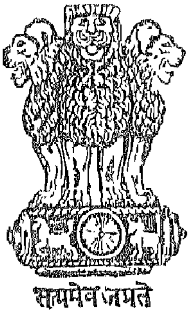
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THE GEOGRAPHY OF THE FLOWERING PLANTS

that grand subject, that almost keystone of the laws of creation,
Geographical Distribution."

CHARLES DARWIN

in a letter to Joseph Dalton Hooker in 1845.

Plate 1.

Forest
vegetation
in Java

(from Schimper, Pflanzen-Geographie)

THE
GEOGRAPHY OF THE FLOWERING PLANTS

BY

RONALD GOOD, M.A., Sc.D. (Cantab.)

Professor of Botany, University College, Hull

ILLUSTRATED BY
75 LINE DRAWINGS
9 MAPS IN COLOUR
AND
16 PHOTOGRAVURE PLATES

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PREFACE TO THE SECOND EDITION

IT was explained, in its preface, that for various reasons the first edition of this book depicted in the main our knowledge of the distribution of the Angiosperms as it was in 1939, and that more recent information would have to be dealt with on some later occasion. The demand for a new edition has, in very welcome fashion, provided this occasion, and I am most grateful to the publishers for allowing me to take full advantage of it.

In this new edition the book has been revised throughout, and parts of it, especially Chapters 4 and 20, largely rewritten. Its whole contents has been reviewed, and in many places elaborated by the inclusion of new material or by additional emphasis. Special care has been given to the floristic classification in Chapter 2 and its accompanying map (Plate 4) and it is hoped that in their improved form these will more completely meet the wider demand which clearly exists for a reasonably simple arrangement of this kind. Several of the weaker photogravure plates have been replaced; several text-figures have been added; Appendix B has once more been re-edited; a subject index has been provided; and the bibliography has been greatly enlarged. With regard to the last I regret that I have not been able to see a copy of item 117, which, I am given to understand, was originally announced under a different title.

Particular pains have been taken to bring the book up to date, or at least as up to date as the rapid development of the subject of plant geography permits, and to ensure its factual accuracy, and it is especially to these ends that I am in the debt of so many correspondents, both at home and abroad, for their ready and generous responses to my enquiries. I am particularly indebted to Mr. H. S. McKee, who has long constituted himself an invaluable and untiring intermediary in all matters Australasian, and to Prof. R. S. Adamson, Dr. C. E. P. Brooks, Mr. I. H. Burkill, Mr. E. J. H. Corner, Dr. P. Dansereau, Mr. W. N. Edwards, Mr. D. W. Ferguson, Prof. E. Hultén, Mr. L. A. S. Johnson, Prof. H. J. Lam, Mrs. M. R. Levyns, Mr. J. E. Lousley, Dr. H. E. Moore, junr., Prof. C. Skottsberg, Dr. W. A. Sledge, Dr. H. Sleumer, Dr. F. A. Stafleu, Dr. P. C. Tsoong and Dr. C. G. G. J. van Steenis. I am also most grateful to Mr. J. E. Dandy, Mr. A. W. Exell, Mr. C. E. Hubbard, Mr. N. Y. Sandwith, Mr. W. T. Stearn and other members of the staffs of the Herbaria at the British Museum and at Kew for always making so readily available to me their special knowledge and experience. I trust that all those mentioned, as well as the many others also who have helped me, will accept this warm expression of my thanks.

Since the first edition was prepared there has been completed an additional important general source of condensed information about the Angiosperms, namely Lemée's great *Dictionnaire descriptif et synonymique des genres de plantes phanérogames*. This is at present the most recent complete conspectus of the Flowering Plants and I have made considerable use of it, especially as a source of comparable figures.

It will be noticed that all specific epithets in this new edition have been spelt without capital letters, this being in accordance with the recommended practice now being generally adopted. As to nomenclature the same sources have been followed as before, except that I may here and there, and entirely on my own responsibility, have used names which are, perhaps, not in strict accord with the letter of the Rules.

RONALD GOOD.

Hull, October, 1952.

PREFACE TO THE FIRST EDITION

THE manuscript of *The Geography of the Flowering Plants* was completed in the summer of 1939 and immediate publication was intended, but the vicissitudes of the war have caused its postponement until now.

In the seven years that have thus elapsed great changes have come about in the life of nearly every part of the world, and in two notable respects these changes are likely to increase interest in the study of plant geography. The spectre of starvation and the rigours of rationing have brought about a much more vivid appreciation of what man owes to the plant world; and the global military struggle has made familiar to the layman many of those more remote parts of the world (such as the islands of the Pacific Ocean) that are of special interest to the student of plant distribution.

On the other hand the war has brought chaos to the co-ordination of learning and research, and years are likely to pass before the advances in knowledge that may be expected from the opening up of hitherto little-known parts of the world can be fully recorded and integrated.

Therefore, although the text of this book has been as far as possible brought up to date, it must be regarded in the main as depicting the state of our knowledge at the outbreak of war, and subsequent advances must await full treatment at a later date.

This unavoidable delay in publication, though regrettable, has had one advantage. The plan of this book has permitted only a comparatively brief reference (notably in Chapters 3 and 14) to certain matters which are of considerable interest and about which the reader may well wish to know more, and it is now possible to refer to two other works in English which deal with them much more completely. These are the authorised translation of Wulff's *Historical Plant Geography* (610) and Cain's *Foundations of Plant Geography* (74). The latter, in particular, includes not only an up-to-date account of the evolutionary background to the subject (especially with regard to modern ideas on the origin of species), and of various questions relating to the distribution of plants in the past, but also a very extensive bibliography. Both books are valuable complements to *The Geography of the Flowering Plants*

It is inevitable in a book of this kind that many facts are quoted without critical comment, since to verify them in detail would be impossible, but every care has been given to the selection of the sources from which they are taken. Also it must be remembered that there is no single complete modern revision of the whole group of the Angiosperms, nor, considering the amount of work it would involve, is there any such in prospect, and the literature is very scattered and often difficult to correlate.

As far as seems practicable the sources of all the major statements in the text are given in the selected bibliography at the end of the book, but there are four outstandingly comprehensive works to which I have had such constant recourse that they must receive special mention and acknowledgment here. They are *Index*

Kewensis (277), *Das Pflanzenreich* (156), *Die natürlichen Pflanzenfamilien* (159, 160) and Willis' *A Dictionary of the Flowering Plants and Ferns* (597).

Further, with regard to examples and statistics, it should be borne in mind that these are useful chiefly for illustrative purposes. Figures must, generally speaking, be looked upon as relative, and of most value as a means of comparison. To treat them as absolute and immutable would be to misinterpret both the figures themselves and their function, for even when they are computations made specially for this book, they are ultimately based on what are, in many cases, no more than personal estimates and opinions.

So many of my friends and colleagues have contributed, in one way or another, to the writing of this book that it is quite impossible to acknowledge in detail all the help I have received in this way, and I can only hope that they will one and all accept this general expression of my thanks.

I must, however, express my very special gratitude to my old master, teacher and friend, the late Sir Albert Seward, whose death in 1941 deprived the botanical world of one of its wisest and kindliest figures. It was characteristic of him that he should find time to read the whole lengthy manuscript critically at a period which must have been most inconvenient for him, and it is a peculiar satisfaction to me to have this opportunity of paying a personal tribute to his memory. His many suggestions and comments, especially in connection with the geological history of the Flowering Plants, were of the greatest service.

My very grateful thanks are due also to my former colleague, Mr. J. E. Dandy, who has devoted a great deal of time to reading the proofs. His ready and generous help has been invaluable in many problems, and particularly in those touching the vexed question of plant nomenclature. Concerning this matter the use of the names at present regarded as correct has sometimes led to the supersession of particularly familiar names, and where this has happened the latter have been added in brackets. In the case of British plants the nomenclature follows that of the recently published "Check List of British Vascular Plants" (98), except that I have retained initial capital letters for certain of the species names.

The numbers in brackets refer to the entries in the Bibliography, which includes also a number of general works on plant geography not specifically referred to in the text.

For the excellent plant drawings I am indebted to Miss Lorna Pillow.

RONALD GOOD.

Hull, 1946.

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INTRODUCTION

The Importance of Plant Geography

PLANT geography is that branch of botany that deals with the spatial relationships of plants both in the present and the past. Its aim is to record, and then if possible to explain, the distribution of plants over the world's surface.

This book is arranged on a similar plan. The first part consists of a purely descriptive account of the facts of distribution in one great group of plants, and the second consists of a theoretical consideration of these facts and concludes with an attempt to give a generalised explanation of them.

Compared with many other aspects of botany, plant geography is remarkably free from technicalities and their attendant terminologies. It is naturally, too, an out-door subject rather than one involving exact experiment in a laboratory and its study needs neither complicated nor costly equipment. It therefore appeals not only to the trained botanist but also to many whose interest in plants, though just as real, is less academic, and especially those who delight in their gardens. For the same reasons it should be possible to prepare an account of the subject acceptable to all these, provided only that it incorporates, for the benefit of the less scientifically minded, an introduction to those aspects of biological thought and method of which some appreciation is necessary if the geography of plants is to be understood properly. Such an introduction is provided in these first pages, but they are in the nature of a preamble to the main parts of the book and the more scientific reader need not be detained by them.

Plant geography is so closely related, not only to many other branches of botany, but to zoology and anthropology, that it is a subject of great importance to man. The enormous advances that have been made in applied sciences make it ever more difficult to recognise in their proper proportions the foundations on which human civilisation rests and the influences that have determined the main trends of its development. Civilisation has been defined as man's gradual conquest of his environment, but how far this process has, in sober fact, gone is a matter for careful thought. In some ways certainly man's mastery over nature is complete enough. He has, for almost all practical purposes, annihilated space; he has explored and exploited the resources of the mineral world to a remarkable degree; he has gone far towards the control of infectious disease, especially in the warmer parts of the world.

These are great achievements, but they must not blind us to the fact that in other ways his efforts have been comparatively unavailing. His control of the elements, for example, can only be described as poor, and although he can often modify their dangers they not infrequently reveal their potentialities with disconcerting clarity.

Another direction in which he has been less successful, and which is of chief concern here, is his relation with the plant world, which still remains what it has always been, the only true basis of human economy. Naturally enough vegetation is as susceptible to man's destructive propensities as any other part of nature, and in many respects it can be as easily exploited by him, but unlike the rest he cannot entirely bend it to his will. Above all, there are two important things which, with all his knowledge, he cannot do—he cannot appreciably control, under all conditions, the speed at which crops mature and ripen; and he cannot grow every kind of plant where and when he likes. In consequence the business of maintaining and distributing his food supplies requires a complicated prevision and an intricacy of movement which makes it extremely vulnerable to disruptive factors. For the explanation of this the reader must refer to sources where the problems are dealt with at greater length (215, 482), but at this particular juncture in world history the statement itself needs no special demonstration. In latter years the nations have presented one another with many and terribly imminent dangers, but behind them all has loomed the one ultimate and over-riding peril that the disorganisation of agriculture and transport arising from them may spread so widely and uncontrollably that there will come about, over much of the world, absolute dearth beyond remedy and the destruction by starvation of a great part of the human race.

Although modern conditions have accentuated this danger and contemporary events have made its possibility all too clear, it has always been in existence and the distribution of plants, which is one of the factual bases of it, has been a controlling influence in mankind's development throughout his history. It is no mere caprice that the earthly paradise depicted in the Book of Genesis—the Garden of Eden—is a place where, to use the words of the Authorised Version, there grew "every tree that is pleasant to the sight and good for food," because that is simply the pictorial rendering of an age-long ideal.

But apart from myth there is abundant evidence of the way in which plant geography has determined the course of history and the destinies of man. To consider this evidence at length would be equivalent to writing a history of the human race and is therefore impossible here, but the more salient points must be stated.

The natural vegetation of any part of the world can, in general, be described as belonging to one or other of three types only (Plate 2). It is either forest of a sort, grassland of a sort, or some kind of desert. There are, of course, considerable areas where somewhat intermediate conditions prevail, but from the human point of view these are the three main conditions. In the forests the plants are mainly trees; in the grasslands they are mainly grasses; while deserts may be described as areas where the total plant life and cover are scanty and incomplete, producing neither woodland nor pasturage. The potentialities of these three to a human population are obviously very different. Deserts are, by definition, unlikely to provide a sufficiency of food and such as there may be is likely to be of little value since it will not include the products of trees or grasses. Forest, while it may in total contain large potential supplies, offers many obstacles to exploitation by man, unless he is at one or other extreme of his development. A very primitive human society, sparse in numbers, may derive sufficient from it, and modern industrial societies can remove and destroy it, but to most peoples this type of vegetation is a serious barrier to progress, because it deprives them of two prime necessities, space for expansion and the opportunity for an economic form of agriculture by which their supplies may be increased in proportion to their growing needs. The grasslands, on the other hand, meet both these primary requirements, providing huge open spaces as stages for the playing of the human drama, and room wherein the most convenient and desirable forms of human food can be produced. It is here, too, that the climatic conditions most suitable for the human race are to be found.

If the world distribution of these three types of vegetation is studied, it is seen that it follows fairly closely the distribution of certain climatic values. Briefly, deserts are found where the prevalent conditions are excessive heat or cold, usually accompanied by lack of moisture, at least at some seasons. Forests, conversely, are found where precipitation is high and especially where temperature also is considerable. The climate of some forest regions is not in itself unsuitable for man, but, as has been said, the nature of the vegetation militates against him. Grassland, however, reflects medium climate values, where there is rain in sufficiency but not in excess and where the temperature is mild. In short it tends to have just the climate which is usually regarded as the best not only for the physical but also for the mental activities of mankind.

It may well be doubted whether primitive man consciously realised the climatic significance of the grasslands, but of their spatial advantages and of the ease with which animals could be hunted on them he must soon have become aware, and for this reason the association of man with this particular kind of vegetation is not hard to understand.

His dependence on the grasses for his own staple food, however, is an aspect of the subject which, by its very familiarity, excites much less interest than it deserves. To-day the pre-eminence of the grasses among the useful plants of the world is due to their double rôle of providing fodder from their vegetative parts and food from their fruits. The first of these two rôles is presumably the older, and with it the whole earlier history of mammalian evolution is intimately involved. The second is younger and its origin is mysterious. It is easy to imagine how, in the dawning of his intellectual powers, man might conceive the possibility of growing deliberately, in order to provide himself with food, plants whose fruits are large and conspicuous, but it is difficult to understand the circumstances by which his early agriculture became, as it did and as it has remained, concentrated upon the cultivation of grasses for the sake of their grain. For the most part the fruits of wild grasses are, in comparison with the fruits of many other plants, neither conspicuous nor bulky, and that their great potentialities as human food were so soon and so unerringly realised is one of the most intriguing sides of the story of primitive man, and may indeed be a valuable clue to problems which still remain to be solved.

But however it may have come about the development of mankind has been and presumably will long continue to be essentially a grassland development. Of the grazing or fodder aspect of this no more need be said here, but the subject of cereals as human food affords a peculiarly vivid picture of the influence of plant geography and a useful introduction to that study.

Although there are small but familiar exceptions it is true to say that even to-day, when diets have become so greatly diversified, the staple food of practically the whole human race is some kind of grain. Anything like a comprehensive list of the grains used would be lengthy, but of them all no more than half a dozen have an importance far greater than that of all the others put together. These are wheat, barley, rye, oats, rice and maize, the last named being on the whole less important than the rest. Broadly speaking, the first four are crops of temperate regions, the last two of tropical countries. That is to say, these are their present cultivation zones, but it is of more particular interest to enquire into their natural ranges. In detail this is a subject of great controversy, but in general it may be said that wheat probably had its home somewhere in western or central Asia, barley and oats in rather more northerly parts of the same region, and rye somewhere more to the north again. Rice comes from the monsoon tropics of eastern Asia and maize, the only important New World grain, probably from somewhere in central America, though there is more than one opinion about this (357).

When maps showing the distribution of the earlier human civilisations are consulted it will be seen that these occur almost entirely in three parts of the world, namely western and central Eurasia, eastern Asia, and to a lesser extent in central America. That is to say, they have much the same natural distribution as the chief grain crops. This correlation can be elaborated in many interesting ways and one or two may well be mentioned here.

Africa has conspicuously never been the site of a comprehensive and powerful civilisation. Whether or not it may have been the cradle of the human race, as some believe, it has remained the home of a loose-knit collection of comparatively primitive races. Nor has it any outstanding cereal of its own. Most of the African peoples have their own peculiar grains, but none of these is of more than local significance and range, a point strikingly emphasised by the fact that the semi-industrialised African natives of to-day have adopted maize as their staple food and that its use is spreading to other parts of the population.

Temperate North America has contributed nothing of moment to the world's list of cereals and this is not unrelated to the fact that the native race of this part of the world was a scanty nomadic pastoral one, mainly without the localised and fixed type of agriculture which has always proved one of the foundations of human progress.

Until the period of European settlement the human population of Australia consisted of a sprinkling only of a race in a most primitive state of existence, comparable indeed to the Stone Age of Europe, and it is difficult to imagine that the absence of a well-characterised indigenous cereal is not a reflection of this low level of culture, or conversely, that the exploitation of some such crop plant would not have been accompanied by great changes in the mode and standards of life of the aborigines.

These instances show clearly enough, if only in one way, the relation between the distribution of plants and the development of man, but neither the one nor the other has grown up suddenly. Each is the outcome of a long and complicated series of events, extending in the case of the plants over many millions of years. Human history is much shorter and covers only the later chapters of the history of plants, but there is no doubt that where the two are concurrent a knowledge of each contributes greatly to an understanding of the other.

The plant geographer concerns himself not only with the distribution of plants in space but also with their distribution in time, and it is one of the purposes of this book to discuss some of the great changes in the distribution of plants that have taken place in the course of geological time. It will appear that the primary cause of these changes has been variation in the distribution of climatic values, but one of their most important aspects is that, acting through the intimate association already described, they have, during the short time that man has occupied the earth, been accompanied by equally great changes in the distribution of human populations. To this cause, for instance, are to be attributed at least two of the major features of human history—the repeated human migrations from the interior of Asia, which have occurred time after time almost throughout the historical period, and that gradual northward trend of the centre of world civilisation which is often called "the Northern March of Empire."

Thus it is to be seen in two quite different ways that plant geography is a subject so intimately connected with human affairs that however academic some aspects of it may seem, it is worth the careful attention of all whose aim and hope it is to reach some understanding of mankind and its difficulties. It can throw light not only on many present-day questions but also on many relating to the past. This being so, may it not also have some value as indicating the way in which some aspects of affairs at any rate may trend in time to come, and thus to do something towards lessening the greatest of all limitations under which man labours, his inability to see into the future?

Vegetation and Flora

Within the science of botany plant geography is most intimately connected with plant ecology, these together making up the wider subject of *geo-botany*, which comprehends all aspects of the relation between plants and the surface of the earth that is the substratum of their lives. Plant ecology is particularly concerned with the way in which plants are mutually related to one another and to the conditions of their habitat. Plant geography, on the other hand, is concerned primarily with the correlation between plants and the distribution of external conditions. The former is essentially physiological; the latter is essentially geographical. Expressed in another way, the difference is that between *vegetation* and *flora*, and a clear understanding of these two terms is important.

The chief features of vegetation reside in its quantitative structural characters because of their obvious influence on all other kinds of associated life. These structural characters are, as has been shown, closely related to climatic conditions, and hence the same kind of vegetation, that is to say the same kind of dominant growth form, tends to recur in many parts of the world. For example, deciduous woodland is found not only in the British Isles and other parts of Eurasia, but also in parts of North America, as well as elsewhere, and in all these places it possesses much the same general features and dimensions.

The word *flora* is a purely scientific term and therefore has no common usage (which is itself an interesting commentary on the conception behind the word *vegetation*), and its meaning is best expressed by extending the example employed in the last paragraph. Although the deciduous woodlands mentioned there are alike in their vegetational features they will be found on closer examination to differ greatly and perhaps entirely in their floral (or floristic) constitution. The vegetation will be the same in all cases, but the actual kinds of plants which comprise it—and which together compose its flora—will be different. The beech of English woodlands is not the kind of beech which grows in the North American forests, nor do either of these occur in the southern hemisphere, where their place is taken by other related species.

Just as vegetation is chiefly a matter of quantitative characters so flora is chiefly a matter of quality, in the sense that it concerns the family relationships of the plant life rather than its visual resemblances. The flora of a region is the total of the species within its boundaries, but the vegetation is the general effect produced by the growth of some or all of these in combination.

The Flowering Plants and their Classification

The plant kingdom as a whole can be divided into two parts or sub-kingdoms—the Phanerogams, comprising all the plants which reproduce by means of seeds, and the Cryptogams, comprising all those which reproduce by means of simpler structures called spores. None of the latter, which includes fern, mosses, seaweeds, fungi and the like, are concerned here.

The Phanerogams or Seed Plants themselves consist of two groups. In one the seeds are generally borne in cones and are not protected by any exterior structures except in so far as the cones themselves may shelter them. This is the group of the

Gymnosperms (a word meaning "naked-seeds"), and it includes the Conifers and their allies. With these also we are not concerned.

In the other group, which is immeasurably the larger, the seeds are borne in flowers and are protected by being produced in enclosed structures called carpels. This is the group of the Flowering Plants or Angiosperms (a word meaning "concealed seeds"), and it is with these alone that this book deals.

The Flowering Plants or Angiosperms are the dominant plant group in the world to-day and represent the highest expression yet attained of plant evolution. They have gradually supplanted all other groups in prominence, and now comprise the great bulk of the vegetation of the land on all but some of the smallest areas. Practically all the plants used and cultivated by man belong to this group. They range in form from gigantic forest trees to tiny ephemeral herbs lasting but a few weeks. They have colonised practically all the land, they are common in fresh water and are even to be found occasionally in shallow seas. It is difficult to say how many different species of them there are, but there may well be 250,000 or more.

For present purposes by far the most important general point about the Flowering Plants is that they represent the most modern type of plants and are the culmination, to date, of evolution in the plant kingdom. As might be expected from this they have a geological history much shorter than any of the other great groups of plants, and it is for this reason that this book deals with them alone. Time is a most important factor in matters of plant geography and it is therefore fundamentally unsound to treat together groups of plants whose length of history is widely dissimilar. To the older groups it is possible to apply generalisations which, owing to their shorter history, are quite inapplicable to Flowering Plants, and conversely much of what is true of these plants cannot be applied to other groups because these are of far longer ancestry.

With regard to the definition which was given above it must be remembered that many of the Flowering Plants which are grown in gardens, and particularly some of the shrubs, have come from regions far away, and when cultivated in countries which are to them strange lands they do not always find the conditions which will enable them to bear flowers. Nevertheless these plants are true Flowering Plants, blossoming normally in their natural haunts, and the fact that they do not do so in gardens is no indication that they do not belong to this group. The only spore-bearing plants which are cultivated to any extent are some of the ferns, and their general characteristics are enough to distinguish them at sight from Angiosperms.

The primary classification of the Flowering Plants is into two great divisions, the Monocotyledons and the Dicotyledons, separated mainly by differences in the seeds. To the former, smaller, group belong such plants as grasses and lilies which, for the most part, have long narrow leaves with parallel veins; while to the latter and larger group belong, in general, the plants with broad and net-veined leaves, including nearly all woody Angiosperms.

Each of these great divisions is classified into *orders*, based on very wide characters, chiefly of the flower. There are about a dozen orders of Monocotyledons and about forty of Dicotyledons. The order is too large a category to be of much practical importance and there will be no occasion to refer to it again.

Each order is classified into *families*. Some orders contain only a single family; others have as many as twenty or thirty. The word *family* here has exactly the same meaning as the older term *natural order*, and this emphasises the special feature of the family, namely that it is, broadly speaking, the largest category in which a general superficial resemblance reveals the close relationship between all its members. All classifications to-day are, theoretically at any rate, natural, in as much as they are based on characters presumed to indicate evolutionary relationship as well as mere similarity, but obviously the larger the category the more diffuse and uncertain will be the inter-relationships within it, and the importance of the family is that it is, in effect, the largest reasonably natural unit for most practical purposes. In short, it should be possible to regard the contents of any one family with some confidence as having had a fairly close community of origin and similarity of history.

Each family is made up of one or more *genera* (the plural of the word *genus*), and just as in the *family* there are brought together plants of a general degree of relationship, so in the *genus* there are brought together the plants of a more particular degree of relationship. In practice this means that a genus usually comprises all the plants closely resembling one another. Thus, all the pansies and violets form one genus, and the roses and willows respectively form others.

The *genus* may, above all others, be called the natural category. Families, despite their natural basis, are often so large and heterogeneous that there may well be some confusion between mere resemblance and real affinity, and many families are not entirely free from the suspicion of being to some extent unnatural for this reason. Genera, on the other hand, are smaller, and for that reason alone tend to be more natural; but apart from this their characters usually emphasise this so much that for the most part they can be regarded reliably as true natural groups, that is to say as groups of plants the members of each of which have a common ancestry from a comparatively recent origin.

Finally, each genus consists of one or more *species*. In some ways the species is an unsatisfactory unit, for it is the subject of much controversy, and some reference to the cause of this must be made here. Difficulty arises primarily because the word has been current much longer than the idea of organic evolution, having been used originally to denote the different kinds of animals and plants which, according to the old cosmogony, had been *specially* created. In this sense the word had a normal conception and meaning, but unfortunately it continued in use after the doctrine of evolution became established and then came to mean (as far as can be expressed in words) any collection of individuals virtually like one another but more unlike any others and presumably the descendants of some one earlier individual parent. This is a theoretical definition, and thus the word species has come to have a subjective rather than an objective meaning.

It is this confusion that causes the practical problem. In the earlier view every species was an entity distinct from all others, with recognisable limits, and, having the same kind of origin, all were, in a sense, of equal value. In the later view the species is simply a collection of individuals related by descent, but how and to what extent it is usually impossible to say. Relationship can in fact only be estimated in terms of superficial resemblance, but the significance of similarity is a matter of personal opinion and hence it has come about that the word "species" scarcely means more at present than that it denotes a number of individuals which on account of their mutual resemblance are believed by fewer or more people to be descended from a single similar individual. This being so there is no real practical criterion of what constitutes a species and there are many different opinions. For this reason statements about species, and particularly estimates of their number, must always be treated with caution and regarded as indicative rather than absolute.

Families, genera and species are all three important in plant geography. A family is not only a collection of genera but there is usually running through it some fairly well-marked structural feature (such as the capitulum of the Compositae) which is more or less peculiar to it. Because of this the distribution of families is often of considerable interest with regard to the possible place of origin of the main types of Angiosperm structure, and their significance in the evolutionary story. The larger families, too, are often particularly characteristic of certain parts of the world, and this enables the salient features of different floras to be visualised in a way which is impossible with smaller categories.

The genus is the most natural category and can generally be accepted as combining together species which have had a common and close descent from a comparatively recent ancestor. This being a matter of great significance from the point of view of spatial relationships makes the genus the most important category for distributional studies.

The species is of value chiefly as a means towards statistical analysis. For such purposes, at any rate, species may be regarded as units of equivalent importance, and on this basis can be of great service in assessing geographical phenomena. For instance, to say that the flora of one region contains 100 species while that of another has 10,000, or to say that one genus has 5 species while another has 250, portrays the actual state of difference between the floras or genera in a particularly vivid way. Indeed, it is often only by using figures that qualitative resemblance or difference can be expressed quantitatively.

The Nomenclature of Plants

The nomenclature of plants, or the science of their names, is often a cause of bewilderment to those who are not familiar with its principles.

In the early days of botany, when the number of known plants was much smaller than it is to-day, there was no definite method of giving distinctive names to different kinds of plants and these could be distinguished verbally only by means of a short descriptive phrase embodying their more prominent characteristics. As the number of known plants increased this became more and more difficult because longer and longer descriptions became necessary, and after a while great confusion arose.

The credit for removing the difficulty belongs to the great Swedish botanist Linnaeus, who flourished about the middle of the eighteenth century and whose method of naming plants is reckoned to date from 1753 (343). His solution was what is termed the binomial system, by which each kind or species of plant is given two names and two names only, the combination of names given to one species never being given to any other. There was really nothing startlingly original about this procedure because it is what in fact is done in the case of human beings in most countries, and Linnaeus' two names were indeed almost exactly comparable with the surname and Christian name of a person. His genius lay in applying this system to plant species and genera, and more particularly in doing so in such a way that no two different species possessed the same name.

The names were not, of course, called surnames and Christian names, but *generic* and *specific* names. Each distinct kind of plant was called a species and the various species were collected into genera according to their mutual degrees of resemblance. The specific name thus corresponds to the Christian name and the generic name to the surname. An example will be the best way of making the working of the system clear. All the species of buttercup were collected together into a genus to which the name *Ranunculus* was given, so that every kind of buttercup possessed the first or generic name of *Ranunculus*. Then each species was given a second and distinctive name, this being made as descriptive as possible and being reserved solely to the one species. The creeping buttercup, for instance, was called *Ranunculus repens* (the Latin for "creeping"), the hairy buttercup was called *Ranunculus hirsutus*, the bulbous buttercup *Ranunculus bulbosus*, and so on, and since each species had its own particular name confusion between them was avoided.

At first, and for a considerable period, this method proved almost perfect and in theory remains so to-day, but difficulties began to crop up when, after Linnaeus' death, others carried on his work. New species were constantly being discovered by all sorts of people, and it became the inevitable practice for the discoverer or describer of a new species to give it a name. There was no means of correlating this scattered work, and so it frequently happened that what was in fact one and the same species was given two or more different names by different workers ignorant of each others' actions. It then became necessary to decide which of the names was to stand and which were to be abandoned. In general the principle of priority was adopted by which the earliest or first-given name was chosen, but priority was often difficult to establish and gradually a great deal of confusion grew up. It is enough here to say that it ultimately became necessary to compile a most complicated set of rules for the naming of plants, but even so there are still great difficulties. It not infrequently happens that to fulfil these rules familiar and long-established names have to be replaced by new and strange ones, and this, when the reason is not fully appreciated, causes much confusion and sometimes much heart-burning. The changes are, however, made in good faith with the intention of trying to make things easier ultimately.

Another feature of Linnaeus' system which tends to be misunderstood to-day was his use of the Latin language for the purpose. The reason is really an excellent one, namely, that Latin was then and indeed is even now the nearest approach to a *lingua franca*. Latin was in fact used as a substitute for a universal language and in order to avoid the necessity of translating the names into various national tongues. It would probably have been impossible to invent any reasonable system of nomenclature without it, and it really needs no defence. Unfortunately, most of us are concerned only with our own language and in these circumstances the use of Latin seems pedantic. Quite apart from the fact that it is indeed not so, there is a stronger reason for using Latin names. The alternative to Latin names is to use national names; but national names have never been given on any system and have simply grown up by common usage which varies from place to place. Thus a plant may be known by several English names in different parts of the country and what may be intelligible in one part may be meaningless in another. Furthermore, all the English names are likely to be meaningless, let us say to a German or Russian. The use of Latin names avoids this difficulty because a species has one and the same Latin name throughout the world.

Specific names derived from human proper names, or from vernacular or generic names, used to be spelt with a capital letter, but this practice, which has little to commend it, is now being abandoned.

The History of Plant Geography

The history of the study of plant geography needs mention here only in so far as it throws light on the theoretical background of the subject and on its relations with other branches of knowledge. In brief it falls into five periods. The first, and considerably the longest, is the pre-Darwinian period, which lasted from the earliest times to the middle of the nineteenth century. This was particularly the period of exploration and discovery and its essential achievement was the gradual description of the world's plant life, that is to say the accumulation of the main facts of plant distribution. The next period, the Darwinian, was a short but most important one reflecting, as it did, the great revolution in thought which its name implies. Darwin and his scarcely less notable contemporaries, Wallace, Huxley and Hooker, early realised that the geography of living organisms, which in terms of special creation might be a matter for wonder but not for speculation, provided, in terms of evolution, one of its most valuable lines of evidence, and it is only necessary to read the *Origin of Species* (124) itself to realise the change that evolution brought to plant geography. Since evolution has ever since remained a fundamental tenet of biological thought plant geography is in one sense still in the Darwinian period, but it is more revealing to limit this stage to the years say from 1850 to 1875, which was the testing time of the new theory. The rest of the nineteenth century may be called the German period. During it a great many workers reinvestigated and reorganised the whole subject of the distribution of plants in the light of its new theoretical background and among them the German school of Grisebach, Drude, Engler and others was pre-eminent. With the turn of the century two new branches of botany—ecology and genetics—arose in spectacular fashion. The former in particular diverted to itself much of the interest formerly enjoyed by plant geography, and during this time, which may be called the period of ecology, floristic plant geography suffered a partial eclipse. Finally, the last thirty years have seen not only the rehabilitation of plant geography, mainly as a result of stimulating new theories relating to it, but what is even more important, much progress towards a proper synthesis of it with ecology, genetics and other aspects of botany which, far from being its rivals, are in fact its close allies. To-day, the study of plant geography has recovered much of the position it held seventy or eighty years ago. There is once more evidence that it may hold the key to much that is hidden and that it must therefore receive the proper measure of attention which it merits not only on this account but also because of its intrinsic interest.

PART ONE

CHAPTER 1

THE GEOGRAPHY OF THE WORLD

IN plant geography almost all aspects of the physical geography of the world are involved, but there are four subjects in particular of which an adequate understanding is so essential that a brief account of them is desirable here. They are the continents and oceans, the islands, the mountains, and the deserts.

Continents and Oceans

The continental land masses of the world are in effect six in number, namely, Eurasia, Africa, Australia, North America, South America, and Antarctica. The last named has now virtually no plant life and is covered with ice and snow, although it possessed a considerable vegetation in former ages.

The distribution of these masses in respect of the equator is such that the northern and southern hemispheres are almost exactly the opposite of one another, so that where there is land in the north, there is sea in the south, and *vice versa*. The Arctic Ocean in the north is balanced by Antarctica in the south, and so on. Arising from this, the distribution of the world's land masses can be described concisely in two useful ways. It may be pictured or represented by two cogwheels, each with three teeth, fitting into one another, the one wheel being the land of the northern hemisphere and the other the oceans of the southern hemisphere. A model made on these lines, with the land wheel black and the sea wheel white, is quite a good rough diagrammatic representation of the map of the world.

It will be apparent from this that the northern hemisphere is predominantly a land hemisphere and the southern one of sea, and in fact the general distribution of land can also be described as having the form of a more or less continuous northern ring from which three branches extend southward across the equator to varying distances.

This peculiar distribution of land leads to what is probably the most significant of all geographical features from the point of view of the general geography of plants and that which does more to explain the facts to be presented below than any other. It is that while in the higher northern latitudes there is a more or less continuous belt of land all round the world, this belt becomes more and more incomplete towards the south, until in southern temperate latitudes there is practically no land at all.

The three extensions southward from this northern belt are South America, Africa, and Malaysia with Australasia and they differ considerably. The first reaches further south than the others and tapers to a point; the second is blunt and does not extend far beyond the Tropic of Capricorn; the third is intermediate in length and, beginning as an archipelago, ends in a detached continent.

But there is a further point about the continents which is apparent only if the distribution of the contours of the seas is studied. If a bathymetric map of the world (Plate 3) is examined, it will be seen that along some parts of the edges of the continents the passage to great depth is very rapid so that deep water lies close to the actual outlines of the land, but that in other parts the seas, for a considerable distance out from the coast, are shallow, the sudden deepening being much further away. Always, however, there is some point at which the waters become suddenly much deeper. The full significance of this will be discussed at greater length in Chapter 20, but it will be clear enough here that this sudden deepening of the sea marks the real edge of the continents and that where this is far seaward of the actual coast line this is because the edges of the continents lie at such a level as to be shallowly submerged. In other words, the absolute level of the edges of continents varies considerably. In most places they stand clear of the water to their very boundaries, but in others they pass gently below the sea level before their actual abrupt edges are reached.

This being so, the seas of the world can be classified into deep seas or oceans proper, bounded by the true edges of the continents, and shallow or marginal seas which are really shallow flooding of the peripheral parts of continents. These latter are appropriately called epicontinental seas. As has been said, this distinction and its meaning will be referred to again later, but it is of immediate importance here in connection with the classification of the islands of the world, which must next be described.

Islands

The number of islands in the world is very great, but the absolute figure is of no particular concern here, their size and distribution being of much greater importance. Obviously all land masses are in a sense islands since there is none which completely girdles the earth, but convention restricts the use of the term to areas which are conspicuously less than those which habitually go by the name of continents. Greenland is generally described as the largest island and is considerably smaller than Australia or Europe, the least of the continents. Other large islands are Baffinland, Japan (three islands), Sumatra, Borneo, New Guinea and Madagascar, while on a somewhat lesser scale, Great Britain, Celebes and New Zealand (two islands) may be added.

Islands of what may be called second size are several in the Arctic, Ceylon, Cuba, Formosa, Fuegia, Haiti, Iceland, Ireland, Java, Luzon and Mindanao (Philippines), Newfoundland, Sakhalin, Sardinia, Sicily, Tasmania and Vancouver. Smaller again are Corsica, Crete, Cyprus, Jamaica, New Caledonia, Porto Rico, Trinidad, and a number of islands in the Malayan Archipelago, the Bismarck Archipelago and in the Solomons.

Lastly there are certain groups of still smaller islands and some very small isolated islands. These are too numerous to mention in detail, but this is a good opportunity for listing those of more particular botanical interest and giving a rough indication of their whereabouts. It is easiest to do this ocean by ocean, and it is perhaps worth while to recall that in a few cases islands which are habitually referred to in the singular, e.g. Lord Howe Island, are in fact small groups.

In the Arctic Ocean are Jan Mayen, half-way between Norway and Greenland, and Bear Island, half-way between Norway and Spitzbergen.

In the North (extra-tropical) Atlantic are, first, the three groups off Portugal and

North Africa, namely Madeira, the Canaries and, furthest from land, the Azores, On the west side of this ocean are the Bermudas and the Bahamas.

In the Tropical Atlantic are the smaller islands of the West Indies; the Cape Verde Islands off Senegal; the group of Fernando Po and S. Tomé, in the Gulf of Guinea; Fernando Noronha, off the point of Brazil; and Ascension and St. Helena.

In the Indian Ocean the Comoros, the Aldabras, the Seychelles and the Mascarenes (Mauritius, Réunion and Rodriguez) lie respectively north-west, north, north-north-east and east of Madagascar; Zanzibar is close to the African mainland a little south of the equator; Socotra lies off the tip of Somaliland; and there are several small islands off the south-east coast of Arabia and in the Persian Gulf. To the south-west of India and Ceylon are the Maldives and Laccadives and the Chagos Islands; the Andamans and Nicobars lie between India and Malaya, while south-west of Java are Christmas Island and the Cocos-Keeling Islands.

In the North (extra-tropical) Pacific there are three remarkable festoons of islands between China and Alaska, namely the Riukiu Islands between Formosa and Japan; the Kuriles between Japan and Kamchatka; and the Aleutians between Kamchatka and Alaska. The Bonin Islands are south of Japan.

Further south, within the tropics, the small islands are innumerable, since they comprise not only many in the Malayan Archipelago but almost all those further east (264, 408). Many of the latter are merely coral atolls and of little botanical interest, but the following groups are all of some, and mostly of considerable, importance. Across the Tropic of Cancer, and rather nearer America than Asia, lie the Hawaiian Islands. East of the Philippines come, first, Palau and Yap; next, the Marianne Islands and the Caroline Islands, and then the Marshall Islands. South of these, and east of the Bismarck Archipelago and the Solomons are the Santa Cruz Islands and, rather further off, the Gilbert and Ellice Islands. To the south again, and east of the northern part of Australia are, from west to east, the New Hebrides, the Fiji Islands, the groups of Samoa and Tonga, the Cook Islands, the Society Islands, the Tuamotu Islands and the Marquesas. Finally, far removed from all these across the ocean, are the four small Revillagigedo Islands, west of southern Mexico, and the more numerous Galapagos Islands, west of Ecuador.

In the South (extra-tropical) Pacific there are few islands but all of them are of interest. North-west of New Zealand are Lord Howe Island and Norfolk Island; north-east are the Kermadecs; to the east are the Chatham Islands and the Antipodes Islands; and to the south are Auckland Island and Campbell Island. Nearer the tropic and about half way between New Zealand and America are Pitcairn Island and Easter Island, famed for its strange statues. Lastly, rather more to the south and not far from the Chilean coast are the Juan Fernandez Islands.

Finally to be mentioned are the Falkland Islands and the tiny and very scattered islands situated in the great continuous sea surrounding Antarctica which it is convenient to call the South Temperate Oceanic Islands. The flora of these last is in total small but of peculiar interest (see p. 203) and it is appropriate to give a list of them here. Working east from the tip of South America they are South Georgia, Tristan da Cunha and Gough Island, Marion Island, the Crozets, the Kerguelen Archipelago, Heard Island, St. Paul and Amsterdam Islands, and Macquarie Island.

Islands are most often classified into two classes, according to their positions in respect of continents. Some, including most of the larger islands, are parts of the shelves of continents and are separated from the mainland only because the intervening land is shallowly submerged. These are called continental islands and the British Isles, Japan, Borneo and New Guinea are good examples of them. Others, including the great majority of smaller islands, arise directly from the floors of the oceans and are separated from the nearest continents by deep water. These are called oceanic islands and are well exemplified by many of the smaller Pacific Islands. Biologically this distinction, though somewhat arbitrary, is a very important one, because the criterion really employed is that of isolation. Continental islands, as integral parts of a continental mass, obviously have a close connection with the adjacent mainland, and this is reflected in their plant and animal life. Oceanic islands on the other hand have no such connection, although they may be fairly close to continents. They are independent of any large land mass and thus their biology presents features and problems of the greatest interest. In their cases isolation and age have been the predominant factors in controlling and determining their floras and faunas.

Several different kinds of oceanic islands have been distinguished (230). First are certain large islands, composed in part at least of sedimentary rocks, which though situated fairly close to continents are separated from them by comparatively deep seas and which are clearly not parts of continental shelves. Such are Madagascar, Jamaica and Iceland. Second are certain similar but smaller and more isolated islands such as New Caledonia. Third are the small islands of igneous rocks arising abruptly from the beds of deep waters and exemplified by the Hawaiian Islands and St. Helena, which are in fact the summits of active or extinct volcanoes. Fourth are small isolated islands largely or entirely of coral rock which are believed to be the remains of coral atolls which have become well elevated above the present level of the sea, and of which there are many instances in the Pacific. Fifth are the coral islands or atolls proper of which there are enormous numbers, chiefly in the same ocean. Those of the third and fourth kinds are often spoken of as "high" islands in contradistinction to the "low," or atoll, islands. Biologically interest centres chiefly in the smaller islands because of their greater average isolation and wider variety, and it is to these, indeed, that the term "oceanic" is more loosely and generally applied. There is little or no geographical segregation between the kinds and since their differences are strikingly reflected in their floras it is important to realise to which class any individual island belongs. Thus the Seychelles consist of two groups, one of granite islands and one of coral atolls. The main distinction is also well seen in the Cocos-Keeling Islands (605) and the neighbouring Christmas Island (16), south of Malaysia, the former being coral atolls and the latter a high volcanic and coral rock island.

Oceanic islands and especially the more isolated of them have long been of particular interest to students of plant geography (239, 258, 274, 570) and a good deal will be said about them in due course. Darwin (124) first drew attention to the chief botanical features of the first four kinds of oceanic islands mentioned above, namely, that they have fewer species than similar sized areas on continents; that they have higher proportions of endemics; and that the order of importance and representation of the larger plant groups are often materially different from those usual on continents. These characteristics are repeatedly exemplified in the following chapters and for this and the other reasons given above there are tabulated here, together with their distances from the nearest large land surface, those oceanic islands (see Plate 3) to which most frequent reference will be made later.

They are:

The Hawaiian Islands .	3,900	miles	from	Japan; 2,400 miles from America
Kerguelen . .	2,500	„	„	Australia; 2,100 miles from Madagascar
Tristan da Cunha .	2,200	„	„	America; 1,800 miles from Africa
Tahiti . . .	2,200	„	„	New Zealand
Samoa . . .	1,700	„	„	„ „
Fiji	1,300	„	„	„ „
St. Helena . .	1,200	„	„	Africa
Ascension . . .	900	„	„	„
New Caledonia .	800	„	„	Australia
Rodriguez . .	800	„	„	Madagascar
The Azores . .	800	„	„	Portugal
The Galapagos Islands	650	„	„	America
The Bermudas . .	650	„	„	„
The Seychelles . .	650	„	„	Africa; 600 from Madagascar
The Kermadecs . .	600	„	„	New Zealand
Mauritius . . .	500	„	„	Madagascar
Norfolk Island . .	450	„	„	New Zealand
Réunion . . .	400	„	„	Madagascar
Juan Fernandez .	400	„	„	Chile
Madeira . . .	350	„	„	Africa
Lord Howe Island .	350	„	„	Australia

Two more points about islands must always be remembered, namely, that their number and distribution depends to a large degree on the general water level of the oceans, and that they have not necessarily all existed as islands for the same length of time. The first of these points is sufficiently illustrated, as far as continental islands are concerned, by Plate 3 and what is said about it in Chapter 20. The same remarks apply to oceanic islands but much less obviously. Many of these arise abruptly from the ocean floor and only just break the surface or, as often in atolls, just fail to do so, and considering the depth of water concerned, the likelihood that there are other considerable submarine elevations which, nowadays, remain hidden below the surface, is clearly strong. A number of such "submerged islands" or *guyots*, as they are technically called, have now been detected in the Pacific (261) and are a reminder that some of the islands listed above may not always have been so isolated as they appear to-day. A very interesting suggestion regarding these guyots is that they are islands which have become submerged through the rise of sea level caused by the accumulation of sediments on the ocean floor.

The age of islands is a much more thorny and controversial subject in which any estimates, such as those of Arldt (21), must depend very much on what their authors believe about various germane matters, such as those dealing with the history of the continental masses. It is probably safe to regard most oceanic islands as having existed in that form longer than most continental islands, and also to regard the first kind as the oldest and the atolls as the youngest, but beyond this there is little that can be said here, and there are almost certainly exceptions to all these statements.

Mountains

The importance of mountains in plant geography lies in the fact that, as altitude increases, the climate tends to become more and more temperate or frigid in character, so that a mountain at a lower latitude has, in its higher parts, a climate very like that prevailing at sea levels at higher latitudes. Owing to this a mountain nearer the equator is often able to support species or vegetation occurring at sea level further north. Moreover since high altitudes are usually combined into mountain ranges which may be of great length, the mountain systems of the world often provide connecting links or paths for the spread of plants.

In the broadest sense the great mountain systems of the world are only three, namely the western American system comprising the Rocky Mountains in the north and the Andes in the south; the Eurasian-Australasian system, comprising the Pyrenees, Alps, Caucasus, the Sino-Himalayan mountains, the plateaux of Central Asia, the mountains of Malaysia, and those of eastern Australia; and the very different (both in size and form) African system, but the picture is too complicated to be painted in quite such bald terms, however desirable it may be to simplify matters, and a rather more detailed classification is required if all the necessary facts are to be revealed. On this basis the mountains are best described and arranged as follows.

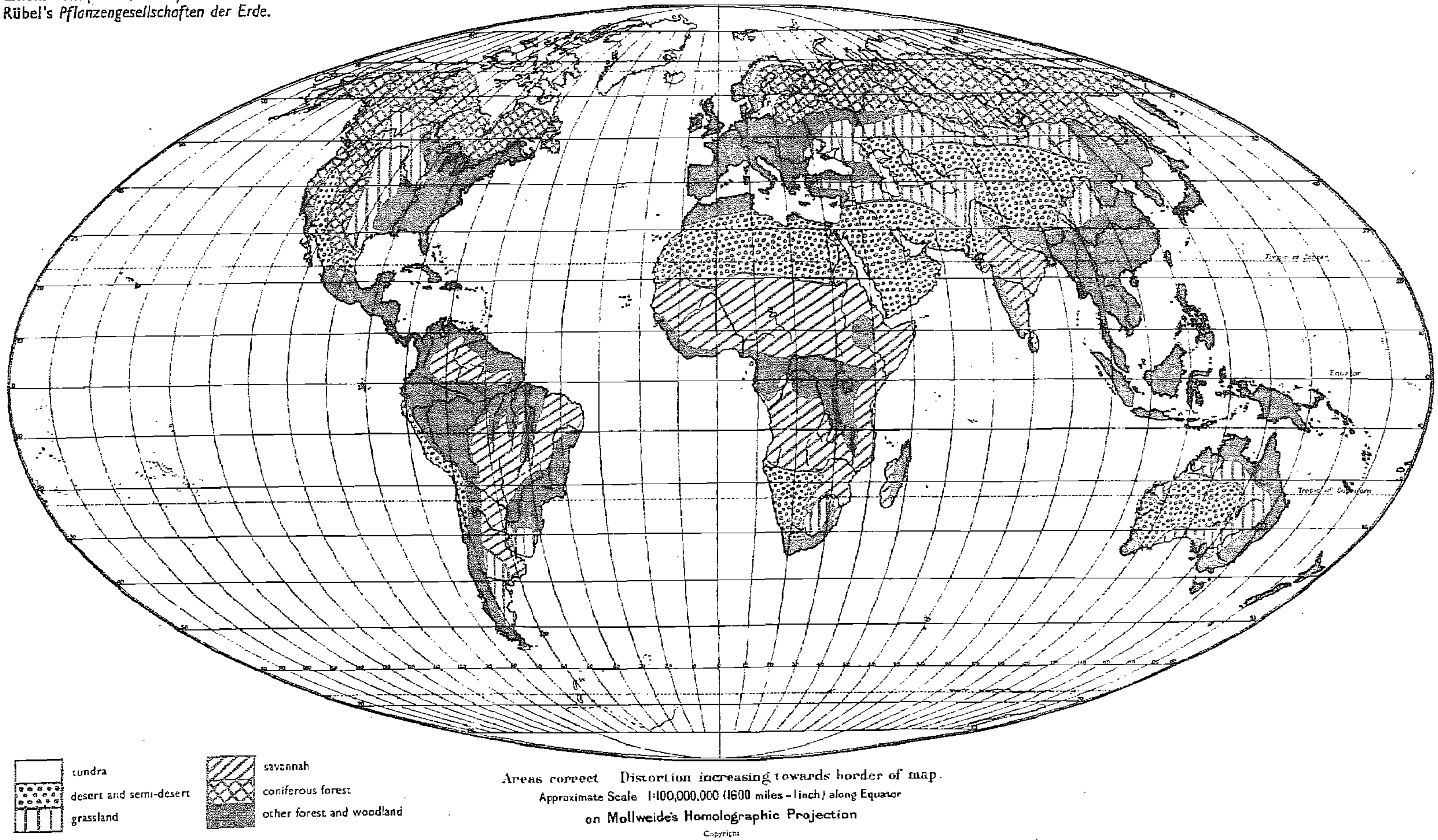
The great western American chain consists of two parts with distinct names, the compound system of the Rockies in the north and the much simpler system of the Andes in the south, but these are really only portions of one great whole which reaches, in a more or less southerly direction, from Alaska in the north to Cape Horn in the south, that is to say through the whole length of the continent of America, and it is probable that the existence of this great transtropical "bridge" has had profound biological consequences. It is not unnaturally least obtrusive in the narrow isthmus of middle America, but even here it has elevations of over 12,000 ft. In the Rockies the greatest heights are in the extreme north-west (Mts. McKinley, Logan and St. Elias all approaching or exceeding 20,000 ft.) and in Mexico (Orizaba and Popocatepetl, both *c.* 18,000 ft.). In the Andes the highest mountain is Aconcagua, 22,800 ft., in latitude 33°, the most southerly of all the great Andean peaks. In eastern North America is the minor north-south range of the Appalachians, and in South America the south-eastern part of Brazil is also mountainous. It must also be remembered that Greenland is almost entirely an elevated plateau, but owing to the high latitude this is not very significant biologically.

In Europe the chief ranges are the Pyrenees, up to 11,000 ft.; the Alps, up to 16,000 ft.; the Apennines, up to 9,600 ft.; the Carpathians up to 9,000 ft.; and the Caucasus, up to 18,500 ft. All these run more or less west and east, as do also the Atlas Mountains, which although in Africa belong to the same general system, and which attain a height of nearly 14,000 ft. In addition to these, the Balkans are largely mountainous. In the north of Europe also there are two elevated regions, western Norway, where there is a height of 8,500 ft., and the Urals, where the highest point is some 5,000 ft. Both these latter systems run north and south.

In Asia the mountain systems are so vast and complicated that they can only be described in general terms. First, from the Bosphorus to north-west India there stretches a series of ranges, all running approximately west and east and mostly of medium height, but containing a few great peaks, such as Ararat, *c.* 17,000 ft., and with a notable outlier, the 13,000 ft. Jebel Akhdar, in eastern Arabia. Next, south-east of these, much of the Indian Peninsula is mountainous, culminating in heights of more than 8,000 ft. in South India and in Ceylon. The main ridge of this system is along the west coast of India. Lastly the whole of the vast triangle N.W. India—Kamchatka—Siam is one huge and complex system of multitudinous mountain ranges which comprise the most extensive area of elevated land in the world as well as all the highest altitudes. Along most of the south side of this triangle runs the

PLATE 2

Map of the World showing the distribution of Vegetation. Simplified, chiefly after Brockmann-Jerosch in Rübel's *Pflanzengesellschaften der Erde*.



Areas correct Distortion increasing towards border of map.
Approximate Scale 1:100,000,000 (1600 miles - 1 inch) along Equator
on Mollweide's Homolographic Projection

huge wall of the Himalayas, themselves a great plexus of ranges culminating in the extreme world height of Mt. Everest, 29,000 ft. and coalescing westwards with the mountains of Persia. Northwards the Himalayas pass into the highly elevated Tibetan plateaux and these again north into the plateaux and ranges of Central Asia, North China and eastern Siberia. The axes of all these are roughly west and east, but in Manchuria, Korea, Japan and Kamchatka they become more or less north and south in conformity with the coastline. Both Japan and Formosa have heights of over 12,000 ft.

Passing back to the south-east of Asia we find one of the major features of world relief. At the junction of Burma, Tibet and China the great west-east mountain chain, which we have traced all the way from the Pyrenees to and through the Himalayas, suddenly changes its course and its constituent ranges turn southwards, continuing through Burma, Siam and Indo-China. Many of the mountains reach a great height, but this region is not very well known and it is best to avoid using figures which may be misleading. The main line of this system is along its centre and runs right down the Malay Peninsula and into the Malayan Archipelago. The geography of this latter region is broken and scattered but it can be said that the main mountain line of the Malay Peninsula continues in a curve through Sumatra, Java and the Lesser Sunda Islands. In both the former there are heights of over 12,000 ft. Practically all the other great islands of the Archipelago are also mountainous, although the axes of their ranges do not follow any well-defined line. In Borneo, for instance, Mt. Kinabalu is over 12,000 ft., and there are peaks of more than 10,000 ft. in the Philippines. Further east again, in New Guinea, the general west-east trend of the mountains is once more apparent, and here there are heights of more than 16,000 ft.

In Australia the main mountain system is that which follows the east coast down into Tasmania, thus running north and south, and this, whatever its historical relation to the rest may be, is the ultimate stretch of the great mountain line which begins in western Europe. The highest point is Mt. Koskiusko, about 7,000 ft., in New South Wales. In the rest of the Pacific New Zealand exhibits strong relief, culminating in Mt. Cook, in South Island, which exceeds 12,000 ft.; the Hawaiian Islands have summits of over 13,000 ft.; and there are peaks of 10,000 ft. in the Solomons.

In Africa the mountain system is mainly different from elsewhere in the world. A ridge of elevated land runs north and south all the way from the Red Sea to the Cape but is broken up in a striking way. In the north is the plateau of Abyssinia, with peaks exceeding 15,000 ft., and in the extreme south-east the mountains of the Transvaal, Natal and the Cape Province also form a more or less definite whole, attaining locally heights of 11,000 ft., but in between the highest land consists mainly of a number of very distinct and isolated mountains surrounding Lake Victoria. Nothing quite like these mountains exists elsewhere and they are frequently referred to as "island mountains." Chief amongst them are Kilimanjaro, nearly 20,000 ft., Mt. Kenya and Ruwenzori, both nearly 17,000 ft., and Mt. Elgon, nearly 15,000 ft. In addition to these eastern mountains there is a secondary series of elevations along parts of the west coast which reach their highest altitude of nearly 14,000 ft., in the Cameroon Mountain. A third series, of widely separated mountain massifs, forms a line between Abyssinia and the Atlas Mountains, thus forming, as it were, stepping stones across the Sahara, and they are for this reason noteworthy. They are not very well known, but it is certain that some at least reach 12,000 ft. In Madagascar, too, there are considerable elevations.

Antarctica is also largely mountainous and said to contain peaks of more than 13,000 ft. (358).

Deserts

Everyone knows what is meant in general terms by the word desert, but it is difficult to define it scientifically. Heat and drought are the commonest characteristics of deserts, but the two are not always combined, and deserts may, in fact, be either hot or cold, according to their latitude and altitude. In all, however, there is, for one reason or another, a deficiency of available moisture, and this is usually due to lack of rain. Botanically deserts have been defined as areas where, because of the climate conditions, there is less than a continuous covering of vegetation, and this criterion includes also the entire absence of it. It is not easy, however, to know exactly where the line is to be drawn, and this definition breaks down if applied too narrowly.

Actually, although these points merit mention, there is no need here to attempt a rigid definition, and it will suffice to give a short survey of those parts of the world to which the name desert is generally applied. It may, however, be noted that they are, roughly speaking, those areas where the annual rainfall measures less than 10 ins. (Plate 23).

Deserts are for the most part to be found on the leeward side of mountain ranges because the heights discharge the rain-bearing clouds from the sea before they pass further inland. This is specially true of the warm deserts, which may be mentioned first.

The North American warm desert of the Great Basin exemplifies this well, lying as it does between the constituent ranges of the southern Rockies. Another desert occupies parts of northern Mexico and the adjacent states of the Union. Both these have elevations of several thousand feet. In South America the arid parts of western Argentina are similar, but there is also the coastal and more tropical desert of Peru and Chile.

The deserts of Africa and Asia must, in part at least, be considered together because the greatest desert in the world covers parts of both continents. This is the great series of varyingly dry regions which stretches, with but few breaks, all the way from the west coast of North Africa to north-eastern Mongolia, and which has six main constituent areas. Of these the Saharan, Arabian and Persian deserts are warm deserts, while those of Turkestan, Tibet and Mongolia (Gobi) are mostly cold deserts.

The Sahara is, in a popular sense, the most typical and absolute of all deserts, and over much of it the surface is mobile sand and bears no plant life. This is, however, by no means continuous but is broken by mountains and oases. The Saharan, Arabian and Persian deserts form a more or less single belt of dry lands all the way from north-west Africa to north-west India. It is also noteworthy that this great region is less intimately associated with mountain ranges than most deserts.

Much of the western part of southern Africa is also arid, and this area comprises the well-known Kalahari and Karroo deserts and most of South West Africa.

Finally, there is the great central warm desert of the interior of Australia, which covers much of western Australia and South Australia and the southern part of the Northern Territory. It illustrates well another feature often seen in deserts, namely, that they occupy the regions most distant from the coasts. The moisture-laden winds from the sea tend gradually to lose their water as they pass inland and distance has much the same result as that of a single mountain range.

The three chief cold deserts of the world have already been mentioned incidentally since they are part of the vast African-Asiatic desert. Among them, the Turkestan desert is the least extreme and has a fairly well-developed vegetation.

Both the Tibetan and Gobi deserts are good examples of cold deserts in which the low temperature is due to great elevation. Both, too, consist chiefly of the plateaux between mountains. The Tibetan plateau desert is often called "the roof of the world" and has an average elevation of some 15,000 feet. The Gobi desert in general exceeds 5,000 ft. The most important climatic feature of these deserts is the variation of temperature during the year, for a greater part of which they are exceedingly cold. Incidentally, even in warm deserts there is generally a great difference between day and night temperature.

In conclusion Antarctica is in one sense a cold desert because it is glaciated, and affords practically no niches for flowering plants, and the same is true of similar parts of the Arctic. In some other parts of the Arctic the precipitation is very low and something like desert vegetation results.

To summarise, the desert regions of the world comprise the warm deserts of North America, Mexico, Chile and Peru, Argentina, the Sahara, Arabia, Persia, north-west India, southern Africa and Australia; the cold deserts of Turkestan, Tibet and Mongolia; and the polar deserts of the Arctic and Antarctic.

There is considerable difference of opinion as to the length of time that the present deserts of the world have existed as such (25). One view is that desert conditions have been a feature of the world throughout geological time, and that some at least of the deserts of to-day have been so far longer than the history of the Angiosperms. Another opinion is that desert conditions may have occurred at intervals throughout geological time but that all the present deserts are comparatively modern. Some, on the other hand, hold that desert conditions were unknown anywhere until late geological time. All that can usefully be said here on this issue is that the last would seem, on grounds of general evidence and experience, more unlikely than either of the other two, and that of these the first is perhaps the simpler proposition and therefore to be preferred in the absence of any definite evidence to the contrary. The present desert floras certainly suggest that they are not all the same age, for they vary much in floristic diversity and in specialisation. Thus the desert floras of southern Africa are peculiarly rich in specialised xeromorphic groups, while the great African-Indian desert region and the Australian desert region are notably deficient in them.

Map Projections

It is almost impossible to depict exactly, on a flat surface like a page of paper, the surface of a sphere, and maps of the world as a whole or of any large part of it therefore almost inevitably contain some distortion unless very complicated and impracticable outlines are used. Various methods, often involving rather abstruse mathematics, are employed in order to reduce this distortion and one or two of these methods, or projections as they are called, require comment here.

The simplest method is perhaps that of picturing the world as it would appear if seen from a very long distance away, but since this view would reveal only the half of the sphere nearer the observer, the whole globe can only be shown thus by two separate circular maps. For most purposes this is a great drawback, but occasionally, as for instance when the polar regions are to be mapped, such a polar stereographic projection has its uses, and it is employed in one or two cases in this book.

The commonest of all projections is Mercator's projection, which shows the surface of the world in rectangular form, but this is only achieved at the expense of a seriously increasing distortion away from the equator. For everyday political maps whose interest centres in lower latitudes this disadvantage can be neglected, and this explains the constant use of this projection in simple generalised maps, but for scientific purposes it is almost useless since it distorts not only the relative position but also the relative size of land masses. Moreover, even this distortion is not constant but increases towards the poles. For these reasons Mercator's projection is particularly unsuitable for problems of plant geography and it is much to be desired that its use in this connection should cease.

For all but very special purposes Mollweide's projection, in one or other of its forms, is perhaps the most convenient since it removes many of the drawbacks of Mercator while still permitting a fairly simple total outline. Mollweide's projection shows the world as an ellipse having the equator as its longer axis. It is an equal area projection, so that the relative sizes of different parts of the world are true, and this is a point of great value. On the other hand, there is some distortion of shape, especially towards the ends of the ellipse, but if, as is usual, Africa is made the central feature, this disadvantage is much reduced.

Although far from perfect it is difficult to find a better projection than that of Mollweide if the whole world is to be covered and if the shape of the map is to remain continuous and simple, and since this is essential when biological problems are under discussion his projection is used almost exclusively in this book.

It need only be pointed out further that, with regard to maps showing less than the whole world, the smaller the area depicted the less important are problems of projections until, where quite small areas are concerned, the lines of latitude and longitude can be drawn truly horizontal and vertical without appreciable distortion.

Definitions

Most parts of the world have received their names without particular regard to biological problems, and hence, when these questions are at issue, it is sometimes necessary to refer to areas which are without convenient comprehensive names.

It is for instance useful to refer to the islands which lie in the eastern North Atlantic off the coasts of north-west Africa and Europe, that is to say the Azores, the Canaries, Madeira and the Cape Verdes, by the inclusive name of Macaronesia.

A more difficult case is that of the islands off the east coast of tropical Africa, which comprise Madagascar, the Comoros, the Aldabra Islands, the Mascarenes and the Seychelles, for there is no general term to cover them all. In the following pages they are considered to form the Madagascar Region and this name is used for them. Unless qualified it may be taken to include all these islands.

Australasia, again, is a common enough term, but it has some ambiguity. Here it is used to mean Australia, New Zealand and its satellite islands, and, generally, New Caledonia, Lord Howe Island and Norfolk Island in addition.

The name Malaya and its associated forms are also the source of some confusion. In this book the usage is to refer to that part of continental Asia south of the Isthmus of Kra as the Malay Peninsula; to the islands thence as far as and including New Guinea as the Malayan Archipelago; and to both together as Malaysia (531).

Finally, the phrase "the Pacific Islands" is used to denote some or all of the islands east of the Malayan Archipelago and north of Australasia (as just defined).

Chapter 2

THE DIVISION OF THE WORLD INTO FLORISTIC REGIONS

Major Zonations

The major and most obvious segregation of the plant life of the world to-day is into three latitudinal zones—polar, temperate and tropical. These, owing to the shape of the earth and its position in relation to the sun, are symmetrical about the equator. For most practical botanical purposes, however, this zonation is scarcely detailed enough and it is usual to incorporate a fourth zone and to speak of arctic (polar), temperate, subtropical and tropical zones.

A still fuller and more scientific classification is that quoted by Hansen (248), for example, which is as follows:

1. Equatorial zone .	0·0–15·0	degrees on either side of the equator
2. Tropical zone . .	15·0–23·5	,, ,, ,, ,, ,,
3. Subtropical zone .	23·5–34·0	,, ,, ,, ,, ,,
4. Warm temperate zone	34·0–45·0	,, ,, ,, ,, ,,
5. Cold temperate zone .	45·0–58·0	,, ,, ,, ,, ,,
6. Subarctic zone . .	58·0–66·5	,, ,, ,, ,, ,,
7. Arctic zone . .	66·5–72·0	,, ,, ,, ,, ,,
8. Polar zone . .	72·0–90·0	,, ,, ,, ,, ,,

This would be a satisfactory and accurate indication of the major distribution of plants were it not that it ignores one factor which actually complicates it very much, namely, the influence of the elevation of the land. It is well known that at any latitude a sufficient vertical rise from sea level epitomises in a very short distance the climatic zonation which is to be observed at sea level between the latitude in question and the nearer pole. Since climate and vegetation are in general very closely correlated, it follows that a vertical rise similarly epitomises the botanical changes which are to be observed at sea level between the latitude in question and the nearer pole. This is illustrated by the familiar fact that as one ascends a mountain the plant life changes with increase in elevation until, if the rise is sufficient, a condition characteristic of polar latitudes is reached, so that the highest mountains, even if on the equator, have permanent ice and snow at their summits.

