis*. This is just what would be expected on the basis of theories which take into account the genetic nature of species populations (Cain 1940, 1944, Chap. XVI, Stebbins 1942b, Mason 1946a,b).

The same consideration holds in respect to the generalization which assumes that the age of a group is proportional to its size. It is probably true in general that any successful group of or-

ganisms is small at the beginning and gradually increases its size through the evolution of new species. But fossil evidence indicates that this increase may be slow or rapid, and may persist until the group has become very large, or it may stop and be followed by a decrease before many species have evolved (Simpson 1944). For these reasons, the elaborate calculations of Small (1937a,b, 1945, 1946, Small and Johnston 1937) are based on a fallacy. Furthermore, the interpretation by Willis and Small of the regular "hollow curves" which are obtained when the size of the groups is plotted against the frequency of groups of a particular size is also fallacious, as Wright (1941b) has pointed out. In fact, such hollow curves can be obtained by plotting the frequency of almost any series of categories of different sizes, such as the college graduates of any class with a certain income or the surnames in a telephone book.

Still another series of generalizations which are subject to numerous qualifications are those which seek to establish rules for determining the place of origin of a particular group. The best known of these is that the place of origin of a group is the region in which the largest number of representatives of that group exists at present. As applied to the origin of genera and families in terms of the distribution of living species, this generalization forms part of the Age and Area theory of Willis. But the gene center theory of Vavilov (1926), which states that the place of origin of a species of cultivated plant is that which contains at present the largest number of genetic varieties of that plant, is essentially similar. The center of origin theory as applied to genera and families has been criticized by Fernald (1926), Wulff (1943), Cain (1944), and many others, while the gene center theory has been similarly criticized by Schiemann (1939) and Turesson (1932). These criticisms have all been essentially similar. If the group in question is a young one, and if the selective forces of the environment, including competition with other organisms, have been operating in about the same manner throughout its evolutionary history, then the center of diversity and the primary center of origin are likely to be the same. But if the group is old, and particularly if it has formerly existed in regions where it is no longer found, or if it has survived great alterations in the environment, secondary centers of diversity are likely

to have arisen in areas which more recently became favorable to the members of the group, and it may even have died out in the place where it originated.

Matthew (1939) has shown that for orders, families, and genera of mammals the fossil evidence is absolutely contradictory to the center of diversity—center of origin hypothesis. The horses, for instance, originated in North America, which now contains no indigenous species of this family. Its present centers of diversity, southwestern Asia and central Africa, were not occupied by the ancestors of its modern representatives until late Pliocene or Pleistocene time. For the order of marsupials, Australia is a center of diversity as prominent and striking as any which can be found for a group of animals or plants. But the evolution which produced this diversity is relatively recent and has obviously resulted from lack of competition with other mammals. The original marsupials probably entered Australia in the latter part of the Cretaceous period. With this example in mind, botanists should be very hesitant to assume that such genera as *Eucalyptus* and *Acacia*, which have equally prominent centers of diversity in Australia, originated on that continent. In fact, Diels (1934) has postulated that these and many others of the subtropical groups endemic to or strongly developed in Australia are of Malaysian origin. His hypotheses on the origin of the Australian flora are entirely in accord with the fossil evidence, both old and new.

On the basis of his evidence from mammals, Matthew produced another generalization about centers of origin, namely, that the center of origin is the region in which the most advanced species are found, while the most primitive species may be expected near the periphery of the range of the group. This generalization is, however, as dangerous as the previous ones. It is based on the following assumption (Matthew 1939, pp. 31–32).

Whatever be the causes of evolution, we must expect them to act with maximum force in some one region; and so long as the evolution is progressing steadily in one direction, we should expect them to continue to act with maximum force in that region. This point will be the center of dispersal of the race. At any period, the most advanced and progressive species of the race will be those inhabiting that region; the most primitive and unprogressive species will be those remote from this center.

If a group has lived through a period of great changes in climate, the selective forces guiding evolution will have changed their intensity and geographic position, and the above assumptions are obviously invalid. This has been true of all genera of plants and animals of the North Temperate Zone, since they all antedate the mountain-building period of the later Tertiary and also the glaciations of the Pleistocene. Direct evidence bearing on Matthew's hypothesis of the peripheral distribution of primitive types can be obtained from the cytology and distribution of polyploid complexes. Their diploid members must be older than the polyploids, although they are not more primitive in the sense that they are less specialized in structure. Nevertheless, on the basis of Matthew's assumption, their greater age should have permitted the diploids to migrate farther toward the periphery of the range of the group, while competition with more aggressive polyploids should tend to eliminate them near its center. Actually, as stated in Chapter IX, a survey of a large number of polyploid complexes has shown that the number of those in which the diploids are peripheral is about equal to those in which the diploids are centrally located and the polyploids are peripheral.

Matthew's hypothesis makes certain assumptions in addition to those which he states. The oldest members of a group will occupy a peripheral position only if their ability for migration and establishment is equal to that of the younger ones. But in many groups of plants, the principal trend of evolution is toward the development of more efficient means of migration and establishment. In many families and genera, the more specialized members differ from the primitive ones in possessing smaller and more numerous seeds and also in the higher development of specialized methods of seed dispersal, such as the pappus of the Compositae, the awns of the Gramineae, and the baccate fruits of many groups. Such species may be expected to overtake their less efficient ancestors in colonizing the globe. Furthermore, the trend in many groups is from long-lived perennials, which as members of climax formations establish themselves very slowly in a new region, to short-lived annuals, which become established quickly and easily. Finally, new polyploid forms, particularly amphiploids, may be able to establish themselves more easily than their diploid ancestors in new, peripheral areas, because of their

greater supply of potential new gene combinations. Matthew's hypothesis may be expected to hold to a different degree in various groups, depending on certain specific properties of their course of evolution. It can thus be weighed in each example against the other hypotheses, according to the available evidence.

Still another type of generalization which may be as misleading as it is helpful consists of those hypotheses which attempt to establish a single region for the origin and differentiation of angiosperm groups and a single basis for their migration from one continent to another. Thus, Wulff (1943, Chap. V) speaks of hypotheses of a polar or a tropical origin of angiosperm groups in general, as if these were mutually exclusive, and he similarly indicates that intercontinental migrations must have been either entirely by land bridges across the present oceans, by migrations southward and northward from the two poles, or that they must all be explained on the basis of the previous union of the continents and the hypothesis of continental drift. Similarly, Camp (1947), by assembling a great number of distributional maps, has attempted to show that the differentiation of angiosperm families took place almost entirely in the Southern Hemisphere. But certain facts of distribution of both living and fossil organisms suggest that families have been differentiated on most if not all of the major land masses, and that migrations of plants have taken place in many different directions and via a number of different intercontinental connections, both past and present, as well as across the "stepping stones" afforded by groups of neighboring islands.

In the first place, certain specialized families of flowering plants are either endemic to or occur so predominantly on one continent that they must be assumed to have originated there. Thus, one can hardly doubt that the Bromeliaceae originated in South America, the Polemoniaceae and the Hydrophyllaceae in North America, the Valerianaceae and the Dipsacaceae in Eurasia, the Bruniaceae in Africa, and the Goodeniaceae and the Candolleaceae in Australia. Cain (1944, p. 245) has presented data from Irmischer to show that such endemic families are not predominant on any one continental mass. By analogy, one can suggest that the most likely situation is that the origin of the more widespread families has likewise been shared by various continental masses,

with no one continent contributing an overwhelming proportion of them. In regard to the origin of the class of angiosperms as a whole, the present condition of our knowledge has been aptly expressed by Chaney (1947, p. 141) as follows.