The vegetational zonation of mountains, and especially of tropical mountains, has been much studied and has been described and expressed in a number of classifications. The following, which is a combination of several, is a fairly familiar one. On a high mountain situated in the more equatorial parts of the tropical zone in the old world, for instance, the lowest levels, namely those between sea and 600 metres, are occupied by a truly equatorial vegetation characterised by palms and bananas; above them comes a tropical but less equatorial kind of vegetation in which tree-ferns and figs are prominent; above this is a zone of subtropical types like myrtles and laurels; above them another warm temperate zone of evergreen trees; next a zone of deciduous trees such as are familar in temperate regions; then a zone of coniferous trees; then a zone of alpine shrubs; and finally a zone of alpine herbs. Above this there is no appreciable vegetation.

This zonation may be summarised with figures as follows:

0– 600 metres	Zone of palms and bananas
600–1,250 ,,	,, tree-ferns and figs
1,250–1,900 ,,	,, myrtles and laurels
1,900–2,600 ,,	,, evergreen trees
2,600–3,200 ,,	,, deciduous trees
3,200–3,800 ,,	,, coniferous trees
3,800–4,450 ,,	,, alpine shrubs
4,450–5,050 ,,	,, alpine herbs
5,050– ,,	Permanent ice and snow

Another and more extensive presentation of this zonation is illustrated in fig. 1.

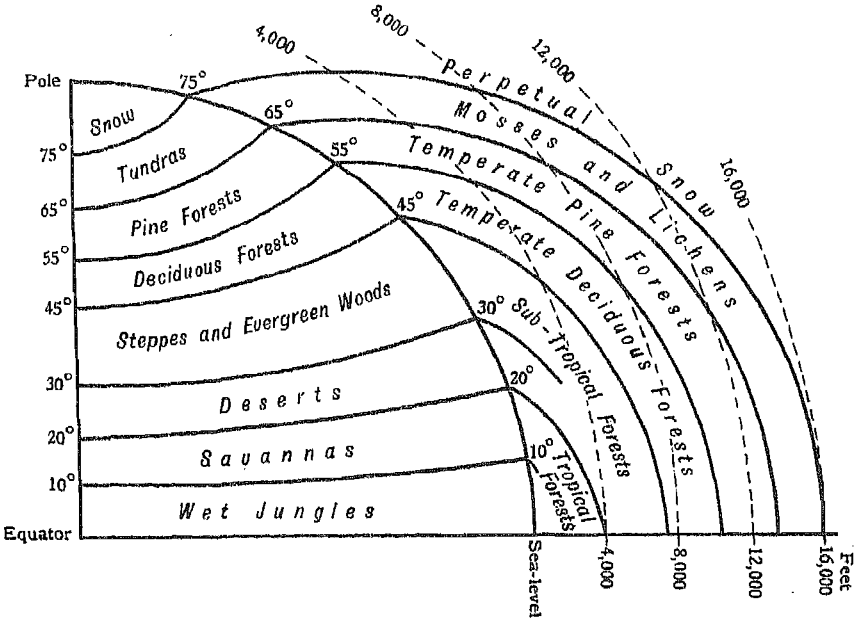


FIG. 1.—Diagrammatic representation of the vegetation zones of latitude and altitude. (Redrawn from Herbertson's *Outlines of Physiography*, Edward Arnold & Co.)

It follows from what has been said that unless the relief of the land is very slight, each latitudinal zone of the world will afford suitable conditions for the appearance of plants in general characteristic of a zone or zones in higher latitudes. Subtropical plants will occur here and there in the tropical regions according to the relief; temperate plants will occur in both subtropical and tropical zones, and so on. If the elevation is sufficient, each type of plant or vegetation will find a congenial home somewhere at all latitudes nearer the equator.

From this there is to be drawn the very important conclusion that in no latitudinal zone is the total land area exclusively available for the type of vegetation characteristic of the lowest levels in that zone. Some of it will be occupied by vegetation characteristic of the lowest levels of zones nearer the poles.

Detailed tables of figures relating to this interesting generalisation are given in Appendix A, but the two chief conclusions to which they lead may be summarised here.

The first relates to the absolute areas of the land occupied by the different kinds of vegetation on each side of the equator, and the figures show these to be, in thousands of square miles:

	No Vegetation.	*Arctic Alpine.*	*Temperate.*	*Subtropical.*	*Tropical.*
North hemisphere .	2,658	9,065	11,137	8,673	6,571
South hemisphere .	155 add Antarctica	436	1,317	5,849	5,571

The second series of figures relates to the proportion of each of the climatic zones available for the different types of vegetation. Taking the corresponding zones in the two hemispheres together, and using a somewhat simplified phraseology, the figures are:

1. In the tropics only about 77 per cent. of the total land is occupied by tropical vegetation; 17·5 per cent. is occupied by subtropical plants; 4 per cent. by temperate plants; and 1·5 per cent. by arctic alpine plants.
2. In the subtropics only about 67·5 per cent. of the total is occupied by subtropical vegetation; 17 per cent. is occupied by temperate plants; and 9 per cent. by arctic alpine plants.
3. In the temperate regions only about 74 per cent. of the total is occupied by temperate vegetation; 18·5 per cent. is occupied by arctic alpine plants.

The residue of each zone is too elevated to bear flowering plants.

Further Classification

The average range of species is comparatively small. No doubt a laborious computation could be made to give a fair idea of the actual dimensions involved, but in the absence of any such figure it is enough to say that the area occupied by any one of the vast majority of species (and, it may be added, of most genera also) is far less than that of any one latitudinal zone. As a result of this some or all the species present in one part of a zone are different from those in other parts of the same zone. Many factors help to determine the degree of this difference, and since these factors themselves show no regularity or constancy, it may be larger or smaller, so that the extent of geographical separation between two floras cannot alone be taken as a measure of the differences between them. Other means of estimation must be sought. From this it is also clear that the plant life of the world can be classified geographically, not only on a vegetational basis, but also floristically, that is, into distinct floras, and a classification of this kind is an important adjunct to plant geography. It is, however, not easy to make because of the absence of any ready means of estimating floristic differences and relationships.

The situation may be made clear by an illustration. Take the case of a botanist familiar with the British flora, who for the first time visits North America. There he will find many plants which he has not encountered before, but for the most part they will be so like those with which he is acquainted at home that he will be able to identify them fairly easily. If the same botanist now visits New Zealand he will again find many unfamiliar plants, indeed even more, but on this occasion his previous experiences will be of little or no help in diagnosing them. In short, the differences between the floras of the British Isles and New Zealand are greater than those between the floras of the British Isles and North America. This is clear enough, but the difficulty is to put an absolute value on these differences and to compare them with others, as for instance those between the floras of North America and New Zealand.

Actually the fact that species are not equally closely related to one another makes it almost impossible to measure floristic resemblances and differences, and all that can be done is to utilise such evidences as may be available (and these are more often than not imponderable and intangible) to make what can be no more than a rough estimate. Of these possibilities the evidence based upon the endemic or peculiar elements of a flora is perhaps the most fruitful, but even this has a strictly limited value. To know, for instance, that half the species of any particular flora are peculiar to it, is often of interest and value, but more than one flora may show a similar degree of endemism and the statement affords no indication of the relationship between them. Indeed, expressions based on endemism serve really only to show how distinct from all others any one flora may be and help little in deciding closeness of affinity. Nevertheless, figures relating to endemism are useful and are frequently quoted in later chapters.

Again it is necessary in making a floristic classification to estimate the relative importance of different floras, and here too endemism can be of only minor assistance. There are other difficulties which it does not touch such as deciding the comparative values of the floras of two regions of very different size or of two floras of which one is large and the other small. How, for instance, is the flora of St. Helena, with perhaps under 100 species, to be compared with that of all Brazil, with many thousands of species? Yet both have the same degree of endemism. Must they, on this account, receive equality of status? There are many questions of this sort and many are the attempts which have been made to solve them, most commonly by the use of formulae by which the various ingredients of a flora may be recognised and given some relative value, as, for instance, in the interesting studies by Exell (168) and Williams (593, 594). It is, however, no criticism of these essays to say that they are not likely to achieve anything more than a rough answer for the simple reason that the classification of plants, on which they must be founded, is man-made and far too clumsy to express all the relevant information.

On the other hand, if we picture, as is surely correct, the floras of different parts of the world meeting and mingling either mutually or unilaterally with one another in the course of time, it may be expected that while, in some circumstances and places, infiltration will be mutual and gradual, in others it will result in comparatively sudden changes of floristic composition, such points or lines of change marking, as it were, the advancing front of the more aggressive flora or the position of barriers which retard further progress. Such places are clearly of great help in determining the boundaries of floristic regions, and they have been particularly studied in respect of the Malaysian flora by van Steenis (531), who refers to them as "demarcation knots." It may well be that the geographical conditions of this part of the world give to these knots an emphasis which may not prevail everywhere, but they must clearly occur at least in some form all over the world, and they are so important a phytogeographical conception that the whole subject of them deserves very careful attention, because, apart from their aid in delimiting floristic areas they are likely to throw valuable light on the direction of migration.

But the difficulties need not be further stressed and in spite of them many floristic classifications have been made, one of the earliest and most illustrative of these being by Schouw in 1823. This is quoted below rather fully, not only for its intrinsic value as a forerunner of modern systems, but because it shows the character that may be imparted to a region by the strong development therein of particular plant groups (467). Schouw divides the world into 25 kingdoms, naming them, wherever possible, after the most characteristic plants, as follows:

1. Kingdom of saxifrages and mosses. Alpine arctic.
   a. Province of sedges. Arctic.
   b. Province of Primulaceae. Eurasian alps.
   c. Province of shrubby alpine Composites. American alpine.
2. Kingdom of Umbelliferae and Cruciferae. North Eurasia.
   a. Province of Cichoriaceae. North Europe.
   b. Province of *Astragalus*, halophytes, thistles. North Asia.
3. Kingdom of Labiates and Caryophyllaceae. Mediterranean region.
   a. Province of Cistaceae. Spain and Portugal.
   b. Province of *Scabiosa* and *Salvia*. South France, Italy and Sicily.
   c. Province of shrubby Labiates. Eastern Mediterranean.
   d. Province of North Africa.
   e. Province of *Sempervivum*. North African Islands and Morocco.
4. Kingdom of *Aster* and *Solidago*. Northern North America.
5. Kingdom of Magnolias. Southern North America.
6. Kingdom of Camellias and Celastraceae. China and Japan.
7. Kingdom of Scitamineae. India.
8. Kingdom of the Himalayas.
9. Kingdom of Polynesia.
10. Kingdom of the Malayan Mountains.
11. Kingdom of Oceania.
12. Kingdom of balm trees. South-west Arabia.
13. Kingdom of deserts. North Africa and North Arabia.
14. Kingdom of Tropical Africa.
15. Kingdom of Cactaceae and Piperaceae. Central America and Northern Tropical South America.
16. Kingdom of the Mexican mountains.
17. Kingdom of *Cinchona*. Northern Andes, lower levels.
18. Kingdom of *Escallonia* and *Calceolaria*. Northern Andes, higher levels.
19. Kingdom of the West Indies.
20. Kingdom of palms and Melastomataceae. Eastern tropical South America.
21. Kingdom of woody Composites. Middle Andes.
22. Kingdom of Antarctica. Patagonia, Fuegia and Falklands.
23. Kingdom of *Stapelia* and *Mesembryanthemum*. Extra-tropical South Africa.
24. Kingdom of *Eucalyptus* and Epacridaceae. Extra-tropical Australia.
25. Kingdom of New Zealand.

It is remarkable that at such an early date so complete a classification should have been made. It is naturally open to much criticism in the light of modern knowledge, but its imperfections and incompleteness are largely due to the lack of knowledge of its time. In many respects it compares favourably with much more modern schemes.

Another, though much later, regional classification which deserves notice here, for much the same reason as did that of Schouw, namely that its approach to the problem is such as to throw into useful relief certain important facts, is that of Delpino (129). This in contrast to many others is a dichotomous classification and to that extent an obviously artificial one, but it has the two merits of being easy to visualize and remember and of showing what regions are analogous, not only above and below the equator but in other directions also. The following is a free and slightly modified rendering of Delpino's arrangement.

- continental
  - north
    - polar
      - ARCTIC-ALPINE
    - temperate
      - east
        - near
          - colder
            - WESTERN EURASIA
          - warmer
            - MEDITERRANEAN
        - far
          - colder
            - EASTERN EURASIA
          - warmer
            - CHINA—JAPAN
      - west
        - near
          - colder
            - EASTERN N. AMERICA
          - warmer
            - FLORIDA
        - far
          - colder
            - CALIFORNIA—OREGON
          - warmer
            - CALIFORNIA—MEXICO
  - tropical
    - west
      - TROPICAL AMERICA
        - Caribbean
        - Guiana
        - Brazil
        - Paraguay
        - Colombia
        - Peru
        - Bolivia
    - east
      - TROPICAL AFRICA—ASIA
        - Africa
        - Arabia
        - India
        - Malaysia
        - New Guinea
  - south
    - temperate
      - east
        - far
          - AUSTRALIA
            - North
            - South-east
            - South
        - near
          - CAPE
      - west
        - near
          - warmer
            - ARGENTINA—URUGUAY
          - colder
            - PATAGONIA
        - far
          - CHILE
    - polar
      - ANTARCTIC—ALPINE
- oceanic
  - Pacific ocean
    - POLYNESIA
  - Indian ocean
    - MASCARENES
  - Atlantic ocean
    - south
      - OLIGONESIA
    - north
      - MACARONESIA

Modern attempts to divide the world up into more or less equivalent floristic units mostly trace back to Engler's scheme (158), and vary from it more in detail than in principle. No one of these however can be considered entirely satisfactory, especially from the point of view of this book, and the writer has therefore compiled the classification given below, which although based on those of Engler and others differs from them in a number of important respects. The object has been to divide the land surfaces of the world into a convenient but not too large number of regions, each of which may be regarded as supporting a flora of its own, that is to say a flora which is characteristic of the region; which, allowing for possible global floral migrations, has largely developed within the region; and which has, to a like extent, been conditioned by the history and circumstances of the region. This essentially historical and phylogenetic conception of the regions is of great importance not only as a step towards the broader understanding of plant geography in general, but also because it helps to lessen the problem of treating as equivalent floras which are in fact very different in nature, size and richness.

Quite apart from the more theoretical difficulties to which allusion has already been made, it is extremely difficult in practice also, to make a floristic classification of this sort and although much care and attention has been given to it (see Preface) a few words of special explanation are called for here, particularly with regard to the changes which have been made since the first edition of this book.

First and foremost there is to be remembered the general lack of agreement in the literature as to where many of the boundaries between regions should be drawn. This is chiefly of interest here because it stresses what is really the inherent problem in such matters namely that of deciding how and what criteria are to be applied, but it also means that in some cases decisions have had to be taken on general rather than particular evidences.

Second, it cannot be over-emphasized that the classification and its map depict a *world-wide floristic arrangement* and take no account of any extraneous and unrelated values. This is an important point because many similar classifications made by botanists of the northern temperate regions are marred by the exaggerated importance given to this part of the world, no doubt chiefly because these are better known botanically, but almost certainly also to some extent because of their preeminence in quite other respects.

Third, the map in Plate 4 is necessarily on a very small scale and in consequence the boundaries of the regions cannot in every case be made as accurate or as free from ambiguity as is theoretically desirable.

Fourth, it has been felt that pure convenience cannot always be ignored if the classification is to make its widest appeal, and a few boundaries have been deliberately drawn with this in mind, as is illustrated, both in general and particular, in the Malaysian region. This has been defined in accordance with the key maps in the first instalment of the *Flora Malesiana* now being published, but this obviously desirable course begs at least two minor problems which deserve notice. Some writers (342, 386) consider that the flora of the small island of Botel Tobago, a little to the east of the south point of Formosa, has more affinity in some ways with that of the Philippines that with that of Formosa itself, but to attempt to show this on so small a map, however strong its justification, would only lead to confusion, and a more generalised boundary has been used. In the south-east of the region the line is drawn between New Guinea and New Britain and this again is certainly the most convenient way of dealing with the puzzling relationships of the latter, even if it does not do full justice to all the evidence. It may be added here that although many parts of the world have their similar problems the classification of the Pacific is especially difficult, not only because of the great isolation and tiny area of many of its land surfaces, but also because as yet little certain is known about their history, and the arrangement adopted here, though it now seems to be the most realistic, may need revision in the light of further information. The Pacific part of the world is undoubtedly of special significance in plant geography because there are reasons for supposing that it may hold the keys to many problems which at present perplex us, and it is promising that much more is now familiar about it than was the case some years ago. The war-time books of Merrill (386), and Osborn (408), for instance, are full of interesting facts, and other more particular references will be found in the bibliography, especially in connection with Chapter 20.

As regards other parts of the world only a few points need be mentioned. In Africa the northern boundary of the South African region has been drawn more directly across the continent, the general convenience of this on a small map being felt to outweigh the advantage of attempting to show the transitional nature of the flora along the south-east coast. Rather similarly the word "transitional" has been dropped from the titles of two of the regions because its retention tends to particularise these regions in a way which is perhaps not altogether justifiable. Chiefly because of its ambiguity the name of the East African Island region has been changed to "the Madagascar region." In South America the earlier and unwieldy Brazilian region has been divided into two, the Amazon region and the South Brazilian region, thus making, in the former, an entity properly and strictly comparable with the equatorial forest regions of West Africa and Malaysia. The boundaries of the Amazon region are, however, difficult to assess and those drawn are frankly somewhat tentative. The actual outlines of some of the regions have been amended considerably in order to include within them, as seems most appropriate, such very isolated small islands as have an appreciable, though not necessarily characteristic, Angiosperm flora, as for instance the Chagos Archipelago and Christmas Island.

Finally it will be seen that two regions, the Atlantic North American region and the Euro-Siberian region, have each been divided into two halves or sub-regions. This is not intended to suggest that they each contain two floras approaching regional status but is meant to emphasise that, largely on account of their exceptional extents, the one latitudinal and the other longitudinal, there is considerable difference between the two ends in each. It should also be noted that these are the only two regions which lie predominantly in the colder north temperate zone above latitude 50°, a value which, as is suggested in Chapter 9, may be of critical importance in plant geography, and it may well be that, on this account, the developmental histories of their floras, are at least sufficiently different from those of other regions to justify this slightly different treatment.

Certain other details about the regions will be referred to in Chapters 7 and 10 as they arise and it only remains to say here that, while the following classification and its accompanying map have been made primarily for the purposes of this book, they have, in this new edition, been revised with the particular hope that they may more widely meet the need which undoubtedly exists for a convenient classification of this kind.

Classification of the World into Floristic Units

(Plate 4)

Boreal Kingdom

1. Arctic and Sub-arctic Region
    a. Eurasian province
    b. Greenland
    c. Nearctic

2. *Euro-Siberian Region*
  A. European Sub-region
    a. Western Europe
    b. Central Europe
    c. Scandinavia
    d. Russia
    e. Danube basin
    f. European alpine
    g. Caucasus

  A. Asiatic Sub-region
    h. Western Siberia
    i. Altai—Trans-Baikalia
    j. North-eastern Siberia
    k. Kamchatka

3. Sino-Japanese Region
    a. Manchuria and South-eastern Siberia
    b. North Japan and South Sakhalin
    c. Korea and South Japan
    d. North China
    e. Central China
    f. Sino - Himalayan - Tibetan mountains

4. Western and Central Asiatic Region
    a. Armenian-Persian Highlands
    b. South Russia—Trans-Caspia
    c. Turkestan and Mongolia
    d. Tibetan plateau

5. Mediterranean Region
    a. Lusitania and western North Mediterranean coasts and islands
    b. *Eastern North Mediterranean coasts and islands*
    c. Morocco—Tunis
    d. Libya, North Egypt and Syria

6. Macaronesian Region
    a. The Azores
    b. Madeira
    c. The Canaries
    d. The Cape Verdes

7. Atlantic North American Region
  A. *Northern Sub-region*
    a. Canadian Conifer province
    b. The Great Lakes
    c. The Appalachians
  B. Southern Sub-region
    d. The Prairies
    e. Atlantic and Gulf coasts
    f. Mississippi basin

8. Pacific North American Region
    a. Southern Alaska and the Aleutian Islands
    b. Sitka, British Columbia, Washington and Oregon
    c. Californian coast
    d. The Great Basin
    e. Rocky Mountains
    f. Sierra Nevada
    g. Mexican Highlands

Palaeotropical Kingdom

A. African Sub-kingdom

9. North African—Indian Desert Region
    a. Sahara—Arabia (except the South)
    b. Mesopotamia—South Persia—North-west India

10. Sudanese Park Steppe Region
    a. Senegambia—Sudan
    b. Upper Nile-land

11. North-east African Highland and Steppe Region
    a. Abyssinia and Eritrea
    b. Galaland and Somaliland
    c. Yemen and South Arabia
    d. Socotra

12. *West African Rain-forest Region*
    a. Upper Guinea
    b. Cameroons and Islands
    c. Congo Basin

A. African Sub-kingdom—*cont.*

13. East African Steppe Region
    - *a.* Southern Portuguese East Africa
    - *b.* The East African Steppes
    - *c.* The East African high mountains
    - *d.* The Central African lake zone
    - *e.* The Rhodesias
    - *f.* Angola
14. South African Region
    - *a.* High veldt of the O.F.S. and Transvaal
    - *b.* The Kalahari
    - *c.* The Karroo
    - *d.* Namaqualand and Damaraland
    - *e.* Natal and eastern Cape Province
15. Madagascar Region
    - *a.* Madagascar and the Comoros
    - *b.* The Seychelles
    - *c.* The Mascarenes
16. Region of Ascension and St. Helena

B. Indo-Malaysian Sub-kingdom

17. Indian Region
    - *a.* Ceylon
    - *b.* Malabar coast and southern India
    - *c.* Deccan
    - *d.* Ganges Plain
    - *e.* Flanks of the Himalayas
18. Continental South-east Asiatic Region
    - *a.* Eastern Assam and Upper Burma
    - *b.* Lower Burma
    - *c.* South China and Hainan
    - *d.* Formosa and the Riukiu Islands
    - *e.* Siam and Indo-China
19. Malaysian Region
    - *a.* The Malay Peninsula
    - *b.* Java, Sumatra and the Sunda Islands
    - *c.* Borneo
    - *d.* Philippines
    - *e.* Celebes and Moluccas
    - *f.* New Guinea and Aru

C. Polynesian Sub-kingdom

20. Hawaiian Region
21. Region of New Caledonia (with Lord Howe and Norfolk Islands)
22. Region of Melanesia and Micronesia
23. Region of Polynesia

NEOTROPICAL KINGDOM

24. Caribbean Region
    - *a.* Mexican lowlands and coast
    - *b.* South Florida, West Indies, Bahamas, Bermudas
    - *c.* Guatemala—Panama
    - *d.* North Colombia and North Venezuela
25. Region of Venezuela and Guiana
    - *a.* Orinoco Basin
    - *b.* Uplands of Venezuela
26. Amazon Region
27. South Brazilian Region
    - *a.* Eastern coasts
    - *b.* Uplands of Central Brazil
    - *c.* Highlands of Eastern Brazil
    - *d.* Grand Chaco
28. Andean Region
    - *a.* Flanks of the Andes
    - *b.* Montane Andes
    - *c.* The Galapagos Islands
    - *d.* Atacama Desert
    - *e.* Chilean sclerophyll zone
29. Pampas Region
    - *a.* Uruguay and South-eastern Brazil
    - *b.* Argentine pampas
    - *c.* Western Argentina
30. Region of Juan Fernandez

SOUTH AFRICAN KINGDOM

31. Cape Region

AUSTRALIAN KINGDOM

32. North and east Australian Region
    - *a.* Northern forests
    - *b.* Queensland forests
    - *c.* South-eastern forests
    - *d.* Tasmania
33. South-west Australian Region
34. Central Australian Region
    - *a.* North and east savanas
    - *b.* Central deserts
    - *c.* South Australia

ANTARCTIC KINGDOM

35. New Zealand Region
    - *a.* North Island
    - *b.* South Island
    - *c.* New Zealand Alps
    - *d.* Kermadec Islands
    - *e.* Chatham Islands
    - *f.* Auckland and Campbell Islands
36. Patagonian Region
    - *a.* Patagonia and Fuegia
    - *b.* Southern Andes
    - *c.* Falkland Islands
37. Region of the South Temperate Oceanic Islands

This floristic classification may be epitomised by saying that it divides the land surfaces of the world into 37 regions, which may, at least for theoretical purposes, be regarded as roughly equivalent in floristic value and importance, though not of course in size or, necessarily, in interest. Where appropriate, as in the discussion of endemics, the subject matter of later chapters is arranged under these regions, and futher details concerning them will be noticed as occasion demands. The constituent provinces of each region have been listed for purposes of general interest and amplification and to provide a more detailed framework where such may be useful to add more detail to the treatment of the regions, but otherwise they will not receive further attention here.

CHAPTER 3

SOME GENERAL ASPECTS OF PLANT GEOGRAPHY

The Evolutionary Background

THE short history of the study of plant geography in the Introduction is enough to show the enormous influence that evolutionary conceptions have had on the development of the subject, and it is no exaggeration to say that its whole background has become an evolutionary one, as, indeed, is true of any biological subject. Evolution is, as it were, the medium in which the picture of plant distribution is painted.

All the latter part of this book is devoted to a consideration of what are usually called the factors of distribution, that is to say the influences which may be looked upon as the immediate causes of the observed facts, but it will be clear from what has just been said that all these, critical as they may be, are to be regarded as secondary. Behind and beyond them is the infinitely broader cause inherent in the nature and course of organic evolution in general and of plant evolution in particular. Whatever the more precise explanation of them, the facts themselves are primarily due to something innate in the very order of nature. This something is the ubiquitous periodic production of new forms (which we call species, genera and families) by the processes of evolution. This is the general theme of which the so-called factors of distribution provide the variations.

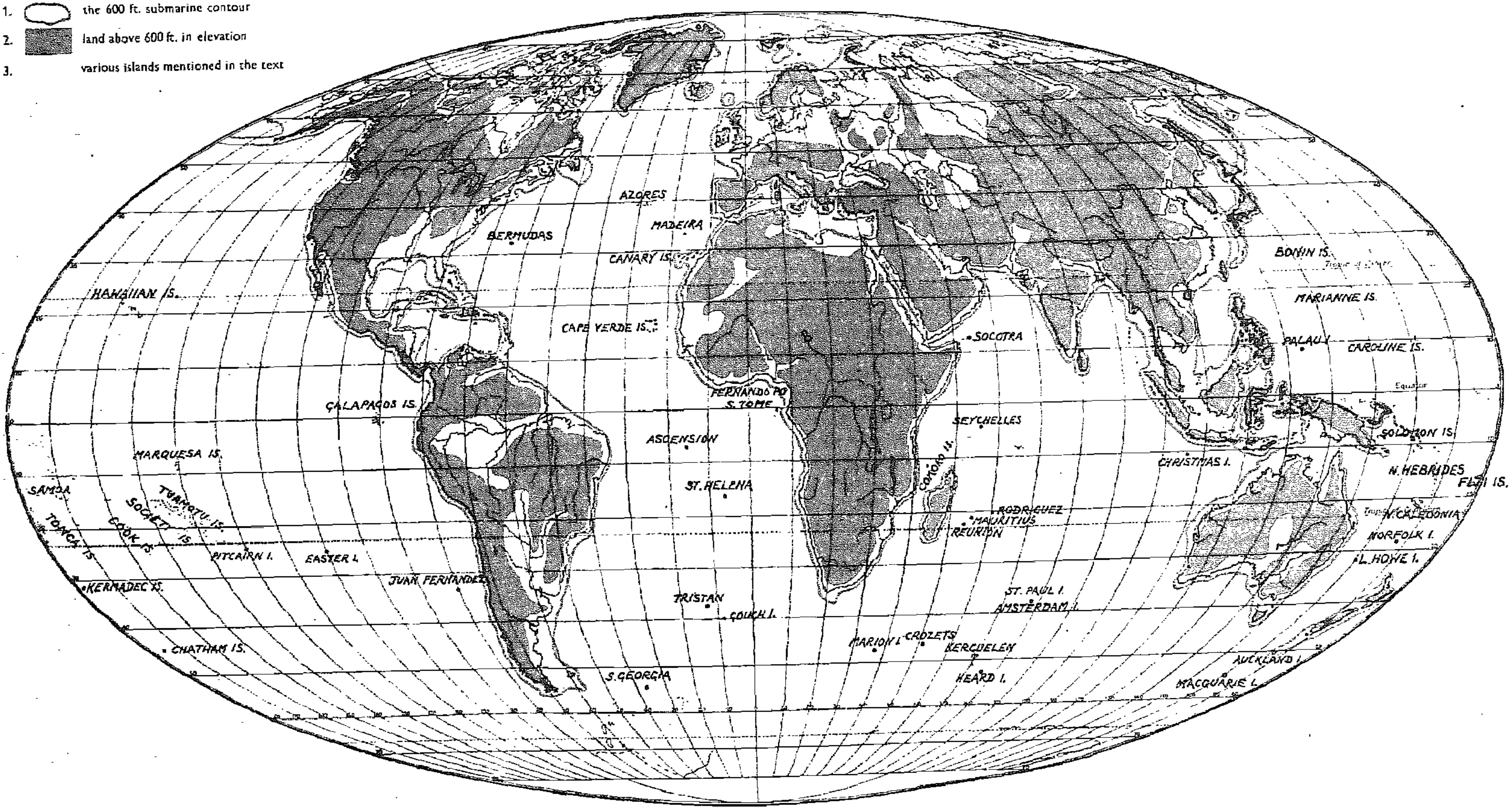
Clearly then the study of plant geography must be approached with this evolutionary conception in mind, and such an approach at once reveals two of the most fundamental features of the subject. The first is that plant geography must always be regarded as a developmental study, and as dynamic rather than static. Whatever the particular facts under discussion it must always be remembered that they are not isolated and unrelated facts, but the culmination of a long series of events and changes which have been in operation at least for some time and often for very long periods. They are the outcome of that gradual change which is the essential feature of evolution, and if they are to be understood properly due account must be taken of the past as well as of the present. Second, it is manifest that time must always be one of the most important factors in all aspects of plant geography. Evolution is generally visualised as a continuous, though perhaps unevenly continuous, process and one in which the state of affairs is constantly changing, so that, in theory at any rate, the constitution and distribution of the world's plant life can only be described in relation to time itself, and it must not be assumed without other evidence that the circumstances controlling plant distribution to-day are necessarily those which have controlled it in the past.

The central problem of evolution has always been that of the methods by which new and distinct forms arise, that is to say of the processes involved in the "origin of species." It would be inappropriate, if nothing more, to discuss this huge subject at any length here, but it is also impossible to neglect it altogether because of its bearing upon a question to which, before commencing the study of plant geography, an answer is an urgent necessity. This is the question of whether a species originates once and once only in the course of evolution or whether one and the same form

PLATE 3

Map of the World showing, from various sources:

1. ◯ the 600 ft. submarine contour
2. ▨ land above 600 ft. in elevation
3. various islands mentioned in the text



Areas correct Distortion increasing towards border of map

Approximate Scale 1:100,000,000 (1600 miles - 1 inch) along Equator

on Mollweide's Homolographic Projection

may arise more than once at intervals of space and time. To give the problem greater definition, species may be said to consist of a number of closely similar individuals. Are these individuals all to be regarded as directly descended from a single and comparatively recent ancestor, that is to say as being *monophyletic*? Or are they to be regarded as having originated, some by one line of descent in one place and others by different lines elsewhere, that is to say as being *polyphyletic*? Is it, in short, safe to assume that all the individuals comprising a species are blood relations, or is it more likely that mere superficial resemblance is the chief bond between them?

A moment's reflection will show the importance of this question to the plant geographer. If a species is strictly monophyletic, then all its individuals are the descendants of one and the same ancestral plant and their total range, however extensive and peculiar it may be, must have grown by the processes of dissemination from the tiny area occupied by this ancestor. However wide may be the space between two or more individuals, this space must be the consequence of progressive geographical divergence in the course of time. If, on the other hand, a species is polyphyletic, then most of the features of its geography, however striking they may be, lose much of their interest and become almost meaningless and inexplicable, since there is nothing to show and no reason to suppose that the positional relationship between the individuals is anything but fortuitous.

In view of this it is obviously imperative before going further to come to some conclusion on this matter, and since this cannot be done without some reference to the subject of evolution in general and its theories, no further justification need be sought for making such a digression here.

Evolution is the natural antithesis of the conception of "special creation," which was the previously accepted explanation of the facts revealed by the study of animal and plant classification. Darwin (124), therefore, when he first propounded his views on evolution, was at some pains to do so in such form as would demonstrate, in the most telling fashion, the inadequacy of special creation as an explanation of the facts, He was also under the necessity of outlining some mechanism by which evolution might be supposed to come about, since without this his views would have been little more than academic. To meet these requirements he postulated his theory that evolution was brought about by "natural selection by survival of the fittest." The facts upon which he based this hypothesis were those of variation, the observed circumstance that no two individuals, even if of the same parentage, are ever exactly alike. He suggested that some of these differences would confer on their possessors advantages in the struggle of life, while others would be detrimental, and that since, as Malthus (356) had already shown, not all the individuals born can hope to survive, those best equipped would tend to be selected. This process he envisaged as accumulating with the passing of generations until some individuals had become sufficiently different from their earlier ancestors to merit recognition and description as new species.

There was nothing in the conception of special creation to preclude the possibility that similar individuals might have been created more than once and in different places, and in order to support his evolutionary views Darwin therefore devoted considerable time and space to an attempt to demonstrate that the weight of evidence was in favour of the opposite view, and that species were in fact normally monophyletic rather than polyphyletic. It was moreover important to do this from the point of view of the details of the suggested process of natural selection because, if this is indeed the mechanism of evolution, it is almost impossible to imagine that species can be anything but monophyletic. The chances that natural selection will, in two different parts of the world or at different periods, lead to exactly the same morphological result, can only be regarded as most improbable.

Perhaps on much the same grounds, Darwin and his contemporaries did not attach much importance to sudden and comparatively large evolutionary changes, but concentrated upon what are generally called "infinitesimal variations." If there is no theoretical limit to the magnitude of evolutionary change there must be visualised the possibility of some new form, widely different from anything hitherto existing, arising quite suddenly and unheralded, and there would be considerable difficulty in divorcing this kind of origin from the suggestion of an act of special creation. It was all-important rather, to show that evolution was an orderly process as opposed to the condition of arbitrariness, which must in one sense at least be inherent in the conception of special creation.

But it was also actually from the point of view of plant geography that Darwin saw the importance of demonstrating the monophyletic origin of species. As he himself expresses the point in the *Origin of Species*—"If the difficulties be not insuperable in admitting that in the long course of time all individuals of the same species belonging to the same genus have proceeded from one source, then all the grand leading facts of geographical distribution are explained on the theory of migration, together with subsequent modification and the multiplication of new forms." That is to say, given a monophyletic origin of species, the facts of plant and animal geography afford useful evidence in support of the theory of evolution.

It is for such reasons as these that the present-day reader of the works of Darwin and his contemporaries is often impressed with the extreme importance which is paid to minute variations and to the establishment of a general belief in the monophyletic origin of species, an importance which in the light of modern knowledge seems exaggerated. It seems so, however, only because the views that it seeks to establish have in fact been implicitly if not explicitly accepted by biologists for many years, and because it is difficult to realise, in the light of after-knowledge, how essential it was to establish them. It might therefore be deemed justifiable to accept these opinions as a general premise to a consideration of plant geography without more discussion, but the state of biological knowledge has advanced enormously since Darwin's time and it is necessary to be satisfied as to how far, if at all, these views now require modification (560).

At the time when Darwin was writing his classics, knowledge concerning the cell and its structures was slight. It was but comparatively recently that the nucleus had been discovered and nothing was known of its internal organisation. Moreover, the work of Mendel on inheritance had still to be discovered by the scientific world. At this time, therefore, the evolutionist was unavoidably at a grave disadvantage because whatever mechanism he might suggest as being the vehicle of evolution, it was impossible to suggest any structural features in the living organism which might be the physical expression of it. Darwin fully realised this difficulty and indeed found it necessary later to augment his original exposition of Natural Selection by the additional hypothesis of "pangenesis" in which he tried to picture how reproductive cells might be capable of transmitting characters to their progeny. Incidentally it is no small measure of Darwin's greatness that his guesses in this matter have very largely been substantiated, though not exactly in the terms he employed.

It was partly due to this difficulty that while evolution as a general theory became widely accepted, a mechanism which stressed the importance of small variations was less acceptable. Indeed there gradually grew up the view that evolution proceeded rather as a result of larger and more sudden changes, called mutations (130). Such large changes were observed in many plants and it was found that their occurrence could be accelerated by certain experimental methods, but the mutationists were at first in much the same difficulty as Darwin because of their ignorance of cytology and genetics.

The enormous advances which have been made in these two subjects since the beginning of this century now enable a more scientific view to be taken of these apparently antagonistic opinions and it is clear that they are far less opposed than was originally thought, this conclusion being in great part the fruit of the remarkable investigations that have been made into the microscopic structure of the cell-nucleus.

It is now believed that the inheritance of characters between parent and offspring is by the agency of the chromosomes, which constitute the essential part of all cell nuclei. There is, moreover, reason to think that these characters are actually resident on the chromosomes in or as entities which are called *genes*, and that alteration in transmissible characters is due to actual alterations of some kind in one or more genes. When an individual differs markedly from its forebears in an inheritable character it is generally supposed that this difference originates as a definitive change in the nature or potentiality of one or more genes.

At first sight this "theory of the gene," as it is called, seems strongly to support the views of the mutationists, in as much as it puts into the general category of mutations all changes in characters since these must, by the nature of the case, be sudden and more or less sharply defined. But this is not quite a fair statement of the position. There are no particular limits in either direction to the magnitude of changes. Some may be large, but others are very small, and indeed are only to be compared with such minute modifications as were comprehended by Darwin in the phrase "infinitesimal variations." The fact of the matter appears to be that gene changes may be of almost any magnitude. If they are large, then they result in what is normally called a mutation: if they are small, they cause no more than minor variations. The distinction between them is primarily one of degree only.

The last forty years or so have also seen the accumulation of a vast amount of information concerning the laws and phenomena of Mendelian inheritance, by which are expressed the ways in which the characters possessed by parents are distributed among and appear in their offspring. Here, again, there is more than one circumstance which may lead to the sudden and unexpected appearance of a form appreciably unlike any of its immediate ancestors which may in favourable conditions be the origin of a new species or at least of a new line of descent.

In brief it may be said that at the present time it seems that the novel morphological forms which are the basis of the recognition of new species arise chiefly by one or other of the following three processes:

1. By gene mutation.
2. By hybridisation, namely the combining together of the characters of relatively unlike parental forms (409), and by the segregation of such characters according to the laws of inheritance.
3. By changes in the number of chromosomes and genes (74).

Any further general consideration of the details of these processes would be beyond the scope of this book, and the reader who wishes to pursue the matter should consult some of the references given in the bibliography (13, 74, 293, 526, 527), and textbooks of cytology and genetics. In particular Babcock's great study of the genus *Crepis* gives a most interesting insight into the processes of speciation (26). There are, however, some few particular aspects of the relation between evolution and plant geography which are so important that some further exposition of them is called for here.

Polytopy and Polychrony

The question whether species are normally to be regarded as monophyletic or as polyphyletic has already received some attention but there is more to be said about it if confusion on the matter is to be altogether avoided.

Both these words are among the older evolutionary terms, and in their earlier days at any rate were applied to the descent of large groups such as phyla or even of whole kingdoms, though their use has since become extended. They are in one sense the opposites of one another and describe, respectively, descent from a single ancestral source and descent from two or more different ancestral sources. What constitutes the appropriate degree of "difference" cannot be defined satisfactorily, but the implication is clear enough, namely, that the products of monophyletic descent are blood relations in a way in which the products of polyphyletic descent are not, or, to use the words of taxonomy, that the former constitute a natural group while the latter do not. The nouns monophylesis and polyphylesis, derived from these adjectives, are sometimes used.

The word *polyphyletic* can be disposed of here shortly. Anything to which it is properly applicable is by definition of mixed origin in the taxonomic sense and in matters of plant geography must be treated with all the caution and restraint that such a condition demands. The word *monophyletic*, on the other hand, needs more consideration. Much depends upon the exact interpretation put upon it, and the narrowness of its definition. In its strictest sense monophyletic suggests origin by a single and unrepeated act of species formation, or speciation, from a single individual ancestor, but this by no means exhausts the ways in which what must be regarded as a natural group as defined above may arise. To write in terms of species there are, indeed, three other possibilities. The first is that the individuals of a species may have come into existence by acts of speciation repeated at intervals of time by the same individual ancestor, or by one or more of that ancestor's immediate descendants. Species arising thus at more than one point of time are said to be *polychronic* and to arise by *polychrony*. The second possibility is that the individuals of a species may have arisen from a number of conspecific parents and hence, in more than one place. Species so arising in more than one place are said to be *polytopic*† and to arise by *polytopy*. Since it is difficult to imagine that polytopic origins can often be strictly synchronous, it may be assumed that polytopic species are also polychronic. In the strictest sense polychronic species are not polytopic but there is the third possibility of a combination of both these conditions. In all three the resultant species is monophyletic within the ordinary meaning of that word.

How does this relate to the main problem of the relative probability of monophylesis and polyphylesis? To answer this we must revert to p. 35. It will be noticed that the suggested primary causes of speciation there set out do not include "that accumulation of small variations" by which natural selection is presumed to

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† There seems to be some confusion about the meaning of this word. The usage here accords with the discussion in Hayek (254) and with the definition in Daydon Jackson's *Glossary of Botanical Terms*. See also the *Oxford English Dictionary* under "polyphylesis."

operate, and this process, if indeed it exists at all, is believed now to play but a minor part in the origin of species. This is important, because this is, of all kinds of speciation, the one most likely to result in monophylesis, because of the very small chance that individuals arising in this manner in different places and circumstances would be sufficiently alike to be regarded as conspecific. On the other hand, the comparative abruptness of mutational change, both in time and degree, makes it very much easier to imagine their repetition, and the circumstances in which this may occur. It is largely to accommodate the possibilities inherent in mutation that the various shades of monophylesis just described have been distinguished.

It would seem then that the likelihood of some species being monophyletic in less than the strictest sense is much greater in the light of modern ideas of speciation than it used to be, but one must be careful not to swing too far in the other direction. We know that the same mutations may be repeated in a population under experimental control, but whether the same thing can and does happen in nature, and if so with what frequency, has yet actually to be demonstrated, and bearing in mind the extreme diversity of natural habitats where there is ordinary competition compared with that of cultivated conditions, it may legitimately be doubted whether it is ever likely to be more than rare. Moreover, the whole plan of character-discontinuity in organisms, which is the objective basis of classification seems to be consistent with the opinion that polychrony, polytopy and, of course, all the forms of true polyphylesis, are, except perhaps in purely local circumstances, of comparatively unusual occurrence. Were they commonplace the fact would surely have revealed itself in the study of classification much more unmistakably before now, and indeed would be likely to make such classification even more difficult than it is. We must be prepared to accept the contingency of their occurrence and to judge each possible case on its merits in the light of this, but it seems doubtful whether it is necessary to regard them as of more than local significance, and as such unlikely to confuse the general picture of plant distribution, and especially discontinuous distribution, to any serious degree.

Differentiation and the Conception of Age and Area

It has already been suggested that if it can be conceded that mutations may be of any magnitude there is little cleavage between the selectionists and the mutationists. But if, on the other hand, it is maintained that evolution comes about largely or exclusively by mutational changes of the larger kind only, there is a great gulf between the two. Indeed the difference then involves the whole conception of the order in which the events of evolution have occurred. In terms of natural selection there is to be pictured a slow divergence of form, resulting from a gradual accumulation of difference and leading to the successive appearance of species, genera and larger categories in that order. Under such conditions it is possible to speak of evolution as working "upwards" from smaller to larger unities. In terms of large mutations the reverse holds. There is to be pictured sudden, abrupt and discontinuous divergence, without intermediate links, producing new forms which become at once foundation members of larger groups, which only subsequently resolve themselves into their constituent genera and species. Under these conditions it is possible to speak of evolution as working "downwards" from larger to smaller unities. The former process may be thought of as one of accumulation; the latter as one of differentiation. Whether there is indeed any clear antithesis between the two is a matter of debate, but there is at least an appearance of this, and in fact the Theory of Differentiation, which expresses only the latter view, is often used as an alternative to the Theory of Natural Selection.

The Theory of Differentiation has been long extant in one shape or another but as far as plant geography is concerned it is especially associated with the names of Guppy (241, 244, 245) and Willis (596, 598, 599). Guppy's interest in it lay chiefly in the light it seemed capable of throwing on the general history of the Angiosperms as a group and he defined it as the view that "the history of our globe, as far as secondary causes are in operation, is essentially the history of the differentiation of primitive world-ranging generalised types in response to the differentiation of their conditions." He was much impressed by the fact that the families of flowering plants tend to fall, on a combination of geographical and structural characters, into two classes, wide-ranging primitive families and restricted derived families, and he mentions in particular the families of the warmer zones, which are for the most part pan-tropical, and which show little association with the geographical distinction between the Old and New Worlds. He also emphasises, that as regards the larger groups, and especially again, the families, the principle that community between these families is an affair of the north is not true.

These circumstances he associates in an interesting way with the known course of climatic and plant history, and particularly with the belief that the earlier history of the development of the Flowering Plants was one of widespread general and more or less constant climate, while their later history has been linked with great climatic diversity and austerity (see Chapter 19). A similar belief is arrived at on various grounds in the course of this book and is discussed at length in the final chapter, but the reason for mentioning it here in connection with differentiation is that Guppy associates it definitely with problems of species formation and in so doing makes a noteworthy contribution to the evolutionary background to the study of plant geography.

He (245) postulates for terrestrial plants "an era when uniformity in environment was the rule—an era, one might imagine, of great atmospheric humidity, when persistent cloud-coverings blanketed the globe and when the same equable temperature everywhere prevailed," and he pictures a plant organism "under such conditions as behaving very much like a ship in a calm, drifting in a morphological sense in all directions and displaying unchecked and irresponsive variations of the floral organs. . . ." Again, he says, "this would imply that the mutations of the floral organs of our own day represent all that remains of the capacity for great morphological changes in the early ages of the history of the Angiosperms." In short, he expresses the view that changes in environmental conditions may be reflected in plants in the manner in which their evolution proceeds, so that while in one set of conditions one method of evolution may predominate, another may prevail when conditions become markedly different. He infers, indeed, that the past may well have seen certain periods and conditions in which species production was especially copious (492). It has already been said that there is some reason for supposing this to have been the case, but it is of particular interest to see this very important conception put forward in the vivid way quoted.

Willis's approach to differentiation was from a different direction. He tells in some of his writings (598, 599), how increasing familiarity with tropical plant life soon caused him to abandon the Theory of Natural Selection, in which he had been nurtured scientifically, as an explanation of evolution, and how he began a search for something more satisfactory. This search led him to the mutationist point of view and to the Theory of Differentiation, and his work became more and more focused on the possibility of obtaining evidence which would demonstrate this view rather than that of the selectionists.

In this search he became attracted to some of the more statistical aspects of biology because he believed that the nature of the evolutionary process which had exclusively or mainly occurred was very likely to reflect itself in the proportionate numbers of species with various definitions and in the numerical relationships of their distributions. This belief was related to what he regarded as the essential features of natural selection, one, that it involved an enormous destruction of less "fit" forms which were *ipso facto* unable to survive, and another that it involved the general assumption that species would at once and almost inevitably be supplanted by their "fitter" progeny so that parent and offspring species would not as a rule coexist for any significant length of time. Of the first he could not, like so many others, find any evidence at all, and he was unable to understand, in the circumstances of the second, how the enormous numbers of existing species had ever accumulated, or indeed how the world had ever become populated so variously at all. Neither of these difficulties would have to be overcome if, on the other hand, a mutational method of evolution had prevailed, for this would not require the elimination of parental forms, which could instead go on living side by side with their progeny for an indefinite time and no doubt producing additional offspring in due course, so that far from there being an extensive elimination of species there would in fact be a rapid accumulation easily able in theory to account for the actual numbers extant. Not only so but this increase would, arithmetically, be of the nature of a geometrical progression or compound interest increase, approaching, if not reaching, the series value 1, 2, 4, 8, etc. Willis concluded therefore that if the existence of some such numerical series could be demonstrated then there would be strong presumptive evidence that mutational evolution and not selection had occurred. It should be added that he regarded the evidence of character-discontinuity as also showing that evolution had included or been composed largely of mutations of large magnitude and that the order of events had been that envisaged in the Theory of Differentiation.

Such geometrical progressions Willis claimed to find especially in two connections, namely, in the relative areas occupied by the constituent species of larger units, and in the numbers of species in genera. In these two cases respectively he found that the numbers of very widespread species and also of large genera were small; that the numbers having intermediate values were larger; but that the numbers of very restricted species and of very small genera were very much and disproportionately greater. The full story of the gradual elaboration of Willis's theories must be read in his own books (596, 598, 599), but these two aspects of it are so closely associated with plant geography in the Theory of Age and Area and in the problem of the so-called "hollow curves," that they must be considered with some care here.

The full presentation of the Theory of Age and Area appeared in 1922 (596), and in it the author postulated that, with certain reservations, the area occupied by a species is, within comparable circles of affinity, proportionate to its age, which is, of course, the time that it has existed. Actually this has long been something of an axiom in plant geography, as is clear from the writings of Hooker in the middle of last century, and there is the same conception, though its expression is rather different, in the principle, discussed by Babcock (26) in connection with the genus *Crepis*, that at any one time, in a large group of organisms showing close phylogenetic relations, the most conservative members will be found furthest from the centre of origin, and the most advanced nearest to it. Willis, however, puts the idea in the form of a much more definite proposition.

That age and area may be, and often in individual cases no doubt are, closely related is beyond question, and it would be difficult to find anyone who would deny this totally, but there are great differences of opinion as to what extent it is in fact true, and Willis's theory aroused unusual controversy, not always of the mildest kind. Two aspects of the presentation of the theory tended to increase opportunities for disagreement. Instead of making, without qualification, a comparatively simple and limited postulation, Willis not only made his theory too wide and was thus obliged to incorporate in the statement of it a number of troublesome reservations, of which his critics were not slow to avail themselves, but he also associated with it some of the statistical arguments mentioned above, showing, in particular, that many facts of distribution, both geographical and taxonomic, were expressible by the sort of graph called the hollow curve.

Unfortunately this mathematical treatment did not enhance his theory. The real meaning and significance of the hollow curve was not at once apparent, and it was soon shown that similar curves could be obtained from many sources unconnected with plant distribution. Moreover, many botanists found it difficult to understand the importance which Willis attached to these curves, or their relation to the conception of Age and Area, and there was almost inevitably imparted to the theory a sense of unreality that was unfortunate. Many felt that if the theory was really sound it should not depend so much on this kind of evidence, and the result was that it met with considerable criticism.

The lapse of time and the recent publication of the longest of Willis's books, *The Birth and Spread of Plants* (599), combine to make possible now a more definitive appraisal of these two sides of his work than has hitherto been easy. With regard to the theory of Age and Area the idea of a relationship between the geographical extent of a species and the time that it has existed is undoubtedly sound in theory, but there is equally little doubt that in practice it is, owing to all manner of complicating circumstances, much less widely applicable than Willis maintains. Indeed it could only be of general application if it could be imagined that the circumstances in which evolution has proceeded have been uniform for vast periods of time, and this almost every aspect of plant geography disproves. It has therefore been said, with some truth, that the theory is no more than a well-known axiom in disguise, namely, that if two species with the same potentiality of movement begin to move at different times the earlier will, at any one future time, have extended further than the other. This criticism is perhaps over-severe, but it is nevertheless very difficult, in view of all the facts, both past and present, to see how the conditions necessary for this age and area relation can ever have prevailed to any appreciable extent. It must also always be remembered that the theory is not, in one sense, primarily a phytogeographical theory but was an integral part of the presentation of its author's views on evolution, which in his latest book just mentioned are fully set out as the Theory of Divergent Dichotomous Mutation.

The problem of the hollow curves was first analysed, in admirable detail, by Chamberlin (88) as long ago as 1924, and Nicholson has recently put the essential points even more concisely (400). In brief, Willis's contention is that the hollow curves are indisputable evidence that evolution has proceeded in such a way as to be expressed as an exponential or "compound interest" function, that is to say that they result only when a geometrical progression, such as might well exist if his views on evolution are correct, is plotted. This is, however, not the case. It is true that hollow curves are given by progressions of this sort but this is not the only source of them. They may also arise when frequency or probability distributions having a certain inherent limitation are plotted. This limitation is that the variate, or in other words the values concerned, shall not be less than one, all hypothetical lesser values being reckoned as one. This happens, for example, when the numbers of persons are concerned, since there cannot be a fraction of a person, and also when species are involved since biological classification does not recognise fractional species. The effect is to make the numbers reckoned as having the value of one disproportionately large and the graphic consequence of this is a hollow curve.

Hollow curves may therefore be the result of one or other of two quite distinct causes; they *may* result, as Willis says they do, by the multiplication of species or their areas according to a geometrical progression, but they *may* also express no more than an ordinary probability distribution without any exponential implication. At present it seems impossible to be sure which of these two a hollow curve belongs to, and until this can be done the hollow curve is in fact valueless as evidence either for or against Willis's theories. In this connection it may be remarked that the reader will find an interesting and simple account of many of the statistical aspects of plant distribution in a paper by Thacker (550).

Despite the considerable criticism that the detailed theory of Age and Area has received (45, 199, 208, 229, 466, 493, 494) it must always be remembered that Willis did the cause of plant geography a great service by publishing it. As a result the subject of plant distribution quickly became topical and gained once more the attention it had largely lost, and it served also to focus study on just those aspects of the subject where it was most needed in view of other modern theories. It must also be remembered that criticism of Age and Area does not necessarily imply criticism of or disbelief in its author's opinions concerning the processes of evolution.

The Cycle of Distribution

The next question to be discussed is that of the geographical fate of species or genera after they have arisen by one or other of the processes of evolution mentioned, and in accordance with the conclusions arrived at there we may assume that this origin has been monophyletic.

If the monophyletic origin of species be accepted in its most extreme form it must be believed that a new species, when it first appears, does so as one or very few individuals only. In this condition it may be described as having no distribution in space, but this will persist only until such time as the first generation produces progeny. This stage is generally a very short one, for as soon as the species reproduces its range must increase, if for no other reason than that no two plants can occupy exactly the same position. If the new species is biologically sound and able to maintain itself normally among pre-existing species it will tend to increase its range further, roughly in accordance with the number of its individuals. At some point or other various external factors tending to restrict its spread will almost inevitably come into play, but for a time at any rate it will continue to increase its range at each reproduction. This checking point may come soon, in which case the species will never be widespread, or it may be long delayed, in which case the species will gradually attain a considerable range. In either case the first stage in its geographical history will be one of spread culminating in the attainment of an appropriate degree of distribution, and of an equilibrium in respect of associated species.

During this stage, however, the processes of evolution are continuing, and sooner or later the erstwhile new species will in turn produce new species itself. This it may do from individuals at any point of its range, or from individuals in certain parts of its area only, but whichever prevails the result will be that new specific distributions or ranges will arise within the area of the parent form or at least in close proximity to it.

There is good reason to believe that the life of a species has much the same course as the life of an individual, and that it passes fairly early through a stage at which it exhibits a maximum vitality. From a phyletic point of view this expresses itself in a maximum evolutionary activity, and hence we may characterise this second stage in its history at that at which it produces a maximum of new forms.

As time goes on this vitality will appear to ebb, possibly because the original stock has produced all the new forms of which it is capable, or, to put it rather differently, will be passed on to succeeding generations and the original will gradually diminish and die out. It will pass in fact into what might be compared with a condition of incipient senility. Its powers of producing new forms will decrease or cease altogether and it will have greater and greater difficulty in maintaining itself against the competition of younger and more virile strains. This stage again may come soon or may be long delayed, but come it must, and the species will eventually die out altogether. Concurrently, and with the consequent diminution in the number of its individuals, the range of the species will also tend to diminish until in the final stages both the plant and its range will disappear entirely.

From a geographical point of view this late stage is a very interesting one. Throughout its history the conditions in which the species exists are constantly changing through a variety of circumstances, and it is likely, and indeed almost inevitable, that the disappearance of the species will be a differential disappearance, that is to say will take place first in one part or another of its range rather than everywhere simultaneously. Geographically the result of this will be a strong tendency towards the development of a discontinuous range, one indeed which will consist of two or more disjunctive constituent parts. Such ranges form one of the most intriguing subjects of plant geography, and since on the assumption of a monophyletic origin they can scarcely arise otherwise than has been outlined their significance as an indication of the state of the species showing them is very great.

Ultimately, and for a varying time before its complete disappearance, the species will have but a very restricted range. If earlier it was discontinuous the further passage of time will see the gradual elimination of all but one of the constituent areas until eventually the range of the species returns to a condition comparable with that which it possessed at the earliest stages of its existence.

To summarise, it would seem therefore that the history of a species or genus, expressed in its geography, will normally consist of four successive stages, each represented by a different and well-marked condition, and this view has been called the Theory of Generic Cycles (74). The first stage may be called the juvenile stage, and during it the species is establishing itself and gradually extending its range from nothing to a maximum determined by various external conditions. The second stage represents the maturity of the species. During this it will exhibit a maximum phyletic activity and give rise to various new forms, numerous or the reverse. It will meanwhile in general maintain its maximum range, within or associated with which there will appear the incipient ranges of many closely related younger forms. It will, indeed, tend to show what may be described as a parental range inclosing a number of offspring ranges. In the third stage the species is passing gradually into obscurity. It no longer produces many new forms and it is giving place to the newer and more virile generations. For a time it may maintain its range, but sooner or later this must tend to decrease. This decrease is likely to be accompanied by a breaking up of the range into disjunctive parts owing to the disappearance of the plants earlier in some places than in others. The fourth and last stage marks the final disappearance of the species and the ultimate contraction of its range to vanishing point. As in the course of this extinction the range decreases, it approximates more and more closely in extent to that which the species possessed in the earliest stage of its career. Finally, for some time before final extinction the size of its range will be indistinguishable at sight from that of a species but newly formed.

It must not be supposed that all species follow exactly the same course in their development and decay, but there can be no doubt that this is a fair picture of their general prospects. The actual details will, however, obviously depend on many considerations. One or other of the stages may be unduly prolonged or much shortened; the length of them will always tend to be controlled by extraneous circumstances. Some species may never attain an appreciable range and may die out without showing either the second or third distributional stages. Others may early attain and long maintain a wide distribution. There is no doubt, too, that the matter of evolutionary vitality, as it has been termed, namely the ability to produce new forms, varies enormously not only among different kinds of plants but also in different circumstances and in different places (492), and it may well be that external changes may induce copious species production in forms which formerly gave rise to them but sparsely. It is difficult also to avoid the conclusion that certain parts of the world are, from time to time, peculiarly favourable for intense and rapid evolution.

The idea of this geographical life cycle in species derives in the main of course from the evidence of the geological record, of which the most striking features are the successive appearance of new groups, their rapid expansion, and their replacement one after another, though only after long passage of time, by something more highly differentiated. It is true that some types seem to have lasted much longer than others, though their constitution has changed, but there has apparently never been any progressive or absolute accumulation of types. Instead, one series gives way to another that replaces it, and it seems beyond doubt that in the course of geological time there is an almost complete "turnover" of plant types, so that unless we ascribe this to some form of periodic catastrophism something of the sequence of events outlined above would seem to be inevitable.

At the same time the theory of generic cycles has, for reasons of simplicity and clarity, been expressed above in terms which are frankly anthropomorphic, and Cain (74) has very properly commented upon this. It may, indeed, well be debated how much objective reality there is in such a phrase as "the senility of species," which, it should be noted, not only postulates the existence of entities called "species" but also endows them with certain physiological attributes, but it is nevertheless helpful to draw an analogy between the course of geographical history and some more familiar sequence of events, and for this reason the particular phraseology employed may be excused.

Such are some at least of the kinds of complications which may and do obscure the simplicity of distribution. Were it not for these complications it would no doubt be possible to describe and explain plant geography much more concisely and completely than it is at present, but it would certainly be a far less interesting subject.

Endemism

To quote the *Concise Oxford Dictionary* the word *endemic* means "Regularly found among (specified) people, in (specified) country." That is to say, it is applied to things which are peculiar to a given situation.

In botany the word *endemic* is applied to any species or other taxonomic unit which is so distributed as to be confined to one particular country or region. It will therefore be seen that without further qualification the word is almost meaningless because every species is confined to some area, though that may be a very large one. In the geography of plants and animals, therefore, the use of the word is restricted somewhat conventionally to species or other units having a comparatively or abnormally restricted range. It should also properly be used with due regard for the size of the taxonomic unit under consideration. Although it is generally indescribable in words, there is an average range of families, an average range of genera, and an average range of species, these being progressively smaller, and the best practical limitation of the use of the word endemic is to restrict it to units whose ranges are obviously less than the average for their kind. For example, it is appropriate and valuable to consider families which are found in only one continent as endemic because the average distribution of families is greater than this. On the contrary it is almost meaningless to speak of species in terms of continental endemism because comparatively few species are as widely or more widely distributed. Areas beyond a certain size will always tend to have a large percentage of endemic species for the simple reason that the great majority of species have ranges of less than these dimensions.

At the same time it is difficult to lay down any hard and fast rules and all that can be done is to bear in mind the importance of denoting in some way the sense in which the term endemism is used. It may be desirable to use it in one set of circumstances and indefensible in others.

It has already been explained that endemism may be particularly useful in the recognition of different floristic regions and also in determining or expressing the degrees in which floras are peculiar. In the first case it is often to be noticed that while one part of a large region possesses a high proportion of endemics another and adjacent region may have considerably fewer, and this is often a useful guide to the delimitation of the two. This is seen, for instance, between the Cape Region and other parts of South Africa, and between south-west Australia and other parts of that continent.

The second case may be well illustrated by three island groups, the Galapagos, Juan Fernandez and Hawaii. The first has many endemic species but very few endemic genera, and even the endemic species are comparatively closely related to continental American types. Juan Fernandez is situated fairly close to Chile and has a small flora only, but this is peculiar, its endemics including numerous genera and even one family. The Hawaiian Islands are very isolated and have a flora much larger than those of the other groups. Moreover, it has a very high degree of endemism, about 90 per cent. of its species being confined to the archipelago. There are also many endemic genera. Although the number of species in each of these floras is very different, the facts of endemism indicate clearly that the floras of Juan Fernandez and Hawaii have a much greater and more similar proportion of peculiarity than the Galapagos Islands. It is partly for this reason that, in the floristic classification given in Chapter 2, a higher rank is given to the former than to the last.

It is clear that species will be of such a narrow range as to merit the name endemic at two distinct periods of their existence, namely at the beginning and at the end, when they are very young and very old. A third possibility, that species may retain a very small area without expansion or contraction for a very long time, is a hypothetical contingency scarcely susceptible to proof or disproof, but the first two are very important in relation to other problems.

It is one of the principal features of plant geography that endemic (narrowly distributed) species are much more numerous than others and this may be explained in two completely different ways according to one's view of evolution. Those who favour the selectionist explanation contend that these endemics are for the most part almost extinct species, and regard their large numbers as evidencing that widespread extinction of forms which their theory requires. Those, like Willis for example, who favour a mutational view of evolution believe that endemics are mostly new species and that their superior numbers point to the kind of exponential increase that should be associated with such a process. This is why the discussion of endemism enters so largely into the presentation of evolutionary theories, each author trying to find, among the facts of endemism, the support which he seeks for his opinions.

Unfortunately there is no ready means, except in very rare cases, of knowing whether an individual endemic species is new or old and hence their value as evidence is strictly speaking, very little, however the more probable one or other mode of origin may be. It is nevertheless a common practice to distinguish these two sorts of endemics by name, if by nothing else, the "old" being referred to particularly as "relics," or even by the special name of "epibiotics" (448, 449).

Discontinuity

Discontinuity, or disjunction as it is often called, is the occurrence of a species or other unit in two or more separated regions, and is by no means an uncommon phenomenon. Sometimes the extent of discontinuity is very small and the range as a whole is almost continuous; sometimes the discontinuity is great and even to be measured in thousands of miles. Between these two extremes there is almost every intermediate condition.

In theory, of course, all species are discontinuous to some extent in so far as they rarely if ever cover their general range so completely that the individual plants are actually in contact, and the greater the detail in which distribution is considered the more apparent this point of view will become. In general, however, and especially in considering the whole ranges of species and genera, it is impossible to take into account, or indeed to mark, this degree of discontinuity, and the term is restricted in practice to ranges which on a large and obvious scale consist of two or more parts. Even so the term remains comparative and this must always be remembered, and in reference to it the degree of discontinuity comprehended should if possible be stated explicitly.

Discontinuity is closely related to two matters which have already been mentioned in this chapter. The first is the problem of the monophyletic origin of species. If this view is maintained, then obviously the phenomena of discontinuity take on a very great interest and importance because it may be assumed that whatever is the present separation between the constituent areas they must once have been continuous, or at least the individuals contained in them must once have come from one ancestral plant. This being so, then the discontinuity has to be explained, and there must be taken into account all the factors which might possibly have caused it, and this often leads the investigator into fascinating by-ways of his subject. On the other hand, if species are polyphyletic or polytopic then discontinuity loses much of its potential importance because it can always be explained on the supposition that the same species has arisen independently in each of the separated portions of its total range.