The ultimate origin of angiosperms is not clearly indicated by the Mesozoic record; much collecting by paleobotanists, followed by broad investigations both by paleobotanists and botanists, must precede our understanding of the nature and relationships of the earliest angiosperms, and our designation of the area or areas from which they have spread out to colonize the earth.

In regard to migration routes, Matthew (1939) has assembled a great body of fossil evidence to show that all migrations of land mammals from the Old World to the New, and vice versa, have been by Holarctic continental connections. But this does not mean that mammalian faunas have all been differentiated near the North Pole; on the contrary, the great centers of mammalian differentiation have been at middle latitudes in the centers of the large land masses of Eurasia, North America, and South America, with lesser centers of differentiation in Africa and Australia. The Holarctic higher latitudes have served as routes of migration, not as centers of differentiation. For the most part, these intercontinental connections have had a temperate climate, but, as previously mentioned, evidence from plant fossils indicates a subtropical climate during the Eocene epoch and perhaps at other earlier periods over at least a large part of the southern fringe of the Asiatic-American land bridge, in the site of the present Aleutian Islands and Alaska Peninsula.

On the other hand, Florin (1940, 1944b) has shown from fossil evidence that the conifers of the Southern Hemisphere have migrated freely from Australasia to South America and vice versa, while since the Jurassic or the Cretaceous period these conifers have remained entirely distinct and separated from those of the Northern Hemisphere. The apparent discrepancy between these two lines of evidence can be resolved on the basis of the different potentialities for migration possessed by these very different types of organisms. Mammals possess very limited capacities for crossing large bodies of water. This is a matter of observation and is also attested by their absence from most oceanic islands. On the other hand, the seeds of plants may occasionally be transported

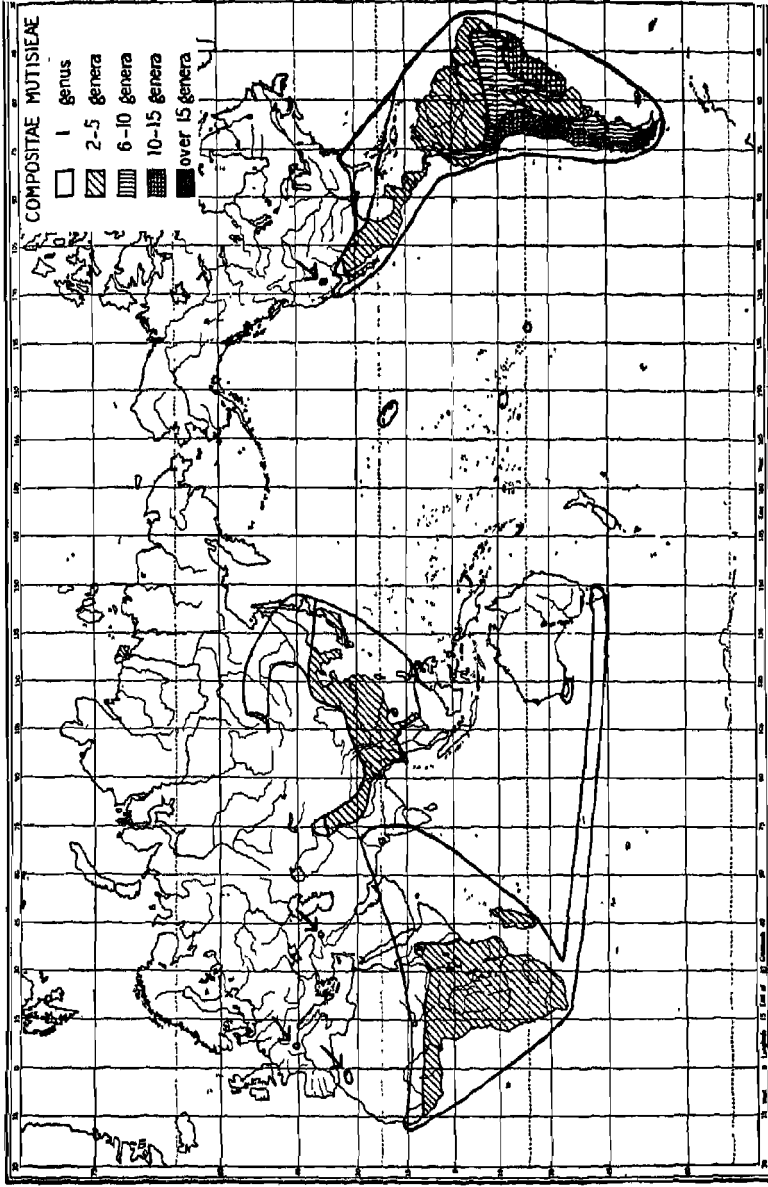


FIG. 50. Map showing the distribution of the tribe *Mutisaceae* of the family *Compositae*, a group at present of austral distribution, but possessing relict genera in the Northern Hemisphere (shown by the arrows), which suggest a northern origin for the group. From Stebbins 1941c. Base map, Eubank's outline map of the world, by permission of Standard Process and Engraving Co., Berkeley, Calif.

over many hundreds of miles of ocean and may establish themselves on remote oceanic islands like Hawaii, Juan Fernandez, St. Helena, and the Canary Islands. We may therefore postulate that the antarctic connection between Australasia and South America existed for plants, but not for vertebrates. It probably consisted of an enlarged antarctic continent, with a temperate climate, which even now is near enough to South America so that seeds could be borne from one land mass to the other without difficulty, plus a series of islands partly connecting Antarctica with Australia and New Zealand (Hill 1929).

On the basis of this evidence, we should expect to find at least two different origins for those plant groups which are now predominant in the Southern Hemisphere. Some of them, like the southern mammals and reptiles, may be relict survivors of migrations from the north or groups derived secondarily from such relicts. Such an interpretation was suggested by the writer (Stebbins 1941c) for the primarily South American tribe Mutisieae of the family Compositae, on the basis of the virtual absence of this tribe from Australasia and the occurrence of isolated relict genera both in North America and in Eurasia (Fig. 50). As mentioned in Chapter IX, the fossil evidence suggests a similar northern origin for the numerous temperate South American species of the grass genus *Piptochaetium*. On the other hand, there is now little doubt that the Podocarpaceae, the Araucariaceae, and other southern groups of conifers originated in the south, or at least underwent their greatest differentiation on the southern continents. The same is most probably true of *Astelia*, *Luzuriaga*, *Acaena*, *Eucryphia*, and many other genera of flowering plants listed and mapped by Hill (1929), Skottsberg (1936), Camp (1947), and others (Fig. 51). DuRietz (1940), in his extended discussion of bipolar distributions, has clearly recognized these two types of origin.

DISJUNCT DISTRIBUTIONS AND THEIR SIGNIFICANCE

The data from plant geography which may be compared most directly with the data from paleobotany, on the one hand, and those from genetics and cytology, on the other, and thus provide indirect evidence for estimating evolutionary rates, are those data obtained from studies of disjunct distributions of species, genera,

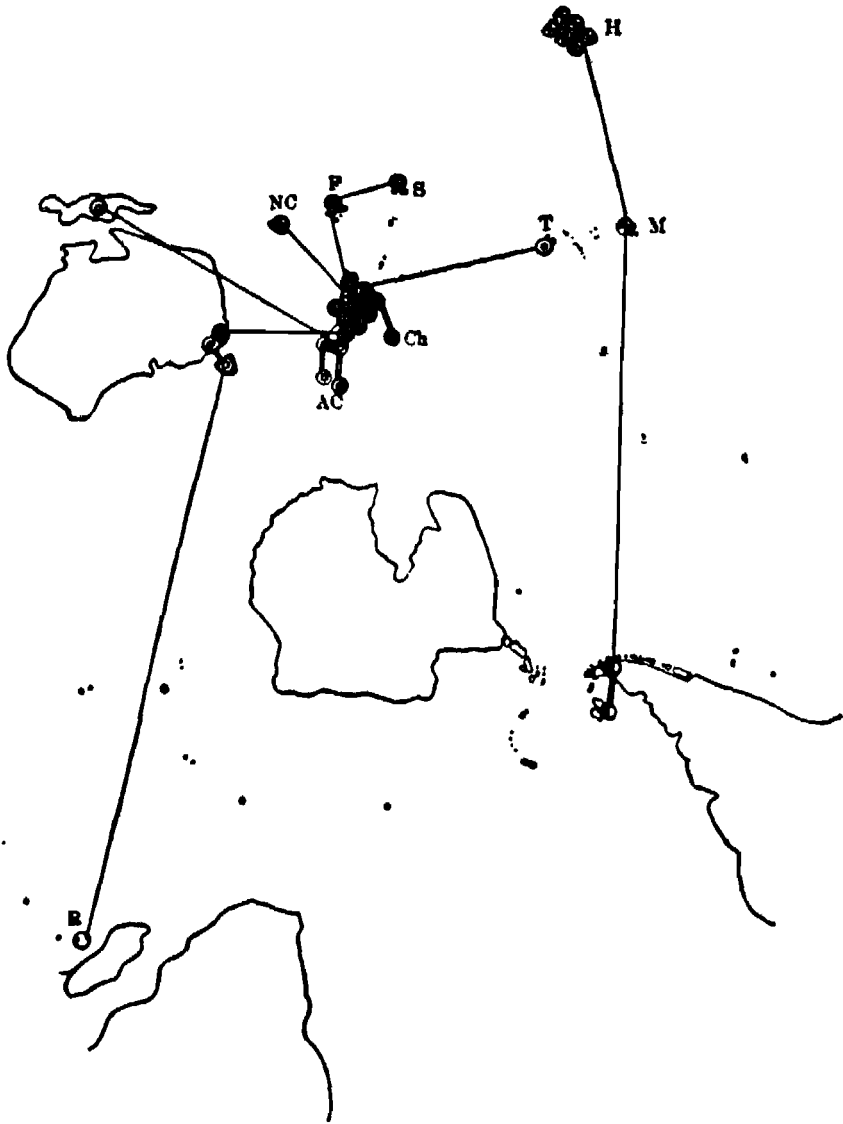


FIG. 51. Map showing the distribution of *Astelia* and *Collospermum*, two typical Antarctic genera. Antarctica is in the center of map, Australia at upper left, South America at lower right. From Skottsberg 1936. By permission of the University of California Press.

AC — Auckland and Campbell Islands
 Ch — Chatham (Warikauri) Island
 F — Fiji Islands
 H — Hawaiian Islands
 M — Marquesas Islands

NC — New Caledonia
 R — Reunion
 S — Samoa
 T — Society Islands

and families of organisms. The significance of such distribution patterns was clearly recognized by the early evolutionists of the nineteenth century, such as Darwin, Wallace, Hooker, and Gray, and many of the most important patterns were already described by these authors. A great succession of plant geographers has amplified and partly clarified our knowledge of these patterns, while more recently several paleobotanists, like Seward, Reid and Chandler, Kryshstofovich, Florin, Berry, Chaney, and Axelrod, have related these patterns to the evidence from the fossil record, and in general have supported the major hypotheses developed by plant geographers. Finally, cytological and genetic studies are beginning to provide an evaluation of the amount of genetic difference between the isolated populations of some disjunct groups, and therefore of the amount of evolutionary divergence which has taken place since they became separated from each other.

Disjunct distributions may involve taxonomic categories of all degrees of size. Single species which occur in two widely separated areas are *Cypripedium arietinum*, *Symplocarpus foetidus*, *Brachyelytrum erectum*, and *Polygonum arifolium* (Fig. 52), all of which

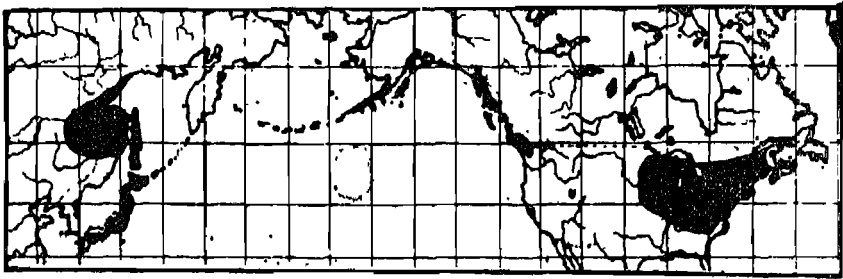


FIG. 52. Distribution of *Symplocarpus foetidus* in Asia and North America. From Fernald 1929.

have one area of distribution in eastern North America, and the other in eastern Asia (Fernald 1929). The distance between the separate areas of these species, which is nearly half the circumference of the earth, is probably the greatest which can be found. All degrees of separation can be found from this maximum down to the isolation of the separate populations of a species on different islands, mountain tops, or other areas which are only a few miles apart. If populations occupying separate areas are clearly

descended from an immediate common ancestor, but are distinct enough in external morphology so that the systematist can always tell them apart, they are known as *vicarious species*. The different types of vicariads have been discussed and classified by Cain (1944,

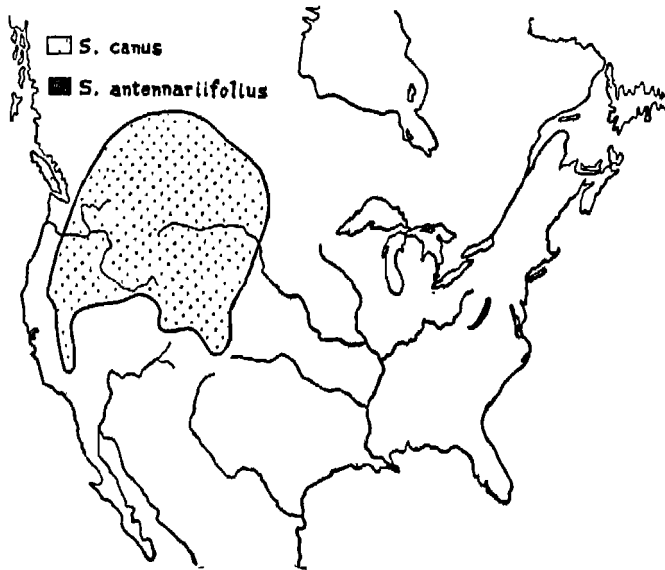


FIG. 53. Distribution of two closely related vicarious species, *Senecio canus* of the western Cordillera and *S. antennariifolius* of the Appalachian shale barrens. From Stebbins 1942b.

Chap. XVIII). Some of them are the sole representatives of their genus in each area, as in the genera *Diphylleia*, *Podophyllum*, *Cercis*, and *Platanus* of Eurasia and North America (Fernald 1931). In other instances, such as *Senecio canus* of the western United States and *S. antennariifolius* of the Appalachian shale barrens of the eastern states, the genera concerned are represented by a large number of species in each area, but the two vicarious species are more closely related to each other than either is to its associates in the same area (Fig. 53). Disjunct distributions for entire genera are well known. Among the widest disjunctions is that of *Hypochaeris*, with one group of species in Eurasia and another in temperate South America (Stebbins 1941c). Disjunct families or subfamilies are also well known; numerous examples are given by Fernald (1931), Cain (1944), and Camp (1947).