As has been said, discontinuity is quite common, and appears in all sorts of forms, and it is unlikely that any serious critic would be found to maintain that all and every of its examples are due to the species concerned having had a polyphyletic origin. On the contrary, the detailed facts are generally such as to indicate very strongly that this is not the case and that discontinuity is the result of real disjunction.

Discontinuity is also closely related to the Theory of Generic Cycles outlined above and will be seen from it to be in some form or other an almost inevitable concomitant of the phase of senility. Hence discontinuity is only to be expected and is to be regarded as a normal phenomenon of distribution. It is of course affected, like the other phases, by all kinds of extraneous causes, and extreme discontinuity is no doubt to some extent abnormal, since it can arise only in definite circumstances. It is for this very reason of special interest and importance, particularly from a theoretical point of view.

Actually the present geography of the world is such that any unit with an extensive range must of necessity be discontinuous. Even northern circumpolar ranges are broken by the gaps of the north Atlantic and the north Pacific, and the increasing segregation of land makes this more and more noticeable the further south we go from the North Pole. The tropical region, for example, is divided by oceans into three main masses corresponding to the continents, while the same kind of segregation is seen even more markedly in the southern temperate latitudes. Hence all the plants which range completely over at least one major climatic world belt must be discontinuous in total distribution. Clearly, to include these under the consideration of discontinuity would make for complexity, and therefore it is a working convention that by discontinuity is meant only such disjunction as is, so to speak, over and above that due to major land and sea distribution. For example, units which are pan-tropical in range are not usually considered or treated as discontinuous. Their ranges are in fact of necessity discontinuous, but this is not their primary interest. On the other hand, units which are found only in certain parts of the tropics separated by areas of ocean are so considered.

It is also apparent that discontinuity can be water discontinuity, land discontinuity (where a unit is irregularly distributed over a large land surface), or a mixture of both. Each kind involves rather a different combination of considerations and in theoretical matters the distinction between them should not be lost.

CHAPTER 4

THE DISTRIBUTION OF FAMILIES

The Number and Size of Families

ESTIMATES of the number of families into which the Angiosperms should be divided vary considerably. Bentham and Hooker (39), whose system of classification is that most familiar to British botanists, recognised about 200; Engler's system (158), which is more generally used on the Continent, makes about 285; Hutchinson's arrangement (291) increases the number to 332; and the recent compilation of Lemée (339) also admits over 300. There is indeed a general tendency for the number to increase as time goes on, not only because new families are discovered but because better knowledge makes it ever clearer that the earlier conceptions of many families were too wide, and need to be restricted. This process of augmentation is, however, still far from complete and there is little doubt that the number of families usually recognised to-day is insufficient to give an entirely realistic picture of their relationships. Some families, as, for example, the Sterculiaceae and the Flacourtiaceae, contain numerous divergent subgroups, while others include either isolated and often monotypic subfamilies or conspicuous *genera incertae sedis* which may well represent distinct families. Certain other families again, which are commonly used, such as the Myoporaceae, Cornaceae and Loganiaceae, are notoriously unsatisfactory and are probably aggregations of genera whose claims to mutual relationship are very slight. Nor are the differences between the various systems in these respects merely those of simple addition or subtraction, for families recognised in one system need not necessarily be admitted in another, which itself may contain others not included in the first.

In a geographical review, therefore, where the main purpose is to describe the distributions of the various groups concerned, it is desirable to refer to as many families as is reasonable, without attempting to follow any particular system of classification, and this is done below. In all nearly 400 families are mentioned, this number including all those in the four classifications noted above as well as some others which for various reasons call for recognition. It should be noted that as a result of this procedure individual families are normally defined in their narrower sense or, in the phrase of the taxonomist, *in sensu stricto*, and this is emphasised, where it seems especially necessary, by the use of an asterisk.

Families vary enormously in size, as is illustrated by the following figures, which are in round numbers based on Lemée (339). At one end of the scale is a family with more than 1,000 genera and 20,000 species and at the other there are several families (see below) which consist each of a single monotypic genus, and which are therefore of the smallest possible size, while between these extremes are others of almost every magnitude. Size can be expressed either in number of genera or in number of species, the former, since a genus may contain any number of species, being on the whole less expressive than the latter.

Heading the Dicotyledons and Monocotyledons respectively are two families considerably larger than any others,

	Genera	Species
Compositae .	1,000	20,000
Orchidaceae .	700	17,500

followed by about twenty others having some 2,000 or more species, namely,

	Genera	Species
Papilionaceae .	440	10,750
Rubiaceae . .	500	9,000
Gramineae .	600	7,500
Euphorbiaceae .	300	5,750
Labiatae . .	185	4,550
Scrophulariaceae .	235	4,150
Cyperaceae .	90	4,100
Melastomataceae .	200	3,750
Myrtaceae . .	95	3,600
Asclepiadaceae .	300	3,500
Acanthaceae .	250	3,100
Umbelliferae .	350	3,050
Liliaceae . .	200	3,000
Cruciferae . .	350	2,550
Solanaceae . .	88	2,300
Ericaceae . .	60	2,250
Piperaceae . .	5	2,200
Apocynaceae .	195	2,150
Rosaceae* . .	110	2,100
Mimosaceae .	50	2,100
Palmae . .	250	2,000
Araceae . .	115	2,000

The Cactaceae are also credited by some with about 2,000 species but the peculiarities of this family make comparison of it with others difficult.

It may be added that, taking the total of known Angiosperm species to be about 225,000 (see p. 140), the average family size is 600 species.

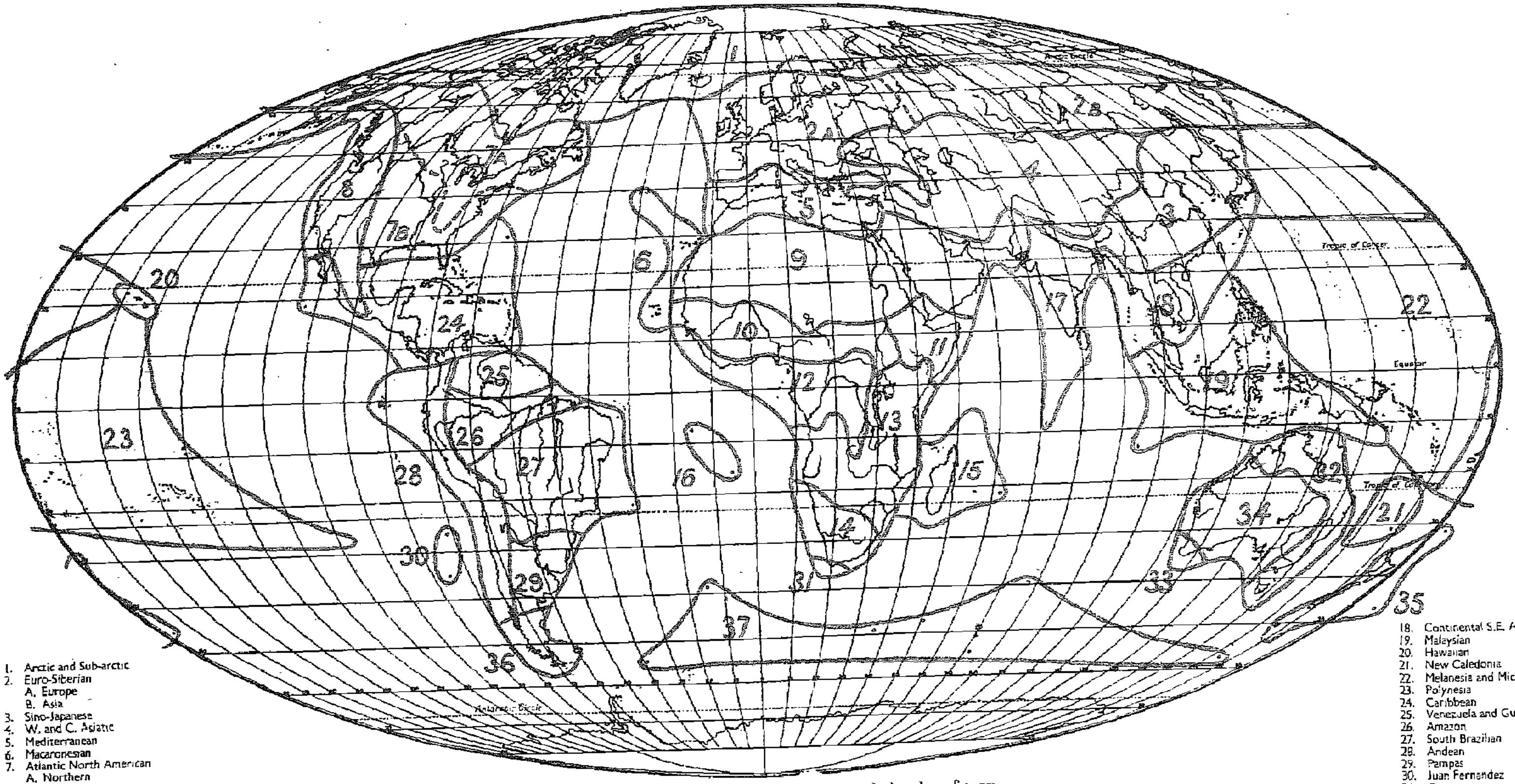
The Local Representation of Families

Another interesting facet of the distribution of families is that of their proportionate representation in the floras of different parts of the world, which is usually expressed by a local version of the world order just quoted, that is to say by arranging the families according to the numbers of their species in the different floras.

If there were no widespread families at all the correlation between lists of this kind would be very small, and indeed absent except perhaps for almost adjacent regions. On the other hand, if a few families were greatly outstanding in ubiquity and size, they would everywhere head the lists. The truth lies much nearer the latter than the former. Almost everywhere Compositae, Gramineae, Leguminosae (in the wide sense) and Cyperaceae are among the first six, but thereafter much depends on whether the area concerned is temperate, in which case such families as Caryophyllaceae, Cruciferae, Ranunculaceae, Rosaceae and Scrophulariaceae rank high, or whether it is tropical, in which case such families as Orchidaceae, Euphorbiaceae and

PLATE 4

Map of the World showing Floristic Regions. Original.



1. Arctic and Sub-arctic
2. Euro-Siberian
    A. Europe
    B. Asia
3. Sino-Japanese
4. W. and C. Asiatic
5. Mediterranean
6. Macaronesian
7. Atlantic North American
    A. Northern
    B. Southern
8. Pacific North American
9. African—Indian Desert
10. Sudanese Park Steppe
11. N.E. African Highland
12. W. African Rain-forest
13. E. African Steppe
14. South African
15. Madagascar
16. Ascension and St. Helena
17. Indian

Areas correct. Distortion increasing towards border of map.

Approximate Scale 1:100,000,000 (1600 miles - 1 inch) along Equator

on Mollweide's Homolographic Projection

Copyright

18. Continental S.E. Asiatic
19. Malaysian
20. Hawaiian
21. New Caledonia
22. Melanesia and Micronesia
23. Polynesia
24. Caribbean
25. Venezuela and Guiana
26. Amazon
27. South Brazilian
28. Andean
29. Pampas
30. Juan Fernandez
31. Cape
32. N. and E. Australian
33. S.W. Australian
34. C. Australian
35. New Zealand
36. Patagonian
37. S. Temp. Oceanic Islands

FIG. 2.—A. *Stylidium scandens*, B. *S. tenellum*, and C. *S. pycnanthum*, somewhat reduced, after Mildbraed.

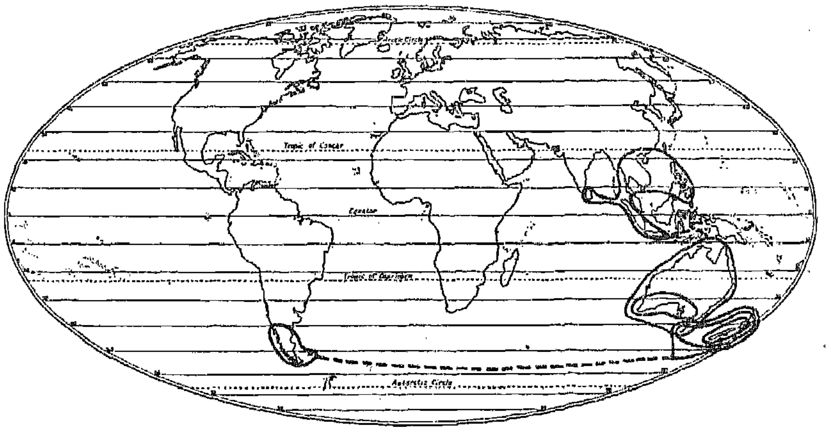


FIG. 3.—Map showing the distribution of the five genera of the family *Stylidiaceae*, i.e. *Stylidium*, Australia-Asia: *Levenhookia*, southern Australia: *Oreostylidium*, New Zealand: *Forstera*, New Zealand and Tasmania: *Phyllachne*, New Zealand, Tasmania and S. America.

Rubiaceae take their places. Departures from the world norm are actually greatest in equatorial forest regions, where leguminous plants are unusually common and Compositae and Gramineae unusually few; in some extra-tropical parts of the southern hemisphere, especially Australia, where Myrtaceae, Proteaceae and certain other families replace many of those more familiar elsewhere, and in some isolated islands, notably New Caledonia where the Gramineae, Compositae and Papilionaceae are remarkably few, and Hawaii where the Lobeliaceae are in the lead and Orchidaceae remarkably few.

Sprague (519) has made a useful contribution to this subject, though his estimates of family size have a basis different from those given above. After quoting a valuable series of figures he comes to several conclusions, which, it may be said, receive general support from many other lines of evidence. Chief among them are first, that the various floras of the world arose by segregation, under the influence of climate, from an ancient world-wide flora of a tropical or semi-tropical character, and second, that the history of the Flowering Plants in the two hemispheres has been quite different because of the near elimination of the southern cold flora during the Pleistocene as a consequence of the discontinuity of the land in the higher latitudes of that hemisphere.

The Geographical Classification of Families

Sundry attempts have been made to classify the families of Angiosperms according to their distributions but this is not an easy thing to do, partly because of the ill-defined taxonomic limits of some groups and partly because of the difficulty of determining the true status, in all parts of the world, of individual species. A particularly elaborate study of this kind had been made by Vester (568), who not only gives a map of each family but also a short verbal account of its distribution. Vester's work brings together in compact form a great deal of information, especially about the northern and southern limits of families, and, although many of the maps need correction, it is a source of great value. At the same time the degree of detail in his classification shows very clearly how hard it is to make anything of the sort both simple and complete. No two families have exactly similar distributions and there is almost infinite variety in detail. Moreover, though the total ranges of certain families may be much alike in outline they may differ considerably in many other respects, such as intensity of distribution, massing of species, proportions of endemism, ecological segregation and so on, all of which must be taken into account.

Here the main concern is to draw attention to the more prominent geographical features of each family as a contribution to the over-all picture of Angiosperm distribution which it is the purpose of this book to draw, and on this basis geographical classification need not be so detailed. Indeed the main considerations are but two, the general degree of distribution and whether the families are essentially tropical or temperate, and combining these it is enough to divide the families under six heads—cosmopolitan or nearly so, tropical, temperate, discontinuous, endemic and anomalous, subdividing each of these independently as required.†

Cosmopolitan and subcosmopolitan families

These are the families which, in extent of range, cover the major portions of both the tropical and extra-tropical parts of the world, and the first question therefore that may well be asked is whether there are any truly cosmopolitan, in

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† In this connection see the interesting maps in Axelrod (618).

FIG. 4.—*Drimys winteri*†, about natural size, after Baillon.

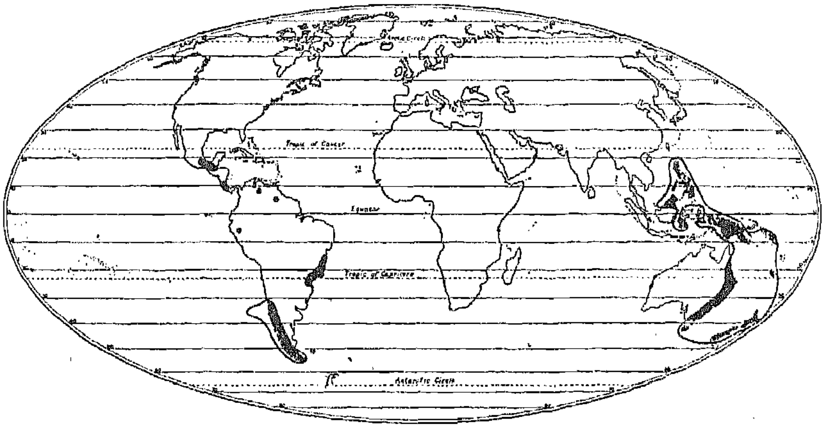

FIG. 5.—Map showing (black) the distribution of the family Winteraceae, mainly after Smith (513).

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† According to Smith, in *Journ. Arnold Arboretum*, 24, 1943, the plant depicted is the variety *punctata*.

the sense of ubiquitous, families. In so far as Antarctica and some of the Arctic regions are permanently glaciated and therefore virtually devoid of seed plants, there are none, but the term cosmopolitan in plant geography is generally used in a less rigid sense and thus to apply to distributions which cover all or nearly all those parts of the world where there is a reasonably well-developed flora of these plants, and within this definition quite a number of families fall.

Pride of place must certainly go to the Gramineae (253), the great family of which much was said in the Introduction. Not only do the grasses reach to the furthest land in the north and to the borders of Antarctica in the south, but their degree of distribution is usually particularly complete and continuous. Almost alone among the families of flowering plants they form the dominant element in vegetation over great areas of the world, and nearly everywhere else too, except perhaps in some forest regions, the proportion of these plants is high.

In general ubiquity the Compositae almost certainly rank next to the Gramineae. They are in fact much more numerous in genera and species but they never form so prominent a part of vegetation. Nevertheless the genera are well-scattered, and nearly every flora contains a good representation of them. In some places, especially within the drier mid-latitudes, the Compositae are particularly abundant, though there is no outstandingly disproportionate local massing.

The Cyperaceae are another remarkably widespread family and, in many ways a counterpart, in rather damper conditions, of the Gramineae, but they are a much smaller family, especially in genera, with a narrower ecological range. Two very large genera, *Carex*, which is mainly temperate, and *Cyperus*, which is mainly tropical, account for most of the distribution.

In purely superficial extent of range the still smaller family Caryophyllaceae probably comes nearest to the Gramineae, for it has not only many arctic forms, but it is the only other family in Antarctica, as well as being a prominent feature in the floras of the South Temperate Oceanic Islands. It has not, however, anything like the same intensity and completeness of distribution, and there are many tropical areas, notably some of the forest regions and the western half of Australia, where it is almost or quite unrepresented. Moreover its breadth of range may to some degree be misleading since the family includes some of the most widespread weeds.

Seven families, in order of size Orchidaceae, Papilionaceae, Labiatae, Scrophulariaceae, Liliaceae*, Boraginaceae* and Gentianaceae*, come next to those above because they are, in the main, equally characteristic of both tropical and temperate regions, though in the Orchidaceae the actual number of species is immensely greater in the tropics. The first three have rather lower northern limits than the rest. The Gentianaceae is the smallest and most thinly spread of the six and owes its wide range chiefly to the development of a minority of notably arctic types.

Similar in general extent of range are the great, predominantly temperate families Cruciferae, Umbelliferae, Ranunculaceae and Rosaceae*. The first of these is probably the nearest approach to an exclusively temperate large family that there is, because its occurrences within the tropic lines are nearly all montane, though to a lesser degree this is true also of the other three. The family Rosaceae is the first to be mentioned in which there is an appreciable number of woody plants. Umbelliferae have a lower northern limit than the others. It is interesting also to note here that both the Cruciferae and Umbelliferae have closely related tropical families, the Capparidaceae and Araliaceae respectively.

Eight others are also predominantly temperate and almost as widely spread,

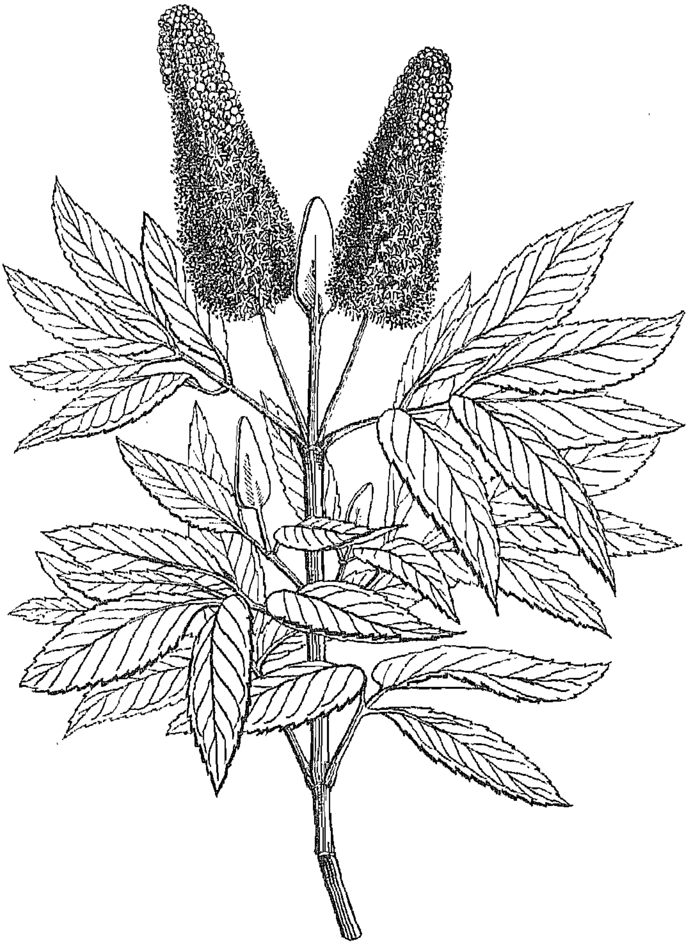

FIG. 6.—*Cunonia capensis,* about half natural size, after Baillon.

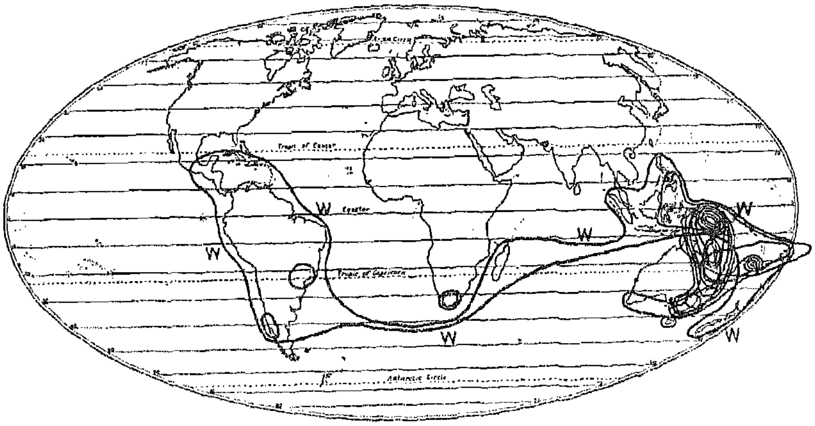

FIG. 7.—Map showing the distribution of the genera of the family Cunoniaceae. One genus, *Weinmannia*, represented by the letter W, is very widespread; all the rest are more or less narrowly endemic and much concentrated in New Guinea and Australasia.

namely Campanulaceae*, Juncaceae, Onagraceae, Polygonaceae, Cuscutaceae, Plantaginaceae (see p. 146), Hypericaceae and Primulaceae (see p. 71) but they are smaller and on the whole less evenly distributed. The first four are the most widely spread and the last two, especially, show considerable gaps. Each of them has one large genus covering nearly all the family range, and the Onagraceae and Polygonaceae are rather particularly characteristic of the western parts of North America.

The Ericaceae pose problems of great geographical interest. In its narrower sense here used the family comprises three groups, the Rhododendroideae, the Arbutoideae and the Ericoideae. It is doubtful, however, whether the over-all differences between these are in fact any less than those between them and two families recognised here as distinct, the Vacciniaceae and the Epacridaceae, and it is more satisfactory from a geographical point of view to think of all these as five groups of similar importance and more or less equal relationship. When this is done some very interesting facts emerge. In total area the five together are as completely cosmopolitan as almost any other single family, but the five constituents have very different distributions. The Arbutoideae are almost world wide, but very predominantly north temperate and scarcely represented in Africa and Australia. The Rhododendroideae are similar but less widely distributed and are absent from Africa. The Vacciniaceae again have a very similar total range, though with representation in Madagascar but not in tropical Africa, but are conspicuously most strongly developed in tropical America and, to a lesser degree, in tropical Asia and Malaysia. The Ericoideae, in marked contrast, are confined to Africa and Europe, with an enormous preponderance south of the Tropic of Capricorn. Finally the Epacridaceae are also southern, being essentially an Australasian group, having also a single monotypic genus in Patagonia. Thus, within a cosmopolitan whole, there are two northern groups, one trans-equatorial chiefly New World group, and two southern Old World groups (see p. 69). It should also be noted that these five comprise woody plants, many of them of a characteristic type, and constitute the most widely distributed of all such groups.

Four families, Convolvulaceae*, Malvaceae, Solanaceae and Urticaceae, are essentially tropical though they have a considerable and widespread temperate representation. They do not, however, reach quite such high latitudes as any of the foregoing. The temperate members of the Urticaceae are rather uncharacteristic of the family as a whole and thus illustrate a not uncommon condition, best seen in the next seven families.

These are the Rubiaceae, Euphorbiaceae, Linaceae*, Violaceae, Polygalaceae, Verbenaceae and Lythraceae, though the last is rather less widely distributed than the rest. All are predominantly tropical families and their wide distributions are due in each case to the occurrence of one or two herbaceous types more or less unrepresentative of the family as a whole. In Rubiaceae the members of the *Galieae* are very unlike the numerous tropical woody genera; in Euphorbiaceae virtually only the highly specialised herbaceous species of the genus *Euphorbia* range into high latitudes; the herbaceous genera *Linum*, *Viola* and *Polygala* are almost the only temperate members of their predominantly woody groups; while in the Verbenaceae and Lythraceae there is a similar, though less marked, state of affairs.

Next come six families in which the main geographical feature is a preponderance south of the equator, and these are best dealt with in pairs. The Santalaceae and Thymelaeaceae are both fairly evenly spread, though they have gaps, but are respectively most plentiful in Australasia and South Africa. The Geraniaceae and

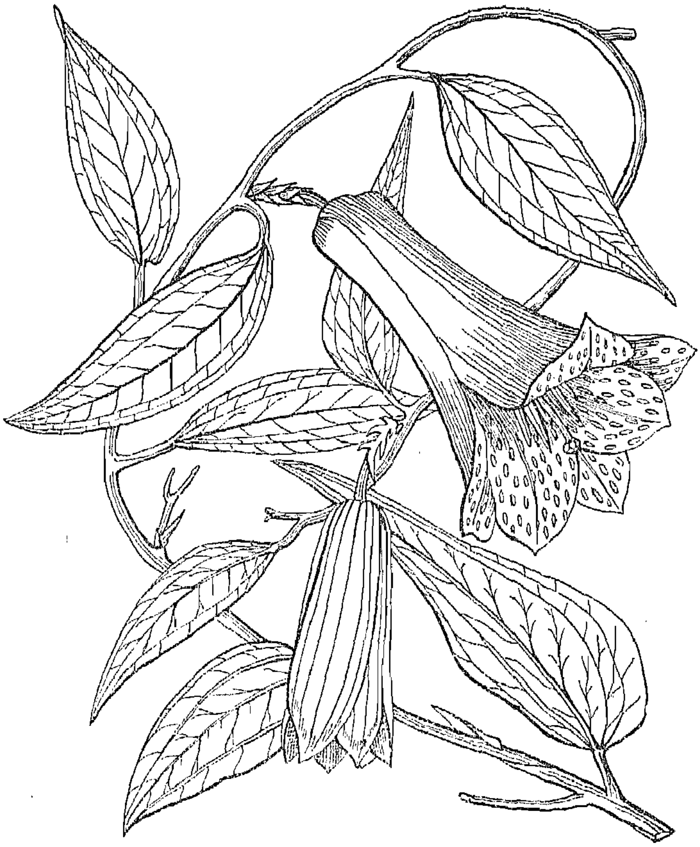

FIG. 8.—*Lapageria rosea*, a familiar member of the Philesiaceae, slightly reduced, after Hutchinson.

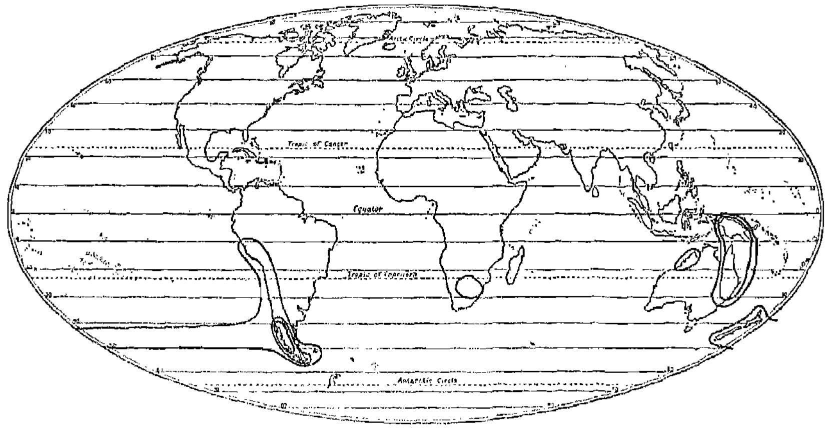

FIG. 9.—Map showing the distribution of the genera of the family Philesiaceae.

Oxalidaceae are both greatly concentrated in South Africa and South America and are world wide only by certain species of the genera *Geranium* and *Oxalis*. The Crassulaceae and Portulacaceae are concentrated respectively in the South African, Macaronesian and Mediterranean regions and in South America and Australia, and are both cosmopolitan only because of the exceptionally wide range of one or two small aquatic members.

Four more woody families are sufficiently widespread to be included here though by the nature of the case they have not quite the same extent as many of those above. They are the Oleaceae, Caprifoliaceae, Celastraceae and Rhamnaceae, and the first two are chiefly temperate while the others are chiefly tropical. The Caprifoliaceae are much less completely distributed than the others.

Another five families may also be included here on the grounds that they are found practically all over the world within their ecological limits but which, on account of these, are certainly much less completely distributed than most of those mentioned above. Two of them, Chenopodiaceae and Plumbaginaceae, are rich in halophytes and are therefore mostly plentiful in either salt desert or coastal areas, and to a less extent the same is true of the Illecebraceae, but the Droseraceae and the Lentibulariaceae are chiefly marsh and bog plants and therefore absent from the more arid parts of the world. The Chenopodiaceae are described (160) as having ten main centres of concentration widely scattered over the world's deserts; the Plumbaginaceae and Illecebraceae are most developed in the Mediterranean and Central Asiatic regions; the Droseraceae are predominantly southern and especially Australian (160); the Lentibulariaceae are more evenly distributed but show one or two gaps.

The subject of edaphic limitation leads on conveniently to the last group of widespread families, the aquatics, in which it is seen in even more pronounced form. These number fifteen, namely:

Alismataceae, Callitrichaceae, Elatinaceae, Hydrocharitaceae, Haloragaceae*, Lemnaceae, Menyanthaceae, Najadaceae, Nymphaeaceae, Potamogetonaceae, Ruppiaceae, Zannichelliaceae and, less completely perhaps, Butomaceae, Ceratophyllaceae and Typhaceae.

Each of these occurs in fresh water (or rarely, in salt water also) in most parts of the world but the necessarily restricted nature of their habitats scarcely allows direct comparison with other families, and it would be unprofitable to try to assess how much more or how much less any one of them is in fact distributed. Their chief geographical interest is in relation to problems of dispersal (see Chapter 18). The largest of them, Hydrocharitaceae, has less than 20 genera, and the largest genus among them is *Potamogeton* with more than 100 species.

Tropical families

Because the area of land available within the tropical and sub-tropical zones of the world is nearly twice as great as that within the temperate and polar zones (see Appendix A) the families widely spread in and characteristic of the former naturally come, in point of distribution, next to those already discussed. There is, however, no very clear line of demarcation between the members of the two categories for the noteworthy reason that comparatively few families range widely through the tropics, that is to say well over all three constituent regions, without some, and usually considerable, extension into temperate latitudes. Indeed such families as the Orchidaceae, Rubiaceae and Euphorbiaceae, which are essentially tropical groups, are, as has been seen, so widespread actually as to merit the term

FIG. 10.—*Hypolaena fastigiata*, a typical member of the Restionaceae, about natural size, after Hooker.

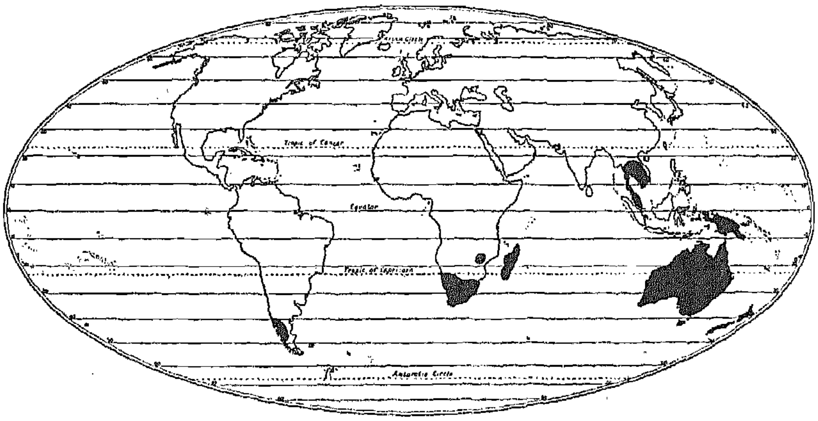

FIG. 11.—Map showing (black) the distribution of the family Restionaceae, partly after Hutchinson.

subcosmopolitan. Hence the first families to be considered here under the "tropical" heading are those in which this latitudinal extension is most marked, though not to the degree which would place them in the previous category.

Nine of these families are familiar in the floras of north-west Europe because, in these latitudes, where the effect of the Gulf Stream is felt, they reach, if only by a single species, parallels higher than elsewhere. Perhaps the most remarkable instance is the Asclepiadaceae, in which the genus *Cynanchum* reaches south Finland. Strangely enough this family is not present, even as adventive, in the British Isles. The other nine families, Amaryllidaceae*, Aquifoliaceae, Araceae, Aristolochiaceae, Cucurbitaceae, Dioscoreaceae, Loranthaceae, Tiliaceae and Ulmaceae, include members of the British flora.

The Eriocaulaceae and Lobeliaceae (see below) have an interesting point in common, namely, that the most northerly species in western Europe are found in North America also but not in eastern Europe or Asia, and in the former there is no representation between Britain and India.

More than a dozen families are of special note, particularly in contrast with those just mentioned, because they tend to reach their highest latitudes in North America and/or Asia, and north of the Sahara to be represented only by one or a few more or less isolated species. The best examples of this are:

> Acanthaceae, Apocynaceae, Araliaceae, Gesneriaceae, Lauraceae, Menispermaceae, Moraceae*, Sapotaceae, Smilacaceae, Vitaceae,

but the same feature appears in less striking form in:

> Amaranthaceae, Anacardiaceae, Caesalpiniaceae, Capparidaceae, Commelinaceae, Mimosaceae, Nyctaginaceae, Phytolaccaceae.

The first, and the last two, of this latter group are especially American families. All eighteen are represented in temperate South America; of the first group all but Acanthaceae, Menispermaceae and Vitaceae are found in New Zealand, but of the second group only Amaranthaceae and Nyctaginaceae have a very slight representation there. Iridaceae and Rutaceae are rather similar, but they are on balance southern families.

The remaining families which, large or small, are found in all three main regions of the tropics, number 46, and can be grouped in various ways. Here it is most appropriate in view of what has already been said to arrange them according to their latitudinal limits, and to do this with special reference to North America, where, for reasons perhaps associated with the Pleistocene glaciations, separation on this basis is particularly clear.

Three small families, Hypoxidaceae, Pontederiaceae and Xyridaceae, actually occur north of the Canadian border and the first is widest below the equator, reaching New Zealand.

Nine families reach to between 40° and 45° N. in the U.S.A. and for the most part occur in Japan also. The Agavaceae, Bignoniaceae (see p. 136), Loganiaceae, Passifloraceae and Sapindaceae reach as far south in Australasia as New Zealand; Annonaceae, Ebenaceae, Ehretiaceae and Melastomataceae reach temperate Australia. All these are considerable families, and among them Agavaceae, Bignoniaceae, Melastomataceae and Passifloraceae show preponderance in the New World, while Annonaceae and Ebenaceae are rather the reverse.

The four large families Palmae (whose northern extreme is actually in Mediterranean Europe), Malpighiaceae, Sterculiaceae and Marantaceae, and the much smaller family Simaroubaceae, reach between 30° and 40° N. in the U.S.A. The first is in New Zealand, and all but the Marantaceae occur in Australia. The

Marantaceae and Malpighiaceae are predominantly American: Sterculiaceae richest in Africa.

The great predominantly southern family Myrtaceae resembles the palms (for which a southern preponderance is claimed on p. 70) in having its northern limit in Europe, but south of the tropics it is much more completely distributed.

Nine more families reach Japan but not (or scarcely only) the U.S.A., namely, Balanophoraceae, Meliaceae, Myrsinaceae, Olacaceae and Piperaceae, all of which are found in New Zealand; Flacourtiaceae, Triuridaceae (very local in Africa) and Zingiberaceae, which reach Australia; and Begoniaceae. Of these Myrsinaceae, Piperaceae and Begoniaceae are relatively few in Africa, Zingiberaceae are predominantly Asiatic (compare Marantaceae), and Flacourtiaceae are rich in Africa. Similar, but with their Asiatic extremes on the mainland, are Combretaceae and Icacinaceae, both with species in New Zealand.

A further twenty, mostly somewhat smaller, families do not much, if at all, cross the tropic anywhere in the northern hemisphere, and these can be grouped according to their Australasian ranges as follows:

1. Monimiaceae* are found in New Zealand.
2. Dilleniaceae have their southern limit in Tasmania.
3. Barringtoniaceae, Bombacaceae, Burseraceae, Chailletiaceae, Chrysobalanaceae, Connaraceae, Erythroxylaceae, Guttiferae*, Hernandiaceae†, Hippocrateaceae, Myristicaceae, Ochnaceae, Opiliaceae, Rhizophoraceae and Samydaceae occur in Australia.
4. Gnetaceae, Hugoniaceae and Ixionanthaceae do not reach Australia.

Finally there are twelve more or less pan-tropical families which call for individual notice because they do not easily fit into any of the groups already mentioned. Eight of these are best described as incompletely pan-tropical because, while they occur in all three parts of the tropical zone, there are significant local gaps in their distributions. Podostemaceae, Tristichaceae, Rafflesiaceae (very scattered) and Zygophyllaceae are absent from parts of Malaysia and Australia; Theaceae scarcely occurs in Africa or Australia; Taccaceae are absent from much of tropical America; Burmanniaceae and Thismiaceae are also incompletely distributed. Four others can only be described as anomalous, namely, the Aizoaceae and Molluginaceae, which are families of arid regions and predominantly African, the Cabombaceae which is a small but widely spread freshwater aquatic family, and the Basellaceae, which is a very small family of uncertain status in parts of the Old World tropics.

Temperate families

Four features of the temperate regions of the world make them, from the point of view of plant distribution, very different from the tropics, quite apart from their climatic values. First, they are mainly in two parts, north and south of the tropics. Second, there are enormous differences of both area and latitudinal range between the north and south temperate (see Appendix A). Third, whereas the north temperate zone is an almost continuous belt of land, the south temperate zone comprises three widely separated parts, South America, South Africa, and Australasia. Fourth, and in many ways most important to remember, while there are in the temperate regions no tropical areas, there are, because of altitude, many well-scattered areas of temperate climate within the tropics. For this last reason the

† If the Queensland genus *Valvanthera* is rightly attributed.

most widely and completely distributed temperate families are in fact more or less cosmopolitan and have already been considered under that heading. Again, because of the first circumstance, it is not surprising that there are no strictly pan-temperate families in the narrower sense of groups which are found throughout both the north temperate and the south temperate but which are unknown in between.

In short there are, apart from the predominantly temperate subcosmopolitan families already referred to, only about 20 families, most of them quite small, which are more or less strictly confined to temperate climates and which are neither so broken in distribution as to be discontinuous (as must be all purely southern temperate groups) or so restricted in area as to be endemic, and these fall simply and clearly into two groups, namely, those which, while mainly in the north temperate regions, extend on higher ground into or even across the tropics in places, and those which are strictly confined north of the Tropic of Cancer.

Of the families in the first group, which number twelve, the Vacciniaceae (see above) is not only the widest, occurring all through the north temperate; throughout America as far as 40° S.; in East Africa and Madagascar; throughout tropical Asia and Malaysia to Queensland; and, if *Ericopsis* is rightly attributed, in south-western Australia, but is also the most anomalous, since its greatest concentrations are in the mountains of warm America and Indo-Malaysia. The Salicaceae are somewhat similar, but present in all Africa and absent from much of Malaysia and from Australasia. The Hydrangeaceae are also extensive, right through America, through Malaysia to New Guinea and to Hawaii. The Fumariaceae have southern extensions in the two parts of the Old World but not in the New, and cover all Africa as well as parts of Tropical Asia. The Saxifragaceae* also cover much of Africa and extend far down America. Two families, Aceraceae and Elaeagnaceae, are widespread in the north, and reach into Malaysia and Australia respectively. Berberidaceae, Juglandaceae and Pirolaceae extend south in both America and Malaysia, the last-named slightly only. Grossulariaceae (see fig. 18) and Polemoniaceae extend widely through America only, and Betulaceae the same on a smaller scale.

The seven families of the north temperate which have no notable extensions into the tropics are—Diapensiaceae, Trilliaceae, and the monotypic Adoxaceae and Scheuchzeriaceae, all of which are more cold temperate, and Corylaceae, Cannabinaceae and Monotropaceae which are rather more warm temperate. The Diapensiaceae (with seven genera) is the nearest approach to a widely distributed northern arctic-alpine family.

Discontinuous families

Speaking very generally the foregoing three categories account for the more widespread families, and there have now to be described those whose ranges are on the whole smaller. There are two classes of such families, the discontinuous, in which the actual areas occupied are in two or more distinct and separate parts, and the endemic, in which the total range is more or less strongly restricted.

The discontinuous families are best divided into groups by recalling and using for the purpose the two geographical circumstances that the temperate zones are separated by the intervening tropics, and that there are three separate land masses extending south from the almost continuous circumboreal belt, because many discontinuities are due to the restriction of families either to both of the temperate zones or to some or all of the three southern extensions. Apart from these discontinuity is usually the result of incomplete distribution within the north temperate or the tropical zones. It must be remembered that all pan-tropical families are in a sense discontinuous although they are more properly and usefully considered a class by themselves, and also that many of these and other families already dealt with are doubtless discontinuous to some degree, though not to the extent which makes it desirable to recognise them as such here.

It is convenient to record the discontinuous families in tabular form because this enables the very varied facts to be presented most simply and also indicates the relative prevalence of each kind. The table given here is capable of much greater subdivision but it is unnecessary to go into more detail because in many cases discontinuity is due to the distribution of particular genera, which receive further notice later on.

The Discontinuous Families of Angiosperms

A. Families of the north and south temperate regions:

Cistaceae	North America and western Eurasia; South America
Empetraceae (fig. 38)	north temperate; South America, and Tristan da Cunha
Fagaceae	north temperate and from Asia to New Zealand; South America
Frankeniaceae	North America; western Eurasia and Africa; South America; Australia and Tasmania
Hippuridaceae	north temperate; South America
Juncaginaceae	north temperate; Central and South America; South Africa; Australia and New Zealand
Lardizabalaceae	East Asia; Chile. A most unusual distribution which may indicate that the family is not a natural group
Orobanchaceae	north temperate; South America; ? South Africa and Australia
Papaveraceae*	north temperate and from North America to the Andes; South Africa; Australia
Philydraceae	South-east Asia; New Guinea and eastern Australia; south-western Australia
Posidoniaceae (marine)	Mediterranean; Australia
Sparganiaceae	north temperate; Australia and New Zealand
Tecophilaeaceae*	California; South Chile; South Africa.
Valerianaceae	north temperate and from North to South America; South Africa; part of Malaysia
Zosteraceae (marine)	north temperate; South Africa; Australia and New Zealand

B. Families of America and of Eurasia and/or Australasia:

1. Families found entirely or predominantly in the northern hemisphere—

a. America and western Eurasia:

Platanaceae

b. America and eastern Eurasia:

Calycanthaceae
Magnoliaceae*
Nyssaceae
Penthoraceae
Phrymaceae
Saururaceae
Schisandraceae

c. America, western and eastern Eurasia:

Datiscaceae
Styracaceae
Hippocastanaceae
Staphyleaceae

2. Families found predominantly in the tropics:
    - Chloranthaceae
    - Illiciaceae (514)
    - Roxburghiaceae
    - Sabiaceae
    - Sauraujaceae
    - Symplocaceae
    - Trigoniaceae

3. Families found entirely or predominantly in the southern hemisphere:
    - Centrolepidaceae
    - Corsiaceae
    - Epacridaceae
    - Eucryphiaceae
    - Goodeniaceae (includes two species very widely distributed on tropical shores)
    - Stylidiaceae (fig. 3)
    - Tetrachondraceae
    - Winteraceae (513)

C. Families of America and of Africa and, often, the Madagascar region:

1. In Africa and the Madagascar region:
    - Canellaceae
    - Hydnoraceae
    - Strelitziaceae
    - Turneraceae
    - Velloziaceae

2. In Africa but not in the Madagascar region:
    - Bromeliaceae
    - Caricaceae
    - Humiriaceae
    - Loasaceae
    - Mayacaceae
    - Rapateaceae
    - Vochysiaceae

D. Families of Africa and/or the Madagascar region and of Asia and/or Australasia and the Pacific Islands:

1. In both Africa and the Madagascar region
    - Alangiaceae
    - Aponogetonaceae
    - Dipterocarpaceae
    - Flagellariaceae
    - Musaceae
    - Pandanaceae
    - Pittosporaceae
    - Trichopodaceae

2. In Africa but not in the Madagascar region
    - Ancistrocladaceae (fig. 28)
    - Ctenolophonaceae

3. In the Madagascar region but not in Africa:
    - Nepenthaceae

E. Families found in all three parts of the southern hemisphere:
    - Cunoniaceae (fig. 7)
    - Escalloniaceae
    - Gunneraceae (fig. 45)
    - Philesiaceae (fig. 9)
    - Proteaceae (fig. 15)
    - Restionaceae (fig. 11)

F. Other discontinuous families:

Atherospermaceae .	Tropical America; West Africa; Australia; New Zealand; New Caledonia
Clethraceae (fig. 32).	America; Asia; Malaysia; Madeira
Cneoraceae . .	Mediterranean; Canaries; and, if *Cubincula trimera* is rightly attributed, Cuba also
Cochlospermaceae .	Tropical America; tropical Africa and (if *Sphaerosepalum* is included) Madagascar; India and south-east Asia; tropical Australia
Coriariaceae (fig. 37)	Central America and western South America; Mediterranean; East Asia; New Guinea; New Zealand, etc.
Cornaceae . .	North temperate; Asia to New Guinea; South America; South Africa and Madagascar; New Zealand, etc.
Cynocrambaceae .	Canaries; Mediterranean; Tibet; Japan
Elaeocarpaceae .	Tropical America and Chile; Madagascar; Mascarenes; Socotra; India and Japan to New Zealand and Hawaii. Compare B3 and E above.
Haemodoraceae .	America; South Africa; Australia and Tasmania

Hamamelidaceae .	North America and Mexico; West Asia; India; Japan; Malaysia; Africa and Madagascar; and, if *Ostrearia* is rightly attributed, Queensland
Hydrocaryaceae .	Europe; parts of Africa; parts of Central Asia; eastern Asia.
Myoporaceae . .	a dubious family, chiefly Australian and thence to Asia; Mascarenes; South Africa; West Indies
Peripterygiaceae .	Malay Peninsula; Borneo; New Caledonia
Resedaceae . .	western Eurasia and North Africa; eastern tropical and South Africa; south-west North America

Endemic families

As was explained in an earlier chapter the term "endemic" is not an absolute one but varies in value according to the circumstances of its use. Generally speaking the larger the taxonomic category concerned the wider the conception of endemism can be and in this chapter it is used to describe families which are found either within one of the continental land masses or within some area of roughly equivalent size. Many families are of course much more restricted even than this, and some are confined to single floristic regions, but to make the category less wide in scope would complicate things undesirably. It must also be noted that many families, which is this sense are endemic, are also, like various wide families, to some degree discontinuous, though not to the extent which would warrant including them in the last category in preference to this.

The endemic families are here tabulated geographically, and with them are given figures of the approximate number of species in each, since this is a matter of particular interest in more narrowly distributed groups. In connection with this table two families call for special remark, the Cactaceae and Bromeliaceae. The former is commonly reported as occurring in the Old World, but as far as can be judged, all these records are of adventive plants and the family is native only in the New World. Here, however, it has a much wider latitudinal range than any other purely American family and is also very much larger, and it has therefore been treated as an exceptional endemic with a place of its own in the tabulation. The Bromeliaceae, on the other hand, which is of similar size, has generally been regarded as confined to America, but the single species found some years ago in West Africa appears to be native there and the family therefore finds a place on p. 62.

The list below includes 124 families in all, about a dozen of which are also discontinuous to a small extent.

The Endemic Families of Angiosperms

A. America:

1. General . .	Cactaceae	1,250–2,000
2. Northern . .	Crossosomataceae	3
	Fouquieriaceae	5
	Garryaceae	20
	Koeberliniaceae	1
	Leitneriaceae	2
	Lennoaceae	5
	Limnanthaceae	5

3. Tropical . .	Achatocarpaceae	10
	Alstroemeriaceae	175
	Batidaceae	1
	Bixaceae	1
	Brunelliaceae	10
	Cannaceae	50
	Caryocaraceae	20
	Cyclanthaceae	50
	Cyrillaceae	9
	Desfontaineaceae	3
	Diclidantheraceae	3
	Julianiaceae	5
	Lacistemaceae	20
	Lecythidaceae*	190
	Lissocarpaceae	1
	Malesherbiaceae	25
	Marcgraviaceae	50
	Martyniaceae	10
	Pellicieraceae	1
	Picrodendraceae	3
	Quiinaceae	25
	Theophrastaceae	45
	Thurniaceae	2
	Tovariaceae	2
	Tropaeolaceae	30

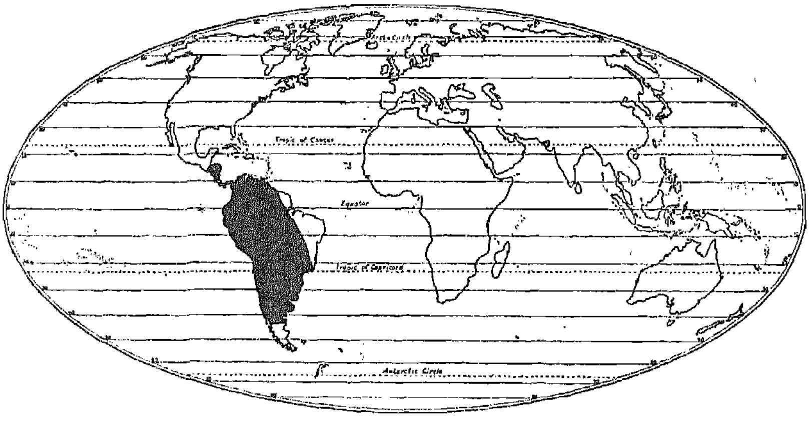

FIG. 12.—Map showing (black) the distribution of the family Tropaeolaceae, after Hutchinson.

4. Southern . .	Aextoxicaceae	1
	Calyceraceae	30
	Gomortegaceae	1
	Lactoridaceae	1
	Myzodendraceae	12
5. Others . . .	Columelliaceae	2
	Heterostylaceae	1
	Nolanaceae	30
	Sarraceniaceae	10

PLATE 5

Map of the World showing Climatic Provinces. After Supan in Bartholomew's *Physical Atlas*, vol. III.

1. Arctic
2. West European
3. East European
4. West Siberian
5. East Siberian
6. Kamchatkan
7. Sino-Japanese
8. Asiatic Mountain and Plateau
9. Aral
10. Indus
11. Mediterranean
12. Saharan
13. African Tropical
14. Kalahari
15. Cape
16. Indo-Australian Monsoon
17. Inner Australian
18. S.W. Australian
19. East Australian
20. New Zealand
21. Polynesian Tropical
22. Hawaiian
23. North Canadian
24. N.W. American Coastal
25. Californian
26. N. American Mountain and Plateau
27. Atlantic American
28. West Indian
29. Tropical Cordilleran
30. S. American Tropical
31. Peruvian
32. North Chilian
33. South Chilian
34. Pampa

Areas correct. Distortion increasing towards border of map.
Approximate Scale. 1:100,000,000 (1600 miles = 1 inch) along Equator
on Mollweide's Homolographic Projection

B. Mediterranean in a wide sense, or at least centred there:

Cynomoriaceae	1	
Globulariaceae	25	
Punicaceae	2	
Ruscaceae	150	

C. Africa:

1. Tropical or tropical and southern Africa, and the Madagascar region

Hydrostachyaceae	12	
Myrothamnaceae	1	
Selaginaceae	250	

2. Tropical . . .

Barbeyaceae	1	and Arabia
Cyanastraceae	5	
Dioncophyllaceae	3	
Hoplestigmataceae	2	
Huacaceae	2	
Lepidobotryaceae	1	
Medusandraceae	1	
Melianthaceae	20	and South Africa
Nectaropetalaceae	6	
Octoknemataceae	5	
Oliniaceae	1	and South Africa; St. Helena
Pandaceae	1	
Scytopetalaceae	12	
Sphenocleaceae	2	

3. Madagascar or Mascarenes only

Chlaenaceae	30	
Didieraceae	4	
Geosiridaceae	1	
Humbertiaceae	1	
Medusagynaceae	1	Seychelles
Rhopalocarpaceae	5	

4. South Africa . .

Achariaceae	1	
Bruniaceae	30	
Geissolomataceae	1	
Greyiaceae	3	
Grubbiaceae	3	
Heteropyxidaceae	2	
Penaeaceae	30	
Roridulaceae	2	

D. Asia:

1. Reaching Australia or New Zealand

Apostasiaceae	25	
Sonneratiaceae*	12	

2. Continental Asia, with Japan and Formosa

Bretschneideraceae	1	
Cercidiphyllaceae	2	
Circaeasteraceae	1	
Eucommiaceae	1	
Eupteleaceae	5	
Pentaphylacaceae	1	
Rhoipteleaceae	1	
Sargentodoxaceae	1	
Stachyuraceae	5	

	Tetracentraceae	1
	Trochodendraceae	1
3. Asia and Malaysia	Actinidiaceae	12
	Crypteroniaceae	8
	Daphniphyllaceae	30
	Erythropalaceae	4
	Pentaphragmataceae	15
	Petrosaviaceae	3
	Sarcospermataceae	9
4. Malaysia only .	Gonystylaceae	7
	Lowiaceae	2
	Scyphostegiaceae	1
	Stenomeridaceae	1
	Tetrameristaceae	2

E. Australasia and the Pacific Islands, or at least centred there:

1. Australia only .	Akaniaceae	1	
	Austrobaileyaceae	1	
	Brunoniaceae	1	
	Byblidaceae	2	
	Cartonemataceae	1	
	Cephalotaceae	1	
	Davidsoniaceae	1	
	Dysphaniaceae	6	
	Gyrostemonaceae	5	
	Petermanniaceae	1	
	Tremandraceae	30	
2. Others	Amborellaceae	1	New Caledonia
	Balanopsidaceae	1	North-east Australia and New Caledonia
	Casuarinaceae	55	Australia, Fiji and New Caledonia to Burma
	Corynocarpaceae	4	New Zealand, New Caledonia, New Hebrides, North Queensland, southern New Guinea
	Degeneriaceae	1	Fiji
	Eupomatiaceae	2	Australia and New Guinea
	Himantandraceae	3	Australia and New Guinea
	Oceanopapaveraceae	1	New Caledonia
	Stackhousiaceae	25	Australia, New Zealand, New Guinea, Philippines, Palau and Yap
	Strasburgeriaceae	1	New Caledonia
	Xanthorrhoeaceae	12	Australia and New Caledonia

Anomalous families

There remain about ten families which do not easily fit into the foregoing classification (though most of them are fairly clearly related to groups therein mentioned) and which are therefore best treated separately here. In the main they are families which, less than world-wide, cannot be described satisfactorily as either tropical or temperate.

The Moringaceae, Pedaliaceae and Salvadoraceae belong to the tropics of the Old World but are mainly in arid countries and their distributions are therefore more or less continuous through Arabia and north-west India.

The Dipsacaceae and Tamaricaeae are found widely in Eurasia including India, and are also well distributed in Africa.

The family Hydrophyllaceae is, like the nearly-related Polemoniaceae, essentially North American, but it includes one small genus (*Hydrolea*) which has species in all three sectors of the tropics. Balsaminaceae are in some ways an interesting contrast to Hydrophyllaceae in that they are essentially plants of the Asiatic and African tropics, but there are a few species which are widely distributed through the northern temperate regions.

As is shown by their maps in Vester (568) the distributions of Myricaceae and Buxaceae are, in differing respects, particularly anomalous, and inevitably raise a doubt as to whether these families as thus comprehended are really complete natural groups.

Southern families

Any general survey of the distribution of the families of Angiosperms such as has just been made leads directly to one of the most fascinating, and at the same time fundamental, problems of plant geography, the question of whether there is or is not recognisable a "southern" flora peculiar in origin to those parts of the world below the equator, and more particularly below the Tropic of Capricorn, and, if there is, what portions of the Angiosperms may be considered to belong to it. It is plain enough and will become even plainer as we go on, that a great many taxonomic units are to-day largely or entirely confined to this part of the world, but there are many others that are found in both extra-tropical zones, and others still which have, in addition, occurrences, usually at high elevations, within the tropics, so that it is certainly not possible to regard the northern and southern extra-tropical floras as two unrelated and isolated entities. There is in fact a continuity between them, and the problem, in its rather narrower expression, is to decide the relative significance of what at least appear to be two intermingled components.

It is well first of all to recall and to bear in mind one or two points of history. Because of the peculiar distribution of land and sea the land area of the northern flora is enormously greater than that of the southern (see Appendix A). Not only so but because of climatic conditions virtually nothing is known of the history of what, in the present connection, is likely to be the crucial part of the south, namely, Antarctica. The North has therefore at the outset an inherent predominance in many respects and this has been intensified by the fact that while this flora has been familiar to man for thousands of years and has been the subject of his interest ever since he became lettered, the southern flora has for the most part been known for less than 200 years. Added to this is the circumstance that the movement of almost all man-made influences has been predominantly in the one direction from north to south.

There is consequently an inherent tendency to assume that botanically, as well as in so many other ways, the south has been stocked from the north rather than the reverse, but this view has also in the past received a good deal of scientific support. Interest in the origin and migrations of floras quickened greatly after the coming of the Darwinian theory of evolution in the middle of last century and most of the great protagonists of that time had their views upon these questions (570), or at least realised how difficult they were. Hooker, who was one of the first to study the flora of the antipodes, was greatly impressed by the reappearance almost everywhere from Europe to Tasmania of genera, and sometimes even of species, belonging to the Scandinavian floras, as if, as he put it, there was a "continuous current of vegetation . . . along . . . the whole extent of that arc of the terrestrial sphere which presents the greatest continuity of land" (271), and from this there sprang the conception of the aggressiveness of the Scandinavian flora, an idea which, buttressed by such other observations as the extreme speed and ease of spread of many weed species emanating from the north, for long sustained belief in the overwhelming preponderance of north to south migrations. Even as recently as 1910 Thiselton-Dyer (551) expressed the opinion that the great floristic richness of certain parts of the south, such as South Africa, was due to the fact that they were *culs-de-sac* in which successive waves of migration from the north had piled up.

Gradually however this point of view underwent modification and it is interesting to note some of the stages by which this came about. Comparatively early the attribution of various northern Angiosperm fossils to typically southern families and genera came to balance the identification of southern fossils with northern plants, and although the value of these determinations is highly problematical (see Chapter 14) they served to adjust the focus a little. Much later came the change of ideas resulting from a better knowledge of both the past and present geology of many parts of the world and particularly from the doubts which began to be expressed concerning current beliefs regarding the permanence of continents and oceans, doubts culminating in the various theories now associated with continental drift, a conception which peculiarly involves the history of the southern land masses. In later years, too, the floras of the southern hemisphere and their resemblances and relationships to those of the north have been studied again and in greater detail by many botanists, especially by Skottsberg, whose many writings on this subject (see bibliography) have done much to put it on a sounder basis, and who has, in particular, given a vivid impression of the successive floras which in the course of geological time have occupied Antarctica (497, 508). A useful survey of these and various related publications has also been given, with special reference to the crucial problem of bipolar plant distribution (see later), by Du Rietz (147). At the same time belief in the supposed greater migratory powers of the northern flora has been modified by such studies as those of Allan on the introduced plants of New Zealand (7, 8, 9), in which he shows that the predominance of alien species is, for reasons more fully set out later (see Chapter 18), largely illusory and that they seldom make headway against native plants in their natural habitats. An interesting account of this particular change of outlook since Hooker's day has recently been given by Wright Smith (607).

These are some of the reasons why ideas as to the part which may been have played by the southern flora in the general development of the distribution of the Flowering Plants have so much changed in recent years. To-day opinions quite the reverse of those earlier held are not uncommon, as may be exemplified by reference to two of them. Croizat, in a discussion of the genera *Trochodendron* and *Tetracentron* (116), reaches the conclusion that not only certain families (he mentioned Cornaceae and Saxifragaceae especially), but most Angiosperm families, are united phylogenetically more closely with the southern hemisphere than they are to "holarctica." Camp, in a long survey of some of the more striking examples of distribution (78), goes even further and subscribes to the view that a study of distribution patterns in relation to phylogeny points to a southern origin of the Angiosperms as a whole. Gordon (225) has also made useful comments on this and its related problems.

Whether or not one can, in face of so many facts concerning the tropical floras of the world, agree with some of the more extreme of these views, it is clear that the phytogeographical facts which may bear on this question of the southern floras and their history call for careful scrutiny here, and this can best be done by a further survey of the families from this particular aspect.

For this purpose southern families may be defined as those in which a considerable majority of the species are found below the equator and to some extent at least below the Tropic of Capricorn. In theory greatest species concentration and greatest superficial extent need not occur in the same hemisphere, that is to say a group may have most of its species on one side of the equator and most of its range on the other, but for simplicity these may, if any of them exist, be ignored here.

On this definition about 75 families may be described as "Southern," and the easiest way to deal with them is to eliminate group by group from the discussion, especially since it will be found that interest mainly centres round a residue of a few, fairly large, families.

To begin with there are eight endemic families partly or entirely in temperate South America (see above); eleven in southern Africa (including Melianthaceae, Oliniaceae and Selaginaceae); six in the Madagascar region; eleven in Australia; three in New Caledonia, and one in Fiji. To these may be added five rather more widely endemic in Australasia, and three (Casuarinaceae, Philydraceae and Stackhousiaceae) which range from Australia or New Zealand northward across the equator. These in all account for over one-third of all the endemic families noted on pages 63–66 above.

Then there are eight families discontinuously distributed between South America and Asia/Australia, five of them quite small and three considerably larger, namely Epacridaceae, Goodeniaceae (ignoring the two pan-tropical shore species) and Stylidiaceae. These last three show a feature which is strikingly noticeable in many of the southern families, a considerable though absolutely minor extension northward across the equator into Malaysia and even into continental south-east Asia (see figs. 3, 15).

Three families, Flagellariaceae, Pandanaceae and Pittosporaceae, range widely over the warmer latitudes of the Old World. The family Flagellariaceae is too small to have much numerical preponderance anywhere; the Pandanaceae are more evenly and widely spaced, but have most of their species in the south, including a notable number in the Madagascar region and comparatively few in Africa; the Pittosporaceae have a most remarkable distribution shown in fig. 42, including a strong representation in Hawaii, and are predominantly Australasian.

Next are four families each of which, though totally widespread, has an enormous southern species concentration, either, as in the cases of Aizoaceae, Geraniaceae and Thymelaeaceae, in South Africa, or, in the Oxalidaceae, in both South America and South Africa. In view of what was said earlier about the Ericaceae it is perhaps fair to mention the Ericoideae here, as if they were a distinct family, for its South African concentration is very striking and it contrasts with the foregoing because of its comparatively restricted range north of the equator.

Two series of families remain. The larger consists of eleven which are chiefly notable because they are found in all three main sectors of the extra-tropical south without having any very wide range above the equator, and in this sense they may be regarded perhaps as the most characteristic of all southern families. Four of them, Cunoniaceae, Proteaceae, Restionaceae, and the considerably smaller

Philesiaceae, are illustrated here by maps and scarcely need further comment than perhaps to call attention again to their extensions north towards or into Asia. Closely related to these are four families in which the southern predominance is, however, somewhat masked by their more considerable expression within the tropics. They are the Escalloniaceae, which in the New World extend to Central America; the Monimiaceae, which are also strongly represented in the New World; the Elaeocarpaceae, which have many points of particular interest including their occurrence in the Madagascar region but not in Africa, and the Dilleniaceae which are widely distributed in the tropics, though least be it noted in Africa, and which are definitely southern by virtue of the great genus *Hibbertia* (see fig. 24) which has no counterpart north of the equator. Finally there are the two smaller families Haemodoraceae and Hypoxidaceae, together with the Zygophyllaceae, a family characteristic of arid countries, in total very widespread, but with a majority of species in the south, especially in South Africa and Australia.