For the purpose of linking paleontological with cytogenetic

evidence on rates of evolution the significant disjunct patterns are obviously those in which the populations in the separate areas are related closely enough to each other so that they can be intercrossed, that is, disjunct species and vicarious species of the same genus. The significant data on such species are only in part those obtained by the systematist on the basis of external morphology. A much more accurate picture of the amount of evolutionary divergence between the vicarious forms can obviously be obtained by growing them under uniform conditions, by studying the number and morphology of their chromosomes, and especially by crossing them and determining the chromosome behavior and degree of fertility of their hybrids.

As has been brought out by Wulff (1943) and by Cain (1944), three explanations may be offered for any example of vicarious areas of distribution. The first assumes that the forms originated independently in the areas which they now occupy and that their present similarity is due to parallel or convergent evolution. The information which we now have on the genetic nature of the morphological differences between subspecies and species, as outlined in earlier chapters of this book, makes this hypothesis so improbable as to be untenable for all examples of single species with disjunct distribution patterns. Species differences are based largely on systems of multiple factors, which are built up by the occurrence and establishment of large numbers of genetically independent mutations. Hence, the probability that two isolated populations will evolve in exactly the same way in all of their characteristics is astronomically low, and the convergence in every respect of previously dissimilar organisms is even less probable. In regard to morphologically different, but apparently related, species, hybridization experiments can provide decisive evidence to show whether their similarity is due to true relationship or to convergent evolution. If the vicarious forms are more easily intercrossed and produce more fertile hybrids with each other than either of them does with any of its associates in its own area, the hypothesis of a common origin is by far the most probable one. But in many instances such elaborate experiments are not necessary. If the forms concerned possess no other relatives in one or both of their vicarious areas of distribution, their independent origin is extremely improbable. Wulff (1943, pp. 55-56) points

out that isolated species of a number of arctic or boreal genera, such as *Primula*, *Draba*, *Saxifraga*, *Gentiana*, *Carex*, and *Phleum*, occur in the southern tip of South America, separated by many thousands of miles from their numerous northern relatives. These species could not have originated in their present habitat, since no possible ancestors exist there. They or their ancestors must have migrated southward from the north temperate regions.

Assuming that the two separated or vicarious populations have had a common origin or are immediately descended from a single common ancestor, two extreme hypotheses are often suggested to explain their present disjunction. Either they have always been separated, and migration took place by long-distance dispersal of seeds across the intervening territory, or the present disjunct areas are relicts of a former continuous distribution of the group. These two hypotheses are not sharply distinct or mutually exclusive. In many instances, two widely separated vicarious areas may never have been completely joined, but may have been closer to each other or partly connected by a series of intermediate, but still disjunct, areas. Furthermore, the hypothesis of a past continuous distribution need not imply that the former range of the group included both of the present areas plus the entire distance between them. They may have radiated from a third region and have become disjunct before they reached their present areas. Figure 54 illustrates five different methods of origin of vicarious areas: long-distance dispersal, past greater proximity, past continuity, "stepping stones," and divergent migration from a third area. Various combinations of these hypotheses may, of course, be imagined.

Evidence exists that each of these explanations is true for different ones of the modern vicarious areas. Long-distance dispersal has most probably been the method of colonization of remote oceanic islands, like Juan Fernandez, St. Helena, and the Canary Islands. Geological evidence is strongly against the hypothesis that these islands ever formed part of a major continent, and the absence or scarcity on them of mammals, fresh-water fishes, and other forms of life which could not possibly cross salt water is likewise significant. In recent years Skottsberg (1925, 1938, 1939) has championed the hypothesis of continuous distribution over past land bridges to explain the origin of the flora of all the Pacific

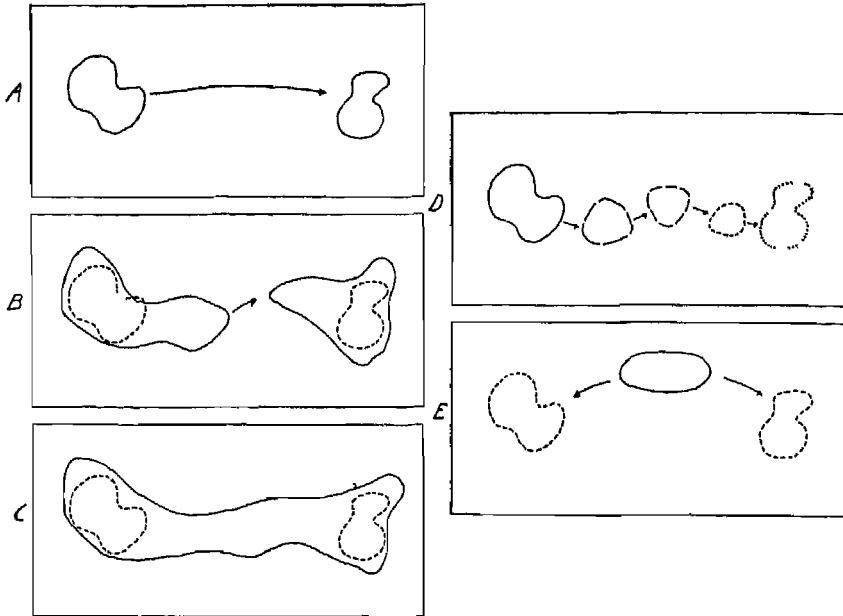


FIG 54. Diagrams showing five different ways in which an instance of a disjunct distribution can arise. A, direct dispersal over a long distance; B, dispersal over a shorter distance through wider distribution and greater proximity of the two areas in the past; C, wider distribution with complete continuity between the two areas in the past; D, dispersal over a series of short distances by means of "stepping stones"; E, migration from a former area outside of the two present areas. Original.

islands. The chief arguments in favor of this have been the difficulty involved both in the transport of seeds over such long distances and in the establishment of the plants once these have arrived. But Mayr (1939, 1943) and Zimmerman (1942, 1948), basing their opinions, respectively, on the distribution of land birds and of insects, see no insuperable difficulties in the transoceanic migrations of these animals to all the islands which they now occupy. Zimmerman points out that such migrations need not have been over the entire distance now separating an island from the nearest land mass with similar ecological conditions. At least in the Pacific, numerous islands undoubtedly existed which are now represented only by low atolls, while other islands were formerly much larger than they are at present. Both authors agree that given sufficient time, extremely improbable events could occur. Their reasoning can be transferred to the colonization of

mountain peaks by alpine plants and to other similar types of dispersal over land, as Mason (1946b) has pointed out.

The "stepping stone" method of long-distance dispersal is the most likely one to explain the antarctic migration and radiation of plants. Guppy (1906, cited by Cain 1944) has suggested this as the way in which arctic and cool temperate plants migrated from the north temperate to the antarctic regions, using as temporary refuges the higher mountain peaks of the tropics. This hypothesis has much to recommend it. A notable fact is that, with the exception of the subtropical and the desert floras, the vicarious elements which have a bipolar disjunction in North and South America (DuRietz 1940) are herbs with efficient methods for the transport and establishment of propagules. The floras of California and central Chile have many genera in common, such as *Chorizanthe*, *Acaena*, *Godetia*, *Phacelia*, *Mimulus*, *Blennosperma*, *Madia*, and *Agoseris*, and in most of these genera closely related vicarious species exist on the two continents. But the trees and shrubs of these two regions, although they possess very similar ecological adaptations, have entirely different relationships. Whereas the forests and the scrub areas of California are dominated by *Pinus*, *Quercus*, *Sequoia*, *Pseudotsuga*, *Arctostaphylos*, *Ceanothus*, and *Adenostoma*, those of Chile are characterized by *Araucaria*, *Podocarpus*, *Nothofagus*, *Fitzroya*, *Persea*, *Quillaja*, *Kageneckia*, *Adesmia*, and other types totally unfamiliar to northern botanists. The Magellanic flora, likewise, although it contains many species of arctic derivation, is entirely antarctic so far as its dominant elements are concerned. This condition is explained more easily on the assumption that the plants which crossed the equator possessed superior means of transport and establishment, rather than on the assumption that there was ever a continuous pathway of migration across the tropics for all types of temperate plants, as DuRietz (1940) has postulated.

The explanation of divergent migration is the most likely one for the disjunct distribution of many arctic and boreal species, as discussed by Hultén (1937). These have radiated outward from refuges which they occupied during the periods of glaciation, and in many instances they now occur in widely separated areas. On the other hand, there are undoubtedly many other vicarious and disjunct species of these regions which had contin-

uous distributions before the last advance of the ice and have persisted only in unglaciated refugial habitats. The nunatak hypothesis of Fernald (1925) and the postglacial migration hypothesis of Wynne-Edwards (1937) in regard to the origin of the numerous isolated populations of far western species and local endemics centering about the Gulf of St. Lawrence may not be entirely contradictory. Some of these species may be preglacial relicts and others, postglacial immigrants.

The two hypotheses of complete and of partial continuity of distribution in the past are very difficult, if not impossible, to differentiate from each other. For both of them we have ample supporting evidence from fossils in the case of certain modern disjunctions. The most important of these are the tropical and subtropical discontinuities and the temperate discontinuities between Eurasia, particularly eastern Asia, and either the eastern or the western part of North America. The greater extension northward of subtropical floras in early Tertiary times has already been discussed. There is at present no evidence that these floras extended continuously across the Bering land bridge from Asia to America, but the Asiatic and American segments of these subtropical floras undoubtedly were closer to each other in the Eocene epoch than they are at present. They must have been at least close enough so that migration of subtropical species across this bridge was possible. The Asiatic-American disjuncts of temperate climates almost certainly ranged continuously from one continent to the other during the early part of the Tertiary period. Fossils of woody genera, such as *Carpinus*, *Castanea*, *Fagus*, *Juglans*, *Quercus*, and *Ulmus*, are known from a great number of localities in both the Old and the New World, in addition to Alaska (Chaney 1940a,b, 1947). During the Miocene epoch this bridge probably became closed to mesophytic trees and forest-loving types, except for boreal groups like *Picea*, *Salix*, *Alnus*, *Betula*, and *Acer*. The data of Smith (1919) indicate that the marine climate at that time was as cold as it is now, and the late Miocene floras of the western United States also indicate a climate as cold as the present one, as well as the beginning of arid conditions in the Great Plains area, effectively isolating the eastern American forests from the western ones.

The establishment of these past intercontinental connections

between floras and the approximate determination of the time when they existed gives us, finally, an opportunity for estimating the rate of evolution, or the degree of evolutionary stability, of certain plant groups which have discontinuous distributions in these areas. We can assume with some degree of certainty that vicarious species with disjunct distributions in the tropics of the Old World and the New World have not been able to exchange genes since the middle of the Eocene epoch, 40 to 50 million years ago, while the numerous species with disjunct distributions in the temperate forests of Asia and America have not exchanged genes for 15 to 20 million years.

The subtropical and the tropical disjuncts consist mostly of genera with one area of distribution in the Old World and one in the New World. These are very irregularly distributed through the plant kingdom, as judged from a survey of distribution patterns as they are given in Engler and Prantl's *Die natürlichen Pflanzenfamilien*. Among the 84 genera of the Gesneriaceae, no examples are given. The genera of Palmaceae contain only a doubtful example in *Elaeis*, as well as *Cocos nucifera*, which is probably an example of recent long-distance transport by water or man. There are likewise very few examples of pantropical distributions among the 450 genera of Orchidaceae, the 100 genera of Araceae, and the 217 genera of Asclepiadaceae. But of the 40 genera of Convolvulaceae, 10 are pantropical, and in the Begoniaceae the only large genus, *Begonia*, is strongly represented in both the Old World and the New. Among the tropical genera of Gramineae and Cyperaceae, not only are there many which occur in both hemispheres, but in addition some of these contain closely related vicarious species. In the grasses, for instance, *Erianthus maximus* of Polynesia has its closest relative in *E. trinii*, of Colombia, Brazil, and Paraguay (Grassl 1946). In the related genus *Imperata*, *I. cylindrica* of subtropical regions in the Old World is closely related to *I. hookeri* of the southern United States. In the genus *Pennisetum*, *P. trachyphyllum* of Africa is vicarious to *P. latifolium*, *P. bambusaeforme*, and *P. tristachyum* of tropical America. These genera are not primitive, but highly advanced, specialized members of their family. The vicarious pantropical distribution of certain species groups indicates, nevertheless, that they were already well differentiated in the Eocene epoch, and

suggests that much of the differentiation of genera in the Gramineae took place before this time. The same may be said of the Cyperaceae and the Convolvulaceae. Evolution in certain genera of these families during the last 50 million years has consisted only in the differentiation of species essentially similar to those already existing, and some of the modern species may be only slightly different from their Eocene ancestors. On the other hand, the fossil record of the Stipeae, mentioned earlier in this chapter, suggests that other genera of grasses, particularly those of temperate climates, were evolving actively during the Tertiary period.

Although the presence of vicarious pantropical patterns of distribution indicates great age and evolutionary stability for the group concerned, the absence of such patterns does not necessarily mean that evolution has been rapid. *Chaetoptelea mexicana*, which is the almost unchanged descendant of the Eocene *C. pseudofulva* (MacGinitie 1941), has a single area of distribution in Mexico, and the restricted relict distribution of many other early Tertiary and Cretaceous types forms, not a disjunct pattern, but a single area. We must not therefore assume that the genera of palms, aroids, orchids, asclepiads, and Gesneriaceae are nearly all recent as compared to *Erianthus*, *Pennisetum*, *Oryza*, and other tropical genera of grasses. Nevertheless, there is some reason for believing that generic differentiation has been considerably more active during the Cenozoic era in these families, than it has in the grasses, sedges, and Convolvulaceae.

Turning to the Asiatic-American disjunctions of the temperate zone, the North Pacific disjunctions of Wulff (1943), we find that nearly all of the genera of woody plants in these regions are involved. As has already been mentioned, ample fossil evidence has shown that these genera were well differentiated and practically in their modern form by the Eocene epoch. An equally large list of herbaceous genera could be cited, as was first noted by Asa Gray and has been repeatedly observed by other botanists (Cain 1944, pp. 251-257). Nearly all the herbaceous genera of the deciduous forests of the North Temperate Zone were probably well developed by the Eocene epoch 50 million years ago, and many of them may be much older (Fernald 1931). Furthermore, some species of herbaceous plants have disjunct distributions in eastern North America and eastern Asia (see Figure 52).

All available evidence suggests that these species have evolved little or not at all during the past 15 to 20 million years. In the case of two annual species, *Polygonum arifolium* and *P. sagittatum*, this means that they have gone through more than 15 million generations without evolutionary divergence.

The evidence from distribution thus supports that from fossils in indicating great evolutionary stability in the floras of the temperate forest belts, and in at least some elements of the mesophytic floras of the tropics. Both of these lines of evidence, however, are of such a nature that they make hypotheses of evolutionary stability much easier to support than those which favor evolutionary progress. For the plant groups which they represent, they indicate stability, but they do not preclude the possibility that much more active evolution has been going on contemporaneously in other groups.