Seven families forming the second series remain to be mentioned. The Haloragaceae, Juncaginaceae and Droseraceae (see fig. 16) are very widespread but all three have the great bulk of their species south of the tropics and are indeed most characteristic of Australia. Also widely distributed but with a much more restricted range in the north temperate are the much larger families Rutaceae and Araliaceae. The limits of the former are not too well-defined but it is clear that the great bulk of the species of the genera usually assigned to it are southern and the family is particularly conspicuous in the floras of South Africa and Australia. It may be that a future re-estimation of the family will make it even more obviously southern than it is now by the removal from it of some of the northern genera. The Araliaceae is a well-defined family but its genera are much confused, and this is unfortunate because the reputed distributions of many of them are of exceptional interest. As a whole the family has a notable Australasian preponderance and is particularly significant in New Caledonia and the Pacific Islands.

It may cause surprise that the Palmae should be claimed as a southern family but there are cogent reasons for doing so. True, the overall distribution of the family is fairly symmetrically pan-tropical and there is no really outstanding concentration of species in the south, but it shows (see pp. 72–74) several points in common with many of the foregoing families. The family is less well-developed in Africa than in America and Asia; but it is notably rich in the Madagascar region; it is strongly associated with New Caledonia and some of the neighbouring parts of Australasia; and certain constituent parts of the family, and particularly the Areceae, are much more strongly represented south of the equator than north of it, and there is no corresponding group in the north.

Lastly there is the largest of all the families to be mentioned here, the Myrtaceae, which though pan-tropical and even with some extra-tropical northern representatives is in total overwhelmingly southern. In one half of the family, the Leptospermeae, one of the two constituent groups is exclusively Australian, and the other, which includes the great genus *Eucalyptus*, very largely so. In the other half are various instances of relationship between South America and Australasia. There is notable paucity in Africa and also, in this case, in the Madagascar region.

Space will not permit us to pursue this very interesting subject of the southern flora here, though one or two other families, e.g. Portulacaceae, Strelitziaceae and Lobeliaceae, might have been mentioned, but enough has been said to show how considerable a factual basis it has, a basis that the progress of phylogenetic taxonomy is likely to widen. It must be remembered also that only whole families have been alluded to and there are many individual genera, as for instance *Acacia* and several of those familiar in the north temperate zone, whose details suggest that the families to which they belong or at least parts of them, may also have had a southern origin. There is still too much to be learnt about the course of botanical events south of the tropics to justify any dogmatic statement but we can at least be reasonably sure that the southern flora, that is to say the flora now characteristic of the southern temperate regions, is not the derivative of the north that it was long believed to be.

Details of some Particular Families

The total range of a family is simply the sum of the ranges of its constituent genera and species, and except in very small families reveals little about the relative and proportionate distribution of these minor units, which is actually often the most noteworthy feature in their distribution as a whole. Moreover, this varies greatly, with the result that families whose total ranges are very similar are often very distinct in terms of the distribution of their genera. Indeed, it would be quite possible to arrange all the families actually on this basis, but this would occupy too much space here. As a substitute, the remainder of this chapter is devoted to a review of four particular families and one comparable lesser group which, taken together, illustrate most of the salient features that a classification of this kind would show. These are the Primulaceae, Palmae, Proteaceae, Lobeliaceae and the Bambuseae.

The Primulaceae

The Primulaceae may be described as an outstanding example of a family made up of a few, and comparatively widely different, genera which vary considerably in distributional extent. Its total range is practically world-wide, but most of the genera are much more restricted. The classification used here is that of Pax (156), with the figures brought reasonably up to date.

There are 17 genera, namely, *Primula, Androsace, Soldanella, Pomatosace, Bryocarpum, Dodecatheon, Cyclamen, Lysimachia, Trientalis, Asterolinon, Pelletiera, Glaux, Anagallis, Centunculus, Samolus, Hottonia* and *Coris*. Most of them are temperate genera and generally familiar, so that a glance at the list shows how varied an assortment of types may go to make up a family which is nevertheless a well-defined natural group.

The world-wide distribution of the family is due chiefly to the exceptionally wide areas of *Anagallis* and *Samolus*. *Anagallis* especially is a genus of disturbed ground and much of its range may be adventive, but *Samolus* appears to be truly and naturally almost cosmopolitan.

Primula is by far the largest genus, with several hundreds of species. Geographically it is both discontinuous and locally centred. It ranges throughout the northern temperate regions with some extension into the tropics and has also one species at least in temperate South America, but the vast majority of its forms are confined to the great Sino-Himalayan mountain region. This latter region has been carefully explored only in recent years, and the discovery and frequently the subsequent introduction into European gardens of many new *Primula* species has been a marked feature in the horticultural history of this century. The genus *Androsace*, though smaller than *Primula*, rather closely resembles it, but is confined to the northern temperate zone.

Lysimachia is also a large genus and is found in almost all the temperate and subtropical parts of the world, as well as on some tropical mountains.

The remaining genera are all small in species number and also in range, and fall into several well-marked groups each of special interest. *Hottonia*, with 2 spp., is found in eastern North America and in Europe, and *Dodecatheon*, with about 15, occurs in North America and eastern Asia. *Bryocarpum* and *Pomatosace* are monotypic (of one species only) endemic genera of the Sino-Himalayan mountains. *Cyclamen*, 12 spp.; *Asterolinon*, 2 spp.; *Coris*, 2 spp.; and *Soldanella*, 7 spp., are all found only in Europe or the Mediterranean region, the last named being one of the few genera endemic to the European Alps. *Glaux*, 1 sp.; *Centunculus*, 3 spp.; and *Trientalis*, 2 spp., are fairly widespread in the northern temperate zone. Finally, *Pelletiera*, 2 spp., is found only in temperate South America; and *Samolus*, 12 spp., though almost cosmopolitan, has species in both north and south temperate zones.

The family thus illustrates the following points. It consists of comparatively few but markedly distinct genera. The genera vary in size from monotypes to one with hundreds of species. There is discontinuity both within the northern temperate zone and between the north and south temperate regions. It is in total world-wide but only by the exceptional ranges of one or two forms. Endemism is fairly well marked, and one genus, *Primula*, is an outstanding example of a group with the bulk of its species massed in one part of the world. The family is very predominantly temperate in character.

The Palmae

(Plate 25)

The family Palmae, containing that remarkable and almost unique group of plants known as the palms, differs from the Primulaceae in almost every way. It is a large group both in genera (about 250) and species (about 2,000) but it is at the same time a very natural one with a most distinctive appearance. Its geographical range also is distinct (fig. 13), being rigidly limited by climatic conditions and almost entirely within the tropics. Indeed the Palmae are one of the most exclusively

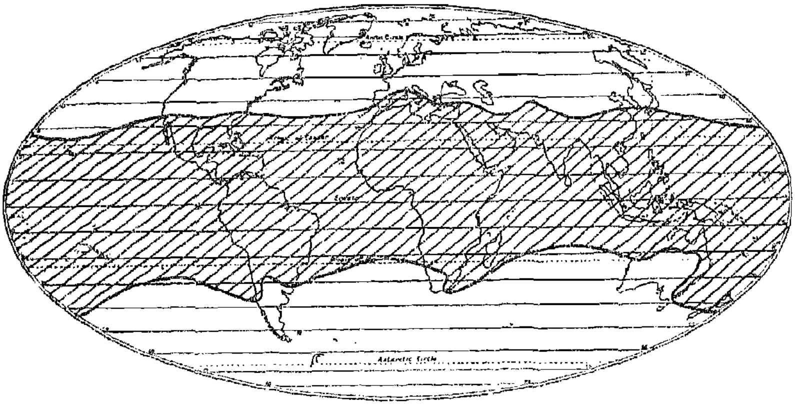

FIG. 13.—Map showing (shaded) the general latitudinal distribution of the family Palmae.

tropical of all the larger families. Such climatic limitation is never absolute in a family of any size, and to this the Palmae are no exception, having a slight representation in several subtropical and even warm temperate regions, but this only emphasises the tropical character of the family as a whole.

Within the tropics the distribution of the palms is almost ubiquitous, though they are said to be absent from a few small areas such as the Galapagos Islands, but by the nature of the case it is divisible into three parts. Rather more than one third of the genera are confined to the New World; a rather larger proportion to Asia, Australia and the Pacific Islands; while only about one-seventh are restricted to Africa and the Madagascar region. Fewer than half a dozen genera range over more than one of these areas and none is found in all three. *Phoenix*, *Borassus* and *Calamus* are found in both African and Asiatic sectors. *Raphia* is in both American and African sectors, and *Elaeis* was formerly credited with the same distribution, but the American plants have now been made the genus *Corozo*. Apart from these the most widely spread genera are some half dozen which range from south-east Asia to Australia or Polynesia.

The genera vary greatly in size. The largest is *Calamus* with some 250 species; *Bactris*, *Daemonorops*, *Geonoma* and *Pinanga* have about 100 each; while *Chamaedorea* and *Licuala* are not much smaller. On the other hand about 75 genera are monotypic, and more than 50 others are generally reckoned to have fewer than 5 species each.

The absence of wide genera has already been remarked, but in addition to this the number of genera with narrow ranges, namely endemics, is very large. Using the term endemic in quite a conservative sense, over 100 merit it, and these are well scattered, few warm regions being without them. They are least plentiful perhaps in Malaysia, though there are some 30 confined to this great region as a whole, and most abundant and conspicuous in certain small insular areas. Thus in the Seychelles and Mauritius all the genera are endemic, and in New Caledonia 12 out of 15 genera are endemic. In Madagascar 13 out of 18 are found nowhere else, and among other regions Central America, the West Indies, New Guinea and, especially, the Pacific Islands are notable for endemic genera.

Species endemism is even more marked and it has been calculated that no less than 95 per cent. of all species in the family are so narrowly distributed. Not only this, but in nearly 150 genera there are none but endemic species. In Hawaii, Madagascar and the Mascarenes, and New Caledonia all the native species are endemic, while even in such continental regions as Central America, South America and tropical Africa the percentage is over 90. Similarly in New Guinea and the Pacific Islands; but in other parts of Malaysia the proportion of endemic species (as also of endemic genera) is lower than almost anywhere else, as, for instance, 50 per cent. in Java and 38 per cent. in Sumatra.

Even more noteworthy is the relationship between endemism and geographical isolation in the form of insularity, which is seen in both genera and species. Nearly 40 genera are restricted to what may reasonably be called small islands. There are, for instance, 12 endemic genera (with about 25 species) in New Caledonia and 9 among the smaller islands associated with Madagascar, including 6 on the Seychelles alone. There are also about 6 on various small islands of the Pacific as well as three on the tiny Lord Howe Island near Australia, one on Cocos Island (America) and one on Juan Fernandez.

This marked restriction of many palms to small islands is still better seen in the species, as the following table shows.

Species of Palms on Small Islands

Hawaiian Islands *c.* 30, with very segregated distributions (506)	
Bismarck Archipelago	12
Mauritius	11
Fiji	9
Solomons	8
Seychelles	7
Trinidad	7

4 species each on Martinique, Samoa, the Carolines, Lord Howe I., the Comoros, and St. Marie de Madagascar.

3 species each on the Andamans, the Nicobars, Aru, Ternate.

2 species each on Guadeloupe, Ceram, Nossi Bé, Tobago, Palau and St. Vincent.

Among the islands from which single endemic species have been recorded are: St. Thomas, Barbados, the Isle of Pines, Mergui, Bird Island, Bermuda, Fernando Po, Corisco, Key, Bougainville, Billiton, Christmas, Grenada, Croker Island, Batjan, Norfolk, St. Kitts, the Kermadecs, and one or two single islands of the Tuamotus.

To summarise, the Palmae are a very natural group of considerable geological age, with a very isolated systematic position—features once vividly described by Hooker, in a letter to Darwin (294) in the words "a very ancient group and much dislocated, structurally and geographically." The genera vary greatly in size, but an unusually large number of them are very small. The family is rigidly limited geographically to the warmest parts of the world's surface except for one or two quite minor extensions. No single species or even genus covers anything approaching the whole range of the family and widespread genera and species are very few. Such as there are show discontinuity over two of the three major land divisions of the tropics. Endemism in both genera and species is exceptionally high and is accompanied by an almost unique degree of geographical isolation, a number of species being confined to islands so small as to be difficult to find even in the largest atlases, a state of affairs all the more remarkable because the fruits of only a very few species of palms are known to be capable of drifting unharmed in sea water.

The Proteaceae

(Plates 12, 17, fig. 14)

This family is best known for the relationship it shows between southern Africa and Australia, but undue emphasis on this point has tended to obscure the main geographical feature of the group, namely, that it is one of the best examples of a large southern family well represented in all the continents below the equator.

As will be seen from the map (fig. 15) there are three extensions northwards from the main areas of distribution, one in each continent. That in America is largely due to the genus *Roupala* which is well represented in Brazil and other parts of the neighbouring tropics, and in this continent the southern species are comparatively few. These show, however, a strong relation with Australia, *Lomatia* (fig. 35), *Oreocallis* and *Orites* being discontinuous between the two continents.

The northern extension is least in Africa and is due entirely to the tropical distribution of members of characteristically South African genera such as *Leucospermum* and *Protea*, which ranges as far north as Abyssinia. There is a monotypic genus in Madagascar.

As in the New World the tropical extension of the family in Asia is due to one large genus, *Helicia*, which covers the whole of the monsoon region proper to the Bismarck Archipelago, and which even has a single species in Japan. In the eastern Old World, however, the more equatorial species are in a great minority owing to the strong development of the family in Australia and New Caledonia. There are a couple of species in New Zealand, and one in Fiji.

The relatively enormous massing of the species of the family in South Africa and in Australia, which is so frequently cited, may be gauged by the statement that about two-thirds of the species are Australian and about one-quarter South African, so that only one-twelfth is left in the whole of the rest of the family area.

The family is divided into two subfamilies, the Persoonioideae and the Grevilleoideae, and the relative distribution of these can be best visualised by saying that the former has no American representatives and that the latter has no African representatives. It will be seen from this that the former is the characteristic group of South Africa, and the latter of Australia. The segregation between the two is, however, not complete, because no fewer than 14 genera of the Persoonioideae are found in Australasia, sometimes in considerable numbers of species.

The family as a whole therefore exhibits (apart from almost indisputable evidence of a southern origin) major discontinuity between Africa and Australia; extension north across the equator in all continents; massing of species in Africa, Australia and New Caledonia; minor discontinuity between Australia and New Caledonia and between Australia and New Zealand; well-marked systematic segregation between America and Africa and less marked segregation between Africa and Australia.

The Lobeliaceae

The Lobeliaceae illustrate many points of interest of a rather different kind. In total the family has a very wide range throughout the tropics, and over much of the warm temperate and even temperate parts of the world, but in the latter is represented by comparatively few small herbaceous forms. The main feature of the family is the occurrence in many isolated regions of endemic genera or species with peculiar growth forms, many of which may be described as giant herbs, though some of them are branched shrubs or even small trees.

Lobelia, for instance, which is the central and largest and widest genus of the family, while consisting mostly of herbaceous forms, contains several groups of very distinctive-looking plants. Best known of these, perhaps, are the remarkable columnar giant species which are so conspicuous a feature of the vegetation of the high mountains of tropical Africa (Plate 13), but similar plants are found also in parts of Asia and elsewhere (499). There is also a peculiar shrubby species on St. Helena. In Central and South America, too, there are groups of tall herbs and shrubs.

Very closely allied to the small herbaceous Lobelias are a series of genera chiefly in the southern temperate regions and often showing very remarkable distributions. These, however, are almost certainly artificial groups derived from *Lobelia* and may be polyphyletic, so that the geographical facts associated with them must be regarded with caution. They include, however, one monotypic endemic genus, *Brighamia*, in Hawaii.

In the tropical parts of America there are two large genera, *Centropogon* and *Siphocampylus*, consisting of branched shrubby forms, some of which have a climbing habit.

Finally, there are six very remarkable genera of trees, or more commonly shrubs, of various habit with a very noteworthy distribution. Four of them,

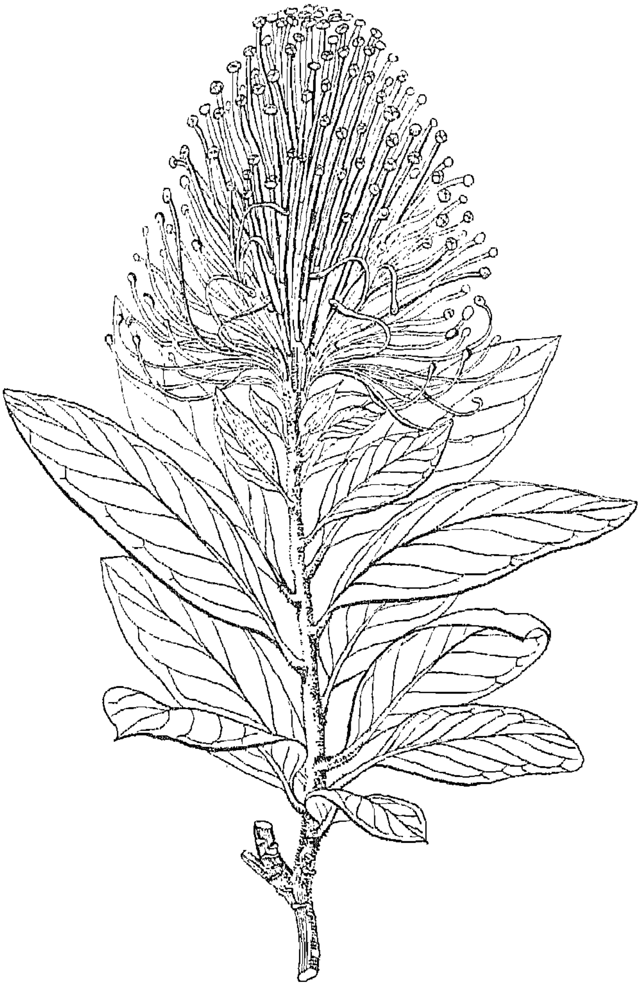

Fig. 14.—*Oreocallis* (*Embothrium*) *grandiflora*, a typical member of the Proteaceae, about half natural size, after Baillon.

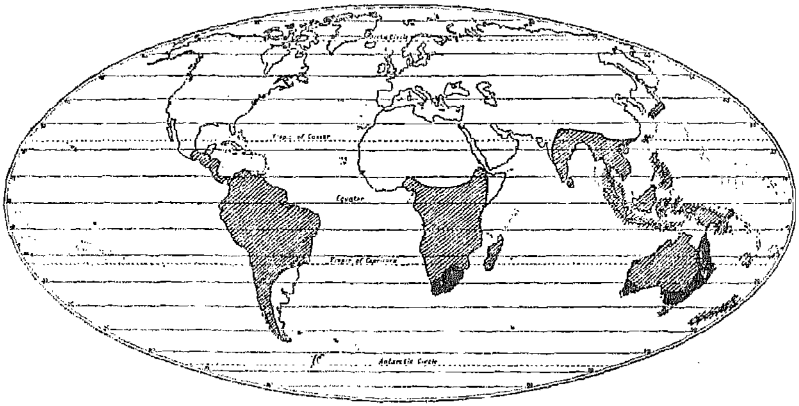

Fig. 15.—Showing the distribution of the family Proteaceae. The solid black areas are those of greatest species concentration.

Clermontia, *Rollandia*, *Delissea* and *Cyanea*, are absolutely confined to the Hawaiian Islands, where they are a conspicuous feature of the flora of the mountains and where also they exhibit extreme specific segregation among the different islands. There are also endemic Lobelias in Hawaii, and altogether, according to one estimate (521), there are in the archipelago no fewer than 150 endemic Lobeliaceae including varieties. The other two genera, *Apetahia* and *Sclerotheca*, both very small, are similar in growth form and endemic to the Society Islands. These peculiar Pacific genera have excited much interest, and their theoretical significance has been discussed at length by Guppy (241) and others.

To summarise, the Lobeliaceae show markedly the production of widespread generalised herbaceous forms and extreme endemism associated with marked peculiarity of growth form.

The Bambuseae

Finally, although it is not formally recognised above as a separate family, this very well-marked section of the Gramineae, comprising its woody members the bamboos, has a very interesting geography particularly illustrative of certain features not uncommonly seen in the distribution of families and referred to elsewhere in these chapters.

The bamboos consist of upwards of 50 genera and of about 500 species, and are found in general throughout the warmer parts of the world, though their northern and southern limits are very uneven longitudinally. In the northern hemisphere they reach as far as 45° in Asia (the Kuriles), and 40° in eastern North America, but there are no native species in Europe, south-west Asia or in North Africa, their extreme in this sector being about 18° in the Sudan, south of the Sahara (compare various families above). In the southern hemisphere they reach about 43° in Chile; they are in all parts of southern Africa; but in Australia they extend no further than about 18° in Queensland.

Unless the somewhat doubtful American species are correctly associated with the Asiatic species of *Bambusa*, only the more or less pan-tropical genus *Arundinaria* is found in both Old and New Worlds. *Oxytenanthera* occurs in Africa and Asia; *Schizostachyum* in Madagascar, Asia and some of the Pacific Islands including Hawaii; and *Cephalostachyum* and *Ochlandra* are both in Madagascar and Asia. No other genus occurs in more than one sector of the tropics and some are quite narrowly distributed.

It has been calculated that 90 per cent. or more of the 500 or so species are either Asiatic or American, the former being much more numerous than the latter. The representation of the bamboos in tropical Africa is remarkably small and one of their most striking features, consisting of only about 6 genera and 14 species, which is much less even than that of Madagascar, where there are 9 genera and perhaps 30 species. There are 3 species (of *Arundinaria* and *Bambusa*) in the northern part of Australia. As for the Pacific, the genus *Greslania* is endemic to New Caledonia; there are believed to be bamboos in the Solomon Islands; and *Schizostachyum glaucifolium* occurs in Hawaii, Fiji, Samoa, and possibly on other islands too.

CHAPTER 5

THE DISTRIBUTION OF GENERA—I

WHEN classification was discussed in an earlier chapter, it was pointed out that, from a geographical point of view at any rate, the genus is the most important and illuminating of all categories. The species is, generally speaking, too small a unit to be of much use in the consideration of world-wide problems, and it is moreover an ultimate category not amenable to further statistical analysis. It is encumbered, too, by the confusion arising from the divergence of opinion as to its value. The family, on the other hand, is more often than not too large a category for convenient handling and the total number of families is small. It is, certainly, like the genus composed of constituent units (the genera) and can be analysed in various ways, but the relationship between genera is not even theoretically constant.

The genus, on the contrary, tends to possess the advantages of both the family and the species without their disadvantages. Genera are mostly of convenient size, both taxonomically and geographically, and are made up of constituent parts, the species, which, at least in theory, all possess the same value. Moreover, the conception underlying the genus is very definitely monophyletic, that is to say, the genus more than any other category is presumed to consist of forms closely related not only by structure but also by descent from a common ancestor.

For these reasons genera need special attention, and the next three chapters, which describe their distribution, are to be regarded as among the most important in this book.

Number and Size of Genera

Taxonomically the size of a genus is reckoned by the number of species it contains, and genera vary enormously in this respect. A great many are monotypic, that is to say consist of only one species: at the other extreme are several genera containing upwards of or more than 1,000 species. It is obviously difficult to give definite figures because of the differences of opinion which often exist as to what does or does not constitute a species, just as it is often difficult to say how many genera there are in a given family. There are striking examples of both these points. The most recent revision of the family Cruciferae (160) puts the number of genera at over 300, but these are in general so closely similar to one another that the suggestion has even been made that they really constitute only one enormous genus. Again, *Mesembryanthemum* used to be treated as a single genus with some hundreds of species, but it is now (160) generally split up into many genera, most of which are very small. It is important to bear these difficulties in mind because of the constant quotation of figures in this and succeeding chapters. Such quotations are in the opinion of the writer quite essential in order to give some measure of reality and precision to what would otherwise be merely generalised statements, but all such figures are open to some degree of criticism. It must be remembered, therefore, when reading them, that they cannot claim to be definitive or absolute and are of value only in so far as they afford a useful means of comparison between genera. They can but represent one opinion on what may be, and often are, controversial questions. The figures actually used are taken not only from the writer's own compilations, but from various other sources, prominent among them being Lemée's dictionary (339) which is the most up-to-date source of its kind, and the works mentioned at the end of the Preface to the first edition.

Estimates of the total number of genera of Flowering Plants known to-day are generally in the neighbourhood of 12,500, giving an average content of about 18 species each.

According to Lemée fourteen genera have more than one thousand large species each, these being led by *Astragalus*, with some 1,800, and *Senecio* with 1,500. Then come *Eugenia*, *Piper* and *Ficus* with between 1,250 and 1,500 each; followed by *Bulbophyllum*, *Carex*, *Dendrobium*, *Epidendrum*, *Eupatorium*, *Euphorbia*, *Psychotria*, *Rhododendron* and *Solanum*. The estimated numbers appear in some cases to be on the conservative side, for *Senecio, Carex* and *Euphorbia*, for instance, have often been credited with many more and the same is doubtless true of others. The reference to large species is necessary because there are certain genera, notably *Salix, Hieracium, Rubus* and *Crataegus,* which are extremely polymorphic and have been divided into huge numbers of closely similar forms. If these are regarded as normal species then the genera containing them are certainly among the largest but they are more reasonably treated as micro-species, and it is relevant to point out that at least certain of these genera depart from the normal in some aspects of their reproduction, so that there may be a real reason for the usual practice of regarding them as special cases.

For the rest there are genera of almost every species number down to the extreme condition of monotypy. These last are particularly numerous, some compilations estimating them at one-third of all genera, while the number of ditypes (two species) is also high, perhaps, according to the same compilations, one-eighth of all genera, so that the two may account for half the total. With increase in species-content so there is decrease in numbers, as is shown by the following figures.

Quoting again the figures derived from Lemée there are some 470 genera in all with one hundred or more species each. Of these 270 have between one hundred and two hundred species each, among the more familiar being *Anemone*, *Asclepias*, *Asparagus*, *Buddleja*, *Coleus*, *Crinum*, *Eschscholzia*, *Linum*, *Lysimachia*, *Olearia*, *Phacelia*, *Restio*, *Rhus*, *Thunbergia* and *Verbena*. About 100 genera have between two hundred and three hundred species each, including *Aconitum*, *Calamus*, *Calceolaria*, *Clerodendrum*, *Cynanchum*, *Dianthus*, *Eriogonum*, *Gladiolus*, *Hoya*, *Jasminum*, *Pelargonium*, *Penstemon*, *Plectranthus*, *Strychnos* and *Tibouchina*. About 65 genera have between three hundred and five hundred species each, including *Allium*, *Campanula*, *Diospyros*, *Eucalyptus*, *Helichrysum*, *Hibiscus*, *Justicia*, *Lobelia*, *Mimosa*, *Passiflora*, *Pedicularis*, *Ranunculus*, *Smilax* and *Vaccinium*. Some 30 genera have between five hundred and one thousand species each, namely, in alphabetical order, *Acacia*, *Anthurium*, *Aster*, *Begonia*, *Cassia*, *Centaurea*, *Croton*, *Dioscorea*, *Erica*, *Gentiana*, *Habenaria*, *Impatiens*, *Indigofera*, *Ipomoea*, *Loranthus*, *Mesembryanthemum*, *Miconia*, *Myrcia*, *Oncidium*, *Oxalis*, *Panicum*, *Peperomia*, *Pleurothallis*, *Polygala*, *Primula*, *Quercus*, *Salvia*, *Sedum*, *Symplocos* and *Vernonia*.

The types of distribution exhibited by these largest of genera are extremely varied and many of them will be mentioned again in due course, but the following table, in which the numbers of genera are slightly rounded off, is a useful summary:

1. More or less cosmopolitan		50
2. Tropical		305
a. pan-tropical	135	
b. only in the Old World	85	
c. only in the New World	60	
d. America and *either* Asia or Africa	25	
3. Temperate		90
a. wide temperate	20	
b. north temperate	45	
c. only in the Old World	18	
d. only in the New World	7	
4. Southern		30
		475

Distribution of Genera

The same broad geographical classification which was used for families may be employed for genera, but the size and relative importance of the categories work out rather differently. This is owing, first, to the natural fact that the average range of genera is much smaller than that of families, and, second, to the arbitrary limitation to be attached to endemism. In the families, it will be remembered, endemism was measured in continental terms, but this is much too wide a conception for genera, and something smaller must be taken. Taking the general purpose of this book into consideration, we cannot do better than to interpret generic endemism broadly in terms of the thirty-seven regions which were outlined in the floristic classification in Chapter 2. Not only will this provide a suitable conception but it will also serve usefully to throw into relief many features in the floras of these regions. In this account of the distribution of genera then, endemic genera are those which are confined to one only of the floristic regions of the world as outlined in the scheme given there, or whose ranges are not much greater than the average size of the continental regions therein mentioned.

But with such a conception of endemism it is clear that there will inevitably be many genera which, though too widely distributed to be considered endemic, will nevertheless be far from completely spread through any one major climatic zone. It will be found, on this account, that a category which in the case of the families was almost negligible, namely the "medium wide" category, is in the genera of much greater size and importance, especially from many theoretical points of view. So much so indeed that it must receive very detailed treatment.

Genera may then, for our present purpose, be divided into the following categories:

Cosmopolitan and subcosmopolitan
Tropical
Temperate
Other wides
Discontinuous
Endemic

This arrangement is roughly one of diminishing areas, and it is therefore convenient to take the categories in the order given, as was done for the families. The

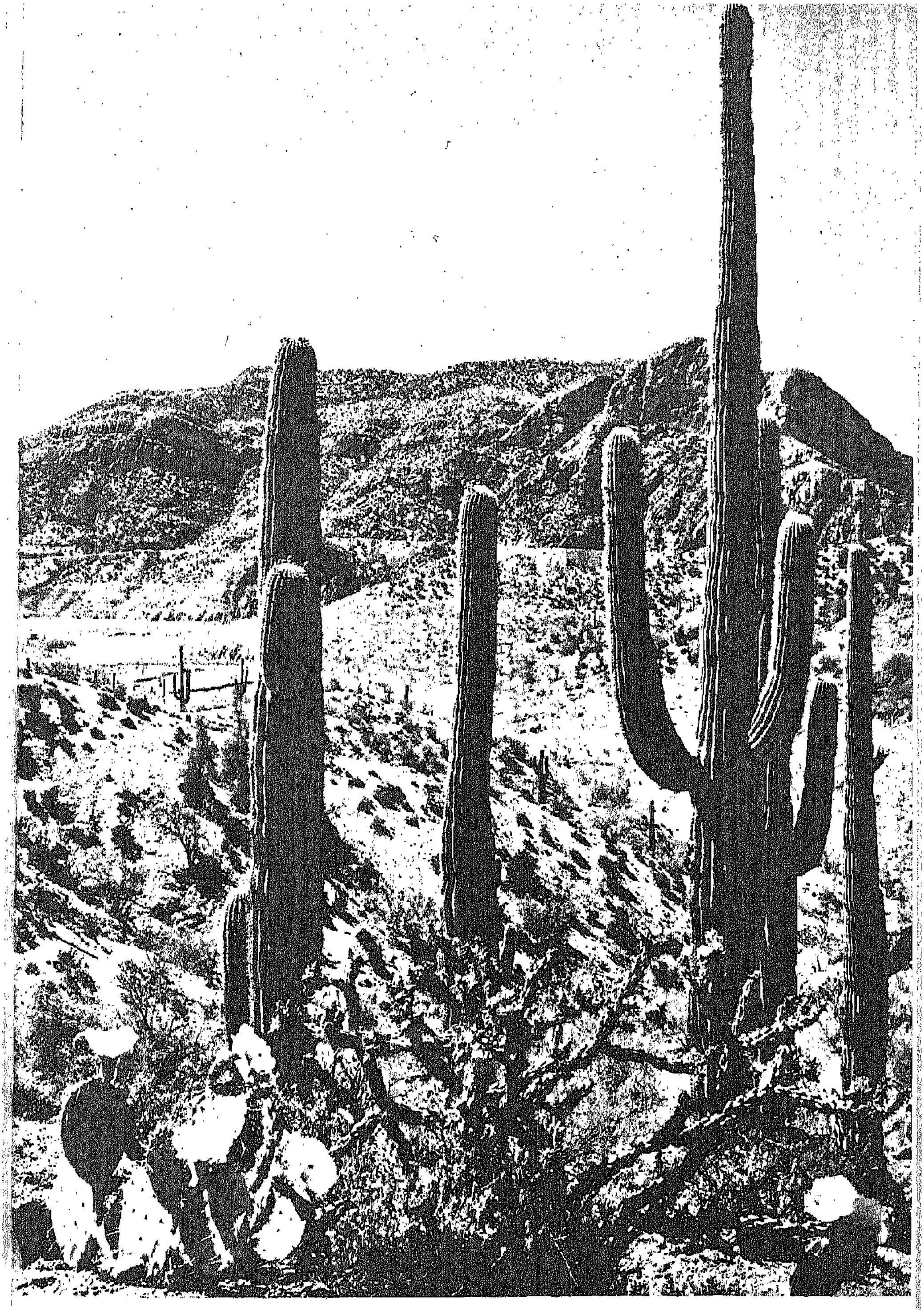

Plate 6. A cactus landscape in Arizona. The large columnar species is *Carnegiea gigantea*: in the foreground are two species of *Opuntia*

(*Photo: Josef Muench*)

number of families is such that it was possible to mention each one individually. This is manifestly impossible with the genera, and instead a rough estimate of the number of genera in each category is given together with examples from among the more familiar. In special cases all the genera are mentioned.

Cosmopolitan and Subcosmopolitan Genera

What was said, under the heading of families, about the use of the terms cosmopolitan and subcosmopolitan is even more to the point in respect of genera. Families, especially if they are large, may contain genera of widely different tolerances and may therefore be found in very diverse circumstances, but the species of genera usually follow a much closer pattern of environment and it is rare to find a genus equally well represented at sea level in all the various parts of both the tropical and temperate zones. Indeed, if we define a cosmopolitan genus in its strictest sense, as one which is found in both high and low latitudes and which has roughly equal numbers of localised species in all the major parts of the world, then perhaps there is only one, *Senecio*, to be mentioned, and it should not be forgotten that this belongs to a family in which generic distinctions are notoriously hard to draw. *Euphorbia* is in some ways a better example but here there is a distinct falling off and specialisation in the colder zones. There is a similar diminution in *Solanum*, which, in addition, is unbalanced by its preponderance in the New World. *Carex*, on the other hand, which in simple terms of extent is almost certainly the most widespread genus, is unbalanced because its low altitude tropical representatives are comparatively few. These four are, as might be expected, very large genera, but four others, notably smaller, namely *Polygala*, *Scirpus*, *Drosera* and *Utricularia*, are also exceptionally well distributed in a native state. In fact, the last two are, in view of their peculiar specialisations, the most noteworthy of the eight.

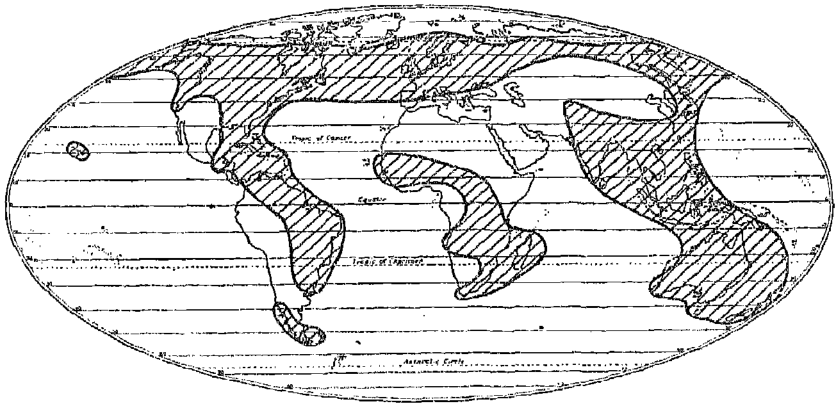

FIG. 16.—Map showing (shaded) the distribution of the genus *Drosera*, after Diels and Irmscher.

Going now to the opposite extreme, and considering as at least subcosmopolitan all the genera which are considerably more than purely tropical or purely temperate in distribution, a number of different types can be recognised.

Nearest to the above, at least in mere extent, are those large genera, which although essentially temperate in character, have nevertheless a notable distribution through the more elevated parts of the tropics, namely *Anemone, Bromus, Cardamine, Clematis, Convolvulus, Cuscuta, Cynoglossum, Deschampsia, Eleocharis, Galium, Geranium, Hierochloe, Hypericum, Juncus, Luzula, Plantago, Poa, Polygonum, Ranunculus, Rhamnus, Rubus* and *Teucrium*. It is particularly difficult to draw any hard line between these and the first group of temperate genera on p. 86 below, with which the link is almost unbroken. The converse of these is seen in a smaller group of large genera, which, essentially tropical, have also a considerable extension into higher latitudes, namely *Andropogon, Aristida, Aristolochia, Cynanchum, Cyperus, Eragrostis, Eupatorium, Heliotropium, Panicum, Smilax, Sporobolus* and *Stipa*. This again is a difficult group to define because there are tropical genera with almost every kind of extension north and south, and the distinction here can be little more than arbitrary, a point which should be recalled when tropical genera are under discussion.

Another conspicuous group consists of very widespread, but in species numbers often very small, genera, which are either completely aquatic or are at least characteristic of subaquatic habitats. These are *Apium, Callitriche, Ceratophyllum, Cladium, Elatine, Hydrocotyle, Leersia, Lemna, Limnanthemum, Limosella, Ludwigia, Montia, Myriophyllum, Najas, Nasturtium, Nymphaea, Phragmites, Potamogeton, Rhynchospora, Ruppia, Samolus, Tillaea, Vallisneria, Wolffia* and *Zannichellia*.

It would seem that the only other small genera which can claim to be of comparable distribution are *Anagallis, Calystegia, Cynodon* and *Prunella*, but these serve the useful purpose here of bridging the gap between the foregoing and another large group of very widespread genera, those which are found to-day practically all over the world but which owe a now indeterminable part of their ranges to introduction as weeds or crops or as more miscellaneous adventives. These amount to at least 30, are nearly all of medium size, rather by the nature of the case are chiefly typical of temperate climates, and include numerous grasses. They are *Agrostis, Agropyrum, Amaranthus, Anaphalis, Arenaria, Atriplex, Avena, Bidens, Centaurea, Cerastium, Chenopodium, Coronopus, Celosia, Datura, Erigeron, Erodium, Festuca, Gnaphalium, Glyceria, Lepidium, Lolium, Oxalis, Phleum, Polycarpon, Portulaca, Rumex, Sagina, Sonchus, Spergula, Stellaria* and *Taraxacum*.

All the foregoing may be described as cosmopolitan, and the term subcosmopolitan is best and most conveniently confined to those genera which are incomplete in their distribution in the sense that they are but poorly represented in, or even completely absent from, one major region or broad type of habitat. Such genera, which number about 24, fall into a number of smaller groups according to the details of their geographical deficiencies. *Brachypodium, Impatiens, Lysimachia, Mentha, Schoenus, Swertia* and *Typha* are notably deficient in warmer America; *Parietaria, Sambucus, Scutellaria* and *Vaccinium* are so in Africa; and *Linum, Salix, Sanicula, Satureja* and *Stachys* are the same in tropical Asia and/or Australasia. *Orobanche, Sagittaria* and *Verbena* are almost absent from the tropics of the Old World. *Eriocaulon* and *Lobelia* are an interesting pair in which the chief feature is absence from western Eurasia except for occurrences on the Atlantic margin. Finally there is an important minor group of halophytic and desert genera, *Frankenia, Limonium, Salicornia, Spergularia, Suaeda* and in less degree *Salsola*, which in superficial area are fairly world wide but which are restricted to certain kinds of soil condition only.

To summarise, the genera which are so widely distributed that they are notably more than either pan-tropical or wide temperate, and are therefore treated here as cosmopolitan or subcosmopolitan, number about 130. This is probably about 1 per cent. of all genera, a figure which demonstrates vividly how few genera have succeeded in spreading themselves with any degree of completeness over all the available land surfaces of the globe, or to put it another way, how few genera have exploited both tropical and temperate conditions. When the aquatic genera, which are rather a law unto themselves, special groups like the halophytes, and the numerous instances including weed species, are subtracted from the total, this circumstance becomes even more striking.

Pan-tropical Genera

Of genera which are found in all three sectors of the tropical zone (America: Africa—Madagascar: Asia—Australasia), and which may thus, in one sense at least, be considered as pan-tropical, there are many familiar examples, but to give anything in the nature of a complete account of this kind of distribution is difficult, partly because the published data, especially the less recent, are seldom detailed enough to reveal the actual extent of range in the countries concerned, and partly because the tropics have, like the temperate regions, weed species of their own, so that it is often impossible to know whether a genus is of natural occurrence or not. For these reasons emphasis here is laid on the various types of pan-tropical distribution and the quotation of examples of these is confined to genera in which the facts are generally held to be beyond dispute.

Nor is it easy to arrive at any very exact figure of the numbers of these genera, but it would seem that rather more than 250 are pan-tropical in the sense used above. Somewhat fewer than half of these have more than 100 species each; the rest are of all sizes, including even monotypes, such as *Gyrocarpus*. Some have probably little geographical significance. Uncertainties of classification make it impossible to say just how the leading families are represented in this total, but it is safe to say that the Leguminosae (comprising Mimosaceae, Caesalpiniaceae and Papilionaceae) and the Gramineae stand out conspicuously. A rough compilation shows, indeed, that about 40 genera of the former group are found throughout the tropics and that nearly three-quarters of these have at least one pan-tropical species each, while a recent revision of the subfamily Panicoideae of the Gramineae (160) shows that it, alone, contains some 24 pan-tropical genera. This exceptional position may, in the former, be due largely to the number of species which are tropical strand plants, and in both cases in some measure to human exploitation, but this is certainly not the whole explanation. It may be added that the Compositae and Orchidaceae, the only conspicuously larger comparable groups, contain very few pan-tropical genera, a distinction which may reflect major historical differences.

The pan-tropical genera as a whole can be classified in much the same way as were the cosmopolitan ones, into three main headings—those evenly distributed with much the same species numbers in all sectors; those in which the species numbers are either notably higher or notably lower in one or more sectors; and those which are associated with particular edaphic conditions.

The evenly spread genera are not unnaturally mostly large genera (more than 100 species), and are exemplified by *Bauhinia*, *Costus*, *Dalbergia*, *Dioscorea*, *Eugenia*, *Hibiscus*, *Justicia*, *Mimusops*, *Peperomia*, *Phyllanthus*, *Psychotria*, *Rhynchosia*, *Strychnos* and *Vitex*, but there are quite a number of smaller ones, including

Corchorus, *Erythrina*, *Fleurya*, *Geophila*, *Melothria*, *Ocimum*, *Ruellia*, *Tacca* and *Vanilla*.

The variations among the unevenly distributed genera are best set out in tabulated form as follows:

1. Genera with most of their species in the New World.
   e.g. the large genera *Cassia*, *Chrysophyllum*, *Cordia*, *Croton*, *Erythroxylum*, *Hyptis*, *Ipomoea*, *Mikania*, *Mimosa*, *Pavonia*, *Vernonia* and the smaller genera *Coldenia* (with only one species in the Old World), *Hybanthus*, *Sauvagesia* (pan-tropical by only one species) and *Tetracera*.
2. Genera with most of their species in the two sectors of the Old World.
   e.g. the large genera *Ampelocissus*, *Aneilema*, *Barleria*, *Bulbophyllum*, *Clerodendrum*, *Commelina*, *Crotalaria*, *Jasminum* (the one species in America is but doubtfully native), *Randia* and *Tephrosia*, and the smaller genera *Ehretia* and *Morinda*.
3. Genera with an outstanding proportion of species in Africa–Madagascar.
   e.g. the large genera *Combretum*, *Eulophia*, *Hermannia*, *Indigofera* and *Pavetta* and the smaller genera *Cassipourea*, *Hypoxis* and *Rinorea*.
4. Genera with an outstanding proportion of species in Asia–Australia.
   e.g. the large genera *Acacia*, *Diospyros*, *Ficus*, *Ixora* and *Sterculia*, and the smaller genera *Gnetum*, *Laportea*, *Uncaria* and *Ziziphus*.
5. Genera which are least strongly represented in Africa–Madagascar.
   e.g. the large genera *Begonia*, *Marsdenia*, *Piper* and *Pithecellobium* and the smaller genera *Caesalpinia*, *Cleidion* and *Crataeva*.
6. Genera which are least strongly represented in Asia–Australia.
   e.g. the large genera *Dorstenia* (one species only), *Eriosema* (one species only), *Hippocratea and Xyris*, and the smaller genera *Aeschynomene* and *Biophytum*.

No strict comparison of the relative importance of these various categories can satisfactorily be given because of the many different factors which would have to be taken into consideration, but the impression is that the first is the most considerable and that the last two are the smallest, and this seems to suggest that such real segregation as there may be is chiefly between the New World and the Old.

In the third class of pan-tropical genera the subdivisions parallel those already used for the cosmopolitan genera, namely, aquatics, adventives, and desert plants and halophytes, except that the latter are represented here chiefly by members of the tropical strand flora. The aquatics are very few, presumably because such plants are less controlled by temperature factors and thus tend to have a wider latitudinal range. *Pistia* is perhaps the best known and is notable in being monotypic. It may be added that the rather similar *Eichhornia*, now seen in many parts of the tropics, has spread adventively from America, and thus leads conveniently to this next category of genera which now occur more or less throughout the tropics mainly because of the wide distribution of one or more species which are either weeds or actually subjects of cultivation. Among the former there may be mentioned *Ageratum*, *Cassytha*, *Catharanthus*, *Celosia*, *Dactyloctenium* (one species only), *Gynandropsis*, *Quamoclit*, *Sida* and *Waltheria*, and among the latter *Cocos*, *Coix*, *Gossypium*, *Terminalia* and *Urena*.

Pan-tropical genera of arid conditions again are very few also perhaps because their climatic relations give them a wider tolerance to temperature and only *Glinus* (which has one species in America and one in the Old World), and *Tribulus* need be mentioned. The tropical coastal plants are of special interest to the plant geographer because of their connection with problems of dispersal and they are discussed at greater length in a later chapter. By the nature of their habitat they cannot of course compare in extent of occupation with many other types and they are often discontinuous, but rather less than a dozen are found, within these limitations, in all three sectors of the tropics. They may conveniently be divided into genera, including *Dodonaea* and *Scaevola*, which are pan-tropical only because one or more of their species are widespread coastal species; genera of mangroves which occur in both western and eastern hemispheres, namely *Avicennia* and *Rhizophora*; and one or two genera consisting only of single coastal species, as in *Remirea* and *Suriana*.

At this point, as we are about to pass from what have been described as tropical genera to those categorised as temperate, it is well to stress again that there is by no means so clear-cut a distinction between the two as this method of treatment might suggest. This is chiefly because many tropical genera have a minority of temperate species and *vice versa*, rather than to the fact that any considerable number of genera can be said to be neither tropical nor temperate but something in between. It is true that there are some genera which are more particularly characteristic of mid-latitudes, such as *Rhus*, *Vitis* and *Lespedeza*, but it would be very misleading to separate these as a third category. Indeed the small representation of such a type is probably a matter of considerable significance in the historical evolution of the Angiosperms, reflecting, among other things, the shape of the earth and the consequent ever-critical nature of the middle latitudes (see p. 161).

Temperate Genera

The circumstances of world geography and relief are such that it is difficult to include, in one category, all the genera to which, broadly, the term "temperate" might be applied. For instance genera which are found in all temperate regions are of necessity almost world-wide and have in fact already received notice; while those confined to temperate latitudes are discontinuous, and are dealt with in the next chapter. There remain, however, two great groups of genera which may appropriately be called temperate genera in the narrower sense and which may therefore be considered here. The first of these consists of genera found throughout

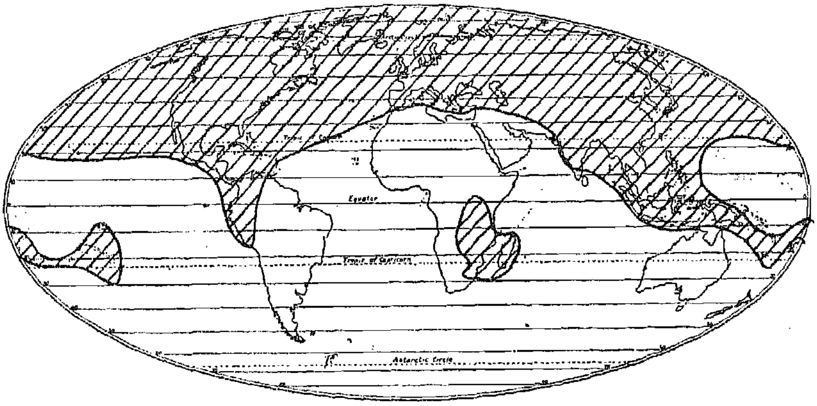

FIG. 17.—Map showing (shaded) the distribution of the genus *Vaccinium*.

the northern extra-tropical latitudes, and also to some extent, but incompletely, in the more elevated regions of the tropics, sometimes actually reaching the southern temperate zone. The second consists of genera distributed through but entirely confined to the northern extra-tropical zone, that is to say, to the northern temperate and arctic regions. Many of the members of these groups will be familiar, at least by name, and it is rather surprising to find that they do not number more than about 165.

There are also a few genera, of which *Vaccinium* (fig. 17) is perhaps the best example, which are equally characteristic of the northern temperate regions and of some parts, but not all, of the tropics, especially the more mountainous. In this genus many species have, for instance, been described from New Guinea, and other parts of Malaysia also have their representatives. There are also many species within the tropics of America. It is least in evidence in Africa, where it is to be found only on the east, but there are a number of species in Madagascar.

The first group can be divided into a number of sub-groups according to detail, and these can be tabulated, with examples, as follows:

1. Genera so widely spread, either naturally or as adventives, as to be almost sub-cosmopolitan:
   Epilobium, *Hordeum*, *Trifolium*, *Urtica*.
2. Genera with some extensions southwards in all directions, usually to certain tropical mountains only:
   Artemisia, *Rosa*, *Thalictrum*.
3. Genera extending south in America and Asia:
   Prunus, *Viburnum*.
4. Genera extending south in America and Africa:
   Astragalus, *Sedum*, *Silene*.
5. Genera extending south in America only:
   a. Into the tropics—
      Cotoneaster, *Juglans*.
   b. Into temperate South America—
      Alnus, *Berberis*, *Draba*, *Lathyrus* and *Vicia*, *Menyanthes*, *Pinguicula*, *Ribes* (fig. 18).

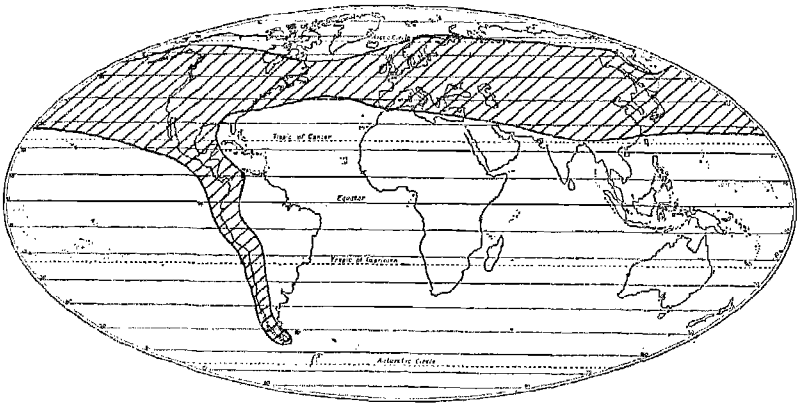

FIG. 18.—Map showing (shaded) the distribution of the genus *Ribes*, after Hutchinson.

6. Genera extending south in Asia only:
Acer, Androsace, Euonymus, Pirola.

7. Genera extending south in Africa only:
Allium, Arabis, Cirsium, Crepis (26), *Subularia.*

The genera which range more or less completely through the northern extra-tropical regions, either at all or some latitudes, can be divided into three according to their constitution. First are those in which the species are fairly numerous and in which the generic area is much greater than that of any one species. This is by far the largest group, and its 65 or so genera include many that are familiar. Mostly they call for no special comment and are well exemplified by:

Aquilegia, Epipactis, Fritillaria, Iris, Spiraea, Trollius and *Veratrum.*

A few are found in part of North America only, while *Dracocephalum* and *Scrophularia* are rather special cases because in each only one species is American. Conversely in *Erythronium, Polemonium* and *Solidago,* all but one or two species are American. In some others, among them *Asarum, Cornus* and *Cypripedium,* there are very few, and sometimes only one, species in Europe.

Second are the genera with more than one species, but in which a single species is more or less circumpolar and accounts for most of the generic range. These number about twenty and include *Diapensia, Dryas* and *Phyllodoce.* It must be remembered that the ranges of the most northerly of these species may be small.

Finally, there are the genera, such as *Adoxa, Calypso* and *Loiseleuria,* which consist of only a single more or less circumpolar species each.

Other Wide Genera

Under this general heading are included all the continuously distributed genera which are, on the one hand, too restricted to merit inclusion in any of the foregoing categories, but which are, on the other hand, too wide in range to be treated as endemics. Not only are these very numerous, but they show almost every variation in range, so that any cursive account of them would be almost impossible. It is essential, therefore, to tabulate them, and in order to do this they must be classified somewhat rigidly. It is also desirable to give rough figures so that the relative size and importance of the different groups can be appreciated.

Actually there are eight main types of wide, continuous distribution in the sense defined above, and although they can be further divided according to detail it is convenient to arrange their description under these heads. They are:

American wide genera.
North Pacific wide genera.
Eurasian wide genera.
African „ „
Asiatic „ „
Australasian wide genera.
African-Asiatic-Australasian wide genera.
Asiatic-Australasian wide genera.

American wide genera

The number of genera confined to America but so widely distributed there as to cover more than one floristic region is about 350 (excluding the more widespread tropical genera, which are dealt with later), and they fall into the following four groups:

1. Genera more or less completely distributed throughout North America. These number about 70 and include:
   Ceanothus, *Heuchera*, *Liatris*, *Monarda*, *Rudbeckia* and *Symphoricarpos*.
2. Genera found in North and Tropical America. These number about 40 and include:
   Predominantly northern genera—*Helianthus*, *Kalmia*.
   Predominantly tropical genera—*Agave*, *Echeveria*.
3. Genera found in tropical and temperate South America. These number upwards of 200 and include:
   Alstroemeria, *Ananas*, *Bromelia*, *Escallonia*, *Hippeastrum*, *Mutisia*, *Salpiglossis*, *Tropaeolum*.
4. Genera found throughout America from north to south. These number about 80 and include:
   Cereus, *Echinocactus* (42° N. to 39° S.), *Gaillardia*, *Godetia*, *Gonolobus*, *Helenium*, *Krameria*, *Metastelma*, *Mentzelia*, *Oenothera*, *Opuntia* (from 50° N.), *Petunia*, *Phoradendron*, *Tagetes*.

   Some of these genera, such as *Gaillardia*, have minor gaps in their range.

North Pacific genera

The wide North American genera and those of Eurasia (below) are linked up by a small group, the members of which are found on both sides of the Bering Strait and which may for this reason appropriately be called North Pacific genera. They number about a dozen.

First come three large genera, *Castilleja*, *Phlox* and *Penstemon*, each with numerous species in the western parts of North America, and with one species in north-east Asia. In *Castilleja* and *Phlox* this latter species is confined to Asia, but *Penstemon* includes one species which ranges from Alaska to Japan.

Bryanthus (fig. 50) is fairly widespread in Eastern Asia but only just reaches America; *Chamaerhodos* ranges from Mongolia to western North America; *Coelopleurum*, *Physocarpus* and *Romanzoffia* are found in north-east Asia and in western North America; and *Erioblastus*, *Leptarrhena* and *Merckia* are monotypic genera distributed narrowly on both sides of the Strait, the last being arctic. *Smilacina* (*Tovaria*) as maintained by Krause (160) may also be included here. It ranges from the Himalayas more or less continuously eastward to Central America.

The four genera *Claytonia*, *Dodecatheon*, *Menziesia* and *Zygadenus* may also be mentioned here because, although they range throughout North America, they have also one or a minority of species in north-east Asia.

Eurasian wide genera

Strict adherence to the definition of endemism given earlier would necessitate treating even the genera which range eastward right from the North Atlantic to the North Pacific as endemic owing to the exceptional width of the Euro-Siberian region. A warning was, however, given in Chapter 2 that this region might on account of its size have sometimes to be treated as a special case, and there is good reason for doing so now. Not only are the actual ranges of these genera far greater than those of the average run of endemic genera as defined, but also to call them endemic without qualification is to distort the general picture of plant distribution and to overshadow what is certainly their most important feature, namely, their relatively great longitudinal range and their more or less complete occupation of the Old World northern temperate zone.

The genera which thus extend across the great Eurasian continent north of the tropics and the subtropics number, at a rough estimate, about one hundred, and among them the families Cruciferae, Gramineae, Compositae and Umbelliferae are conspicuous. At both ends of their range, and more especially in the west, they often show a tendency to extend south into warmer latitudes. The group naturally includes many genera familiar to European botanists either as garden plants or as native wild plants and as far as possible the following examples have been drawn from these

Doronicum, *Eranthis*, *Hedera* (occurs also in Macaronesia), *Lamium* (especially in the west), *Neottia*, *Paris*, *Syringa* (especially eastern), *Tulipa*.

African wide genera

Here are included the genera which are widely distributed in Africa (generally with the exception of the north) and in the Madagascar region. They total between 200 and 300 and are of three main geographical types, excluding the wider genera *within* the tropics, which are dealt with later.

1. Genera found in tropical and southern Africa only. These number more than 100 and include:
    - *Babiana* (discontinuous between Socotra and southern Africa), *Euclea*, *Fadogia* and *Voandzeia*, predominantly tropical.
    - *Blaeria*, *Cliffortia* (581), *Protea*, *Stapelia* and *Ursinia*, predominantly southern.
2. Genera found in Africa and in the Madagascar region. These number about 100 and include:
    - *Myrothamnus* in tropical Africa and Madagascar only.
    - *Clematopsis*, *Faurea*, *Hydnora* and *Sparrmannia* in tropical and southern Africa and in Madagascar.
    - *Aristea* (582), *Lightfootia* and *Selago* with a similar distribution but predominantly found in southern Africa.
    - *Angraecum*, *Disa*, *Philippia* and *Stoebe* more or less throughout Africa and the Madagascar region, *Philippia* being characteristic of the latter and *Disa* and *Stoebe* of southern Africa.
    - *Himantochilus* is found in tropical Africa and the Mascarenes only.
    - *Agauria* is found in tropical Africa, Madagascar and the Mascarenes.
3. Genera found in South Africa and Madagascar, and occasionally in the Mascarenes. These number about 20 and include:
    - *Alberta*, *Cassinopsis* and *Trichocaulon*.

It is very noteworthy that nearly all the genera here represented as in Madagascar or the Mascarenes are found also in South Africa, and that this relationship is, in general, more marked than that between tropical Africa and the islands. It is true that the Madagascar region has many genera in common with tropical Africa, but these mostly extend more widely also, and therefore, as regards this chapter, appear in other categories.

Asiatic wide genera

This group is a large one calculated to contain between 350 and 400 genera, and is moreover difficult to define numerically because the limits of the genera tend to be in regions where it is hard to trace them accurately. One definite feature, however, is that to all intents and purposes all the genera are limited westward in India, that is to say hardly any range from warm Central Asia to Malaya. Actually several such have been described, including *Skimmia*, which ranges from Afghanistan to the Malayan Archipelago, but these serve only as exceptions that prove the rule.

This fact points the way towards a classification of the whole group into distributional types, which is best done by recognising two main types, the first of which shows ranges from India, China or Japan to the Malayan Archipelago and the second from some part of the south-east Asiatic region similarly to the islands. The former are apparently more than twice as numerous as the latter, and both are constantly increasing because of new records in Malaysia.

In the first, the largest number consists of genera which range from India only, the Indo-Malaysian genera proper. It is probable that these amount to at least 200, and many of them touch south-west China. Several of the Dipterocarpaceae, such as *Dipterocarpus*, *Hopea* and *Shorea*, are good examples, as are also several other genera containing important timber trees like *Mesua*, *Tectona* and *Walsura*. *Mangifera* seems to belong here as far as its natural range can be ascertained, and other examples are *Colocasia*, *Daemonorops*, *Hodgsonia* and *Osmelia*. A few genera, including *Aporosa*, range eastward from Ceylon and do not occur in the Indian Peninsula proper. Two other smaller groups in this main type which are related to the above are genera ranging from India and China and from India, China and Japan respectively. The first includes *Beaumontia*, *Dichroa* and *Eriobotrya*, and the second *Camellia*, *Daphniphyllum*, *Heterosmilax* and *Michelia*. Finally there are some genera distributed from China and Japan respectively into Malaysia. The former include *Anneslea* and *Cratoxylon* and the latter *Broussonetia* and *Cladopus*. *Actinidia* and *Thladiantha* exemplify genera which range from north Asia to the Archipelago.

The second of the main types could also be classified into three, though on a smaller scale, according to whether they are, in south-east Asia, found in both Burma and Indo-China or in only one of these, but it is doubtful whether the facts are sufficiently well known to make this worth while here. Examples of this type as a whole are *Achasma*, *Barclaya*, *Duabanga*, *Feroniella*, *Indorouchera* and *Payena*.

The very interesting subject of the detailed distribution of all these genera within the Archipelago is too complex to be dealt with here in what is but a general survey, but it is worth noting that while many genera occur fairly generally on all the larger islands, an appreciable number tend to be found either in Java and Sumatra *or* in Borneo *or* in the Philippines (see p. 127). Of the more generally distributed genera most seem to extend all the way to New Guinea.

It should also be noted that these genera include examples of various types of discontinuity, as for instance, *Sarcosperma* (332); *Herpysma* and *Triplostegia* (529); *Rhodoleia* and *Wightia*.

At first sight the different groups mentioned above are not easy to visualise, and it is therefore useful to summarise them and to repeat the approximate numbers of genera in each. They are:

1. Genera ranging from India, China and Japan to the Malayan Archipelago, 250–300.
    - *a*. Genera ranging from India to the Archipelago, most numerous.
    - *b*. Genera ranging from India and China to the Archipelago.
    - *c*. Genera ranging from India, China and Japan to the Archipelago.
    - *d*. Genera ranging from China to the Archipelago, comparatively few.
    - *e*. Genera ranging from Japan to the Archipelago, comparatively few.
2. Genera ranging from south-east Asia to the Malayan Archipelago, 100–150.

Australasian wide genera

These are comparatively few in number, probably not more than 60, and fall quite simply into two types, those which are confined to Australia and New Zealand (including the Lord Howe and Norfolk Islands) and those which occur also somewhere in the Pacific Islands.

The first number about 30 and include *Celmisia, Persoonia* (only one species in New Zealand) and *Raoulia* (also in New Guinea).

Of the rest the genera found in Australia and the Pacific Islands number about 20 and are exemplified by *Argophyllum* and *Geissois*. Their ranges outside Australia vary a good deal, but for the most part they are restricted to New Caledonia.

The genera of Australia, New Zealand and the Pacific Islands number about half a dozen, among them being *Dracophyllum* and *Epacris*.

Even fewer, among them *Xeronema*, are found in New Zealand and the Pacific Islands only.

Finally *Carmichaelia* occurs in New Zealand and on Lord Howe Island (625), and *Rhopalostylis* in New Zealand and on Norfolk Island.

African-Asiatic-Australasian wide genera

There are included in this very comprehensive category all those genera which, present in Africa, range thence either to Europe and Asia only, or further through Asia into Australasia. From many points of view the category is a very interesting and important one, and must be considered with some care, although any estimate of numbers is difficult for many reasons and especially because it is often impossible to say how continuous a genus is in the desert and semi-desert regions which link Africa and India. As far as can be calculated, the total appears to be about 150, but it must be remembered that this excludes all those old world tropical genera which are widely discontinuous (see p. 101 and Appendix B).

In general the category comprises two main types of range, namely genera more characteristic of the temperate regions, but with extensions into the tropics, and genera more characteristic of the tropics and reaching continuously all or part of the way from tropical Africa to Australasia and the Pacific Islands.

There must be included in the first of these a rather special group of genera which range from Europe and the Mediterranean southward through Africa. *Adenocarpus*, *Asterolinon* and *Crambe*, with most of their species in the north, are good examples of one extreme and these reach no further than the northern tropics. *Punica* has a rather similar range, but extends well eastward into Asia, and its distribution is no doubt confused by long cultivation. *Dianthus*, which extends to Japan, reaches as far south as the Cape (160). At the other extreme are genera like *Erica* and *Gladiolus* (also in Madagascar), both of which are concentrated in South Africa, but extend, chiefly up the east side of the continent, practically all over Europe and western Asia. Between these extremes are such genera as *Holcus* and *Romulea*, which occur in Europe and the Mediterranean region and also in South Africa, but which appear to be more or less absent in between.

The second main type, consisting of essentially tropical genera, is much larger and can be divided into four. First there are the genera which are practically confined to Africa, but which extend therefrom into Arabia. Here belong *Aloe*, *Catha* and *Kniphofia*. Next comes the largest group of all, containing genera which range continuously from Africa to India. Some of these, like *Cometes* and *Salvadora*, occur only in the tropical parts of Africa; others, like *Vahlia*, extend to the south of the continent. *Echinops*, *Hyoscyamus* and *Reseda* exemplify genera found in

Europe and the Mediterranean as well as in tropical Africa. *Caralluma* ranges from South Africa up the east coast and all over North Africa to India. A third minor type comprises genera of similar distribution, but extending still further into tropical Asia. Examples of these are:

Asparagus, South Africa, Mascarenes to Malaysia.
Boswellia and *Cistanche*, Africa to China.
Maerua, Africa, Madagascar and Mascarenes to Siam.

Finally, there are the widest ranging genera of all—those extending from Africa all the way to Australia or the Pacific. It is difficult to estimate the number of these, but they include:

Ceropegia, Macaronesia and South Africa to Australia.
Loranthus, Africa and Madagascar to the Pacific Islands.
Melhania, Africa and Madagascar to Australia.
Viscum, Africa and Eurasia to Australia.

Of all these very varied groups, that of the genera ranging from Africa to India is by far the largest, comprising about one-third of the total, but taking the category as a whole there is represented in it almost every degree of distribution from Africa towards Australia and Polynesia.

Asiatic-Australasian wide genera

In one sense this category is the counterpart of the last in that it includes genera with much the same kind of distribution, but with the emphasis on the east and south-east rather than the west. Moreover, although it contains genera which may well have originated in Asia and have spread thence southward, it certainly comprises many which originated in Australasia and have ranged northward into Asia.

The classification of the category, which in total seems to contain about 200 genera, is into three main groups. In each the genera are represented in some parts of Asia, but in one they occur also in Australasia and the Pacific Islands; in another in Australasia only; and in the third in the Pacific Islands only. Each of these groups can be further divided according to whether the Asiatic distribution includes India, China or Japan, or whether it is limited to Malaysia and/or Indo-China. Moreover, almost every group contains some genera which are predominantly Asiatic and some which are predominantly Australasian, and only in a few cases, as for instance *Aegialites*, which is monotypic and widely discontinuous, is there no such distinction.

But this classification is really too complicated for a running description and the facts are best displayed in tabulated form. As previously, the approximate numbers of genera are given and, unless otherwise stated, the word Australasia may be taken to mean Australia and/or New Zealand. The numbers of the predominantly Australian genera especially are constantly tending to increase because of new records in Malaysia.

Asiatic-Australasian wide genera

1. Genera of Indo-Malaysia, Australasia and the Pacific Islands:
    a. Genera ranging from India and/or China—
        1. Genera predominantly Asiatic, *c.* 30.
            e.g. *Areca, Dendrobium, Dischidia, Hoya.*
        2. Genera predominantly Australasian, *c.* 5.
            e.g. *Calogyne, Melaleuca, Styphelia.*

- *b*. Genera ranging from Malaysia—
    - 1. Genera predominantly Asiatic, *c*. 6.
        e.g. *Codiaeum*.
    - 2. Genera predominantly Australasian, *c*. 15.
        e.g. *Casuarina* (see below), *Grevillea*, *Leptospermum*.

2. Genera of Indo-Malaysia and Australasia:
    - *a*. Genera ranging from India and/or China—
        - 1. Genera predominantly Asiatic, *c*. 60.
            e.g. *Nipa*, *Thysanotus*, *Zingiber*.
        - 2. Genera predominantly Australasian, *c*. 6.
            e.g. *Centrolepis*, *Goodenia*, *Stylidium*.
    - *b*. Genera ranging from Malaysia—
        - 1. Genera predominantly Asiatic, *c*. 12.
            e.g. *Kentia*, *Myrmecodia*, *Tecomanthe*.
        - 2. Genera predominantly Australasian, *c*. 15.
            e.g. *Eucalyptus* (fig. 19), *Olearia*, *Patersonia*.

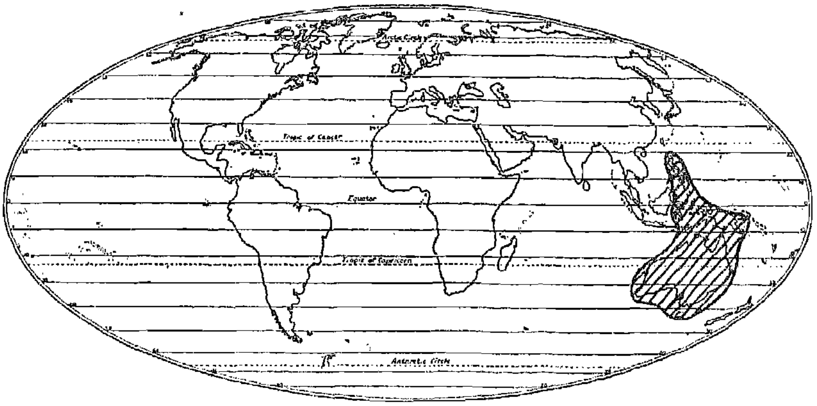

FIG. 19.—Map showing (shaded) the distribution of the genus *Eucalyptus*.

3. Genera of Indo-Malaysia and the Pacific Islands, with New Caledonia:
    - *a*. Genera ranging from India, *c*. 30.
        e.g. *Ailanthus*, *Aleurites*, *Sarcolobus*.
    - *b*. Genera ranging from Malaysia, *c*. 25.
        e.g. *Finschia*, *Metroxylum*.

It may be assumed that all the genera of 3 *a* are predominantly Asiatic, but some of the genera of 3 *b* only extend west as far as New Guinea (e.g. *Agatea* and *Pentaphalangium*), and are equally characteristic of the Pacific Islands, often being plentiful in New Caledonia.

Because of the exceptional interest of the genus *Casuarina* from the point of view of comparative morphology, it is worth while to give a slightly extended description of its distribution, for the details of which I am indebted to Mr. L. A. S. Johnson. The genus has two distinctive sections, one with 40 species and the other with 14. The former comprise 20 in western Australia, about 15 in eastern Australia, and 4 in Java, New Guinea and New Caledonia; and it also includes the now widely planted *C. equisetifolia*, the native range of which is probably from Burma to Australia and Polynesia. The latter section has only one species in Australia (in northern Queensland) and the rest range over the Malayan Archipelago and eastward to Fiji. It will be noted that the genus is not native in New Zealand.

Summary

In order to bring together in conveniently abbreviated form all that has been said in the foregoing pages about the widely distributed genera of Angiosperms, it is desirable to conclude this chapter with a summary of the facts and figures which have been described and discussed. This summary, which comprises all the genera which are neither discontinuous nor endemic, is as follows:

1. Cosmopolitan or very wide genera	*c.* 130
2. Tropical genera	*c.* 250
3. Temperate genera	*c.* 165
4. Other wide genera:	
a. American genera	*c.* 350
b. North Pacific genera	*c.* 12
c. Eurasian genera	*c.* 110
d. African genera	*c.* 250
e. Asiatic genera	*c.* 370
f. Australasian genera	*c.* 60
g. African-Asiatic-Australasian genera	*c.* 150
h. Asiatic-Australasian genera	*c.* 220
Total	*c.* 2050

From this table it therefore appears that about 15 per cent. of all genera may be regarded as wide genera, leaving about 85 per cent. for discontinuous and endemic genera.

CHAPTER 6

THE DISTRIBUTION OF GENERA—II

Discontinuous Genera

THE facts of discontinuous distribution are among the most remarkable in all the geography of the Flowering Plants and on this account alone would demand special attention here, but there is a second and related reason why a careful survey of them is particularly desirable. Discontinuity is a matter which bears upon many problems (especially those concerning the distribution of land and climate in the past) beyond the confines of botany, and it has therefore, not unnaturally, attracted the attention of many who are not botanists, and their statements regarding it are not always to be taken at their face value. Thus there has arisen a certain amount of confusion regarding the facts, and a general survey which reviews the subject as critically as possible may serve also to dispel some of this. Since the story of discontinuity in general is largely the story of generic discontinuity in particular, this chapter comprehends the most important part of such a survey.

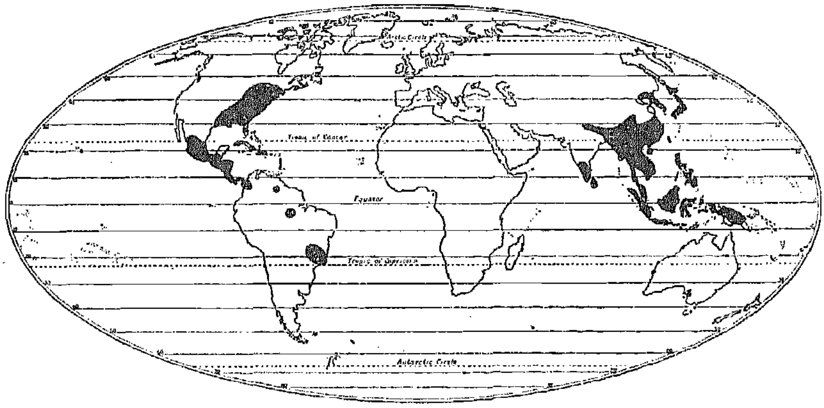

FIG. 20.—Map showing (black) the distribution of the tribe Magnolieae.

When one plant group is found distributed over two or more widely separated regions its discontinuity is significant, in theory at all events, only if it can be assumed that its range was formerly continuous and that the subsequent disjunction has resulted from natural causes. Expressed rather differently, discontinuity is of interest, from most points of view, only when it can be assumed that the group exhibiting it is of monophyletic origin and has had therefore not only a common ancestry but also a single point of origin. It is by the quotation, as discontinuous, of genera which do not fulfil these conditions that confusion has chiefly arisen.

The greatest difficulty lies in deciding which genera are to be regarded confidently as monophyletic groups, because here the only possible criterion is that of personal opinion, but there are two types of genera which must almost certainly be excluded. The first comprises those which consist of two or more very distinct subgenera separated by characters which in other cases are often regarded as of full generic value. Not uncommonly such genera are described as discontinuous because each of the subgenera has a distinct range, but if the relationship between them is open to doubt, so also of course is their discontinuity, and reference to it is merely misleading.

The second case is much commoner and especially concerns certain large and particularly "natural" families. In these families the constituent species are all so much alike that it is very difficult to group them into separate genera and it becomes necessary, in order to do so, to emphasise and rely too rigidly upon characters so detailed and minute that their value as criteria of true relationship can only be described as very doubtful. Thus in some families especially the genera as commonly defined can but rarely be accepted as monophyletic units. This is true, for instance, in the Compositae, where one of the most prevalent types of generic distinction is the minute morphology of the style arms; and, again, in the Acanthaceae, where minor characters of the anthers are much used. Sometimes, of course, other and more practicable features come into play, but the general result is that nearly all the discontinuities recorded for these and a few other families must be treated with reserve.

Another common difficulty is that of deciding whether or not a plant is of natural occurrence in all parts of its range. The heather and certain heaths, for instance, are often quoted as striking examples of wide discontinuity on the strength of their occurrence in eastern North America, but investigation shows that they are by no means free from the suspicion that the American plants are in fact intentional or unintentional introductions from the Old World and that they do not, therefore, confer discontinuity in the phyletic sense on the genera to which they belong.

Misidentifications and errors of fact also lead to misunderstanding. Slips of the pen or tongue have frequently attributed to genera discontinuity which in fact they do not possess. In collecting plants and in dealing with them subsequently data sometimes get misplaced: these errors may eventually pass into print, and once this has happened it is not at all easy to correct them. As regards identification, a wrong conclusion as to which of two genera a new species belongs may lead to great geographical confusion.

It was the realisation of these difficulties that prompted the present writer, years ago, to review all the genera which had from time to time been described as exhibiting wide discontinuity, that is to say discontinuity of approximately continental or oceanic dimensions, and to compile a list of those which could with reasonable confidence be looked upon as good and reliable instances of it, omitting those which for such reasons as have just been mentioned were to be regarded at least with suspicion. In short, the object of the review was to produce a list of all the genera which could be safely quoted as examples of widely discontinuously distributed monophyletic groups. This list first appeared in 1927 (210), and there was a revision of it in the first edition of the present book. A third version of it is given here in Appendix B. This course of printing the list separately has been adopted because to have incorporated it in the text of this chapter would have overburdened this with detail and would have made the cursive reading of it almost impossible.

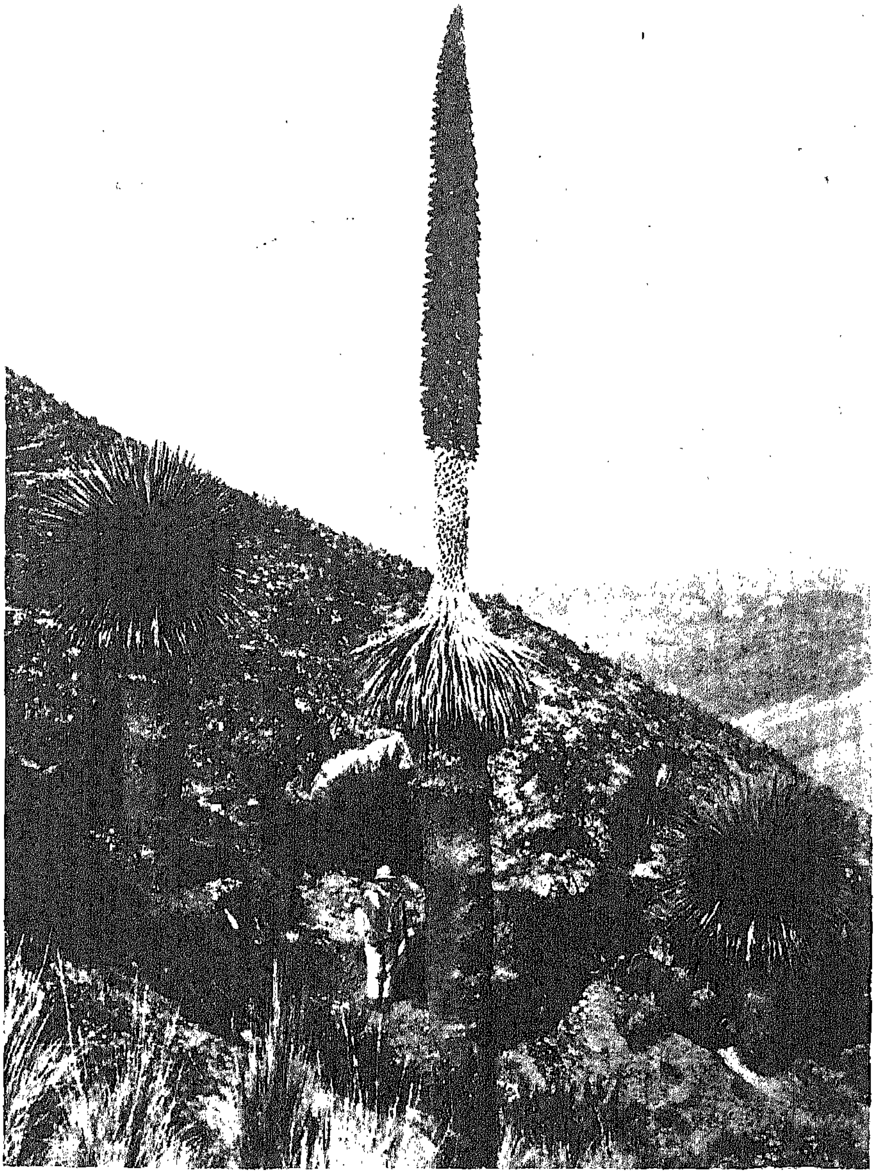

Plate 7. Puya raimondii in the Peruvian Andes

(from Weberbauer in Vegetation der Erde)

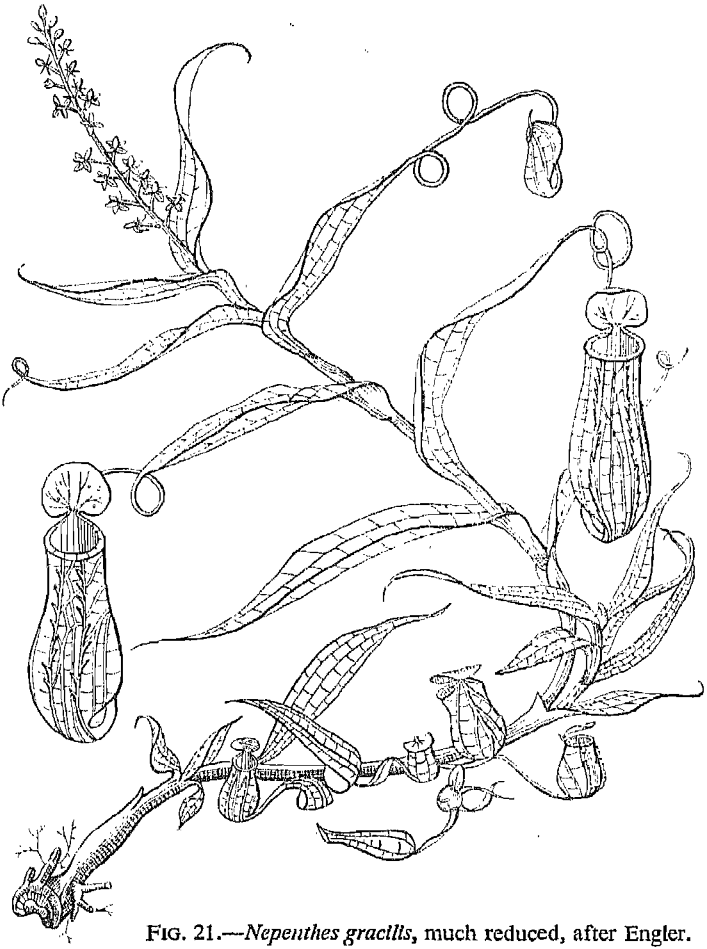

FIG. 21.—*Nepenthes gracilis*, much reduced, after Engler.

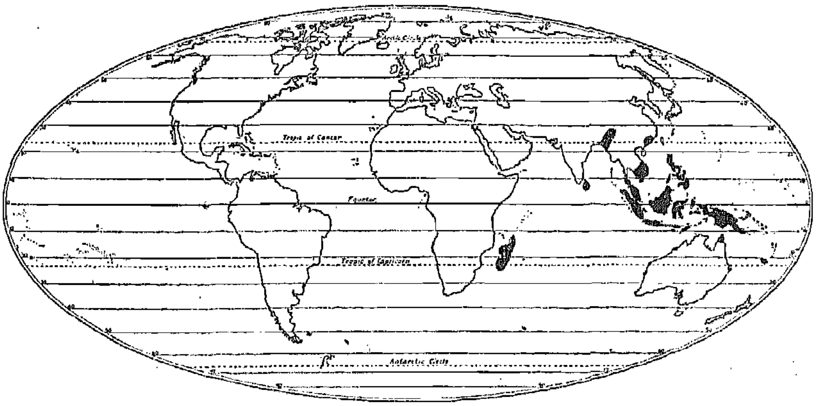

FIG. 22.—Map showing (black) the distribution of the genus *Nepenthes*, after Hutchinson.

The following pages include, however, a more generalised account of the list and of the classification and figures that it presents, and the Appendix can be used to amplify this as may be felt desirable.

The distribution of land and sea and the zonation of climate are such that the discontinuous genera of the Flowering Plants are of five main types, *i.e.*:

1. Genera entirely or predominantly confined to the northern temperate regions.
2. Genera entirely or predominantly confined to the tropical zone.
3. Genera entirely or predominantly confined to the southern temperate regions.
4. Genera occurring in both northern and southern temperate regions.
5. Genera of various distributions, but all occurring in the exceptionally isolated Hawaiian Islands.

Discontinuous genera of the north temperate zone

The northern temperate discontinuous genera comprise, as might be expected from the huge extent of this area, several very distinct types, including some which range over the whole of it and rather fewer which occur at both ends of the Eurasian continent, but the commonest discontinuities are between America and Europe and America and eastern Asia respectively.

The latter is one of the most familiar and important of all and, from the time that Asa Gray (228) first drew special attention to it, has been much studied and discussed (622). These genera number about eighty and there is reason to believe that they may be survivors of a very ancient circumboreal flora which has failed to persist in Europe and western Asia. They can be further classified according to the details of their Asiatic distributions, some occurring only on the continent; some in Japan; and others in both. Some of them, moreover, have marked extensions southward into the tropics of one or both hemispheres.

The total number of genera in this northern temperate category is about 125, and the following are some of the best examples of them:

Liquidambar	According to most authorities there are three species—one in North and Central America, one in south-western Asia, and one in Formosa and south China.
Meconopsis	Taylor (545) regards this genus as consisting of one western European species and about forty in the Sino-Himalayan mountain system. Some taxonomists include also two western North American species.
Corema	A genus of two species—one in North America from Newfoundland to New Jersey and the other in the Azores, Spain and Portugal (fig. 38).
Platanus	There are four species in western North America and Mexico, one in eastern North America, and one in the eastern Mediterranean and in Asia Minor. Seward (479) gives an interesting map of the past and present range of this genus.
Clintonia	This genus has six species—two in western North America, two in eastern North America, one in the Himalayas and one in east Asia.
Paeonia	According to Stern (534), this genus has some thirty species, of which about a dozen are in Asia; seventeen in south Europe, the Mediterranean region and the Caucasus; and two in western North America. See also Barber (33).

FIG. 23.—*Hibbertia volubilis*, about natural size, after Baillon

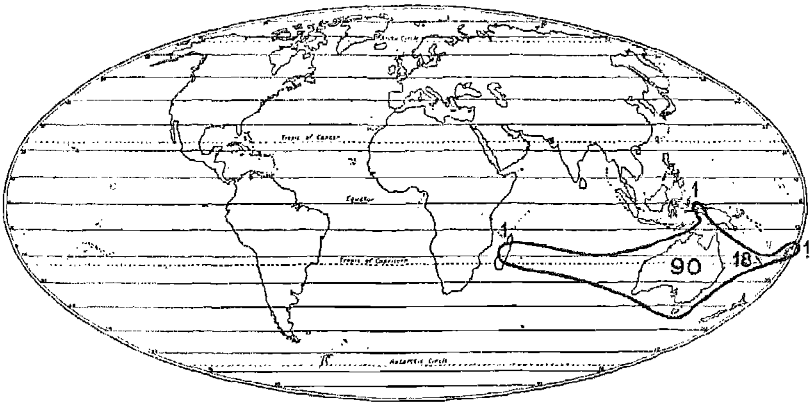

FIG. 24.—Map showing the distribution of the genus *Hibbertia*, partly after Hoogland. The figures are the numbers of the species in the different parts of the range.

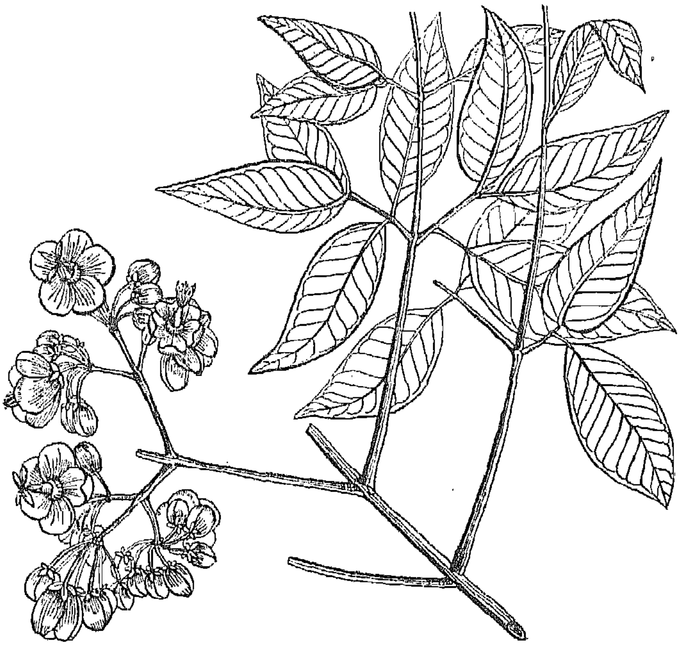

FIG. 25.—*Symphonia globulifera*, about half natural size, after Engler.

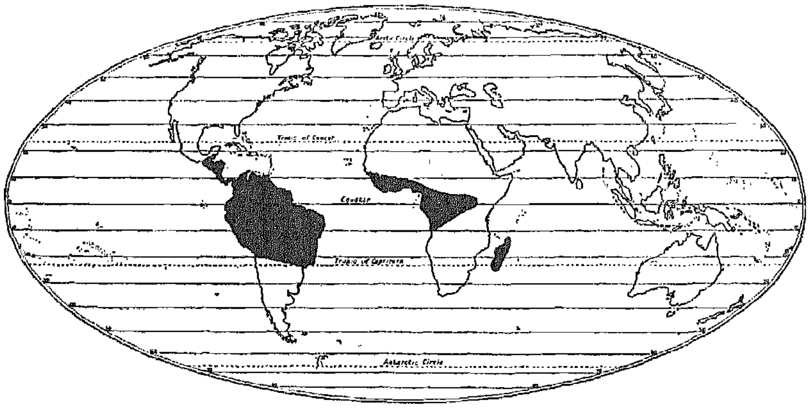

FIG. 26.—Map showing (black) the distribution of the genus *Symphonia*, after Hutchinson.

Menispermum .	According to Diels (156) there are two species—one in eastern North America and one in north-east Asia, north China, Korea and Japan.
Liriodendron .	One of the most striking and often quoted instances of discontinuity. There is one species in eastern North America and one very narrowly distributed in eastern China (Plate 18 and fig. 63).
Chiogenes . .	There is one species throughout eastern North America and one in Japan. Some consider the latter to be only a variety of the former.
Magnolia . .	According to Dandy and Good (247) there are some species in eastern North America and a larger number in eastern Asia, both groups having an appreciable extension into the tropics (fig. 20).

Discontinuous genera of the tropical zone

The tropical genera considered here as discontinuous comprise those which, while not completely pan-tropical, nevertheless occur in two or more of the main land divisions of this zone. Whether or not it is to be interpreted as a measure of the relatively great age of the tropical flora as a whole, the fact remains that the genera of this category are far more numerous than those of all the others put together, amounting indeed to nearly two-thirds of the total.

The three most obvious subdivisions are composed of genera found in America and Africa (*e.g.* figs. 25, 26), in America and Asia (*e.g.* fig. 66), and in Africa and Asia (*e.g.* figs. 27, 28) respectively, but not all the genera which have to find a place can be included in these, and it is necessary to recognise two further groups, one of genera more widely, but still discontinuously and incompletely, distributed over the tropics (*e.g.* figs. 29, 30), and one to include still more anomalous cases.

Of the three first divisions that of the African-Asiatic genera is more than twice as large as the other two together, and in this connection it is relevant to remind the reader that this is the only case in which the two constituent land masses are actually contiguous. Of the two divisions involving the New World that of the American-African genera is nearly three times as large as that of the American-Asiatic and Australasian groups.

The two divisions involving Africa can each be further classified according to whether the genera occur on the continent only; on the continent and in the Madagascar region; or on the islands only. Specially remarkable is the small but distinct group of genera which are found in America and elsewhere only in Madagascar.

The actual ranges of these various tropical types are sufficiently indicated by the titles of the divisions to which they belong and it is unnecessary to quote many examples of them apart from four of which figures and maps are given here. These are:

Nepenthes . .	A well-known genus of pitcher-plants with well over fifty species ranging from South China to north-eastern Australia, and in addition one species in New Caledonia, one in the Seychelles and one in Madagascar (figs. 21, 22).
Cunonia . .	A genus with about a dozen species in New Caledonia and one in South Africa. The latter is illustrated in fig. 6 and the distribution of the genera of the Cunoniaceae in fig. 7.
Hibbertia . .	In some respects like the last, but much larger. There are nearly one hundred species in Australia, about eighteen in New Caledonia, one in Fiji (531), one in New Guinea (195) and one in Madagascar (figs. 23, 24).

FIG. 27.—*Ancistrocladus heyneanus*, about half natural size, after Engler.

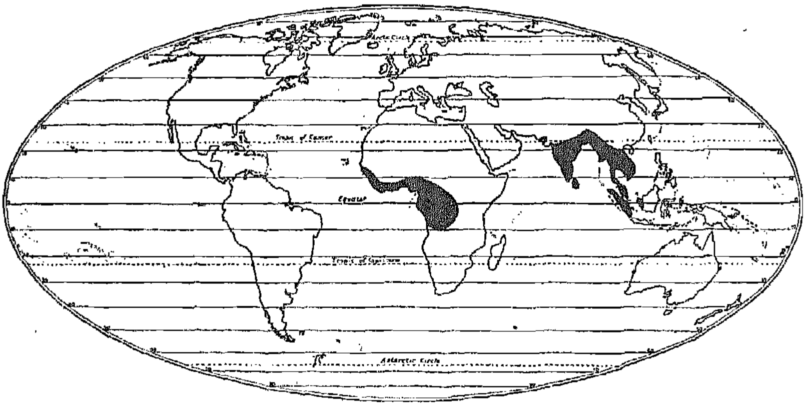

FIG. 28.—Map showing (black) the distribution of the genus *Ancistrocladus*, after Hutchinson.

Fig. 29.—*Hernandia peltata*, somewhat reduced, after Seemann.

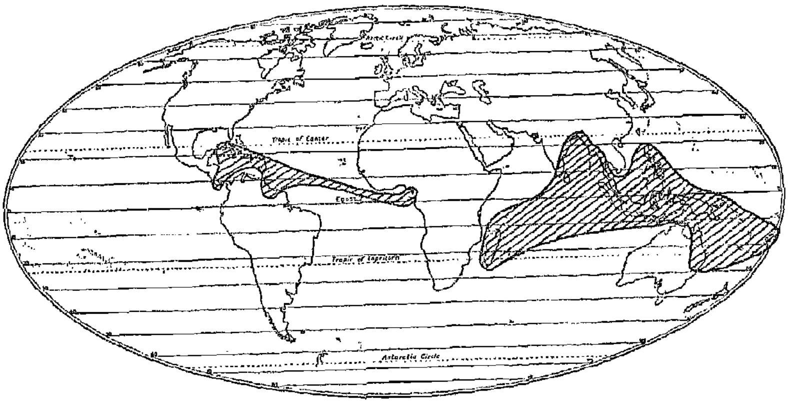

Fig. 30.—Map showing (shaded) the distribution of the genus *Hernandia*, after Hutchinson.

Nelumbo	According to Irmscher (295) one species extends from the Caspian to Japan and through Malaysia to Australia and a second from North America to Brazil (figs. 65, 66).

The more widely ranging discontinuous genera of the tropics are by the nature of the case much more miscellaneous and admit of no general description. Some idea of their details will, however, be apparent from the following, which are some of the more outstanding of them:

Clethra	This genus is almost confined to America and Asia, but one species occurs on Madeira (figs. 31, 32).
Turnera	There are many species in tropical America, and in addition one that ranges from the Seychelles and Réunion to Indo-Malaysia.
Kalanchoe	A large genus with all but one of its species in the Old World. The exception is a plant found locally in Brazil. It is usually described as distinct and as a native, but it is possibly adventive.
Styrax	Very like *Clethra* in that all but one of its species are American or Asiatic, but the exception in this case is found in the Mediterranean region.
Weinmannia	A large genus with the great majority of its species in tropical America, but it is also fairly well distributed in the Madagascar region and in Malaysia and the Pacific Islands, and there are one or two species in New Zealand (fig. 6).

The anomalous discontinuous genera of the warmer parts of the world are even more miscellaneous and nearly every one of them has its own particular interest, and at least the following call for special reference here:

Aldrovanda	A monotypic aquatic genus recorded from the warmer parts of Europe, north-east Asia, India, Japan, central Africa, Timor and Australia.
Brasenia	Also a monotypic aquatic genus and rather like the last except that it occurs also in the New World. It has been recorded from Manchuria, India, Japan, Sumatra, Australia, tropical Africa and from North and Central America.
Cohnia	This genus has been recorded from the Mascarenes and from New Caledonia. This is a very extraordinary range and the relationships of the genus need further study, but it is notable that a somewhat similar distribution is attributed to some other genera (221), and particularly to the next.
Cossinia	This genus is now recorded from the Mascarenes, New Caledonia and Fiji, and the species from the last of these is said to be closely related to that from the Mascarenes (515).
Kissenia	According to Dandy (120) this genus is found only in southern Arabia and Somaliland and in the south-western part of South Africa. The plants in the two areas are much alike and may represent only one species.
Pelargonium	A large genus with the great majority of its species in South Africa, whence it extends to Madagascar and up the east coast of Africa to Arabia and western India. There are also several species in Australia and one occurs in Australia, South Africa and on the Tristan da Cunha islands.
Pharnaceum and *Hypertelis*	Together these form a natural group of species almost entirely confined to Africa and Madagascar, but with one, now very rare, on St. Helena.
Phylica	Very like the last, but occurs on Tristan as well as on St. Helena.

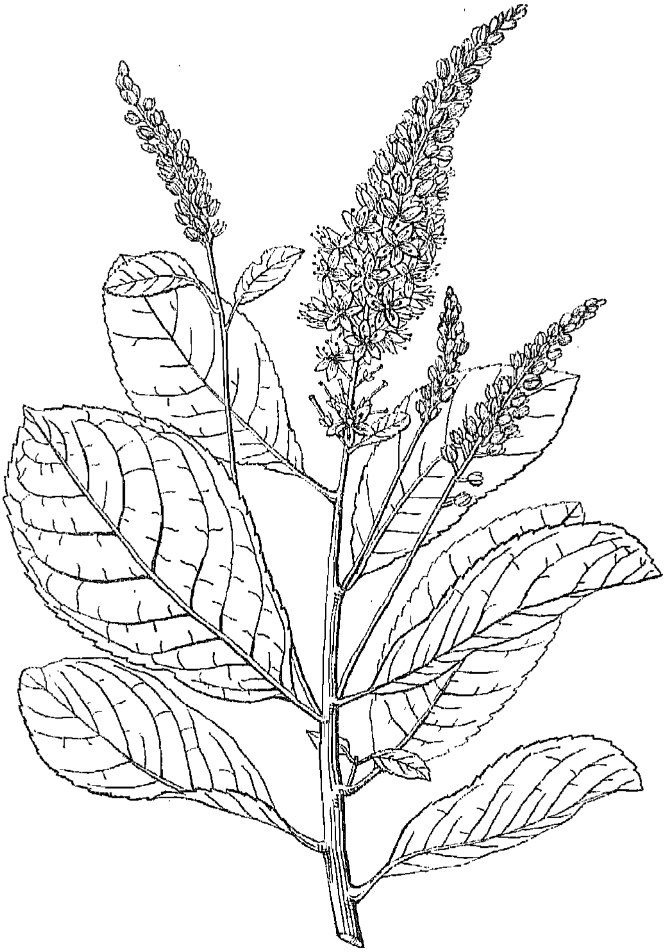

FIG. 31.—*Clethra tomentosa*, about natural size, after Bailey.

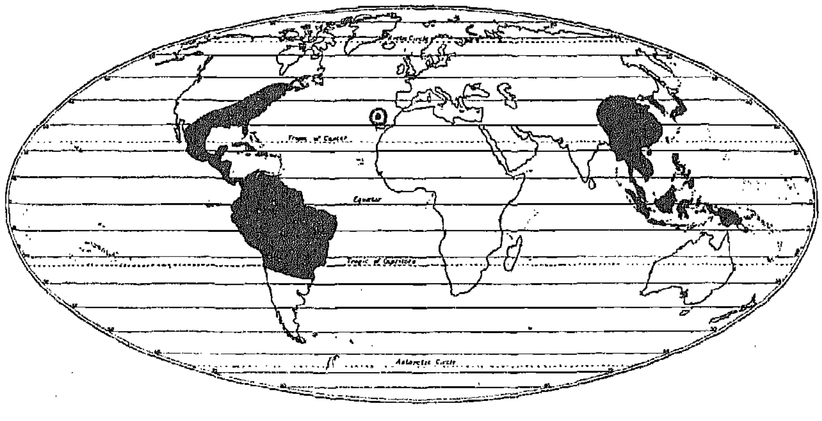

FIG. 32.—Map showing the distribution of the genus *Clethra*, mainly after Irmscher.

Discontinuous genera of the south temperate zone

It will be remembered that of the three land extensions south from the north circumboreal belt those in America and in Asia and Australasia are much longer than that in Africa, and it is, therefore, not surprising to find that among the discontinuous genera of the southern temperate regions (*e.g.* figs. 33, 34), which number some fifty in all, those confined to America and to Australasia are much the most numerous. Some are confined to Africa and Australasia, but other types are scarcely represented. A very few are anomalous.

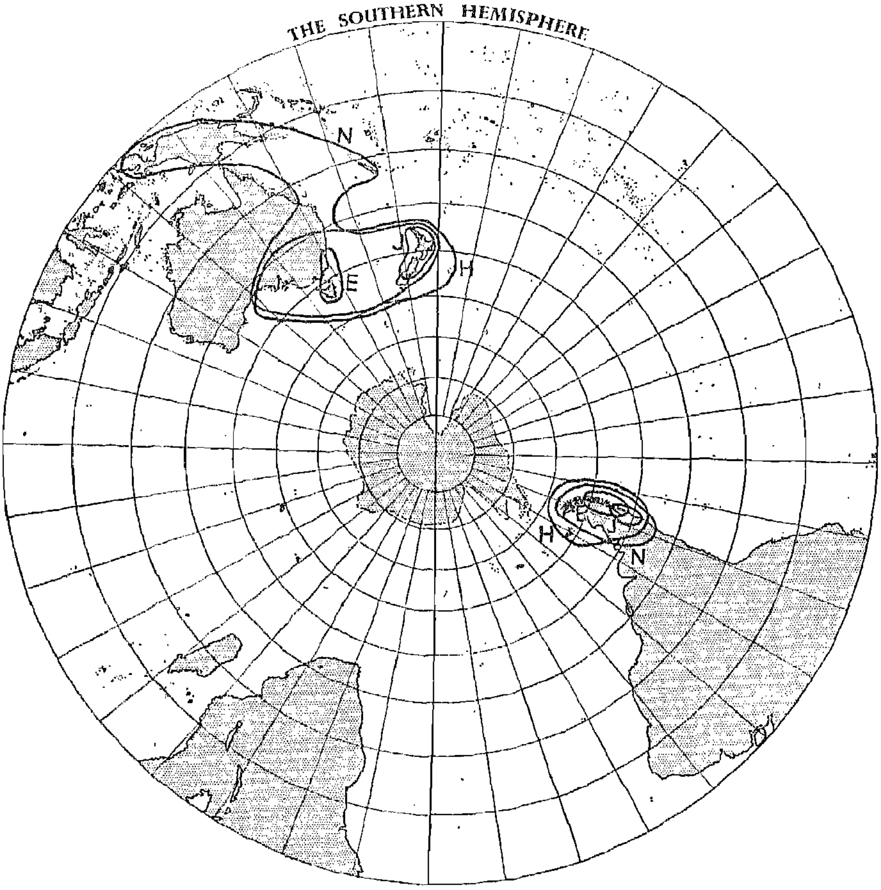

FIG. 33.—Map showing the distribution of the genera N, *Nothofagus*; H, *Hebe*; E, *Eucryphia*; J, *Jovellana.*

The genera of the first of these groups are of special interest and importance in relation to the past history of the Antarctic continent and have been much studied in this connection. The writings of Skottsberg in particular (see bibliography) on this subject are of first importance and should be consulted by all who are interested in the great problems they involve.

These genera can be further subdivided according to whether they are found in Australia and New Zealand or in only one of these. The first condition is, with wenty-one genera, much the commonest, and that of occurrence in *Australia* only is he rarest.

The general features of these southern temperate genera are fairly adequately displayed by their classification, but the following may be noticed in detail as specially noteworthy examples of the group:

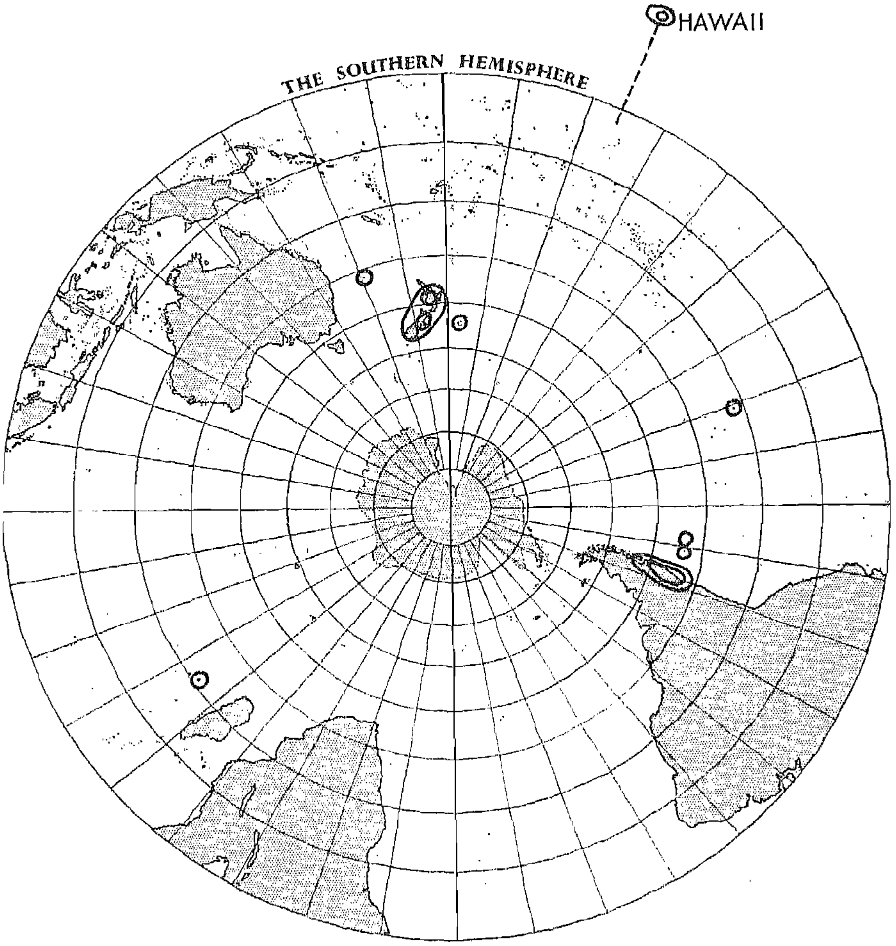

FIG. 34.—Map showing the distribution of the 13 species of the series *Tetrapterae* of the genus *Sophora*.

Colobanthus . .	Most of the species are confined to New Zealand, but one is common to New Zealand and Australia. There are also at least two ranging from New Zealand to South America and occurring also on many of the South Temperate Oceanic Islands.

Haloragis . . According to Tuyama (564) this genus had 59 of its 80 species in Australia, whence it extends to Rapa on the east and to Japan northwards, the latter chiefly by two exceptionally widely distributed species. There are also three species on the Juan Fernandez Islands. The genus thus well illustrates the not infrequent extension of an Australasian group far north of the equator, and the much rarer condition of occurrence in Juan Fernandez but not in continental America.

Lilaeopsis . . A genus of rather problematical species constitution and according to Hill (262) recorded from North America, Mexico, South America and the Falklands as well as from Australia, Tasmania and New Zealand.

FIG. 35.—*Eucryphia glutinosa*, about natural size, after Hutchinson.

Nothofagus . . This genus contains the southern beeches, and although usually kept distinct is closely related to *Fagus*. It has about a dozen species in Chile and Fuegia, about half a dozen in New Zealand, two in Australia, one in Tasmania, while one or two in New Caledonia, and several in New Guinea, have recently been reported (334) though it remains to be seen whether these are all truly congeneric (fig. 33). See also van Steenis (629).

Fuchsia . . Most of the species occur in America and especially in the tropical parts, but there are five, including *F. procumbens*, in New Zealand and one in the Society Islands (395).

Jovellana	A genus closely related to *Calceolaria*, with one or two species in Chile and a few in New Zealand (fig. 33).
Phyllachne	This genus has three species in New Zealand and Tasmania and one in Fuegia, the latter being the only member of the family (Stylidiaceae) in the New World (209) (fig. 3).
Drimys	Most of the species are in the eastern part of the Malayan Archipelago and especially in New Guinea, but there are others in Australia and in parts of South and Central America (fig. 5).
Restio	A large genus confined to South Africa and Australia and well represented in each. The family to which it belongs (Restionaceae) has, in general, much the same distribution.
Carpobrotus	This is one of the modern segregates of the large genus *Mesembryanthemum*. It has about a dozen species in South Africa, several in Australia and one in Chile.
Pringlea	"The Kerguelen cabbage," a monotypic genus once thought to be confined to the island group of that name but now known also from Heard Island, Marion Island and the Crozets. It thus combines very wide discontinuity with a very small actual area of occurrence.

Discontinuous genera of the north and south temperate zones

The fourth great category, of genera found only in the north and south temperate zones, is particularly hard to estimate because of the difficulty of determining the real status of many plants which occur more or less naturally in the temperate parts of the southern hemisphere. Frequently plants which seem, at first sight, to be native there, turn out on further investigation to be, in all probability, adventives, and therefore not to be reckoned as authentic cases of discontinuity. There is also the problem of deciding which of the many genera that extend with more or less marked gaps along the Andes are in fact sufficiently discontinuous to merit inclusion. When these two difficulties in particular are allowed for, the number of genera in the category appears not to exceed about sixty.

These are best further divided according to their ranges below the equator. Some occur, for instance, in all three parts of the southern hemisphere, others in only two out of three, and still others in only one. In all there are seven possible combinations and of these six occur, the only case of which there appear to be no examples being that of distribution in the northern temperate zone and in South America and South Africa. The commonest state is that of occurrence in the north and in South America only, and this is doubtless correlated with the exceptional ease of migration along the great line of the Rockies and the Andes. Details of the numbers in each of these several types must be sought in the Appendix, but the following may be cited as specially interesting examples of the category as a whole:

Triglochin	Among the many interesting features of this genus, which merits a careful geographical study, are the occurrence of several species in both the northern and southern temperate regions and the presence of a number of endemics, which are annuals, in Australia.
Frankenia	The wide total range of the genus (295) is due to the extensive distribution of a single species which is found more or less continuously from Europe to Central Asia and through Africa to the Cape, but there are also a number of other species in the Mediterranean region. Besides these there is a large group of species in Australia, another in Chile, and a smaller one in western North America. The genus is also recorded from St. Helena.

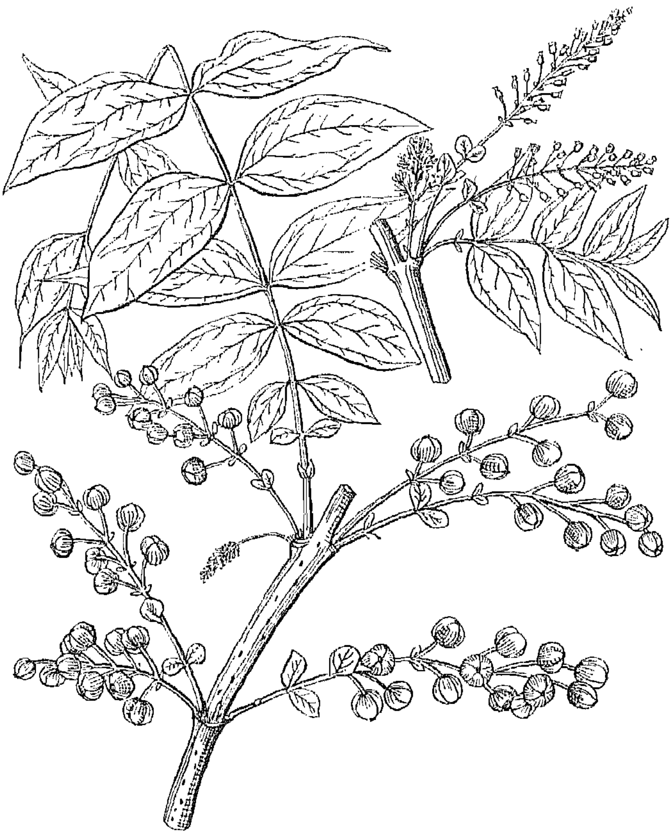

FIG. 36.—*Coriaria japonica*, about half natural size, after Bailey.

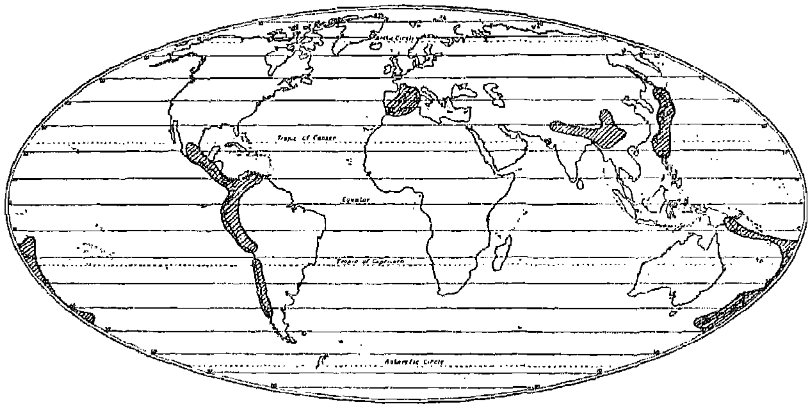

FIG. 37.—Map showing (shaded) the distribution of the genus *Coriaria*.

Myosurus . . . A very small genus found in the northern temperate zone and in all three parts of the southern temperate regions.

Coriaria . . . The only genus of its family and one of the most remarkable examples of discontinuity (213). The few species occur in tropical America, Chile, the Mediterranean region, eastern continental Asia, Japan and New Zealand (406). In addition at least one species is found both in South America and in New Zealand (figs. 36, 37).

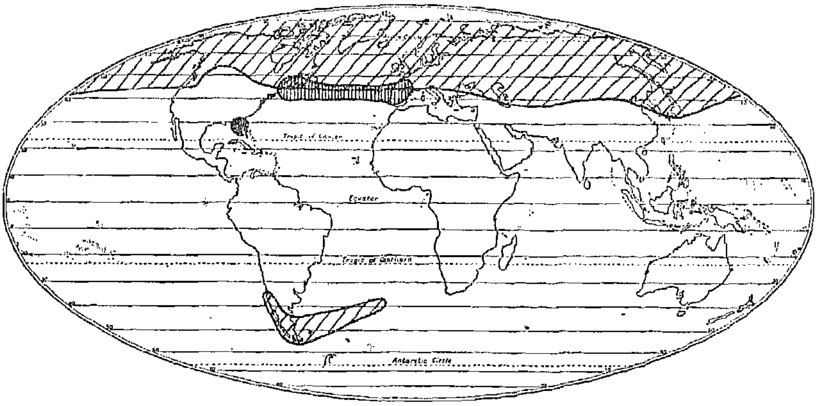

FIG. 38.—Map showing the distribution of the three genera of the family Empetraceae:—
wide diagonal shading—*Empetrum*,
close vertical shading—*Corema*,
solid black—*Ceratiola*.

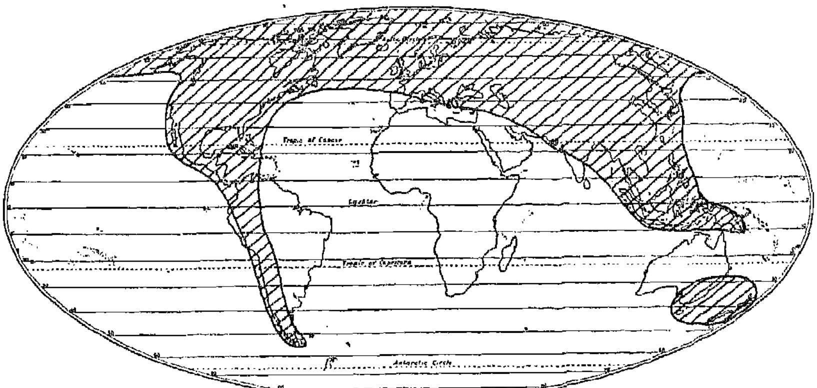

FIG. 39.—Map showing (shaded) the distribution of the genus *Gentiana*, mainly after Irmscher.

Eryngium . . . This genus has an unusual distribution and is a somewhat anomalous member of this category though it cannot be fitted in better elsewhere. It has one species concentration in western Eurasia and the Mediterranean, and another, larger, one in America, especially in the tropics. There are one or two species in Australia and New Zealand. The genus is absent from Asia except in the west; from tropical and south Africa; and is only slightly represented in North America.

Papaver	Almost entirely a northern genus and centred in the Mediterranean region, but there is one species in South Africa and Australia.
Oligomeris	There is one species in the south-west U.S.A. and in western Eurasia, and about seven in South Africa.
Damasonium	Two species occur in the Mediterranean region and there is one in the southern half of Australia.
Empetrum	Another very remarkable instance of discontinuity (211). It is a genus of two species and is completely circumpolar in the north. Elsewhere it is found only in temperate South America, including the Falklands, and on the Tristan group (fig. 38).
Honkenya	Widely distributed in the northern temperate regions and occurs also, apparently native, on the coast of Patagonia. It is a monotypic genus but its subspecies and forms are also completely segregated geographically.
Littorella	A genus of two species, one of which is found in Europe and in eastern North America and the other in Patagonia. It thus combines two distinct types of discontinuity.

Discontinuous genera present in Hawaii

The last of the five categories, that which concerns certain plants found in the Hawaiian Islands, is scarcely comparable with the others but it is, nevertheless, of considerable interest. It is made necessary by the extraordinary isolation of these islands and by their position roughly equally distant from Asia and America. As will be seen later, these islands have many endemic genera and their flora also includes others which are cosmopolitan, pan-temperate or pan-tropical. The fifty-odd genera which comprise the present category are therefore those genera of the flora which, outside the islands, have a fairly restricted distribution and which thus are of special interest as a clue to the general affinities of the flora.

In this connection it is most noteworthy that of these genera thirty-odd are found elsewhere only in the Old World, compared with about half a dozen found only in the New World. The rest are found in both. The category as a whole includes some genera with very remarkable distributions, and in particular the following deserve notice:

Acaena	This genus, besides occurring in Hawaii, is found in temperate Australasia; widely over the south temperate oceanic islands; at the Cape (1 species); rather widely in South America; and has an outlier in California (292).
Coprosma	According to Oliver (404), this genus is massed in New Zealand and in Hawaii, but it is found also in Australia, the Malayan Archipelago, the Pacific Islands and on the Juan Fernandez group (figs. 40, 41).
Pittosporum	A genus distributed widely in the tropical and south temperate zones of the Old World, but massed in Australasia. Secondary species concentrations are found in Madagascar, the Philippines, New Guinea and Hawaii and there is an outlying species in Macaronesia (221).
Cuphea	Another large genus, exclusively American except for one species which is found in Hawaii and also on the Galapagos Islands.
Astelia	According to Skottsberg (502 and in litt.), there are nine species in New Zealand, six in Hawaii, two in Australia, one in Australia and New Zealand, one in New Guinea, one in New Caledonia,

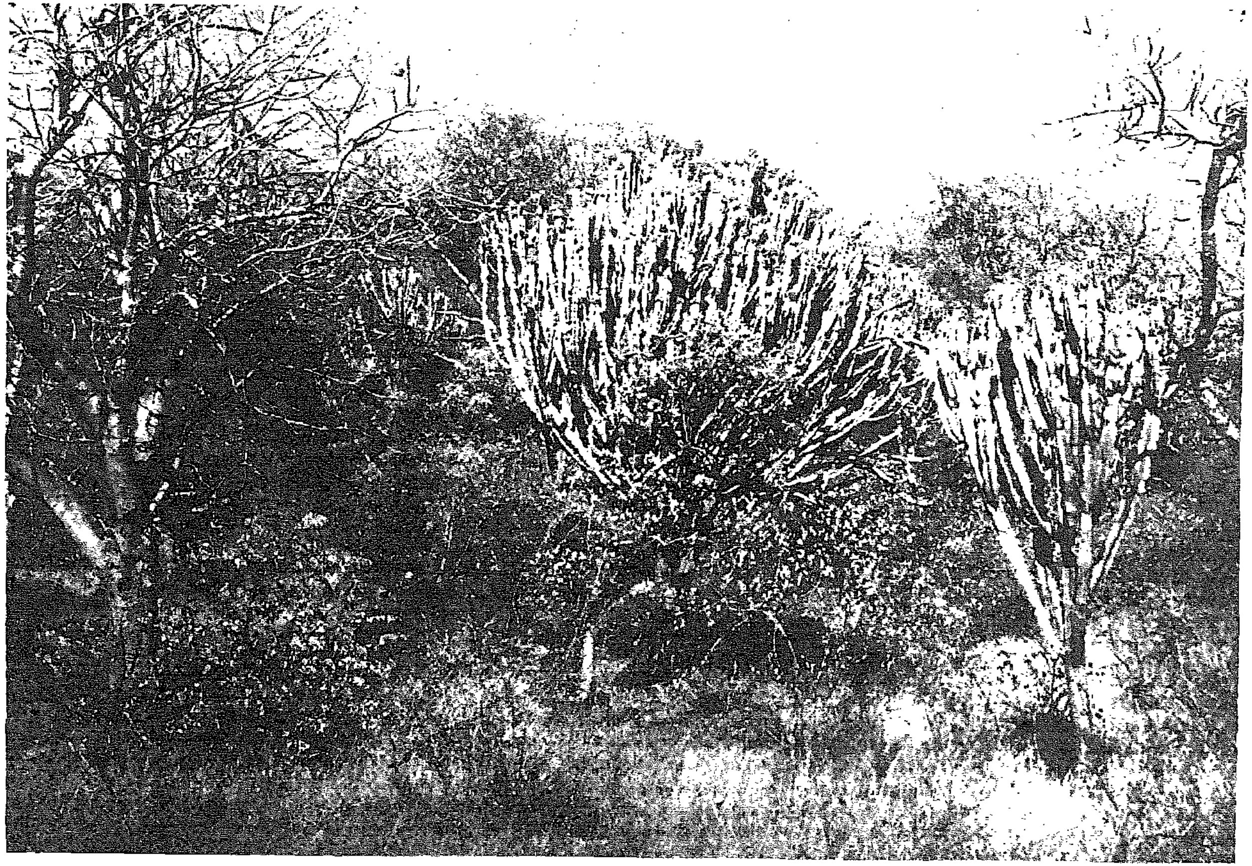

Plate 8. The cactus-like tree *Euphorbia ingens* among other vegetation in the northern Transvaal. Note the terminal flower clusters on the centre specimen

(*Photo: M. R. Levyns*)

FIG. 40.—*Coprosma nitida*, about natural size, after Hooker.

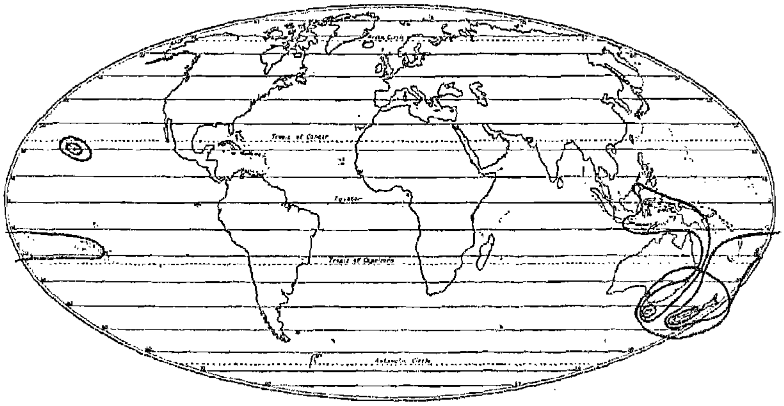

FIG. 41.—Map showing the distribution of the sections of the genus *Coprosma*, mainly after Oliver.

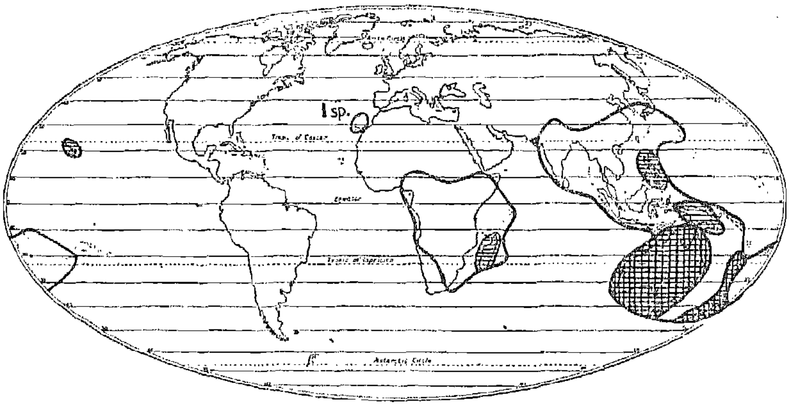

FIG. 42.—Map showing the distribution of the family Pittosporaceae. The areas of highest species concentration are cross-hatched: secondary concentrations are shown by horizontal lines.

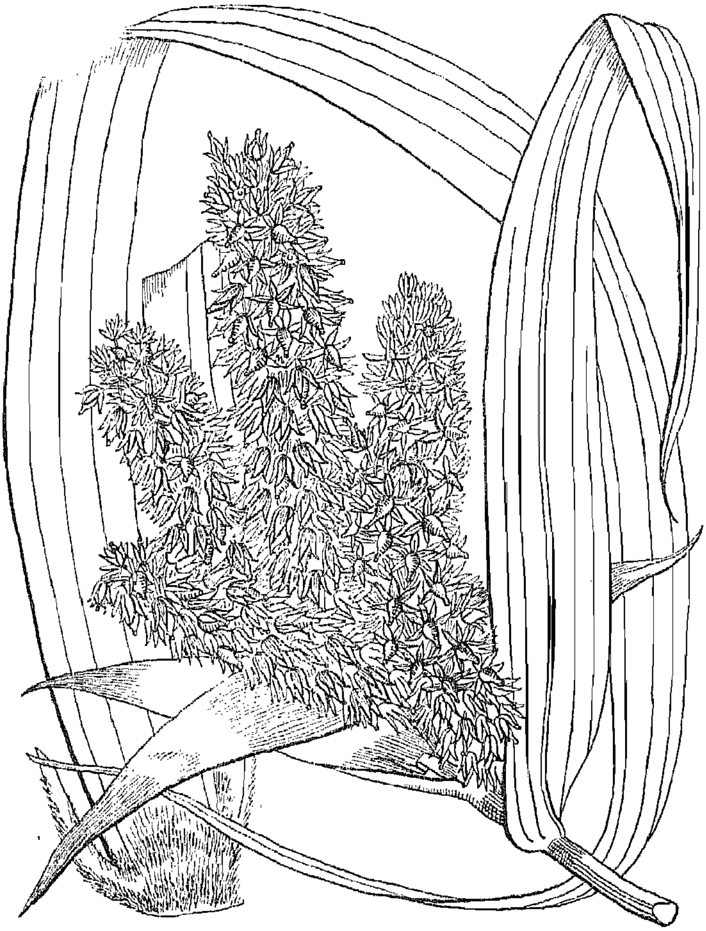

FIG. 43.—*Collospermum montanum*, somewhat reduced, after Seemann.

one in Tahiti, one in the Marquesas, one in Rapa, one in Réunion and Mauritius, and one in temperate South America (figs. 43, 44).

Nertera . . . A genus centred in New Zealand and with some representation in tropical Asia. It includes in addition one very widespread species recorded also from Australia, Tasmania, Hawaii, South America and Tristan da Cunha.

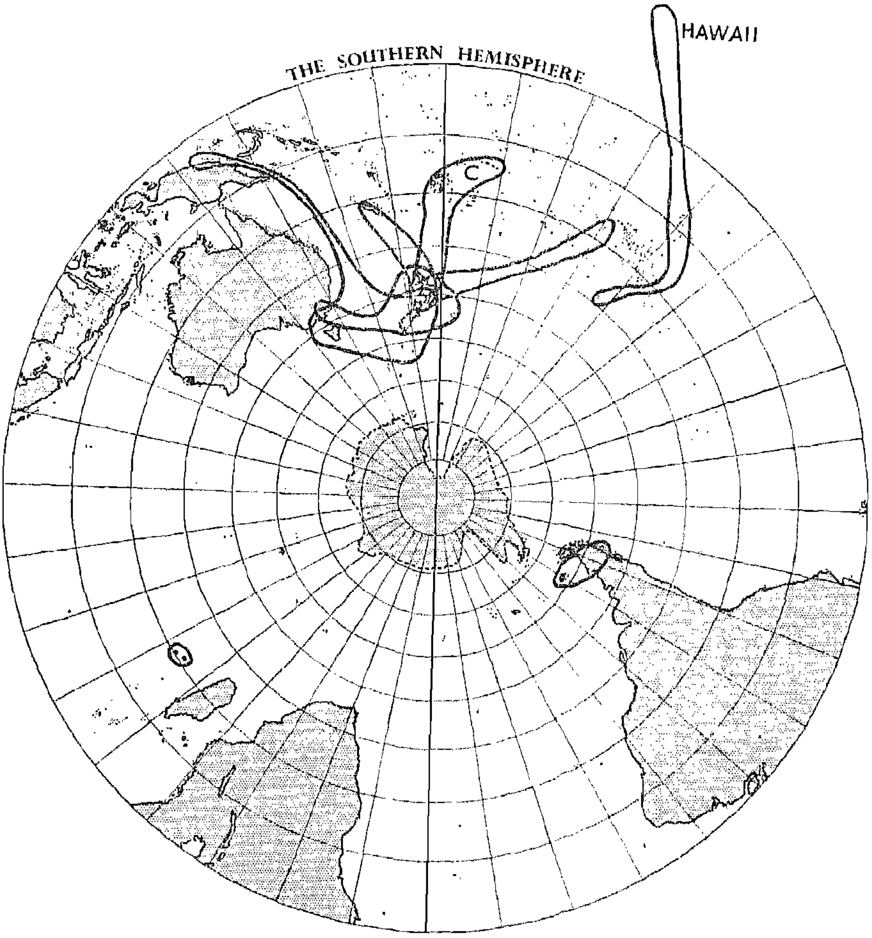

FIG. 44.—Map showing the distribution of the seven sections of the genus *Astelia*, and of the closely allied genus *Collospermum*, C (fig. 43).

Gunnera . . . According to Skottsberg (504) this genus is chiefly South American with a minor group in New Zealand, Tasmania and the Malayan Archipelago. It occurs also in Africa and Madagascar, and in Hawaii (Plate 9, fig. 45).

Metrosideros . The great majority of the species are in the Malayan Archipelago, Australia, New Caledonia and New Zealand, but there is an outlier in South Africa and several in Hawaii and Polynesia.

Three other genera of this category, all of them large, deserve mention together because of their high proportions of endemic species and great development on the islands of Malaysia and the Pacific, namely *Pandanus* and *Freycinetia*, which are closely related members of the same family of Monocotyledons, and *Cyrtandra*. All three have been discussed at some length, especially from the point of view of the problems which the details of their endemism present, by Guppy (241).