DISTRIBUTIONAL PATTERNS SUGGESTING RAPID EVOLUTION

Patterns suggesting rapid evolution are those which consist of many closely related species occurring in adjacent localities within the same general area, particularly if that area is known to be a recently disturbed one. This postulate was suggested some time ago by Sinnott (1916) and has since been repeated by a number of authors. Thus, Marie-Victorin (1929, 1938) has called attention to the apparent sudden burst of speciation of the genera *Crataegus* and *Oenothera* in eastern Canada since the advent of the white man and the clearing of the forests, and to the similar phenomena in *Rosa*, *Hieracium*, and *Rubus* in Europe, as well as *Acacia* in Africa, *Sorbus* in the Orient, and *Hebe* (*Veronica*) in New Zealand. Most of these can be dismissed as special cases. As was mentioned in earlier chapters, the apomicts of the European *Hieracium* and *Rubus* are not equivalent genetically to species in sexual groups, while the peculiar "microspecies" of *Oenothera* in eastern North America and of the *canina* roses of Europe are the results of abnormal types of genetic segregation and are more comparable to the individual genotypes or, at most, to the ecotypes of cross-fertilizing sexual organisms than to their species. *Crataegus* and *Sorbus* are likewise probably agamic complexes, and it is likely that the new "species" of these genera which have populated cleared areas in China and America are mostly, if not

entirely, apomicts of autoploid or hybrid derivation rather than true species. *Hebe* is known to form hybrid swarms (Allan 1940), so that the "species" of this genus may be largely unstable segregates from hybridization, like the "species" of *Iris* from the Mississippi Delta which have been described (cf. page 283).

Nevertheless, the conditions postulated by Marie-Victorin for the rapid evolution of new species, namely, the opening up of new environments to which particular organisms are especially well suited, are undoubtedly valid, and given sufficient time, genetically isolated sexual species can be expected to evolve in them in considerable numbers. Examples should be sought in the weedy floras of those regions which have for the longest time been subject to man's influence, particularly China, India, and the eastern Mediterranean region.

In the genus *Crepis* (Babcock 1947), active evolution of new, highly specialized species has undoubtedly been going on throughout the million years of the Pleistocene and recent epochs. The distribution patterns of the most advanced sections of this genus



FIG. 55. Distribution of the ten species comprising one of the phylogenetically most advanced and recent sections of the genus *Crepis*. From Babcock 1947; based on Goode base map No. 124, by permission of the University of Chicago Press.

show typical clusters of adjacent, closely related species (Fig. 55). In the case of two of the species included in Figure 55, *C. neglecta* and *C. fuliginosa*, the genetic basis of their differentiation is well understood (Tobgy 1943), and the time of this differentiation was probably the early part of the Pleistocene epoch. In a neighboring section, the polymorphic *C. vesicaria* contains eight subspecies, some of which, such as subspp. *myriocephala* and *taraxacifolia*, are beginning to develop sterility barriers between them and appear to be on the way to becoming species (Babcock 1947, pp. 825-863).

Another example of species clusters in a newly differentiated environment is presented by the tribe Madinae of the family Compositae in central California, already discussed in Chapter II (cf. Clausen, Keck, and Hiesey 1941, 1945a). In this tribe there are many examples of closely related species occupying localities which are near each other but nevertheless geographically and ecologically distinct and separated by imperfectly developed barriers of partial hybrid sterility. These are discussed more fully in another publication (Stebbins 1949a). Examples are also cited of probable rapid evolution in perennial herbs and even in woody groups, like *Ceanothus* and *Arctostaphylos*. These, however, are shrubs of pioneer formations; the dominant trees of the Californian savanna area are species of *Quercus* and *Pinus*, which have changed little or not at all since the Miocene epoch (see page 521).

THE POSSIBLE BASIS FOR DIFFERENTIAL EVOLUTIONARY RATES

The presence of widely different rates of evolution, both between different unrelated phyla and between related members of the same order, as well as within a single evolutionary line at different times of its history, has been firmly established for animals by Simpson (1944), on the basis of his analysis of the fossil evidence. He has found that most of the rates found within any order or class fall within a normal curve of distribution as to frequency, and he has designated these rates as horotelic. The normal rate, however, is not measured according to the geological time scale, but in reference to the group of animals under consideration. Thus, the horotelic rates for carnivorous mammals are about ten times as fast as those for pelecypod mollusks.

In addition to these normal rates, Simpson shows that in several

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groups of animals there have existed in the past exceptionally slow and probably also exceptionally fast rates of evolution. The slow rates, termed *bradytelic*, are exemplified by *Lingula*, the well-known modern brachiopod genus which has been virtually unchanged throughout the known fossil record; *Ostrea* (the oyster) and several other genera of mollusks, which have existed since the Carboniferous; and *Sphenodon*, the crocodiles, and the opossum, of which the modern representatives are very similar to their relatives which lived, respectively, in the Triassic, the early Cretaceous, and the late Cretaceous periods. Among plants, bradytelic genera are *Thyrsopteris*, a fern now living on Juan Fernandez Island which closely resembles fossils of the Jurassic period (Seward 1931); *Ginkgo*, *Sequoia*, and probably the living cycads and Gnetales. There is good reason to believe that many genera of thallophytes are as old and conservative as those of mollusks, but these plants are not preserved in the fossil record.

Exceptionally fast rates of evolution, designated by Simpson as *tachytelic*, cannot be directly observed in the fossil record. In even the best series of fossil deposits, events which happened in closer succession than once in a hundred thousand to once in a million years are impossible to observe because not enough fossils are available. Furthermore, on the basis of Wright's conclusion that evolution proceeds the most rapidly in populations of intermediate size which are broken up into partially isolated subunits (see Chapter IV), we should expect members of tachytelic evolutionary lines to be less abundant than those of bradytelic ones, and therefore less likely to be preserved in the fossil record. Simpson has further pointed out that rapid evolution would be expected in organisms imperfectly adapted to their environment or in those adapted to transitory environments, and that such organisms would certainly be uncommon and rarely preserved. For these reasons, Simpson has concluded that the apparent saltations or jumps in the evolutionary progress of many lines, which would include the "revolutions" in the plant world discussed by Sahni (1937), are due to short periods of tachytely rather than to the occurrence of single large mutations. This conclusion is fully in accord with the evidence obtained from living organisms, as summarized in this book. A noteworthy fact is that these bursts of rapid evolution usually occur in the beginning of the develop-

ment of a line, at a time when several different adaptive trends are radiating from an unspecialized common ancestor. This agrees with the interpretation of these bursts on the basis of the occurrence and establishment by selection of many small mutations, since a generalized group with many specialized habitats or new ways of life open to it would be expected to evolve rapidly to occupy these untenanted "adaptive peaks."

It must be emphasized that rates termed tachytelic by paleontologists would not necessarily be rapid in genetic terms. For instance, the horotelic rate of evolution in a typical line, the horses, consists of the evolution of a new species about once every 2,500,000 years, or about every 250,000 generations. The production of a new species in a thousand generations would certainly be considered tachytely. The maximum rate at which new species of animals or plants could be produced by means of the occurrence and establishment by selection of mutations with relatively slight effects is not known, but a little more knowledge of the species-formation processes may make an estimate possible in the not too distant future. At present, the writer ventures to state that given selective forces acting at their maximum intensity, a normal rate of mutation, and the possibility of occasional hybridization between types widely different in morphology and their adaptive norms, a new species, adapted to a different environment from its immediate ancestor and isolated by a barrier of hybrid sterility, could evolve in fifty to a hundred generations. If this is true, there is ample possibility for the occurrence by means of the processes outlined in this book of all of the evolutionary changes which paleontologists have termed sudden, explosive, revolutionary, or tachytelic.