The most widespread of these is *Pandanus*, which ranges from Tropical Africa, through Madagascar (where it is strongly represented), over tropical south-east Asia, and Malaysia, where it has a great number of species especially in the Malay Peninsula, the Philippines and New Guinea, to Australia and far over the Pacific. From this last vast region more than one-fifth of all its species have been described. *Pandanus* has only a single species in Hawaii, but it extends east as far as the Marquesas and Rapa. Many of its species have been described as endemic on tiny islands, but a handful of species are widely distributed coastal plants. A considerable majority of its total species are south of the equator. *Freycinetia* is geographically a lesser version of *Pandanus* having much the same limits in the east but extending westward only as far as Ceylon. In the north it reaches Formosa and in the south New Zealand. Many more species have been described from the Philippines and New Guinea than anywhere else, and there are several in Hawaii. Like *Pandanus* it has most of its species south of the equator. *Cyrtandra*, which is as far removed taxonomically from the others as can well be imagined, ranges south and east from China, Siam and the Malay Peninsula to Australia and far across the Pacific to the Marquesas. Almost all its species, however, are in Malaysia and the Pacific Islands, the former having about twice as many as the latter, and in contrast to the two preceding genera, Hawaii, where all the species are endemic, is one of the greatest centres, the only larger ones being the Philippines and New Guinea. Its species are almost equal in numbers on both sides of the equator with perhaps a slight preponderance in the north.

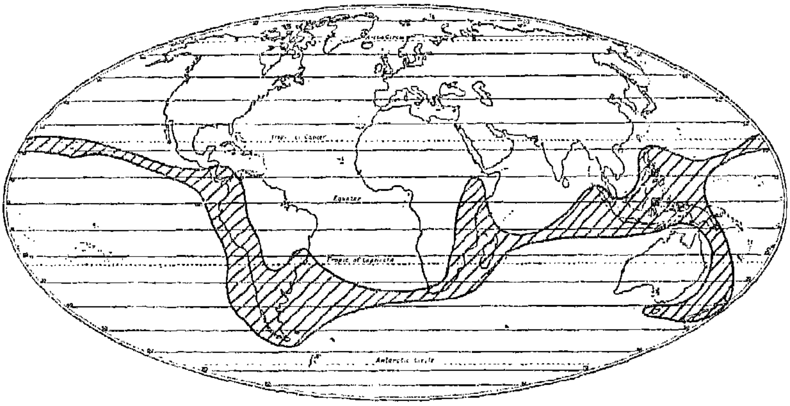

FIG. 45.—Map showing (shaded) the distribution of the genus *Gunnera*.

Finally the inclusion of the genus *Edwardsia* of Salisbury requires explanation. This genus includes various species which are more commonly regarded as belonging to the large genus *Sophora* which has lately been exhaustively studied by Dr.

Tsoong, who has most kindly provided the following as yet unpublished information. The genus *Edwardsia* cannot in his opinion be sustained, but its geographically most interesting species constitute a new series, *Tetrapterae*, of *Sophora*. This series comprises thirteen species distributed as follows (see fig. 34)—two on Hawaii, one on Lord Howe Island, one on the Chatham Islands, three in New Zealand, one in Réunion, two in temperate South America, two on Juan Fernandez (one on Masafuera and one on Masatierra), and one on Easter Island. The occurrence of one of these species on Gough Island is presumably regarded as adventive. A closely related series containing two other species of *Edwardsia* occurs in continental Asia. There are two other related monotypic series, one of which is found on coasts throughout the tropics, and the other in Korea.

The complete list as given in Appendix B contains about 750 genera. For the reasons given earlier this is almost certainly an appreciable underestimate of the total number of discontinuous genera in the Angiosperms, and hence it can at least be said that these amount to more than 5 per cent. of all genera. Among them tropical genera predominate strongly.

It would be particularly interesting to calculate the number of discontinuous genera in the different families, but the method of classification of certain families makes it almost impossible to do this. It is, however, possible to calculate the relative and absolute frequency of the different families represented in the list, and this reveals some interesting facts.

The Leguminosae, using that term in its comprehensive sense, is the most frequent group and is followed in the order named by the Compositae, Euphorbiaceae, Rubiaceae, Liliaceae, Scrophulariaceae and Apocynaceae. Taking into account what has been said about the Compositae in particular, the number here is remarkably high and indicates that, as might be expected from its size, this family probably actually has more discontinuous genera in total than any other.

It is more interesting to note that, as the list stands at present, some of the smaller families show by far the highest *proportion* of widely discontinuous genera. Saxifragaceae, Gentianaceae, Sterculiaceae, Rutaceae, Olacaceae, Meliaceae, Oleaceae, Rhamnaceae, Aizoaceae, Simaroubaceae, Combretaceae and Rhizophoraceae, for instance, have very high figures, but even these are exceeded by the Magnoliaceae and, above all, by the Berberidaceae. In the last indeed practically every genus finds a place somewhere in the list, and this fact, if it is not already sufficiently realised, may well attract the special attention of students of this family.

Mention of the Rhizophoraceae, the family containing the mangroves, serves as a reminder that one very special kind of discontinuous distribution has received practically no notice above. This is the discontinuity which is generally and indeed almost inevitably shown by wide ranging plants whose habitats are in, or closely associated with, shallow marine waters. Such plants fall into three groups, namely, the marine Angiosperms, which live actually submerged in the sea; the mangroves, which inhabit muddy tidal shores; and certain so-called strand plants, which grow either on, or just inland of, sandy shores. Each of these groups contains many genera which are discontinuous and form a conspicuous element in at least the tropical category of the list given in Appendix B. It is clear, however, that their discontinuity is of a very particular and special kind, and for this reason and also because it is, more often than not, a matter of individual species, more detailed consideration is deferred to a later chapter, where it will be described at some length.

CHAPTER 7

THE DISTRIBUTION OF GENERA—III

Endemic Genera

ENDEMIC genera have been defined, for present purposes, as genera either actually confined to one floristic region or having distributions not greatly exceeding the average size of a region. This latter qualification is necessary because many genera, while comparatively restricted in range, actually extend over parts of two regions. On the other hand, many are so local as to occupy much less than the whole of an average region.

Taking into account the figures already given for other categories, it would appear that about 10,000 genera are endemic in the sense just defined, and for the purposes of the short and formal survey which is all that is possible here they can be dealt with most conveniently if they are classified according to the thirty-seven regions which form the basis of the floristic arrangement used here. Here and there it is necessary for special reasons to depart from this treatment, but on the whole it not only permits the easy handling of this great mass of genera but also provides a useful opportunity for drawing attention to special features of interest in the floras of these regions.

As far as possible figures are again quoted, but they are intended only to give some idea of relative numbers. The various examples selected for mention are, whenever possible, those most likely to be familiar to the general reader.

It should also be borne in mind that the inclusion of a genus in any particular regional account does not necessarily mean that it is exclusively confined to that region but only that the region in question is that of which it is most characteristic. Many genera naturally extend somewhat beyond the limits of the region in which the bulk of their range and/or the majority of their species occur.

Arctic and Sub-arctic Region

The arctic provides an excellent instance of the limitations to the use of endemism in estimating floristic rank, because, though it is commonly agreed that the arctic flora is a sufficiently distinct entity to be reckoned as a major unit in floristic classification, it has, in fact, practically no endemic genera. A few, including *Arctagrostis* and *Parrya*, have been described as such, but they are small and not too well defined. It is in this negative quality that the chief interest of the arctic flora lies, because the proportion of endemism in a flora tends to increase with the degree and duration of its isolation. There is good reason to believe that the arctic flora, in its present form, is one of the youngest and perhaps the youngest in the world. It also shows a minimum amount of isolation, consisting merely of the most resistant elements of the northern temperate flora and their derivatives (see pp. 161 *et seq.* below), and the boundary between the two indeed is largely a subjective one. It should also be borne in mind that the arctic region, except for Greenland, which is almost covered by an ice-cap, is a small one and that the polar region proper is occupied by the Arctic Ocean.

Euro-Siberian Region

It was found convenient to deal with the genera which range throughout this exceptionally extensive region in the last chapter, and attention is here confined to genera which are endemic to one or other part of it.

One good reason for dividing this very elongated region into two is that, although these are clearly but parts of one whole, conditions at the two ends of the region are very different. In the west the influence of the Gulf Stream results in a considerable latitudinal depth of comparatively genial climate, especially in winter, and this, coupled with an absence of barriers, not only gives room for a wide development of deciduous forest vegetation but also adds to the general flora a noteworthy element from the Mediterranean region to the south. On the east the coast is entirely icebound in winter and the climate of the interior is one of the most severe in the world, characterised by enormous seasonal variation in air temperature above a subsoil which, for the most part, is permanently frozen. Moreover the direction of continuous mountain ranges not only narrows the region geographically and restricts it vegetationally largely to coniferous forest, but cuts it off from easy general infiltration from China on the south, where the East Asiatic deciduous forest flora is found.

The dividing line between the two subregions (see p. 28) follows the longitude 60° E., partly because such a line is easily recognised and drawn on maps, partly because it follows, reasonably closely, the main physiographic feature of the Urals, partly because, so doing, it marks also the boundary between Europe and Siberia, and partly because it marks, more or less accurately, the limits of various constituents of the European deciduous forest flora.

It is not surprising, in view of these considerations, that the flora of the western part of the region is much richer than that of the eastern part, and this is shown by the fact that while Europe has between fifty and one hundred endemic genera, according to taxonomic taste, and some of these not of the smallest size, Siberia appears to have very few, perhaps no more than a dozen or so, and nearly all of them monotypic. The former include *Bulbocodium*, *Lunaria*, *Melittis*, *Physospermum*, *Stratiotes* and *Pulmonaria*, the last with about a dozen species being perhaps the largest. These are scarcely to be distinguished from genera characteristic of Europe, but which extend somewhat into western Asia, such as *Astrantia*, *Eremurus*, *Laburnum* and *Vinca*. Strictly confined to Europe and actually even more strongly localised are about twenty genera found only in one or other of the mountain systems, among them *Erinus*, *Nigritella*, *Ramonda* and *Soldanella*. *Bryonia*, *Carlina* and *Crithmum* exemplify genera which are very familiar in west Eurasia but which extend also to Macaronesia.

None of the Siberian endemic genera are important or familiar, and *Borodinia*, *Macropodium* and *Redowskia* are examples of the Cruciferae which seem to provide the bulk of them. Certain other genera, however, are rather characteristic of this subregion though they extend outside it, and of these there may be mentioned *Bergenia*, *Caragana* and *Rheum*.

Sino-Japanese Region

This region consists of three main parts—the elevated area of the Sino-Himalayan-Tibetan mountains; the rest of China except the south; and an insular area, Japan. The flora is, on the whole, homogeneous throughout except that the inclusion of the total Himalayan complex brings in extraneous elements to some extent. To regard these mountains as a single whole, however, makes for a very useful simplification and does not obscure any very salient facts.

The total number of endemic genera in this very considerable region is almost certainly three hundred or more, but it is difficult to give figures because new plants are still being discovered in it. Whatever the figures are, the genera divide fairly simply into groups. A few range over almost the whole region, among them *Aucuba*, *Caryopteris*, *Hovenia* and *Metaplexis*. More are found in both China and Japan and thus cover nearly the whole area, and these include *Callistephus*, *Paulownia* and *Rehmannia*. Genera confined to China number well over a hundred and may be many more, but it must be remembered that the southern part of the country belongs to another region. Chinese genera include *Corallodiscus*, *Kerria*, *Litchi* and *Poncirus*. For Japan, Willis (597) lists about seventy for the whole country, but other sources indicate a lower figure. One genus at least, *Fatsia*, is familiar. One or more endemic genera have been described from the Bonin Islands.

The Himalayan system is the native home of many highly prized garden plants, but its strict endemics number less than 100, most of its characteristic genera having wider ranges. Among the better known examples are *Davidia*, *Leycesteria* and *Nomocharis*. Several genera, while massed in the Himalayas, extend somewhat out of the region, as, for instance, *Cremanthodium* (212), which can only be included here by stretching a point, as one or two of its more atypical species reach well into Tibet and North China, and *Codonopsis*, which actually reaches Japan. *Meconopsis* also is essentially a Himalayan genus but in fact, on account of a species in Europe, discontinuous.

On the south the region shows considerable linkage with its neighbours. A number of genera are, for instance, described as ranging from India to Japan, and in another direction a handful of genera extend south towards Malaya, among them being *Aspidistra* and *Schizophragma*.

Western and Central Asiatic Region

This region, which comprises the Caucasus, Armenia, part of Persia, part of Russia, and part of Tibet, as well as the rather indeterminate countries between east Europe and China, is difficult to deal with because its limits bear little relation to political boundaries, a point which always complicates the investigation of plant distribution. It consists of dry mountainous areas or of actual deserts which are often salt, and the vegetation is comparatively limited and specialised.

As far as any estimate can be of value it appears to contain about 150 endemic genera, of which Tibet has perhaps a dozen, and these are almost all small and specialised. Halophytes and xerophytes are well represented, and more than a third of the total belong to the Cruciferae, a family of notoriously difficult generic distinction. Chenopodiaceae and Umbelliferae are also plentiful, and these three families together account for more than half the total. Most of the genera are fairly well distributed, but some, like *Dorema*, are restricted to the western part and others, like *Potaninia* and *Tetraena*, to the east.

Cannabis and *Spinacia* are almost the only very familiar genera. The former, as far as its native range can now be determined, is confined to the region, but the latter extends into Mesopotamia. *Exochorda* extends eastwards into China, and *Phelipaea* is a true endemic parasitic genus.

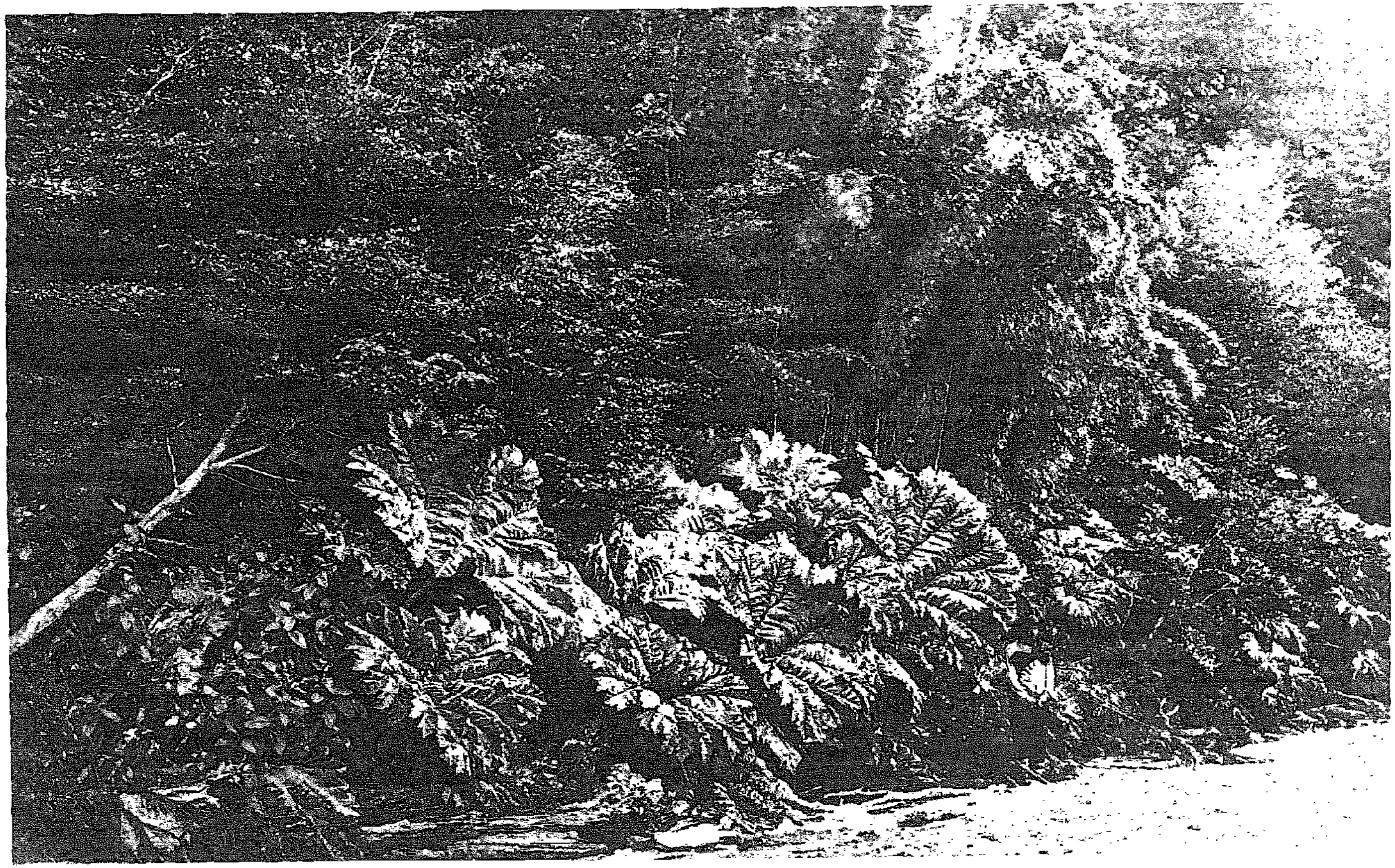

Plate 9. *Gunnera chilensis* in S. Chile

(from Karsten & Schenck, Vegetationsbilder)

Mediterranean Region

The actual area of land within this region is small, being confined, except for the larger part of the Iberian Peninsula, to the littoral zones of the Mediterranean, and it has a very specialised type of vegetation (153, 365), which is reflected in a high proportion of endemic forms. Furthermore, the boundaries between it and the neighbouring regions are not always clear and many genera characteristic of the Mediterranean in fact extend far beyond it. This is specially noteworthy in the north, where many Mediterranean genera range far up into western Europe and some actually reach the British Isles, where, as will be seen later, they form an important element in its flora. Among these are *Anthyllis*, *Atropa*, *Bellis*, *Hippocrepis*, *Jasione*, *Medicago*, *Ophrys*, *Origanum*, *Tamus*, *Ulex* and *Verbascum*. Among others, mainly represented in Britain by garden plants only, are *Centranthus*, *Crocus*, *Galanthus*, *Gypsophila*, *Helleborus*, *Lavandula*, *Muscari*, *Narcissus* (176) and *Nigella*.

Including these the total number of Mediterranean genera is probably about 250. Among them *Aethionema* and *Cistus* stand out as exceptionally large genera, the former having more than fifty species. The latter, though rather smaller, is perhaps the most characteristic of all Mediterranean plant groups because it contributes so largely to the peculiar type of vegetation known as the " maquis." Among other fairly well known examples are *Aubrietia*, *Galega*, *Malope*, *Phillyrea*, *Pisum*, *Rosmarinus* and *Santolina*, all of which range fairly widely over the region.

As examples of rather more restricted genera there may be mentioned—*Helxine* on Corsica and Sardinia; *Triplachne* on Sicily; *Astrocarpus* in Spain; *Argania* in North Africa; *Drosophyllum* in south Spain and neighbouring North Africa and several notable monotypic genera of Cruciferae in south Spain. There are also a few genera, mostly Umbelliferous, recorded only from Syria.

On the east side the region connects up with Central Asia by several genera such as *Chionodoxa*, *Cicer* and *Danae*, but it is difficult to classify genera here, because while parts of the coast of Asia Minor belong floristically to the Mediterranean region the interior belongs to Western and Central Asia. On the west side the region shows relationship with Macaronesia in the presence of several genera, including *Ecballium*, *Echium* and *Ruscus*, which occur in both.

Macaronesian Region

The degree of generic endemism in this region is low and chiefly of interest in relation to its distribution among the island groups. In all there are less than thirty endemic genera. Of these about half are confined to the Canaries, including *Phyllis*, *Plocama* and *Semele*. A few are confined to Madeira. Two only are found on the Cape Verdes, and there is none on the Azores. Of the rest three, including *Isoplexis*, inhabit the Canaries and Madeira; *Lytanthus* is in the Canaries and the Azores: and *Aichryson* ranges over the Canaries, Madeira and the Azores.

It should be noted that the Canaries, though volcanic, are in the position of continental islands, and that they have most endemics, while the most isolated group, the Azores, has none.

Atlantic North American Region

The endemic genera of this region probably number between one and two hundred. It must, however, be remembered that many genera characteristic of eastern North America extend right across the continent and have, therefore, been considered among the wide genera in Chapter 5.

Some of the endemics, like *Baptisia* and *Robinia*, are almost extensive enough to rank as wides, but there are others which are very narrow. *Franklinia* is a particularly interesting case because it appears to be one of the few genera which have actually become extinct in a wild state during the historical period. One single plant of a single species was discovered in the eighteenth century on the Atamaha River in Georgia (175), and from this tree the existing garden individuals are all descended. The original wild tree, however, has disappeared and apparently no other has ever been seen.

Among other genera confined to the Atlantic States of North America are *Ceratiola*, *Dionaea*, *Dirca*, *Gatesia*, *Hudsonia*, *Meehania*, *Neviusia*, *Pleea*, *Sanguinaria*, *Sarracenia* and *Uvularia*.

Pacific North American Region

Various estimates go to indicate that there are at least three hundred endemic genera in this region. The richest part is certainly California, but many genera extend nearly all over it. It is, however, safe to say that the number is greater in the south than in the north.

Eschscholzia and *Abronia* are good examples of wider endemics, while *Sidalcea* and *Tolmiea* exemplify genera of the more northern parts. Others, chiefly of the south, are *Choisya*, *Darlingtonia*, *Dendromecon*, *Lewisia*, *Nolina*, and *Romneya*. *Sarcodes* is a remarkable saprophytic plant from the Sierra Nevada.

As is usual, a number of genera mainly characteristic of the region show transition with its neighbours. *Yucca*, for instance, though characteristic of the southwestern U.S.A., extends widely east in the southern part of its range. *Bigelovia*, similarly, has one species in the east. *Zinnia*, again, is centred in the southern part of the region but has one species which extends right down to Chile. *Garrya* reaches Mexico and the West Indies; and *Calochortus* reaches Guatemala.

North African—Indian Desert Region

This region, though one of the largest, has, as might be expected from the nature of its climate, a comparatively restricted vegetation, and the number of its endemic genera, none of which is large, probably does not much exceed fifty. Among them the Cruciferae and Compositae are particularly well represented.

Some of these genera are relatively widespread, as, for instance, *Anastatica*, *Londesia* (which reaches Mongolia), *Ochradenus* (which reaches Abyssinia), and *Savignya*, but others are confined either to the western part from Morocco to Arabia (e.g. *Cornulaca* and *Zilla*) or to the eastern part from Persia to Afghanistan (e.g. *Fortuynia*, *Reptonia* and *Zataria*).

Among more restricted endemics are *Mecomischus* from the Sahara; *Saltia* from Aden; *Omania* and *Xerotia* from Arabia.

At the other extreme there are certain genera which though ranging variously beyond the strict limits of this region are nevertheless very characteristic of it, and among these *Daemia*, *Glossonema* and *Leptadenia*, all belonging to the Asclepiadaceae, may be cited.

Endemic Genera of Tropical Africa

This is one of the points at which it is convenient to depart from a rigid regional classification, because the different regions into which tropical Africa is divided are so closely related that a large number of genera are not markedly confined to one of them although they are not found outside the tropical parts of the continent. They therefore can scarcely rank as wides, and must receive notice here.

These more extensive endemics probably number several hundred but most of them are small, although *Ritchiea*, for instance, has upwards of fifty species. They include *Cola*, *Erythrocephalum*, *Khaya*, *Margaretta*, *Monotes*, *Octoknema*, *Oricia*, *Pleiotaxis* and *Ricinodendron*.

Some are confined to the mountains and occasionally show some discontinuity. *Thunbergianthus*, for instance, is recorded from the island of S. Tomé in the Gulf of Guinea and from Ruwenzori; and *Pseudagrostistachys* from S. Tomé, Fernando Po and the Ruwenzori region.

Even with the more narrowly distributed endemic genera of tropical Africa it is convenient to modify the regional classification slightly and in two instances to combine together a pair of separate regions. These pairs are the Sudanese Steppe Region and the West African Forest Region, and the North-east African Highland and Steppe Region and the East African Steppe Region, respectively. By reckoning these four as two double regions an important point is emphasised, namely the occurrence of two well-marked floras, one covering what may be called western tropical Africa and the other eastern and southern tropical Africa, and the advantage of doing this outweighs the drawback of departing from the more rigid regional arrangement, and also simplifies the presentation of the relevant facts.

Sudanese Park Steppe Region and West African Rain-forest Region

The total number of endemic genera in these two portions of the African continent appears at present to be about 250, but knowledge of the flora here has increased in late years and this may well prove to be an underestimate. Whatever the number may be, however, there is no doubt that the majority of them belong to the forest rather than to the steppes, not because the forest flora is richer but because the steppe flora is mainly part of one which covers much of the African tropics.

Moreover, except to the specialist, the genera are not very familiar and there need only be mentioned *Anisopus*, *Carpodinus*, *Maesobotrya*, *Napoleona* and *Oldfieldia*.

Several genera, including *Heteradelphia* and *Principina*, are confined to the small islands in the Gulf of Guinea.

North-east African Highland and Steppe Region and East African Steppe Region

Taken together these two regions represent eastern and southern tropical Africa, and reach from the Red Sea to south Angola. The north-east part divides very clearly into two areas, the highlands of Abyssinia and the lowlands of Eritrea and Somaliland, and the flora of the first is closely related to the rest of tropical Africa, while that of the second is more nearly allied with that of the North African-Indian desert region.

The total number of endemic genera in this double region is probably of the order of 200, with the same reservation as in West Africa.

The north-east region does not account for more than about fifty of these, and nearly half of this group are confined to the island of Socotra, which for its position has a remarkably peculiar flora. The rest are fairly evenly divided between

Abyssinia and Somaliland, examples of the former being *Afrovivella* and *Hagenia*, and of the latter *Drakebrockmania* and *Poskea*. *Oreophyton* and *Edithcolea* range southward into East Africa proper, and *Morettia* connects the region with that of the African-Indian deserts.

The endemic genera of the rest of eastern and southern tropical Africa are practically all small and unfamiliar and scarcely form a conspicuous element in the flora. This is due chiefly to the great mingling of floras which has taken place here, and especially to the extension northward in East Africa of many genera more particularly characteristic of the southern parts of the continent.

The more strictly endemic genera are for the most part found either on the east side of the continent (Kenya to Nyasa) or in Angola and northern South West Africa. The former include *Saintpaulia* (*S. ionantha* is a not unfamiliar greenhouse plant) and *Synadenium*, and among the latter are *Corynanthe* and *Umbellulanthus*.

The Madagascar Region

This region comprises Madagascar and its small islands; the Comoros between Madagascar and the mainland; Aldabra and the Seychelles to the north; and the Mascarenes to the east.

The number of endemic genera is large and the total may be well over 200 (221) of which the great majority are found on Madagascar itself, or, as in the case of a few small genera, on the very tiny islands close to it, but estimates of the total vary considerably (416).

The most striking element in the endemic flora of Madagascar is that of the seven genera which make up the endemic family Chlaenaceae, and of which *Rhodochlaena* is perhaps the chief. Perrier de la Bathie (415) has described the distribution of these in some detail. He divides the island into two main floristic regions, an eastern, windward region, including all the mountainous parts, in which the vegetation is evergreen; and a smaller leeward region, where the vegetation is deciduous. The species of Chlaenaceae are massed particularly in the northern corner of the island and in the mid latitudes of the eastern region. In the west, which is the part where human influence has been greatest, there is only one genus of four species.

Among other endemics are *Bembicia*, *Boutonia*, *Hydrotriche*, *Stapelianthus*, *Vomitra* and the extraordinary cactus-like *Didierea*. *Symphytosiphon* is said to be confined to the small island of Nossi Bé.

Certain genera, among them *Dicorypha*, *Humblotidendron* and *Ravenea*, are found on both Madagascar and the Comoros, while a few others, including *Cremocarpus*, are confined to the latter.

Lomatophyllum, *Oncostemon* (which has been described as the largest genus which is confined to islands) and *Poupartia* exemplify a small group of genera which range over Madagascar and the Mascarenes. *Brandzeia* appears to be the only genus restricted to Madagascar and the Seychelles.

The endemics of the Mascarenes number about thirty and are variously distributed. For example *Cylindrocline* and *Roussea* occur on Mauritius; *Hyophorbe* and *Pyrostria* on Mauritius and Rodriguez; *Mathurina* and *Scyphochlamys* on Rodriguez; *Fargesia* and *Guya* on Réunion.

There are about a dozen endemic genera in the Seychelles. *Medusagyne*, which is found only on a single island, forms an exceptionally local family, while *Deckenia* and *Lodoicea* are noteworthy genera of palms.

Region of Ascension and St. Helena

In area this is probably one of the smallest of all the regions, comprising only two small islands. Its natural flora is also extremely small to-day because the rich native vegetation of the larger island has gradually become almost exterminated (562). There is, however, still enough left to show that the original flora was almost entirely distinctive and peculiar. The degree of specific endemism indeed must have been very high (see p. 188), although the number of endemic genera was perhaps not considerable.

To-day there are known only five endemic genera, all from St. Helena. They are *Mellissea*, *Petrobium*, *Nesiota*, *Commidendron* and *Melanodendron*, the last two exemplifying the woody members of the Compositae which are, and still more were, a feature of the flora.

South African endemic genera

Once again, in the case of South Africa it is desirable to depart from the regional classification. Two regions cover the southern part of the African continent (292, 421), but they are very different from one another. The Cape region, which actually constitutes a separate floristic kingdom, consists only of the south-west part of the Cape Province and is thus one of the smallest continental regions, but it has one of the most remarkable, and perhaps the richest, of all the world's floras. It is also of special interest because it has contributed much to the beauty of European gardens. The South African region, on the other hand, has not a particularly rich flora and represents the meeting ground of elements from the more tropical north and from the specialised Cape flora to the south (51). The latter on the whole predominate, or at least do so over much of this region, and it may be regarded more particularly as related to the Cape flora. For this reason alone there would be grounds for combining the two here, but there is also an important practical reason for so doing.

The combined area of both is roughly that of the Union of South Africa, and the flora of this political area has been analysed in great detail by Phillips (418, 623), so that by combining the two regions a great number of statistics are conveniently to hand. According to Phillips the flora of the Union of South Africa contains about 1,500 genera with native species, and of these some 500 are endemic, giving a proportion of about 30 per cent., a figure perhaps not exceeded anywhere. The flora also includes a number of endemic families, but these are for the most part small. As might be expected, the endemic genera vary greatly in size from monotypes, of which there are about 200, to genera with over one hundred species. Among these latter are *Agathosma*, *Aspalathus* and *Heliophila*, and other large genera are *Gasteria*, *Lachenalia* and *Leucadendron*. The endemics are specially numerous in certain families. For example *Elegia*, *Hypodiscus*, *Thamnochortus* and *Willdenowia* belong to the Restionaceae; *Lebeckia*, *Podalyria*, *Priestleya* and *Rafnia* to the Leguminosae; *Grisebachia*, *Salaxis*, *Scyphogyne*, *Simocheilus* and *Sympieza* are closely related genera of the Ericaceae; and *Chrysocoma*, *Eriocephalus*, *Metalasia*, *Oldenburgia* and *Relhania* belong to the Compositae. Among other endemic genera belonging to less conspicuous families are *Duvalia*, *Freesia*, *Galtonia*, *Mimetes*, *Pectinaria*, *Prismatocarpus*, *Rochea*, *Roella*, *Roridula*, *Sarcocaulon* and *Strelitzia*. It must also be remembered that many of the genera included in wider African categories are in fact almost entirely confined to this part of South Africa.

The case of *Mesembryanthemum* (Plate 11), one of the most characteristic of all

South African genera, requires special comment. In its old conception of a single huge genus of several hundred species, *Mesembryanthemum*, although almost entirely confined to South Africa, was not entirely so since a handful of species extended to a considerable distance elsewhere. In recent years, however, this huge genus has been split up into about one hundred smaller genera, mostly of only a few species each. Of these practically all are confined, often very narrowly, to South Africa and have the effect of appreciably increasing the number of genera endemic to that kingdom.

Indian Region

This region divides latitudinally into three distinct parts—the subtropical flanks of the Himalayas, the Indian Peninsula proper, and Ceylon, and the first and last of these are botanically of the greater consequence. Floristically the northern and eastern limits of the region are fairly accurately marked by the southern boundary of the distribution of the Cupuliferae.

Hooker (276), to whom we owe so much of our knowledge of the Indian flora, emphasises that the sub-continent is essentially a meeting place of floras from the west, the north and the east, and that it has little real botanical character of its own, as is reflected in the small size of the endemic element. The total of endemic genera within the region is probably not more than 150, of which the great majority are monotypic and very local. About 20 are confined to Ceylon; a somewhat similar number occur in both India and Ceylon; and the rest are fairly evenly divided between the Himalayas and the peninsula.

The endemics of Ceylon, among which members of the Dipterocarpaceae are conspicuous, include the largest of all, *Stemonoporus*, with a dozen or more species, *Hortonia*, *Nargedia* and *Schumacheria*. Genera of both India and Ceylon include *Heylandia*, *Lagenandra* and *Zeylanidium*. Among the Indian endemics are *Blepharistemma*, *Cruddasia*, *Hitchenia* and an interesting small group of Asclepiadaceae, among them *Utleria*, generally described as the only arborescent member of the family. Among the endemics of the Himalayas may be mentioned *Amphicome*, *Dittoceras* and *Dodecania*.

Continental South-east Asiatic Region

This region comprises the Andamans and Nicobars, Burma, tropical China, Formosa and the Riukiu Islands (368), Hainan, Siam and Indo-China, and has a vegetation comparable in luxuriance with that of Malaysia. Floristically, however, it is not an outstanding region, and indeed might be described as transitional or intermediate between the rich floras of Malaysia in the south and of China in the north. Furthermore, it is still far from completely known. The floristic boundary between this and the Indian region is well marked.

As might therefore be expected the degree of endemism is not remarkable, and is also very difficult to estimate, but the number of endemic genera is probably now over 250, though nearly all of these are small and localised. *Parabarium* is one of the largest, and others that may be noted are *Bousigonia*, *Schizocapsa*, *Tirania* and *Trisepalum*.

Numerous genera link the region with its neighbours north and south and a small but conspicuous group links it with the Indian region. Some of these range from India to Siam, and others to the Malay Peninsula, among them being *Pentasacme*, *Sapria* (Himalayas and Siam) and *Sphinctacanthus*.

There are one or two endemic genera in the Riukiu Islands but the Andamans and Nicobars have none.

The Malaysian Region

For many reasons, and especially for those connected with theories of palaeogeography, Malaysia is, quite apart from its great floral richness, one of the most interesting parts of the world.

A bathymetrical map of the world, such as Plate 3, shows that the western part of the Malayan Archipelago, comprising Java and Bali, Sumatra and Borneo, or the Sunda Islands as they are called, is separated from the mainland of Asia by seas less than 600 ft. deep, and these islands are therefore generally regarded as rising from a continental shelf, the Sunda shelf, which is a prolongation of the Asiatic continent. Some authorities regard the Palawan-Calamian groups of the Philippines as also belonging to this shelf (384), which is believed to have been wholly exposed as land as lately as the Pleistocene (377) and in part perhaps even more recently (36, 512). Similarly in the eastern part of the Archipelago, the islands of New Guinea and Aru are joined in the same manner to Australia and are part of what is called the Sahul shelf which also is thought to have been dry land in the Pleistocene. Between are many islands separated from these two shelves, and for the most part from one another, by much deeper water, and these, which include the Philippines, Celebes, Ceram, Timor, the Lesser Sundas, the Moluccas and Kei, make up what has been called a "zone of disquiet relief," which it is believed has been insular since the early Tertiary. This zone is sometimes called "Wallacea."

It is thus seen that the Malayan Archipelago has three parts, a western, Asiatic zone; an eastern, Australian zone; and an intermediate zone. It has also long been realised that the flora and fauna of the region show a similar segregation, although this is sometimes rather obscure, and many attempts have been made to draw imaginary lines marking the junction of the western and eastern biota (68). One of the earliest, and perhaps the best known of these is "Wallace's Line" which ran between the small islands of Bali and Lombok, east of Borneo, and between Celebes and the Philippines. This, it will be noted, actually marks the edge of the Sunda shelf and was based largely on the facts of animal distribution. The more recent line of Weber put the chief division east of Timor, west of Buru and Halmahera, and between Halmahera and the Philippines, and therefore followed fairly closely the western edge of the Sahul shelf.

Latterly both these lines have been amended in detail, Wallace's line to run along the Mindoro Strait and between Formosa and Botel Tobago, and Weber's to run east of Halmahera, Obi, Ceram, Kei, Timorlaut and Timor (386). These old and new lines and the extent of the shelves are well portrayed in a map by van Steenis (528), and are again reviewed in the *Flora Malesiana* (531), which accepts a third line, that of Zollinger, as best dividing the archipelago into western and eastern parts from a botanical point of view. This line runs round the east of Timorlaut, westwards through the Sunda Sea, north through the Macassar Strait, and east between the Philippines and the Moluccas, thus putting all the Sunda Islands, Timor and the Philippines into western Malaysia, and including Celebes and the Moluccas in eastern Malaysia. Most recently these lines have been discussed by de Beaufort (36) in relation to animal distribution.

It is outside our province here to discuss the merits of these lines further, but they help us to visualise what is the most important botanical feature of the region as a whole, namely that the flora consists of two important elements, the Asiatic and the Australian, and that the middle part of the archipelago particularly shows a great mingling of them. It is also generally true to say that the Asiatic element is the larger and more extensive and that this predominates in the west, while the Australian element predominates, or is at least most obvious, in the east. What has been said also makes clear that any comprehensive botanical account of the region is impossible within the space available here and that it is possible only to refer to some of the leading features. The remarks that have been made should be borne in mind especially in relation to the subject matter of Chapter 20.

For practical analytical purposes Malaysia is best divided† into three parts, southern Malaysia, comprising the islands from Java to Timorlaut inclusive; western Malaysia, comprising the Malay Peninsula, Sumatra, Borneo and the Philippines; and eastern Malaysia, comprising Celebes, the Moluccas, Kei, Aru and New Guinea. Within these three parts the numbers of strictly endemic genera, that is to say genera confined to one island or island group, vary considerably. In southern Malaysia there are only 14, 10 in Java and 4 elsewhere; in western Malaysia there are 150, namely 17 in Sumatra, 41 in the Malay Peninsula, 59 in Borneo, and 33 in the Philippines; in eastern Malaysia there are 132, namely 7 in Celebes, 1 in the Moluccas, and no fewer than 124 in New Guinea. All these total 296 and, remembering the many other genera which though more widely distributed are nevertheless still confined to Malaysia as a whole, it would seem likely that the total number of endemic genera in the region is 500 or more.

Of the wider endemics there may be instanced the larger genera *Anerincleistus, Anplectrum, Boerlagiodendron, Cyrtandromoea, Elettariopsis, Hallieracantha, Kibessia, Schismatoglottis* and *Trichotoria*, and the smaller *Althoffia, Aphanomyrtus, Connaropsis, Dryobalanops, Durio, Gynotroches, Lunasia, Matthaea, Ochthocharis, Pangium, Paraboea, Prainea, Rafflesia, Sindora* and *Trigoniastrum.* In addition there are examples of distribution over almost every combination of two or more islands. *Philbornea* and one or two others, for instance, form a group recorded only from Borneo and the Philippines.

The *Flora Malesiana* also gives an important brief analysis of the geographical affinities of the total flora, showing that, of the 2,178 genera native to the region—

about 25 per cent. are widely spread through Asia, Malaysia and Australia;
about 25 per cent. are essentially Asiatic;
about 40 per cent. are either actually endemic or at least essentially Malaysian;
about 7 per cent. are essentially Australian.

Merrill's extensive studies of the plant life of the Philippines (382, 383, 384, 386) have made this one of the best known and documented of the constituent Malaysian floras, and show it to be not only particularly rich but also, as adumbrated above, of special interest with regard to the question of the paths of plant migration in the archipelago. Thus, although the flora of the Philippines has most in common with that of western Malaysia, it nevertheless possesses a notable Australian element typified by the occurrence of members of the Myrtaceae (see fig. 19). There is also in the flora of the northern islands a distinct Himalayan element, which is an attenuation of a corresponding element in the flora of Formosa. In this connection it has been maintained (342, 386) that the flora of the small island of Botel Tobago is more closely allied to that of the Philippines than to that of Formosa (see p. 27).

The climatic conditions throughout the Malayan Archipelago are in general

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† As in the map on p. xi (Introduction) of the First Instalment of the Flora Malesiana (531).

Plate 10. Forest of *Eucalyptus regnans* in Victoria

(Photo: Victorian Railways)

constant and nearly all the islands are heavily forested, but Timor and its immediate associates are exceptional. Here the climate is effectively much drier and closely resembles that of the north of Australia, and it is interesting to note that the vegetation is similarly parallel, being a much more open one in which species of *Eucalyptus* are among the most prominent features (569).

The Polynesian sub-kingdom (18, 135, 385, 386, 387, 408, 477, 478)

The next four regions all fall within what may, in broad terms, be called the Pacific Islands or "Polynesia," although this latter name is properly applied to only one of them. Although their floras are statistically of very different values, they are all, for theoretical reasons, of exceptional interest, and it is desirable to give as complete a list as possible of their endemic genera. The data are, however, particularly confusing and hard to collect, so that allowance must be made for future modifications, but the particulars given here may assist towards the more conclusive knowledge that is so desirable.

Two of the regions, Hawaii and New Caledonia, have rich and very remarkable floras; that of Polynesia is comparatively unremarkable except perhaps as regards Fiji; and that of Melanesia and Micronesia calls for no particular comment. Indeed, except for the first two, there is virtually no "Polynesian" flora, and what little there is seems to be entirely derived. This is well seen in an overall summary of endemic genera which shows that of about 230 genera, at least 120 are in New Caledonia only; over 40 in Hawaii; and about 20 in Fiji, leaving no more than 50, all of them very small, for the whole of the rest of the area.

Only about fifteen genera occur in more than one of the four constituent regions, namely:

Crossostylis in New Caledonia, Fiji and elsewhere in Polynesia.
Acicalyptus, *Bauerella*, *Kermadecia* and *Storckiella* in New Caledonia and Fiji.
Cyphosperma and *Veitchia* in New Caledonia, Fiji and New Hebrides.
Clinostigma in Lord Howe, New Hebrides and Samoa.
Belliolum in New Caledonia and the Solomons.
Pelagodoxa in New Caledonia and the Marquesas.
Balaka and *Chelonespermum* in Fiji and the Solomons.
Phyllostegia in Hawaii and the Society Islands.
Pritchardia in Hawaii and Fiji.
Pelea in Hawaii and the Marquesas.
Lepinia in the Solomons and Society Islands.

The distribution of the above 200 odd genera over the families is a point of considerable interest. At least 35 of them belong to the Palmae, which is perhaps not so surprising in view of what has already been said in Chapter 4, but more than 20 belong to the Rubiaceae. Other families particularly well represented are Araliaceae, Rutaceae, Euphorbiaceae, Myrtaceae, Apocynaceae and Compositae, though the last has few outside Hawaii. The Gramineae, on the other hand, are repesented only by two genera on New Caledonia.

Hawaiian Region

This is one of the most isolated areas of the world and its flora shows a very high degree of endemism. The two most important elements in the flora apart from this (see p. 194) are the Asiatic and the American, and of these the former preponderates, as is illustrated by the numbers of genera mentioned in the last section of Appendix B.

The number of endemic genera is about forty which is generally considered a proportion of about 20 per cent., and they belong to eighteen families of which one or two are particularly prominent. For instance, *Brighamia*, *Clermontia*, *Cyanea*, *Dellissea*, *Rollandia* and *Trematolobelia*, which include the largest endemics, are all woody members of the Lobeliaceae (see p. 75), while *Raillardia* is one of at least six Composite genera. On the other hand, the orchids are but poorly represented, and there is in general a lack of endemic genera belonging to the Monocotyledons.

For the rest *Kadua*, *Schiedea* and *Stenogyne* are among the largest and others are *Bobea*, *Hillebrandia*, *Labordea* and *Nothocestrum*.

Region of New Caledonia

In our regional classification there are here included, for convenience, Lord Howe Island and Norfolk Island, which would otherwise have to be treated separately since they are equally isolated from more than one other region. They are two of the most interesting oceanic islands in the world but it must be enough here to deal with them merely by the statement that the former has six endemic genera, *Colmeiroa*, *Denea*, *Hedyscepe*, *Howea*, *Lepidorrhachis* and *Negria*, and the latter apparently only one, *Streblorrhiza*, now extinct in a wild state.

The flora of New Caledonia (238), which, though oceanic in isolation is continental in structure, is of the greatest interest not only for its marked endemism but also because of its floral relationships (221). It contains well over one hundred endemic genera in nearly thirty families and this probably means upwards of 20 per cent. of the genera native to the island. These endemics are, however, all relatively unfamiliar and one can here only mention as examples *Arthroclianthus*, *Codia*, *Cyclophyllum*, *Exospermum*, *Greslania*, *Microkentia*, *Normandia*, *Oxera*, *Pancheria*, *Phelline* and *Sparattosyce*.

Region of Melanesia and Micronesia (310, 311)

The following is believed to be a reasonably complete list of the genera which have been described as endemic to this rather dual region.

Bonin Islands—*Boninia*.
Bonin Islands and Caroline Islands—*Bentinckiopsis*.
Marianne Islands—*Guamia*, *Merrilliodendron*, *Saipania*.
Caroline Islands—*Gulubiopsis*, *Palaua*, *Ponapea*, *Protocyrtandra*, *Saffordiella*, *Trukia*.
Bismarck Archipelago—*Peckelodendron*, *Peckelopanax*.
Solomon Islands—*Cassidispermum*, *Homalocladium*, *Pseudomacodes*, *Rehderophoenix* and *Strongylocaryum*.
New Hebrides—*Carpoxylon*, *Physokentia*, *Trichochilus*.

It must be borne in mind that all the larger islands are in the southern (Melanesian) part of the region, and it will be noticed that the largest constituent area of all, the Bismarck islands of New Britain and New Ireland, has apparently only two endemics, neither very remarkable. There is no endemic genus in both parts of the region.

Region of Polynesia

The outstanding feature here is that of thirty or so genera which have been described as endemic, twenty of them are found only in Fiji, a point of great interest in view of the fact that these islands are often said to show certain features more usually characteristic of continental areas. Of these twenty, *Degeneria* forms a monotypic family, five belong to the Palmae, five to the Rubiaceae, and among the rest may be mentioned *Amaroria, Dorisia, Graeffea* and *Pimia*.

The remaining Polynesian genera appear to be *Badusa* and *Vitiphoenix*, on Fiji and on the Society Islands and Samoa respectively; *Naudiniella* and *Reynoldsia* on Samoa and the Society Islands; *Fitchia* on the Cook and Society Islands; and eight on one island group each only, namely *Sarcopygme* and *Solfia* on Samoa, *Hitoa* and *Tahitia* on the Society Islands; *Cyrtandroidea* in the Marquesas, and *Lautea* and *Metatrophis* on Rapa.

Endemic genera of tropical America

Just as in Africa, there are in tropical America many endemic genera with ranges that transcend the limits of any one region. Some of these approach in extent of distribution genera which elsewhere have been described as "wides," but they vary a great deal and it is more generally convenient to include them here as a special more widespread type of American endemics, and this may be justified on the grounds that their interest lies more in the fact that they are confined to tropical America than in the fact that they do not happen to be confined to one region.

This reflects to some extent on the value of the regions as defined in the floristic classification, but enough has already been said to show that these are indeed real entities. It seems rather that in the tropics of the New World, which form an extensive and homogeneous area, geographical segregation and isolation has never been very great and that, as a result, endemism is, as it were, on a rather wider scale.

The total number of genera unknown outside tropical America appears to be about 3,000 and it may be that upwards of one thousand of these are distributed over two or more of the regions here defined and must therefore be considered here.

Their ranges vary enormously but various influences lead to the predominance of three main types. First, there are the genera which extend practically all over the whole area including Central America and the West Indies. Next, there are those confined to the western, Andean, side of the land but which extend so far north and south that they cover two or more floristic regions. Finally, there are the genera which are mostly to be found within the great area of Brazil but which extend thence varyingly westward or north-westward.

These groups as a whole include many large and familiar genera and especially many of the choice orchids commonly grown in hothouses in Europe. Among good examples are:

1. Genera found more or less throughout tropical America:
   Caryocar, Cecropia, Gloxinia, Lycaste, Maranta, Monstera, Ochroma, Oncidium, Tecoma, Theobroma.
2. Genera chiefly in Brazil but extending west and north-west therefrom:
   Cattleya, Cephalocereus, Jacaranda, Jacobinia, Laelia, Miltonia.
3. Genera found chiefly in western tropical America:
   Cinchona, Cosmos, Phytelephas.

Caribbean Region

This region consists of two well-marked areas, isthmian America and the West Indies, and the former has a close relationship with western North America. Owing to the absence of modern floras it is difficult to estimate the total number of endemic genera, but it is probably considerably more than 500. *Bouvardia*, *Guajacum*, *Hura* and *Swietenia* (which is actually said to reach Peru) exemplify genera found more or less throughout the region.

More than half the endemic genera are confined to isthmian America and particularly to Mexico, and the latter include *Dahlia*, *Dictyanthus*, *Euchlaena*, *Martynia* and *Polianthes*.

Less than half the genera are confined to the West Indies and *Crescentia* is but one of many characteristic genera here.

Agave is a good example of a genus which extends rather beyond the strict limits of the region, being centred in Mexico but ranging deep into the U.S.A. and to northern South America. *Furcraea* is similar but less northerly.

The region includes, on the Pacific side, Guadalupe Island and the Revilla gigedo Islands but these have no endemic genera.

The Bahamas are said to have one or two endemic genera but the Bermudas have none.

Region of Venezuela and Guiana

Although there are sufficient reasons for maintaining this area as a distinct floristic region, it is not surprising that its relationships with the next two, the Andean and the Amazon, are very close, and its endemic genera appear to be few, most probably fewer than one hundred. Moreover, none of these are either well-known or familiar plants, and there need only be mentioned *Heliamphora*, *Manicaria* and *Voyria*. Botanically the most remarkable part of the region is the mountainous area along the boundaries of Venezuela and Brazil where the endemics include *Leitgebia*, *Ledothamnus*, *Stenopadus* and several members of the Rapateaceae, and about this more will be said Chapter 10.

Endemic genera of Brazil

The two floristic regions which cover the States of Brazil, Paraguay, and other border areas, have one of the richest floras in the world but also one of the least completely known, and they are considered together here, because although they are both physiographically and floristically quite distinctive, it is not always easy to be sure which genera are strictly confined to one or the other.

A recent compilation based on Lemée (339) shows that the total number of endemic genera in Brazil is about five hundred, though a number of others probably do not extend very far beyond this country. The chief families represented are, as might be expected, the Compositae, Orchidaceae, Euphorbiaceae and the three leguminous families, and, more notably, the Asclepiadaceae, Bignoniaceae and Melastomataceae. The largest endemic genera are *Cambessedesia*, *Chaetostoma*, *Diplusodon*, *Eremanthus*, *Kielmeyera*, *Lavoisiera*, *Lychnophora*, *Nidularium*, *Promenaea*, *Sinningia* and *Tremblya*, but none of these has more than about fifty species. Indeed the total number of species in all the endemic genera is probably not more than about 1,250, a very small proportion of the whole flora, and this reflects very clearly the comparatively wide distribution of most tropical American genera, as mentioned on p. 131 above.

The Amazon region is the third of the great equatorial forest areas and is a simpler and better-defined unit than either of the others because it consists exclusively of the vast basin of the Amazon river system. An important environmental factor in it, which also makes it somewhat different, is the extensive flooding to which, on account of the general lowness of level and the slowness of drainage, much of the region is regularly subjected, and the vegetation can primarily be divided into that above the level of the flood-waters (igapo) and that below it (ete). Here there are probably about one hundred endemic genera, all quite small, and including *Dilkea*, *Hevea* (the Para rubber), *Lacunaria* and *Lissocarpa*.

The South Brazilian region comprises three main constituent parts, the forested mountains of the eastern coasts, the open woodlands of the caatingas, and the savanas of the campos. The flora is large and the number of endemic genera appears to be about four hundred, among them being *Albertinia*, *Antonia*, *Arachis* (to which the ground-nut belongs), *Barjonia*, *Castelnavia*, *Diclidanthera*, *Fernseea*, *Fragariopsis*, *Gearum*, *Hymenolobium*, *Itatiaea*, *Leptotes*, *Mauritiella*, *Nautonia*, *Pamphilea*, *Pygmaeorchis*, *Sapucaya*, *Schlumbergeria*, *Seris*, *Soaresia*, *Spathicarpa*, *Tetraplandra*, *Tetraulacium* and *Wunderlichia*.

The islands of Fernando Noronha (4°S 32°W) and South Trinidad (20°S 30°W) have no endemic genera.

Andean Region

Although the whole Andean region from Colombia to southern Chile is to be regarded as a single elongated region, it is convenient to consider it here as made up of two rather distinct parts, tropical and temperate, and these are fairly clearly marked politically. In the northern tropical part are the four montane countries of Colombia, Ecuador, Peru and Bolivia, while the southern part consists essentially of Chile (though it includes also the western part of Argentina) and may be referred to by this name. The Andean region as defined in our classification also includes the Galapagos Islands.

The flora of the tropical Andes is very rich and also, on account of the range of elevation, very varied. Each constituent country has many endemics, so that the total is probably several hundreds, and they are found chiefly on the tropical flanks of the mountains, the highland element in the flora having generally a wider range. Among the more familiar endemic genera are *Cochlioda*, *Desfontainia* and *Eccremocarpus*.

The flora of the Galapagos Islands (322, 535) is of great interest from the point of view of its species but contains very few endemic genera, *Leiocarpus* and *Scalesia* being the only important ones. It is chiefly for this reason that the archipelago has not been given regional rank.

The flora of Chile has been analysed in some detail in connection with the flora of temperate South America as a whole (216), and from this and more recent sources it appears that there are about 125 endemic genera, a high percentage considering the size of the flora as a whole, *Jubaea*, *Lapageria* and *Lardizabala* are noteworthy examples, the first-named being one of the few palms found outside the tropics, and others include *Berberidopsis*, *Fascicularia*, *Francoa*, *Schizanthus* and *Tecophilaea*.

Pampas Region

This region comprises that part of South America east of the Andes and between the tropical Brazilian flora on the north and the temperate Patagonian flora on the south. Its core consists of the great grass plains of the pampas proper, so vividly described by Hudson (282) and others, but there also falls within it much of drier western and northern Argentina, as well as the southernmost two provinces of Brazil. The botany of the Argentine part of it has lately been well described by Cabrera (71).

The flora is not particularly rich and the endemic or near endemic genera, which are all small, probably do not number more than about fifty, including several in the Cactaceae. Others are *Deinacanthon*, *Holmbergia*, *Jodina*, *Synandrospadix* and *Tricomaria*.

Region of Juan Fernandez

The Juan Fernandez Archipelago, which lies 400 miles off the coast of Chile, has a very remarkable flora which has been particularly studied by Skottsberg (496). It has a very high degree of endemism including about a dozen genera. Among them are *Juania*, a palm; *Lactoris*, which forms an endemic monotypic family; and one or two remarkable Composites, including *Dendroseris* and *Rhetinodendron*.

This region, as here defined (see Plate 4), also includes the tiny Desventuradas Islands (S. Ambrosio and S. Felix) which lie about 500 miles north of Juan Fernandez and 600 miles from the coast of Chile. Their flora (505) is very small, but includes three endemic genera, of which one, *Thamnoseris*, is regarded as most closely related to *Dendroseris*, already mentioned.

Other American endemic genera

As in tropical America there are, in temperate South America, a number of genera which, while not falling under any one region, must nevertheless be considered as endemics. These consist chiefly of genera characteristic of the temperate Andes but which extend therefrom eastward across Argentina and Patagonia for various distances.

In all there are about eighty such genera, and among them are *Azara*, *Cajophora*, *Myzodendron*, *Nassauvia* and *Triptilium*.

Australian endemic genera

The Australian continent supports one of the most peculiar and, in places, one of the richest of the world's floras (80). Indeed, its very degree of peculiarity, which it can scarcely be doubted results from the long geographical isolation of the continent from others, combined with its relative unfamiliarity, makes for difficulty because the flora is in general so different from others (its only considerable relation being with that of South Africa) that there is a natural tendency to regard it as a single unit, whereas in fact there is room for a classification quite as detailed as that of other continental areas of comparable size. Another complicating factor is that the flora is unevenly distributed. It is richly developed in the east and south-east, and also in the south-west, but it is less so in the middle parts of the south coast, and is poor in the interior and over much of the north. There is also a great range of latitude and the flora of northern Queensland is, if but for this one reason, very different from that of Tasmania or that of the south-west.

The constantly recurring theme in nearly all that has been written about the Australian flora is the aridity of the country and the related xerophily of the plant life, a characteristic which is reflected in the general absence of deep shade even where the vegetation is of trees. Andrews (17), for instance, maintains that the "real" Australian flora is essentially one of barren waste places, and Lawson (337) also stresses its striking and varied xerophily as one of its main features. The facts relating to the climate and the correlation of the vegetation with it, are perhaps most prominent in the western part of the continent and for this region have been admirably set out by Gardner (192). In connection with their studies of the South Australian vegetation Crocker and Wood (114) conclude that the general aridity is the result of post-Pleistocene desiccation which has wiped out most of the prior flora, at any rate over much of the interior. The highest rainfall is along the coast of northern Queensland and here the vegetation is comparatively luxuriant and has much in common with that of New Guinea. Here in particular there is, in the flora, a striking mixture of Malaysian and Australian types and Cambage (76, 77) believes that here again the vegetation is in nice balance with existing climatic values, so that any diminution of rainfall would cause a waning of the Malaysian element and *vice versa.* This is a point of special interest in connection with theories of continental movement, according to some of which the position of Australia has altered considerably during the latter part of geological time (see Chapter 20).

The recognition here of three regions in Australia, northern and eastern, south-western, and central, expresses the main segregation of the flora and climate, and also the outline of the geological history of the continent (260), in which a chapter of special significance to the Angiosperm flora was the long submergence of much of mid-Australia with consequent isolation of the west from the east, but, as with other continents, there are many genera which range much more widely than over any one of these three, although nevertheless restricted to the continent, and these must be noticed first.

The total number of genera endemic, or virtually so, to Australia is estimated at over 500, which is generally regarded as representing about 30 per cent., many of them, like those of South Africa, being large and markedly peculiar genera, and of these probably nearly half are so wide-ranging that they cover all or parts of two or more of the three constituent regions.

Many of these are found almost all over the continent, except for the dry regions of the centre and south, and among them are *Actinotus*, *Dryandra*, *Hakea*, *Pultenaea* (80 spp.) and *Xanthorrhoea*; *Banksia* and *Haemodorum*, which occur in New Guinea; and *Ptilotus* (100 spp.) and *Trachymene* which have a wider representation in Malaysia.

Very many others extend more or less completely through the southern latitudes of the continent from west to east. A few, as *Correa*, are more characteristically eastern, but the great majority are centred in the south-west, and have but a few species in the east. Good examples of these are *Boronia* (60 spp.), *Chorizema*, *Darwinia*, *Daviesia*, *Dillwynia*, *Jacksonia*, *Kennedya* and *Pterophila*. *Byblis* is a good instance of a discontinuous genus having one species in the south-west and one in the north and north-east.

North and East Australian Region

This is an unsatisfactory region because of its enormous latitudinal range (compare eastern North America), and it is only to be expected that the flora of northern Queensland which is well within the tropics, will be very different from that of the mountains of the south-east, or of Tasmania which lies beyond 40° south.

The region as a whole appears to contain about 150 endemic genera in all, and few of them range throughout it. Most of them are confined to Queensland, and these are exemplified by *Carnarvonia* and *Darlingia*. At the other extreme Tasmania has a few endemic genera, including *Agastachys*, *Bellendena* and *Cenarrhenes*. The remainder are chiefly in the south-eastern parts of New South Wales and Victoria, and in South Australia, and these include *Blandfordia*, *Brunonia*, *Callicoma*, *Humea* and *Telopea*.

South-west Australian Region (192)

This region stands out among the Australian regions in the richness of its flora and in its high degree of endemism, and it is, indeed, perhaps the only flora which compares (as it does in this and many other ways) with that of the Cape Region of South Africa. Each, it will be noted, occupies the extreme corner of a continental mass.

Its endemic genera, however, do not give a real picture of its peculiarity, because some of the most characteristic genera actually range far outside it and have already been mentioned, and this peculiarity will be plainer when the species are discussed.

The number of more or less strictly endemic genera seems to be in the neighbourhood of one hundred, and by the nature of the case they are mostly local, though *Cephalotus*, which forms a monotypic family, occupies a long coastal strip. Others are *Anigozanthos*, *Dasypogon*, *Eremaea*, *Kingia* and *Loxocarya*.

Central Australian Region

This region needs but little notice here, not only because the number of endemics is small but also because it is still imperfectly known. The endemic genera probably do not exceed thirty, and it must suffice to say that they include *Austrobassia*, *Clelandia*, *Dimorphocome* and several small Cruciferous genera.

New Zealand Region

For many reasons, chiefly connected with its position, the flora of this region is of special interest to the plant geographer, and it has been so much studied that its constitution now is well known (95, 157). This will be discussed in more detail in Chapter 10, but it can be said here that the number of endemic genera is about 25. They are, however, all quite small, and nearly all the endemic species for which the region is remarkable, belong to non-endemic genera. Indeed the contrast between the degrees of generic and specific endemism is very marked. It should, however, be noted that *Celmisia*, with over 50 species, is, except for a single species in Australia, an exclusively New Zealand genus, and that were it not for their occurrence in Macquarie Island the two small genera *Pleurophyllum* and *Stilbocarpa* would also have to be added to the list.

Two monotypic genera, *Coxella* and *Myosotidium* (a familiar garden plant), both coastal and both now becoming rare, are endemic to the Chatham Islands, and *Corokia* occurs here as well as in New Zealand proper. The remainder are all confined to the main islands of New Zealand, and include *Alectryon*, *Haastia* and *Hoheria*, as well as six genera which are the only representatives of their families in the region, namely, *Dactylanthus* (1 sp., Balanophoraceae), *Tetrapathaea* (1 sp. Passifloraceae), *Rhabdothamnus* (1 sp. Gesneriaceae), *Tecomanthe* (1 sp., Bignoniaceae), *Plectomirtha* (1 sp., Anacardiaceae) and *Alseuosmia* (4 spp., Caprifoliaceae).

Patagonian Region

This region, which may be described as comprising the lowland parts of extreme southern America, has a small flora with a few almost or quite endemic genera, among which *Lebetanthus*, *Magallana*, *Niederlinia* and *Saxifragella*, and a small group of Cruciferous genera, may be noted. Some of those already mentioned for Chile and Argentina perhaps actually fall mostly within this region but as they have already been referred to they need not be considered again. The most isolated part of the region, the Falkland Islands, has no well-marked endemic genera at all. The question of the boundaries of the Patagonian region and its subdivisions have been discussed by Beetle (38), Donat (137) and Skottsberg (501).

Region of the South Temperate Oceanic Islands

The flora of this region is extremely small, but it is of exceptional interest for many reasons and will receive detailed treatment later. There are only two endemic genera in it, namely *Lyallia* on Kerguelen and *Pringlea*, whose distribution, owing to the configuration of the region, is discontinuous and which has already been mentioned under that heading.

The proportion of endemic genera in the two hemispheres

This lengthy account of endemic genera may fitly be concluded by an attempt to estimate the number of such genera in each of the two hemispheres, northern and southern. It is not altogether easy to make this computation, because several regions lie across the equator, but if some arbitrary proportionment of these is adopted it appears that there are about twice as many endemic genera in the southern hemisphere as there are in the north. This is using the term endemic as it has been defined for the particular purposes of this chapter. If it is made more narrow in conception, then the disparity in numbers is certainly accentuated, and of extremely restricted genera the great majority are undoubtedly southern.

These bare figures are sufficiently noteworthy, but the position can only be appreciated properly if the relative areas of land in the two hemispheres are taken into account. It was seen in Chapter 2 that the land area open to plant habitation in the north is about 38 million square miles, while in the south it is only 13 million, a proportion of nearly three to one, and it would appear therefore that the density or frequency of endemic genera is six times as great in the south as in the north.

There are good reasons, chief among them being the variation in size of the regions and the differences in the conception of genera, why it is unwise to read too much into the figures and facts set out in this chapter, but on the other hand some generalisation seems to be fully justified. It is clear that in certain parts of the world generic endemism, that is the number of endemic genera and the total of the species they contain, is considerably higher than elsewhere. These parts are isthmian America, the Andes, South Africa, Madagascar, south-west Australia, eastern Australia and Malaysia (especially New Guinea), to which, though rather different because of their smaller areas, Hawaii and New Caledonia must be added. Of all these areas the South African is certainly the most remarkable not only because of its floristic wealth but also because it is almost or quite the least isolated geographically. A lower but still notable degree of generic endemism is seen in western North America, the West Indies, southern Brazil and south-east Asia. Somewhat lower again are China and Japan and Europe and the Mediterranean, though it may be suspected that the intense study which the floras of the latter have received has inflated their figures somewhat. For the rest there are of course parts of the world such as the arctic and the African-Indian deserts where it is scarcely surprising that generic endemism is low, but there are others where the figures are notably less than might, for various *prima facie* reasons, be expected, prominent among these being eastern North America, Venezuela and Guiana, the Amazon, Argentina, tropical Africa generally, India and New Zealand. Finally in relation to these statements it must be borne in mind that generic endemism is neither necessarily nor commonly any measure of specific endemism, which is discussed in a later chapter, and the parallels and contrasts between the two are one of the interesting problems of plant geography.

CHAPTER 8

THE DISTRIBUTION OF SPECIES—I

THE number of families of Flowering Plants is such that it was possible in Chapter 4 to mention them individually. The number of genera is so much greater that even in three chapters only a few of them could be mentioned, but it was possible to make a complete statistical analysis of them. The number of species, however, is so huge that even this is impossible, and only a very generalised survey is possible, in which it is difficult to decide what should be included and what should be left out. Whatever else may be desirable, the essential purpose of such a survey is to demonstrate what is certainly the most conspicuous general feature in the distribution of species, namely that there are representatives of almost every kind of range that the geography of the world permits, and the illustration of this leading fact is the main theme of this and the next three chapters. It must not be supposed, of course, that all these types are represented in anything like even proportions, some are much more common than others, but at the same time it is true to say that there are no particular types of specific distribution which are overwhelmingly more prevalent than others that are properly comparable, nor are there any very conspicuous types that are greatly under-represented. In short there is no simplification of the overall distribution pattern because of the outstanding prominence of a few distribution forms.

That many genera consist of but one species, and that the ranges of others are but the sums of the superposed ranges of their constituent species, are enough indication that there is no real difference between the distribution of species and that of genera, except, of course, that the latter is usually more extensive. This being so, much the same treatment and arrangement can be adopted with regard to species as was used in the case of genera, and if this framework is supplemented by particular reference to certain especially important aspects of species distribution, the main purpose mentioned above can be sufficiently achieved. The subject matter of these four chapters dealing with the distribution of species therefore begins with a discussion of the subject of species numbers in general. This is followed by the description of the distribution of the species in each of a few large genera, selected for their variousness in this respect. Wide species are dealt with next; then comes a survey of endemic species, arranged as far as is appropriate, according to the thirty-seven floristic regions, and finally certain particular matters of species distribution receive special notice.

Number of Species

It is possible to make a reasonably up-to-date estimate of the number of species of flowering plants at present known from the recently completed dictionary of Lemée (339). This work, in nine volumes, includes particulars of all described genera, and from the information given it would appear that the grand total of species is about 225,000, and the grand total of genera about 12,500, giving an average of 18 species per genus. Within these totals the figures for Dicotyledons are several times those for Monocotyledons. Taking into consideration how many parts of the world have yet to be completely explored botanically, it seems likely that the total number of species in existence is appreciably higher than this, and that it probably exceeds a quarter of a million. Jones, calculating on a slightly different basis, has recently (305) arrived at the same figures except that he believes a quarter of a million Angiosperm species to be already known.

The numerical distribution of these species over the world's surface, or what may more shortly be called the species density from place to place, is a subject which has long attracted attention as one likely to reveal facts of importance in the study of plant geography (86, 412), and among the more recent references to it are those of Szymkiewicz (541) and Wulff (609). The latter paper, from which many of the figures quoted below are taken, is the more elaborate study and concludes with an attempt to map the world on the basis of species density using different shadings and colours for different concentrations.

Unfortunately the results are disappointing, for the subject is one beset with difficulties which, as will be seen, render it, except in special circumstances, a less valuable aid in plant geography than might at first sight be expected. In the first place the necessary totals of species can be obtained only from complete floras or floral lists, and even to-day these are readily available only for certain parts of the world, and not necessarily those of greatest interest in this connection. Even the lists which do exist should only be compared with great caution partly because they are seldom contemporaneous and partly because they are the work of many different authors with various ideas about the value of species. Then again it is not always clear from quotations whether totals represent all vascular plants or only Angiosperms, and if the latter, whether these include introductions as well as the native species which alone are significant. Indeed, in the floras of many parts of the north temperate regions, *e.g.* Great Britain, it is probably no longer possible satisfactorily to separate one from the other. There is also the difficulty that more often than not floras are of political rather than natural areas.

But even more important, the figures, whatever their provenance and reliability may be, mean little unless they are expressed in some way which takes into account the size of the areas concerned, in other words unless they are expressed as values of relative density, and this has seldom been done.

Some of the broader aspects of the relation between area and species population have been conveniently summarised by Williams (592), who, applying statistical methods, has constructed a curve based upon the numbers of species present in a great number of areas ranging in size from a few square inches to many thousands of square miles. He shows that the resultant curve consists essentially of three parts and the explanation of this appears to be as follows.

In any very tiny area such as that of a few square inches there is probably only a single individual plant representing a single species, but as area increases the likelihood that the number of species present will rise grows, the augmentation in theory following a probability formula which the writer discusses. This first part of the curve, therefore, shows a fairly steep and even rise up to a point at which it begins to flatten out, showing that the rate of increase has sharply changed. This point of change appears to be that at which the area is of such a size that all the species immediately available to inhabit it in fact do so. That is to say, if an area is ecologically simple there will soon be reached the point at which all the normal species inhabiting that kind of habitat appear in the area concerned. In brief it represents not only the maximum population of a simple habitat but also the average size of such habitats.

The second and more gently rising part of the curves follows, and results from the fact that, beyond the point just described, the larger the area is the greater will its ecological diversity tend to be, and therefore the greater the number of species it will contain. Judging from the curve this relation holds good over a very wide range of area size, a circumstance which is probably related to the fact that the average area of occupation of species is comparatively small, so that with areas above a certain size increase in population continues because the boundaries extend to places where some or all of the original species are replaced by others.

Finally the curve enters a third phase and becomes irregular and of little value partly because areas above a certain size tend to contain all possible kinds of habitats but chiefly because in such enormous areas quite new factors, such as those of relative isolation and independent evolution, come into play.

To recapitulate, as long as an area comprises only one kind of habitat its species population increases rapidly with enlargement according to a certain formula of probability. In large areas species population continues to increase, though more slowly, because, generally speaking, area increase here means also increase of ecological diversity. This increase does not, as might be expected, die out beyond a certain point because the average distribution of species is comparatively small. Finally, however, entirely new factors destroy the validity of the curve.

This work of Williams is a very useful presentation of a difficult subject but it gives perhaps too simplified a conception of the situation as it strikes the plant geographer who is concerned mainly with the medium and large areas such as counties, provinces and countries which compose the second and main part of the curve, and two complicating factors in particular need to be emphasised. One is that while larger areas are admittedly likely to be more heterogeneous ecologically than smaller ones, this is effectively true only when areas of the same general type and of similar latitudes and longitudes are compared. A single European parish is probably more heterogeneous than vast tracts of the Sahara; nor is there, although the respective figures may be interesting, any direct basis of comparison between an area in North Africa and one of similar size in South Africa. The second point is that isolation and its attendant climatic effects influence comparatively small areas as well as very large ones.

An enormous amount depends also on where the boundaries of areas are drawn. With islands and with strongly circumscribed natural continental areas there is not much difficulty but often the arbitrary use of artificial boundaries is very misleading, a point which may be illustrated by two examples. The county of Dorset whose area is less than 1 per cent of the British Isles contains upwards of, or even perhaps more than, two-thirds of all the native British species. In the same way any parish of average size in Dorset probably contains upwards of or above half the county flora. The reason is that both the county and the parish are but constituent parts, above a critical minimum in size, of a more or less homogenous whole.

The second example is taken from North America. Here the state of Arizona is reported to contain about 3,300 species, and the neighbouring state of New Mexico about 3,000. Yet the population of the two combined is said to be no more than 4,000. Clearly this is because the boundaries of these states have little or no relation to the distribution of the plant life of the continent. The same kind of result is obtained if two English counties are similarly combined.

But despite these difficulties and the many possible sources of confusion there is much of interest to be learnt, especially about some wider issues, from a study of species density, and the following summary, in which some of the less debatable figures are used, is intended to illustrate not only the limitations but also the potentialities of the subject. In this summary are given the approximate areas in square miles, the approximate numbers of species, and positive relative density figures obtained by dividing the former into the latter and thus representing the number of species per square mile.

1. Figures showing great differences in density between areas unlike in size, structure and kind.

	area in sq. mls.	species	density
Canada, North-west Territory	1,300,000	400	0·0003
Canada, Eastern Arctic	420,000	286	0·0007
Tibet	460,000	700	0·0015
Nigeria	370,000	3,150	0·008
Chile	290,000	5,500	0·02
Switzerland	16,000	2,600	0·16
Formosa	14,000	3,265	0·23
Isle of Wight	150	850	5·7
Cape Peninsula	200	2,500	12·5
Principe I.	12	275	23

2. Figures showing comparable densities in areas of very different size and situation.

	area in sq. mls.	species	density
Madagascar	228,000	5,500	0·024
Spain	200,000	5,000	0·025
California	160,000	4,000	0·025
Victoria	88,000	2,200	0·025
Korea	85,000	2,165	0·025

3. Figures showing different densities in areas comparable in size but not necessarily in kind.

	area in sq. mls.	species	density
a. Italian Somaliland	220,000	600	0·003
Germany	226,000	2,600	0·012
France	213,000	3,800	0·018
b. Kuriles	34,000	770	0·0225
Sakhalin	30,000	1,166	0·037
Sierra Leone	28,000	1,685	0·06
Austria	32,000	2,300	0·07
Portugal	35,000	2,700	0·08
Ceylon	25,500	3,000	0·12

4. Figures showing different densities in areas geographically related but different in size and kind.

	area in sq. mls.	species	density
Australia	2,975,000	12,000	0·004
South Australia	900,000	2,200	0·0023
Western Australia	975,000	4,400	0·0045
Queensland	670,000	4,400	0·0068
New South Wales	310,000	3,700	0·012
Victoria	88,000	2,200	0·025
Tasmania	26,000	1,100	0·042

5. Figures showing somewhat similar densities in areas relatively similar in position and kind, though varied in size.

	area in sq. mls.	species	density
Texas	266,000	4,900	0·018
Utah and Nevada	185,000	3,600	0·018
New Mexico	122,000	3,000	0·025
California	160,000	4,000	0·025
Colorado	104,000	2,900	0·028
Arizona	114,000	3,300	0·029
Illinois	58,000	1,785	0·031
Oregon	97,000	3,100	0·031
Indiana	36,350	1,900	0·052

Selected figures like the above give little idea of whether there is any underlying order in the distribution of densities, or whether indeed any particular parts of the world are notably richer in species than the rest, but some reply to these questions can be gained by arranging all the available figures in a single list according to the sizes of the areas concerned and beginning with the largest. When this is done it is seen at once that, in general, the density increases as the areas get smaller, that is to say the smaller the area the greater its species density. The significance of one aspect of this will be considered in a moment but meanwhile a more careful inspection shows that here and there are densities which are either higher or lower in the table than is appropriate to the size of the areas concerned. Italian Somaliland and Kerguelen, for example, and various arctic or subarctic regions have densities lower than most places of their size, as a result presumably of their difficult climatic conditions. On the other hand, certain areas have densities much higher than the average appropriate to their size. Prominent among these areas are the Union of South Africa, the Balkans, the Malay Peninsula, Borneo, the Philippines, New Caledonia and Cuba. The figures for these coupled with what is in general known about the species population of certain areas not specifically represented in the tables, such as parts of Australia where the density is notoriously high (17), enables the following general statement to be made with a reasonable degree of confidence.

The species density increases rapidly and fairly regularly from the poles towards the equator down to about 35°, but then in many places falls rapidly owing to the prevalence of arid regions. Within the tropics it rises again to a maximum in the equatorial zone. There is difficulty in making an absolute estimate of what this second maximum may be because in so many places the floras are far from completely known, but such evidence as there is suggests that it is probably not appreciably higher than some of the greatest densities elsewhere. There seems little doubt that the highest densities of all are found in certain comparatively limited areas of the southern warm-temperate and sub-tropics.

Reverting again to the table of diminishing areas it is very noticeable that the smaller areas at the end, which have in general the higher densities, are islands, and this is likely to give the impression, which should be corrected, that, other things being equal, the species density on islands is greater than on continents. This is not so and, indeed, the paucity of species on the more remote oceanic islands has long been recognised (124) as one of their most significant and peculiar features (see Chapter 1). The table gives the erroneous impression simply because the only areas of small size from which there are commonly quoted figures happen to be isolated oceanic islands, this being because by the nature of things an island has an individuality and familiarity often quite out of proportion to its size. For example, it is of general interest to know how many species there are on an oceanic island, but it is rare that corresponding figures are available for areas of similar size on continents. It is due to this lack of comparative figures that such islands appear to have exceptional species density, and comparison with continental areas of similar size would almost certainly show many more species in the latter, provided, of course, that reasonably similar circumstances prevailed in both.

How much the density on small or very small islands may differ is shown by the following tabulation:

a. Density below 0·1
    Kerguelen, Falklands.
b. Density from 0·1 to 0·25
    Ascension, Auckland, Bahamas, Fiji, Galapagos, Hawaii, New Hebrides, Sardinia, Sicily.
c. Density from 0·25 to 0·5
    Corsica, Crete, Cyprus, Macquarie, New Caledonia, Réunion, Samoa, Socotra.
d. Density from 0·5 to 1·0
    Azores, Campbell, Canaries, Carolines and Palau, Easter, Fernando Po, Tahiti, Tristan da Cunha.
e. Density from 1·0 to 10
    Bermudas, Juan Fernandez, Madeira, Mauritius, Micronesia, Rodriguez, Seychelles, St. Helena, S. Tomé, Tonga, Trinidad.
f. Density more than 10
    Annobon, Lord Howe, Norfolk, Principe.

Having discussed some of the smallest areas let us turn in conclusion to the opposite end of the scale and see what information can be gathered about the species density of some very large areas and especially of the three main constituents of the tropical zone. Here some of the difficulties already stressed are particularly great but something may be attempted. A recent estimate (525) gives a figure of 15–20,000 and hence a density of 0·0022 for the whole huge area, 8 million square miles, of the U.S.S.R. Wulff gives a figure for India and Burma of 20,000 species, which yields a density figure of 0·013, but the area on which this figure is based is very heterogeneous. In India in the narrowest sense, that is to say the peninsula south of the Indus and Ganges plains, there are perhaps not more than 4,000 native species (276) giving a density figure of only 0·005. At the same time it is only fair to say that the floras of both the Himalayas and Ceylon are rich and redeem much of the balance for India in the wider sense. Wulff also discusses China and concludes that its flora also contains about 20,000 species which gives a density of about 0·005. Van Steenis (531) considers that 27,000 is a conservative estimate for Malaysia, which gives a density of 0·02, but judging from the figures of constituent areas the total seems quite likely to be as high as 40,000, in which case the figure is 0·033. In the New World there is less to go upon but it is generally believed that Brazil contains not less than 40,000 species which gives it a density figure of 0·012, and this figure probably remains much the same if the rest of tropical America is included. In tropical Africa, however, the facts seem to be very different. Thonner (555) some 40 years ago, estimated the total of species at over 18,000, and even a generous proportionate increase would raise this only to 25,000 now. A figure of this sort is supported also by recent estimates for some particular constituent areas, coupled with the general recognition that the proportion of species

Plate 11. Stone-like plants growing in the Little Karroo, South Africa. The plant immediately below the shaft of the hammer is *Gibbaeum album*; the larger, more plentiful species is *Muiria hortenseae*

(Photo: M. R. Levyns)

widely distributed through tropical Africa is relatively high. Certainly such evidence as there is indicates that the total flora is not likely to be more than 30,000, and even this figure gives a density of only 0·005, which seems to show quite conclusively that the species population of this, the most extensive sector of the tropics, is much lower than that of either of the other two sectors, in both of which, it must not be forgotten, it is likely that just as high a proportion of the total flora remains as yet unknown. This relative paucity of the tropical African flora is a general phenomenon though it is especially evidenced by the relatively scanty representation there of some of the most characteristic and elsewhere plentiful tropical plant groups, notably the orchids, palms, bamboos and aroids. It is also in remarkable contrast with the flora of South Africa, which is one of the richest in the world, and the reasons for this difference merit very careful study. In general African paucity is most often considered likely to be due to climatic changes in the continent, and this view has been put most definitely in the recent work of Aubréville (23, 24) who suggests that it is due partly to great movements of climatic zones over the continent (and in particular a movement of the equator southwards) and partly to the "désertification," or increase of aridity, of large areas by causes associated with the presence of man. With regard to this last, however, it should be noted that this process would seem to favour the spread of savana conditions, and it is in some forms of this vegetation that the tropical African flora actually finds its richest expression. It would also seem that there is little doubt that the paucity has some connection with the geological and physiographic history of Africa since the early days of the Angiosperms, during which it appears to have been much more isolated than either of the other tropical sectors. A very useful summary of what we know about the continent from this point of view has recently been given by Moreau (394).

Such are some of the facts and figures relating to the numerical distribution of species. It would be unwise, for the reasons given, to read too much into them or to base any very profound deductions upon them, but three points, each with a different implication for the plant geographer, seem to emerge fairly clearly. They are that in the absence of adverse conditions the highest species concentrations are found in the warm temperate and in the equatorial zones, and that these are probably much of the same order; that islands do not show, in general, any higher concentrations than those of corresponding continental areas; and that of the three great parts of the tropical zone the flora of tropical Africa is much poorer in species than that of either America or Asia, and that the two latter have very similar values, possibly with Asia a little in the lead area for area.

The statistical comparison of floras

Clearly related to the numerical values of different floras is the problem of comparing them in a way which may be at once concise and realistic. The aim is, generally, to estimate the comparative degrees of relationship between floras in order to determine which have the greatest measure of affinity (and hence are likely to have had the most recent community of origin) and which are the more original and least derivative, questions which are very difficult to answer. For instance, how can a flora of 100 species be compared with one of 1,000 or perhaps 10,000 species? How can the relative degrees of endemism be equated? How does the proportion of wide species affect the matter? And how does relative size of area and consequent density influence the result? These are but a few of the questions which many have tried to answer, without, it must be admitted, very much success. It is not necessary to review these attempts, which often involve complicated statistics, here, but the reader may be referred to the interesting method of presenting the facts, so that their value may be estimated in various ways, outlined by Exell and Williams (168, 593, 594) who in the course of their remarks illustrate many of the difficulties just mentioned and some of the ways in which they may be met.

Many similar aspects of the relation between area and species population have been studied by Jaccard (296) in particular. He stresses the distinction between the number of species present in an area, or the floristic *richness*, and their taxonomic diversity, or floristic *composition*, and believes that the relation between these two can be expressed by a single figure, the generic coefficient, which is the number of genera proportional to every hundred species, or in other words, the quotient, expressed in whole numbers, when the number of species is divided *into* the number of genera. This coefficient, its author states, is higher when uniformity of habitat prevails and lower when there is ecological diversity, and for areas of roughly similar ecological values the coefficient diminishes with increase of area, because of the resulting greater floristic diversity, and he develops these themes in a number of ways. He also states that the coefficient is higher in islands than in continental areas of the same size, because of the greater frequency in the former of monotypic or ditypic genera, a conclusion of particular interest here in view of what is said about islands elsewhere.

Distribution of Species within Genera

Genera vary enormously in the relative distribution of their constituent species, and even those which are alike in total range are often quite dissimilar when the actual distribution of their species is taken into account. In some genera there is a fairly high proportion of wide species; in others the species are practically all, and in some cases entirely, endemics. In the former the wides may be of comparable range and fairly evenly scattered, or there may be one or more which exceed the rest and which may even attain the whole area of the genus. In the latter endemics may be found in all parts of the genus area, or they may be massed in one part of it. Some genera illustrate several of these features to some degree.

In order to illustrate these and other more detailed points, eight large genera have been selected and the detailed distribution of their species is here described. They have been chosen as covering between them most of the world and most aspects of interest in the geography of species. Two, *Plantago* and *Juncus*, are almost world-wide, but chiefly temperate, genera; two, *Begonia* and *Dioscorea*, are almost pan-tropical; *Drosera* is predominantly a southern genus; *Viola* is a wide-spread but discontinuous temperate genus; and *Rhododendron* and *Erica* have each great numbers of endemic species in one particular region.

The distribution of the species of Plantago

The genus *Plantago*, which has been revised by Pilger (156), has about 250 species and is a good example of a genus which is actually found, owing to the cosmopolitan range of one or two widely introduced species, almost all over the world, but which is essentially temperate in its natural distribution.

The total range is almost world-wide except that in many parts of the tropics the genus is represented only by the adventive species, *P. major* and *P. lanceolata*, and even these are absent from the low-lying parts of tropical America.

About twenty species can be said to have a wide range, and of these the only marked examples are *P. media* in Eurasia, *P. asiatica* from the Himalayas to Java, *P. macrocarpa* from Kamchatka to north-western America, *P. erosa* from Ceylon to western China, *P. depressa* in central and eastern Asia, *P. hirtella* from Mexico to Uruguay and *P. triantha* in Australia and New Zealand.

Nine species have discontinuous ranges, namely, *P. maritima*, northern hemisphere and Patagonia; *P. durvillei*, California and the tropical Andes; *P. heterophylla*, North America, Uruguay and Paraguay; *P. trimenta*, Chile and Juan Fernandez; *P. crassifolia*, Mediterranean and South Africa; *P. canescens*, eastern Siberia and north-west America; *P. amplexicaulis*, Canaries and Mediterranean; *P. ovata*, Canaries and western and central Asia; and *P. lanigera*, New Zealand and, recently, New Guinea.

This leaves over 200 species of what may be called endemics, that is to say, species more or less rigidly confined to one region. The distribution is as follows:

Western North America	5
Eastern North America	15
Mexico	5
Western tropical South America	39
Temperate South America	42
Europe, Mediterranean and west Asia	42
Central Asia	10
East Asia	10
Formosa	2
Java	2
Madeira and Canaries	4
Tropical African Mountains	2
South Africa	4
Madagascar	1
Australia	16
New Zealand	4
Hawaii	9

together with the following very narrowly distributed species:

P. fernandezia	Masatierra.
P. hedleyi	Lord Howe Island.
P. robusta	St. Helena.
P. rupicola	Rapa Island.
P. rapensis	Rapa Island.
P. aucklandica	Auckland Island.
P. picta	E. Cape Island, New Zealand.
P. pentasperma	Amsterdam Island.
P. stauntoni	St. Paul Island.

Among more recently described species are *P. palustris* from a mountain top in New South Wales and *P. gunnii* from mountain summits in Tasmania.

The distribution of the species of Juncus

In contrast to *Plantago*, *Juncus* has very few species which are anywhere adventive. As revised by Vierhapper (160), the genus has about 225 species, and of these something between one-third and one-half are wides—a very high proportion.

The widest of all is *J. bufonius*, which is almost cosmopolitan. It is worth noting that this is the only member of the genus which is a common weed of cultivated land and its great range may be to some extent adventive. This latter is true also of certain other species such as *J. tenuis*, which is widespread in America and introduced here and there in the Old World; *J. capitatus*, which occurs naturally in Newfoundland, Europe and Africa, and which is introduced into Australia; and the Eurasian *J. inflexus*, which is introduced in South Africa and New Zealand. *J. articulatus* and *J. bulbosus* are both characteristic of the temperate parts of the Old World but have a limited distribution in North America.

Other wides include a conspicuous group of arctic-alpine species with a more or less circumpolar range and which occur also in some or all of the north temperate mountains, among them being *J. triglumis* and *J. biglumis*.

Among more temperate northern species are *J. conglomeratus* and *J. gerardii*, and on a narrower scale *J. compressus*.

Several species range more or less continuously from North to South America as, for instance, *J. dichotomus*, *J. andicola* (from Alaska to Patagonia), and *J. marginatus*. Similarly in the eastern part of the Old World there is a link between the north and south by *J. pauciflorus* from east Asia to Australasia and the Pacific Islands, and *J. prismatocarpus* from east Asia to New Zealand.

Discontinuity of range is well illustrated, and if the status of the plants is to be relied upon in all cases there are some remarkable examples. *Juncus maritimus* ranges over Europe and part of Africa and occurs again in Australia and New Zealand; *J. acutus* is in Europe, Macaronesia and the Mediterranean, and at the Cape as well as possibly on Juan Fernandez. The well-known east Asiatic-North American discontinuity is illustrated by *J. xiphioides*, while *J. falcatus* exemplifies both this and north-south discontinuity, being recorded from western North America, Japan and also from Australia and Tasmania. Finally, *J. planifolius* occurs in New Zealand, Australia and Tasmania, and again in South America and Juan Fernandez, and *J. antarcticus*, previously known only from New Zealand, has now been found in the mountains of eastern Australia.

Among the remaining wides which are too numerous to be mentioned in detail all sorts of ranges are represented, as, for instance, Australia and New Zealand, both western and eastern North America, and south and tropical Africa.

Actually the most outstanding instance of the last should perhaps be included among discontinuous species. It is *J. lomatophyllus*, which is said to be native in South Africa, south-eastern tropical Africa and in St. Helena. Weimarck has described discontinuities also in some other African species (584).

As regards the endemic species of the genus, these again are spread over nearly the whole world, but three groups stand out. These are some forty species in either western or eastern North America, about thirty in the Sino-Himalayan mountain mass, and about a dozen in Europe or the Mediterranean.

The distribution of the species of Begonia

The huge tropical genus *Begonia* has very few wides, and the vast majority of the species are quite narrowly endemic. Indeed, according to Irmscher's revision of the genus (160), only three species merit the term wide at all, and even these are little more than endemic. They are *B. scandens* found in Jamaica, Guatemala, Guiana, Venezuela and Peru, *B. evansiana*, which reaches from Java to North China and Japan, and *B. mollis*, which is described as widely spread on the larger Sunda Islands.

The segregation of the species over the tropics is also very marked, so that it is possible to divide the genus, without violence to its taxonomy, into four sections containing respectively African species, Asiatic species, American species, and

Asiatic or American species. In other words, the main groups within the genus are confined to the continents as indicated.

In the African section species range varies from that of *B. oxyloba*, which is found in both west and east tropical Africa, to *B. asplenifolia*, which occurs only on the top of one mountain in Gaboon. There are several species in Madagascar, but all are endemic there. Incidentally five very closely related species form a most interesting geographical series in this part of the world. They are *B. oxyloba*, already mentioned as fairly wide in tropical Africa, *B. meyer-johannis* in eastern tropical Africa, *B. cladocarpa* in Madagascar, *B. salaziensis* in Mauritius, and finally *B. comorensis* in the Comoro Islands.

This section includes also several exceptionally narrowly distributed species, as, for instance *B. prismatocarpa* on Fernando Po, *B. thomeana* on the nearby island of S. Tomé, *B. perpusilla* on the island of Nossi Bé off Madagascar, *B. diptera* on the Comoro island of Johanna, and *B. annobonensis* on the west African island of Annobon.

In Asia endemic species are, as the following list of examples shows, to be found in almost every part of the area. *B. roxburghii* is on the Himalayan-Burmese mountains, *B. malabarica* in India and Ceylon, *B. handelii* in China, *B. tricuspidata* in Burma, *B. pseudolateralis* in the Philippines, *B. conophylla* in Sumatra, *B. burbidgei* in Borneo, *B. renifolia* in Celebes, and *B. hirsuticaulis* in New Guinea.

Similarly in the American species, which are more numerous than the others, there are species in every region, as, for instance, *B. franconis* in Mexico, *B. carpinifolia* in Costa Rica, *B. foliosa* in Colombia, *B. ferruginea* in Colombia and Ecuador, *B. maurandiae* in the northern Andes, *B. microphylla* in Venezuela, *B. boliviensis* in Bolivia, *B. columnaris* in Peru, *B. sanguinea* in Brazil, *B. arborescens* in the neighbourhood of Rio, *B. fiebrigii* in Paraguay, and *B. micrantha in* Argentina.

The distribution of the species Dioscorea

The great tropical genus *Dioscorea*, which contains the yams, has been revised by Knuth (160), who estimates that it comprises between six and seven hundred species.

Although it is found throughout the warmer parts of the world, the wide species are very few and in fact there is only one species which can claim even to approach the range of the whole genus. This is *D. bulbifera*, which occurs throughout the tropics, but it is one of the cultivated species and its natural range can now hardly be estimated. The last remark also applies to *D. esculenta*, which is described as ranging from India to the Pacific Islands. Among other wide Asiatic species are *D. glabra* from India to Java (a very common type of distribution) and *D. cirrhosa* from Hong Kong and the Riukiu Islands to the Philippines and Ceram (a much rarer type). Other Asiatic species include *D. nipponica* from Manchuria, China and Japan, an unusually northern range, *D. collettii* of Burma, South China and Formosa, and the equatorial *D. polyclades*, *D. polifolia* and *D. nummularia*. Endemic Asiatic species are found in Japan, in the Philippines and in India. Very few species either reach Australia or are endemic therein.

The Asiatic species, which have also been monographed by Prain and Burkill (432), are connected with those of Africa by *D. triphylla* which ranges discontinuously over the tropics of both continents, but the total representation of the African sector is very slight and much of it actually consists of Madagascan species. Apparently none occurs on both continent and island. *D. quartiniana* and one or two others are widespread in tropical Africa, and there are species in the west, in the east, in the south-east, and even in South Africa proper, where they include the well-known *D. elaphantipes*. *D. lanata* occurs on Socotra.

Mention of the last introduces two species which, geographically, are among the most remarkable of all. These are *D. caucasica* in the Caucasus and *D. balcanica* in Albania. Their nearest neighbour is the Socotran species just mentioned, and their curiously isolated northern range is generally considered to mean that they are relics of a more subtropical flora, most of which has now disappeared. The closely related monotypic genus *Borderea*, sometimes included in *Dioscorea*, is a native of the Pyrenees.

The remainder of the species are American and these are very numerous. Few of them are widespread even in tropical America, but there are endemics in almost every country and many ranging over two or more. They are most plentiful in South America, and here they are found both on the west and on the east. The following, selected at random, will suffice as illustrations: *D. adenocarpa* in Brazil and Paraguay; *D. campestris* in Brazil and Argentina; *D. pilosiuscula* in the West Indies and Guiana; *D. altissima* in Brazil, Guadeloupe and Tobago; *D. convolvulacea* through much of Central America and in Trinidad; *D. glandulosa* in Colombia and Argentina; *D. megalantha* in Venezuela, Colombia and Peru; *D. amazonum* in Venezuela, Guiana and Brazil; and *D. occidentalis* in the West Indies and Brazil.

The distribution of the species of the genus Drosera

(Fig. 16)

The genus *Drosera*, which contains the sundews, has been much studied by Diels (160) and others.

Only five species out of about ninety have what can reasonably be called wide ranges. The widest of all appears to be *D. indica*, which is found in tropical Africa and again from India and China to Australia. It is thus not only very widespread but also markedly discontinuous. The remaining wides fall into two groups, the first of two species, *D. rotundifolia* and *D. anglica*, throughout the northern temperate zone, the latter being slightly more widespread and, incidentally, discontinuous, by its additional occurrence in Hawaii; the second of three species, *D. burmanni*, *D. peltata* and *D. spathulata*, which connect the species of the northern hemisphere with those of the south and of which the last-named ranges from China and Japan to Australia and New Zealand.

D. madagascariensis, which covers almost all tropical Africa as well as Madagascar, is probably the next widest species, and *D. burkeana* has a similar range but is less wide on the continent. Narrower African species are *D. natalensis* in south-east Africa and a group of local species exemplified by *D. capensis* in the south-west Cape region. There are no purely Madagascan species.

D. intermedia, found in eastern North America and western Europe, is another markedly discontinuous species, as also, in lesser degree, are *D. brevifolia* in south-eastern North America and southern Brazil and *D. capillaris* from Texas to Guiana, the latter being the only connections between northern and southern species in the New World.

Other American species are, with the exception of *D. filiformis* in eastern North America, all southern, the widest here being *D. sessilifolia* in Guiana and Brazil; but most of them are Brazilian only, as, for instance, *D. montana*. Finally, one species, *D. uniflora*, is restricted to that part of the southern continent south of latitude 40°, and this is of special interest because the only two close relatives of this species, namely *D. arcturi* and *D. stenopetala*, are confined to Australasia, the former being found in south-eastern Australia and New Zealand and the latter only on the New Zealand mountains.

All the other species of the genus are confined to Australasia and it is here that its great specific wealth lies. Upwards of half the total species of the genus are confined to a comparatively small part of south-western Australia, and are exemplified by *D. gigantea* and *D. myriantha*, but others range widely over the continent, as, for instance, *D. glanduligera*, on both coasts of southern Australia. There are one or two species in south-east Australia, notably *D. whittakeri*, and a group, including *D. banksii* and *D. adelae*, in north Australia and Queensland.

D. petiolaris is found in north Australia and in New Guinea, while *D. pygmaea* and two others (in addition to *D. arcturi* mentioned above) connect Australia with New Zealand. Finally, there is one endemic species in New Caledonia.

The distribution of the species of the genus Viola

Turning now to pan-temperate and therefore more or less discontinuous genera, *Viola* is of much interest. In total its range is almost cosmopolitan, but its tropical representatives are mostly montane and the genus can be considered as essentially temperate. It has been monographed and revised by Becker (160).

The main feature of the distribution of the species is the comparatively large number of wides and the absence of any very marked massing of the endemic species, a contrast to what has been described for *Begonia* and *Dioscorea*. Moreover, the wides are of various ranges and not, as is often the case, restricted to the northern temperate zone, where in general widespread species tend to be plentiful.

It is true that many of the more widely spread species belong to this area, as, for instance, *V. palustris* and *V. selkirkii* (which is more or less completely circumpolar), *V. mirabilis*, *V. canina*, *V. pinnata* and *V. collina*, which are found throughout Europe and Asia, *V. odorata* and *V. hirta*, which occur over much of Eurasia, and various species, including *V. occidentalis* and *V. incognita*, which are widespread in North America; but there are many other types of wide distribution as well.

V. reichenbachiana and *V. riviniana* occur in Europe and west Asia and also in Macaronesia, *V. blanda* and *V. langsdorffii* are found on both sides of the Bering Strait, *V. altaica* and *V. dacica* range from south Europe far into Central Asia, and *V. tricolor* (in the wider sense) ranges throughout Eurasia and occurs also on the Canaries.

In lower latitudes *V. betonicifolia* has one of the widest ranges, extending more or less continuously from Afghanistan, China and Japan to Australia, including Tasmania. With similar but rather less wide ranges are *V. serpens* from Afghanistan to the Malayan Archipelago, *V. diffusa* from India and Japan to the Philippines, and *V. arcuata* from India to Java and the Philippines. *V. etbaica* ranges from Nubia to the north-western borders of India.

In the New World *V. lanceolata*, from Canada to Texas and also in Venezuela, is one of the widest, and others are *V. stipularis* in Central America, the West Indies and northern South America, and *V. scandens* from Mexico to Ecuador.

As has been said, endemic species are found in all parts of the generic range, but they are most plentiful in Europe and in the Mediterranean region. Some of these have a very narrow range indeed, as, for instance, *V. magellensis* in the Abruzzi, *V. fragrans* in Crete, *V. albanica* in Albania, *V. splendida* in south Italy and *V. athois* on Mount Athos. *V. bertolonii* inhabits Corsica and Sardinia.

Three noteworthy species in Macaronesia are *V. paradoxa* in Madeira, *V. cheiranthifolia* on the Peak of Teneriffe and *V. palmensis* on the island of Palma in the Canaries.

The genus is least represented in Africa, where it appears to be absent from the tropics except for *V. somalensis* in Somaliland and *V. etbaica.* In the south there are two species, *V. decumbens* and *V. sentiformis*, at the Cape.

Temperate Asia, and especially China and Japan, are fairly well stocked with endemics and include several in the Himalayas, such as *V. kashmiriana* and *V. forrestiana.*

Endemics are also to be found, although in small numbers, over tropical Asia, as, for instance, *V. celebica* in Celebes, *V. javanica* in Java, *V. ovalifolia* in Sumatra, and *V. lunata* in New Guinea. There are at least two species in Australia and three in New Zealand, one of these also on the Chatham Islands.

In the New World there are endemic species throughout the continent. In the north some are confined to the west (e.g. *V. sarmentosa*) and some to the east (e.g. *V. pedata*), and there are several in Central America and the West Indies (e.g. *V. jalapensis* in Mexico and *V. domingensis* on Hayti).

South America, and especially the southern parts, is rich in species and compares with Europe in this respect. Most of the more equatorial species like *V. humboldtii* and *V. arguta* are found on the Andes, but there are also several species in Brazil. Further south several small groups of species inhabit the Chilean Andes, including *V. pumila* and *V. rubella*, while others are found in the Argentine and Patagonian Andes. Finally, there are several species in Fuegia and Magellansland, an outstanding example being *V. maculata*, which is also in south Chile and the Falklands and should perhaps be considered a wide.

There is one section of 8 species in the Hawaiian Islands, of which 7 are confined to one island only each, and the eighth is on four islands.

Discontinuous species are very few, but there is one outstanding example, *V. rostrata*, which is found in eastern North America and in Japan.

The distribution of the species of the genus Rhododendron

(Fig. 46)

Rhododendron affords a good example of the massing of endemic species in certain areas and the relative absence of wides. Many new species have been described recently, and there is no complete modern revision of the genus, but the main outline of its distribution can be gained from the *Index Kewensis* (277) and certain other sources (380).

The genus is distributed throughout the northern temperate regions with a very marked single extension south and south-east through tropical Asia to the northern part of Australia, and close on 1,100 species have been described. It is probable that if the genus is ever revised completely this number will suffer some reduction, but, on the other hand, new species are still being found, so that the figure may not be much too large.

Of this huge number no less than two-thirds, that is to say over 700 species, are found only in the great Sino-Himalayan mountain system, and of these the great majority are in that part of it where India, Burma, Tibet and China meet—the country of the great river gorges.

From this amazingly highly populated centre the genus has extensions in three directions. Much the strongest of these is through India and Malaysia, and this accounts for at least another 200 species, divided up as follows: India and Lower Burma, 6; Indo-China and Siam, 19; Malay Peninsula, 13; Sumatra, 11; Java, 7;

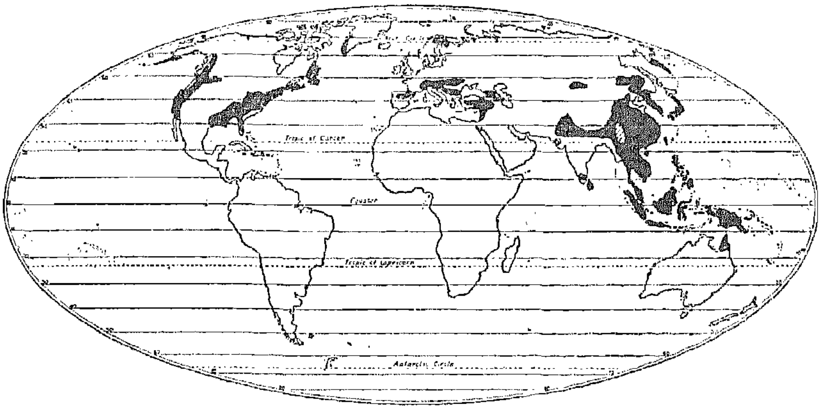


FIG. 46.—Map showing (black) the distribution of the genus *Rhododendron*, after Meinertzhagen. The small shaded ellipse in south-east Asia is the area of greatest species concentration.

Borneo, 32; Philippines, 24; Celebes, 9; Moluccas, 8; and New Guinea about 100. *R. retusum* is recorded from Java and Sumatra; two species have been described from the Solomon Islands; and one species, *R. lochae*, is found in Australia, restricted to the top of Mt. Bellenden-Ker in Queensland.

The second extension of the genus is eastwards through eastern and north-eastern Asia, including Formosa, into and right across the North American continent. This branch of the genus comprises about 120 species distributed as follows: north-eastern Asia, 33; Formosa, 24; Japan, 45; North America, 23. *R. anthopogon* is described as occurring in north Asia and in the Himalayas.

The third and much the smallest branch of the genus is westwards across western Asia and south Europe to Portugal. It consists of only about half a dozen species, but these include three of the best-known, namely, *R. ponticum* of the eastern Mediterranean region, which is the species of longest and most familiar horticultural history, and *R. ferrugineum* and *R. hirsutum*, the well-known "alpenrosen" of the European mountains. *R. lapponicum* has a circumpolar arctic range.

From this summary it will be seen that out of 1,100 species only two, or possibly three, are wide in the sense that they extend beyond the limits of one floristic region. Even these are very narrowly distributed compared with the range of the genus as a whole. This, in conjunction with the fact that over 700 species are confined to what is floristically but part of a region, gives the genus *Rhododendron* a degree of specific endemism and local concentration which is probably unique in one of its size and range.

The distribution of the species of the genus Erica

It is appropriate to pass from *Rhododendron* to a genus which can claim to compare closely with it in the features which have just been emphasised. This is the genus *Erica*, containing the "heaths." As in *Rhododendron*, there is no complete modern monograph, but the situation is here rather better because one or two publications, notably that of Phillips (418), provide useful information about the South African species, while the tropical African species have also been studied (96). Together with the *Index Kewensis* these sources provide a fairly clear picture of the distribution of the genus.

About 700 species have been described, and of these well over 600 are confined to the Union of South Africa, while of these again all but a handful are found only in the very much smaller Cape region.

From this marked geographical terminus the genus ranges in one direction only, up the east side of Africa, across the Mediterranean, and into Europe. This great south-north area is, however, in striking contrast to that of the tiny southern headquarters of the genus, comparatively poor in species, and such as there are fall into two well-marked distributional groups.

Ranging through tropical Africa from Rhodesia in the south to Abyssinia in the north, and to all intents and purposes confined to the mountains of the eastern side of the continent, are some sixteen species. All but one of these are more or less narrowly endemic, and they are more plentiful in the south than in the north. The single exception is the well-known tree heath, *Erica arborea*, found, south of the Sahara, from Tanganyika to Abyssinia, and again, north of the Sahara, from Macaronesia and Portugal to Greece and Crete (292). This, the only wide species in the whole genus, connects the tropical African species with the remaining group of European and Mediterranean species, which number about twenty. They include one outlier, *E. azorica*, found only on the Azores; the three species, *E. ciliaris*, *E. mediterranea* and *E. vagans*, which find their northern limits in the British Isles; and *E. tetralix* and *E. cinerea*, which provide, in northern Europe, the northernmost records of the genus (see fig. 54).

With only one wide species the proportion of endemics in *Erica* is even higher than in *Rhododendron*, but the latter is the wider genus and its great species centre is in the middle rather than at the edge of a continent. Moreover, *Erica* has but one centre, while *Rhododendron* has subsidiary centres in several parts of Malaysia, notably in New Guinea.

The Significance of High Species Concentrations

The last two genera mentioned were selected to illustrate a common feature of distribution, the concentration of great numbers of species in one part of the generic range, and in so doing they inevitably raise the question as to whether these places of maximum species concentration can be regarded as the original homes of the genera concerned or not. In short, is it justifiable, on the strength of the species distribution, to regard *Erica* as having originated in South Africa and *Rhododendron* in the Himalayas?

Actually the two cases are rather different. In *Rhododendron* the marked partial discontinuity and the known glacial history of much of the northern temperate flora goes far to resolve the problem, and it will simplify matters if on these accounts this genus is dismissed with the remark that it would indeed be rash to maintain, merely on the basis of the present distribution of the genus, that it originated in the Himalayas.

Erica is much more difficult, and, as it is but one of a considerable number of genera with rather similar ranges, it calls for more detailed treatment here.

A steep downward gradient of species concentration away from a maximum, especially when that maximum is situated at the very extremity of a great continental mass, gives, when expressed on a map, an overwhelming first impression of migration away from the peak and in the direction of the widest land areas, this impression no doubt partly arising from the circumstance that where the scattering of inanimate objects is concerned this is the usual figure produced.

Moreover, the impression is strengthened, and can to some extent be rationalised, by an appeal to the conceptions of evolution. If, as is believed, species are produced one after another over a long period of time, it would seem that the greater the concentration of species anywhere the longer has the genus existed there.

When they are put into print it is quickly clear that both these arguments, if they can so be called, are false. The first is obviously unjustifiable, simply because a genus is not inanimate and there is no reason to suppose that living species are disposed in the way indicated. The second is unsound, because the assumption in it is based on the supposition that the rate of species production is always and everywhere the same, whereas in fact there is every evidence to the contrary.

The question of the significance of high species concentrations is but one aspect of the much wider problem of how far and by what means it is possible to determine the geographical point of origin of any particular plant group. This information may clearly be of great importance to the plant geographer, and much attention has therefore been given to the consideration of the possible criteria and evidences by which it may be indicated. Cain (73, 74) has dealt with this subject in considerable detail and has listed a dozen such criteria which, it has been claimed at one time or another, can be used as indicators of the centre of origin of a group,

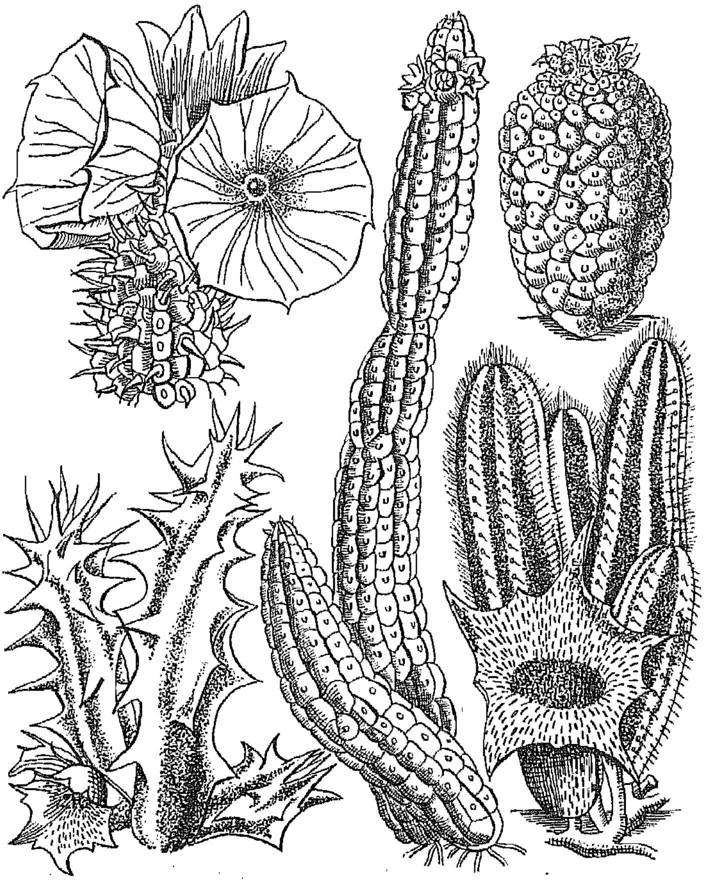


FIG. 47.—Some characteristic members of the tribe Stapelieae, after Wettstein.

but perhaps of greater importance is his conclusion, illustrated and strengthened by his study of these, that plant geography, among other biological subjects, carries too heavy a burden of hypothesis and assumption, and needs to return to inductive reasoning. With this conclusion many will agree.

The application, as well as the limitations, of some of these suggested criteria may be briefly illustrated by a short account of one of the most remarkable of Angiosperm groups, the Stapelieae, a tribe of the family Asclepiadaceae (621). This group of twenty or so genera has been monographed on an elaborate scale (585) and its geography can therefore be described with some confidence. The Asclepiadaceae are, as a family, characterised by marked floral specialisation, but the Stapelieae add to this an equally specialised vegetative form, being one of the three main groups of flowering plants (the others being the Cactaceae and certain species of *Euphorbia*) which, in association with arid habitats, have developed a cactoid habit, that is to say, which have lost their leaves and developed stems which are green, succulent and usually more or less angularly cylindrical.

The geography of the Stapelieae is shown vividly in figs. 48, 49, and it is only necessary here to summarise the chief points of importance. These are:

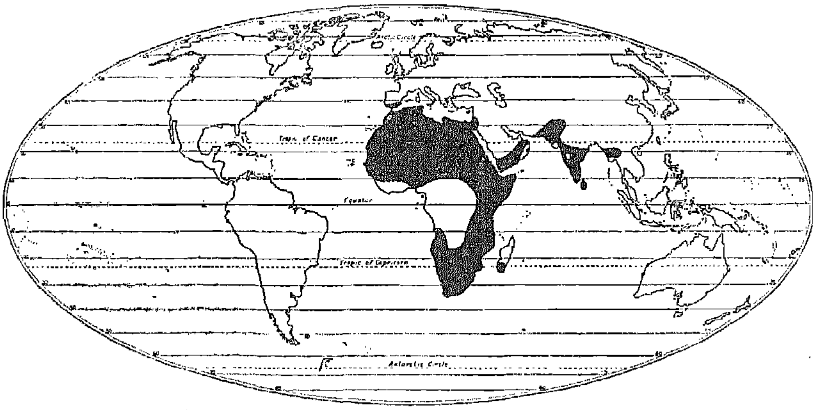


FIG. 48.—Map showing (black) the distribution of the tribe Stapelieae. The small white spot in the Indian Peninsula marks the distribution of the genus *Frerea.*

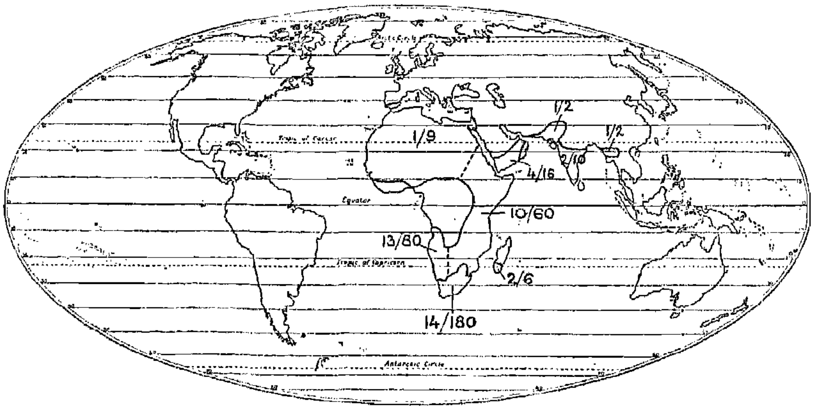


FIG. 49.—Map showing the numbers of genera/species in different parts of the range of the tribe Stapelieae.

1. The group as a whole ranges from Burma to Senegal and down the east side of Africa to the Cape.
2. Of its 370 species more than 280 are found only in South Africa.
3. No fewer than twelve out of twenty genera are found only in southern Africa and Madagascar.
4. One genus, *Caralluma*, has the range of the whole group.
5. This genus has half its 110 species in South Africa; four in East Africa; about thirty round the mouth of the Red Sea; and nearly all the rest scattered along its main west-east axis.
6. Eighteen out of the remaining nineteen genera are restricted to south Arabia, East Africa, South Africa, and very slightly to Madagascar.
7. The only other genus, *Frerea*, is a monotype of very restricted range in the vicinity of Poona in India.

Here, then, is a large group of plants numerically centred in South Africa but ranging widely therefrom both north and east. At first sight it might therefore be supposed that the group originated in South Africa and spread thence, but, as will be seen, there is strong evidence that the contrary is true.

The evidence for this view resides chiefly in the relationship between the different genera of the group. For reasons which need not be considered in detail here it is generally and quite justifiably believed that extremely specialised structural modifications towards life under markedly xerophytic conditions, as in deserts, have been comparatively recently derived from more mesophytic types with more ordinary form and possessing leaves. For these reasons, for instance, *Pereskia*, which is the only genus of Cactaceae with leaves, is generally held to be the most primitive type of the family. It is therefore interesting to find that there is one genus of Stapelieae which has persistent leaves and which is far less xeromorphic than the others, and which therefore may be regarded as the most ancient and primitive of the group, and still more interesting to find that this is the genus *Frerea*, the Indian monotype. Again, *Caralluma*, which is certainly the most generalised of the xeromorphic genera and the most closely related to *Frerea*, is the only other genus found east of Arabia. Still again, the general relationship of its species is along the line from Burma to Senegal, and the South African branch of its range is occupied by its most specialised species. Finally, the South African genera are all to be regarded as among the most specialised of the whole group.

In short, all the evidence seems to show that the Stapelieae are of Asiatic origin and that their extension down the east side of Africa is a branch of their main geographical axis. If this is so, then the group illustrates, not a maximum species concentration at its point of origin, but one at the point furthest from it, and, however much the general distribution of the species may, at first sight, suggest a South African origin for the group, the other lines of evidence are all in favour of the contrary view.

It seems clear then, at least from this example, that, unless it is supported by other evidence, a great local concentration of species cannot necessarily be held to indicate the original home of a plant group, but that every group showing such a concentration must be considered on its merits.

CHAPTER 9

THE DISTRIBUTION OF SPECIES—II

It has already been pointed out that there is no fundamental distinction between the ranges of genera and the ranges of species, and, this being so, it is practicable and convenient to use, in this and the next two chapters, the same general classification of distributional types as was employed in the case of genera, beginning with the most widespread forms and working down to the most restricted endemics. To the former class this chapter is devoted.

Cosmopolitan and Very Wide Species

It can be said with certainty that no species is cosmopolitan in the sense that it occurs naturally wherever flowering plants will grow, but a good many are so widely distributed that they do not fall into any more restricted category. These exceptionally well-spread species are mostly of three kinds, namely freshwater aquatics, temperate species now widely adventive in the tropics, or tropical species to some extent adventive in the temperate zones. Apart from these few species have been credited with comparable ranges, and the mention of *Calystegia sepium*, *Deschampsia caespitosa*, *Luzula campestris*, *Prunella vulgaris*, *Samolus valerandi* and *Sibthorpia europaea* accounts for the best-known of them.

Actually *Phragmites communis*, the common reed, is generally quoted as the most widely distributed of all Angiosperms. It occurs, often in great quantity, in nearly all parts of the world, but is said by Ridley (449) to be absent from the region of the Amazon. It is, however, an aquatic plant and may well serve as an introduction to the other species comprising the first of the three types mentioned above.

Darwin (124) was one of the first to call attention to the exceptional range of many freshwater aquatic species (especially those that live floating or submerged) and paid considerable attention to them. Among them the members of the genus *Lemna* are nearly all very widespread, but their peculiar growth-form tends to favour casual transport of whole plants such as is scarcely known elsewhere, and their geography certainly owes something to this. This is certainly not true, however, of *Potamogeton pectinatus*, which shows an equally wide range. *Typha latifolia* and *T. angustifolia* are similarly widespread, the former being absent only from central and southern Africa and the latter from North America and Madagascar. *Potamogeton crispus* is unusual in that it occurs widely in both the tropical and temperate parts of the Old World but is absent from America (547). Among other wide aquatics are *Ceratophyllum demersum*, *Cladium mariscus*, *Cyperus flavescens*, *Glyceria fluitans*, *Myriophyllum spicatum*, *Najas marina*, *Phalaris arundinacea*, *Scirpus* spp. and *Zannichellia palustris*. Others almost equal in range, but which are less widespread in the temperate regions, include *Rotala mexicana*, *Ammannia auriculata* and *Ludwigia parviflora*.

It must be remembered that aquatic plants have generally, although they may be well scattered, a comparatively limited area of actual occurrence, so that while the total area may be wide the number of individuals may be much less than in the case of more restricted species. This kind of limitation of habitat, as opposed to total range, is also seen in the case of other plants of various special kinds, prominent among them being the halophytes, of which *Suaeda maritima* and *Salicornia europaea* are generally credited with an almost world-wide distribution. They do indeed occur in most latitudes, but their edaphic requirements (see Chapter 17) limit them either entirely or largely to coastal areas or to where inland there are salt deposits, so that the actual size of the area they cover is relatively small. The same thing is true of many temperate species in the tropics. Their occurrences may be widely scattered, but at least if they inhabit very high altitudes the total area they cover may be very small.

The next two types both involve the problem of status (see Chapter 12), and this in particular prevents more than a rather indefinite account of these very widespread species because they may often be no more than transitory casuals.

As regards these partially adventive wides it is instructive to notice that those introduced from temperate to tropical regions have for the most part wider ranges than those in which the movement has been the reverse, which seems to indicate that while many species can live, under somewhat artificial conditions, in surroundings considerably warmer than those to which they are normally accustomed, few can maintain themselves in conditions much colder than the normal. Here two factors are certainly concerned deeply: in colder regions the growing season is shorter and there is less chance of ripening seed, but more important is the fact that the temperate zones nearly everywhere have frost at one time or another, a condition to which tropical plants are not exposed.

It is probably true to say that all temperate weeds find niches somewhere in the tropics as a result of carriage by man, but the following appear to be particularly ubiquitous:

Capsella bursa-pastoris, *Chenopodium album*, *Erigeron canadensis*, *Euphorbia helioscopia*, *Plantago major*, *Poa annua*, *Polygonum aviculare*, *Solanum nigrum*, *Sonchus oleraceus*, *Stellaria media*, *Taraxacum officinale* and *Urtica dioica*.

The opposite condition of tropical species extending into more temperate zones as weeds is shown well by the following, of which some actually occur rarely in the British Isles:

Amaranthus angustifolia, *Asclepias curassavica*, *Cynodon dactylon*, *Echinochloa crus-galli*, *Gnaphalium luteo-album*, *Paspalum distichum*, *Portulaca oleracea* and *Setaria verticillata*.

Pan-tropical Species

The number of species which to-day are found practically throughout the tropics is large, but here again it is very difficult to determine their status in different parts of the world. A few perhaps have, as will be seen, a natural range over the tropics, but the vast majority of them have been introduced widely and especially between the western and eastern hemispheres. Some have been actually planted all over the tropics, like the coconut, whose place of origin is still a matter of argument (378); some have run wild from cultivation; while still others, and these seem most numerous, are weeds of tropical lands occurring like those of the temperate zones wherever there is disturbed ground, though each is native to some part of its range.

The relative absence of natural pan-tropical species has often been commented on, and Ridley (449) calls attention to the fact that the nearest approach to them appears to be such members of the Cyperaceae as *Cyperus haspan*, *Fuirena umbellata*, *Eleocharis geniculata*, *E. chaetaria*, *Rhynchospora corymbosa* and *Scleria lithosperma*. It is fairly certain that these plants at least are not adventives, but with almost all other pan-tropical species there is generally some reason for suspicion except perhaps among some of the strand plants (see p. 219).

Among the widely found escapes from cultivation in the tropics are *Acacia farnesiana*, *Amaranthus caudatus*, *Anacardium occidentale*, *Cajanus cajan*, *Canavalia ensiformis*, *C. maritima*, *Gossypium arboreum*, *G. peruvianum*, *Physalis peruviana* and *Tamarindus indica*.

The widely distributed tropical weeds are of general interest from many points of view, and for this reason the following list of some of the most important is not too long:

Abrus precatorius
Abutilon asiaticum
A. crispum
A. hirtum
A. indicum
Achyranthes aspera
A. indica
Ageratum conyzoides
Amaranthus spinosus
A. tristis
Bidens pilosa
Bryophyllum pinnatum
Caesalpinia bonduc
C. pulcherrima
Capsicum frutescens
Cassia absus
C. tora
Cassytha filiformis
Catharanthus (Lochnera) roseus
Celosia argentea
Cenchrus echinatus
Coix lacryma-jobi
Commelina diffusa
Cressa cretica
Crotalaria incana
C. retusa
Cyathula prostrata
Desmodium triflorum
D. umbellatum
Digitaria sanguinalis
Dodonaea viscosa
Eclipta prostrata
Eichhornia crassipes
Elephantopus scaber
Eriodendron anfractuosum
Evolvulus alsinoides
Gomphrena globosa
Gynandropsis gynandra
Gyrocarpus jacquinii
Heteropogon contortus
Hibiscus cannabinus
H. sabdariffa
Hyptis pectinata
Jussiaea repens
J. suffruticosa
Lantana mixta
Leonotis nepetifolia
Leucas martinicensis
Limnocharis flava
Microglossa pyrifolia
Mikania scandens
Mimosa pudica
Mucuna pruriens
Oxalis rosea
Peperomia reflexa
Phyllanthus distichus
Pisonia aculeata
Sesuvium portulacastrum
Sida cordifolia
S. rhombifolia
S. spinosa
S. urens
S. veronicifolia
Sigesbeckia orientalis
Solanum aculeatissimum
Spilanthes acmella
Tragus racemosus
Urena lobata
Vigna marina

It may be noted that in this list the Malvaceae, Amaranthaceae, Compositae and Gramineae and the three leguminous families are particularly well represented, and that some of the species are strand-plants (see Chapter 11).

Plate 12. *Protea cynaroides* at the Cape

Other Wide Species

The wide species of the northern flora

The great extent of the land surfaces in the colder parts of the northern extra-tropical world, the southern boundary of which (though varying somewhat with latitude), may be drawn at somewhere between 45° and 50° N.; the arrangement of these lands in an almost continuous circumpolar belt; and, doubtless, the marked climatic vicissitudes to which most of them have been subjected since the end of the Tertiary, combine to give their plant life a rare degree of floristic unity, of which the most notable expression is the unusual prevalence of species with wide distributions and a comparative paucity of narrower endemics of the better-marked sort, a characteristic which points clearly to the main feature of this northern flora, which is that it is, in broad terms, a diminished extension northwards of the various floras in the latitudes immediately south of it. Plain as this is in most parts of the north temperate zone it is perhaps most obvious in eastern North America where the floristic change and diminution northward is so gradual that it is almost impossible to find a line at which there is any abrupt passage from one flora to another, with the result that this whole area, covering a quite exceptional latitudinal range can only with some difficulty be divided, on a world-wide scale, into two sub-regions. In eastern Eurasia the situation is rather different, partly no doubt because the effects of the ice ages were there less felt and partly because of the distribution of great topographic barriers, and the boundary between the northern flora and that of the Sino-Japanese region (which is the counterpart of the flora of south-eastern North America) is much more clear-cut. On the other hand the wide diffusion of the northern flora is, in the Old World, exemplified by the exceptional latitudinal extent of the Euro-Siberian region, which also cannot reasonably be divided into more than two sub-regions, and even this more for convenience than on the merits of any strong distinctions.

The existence of this widely diffused northern flora may confidently be attributed in part at least to such fundamental considerations as the shape of the earth and the particulars of its movements in relation to the sun, for, so long as the polar axis has remained in a position approximating to that which it now occupies, and so long as there has been no considerable change (other than minor fluctuation) in the obliquity of the ecliptic, the latitude of 45°–50° or so must always have been a critical one because of the rapidity with which certain climatic and related values change north of it on account of the diminishing angle at which the incident rays of light strike the earth. Thus, the length of day in summer, and the length of night in winter, increase very sharply until at the poles each has a duration of six months, while above this crucial line frost is as much a commonplace as is its absence south of it. It is generally agreed that such austere conditions as these are not likely to be those in which the Flowering Plants attained their mastery of world vegetation and there is thus additional reason to regard the northern flora, as described above, as being essentially the high latitude derivative of more tropical floras and as comprising those plant types which possessed or developed the necessary tolerance to more difficult life conditions and which were thus sifted out from the rest and enabled to colonise the north.

It is therefore especially in connection with the Northern flora that the plant geographer becomes most closely concerned with the problems of changes in chromosome number (526, 527), or polyploidy as it is broadly called (see Chapter 3). Some biologists, among whom may be mentioned Tischler (557) and Muntzing

(396), are of opinion that polyploid forms are proportionately more numerous in climatically less favourable regions, and even that they are more hardy than diploids and hence more suited to high latitude distribution, while Löve and Löve (350) state that there is something of a direct relation between the latitude and the proportion of polyploids in a flora. It has also been shown for particular species and genera, as by Manton (360), Anderson and Sax (14) and Giles (196) that polyploids have, in comparison with diploids, ranges which suggest that they have been especially successful in colonising northward or upward in the direction of retreating ice sheets. There would seem little doubt (see Chapter 19) that the rapidity of climatic change during the Pleistocene was much greater than it had hitherto been in the history of Angiosperms and it is not unreasonable to suggest that the underlying necessity for keeping pace with this change found expression in the intensification of evolution by the most rapid methods such as change in chromosome number, and in this connection it is significant also that those flowering plants in which the normal processes of seed production have been short-circuited by apomixis are also, in the main, high latitude plants. However, other biologists, among whom Senn (474) and Bowden (59) may be cited, deny that polyploids are more hardy than diploids or have more northerly distributions. A useful more extended survey of the problems of chromosomes and geographical distribution is given by Cain (74).

But the latitudes in which this northern flora is seen at its best are also those in which the impact of the human foot has been deepest, with the twin consequences that, while the flora is the most artificially modified in the world, it is also the most intensively studied, with a literature so vast that even the slightest survey of it is impossible here, and any lack of botanical richness there may be in the flora, compared with those of more favoured lands, is more than offset by the great detail in which it has been investigated and the enormous amount of information available concerning it. Unfortunately each of these considerations leads to a difficulty; first, that there are widely divergent conceptions about many species, and consequently of their distribution, and second, that to compress what must be said about it into the space available here is as hard as it is to compare it faithfully with the floras of other and less familiar parts of the world.

In view of these difficulties the best course here is to base our observations on particular sources, and we cannot do better than to use, as these, two works of Hultén, whose knowledge of the geographical distribution of the members of the northern flora is probably unrivalled. The smaller and earlier of these two books, the *Outline of the History of Arctic and Boreal Biota during the Quaternary Period* (284), is the more generally valuable here because of its rather wider scope and the fact that it deals with a less familiar part of the flora. In it the author develops the thesis that during the Pleistocene certain areas in the higher latitudes became refuges in which various species of the pre-glacial flora were able to persist till better climatic conditions returned and from which they were then able to spread more widely again. This he illustrates by a series of maps constructed on the principle of *isochores*, which are lines analogous to such more familiar ones as isotherms, based on the species populations from place to place, and the resultant maps may be described as, or compared with, layered maps in which each successive layer represents a higher proportion present of the total species constituting the group which is thus being analysed. These maps, Hultén considers, illustrate his contention that, to use his own words, "the plants of our area can be grouped around centra from which they must have spread, and that the total areas of all plants spreading from the same centre form more or less concentric and equiformal progressive figures," and this is the expression of his Theory of Equiformal Progressive Areas. From these maps Hultén concludes that the pre-glacial refuges were particularly associated with those regions on both sides of the Bering Strait where the influence of the ice-ages was least felt, and it is the species which now occur in these parts which are the subject of his very detailed analysis.

Hultén's isochore maps are impressive but there is some room for difference of opinion about their real value, especially since they do not necessarily depict the actual distribution of any one or more species, and it may be that they do not express much beyond the fact that the distributions of species can, because of their almost infinite variety of detail, be arranged in many different ascending or descending series of size and shape. Similarly, as Raup has also pointed out in comments on this work (437, 438), the sorting of these distributions into groups, which is fundamental to the isochore method, must, because of the great similarities between many of them, and especially the more widespread, involve a measure of arbitrary decision which is bound to weaken to some extent any conclusions based on it. At the same time this comment is no denial of Hultén's views about the history of the northern biota during the Quaternary, nor does it detract from the vivid way in which his maps reveal some of the outstanding types of plant distribution in this part of the world.