In discussing the causes of bradytely and tachytely, Simpson has concluded that neither the internal, genetic properties nor the influence of the environment can by themselves determine these exceptional rates. Their causes are to be sought in the nature of the relationship between the organism and its environment. This conclusion is amply borne out by the evidence from plants. Among the particular factors responsible for bradytely, Simpson has listed population size and degree of phylogenetic specialization. Bradytelic groups usually have large populations, and are specialized, not primitive, when they become bradytelic.

The importance of population size is borne out by the large proportion of slowly evolving types found among forest trees. But in plants, as well as in animals, exceptions exist in the form of ancient, relict types with restricted distributions. These presumably had large populations when they first became bradytelic, as is known to be true of *Gingko* and *Sequoia*, and their restriction is due to the fact that, as Simpson has suggested, once they are bradytelic, it is very difficult for them to become tachytelic or even horotelic again.

Simpson's next conclusion, that groups are not primitive, but specialized and advanced, when they become bradytelic, is likewise true for plants, as pointed out elsewhere by the present author (Stebbins 1949a). Furthermore, evidence presented earlier in this chapter indicates that another characteristic postulated by Simpson for bradytelic groups is found in woody angiosperms and gymnosperms; they probably evolved considerably more rapidly in past geological ages.

There is, moreover, no reason for assuming that these types show a greatly retarded or static evolution because of an innate quality of "senescence" due to their age. Cain (1944), in a thorough discussion of the examples of so-called senescence, has shown that the morphological constancy and inability for aggressive migration which are sometimes attributed to such a quality can be found in populations which are relatively young in terms of the geological time scale, while other, much older species populations show signs of aggressiveness and invading ability which are ascribed to youthfulness by the advocates of the concept of senescence. As both Cain and the writer (Stebbins 1942b) have pointed out, the characteristics sometimes attributed to senescence are most probably due to a depletion of the genetic variability of the species population, a narrowing of the range of ecological tolerance of its individual biotypes, a restriction of the habitats to which these biotypes are adapted, the possession of poor means of seed dispersal and establishment of seedlings, or to any combination of these four factors.

There is good reason, therefore, for botanists to follow Simpson, as well as Rubtzov (1945) and Schmalhausen (1946), in seeking for the principal factors governing rates of evolution by studying the adaptation of organisms to their environment (Simp-

son 1944, p. 140). Here also the situation in most woody plants is similar to that described for bradytelic animals. Their specialized characteristics are highly adaptive, as is evident from the fact that among trees of the temperate zone are found some of the most striking examples of parallel and convergent evolution. Such families as the Fagaceae and the Juglandaceae, or the Salicaceae and the Betulaceae, have developed very similar adaptations for pollination and seed dispersal, although the bulk of the evidence suggests that they have come from very different origins. Furthermore, these adaptations are of a broad, general type, as is evident from the very wide geographic and climatic range of most of the genera in these families, and in fact of many individual species. The trees of the temperate zone appear to be less sensitive to local differences in soil and other edaphic factors than are the herbs associated with them. Their distributions are governed more by climatic factors, and because of their wide range of climatic adaptability, these woody species could become adjusted to the major alterations which took place during various geological epochs with less change in their genetic composition than could many of the more particularly adapted herbs. The following remark of Simpson can be applied to them; they "are so well adapted to a particular, continuously available environment that almost any mutation occurring in them must be disadvantageous."

The herbs of temperate forests for the most part possess specializations of their vegetative organs which adapt them very well for growth in their chosen habitat, but limit very much their capability for adaptation to new conditions if the forest should be destroyed. Many of them, therefore, are becoming very rare or actually extinct in modern times, as the great temperate forests are being hewn down.

The epiphytes and the parasitic flowering plants of the tropical rain forests likewise are highly specialized for existence in a constant environment, so that each genus or family of such plants tends to possess a relatively constant, standardized type of organization of its vegetative parts. For instance, the epiphytic orchids, even those belonging to different genera or tribes, are remarkably similar in habit, as well as in the characteristics of their fruits and seeds. Their great diversity and extensive evolution is in the structure of the flower, which obviously represents a series of

adaptations to cross-pollination by insects. This is associated with the fact that the upper stories of the tropical rain forest are very rich in flower-pollinating insects, which may still be undergoing considerable evolution. So while the secular environment of the rain forest epiphytes is remarkably constant, their biological environment has been and may still be undergoing considerable changes, which continually call forth new adaptive evolution in their flowers. The evolutionary significance of these plants, already recognized by Darwin, will be very great once their ecology and cytogenetic characteristics are better known. They deserve careful study by modern methods.

ENVIRONMENTAL CONDITIONS PROMOTING RAPID EVOLUTION

From the discussion in this and the preceding chapters, the conclusion is reached that a variable environment strongly promotes rapid evolution and may in fact be essential for speeding up evolutionary change. Both Simpson (1944) and Rubtzov (1945) have reviewed the geological and paleontological evidence indicating that the great mountain-building periods in the earth's history have seen the rise or the extinction of most of the larger groups of animals and plants. Simpson, however, has pointed out that the biological changes accompanying these geological revolutions have been not so much the origin or extinction of whole phyla or classes as the expansion and diversification of classes and the origin of new orders and families. The origin of archegoniate land plants may have coincided with the Caledonian and the Taconic revolutions of the Silurian period, while the diversification of vascular plants took place under the conditions of aridity and oscillation of land and sea which characterized the Devonian period. On the other hand, the mild, equable conditions of the subsequent Carboniferous period saw, not the origin of new groups, but the expansion and perfection of those already existing. The great, world-wide mountain-building revolution which ended the Paleozoic era caused the extinction of the giant Lepidodendrids and Calamites, as well as many archaic groups of ferns and seed plants, and the rise of modern orders of ferns and gymnosperms, such as the Cycadales and the Coniferales. In the early part of the Mesozoic era, which was much more quiescent geologically, the flora, so far as is known, was also relatively static.

The next change in the plant world, the replacement of cycadophytes and other archaic gymnosperms by the already highly developed angiosperms, took place in the lower part of the Cretaceous period, when relatively warm, moist conditions were being replaced by a cooler, but sunnier, climate.

The last two great geological revolutions of the earth's history, namely, the one which ended the Cretaceous period and that which culminated in the Pleistocene glaciation, were accompanied by major changes in the angiosperm flora. The first brought about the differentiation of many, and perhaps most, of the modern genera of woody plants, as well as many herbaceous ones; while during the Pliocene and the Pleistocene epochs there occurred the great expansion and diversification of modern genera of herbs and the breaking up of the more generalized floras into the complex pattern of plant associations which exists today. At present, the mountain-building and glacial revolution of the Pleistocene is being closely followed by a man-made "revolution," in which many preexisting habitats are being destroyed, while new, man-made habitats are being opened up to the weedy plants able to colonize them. At the same time, plant species have been transported to all corners of the earth with unprecedented speed. This "revolution," which is still in progress, began far too recently for us to observe more than the very beginnings of its effects on plant evolution. Nevertheless, there is every reason to believe that the dominant plants of the future will be those best able to colonize the habitats created by man, and that studies of these plants will give us an insight into the future course of evolution in the plant world.

BIOLOGICAL CONDITIONS PROMOTING RAPID EVOLUTION

The summary just given illustrates the fact that varying environments have caused the expansion and diversification of some groups, the decimation and extinction of others, and have left still other groups relatively unchanged. Although environmental change seems to be essential for rapid evolution, the ability of a group to respond to such change by evolving rapidly depends on certain internal, biological characteristics of that group. The most important of these are doubtless the possession of a high degree of genetic heterozygosity and a favorable population struc-

ture, as emphasized in Chapter IV and elsewhere in this book. Two other characteristics are, however, equally important.

The first of these is the possession of morphological or physiological characteristics which are potentially preadaptive in the direction of the environmental change. Thus, if the climate is becoming drier, species which have relatively small, thick leaves and hard seeds capable of surviving long periods of drought have an advantage over thin-leaved, small-seeded types. For instance, fossil evidence indicates that during the Miocene and the Pliocene epochs, when the climate of the North American Great Plains was becoming progressively drier, the essentially mesophytic genus *Celtis* remained static, but the tribe Stipeae of the grass family, the species of which have seeds and leaves admirably adapted to dry conditions, evolved rapidly (Elias 1942). In California during the Pliocene and the Pleistocene epochs the genus *Quercus*, as described earlier in this chapter, evolved little or not at all, while *Arctostaphylos* and *Ceanothus*, both of which have generations not much shorter than those of the oaks, evolved much more rapidly. This difference might be due to differences in the adaptive character of the seeds of the two groups. The acorns of oaks are short-lived, need considerable moisture for germination, and so can initiate a new generation in arid regions only within a relatively limited range of climatic and edaphic conditions. On the other hand, the harder, more drought-resistant seeds of *Arctostaphylos* and *Ceanothus* could produce seedlings under a greater variety of external conditions and so permit the establishment of a larger number of genetic variants. In this way the populations of species of the latter genera might be given greater opportunities for exploring new adaptive peaks.

The final biological characteristic making for rapid evolution is the possession by the species of adaptive mechanisms which are not too general, so that they must be modified in response to the changing conditions. Schmalhausen (1946, cf. Stebbins 1949a) has shown that in animals the character of adaptation depends on the position of the organism in the hierarchy of nutrition. Animals in the lowest position are those which have no defense against aggressors except for rapidity of reproduction. These are indifferent to the particular type of aggressor, and hence will respond little or not at all to changes in their biological environment.

Plankton organisms, the best examples of this type, are well known for their slow rates of evolution. The next lowest position is occupied by all organisms with purely passive forms of defense against their enemies. This category includes all sedentary organisms and therefore practically the entire plant kingdom. According to Schmalhausen, this explains the fact that in general plants have evolved more slowly than animals. Most of the larger animals are contained in the two higher categories of the hierarchy of nutrition, namely, those which actively elude their predators or which themselves prey on other organisms, and thus compete with each other for food.

The writer has pointed out elsewhere (Stebbins 1949a) that an amplification of Schmalhausen's scheme will serve to classify plants and parts of plants according to the rapidity of evolution required by their particular type of adaptation. This is centered about differences in the ecology of their reproduction. The three levels recognized in this hierarchy of reproduction are as follows. The lowest is that containing those organisms which rely solely on the large number of gametes and zygotes they produce. A large number of aquatic plants, particularly among the algae, belong here, and these have tended to retain simple reproductive structures and reproductive cycles. Among land plants, this level is occupied by many of the bryophytes and by homosporous pteridophytes, particularly those with large, unspecialized sporangia which rely entirely on the wind for the dissemination of their spores. Here we find such bradytelic genera as *Psilotum*, *Botrychium*, *Marattia*, and *Lycopodium*. Among seed plants, the conifers, which produce large numbers of pollen grains and seeds adapted for wind dispersal, have been the most successful of the bradytelic lines. In the angiosperms, the relationship between large numbers of pollen grains or seeds produced and slowness of evolutionary change has produced not only slower evolution of the pollen- or seed-producing organs in certain families of genera, but also relative retardation of the evolutionary change of some organs as compared to others of the same plant. The stamens have in general shown less evolutionary change than other parts of the flower, and they have been particularly constant in wind-pollinated groups like the grasses and the sedges, which produce large amounts of pollen. Furthermore, many-seeded capsules show

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much less evolutionary differentiation in the groups in which they occur than do achenes, nuts, or other few-seeded types of fruits.

The middle position in the hierarchy of reproduction is occupied by many plants, ranging from the algae to the flowering plants, which produce large, heavily coated, highly resistant resting spores or seeds. Generic and family differences can often be found in such structures, and then tend to show more diversity than the light, wind-borne spores and seeds of the plants in the lower group. The highest position in this hierarchy is occupied by those angiosperms which are cross-pollinated by insects, which have fruits adapted to dispersal by animals, or which rely on animals for both pollination and seed dispersal. Since there are many more diverse kinds of animals in any locality than there are different climatic or edaphic conditions, many more adaptive gene combinations are possible in plants which rely on animals for their vital reproductive functions. This explains to a large extent the evolutionary diversity and plasticity of such families as Leguminosae, Malvaceae, Labiatae, Compositae, Gramineae, and Orchidaceae. In addition, it explains the fact that this diversity has involved principally those organs involved in the dispersal by animals. Thus, the Orchidaceae and the Asclepiadaceae have highly specialized and complex floral structures, which show an amazing diversity in their specializations for insect pollination, while the seed capsules, which bear enormous numbers of wind-borne seeds, are remarkably similar throughout whole genera and tribes. On the other hand, the wind-pollinated grasses have relatively uniform structures of the flower itself, including the palea, lodicules, anthers, and stigmas. But their great diversity lies in the scales and rachises of their inflorescence, which are structures connected chiefly with seed dispersal, as described in Chapter IV. In grasses, this function is carried out to a large extent by animals.

THE BASIS OF EVOLUTIONARY RATES: SUMMARY AND CONCLUSIONS

The discussion presented in this chapter may be summarized in the following hypothesis, which is essentially that of Simpson (1944) and Rubtzov (1945, cf. also Stebbins 1949a). Rates of evolutionary change are very diverse, not only between different groups of organisms living in different environments or even in

the same environment but also within the same line at different periods in its evolutionary history and between different parts of the same organism. They may range all the way from the extreme rapidity which is considered sudden or explosive in terms of the geological time scale down to rates so slow that the line is essentially static. They are determined primarily by the relationship between the evolving population and its environment and secondarily by forces inherent in the population itself. If the environment is constant in respect to all the forces affecting the adaptive character of the population, evolution will slow down until it stops at a level which represents the attainment in the population as a whole of the most adaptive set of gene combinations possible. This evolutionary stability is an equilibrium, maintained by the selective elimination of new mutations, which are constantly occurring.

If the environment changes, the population will either become reduced in size and eventually extinct or it will evolve in response to this change. The principal factors governing the rate of this change are as follows. First, the amount of genetic variability in the population, in terms of heterozygosity of individuals, and genetic differences between actually or potentially interbreeding races. Second, the structure of the population, whether large or small and whether continuous and panmictic or divided into partly isolated subpopulations (see Chapter IV). Third, the nature of the adaptation of the population to its environment. This includes the degree to which potentially preadaptive gene combinations are possible, as well as the position of the organism in the hierarchies of nutrition and reproduction. Fourth, the intrinsic mutation rate.

The various points of this hypothesis can be tested on a variety of organisms, both plant and animal, by observation, experimentation, and application of data already available. If they are correct, then an intimate study of a group of organisms with these points in mind should enable us to determine their evolutionary possibilities and to accelerate greatly their rate of evolution, provided that the group can be handled experimentally. The control by man of organic evolution is now an attainable goal.