The larger and more recent of Hultén's books, his beautifully produced Atlas of the *Distribution of Vascular Plants in North-west Europe* (285) deals only with the species which occur within that region and is therefore somewhat more restricted in scope, but it is likely to be of greater interest to British and continental botanists because it deals with so many of their indigenous species, and even more will appeal to all who appreciate the fine making of books. Here the same general methods of presentation are employed and the flora of this part of Europe is exhaustively classified with the aid of further isochore maps. So exhaustive indeed is the classification here, where forty-eight groups are recognised, and in the *Outline*, where the number is rather less, that the reader can only be recommended to study them in the original, as no summary will easily do them justice.

A geographical analysis of a rather different kind, dealing with the arctic and European portions of the northern flora is given by Böcher (56). Here the basis of arrangement is latitudinal, and the area under consideration is divided into three such zones, arctic or alpine, boreal, and central European, and each of these is further divided, so that with the addition of one intermediate the total number of latitudinal belts is ten. The species under each of these are then grouped according to whether they are mainly oceanic, or continental, or indifferent in distribution, and each of these is still further divided, so that in grand total the classification contains more than sixty geographical types. It is unnecessary to multiply references to arrangements of this kind, but the reader may be referred to one more general work, which contains a great deal of information, both in the form of maps and otherwise, relating to the northern flora, namely Meusel's *Vergleichende Arealkunde* (388).

The very complexity of these various classifications expresses one of the leading features of the flora, the great geographical diversity shown by its members, and any attempt to give a simpler presentation of the facts meets with difficulties. Some of these have already been touched upon, but there is one in particular so generally inherent in phytogeographical studies, and so well illustrated by the present subject, that a further discussion of it is desirable here.

When the ultimate distribution of the individuals of a species is examined it is invariably found to be discontinuous to some degree, that is to say the individuals are scattered more or less irregularly and are never all in complete mutual contact. In theory, of course, there might be such a continuity, especially if the species consisted of only a few individuals, but it is doubtful whether this has ever been recorded, and it is certainly contrary to all experience. Discontinuity between individuals or populations may be of almost any extent, and of very different degrees in different places. Thus, in one part of its range a species may almost cover the ground to the exclusion of others, while in other places it may occur only as a few widely scattered plants. Similarly its different separate localities may be closely grouped or widely spaced from one another. Because of this it is usually impracticable, except on an impossibly large scale, to describe or depict exactly the discontinuities in distributions and it becomes necessary to ignore them to whatever may be the most appropriate degree. The problem thus becomes one of deciding what this appropriate degree may be, having in mind the purpose immediately in hand, but it is seldom one which reveals more than some, and often very little,

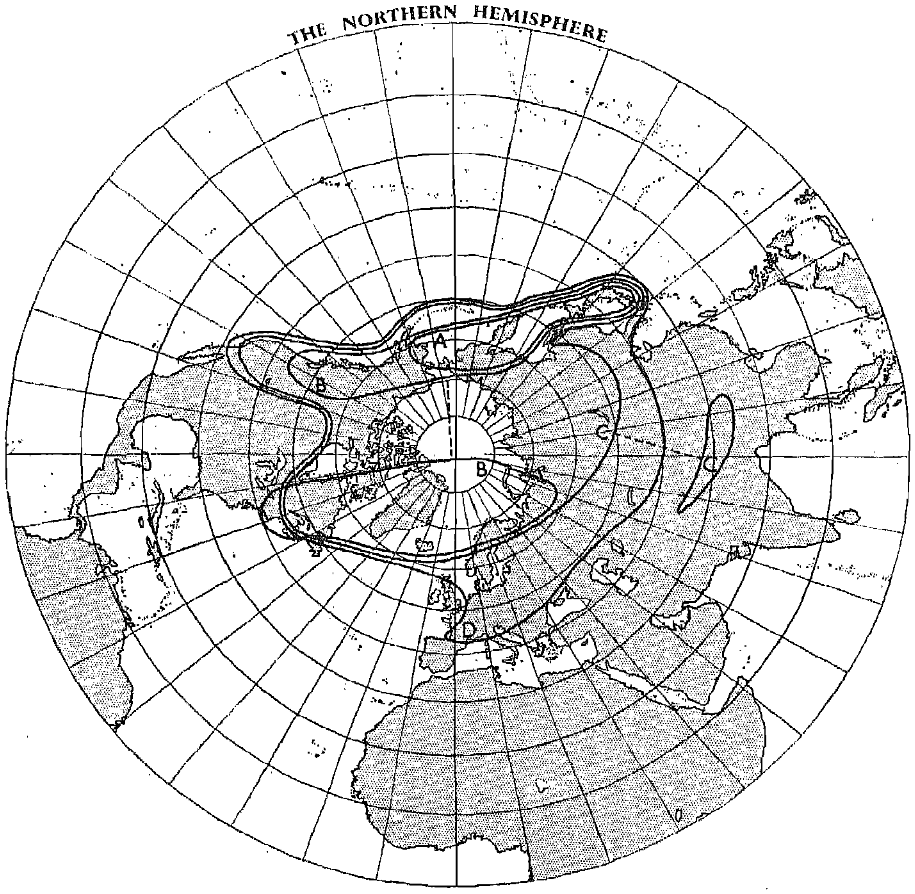


FIG. 50.—Map showing the distribution of the genera A. *Bryanthus*, B. *Harrimanella*, C. *Cassiope* and D. *Phyllodoce*.

detail. This point can be nicely illustrated by reference to the arctic-alpine species *Phyllodoce caerulea.* This plant is often regarded as having a circumpolar range, and this, up to a point, is true, but as Hultén's map (284) shows, the distribution of the species actually comprises some twenty distinct and variously separated minor areas. Even so this only partially reveals its discontinuity, for in another map by Hultén, on a larger scale (285), its Scandinavian area is itself seen to be irregularly discontinuous. Finally even the smallest areas shown on the first map tend necessarily to exaggerate the actual distribution of the plant, as for instance in the case of Scotland, where it is in fact exceedingly local.

What is true of *Phyllodoce caerulea* is true also of other members of the northern flora, and there can be but few species which are not appreciably discontinuous on a relatively large scale, and consequently any geographical analysis, if taken beyond a certain point, tends only to result in the recognition of increasingly large numbers of variously discontinuous and differing types. On the other hand there are certain species in which the discontinuity is exceptionally wide, and these must not be overlooked. In short, it becomes a matter of choosing a method of presentation which will, on the one hand, provide enough elaboration for the current purpose, without, on the other hand, being so highly analytical that generalities will be lost in a mass of detail. The following comparatively simple statement and arrangement of the wider types of distribution in the northern flora has been drawn up with this in view and must be read in relation to the general purpose of this book. Its accuracy can go only so far as its scope permits, and like any other arrangement of species in categories, it necessarily involves an element of arbitrary choice. At the same time it does present, as far as seems feasible here, the general plan of wider distributions over the vast area occupied by the northern flora; the narrower types of distribution are dealt with later under their more particular headings.

The wider types of distribution in the northern flora

A. Distribution more or less completely circumpolar.

A comparatively frequent type of distribution, which may be further subdivided latitudinally.

1. Arctic and sub-arctic, which, because this region is itself circumpolar, will include some of the species endemic to it.
   e.g. *Braya purpurascens, Carex lapponica, Ranunculus nivalis.*
2. Arctic-montane, containing species present also in some of the mountain regions.
   e.g. *Oxyria digyna, Polygonum viviparum, Saxifraga oppositifolia.*
3. Temperate, with ranges all or mostly outside the arctic circle.
   e.g. *Caltha palustris, Comarum palustre, Menyanthes trifoliata.*

B. Distribution incompletely circumpolar.

Comprising the numerous species which occur in both western and eastern hemispheres but which are conspicuously lacking or deficient in one major longitudinal sector.

1. Species notably absent from or deficient in western Eurasia.
   e.g. *Gentiana acuta, Mitella nuda, Veronica americana.*
2. Species notably absent from or deficient in central Eurasia.
   e.g. *Galium triflorum, Juncus stygius, Mertensia maritima.*

3. Species notably absent from or deficient in eastern Eurasia.
    e.g. *Campanula uniflora, Listera cordata, Pinguicula vulgaris.*
4. Species notably absent from or deficient in western North America.
    e.g. *Milium effusum, Oxalis acetosella, Scirpus sylvaticus.*
5. Species notably absent from or deficient in eastern North America.
    e.g. *Adoxa moschatellina, Cypripedium guttatum, Myosotis alpestris.*
6. Species notably absent from or deficient in the neighbourhood of the North Atlantic.
    e.g. *Minuartia arctica, Parrya nudicaulis, Pedicularis sudetica.*
7. Species notably absent from or deficient in the neighbourhood of the North Pacific.
    e.g. *Cassiope hypnoides, Geum rivale, Liparis loeselii.*

C. Distributions more incomplete but still involving both western and eastern hemispheres.

1. On both sides of both the North Atlantic and the North Pacific only.
    e.g. *Cornus suecica* (also Burma), *Lathyrus maritimus, Montia lamprosperma.*
2. On both sides of the North Atlantic only.
    e.g. *Bartsia alpina, Gentiana nivalis, Saxifraga stellaris.*
3. On both sides of the North Pacific only.
    e.g. *Cassiope lycopodioides, Echinopanax horridum, Fritillaria camschatcensis.*
4. Other notably discontinuous species.
    e.g. *Cornus canadensis* (see fig. 5), *Eriocaulon septangulare, Lobelia dortmanna, Phyllodoce caerulea* (almost C.1), *Potamogeton epihydrus, Potentilla fruticosa, Spiranthes romanzoffiana, Swertia perennis, Tofieldia palustris.*

Old World tropical species

Reference is often made in the literature to species which are described as having a distribution throughout the Old World Tropics, with the inference that they are more or less continuous from southern Africa to the Pacific Islands. Probably there are very few if any species which naturally have this range rather than one which falls more appropriately into one or other of the next two categories, but there is certainly a group of species which generally, owing to introduction here or there, or to escape from cultivation, have this range in a more or less complete form. They are therefore to be regarded as the counterpart on a smaller scale of the pan-tropical weeds already discussed, and a short list of some of the more important is of interest. It contains:

Bryonopsis laciniosa, Canscora diffusa, Carapa moluccensis, Conyza aegyptiaca, Cymbopogon citratus, Dichanthium annulatum, Diplachne fusca, Drosera indica, Elytrophorus spicatus, Gymnema sylvestre, Hibiscus aristivalvis, H. caesius, H. panduriformus, H. surattensis, H. trionum, Imperata cylindrica, Musa cavendishii, M. paradisiaca, Ocimum basilicum, Parochetus communis, Polygonum plebeium, Portulaca quadrifida, Rottboellia exaltata, Solanum melongena, S. pseudocapsicum, Sphaeranthus africanus, S. indicus, Tacca leontopetaloides, Trichodesma zeylanicum, Xyris indica.

A somewhat reduced form of this distribution is shown by such species as *Afzelia bijuga* (Madagascar to Queensland) and *Dianella ensifolia* (Madagascar to northern Australia).

African-Asiatic species

As has just been indicated, the wider naturally ranging species of the Old World tropics are either found from Africa to Asia or from Asia to Australasia and the Pacific Islands, and the present category contains the former.

For the most part they are rather xerophilous species, because otherwise they tend to be absent from northern Africa and western Asia and therefore to be discontinuous, but they include quite a number of others as well. Again, most of them range from Africa only as far as India or southern China, but others extend far into Malaysia. Some, too, occur in Madagascar or the Mascarenes as well as in continental Africa.

It will thus be seen that the category is not well defined, but a range of this kind has been attributed to *Aerva javanica*, *Arthraxon lancifolius*, *Asparagus asiaticus*, *Cleome monophylla*, *Desmostachya bipinnata*, *Dicoma tomentosa*, *Grewia villosa*, *Hypericum lalandii*, *Latipes senegalensis*, *Pavonia schimperiana*, *Polygala erioptera*, *Rumex nepalensis*, *Schismus barbatus*, *Sorghum subglabrescens*, *Trichodesma africanum*, *Urochloa panicoides*.

Asiatic—Australasian wide species

In one sense this category is the counterpart of the last and contains in particular those species which range all the way from deep in continental Asia to Australasia or the Pacific Islands, but there are reasons why it is appropriate to include also in our consideration here those many other kinds of distribution which, though less extensive nevertheless considerably exceed the limits of any single one of the floristic regions in this part of the world.

A glance at the maps of Plates 4 and 5 shows that one of the more important differences between them is in the Asiatic sector of the tropics. Floristically this great area is divided into three regions, but climatically these are one, and form all but a small part of the Indo-Australian Monsoon Province. It is therefore not surprising to find that although the floristic distinctions between the three constituent regions, and especially between the two continental regions and Malaysia, are well marked, there are many species whose ranges exceed any one of these and in many cases cover all or nearly all the province or even extend beyond it, more especially towards Japan in the north and further south in Australasia. Many familiar plants of cultivation especially are widely spread in this great area and are thought to have had their orginal homes somewhere within it, though it is now impossible to say more than this, among them being, *Adenanthera pavonina*, *Areca catechu*, *Artocarpus integer*, *Boehmeria nivea*, *Durio zibethinus*, *Mangifera indica*, *Nephelium lappaceum*, *Palaquium gutta*, *Piper betle*, *Piper cubeba*, *Pogostemon patchouly*, *Tectona grandis* and *Uncaria gambier*.

Although some species, such as *Curculigo orchioides*, *Drosera spathulata*, *Finlaysonia obovata*, *Haloragis micrantha*, *Lagenophora billardierii*, *Malaisia tortuosa*, *Morinda citrifolia*, *Nervilia aragoana*, *Osteomeles anthyllidifolia* and *Zoisia matrella*, range from Asia to New Zealand or Polynesia, the commonest type of distribution in this part of the world is probably that from India and/or neighbouring south-east Asia to Australia, a distribution covering the monsoon province more or less exactly. Good instances of this kind of range include *Burmannia disticha*, *Calanthe veratrifolia*, *Casearia tomentosa*, *Deeringia amaranthoides*, *Dischidia rafflesiana*, *Drosera burmanni*, *Epipogium roseum*, *Gnetum gnemon*, *Hoya carnosa*, *Leptospermum flavescens*, *Loranthus falcatus*, *Microcarpaea muscosa*, *Mimusops balata*, *Pholidota imbricata*, *Pluchea indica*, *Pycnospora hedysaroides*.

Of less extensive distributions within these extremes there are so many sorts and the connections between them are so gradual that little would be gained in clarity by attempting any exhaustive analysis of them, but the following table of quoted examples will demonstrate this fact sufficiently.

Actinidia callosa	north-east Asia to Java.
Artemisia capillare	Manchuria to Philippines.
Liriope graminifolium	Manchuria, Indo-China, Formosa, Philippines.
Gaultheria leucocarpa	south-east Asia and Malay Peninsula to New Guinea.
Dendrobium crumenatum	Burma and South China to Moluccas.
Stackhousia intermedia	Sumatra and Philippines to Micronesia and Australia
Erechtites arguta	Lesser Sundas, New Guinea, Australia, New Zealand.
Uncinia riparia	Borneo, New Guinea, Australia, New Zealand
Geranium pilosum	New Guinea, Australia, New Zealand.
Secamone elliptica	Philippines to Australia.
Dianella caerulea	New Guinea, Australia, New Caledonia and Fiji.
Dianella javanica	Sumatra and Philippines to New Guinea and New Caledonia.
Gymnanthera nitida	Borneo to Australia.
Macrosolen cochinchinensis	India and South China to Borneo and Philippines.
Macrosolen avenis	Burma and Siam to Java and Sumatra.
Pottsia cantonensis	India and China to New Guinea.
Homonoia riparia	Ceylon and Yunnan to Timor.
Tecticornia cinerea	South-west New Guinea and northern Australia.
Loranthus estipitatus	South China and Indo-China to Malay Peninsula, Borneo and Philippines.
Korthalsella opuntia	Himalayas to Japan, western Malaysia and Philippines.
Scutellaria luzonica	Formosa to New Guinea.
Bythophyton indicum	south-east Asia and Philippines.
Cryptolepis elegans	India, South China and Java.
Hemidesmus indicus	India, Ceylon, Malay Peninsula.
Trichopus zeylanicus	,, ,, ,,
Streptocaulon griffithii	Burma, Siam, Malay Peninsula.
Ancistrocladus tectorius	south-east Asia to Sumatra and Borneo.

The botanical history of the monsoon province is of great interest especially with regard to the interrelationships of the different parts and has been discussed by van Steenis (529) with particular reference to the montane element in the flora. This work will be mentioned again later, but it may be noted here that the distributions of these species show two distinct lines of connection between continental Asia and Malaysia, one by way of India, Indo-China, Sumatra and Java, and another by way of China, Japan, Formosa and the Philippines. The former is illustrated by *Anemone sumatrana*, *Bucklandia populnea* and *Pyrus glandulosa*, and the latter by *Androsace umbellata*, *Asparagus cochinchinensis*, *Fragaria indica* and *Skimmia japonica*.

African wide species

Under this heading must be included the various types of distribution too wide to be included under any one of the African regions, and here again, as so often before, almost any particular range can be exemplified, but there are certain predominant types.

One comprises species found widely in Africa, or at least the tropics, and also on the islands. Examples of this are furnished by *Celosia trigyna*, *Gloriosa virescens*, *Harungana madagascariensis*, *Maesa lanceolata*, *Sorghum verticilliflorum* and *Strychnos spinosa*.

Much more familiar and numerous are some of the plants which range widely over the continent itself. An extreme condition is seen in such plants as *Clematis simensis* or *Oncoba spinosa*, which actually reach Arabia, but the great majority are found only south of the Sahara, although *Priva cordifolia*, *Myrsine africana* and doubtless some others extend from Socotra or Abyssinia to the Cape.

A few wide African species like *Coleus thyrsoideus*, *Kalanchoe coccinea* and *Zantedeschia aethiopica* (the arum lily) are grown in greenhouses, and the last is perhaps the best-known of all African plants. There are also a few economic plants of at least local importance which now have a wide range. Among them may be mentioned *Butyrospermum parkii*, *Cola nitida*, *Pentadesma butyraceum*, *Ricinus communis*, *Sorghum caffrorum*, *S. guineense* and *Voandzeia subterranea*.

For the rest the following is a selection of the species to which a wide distribution in tropical or warm Africa has been attributed:

Adansonia digitata, *Baphia nitida*, *Bridelia micrantha*, *Chlorocodon whitei*, *Clematopsis scabiosifolia*, *Cleome hirta*, *Clerodendrum thompsonae*, *Cymbopogon giganteus*, *Hymenocardia acida*, *Hypericum roeperianum*, *Leonotis leonurus*, *Myrothamnus flabellifer*, *Nymphaea caerulea*, *Oxytenanthera abyssinica*, *Pennisetum purpureum*, *Pluchea dioscoridis*, *Sorghum arundinaceum*, *Sparrmannia africana*, *Stephania abyssinica*, *Telfairia pedata* and *Telosma extensa*.

Australian and New Zealand wide species

Here two rather distinct types of distribution find a place, namely the wide Australian, which covers more than one of the regions into which the continent is divided, and the Australian-New Zealand type, which is discontinuous but which it is convenient to consider here.

As regards the species widely distributed within the continent their range usually takes one of two forms; they are either plants of the drier interior which actually extend into one or other of the peripheral regions, or they are plants which extend more or less completely across the south of the continent from east to west. The former includes a number of grasses, among them *Panicum decompositum*, *Pappophorum nigricans* and *Triodia irritans*.

The latter are certainly much more numerous, and almost every large and characteristic Australian genus contains one or more of them, though the proportion is always small. *Casuarina distyla*, *Goodenia pinnatifida*, and a number of species of *Eucalyptus* and *Grevillea* are examples.

There is a strong element of relationship between the floras of Australia and New Zealand and the two regions appear to have at least 220 species in common. Among those which are found only in these two countries may be mentioned *Mazus pumilio*, *Scleranthus biflorus*, *Spinifex hirsutus* and *Stipa teretiflora*.

American wide species

It would take far more than the space available here to give even a brief complete survey of the innumerable types of wide distribution exhibited in the huge area of the New World. The task is, moreover, made particularly difficult because of the absence of barriers between the north and south and the facilities for plant movement in this direction afforded by the long chain of the western mountains, and, as a result of these conditions, there is every variation in latitudinal plant distribution. All that can be done is to supplement what will be said later under the various regions. With this purpose in view we may pass somewhat rapidly over certain aspects by saying that there are species like *Erechtites hieracifolia* which are said to occur practically all over America, *Madia sativa* which occurs all down the west side, and others such as *Apocynum androsaemifolium*, *Dodecatheon meadia*, *Symphoricarpos albus*, and various species of *Penstemon*, *Solidago*, *Trillium* and *Carya* which range widely through North America, and pass on to the more detailed and necessary consideration of the widely spread tropical species.

In one sense the tropical portion of America corresponds to the whole of the Old World tropics and may be expected to have in the same way its own widely distributed weeds and denizens. This is so, and in order to make a comparison between the two hemispheres possible it is worth while to give a fairly extended list of the species which are more or less completely distributed now through the New World tropics. The list includes also some of the species whose natural ranges are especially wide, as well as a few species now so widely cultivated that their place of origin can hardly be decided.

Bocconia frutescens
Bursera gummifera
Capsicum annuum
Carica papaya
Cedrela odorata
Chlorophora tinctoria
Clidemia hirta
Cordia sebestena
Crataeva tapia
Cyathula achyranthoides
Cynanchum multiflorum
Desmodium adscendens
Epidendrum fragrans
Epidendrum nocturnum
Epidendrum rigidum
Erythrina corallodendrum
Flaveria contrayerba
Gossypium barbadense
Hura crepitans
Inga vera
Jatropha curcas
Jatropha pungens
Jussiaea peruviana
Maranta arundinacea
Metastelma parviflora
Mirabilis jalapa
Mullugo verticillata
Ochroma lagopus
Oncidium luridum
Peperomia hispidula
Peperomia rotundifolia
Phaseolus multiflorus
Piper aduncum
Piptadenia peregrina
Psidium guajava
Pterocarpus officinalis
Rivina humilis
Seraphyta diffusa
Simarouba amara
Spigelia anthelmia
Spondias purpurea
Tecoma stans
Trema micranthum
Tribulus cistoides

Among species less widely distributed in the American tropics nearly every possible range can be exemplified. A very common one is that of plants common to the West Indies and to the northern part of the South American mainland, often to Venezuela or Guiana only, and among these are *Cecropia peltata*, *Guajacum officinale*, *Mammea americana*, *Oncidium pulchellum* and *Pleurothallis pruinosa*.

Another group has a similar range but extends farther into South America, as, for instance, to Brazil, and here belong *Erythrina velutina*, *Galeandra beyrichii* and *Hedyosmum arborescens*.

Another rather frequent type includes the species which, found in both Central America and the West Indies, also occur in the northern part of South America. Examples of these are *Hippomane mancinella*, *Lonchocarpus latifolius* and *Rubus alpinus*.

Many plants are widely distributed in the tropical parts of South America but do not reach either Central America or the West Indies, and these include *Bixa orellana*, *Hymenaea courbaril* and *Lucuma mammosa*.

Brassavola nodosa and *Phyllanthus caroliniensis* are instances of species which are found in Central America and the West Indies and also on the western (Andean) side of South America.

The floral relationship between the north temperate regions and the north tropics is best left for discussion in the next chapter, but this one may be closed by a mention of *Geranium carolinense*, which is said to occur in both Central America and the West Indies, and northward as far as Canada.

CHAPTER 10

THE DISTRIBUTION OF SPECIES—III

Endemic Species

STRICTLY speaking, a narrower conception of endemism should be employed for species than for genera, but to do this here would mean recasting the geographical background in a way which would certainly make for confusion, and for this reason it is better to give the term endemic the same value in both and to treat the endemic species on the same regional basis as was used for the genera. As before, species falling partly into two or more regions are included under the region of which they are most characteristic.

It will be remembered that the proportion of endemic genera among all genera proved to be about 80 per cent. Species have, on the average, much smaller areas than genera, and hence it may be assumed that, on the present conception of endemism, the proportion of endemics among indigenous species is considerably greater and may well exceed 90 per cent. At all events there have now to be dealt with the vast majority of the species of flowering plants.

Arctic and Sub-arctic Region

The arctic and sub-arctic region as here defined comprises all the treeless land north of the great northern coniferous forest zone but, because of the preponderance of sea at these high latitudes, its area is not as great as might be expected, and is still more restricted as a habitat for flowering plants on account of the fact that its biggest constituent area, Greenland, is very largely covered by a permanent ice-cap.

One of the first general accounts of the flora was given by Hooker (273) but his definition of it was not altogether satisfactory and made his statistics less useful than they would otherwise have been, while most more modern studies have been confined to one or other of the three main geographical divisions, namely the palaearctic (Eurasia), the nearctic (North America) and Greenland (410). A very interesting brief account of arctic plant life, with special reference to the New World has recently been given by Porsild (424) who stresses the peculiar conditions under which it exists, as for instance the circumstance that the precipitation is, widely, so scanty during the growing season that if the water in the subsoil were not permanently frozen and the summer surface melt water thus prevented from draining away, much of the region would be a desert.

Floristically, northern Alaska, which it is important to note is generally believed to have been unglaciated during the Pleistocene, is probably the richest part with about 600 species, a figure also quoted for the larger Canadian arctic mainland (424). The Canadian arctic archipelago has about half this number. The flora of Greenland (which is virtually the only remaining glaciated part of the arctic) has about 400 species, 13 per cent. of which are said to have been introduced by the early Norse settlers. Of the rest about four-fifths are of American affinity, and the others of European relationship. Many of the species are found on both west and east coasts, and of the remainder those found only on the west greatly outnumber those found only on the east. There is a quite considerable flora at the most northerly land latitudes (about 83° N.), and a recent study lists 189 species from north of 71° on the east coast (518). Comparable figures for the Old World are not quite so readily available, but are likely to be of much the same order, as is shown by the estimates of 375 for Iceland, 137 for Spitzbergen, 200 for Novaya Zemlya, 200 for the Taimyr Peninsula and other figures quoted by Wulff and shown on his map (609).

The flora of the region as a whole contains two basic elements, the arctic, whose species are more or less confined to sea level at the highest latitudes, and the arctic-alpine, of species which are found not only in the arctic but also at elevation in one or more of the mountain systems considerably further south. The larger part of the former makes up the endemic part of the flora of the arctic region in its narrowest sense, and is thus our particular concern here. Its numerical value is hard to estimate, partly because many of its species overlap the tree limit to some extent according to merely local conditions, and partly because many of the species concerned are not well defined taxonomically. Perhaps the most noteworthy of these endemics are a few grasses, including *Phippsia algida*, *Colpodium fulvum*, *Dupontia fischeri* and *Pleuropogon sabinii*. The genus *Braya* includes one or two endemics, as also does *Pedicularis*; while several species of *Salix*, among them *S. arctica*, *S. nummularia* and *S. polaris* are so described. Other actual or virtual endemics are *Chrysanthemum arcticum*, *Nardosmia glacialis*, and *Ranunculus pallasii*.

The arctic-alpine part of the flora is, for historical and other reasons already touched upon in pp. 161 *et seq.* in relation to the northern flora as a whole, of special interest in any general study of the distribution of Angiosperms, and calls for some particular notice here. Nor is this unjustifiable on the score that this chapter is about endemic species because the arctic and sub-arctic region as here defined is in a way artificial. Logically, as well as botanically, there should be included in it various localised high alpine areas of the northern temperate zone, thus giving a floristic unit which would comprise three main classes of endemic forms, arctic, alpine and arctic-alpine, but such a region would be almost indefinable and certainly could not be mapped on a small scale, and for practical convenience therefore it has been delimited as described above, and the numerous small southern outliers ignored, their endemics going to swell the numbers of the regions within which they are actually situated.

Although the distribution of arctic-alpine species is, in detail, extraordinarily various, its main outlines can be appreciated fairly easily because of the correlation with major topographical features of the northern extra-tropical regions. With some exceptions the elevated regions of the northern temperate zone are aggregated into three great but distinct systems. These are the Rockies in America; the various isolated *massifs* which constitute the mountains of central and southern Europe and which may here be called comprehensively the Alps; and the enormous system of the Himalayas in Asia.

The interesting immediate point about these three systems is that they vary considerably in their distance from the arctic proper. The Rocky Mountains actually fuse with it in the north; the Alps are roughly along the latitude 45° N.; and the Himalayas are roughly between 30° and 35° N. The floristic relationship is closely correlated with this spatial one. Arctic alpine species are most numerous in the Rocky Mountains, fairly numerous in the Alps, but very few in the

Himalayas. The significance of these relationships will be considered later, but it is relevant to point out here that the Himalayan region is not only the most isolated from the arctic to-day but was even more markedly so during the Pleistocene ice ages.

As between these four constituent areas, the arctic, the Rockies, the Alps, and the Himalayas, there is almost every kind of specific distribution. It would take too long to describe these in detail, but a good impression of them can be given by quoting the distribution recorded by Hegi (256) for a few of the most familiar plants of the European mountains, as follows:

Androsace chamaejasme	Alps, Urals, Altai, Himalayas, Arctic.
Anemone alpina	Alps and Arctic.
Atragene alpina	„ „ „
Bartsia alpina	„ „ „
Campanula scheuchzeri	Alps, Altai, Arctic.
Dryas octopetala	Alps and Arctic.
Gentiana nivalis	Alps, Asia Minor, Arctic.
Hedysarum obscurum	Alps and Arctic.
Myosotis alpestris	Alps, Corsica, Arctic.
Polygonum viviparum	Alps, Altai, Himalayas, Arctic.
Ranunculus glacialis	Alps and Arctic.
Ranunculus pygmaeus	Alps, Rockies, Arctic.
Salix herbacea	Alps, Scotland, Urals, Rockies, Arctic.
Saxifraga aizoides	Alps and Arctic.
Saxifraga oppositifolia	„ „ „
Viola biflora	„ „ „

Certain other familiar plants of the European mountains form as it were a link with the next region to be discussed in being distributed far to the north though scarcely into the arctic proper. Such are:

Arnica montana	widely distributed in Europe and north Asia
Campanula barbata	in the Alps, Carpathians and Norway.
Gentiana purpurea	„ „ Norway and Kamchatka.
Lactuca (Mulgedium) alpina	„ „ and also in north Europe.
Nigritella nigra	„ „ „ „ „

The species of the genus *Diapensia* also illustrate an interesting state of affairs. According to Evans (165) *Diapensia lapponica* is circumpolar and also found in the White Mountains of eastern North America and in Japan; while the other three species, *D. himalaica*, *D. purpurea* and *D. wardii*, are all confined to the eastern parts of the Himalayan system.

The *alpine* flora proper, namely those plants which, while part of the arctic-alpine flora as a whole, are only found in the mountain systems mentioned, is best considered under the regions of which these mountains form part.

Euro-Siberian Region

This region is so extensive longitudinally (see p. 28) that some of the species confined to it and therefore to be regarded, on the definition in use here, as endemics, may in fact range in one direction for several thousands of miles and actually may rank as some of the most widespread species in the world. But these cannot well be separated from the much more numerous species which have something less than this extreme range and to attempt to do this would be artificial, so it is best to consider all these types here, however much some of them, in the peculiar circumstances, strain the more usual conception of endemism. Another difficulty is that, as has been explained on p. 119, the latitudinal depth of the region is greater in the west than in the east, and because of this species which, in the west, are characteristic of the Euro-Siberian region, are often, in the east, more characteristic of Central Asia or of China and Japan. Little would be gained by attempting to sort these out in detail and there are thus included in consideration here species which in general range widely through the Eurasian temperate zone even if they are not altogether confined to the Euro-Siberian region as defined.

A few plants familiar in cultivation are found more or less throughout the region, among them *Asparagus officinalis* and *Campanula trachelium* and this type of distribution is very common among the species native to some parts of the British Isles, as may be illustrated by the mention of *Campanula glomerata*, *Conium maculatum*, *Cypripedium calceolus*, *Geranium pratense*, *Heracleum sphondylium*, *Holcus lanatus*, *Lamium album*, *Paris quadrifolia*, *Ranunculus acris* and *Solanum dulcamara*. Some others which are also widespread from west to east extend also further south in places, as *Sanicula europaea* to the African mountains and into Malaysia and *Brachypodium sylvaticum* and one or two others into the latter.

Among rather less completely distributed species there are some which do not occur in Britain such as *Aconitum excelsum*, *Dianthus superbus*, *Dictamnus albus*, *Eritrichium villosum*, *Rubus humulifolius* and *Trifolium lupinaster*; while conversely, there are others which occur in Britain but fail to reach the Pacific, among these being *Artemisia campestris*, *Butomus umbellatus*, *Lathyrus pratensis*, *Listera ovata*, *Myosotis palustris*, *Senecio jacobaea*, *Stachys sylvatica* and *Verbascum thapsus*. Others again have a like width of distribution in total but are more or less discontinuous, as for instance *Eriophorum latifolium*, *Gagea lutea*, *Pirola media*, *Stellaria palustris* and *Veratrum album*.

Among the considerable number of less widely ranging species of the region it must be sufficient here to deal with three particularly well-defined groups; the species restricted to the western part of the region as a whole, namely those of Europe and the Caucasus; the species restricted to the eastern part of the region, namely Siberia; and the species of the European mountain systems—the alpine flora in its narrowest sense. Since this last is closely related to the arctic-alpine flora, it may be dealt with first while the foregoing pages are still fresh in the mind of the reader.

It is difficult to compare the European alpine flora with others because the areas of high elevation are so different, but it is safe to say that the alpine flora proper is rich and compares favourably with others proportionately. It tends to differ from them, however, because the European mountains comprise a number of isolated *massifs* rather than one continuous range, and for this reason the comparative ranges of species are of special interest.

The alpine flora is part of the arctic-alpine flora and therefore has a close affinity with that of the arctic itself, but it is also related to the European lowland flora and, particularly in the more southern mountains, with the Mediterranean flora.

These several points can be illustrated by citing the ranges, as given by Hegi (256), of some of the more familiar plants of the Alps proper:

Androsace helvetica	Alps.
Campanula thyrsoides . . .	,,
Carlina acaulis	wide in south and central Europe.

Crocus albiflorus	Alps, Pyrenees, north Apennines, Carpathians, Balkans.
Dianthus alpinus	Alps.
Erinus alpinus	Alps and Pyrenees.
Gentiana acaulis	Alps, Pyrenees, Carpathians.
Gentiana lutea	Alps, Pyrenees, Apennines, Carpathians, Balkans, Corsica, Sardinia, Asia Minor.
Geum montanum	Alps, Pyrenees, Apennines, Carpathians, Balkans, Corsica.
Globularia cordifolia	Alps, Pyrenees, Apennines, Carpathians, Balkans.
Linaria alpina	Alps, Pyrenees, Balkans.
Narcissus poeticus	Alps.
Paradisea liliastrum	Alps, Pyrenees, Apennines.
Primula auricula	Alps, Pyrenees, Apennines, Carpathians, Balkans.
Primula glutinosa	Alps and Balkans.
Saponaria ocymoides	Alps.
Sempervivum arachnoideum	Alps, Pyrenees, Apennines, Carpathians.
Trifolium alpinum	Alps, Pyrenees, north Apennines.

The edelweiss, *Leontopodium alpinum*, is said by Hegi to occur in various mountains from the Alps to Japan, but according to Handel-Mazzetti (247) this species is confined to the Alps, Pyrenees and Carpathians.

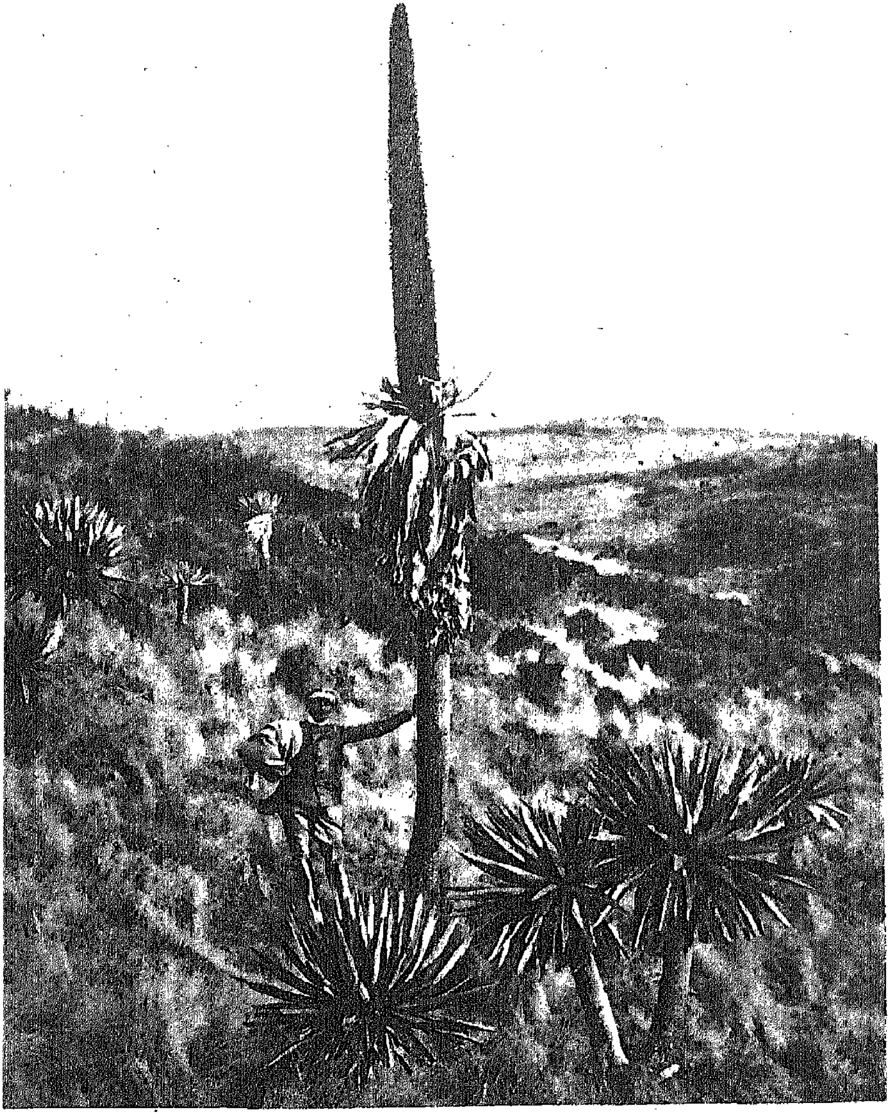
The differential distribution of the species of a single genus is well shown in *Soldanella*. According to Vierhapper (247), there are seven species with the following ranges:

S. alpina	Alps, Pyrenees, Apennines, Cevennes and Dalmatia;
S. carpatica	northern Carpathians;
S. villosa	western Pyrenees;
S. montana	north-eastern Alps, eastern Carpathians and the Balkans;
S. hungarica	eastern Alps, Carpathians and Balkans;

and two species in northern Greece.

One of the most interesting features of the European mountain flora is the occurrence in it of certain isolated genera affording almost the only known temperate examples of families now confined to the tropical regions of the world. By far the most remarkable instance of this is the occurrence in some of the more southerly mountains of Europe of no fewer than three endemic genera of Gesneriaceae, a family which is otherwise one of the most characteristically tropical. One of these plants, generally called *Ramondia pyrenaica*, is familiar to European gardeners, but there are several others also. Hayek (247) has given a good account of them and shows that there are six species in all belonging to three genera. *Ramonda myconi* (*Ramondia pyrenaica*) is found only in the Pyrenees; the remaining five all have varying but very restricted distributions in the mountainous parts of the Balkan Peninsula between the longitudes 20°–26° E. and the latitudes 39°–44° N. (532, 536). These five are *Ramonda nathaliae*, *R. serbica*, *Haberlea rhodopensis*, *H. ferdinandii-coburgii* and *Jankaea heldrichii*.

From the more lowland parts of the European sub-region come many species familiar either as British plants or as plants of economic or horticultural value, among them *Bellis perennis*, *Crataegus oxyacantha*, *Digitalis purpurea*, *Fagus*



3. A giant Lobelia (*L. rhynchopetalum*) of the African mountains

(*from Karsten & Schenck, Vegetationsbilder*)

sylvatica, *Laburnum anagyroides* (*vulgare*), *Malus pumila* (*Pyrus malus*), *Malva moschata*, *Narcissus pseudo-narcissus*, *Primula vulgaris*, *Prunus cerasus*, *Pyrus communis*, *Rosa centifolia* and *Trollius europaeus*. The grape vine, *Vitis vinifera*, may also have had its origin here, perhaps in the Caucasus.

There is not unnaturally an enormous literature dealing with the floras of the various European countries and their geographical affinities, and as an example of it there may be mentioned the very detailed geographical analysis of the German flora by Wangerin (573) which though primarily concerned with the plants of one country contains much of interest about the plants of western Eurasia in general.

The plant life of the Asiatic sub-region is a good deal less familiar, but a number of species either grown in gardens or of some other interest are natives of Siberia or of the neighbouring areas, among them being *Allium sibiricum*, *Bergenia cordifolia*, *Bergenia crassifolia*, *Delphinium grandiflorum*, *Iris sibirica*, *Lychnis fulgens*, *Pyrus baccata* and *Stachys lanata*.

Of the mountain floras of northern east Asia that of the Altai may be mentioned. The alpine flora here consists of nearly 300 species (323) in which the arctic-alpine element accounts for about 60 per cent. and the alpine element about 40 per cent. About half the species are Asiatic only; about a third are circumpolar in distribution; 10 per cent. are Eurasian; another 10 per cent. are endemic; and a handful are Asiatic-American.

Sino-Japanese Region

For two reasons in particular this region is one of the most interesting from the point of view of its species. The first is that its flora is extremely rich and almost certainly the richest of the whole northern temperate zone. It is also especially rich in trees (281) and it has, indeed, been said that the number of tree species here outnumbers that of the whole of the rest of the northern temperate zone. Its endemism is also high, but this is only to be expected from the size of the area. It is in relation to what we believe to have been the history of the region that its richness in species and particularly in trees is so significant.

As will be shown in Chapter 14, the great polar ice-cap of the Pleistocene was not, as at first sight might be expected, symmetrical about the present North Pole but had its centre in what is now the southern part of Greenland. As a result the ice reached particularly low latitudes in eastern North America and in Europe, but covered only a small part of Asia and, in fact, may have made itself felt there little more than does the smaller ice-cap of to-day. It will also be seen that there is good reason for believing that prior to the Pleistocene a single great flora, characterised by the prevalence of woody types, was found throughout the northern temperate regions or at least at the lower latitudes. In view of these facts it is therefore justifiable to suggest that the flora of eastern Asia was comparatively little affected by the Pleistocene Ice Ages, and hence that the present Sino-Japanese flora is in fact a relatively little-changed descendant of it, giving a picture of the kind of vegetation which, before the glaciation, encircled the whole northern hemisphere.

The second reason for the interest of the flora of this region lies in the fact that of recent years it has contributed an enormous number of plants to European gardens. Indeed, the story of the exploration of the remoter parts of the Himalayas, Burma and China by collectors in search of seeds and plants of aesthetic value is one of the romances of twentieth-century botany and geography. It is the story especially of the hitherto little-known mountainous country in the region of the great river gorges near the junction of Burma, China, India and Tibet, and from it the names of Henry, Farrer, Forrest, Kingdon-Ward and many others will always be inseparable. The result of their labours and travels has been the discovery not only of many most valuable garden plants but also of much other botanical and geographical information culminating in the recognition of this part of the world as one of its most remarkable natural features.

The Sino-Japanese region too has contributed greatly to the list of important economic plants, or at least we may say that many such plants had their origin as crops in this region. It is necessary to adopt this somewhat cautious expression, because where a considerable number of cultivated plants are found to have originated there is a rather natural tendency to assume that the local native flora has proved of special value to man as compared with that of other regions. This, it need hardly be said, is an assumption which may not always be justified, and the number of cultivated plants may be a measure of the length of human history rather than any inherent virtue in the flora as a whole.

It is worth discussing this point at some length, because it has often been observed that the important economic plants of the world come especially from certain parts of it and, as often suggested on this basis, especially by the Russian school of botanists led by Vavilov (567), that this circumstance has had an important controlling effect on the distribution and growth of human races. Interesting as this view is, it seems to confuse cause and effect. The early civilisations of the world must have originated to a considerable extent independently of one another, if only because of the virtual absence of long-distance communication, and as each passed from a nomadic or pastoral stage to an agricultural level each must have derived its economic plants from local wild plants. In other words, the early peoples must of necessity have made use for the purposes of agriculture of the plants which were immediately available to them. The longer the history of the human population of any region the more complete would be the exploitation of its native plant life in this way, and it is natural to-day, therefore, to find that the areas from which economic plants particularly derive are those with the longest history of human settlement. It is true that certain types of vegetation and therefore certain regions provide a greater selection of potentially valuable plants, but any suggestion that the cultivation of these plants was the cause rather than the effect of human settlement bristles with difficulties.

It is noteworthy too that in different parts of the world there are different but corresponding economic plants. Almost all aspects of economic botany will illustrate this, but it is perhaps outstanding in the case of the three plants, tea, coffee and cocoa, from which important beverages are prepared. Tea is a native of warm Asia, coffee of Africa, and cocoa of South America. Clearly the peoples of each of these continents have, as occasion demanded, developed their own particular beverage from the most suitable available native plant. They have made use of such plants as were available in the circumstances of their situation.

Moreover, once a plant is in cultivation it, so to speak, loses its nationality and can within certain obvious limits be grown as and where required, and there is no necessity for population to remain closely associated with its point of origin. For example, the New World has provided man with several economic plants of first importance, but the fact that these are natives of America has not made it necessary for human population to concentrate there in order to enjoy them.

But to return to the Sino-Japanese flora, there are within the region many types of specific distribution, and some species like *Clematis montana*, *Diervilla* (*Weigela*) *florida*, *Iris ensata*, *Panax schinseng*, *Rosa rugosa*, *Sium sisarum* and *Stachys* *sieboldii* are widespread, or at least their original homes cannot now be more accurately determined.

Many others occur particularly or exclusively in China and Japan, among them being *Anemone japonica*, *Aucuba japonica*, *Callistephus chinensis*, *Camellia japonica*, *Hydrangea macrophylla*, *Lilium tigrinum*, *Parthenocissus tricuspidata* (*Ampelopsis veitchii*), *Paulownia tomentosa*, *Pyrus pulcherrima*, *Rosa wichuraiana* and *Saxifraga sarmentosa*. The prototypes, too, of cultivated Chrysanthemums are also supposed by most authorities to belong here.

Of plants native to China there may be mentioned *Aspidistra elatior*, *Diospyros kaki*, *Forsythia suspensa*, *Jasminum nudiflorum*, *Kerria japonica*, *Livistona chinensis*, *Lonicera nitida*, *Morus alba*, *Primula malacoides*, *Primula obconica*, *Primula sinensis*, *Rosa banksiae*, *Rosa omeiensis* and *Wisteria sinensis*.

Among natives of Japan are *Astilbe japonica*, *Dicentra spectabilis*, *Fatsia japonica*, *Hamamelis japonica*, *Lilium auratum*, *Lilium longiflorum*, *Magnolia kobus*, *Primula japonica*, *Rosa multiflora* and *Schizophragma hydrangeoides*.

The debt which the horticulturist owes to the plants of the Himalayas is well shown by *Cotoneaster frigida*, *Erigeron multiradiatus*, *Gentiana farreri*, *Gentiana sino-ornata*, *Incarvillea delavayi*, *Magnolia campbellii*, *Meconopsis betonicifolia* (*baileyi*) and *Primula bulleyana*, all of which are native to that zone.

Lastly, *Glycine max* (*soya*) and *Caragana arborescens* come from the Manchurian part of the region, and *Fagus sieboldii* and *Zelkova serrata* from Korea and Japan.

Western and Central Asiatic Region

Botanically the western part of this region, namely north Persia and the interior of Asia Minor, is much the richest, and from it are derived many well-known and valuable plants, among them being *Fritillaria imperialis*, *Hyssopus officinalis*, *Jasminum officinale*, *Nepeta mussinii*, *Papaver orientale*, *Philadelphus coronarius*, *Platanus orientalis*, *Prunus communis*, *Spinacia oleracea* and *Tulipa gesneriana*. It seems fairly certain too that barley (*Hordeum vulgare*) and at least some kinds of wheat (*Triticum* spp.) originated here.

From the great desert and semi-desert areas which form the eastern part of the region come such familiar or characteristic plants as *Astragalus tragacantha*, *Iris halophila*, *Limonium* (*Statice*) *suworowii*, *Lonicera persica*, *Polygonum baldschuanicum* and *Rheum rhaponticum*.

Where, as is often the case, the deserts are saline, halophytes like *Haloxylon ammodendron* and *Salsola arbuscula* are conspicuous.

The Tibetan plateau proper forms a rather specialised area chiefly on account of its great elevation (314). Here *Poa altaica* has been recorded from a height of 19,000 ft., and among other noteworthy species are *Caragana versicolor*, *Kobresia tibetica*, *Myricaria prostrata* and *Primula florindae*.

Mediterranean Region

Perhaps the most outstanding feature of plant distribution in this region is the way in which many of the species (just as do many of the genera) extend out of the region proper far up the western coasts of Europe, often reaching even to the British Isles. Many of these have also been recorded from Macaronesia, but their status there is not always free from doubt. Apart from this, however, the flora is well defined, except perhaps in Asia Minor, and, owing to the marked geography of the region, can be divided up into a number of parts.

It is a very rich flora with considerable endemism and, taking into account that the Mediterranean has been the cradle of many human civilisations, it is not surprising to find that the native plants of it have contributed largely to both horticulture and agriculture. The type of vegetation prevailing over much of the region is the very characteristic "maquis" or thicket, and many of its constituent species, though not of great value, are nevertheless familiar.

The gardeners' debt to the region is well shown by the following, all of which are derived thence: *Anemone coronaria*, *Aubrietia deltoidea*, *Cercis siliquastrum*, *Chrysanthemum coronarium*, *Cyclamen indicum*, *Hermodactylus tuberosus*, *Hyacinthus orientalis*, *Iris stylosa*, *Iris susiana*, *Lavandula spica*, *Lilium candidum*, *Lilium chalcedonicum*, *Malope trifida*, *Narcissus jonquilla*, *Nerium oleander*, *Nigella damascena*, *Paeonia officinalis*, *Prunus laurocerasus*, *Pyracantha coccinea*, *Quercus ilex*, *Reseda odorata*, *Senecio cineraria* and *Viburnum tinus*.

Economic plants include *Allium porrum*, *Capparis spinosa*, *Cynara scolymus*, *Ficus carica*, *Laurus nobilis*, *Mandragora officinarum*, *Olea europaea*, *Petroselinum crispum*, *Quercus suber* and *Scolymus hispanicus*.

In addition to the endemics of the continental parts of the region almost every island has its own peculiar species; Corsica and Sardinia, for instance, are said to have about fifty each. On both continent and islands the endemics are often very restricted littoral species, as is well seen in the genus *Narcissus* (176).

Among the constituent parts of the region the Atlas Mountains are of special interest. Their flora is still by far the least completely known and has many very interesting features. It has been suggested, for instance (355), that it represents to a considerable extent a remnant of the old north temperate flora of the Tertiary epoch which has found there a refuge where it has survived the effects of the Pleistocene glaciation, in much the same way as a vastly greater part of the old flora survived in the mountainous parts of the Sino-Japanese region.

Macaronesian Region

In an insular region of very small total land area such as this the question of the proportion of species endemism is particularly illuminating, but unfortunately the figures are not easy to obtain because the islands have so long felt the influence of man that it is often almost impossible to separate the alien from the native plants.

In the Azores Guppy (243) estimates that the forty or so endemic species represent a proportion of some 20 per cent. of the native species. The flora is essentially the remnant of a forest flora and its general affinities are with western Europe. Among the endemic species are *Campanula vidalii*, *Daboecia azorica*, *Erica azorica* and *Vaccinium cylindraceum*.

Madeira has about 100 endemics and perhaps the proportion is roughly the same as in the Azores. The flora again is a forest flora and closely related to the Mediterranean flora. Cockerell (106) has pointed out that the endemic species are chiefly of two kinds, either isolated, or closely related to European forms. Among the former are *Clethra arborea*, *Pittosporum coriaceum* and *Sideroxylon marmulano*, and among the latter *Sambucus maderensis* and *Sorbus maderensis*.

The Canary flora, again, is a forest flora and chiefly related to that of North Africa. Its endemics have been estimated at about 400, and this is certainly a higher proportion than either of the above. A number of these species are fairly familiar either in gardens or as specially characteristic of the vegetation, including *Canarina canariensis*, *Ceropegia fusca*, *Cytisus canariensis*, *Dracaena draco*, *Euphorbia canariensis*, *Kleinia neriifolia*, *Phoebe barbusana*, *Semele androgyna*, *Sempervivum spathulatum*, *Senecio cruentus*, *Tamus edulis* and *Viburnum rugosum*,

One of the noteworthy features of the flora is the great development of succulent members of the Crassulaceae, and especially the genus *Sempervivum*. These species afford a most interesting study in segregation and endemism, and an excellent account of them has been given by Praeger (427).

The flora of the Cape Verdes has been much less studied than that of Madeira or the Canaries, and it is difficult to say what proportion the sixty-odd endemic species represent. The affinities of the flora are with adjacent Africa, as is instanced by *Lavandula rotundifolia* and *Campanula jacobaea*.

Among species linking the islands together or with the European-African land mass may be mentioned *Laurus canariensis*, *Myrica faya* and *Persea indica*, which occur on the Azores, Madeira and the Canaries; *Cistus monspeliensis* on the Canaries and in the Mediterranean; *Centranthus calcitrapa* and *Oreodaphne foetens* on Madeira and the Canaries; *Ruscus hypophyllus*, which ranges from Madeira to the Caucasus; *Periploca laevigata*, from the Canaries to Cyrenaica; and *Erica arborea* (see p. 154).

Atlantic North American Region (437, 438)

The proportion of endemic species is naturally high in so large an area as is covered by this region, but the main features of the flora are that its northern part has a strong general resemblance to the flora of temperate Eurasia, and that its southern part has a corresponding likeness to the flora of China and Japan, and one of the reasons for recognising two sub-regions here is the wish to emphasize these relationships. In both cases many species of the Old World are represented in the New by others very similar, and many of these afford excellent examples of species-pairs, a subject which will be discussed in the next chapter.

The Eastern North American region as a whole has not contributed many plants of economic value to the common store, most of them being drug plants, such as *Hamamelis virginiana*, *Hydrastis canadensis*, *Lobelia inflata*, *Podophyllum peltatum*, *Polygala senega* and *Ulmus fulva*, but the sugar maples (*Acer saccharum*, etc.) and the hickories and pecans (*Carya* spp.) must not be forgotten.

As might be expected from the similarity of latitudes the region has provided Europe with a number of important garden plants, among them being *Acer negundo*, many Michaelmas daisies (*Aster* spp.), *Catalpa bignonioides*, *Cornus florida*, *Juglans nigra*, *Kalmia latifolia*, *Liatris pycnostachya*, *Lilium philadelphicum*, *Lobelia cardinalis*, *Magnolia grandiflora*, *Monarda fistulosa*, *Phlox subulata*, *Rhus typhina*, *Robinia pseudo-acacia* and *Tradescantia virginiana*. The prairies in particular, have provided a number of Composites, including *Gaillardia aristata*, *Helenium autumnale* and *Rudbeckia hirta*. Among other particularly interesting or characteristic plants are *Castilleja coccinea*, *Chiogenes hispidula*, *Gaultheria procumbens*, *Gymnocladus canadensis*, *Maclura pomifera* (*aurantiaca*), *Menispermum canadense*, *Nyssa aquatica*, *Platanus occidentalis*, *Prunus serotina*, *Rhododendron maximum*, *Rhus toxicodendron* (379), *Rhus vernix*, *Sabal palmetto*, *Saururus cernuus and Vitis labrusca*.

The area around the Gulf of St. Lawrence has been the scene of some particularly interesting studies in plant distribution. Fernald (171–174) showed that there is in this area a considerable group of plants, many of which are endemic, either identical with or very closely related to plants found elsewhere only in the western North American mountains, or more rarely in parts of continental Asia. Moreover he showed that these plants have, in north-eastern America, a very local and restricted distribution and are in fact found only on areas (such as the Gaspé

Peninsula, western Newfoundland, the Magdalen Islands and parts of north-east Labrador) which may have been unglaciated during the Pleistocene. That is to say he suggested that these plants are confined to former "nunataks." His explanation of the many curious facts that he describes is that the species concerned lived throughout the Pleistocene in the Arctic, and that during this time they migrated to where they are now found. There they have since persisted, and have not, as might otherwise seem possible, been derived by migration eastwards from western North America. Wynne-Edwards (611) on the other hand believes the nunatak theory to be untenable and that the localisation of many arctic-alpine species is due to the corresponding localisation of certain soil conditions, notably lime and magnesia-lime-soda combinations. Unlocalised species, he claims, are found on highly silicious and certain more acid rocks which, even if they are nunataks, do not bear local "relicts."

Marie Victorin (364) also investigated the distribution of plants in this part of the world and confirmed many of Fernald's observations, but also emphasised the great interest of the area from the point of view of plant evolution and speciation. He referred not only to the restricted endemic forms already mentioned but also to the more familiar features of such genera as *Senecio* and *Crataegus*, which are here represented by such an array of minor species or forms as almost to defy classification. With regard to the latter especially he expressed the interesting opinion that many of these forms have arisen as a result of deforestation and human settlement. They are, therefore, to be regarded as very young species, and it follows, moreover, that in certain circumstances forms of this kind may be produced in two or three hundred years, which is, of course, the period of European settlement in North America. He also drew attention to the fact that many of the local endemics are found only in estuarine conditions, and that sometimes the local segregation of forms in these conditions is most marked, as, for instance, in *Bidens hyperborea*, and he added something to Fernald's conceptions by recognising certain endemic species as having persisted during glaciation on nunataks, but as having migrated slightly from those areas since. His general conclusions were, first, that the floras of western and eastern North America were long separated by an arm of the sea; second, that eastern North America has become gradually isolated from Europe by geographical changes; and third, that the flora of north-eastern North America has evolved chiefly in response to two more recent factors, namely glaciation and the widespread occurrence of estuarine conditions, both of which have amounted to physiological isolation.

A long and critical account of the "nunatak theory," and of opposing opinions about it, has been given by Raup (437), and a very readable recent account of the eastern North American flora, with special reference to the Gaspé area, by Dansereau (121).

Pacific North American Region

Like the last this region has not contributed much in economic plants, but garden species originating here are very numerous and include *Arbutus menziesii, Ceanothus thyrsiflorus, Clarkia elegans, Cornus nuttallii, Eschscholzia californica, Garrya elliptica, Gaultheria shallon, Godetia* spp., *Lupinus arboreus, L. polyphyllus, Mahonia aquifolium, Mimulus moschatus, Nemophila menziesii, Phacelia* spp., *Ribes aureum* and *Tolmiea menziesii.*

By far the best-marked constituent flora of the region, and in many ways the most interesting, is that of California, which is a good example of " Mediterranean " flora, that is to say one showing the same peculiar type of vegetation (evergreen thicket or scrub) as is seen in that of the Mediterranean region itself. The Californian flora, like all "Mediterranean" floras, has a high proportion of endemism, perhaps as much as 50 per cent. (298, 299), and considerable richness, and a good account of it and its affinities has been given by Abrams (1).

Among characteristic species of this part of western North America may be mentioned *Artemisia tridentata*, *Clistoyucca arborescens*, *Erythronium grandiflorum*, *Fouquieria splendens*, *Lewisia rediviva*, *Penstemon heterophyllus*, *Quercus chrysolepis*, *Rhododendron californicum* and *Washingtonia filifera* (Plate 25).

Well-known species from the more northerly part of the region include *Aquilegia formosa*, *Lupinus nootkatensis* and *Rosa nutkana*.

North African—Indian Desert Region

As is to be expected from the nature of the terrain, the flora of this great region is comparatively poor and specialised, although there are no particularly characteristic larger plant groups such as are so conspicuous in the South African and many other arid regions. There is one very important economic plant *Phoenix dactylifera* (the date palm) and a few minor ones, including *Balsamodendron myrrha*, *Boswellia carteri* and various species of *Acacia*, but rather naturally no garden plants.

A good many of the species are found throughout the region, as, for instance, *Calotropis procera*, *Cistanche lutea*, *Daemia extensa*, *Haloxylon salicornicum*, *Lawsonia inermis*, *Leptadenia pyrotechnica*, *Neurada procumbens* and *Zilla spinosa*. Others range throughout North Africa and Arabia, among them *Anabasis aretioides*, *Anastatica hierocuntica* and *Calligonum comosum*, or from Egypt over Arabia, as *Halopeplis perfoliata*, *Mesembryanthemum* (*Opophytum*) *forskahlei* and *Reseda muricata*, or from Africa to Persia, as *Sclerocephalus arabicus* and *Herniaria hemistemon*, or, as *Rhazya stricta*, from Arabia to India. Narrower species are mostly restricted to the Sahara, or to Mesopotamia and Arabia, or to the eastern side of the Persian Gulf. Examples of the first are *Asteriscus pygmaeus*, *Farsetia aegyptiaca*, *Limonium guyonianum*, *Peganum harmala* and *Retama rhaetam*; of the second *Balsamodendron opobalsamum* and *Catha edulis*; and of the third, *Quercus infectoria*.

Sudanese Park Steppe Region

The flora of this region is not very rich because the vegetation is mainly of a kind in which the species are rarely particularly copious. It is a land of open spaces, and, like its East African counterpart, is better known for its big-game fauna which is, or was, extremely abundant. It is, however, of special interest botanically in relation to the problems of "désertification" referred to on p. 145 because the causes tending towards this process can here be studied better than almost anywhere else.

In one sense it may be considered as a westerly extension of the East African steppes with which it encircles the forests of the Congo and Niger, and its strongest floristic affinities are in this direction.

Species of *Acacia*, grasses and palms are among the most conspicuous of its plants, and instances of these are included in the following list of species more or less characteristic of the region as a whole, namely *Acacia senegal*, *Andropogon gayanus*, *Borassus aethiopicum*, *Cassia senna*, *Cola acuminata*, *Entada sudanica*, *Hyphaene thebaica*, *Kigelia aethiopica*, *Loranthus acaciae*, *Phoenix reclinata* and *Themeda triandra*.

North-east African Highland and Steppe Region

Abyssinia, which comprises by far the larger part of this region, has a rich and interesting flora and one that is of special theoretical importance in regard to the development of the tropical African montane flora in general. It is still not very completely known, but it can be said that in addition to a considerable element of tropical African affinity it also contains a number of types more characteristic of the northern temperate regions.

In *Coffea arabica* it has provided at least one economic plant of first importance, but apart from this its species are not very familiar or important. Among those particularly characteristic of the area may be mentioned *Acacia abyssinica, Aloe abyssinica, Eragrostis tef* and *Euphorbia abyssinica.*

The remainder of the region is, for the most part, of less interest and its flora is a depauperate one chiefly of African affinity, containing no plants of special note.

Socotra, however, has a very interesting flora with, considering its slight degree of isolation, a marked amount of endemism (183). The first comprehensive account of it is that of Balfour (30), who visited the island in the eighteen-eighties. To-day it is known to possess about 200 endemic species representing a proportion of about 40 per cent.

West African Rain-forest Region

This region, which corresponds, as the only equatorial forest zone in Africa, to the whole of the Amazon region or of Monsoon Asia, has a very rich flora which is still far from completely known, but, as might be expected, it has not yet at any rate provided many useful plants, as far as world commerce is concerned. On the other hand, quite a number of indigenous species have been exploited by the native peoples and, in addition, the flora contains a number of valuable timber trees.

Among the economic plants two, *Coffea liberica* and *Elaeis guineensis*, are of outstanding importance, and others with a more local value include *Aframomum melegueta*, *Raphia vinifera*, and the native rubber plants, *Funtumia elastica* and *Landolphia owariensis.* Among timber trees, *Khaya senegalensis, Piptadenia africana* and *Staudtia gabonensis* may be mentioned.

Other species characteristic of the region are *Clerodendrum splendens*, *Erythrina excelsa, Monodora myristica, Pleiocarpa mutica, Spathodea campanulata, Stipularia africana*, *Strophanthus hispidus, Strophanthus sarmentosus* and *Uncaria africana.*

The islands of the Gulf of Guinea have a considerable proportion of endemic species (167). They are mostly mountainous and the floras show some affinity with the other tropical African mountains, but they also possess many species such as *Abutilon grandiflorum, Costus giganteus* and *Xylopia aethiopica* which link them up with the continent in general.

East African Steppe Region

The typical vegetation of this great region is savana, but in the highlands and in the south-eastern part forests are well developed and altogether there is considerable heterogeneity, and the area can be and has been divided up floristically in great detail. Largely because of this the flora is both richer and more varied than that of the Sudanese region, but despite this, few of the native plants are familiar, and there are practically no economic plants of importance except a few timber trees such as *Berlinia baumii, Burkea africana* and *Pterocarpus erinaceus.*

The flora of the eastern highlands is discussed at some length below and apart from this the flora of the region as a whole tends to divide into western and eastern parts, the former comprising Angola and Rhodesia and the latter Portuguese and British East Africa. Among characteristic species of the former are *Brachystegia* spp., *Clematis welwitschii* and *Ziziphus mucronata*, while those of the latter include *Arundinaria alpina, Hagenia abyssinica, Hypericum lanceolatum, Musa holstii* and *Olea chrysophylla*.

The Flora of the Tropical African Mountains

It was seen in an earlier chapter that high mountains are by no means confined to the temperate regions of the world and that there are in fact elevations so great that their summits bear perpetual ice and snow in all continents and at all latitudes. The equatorial mountains, however, are, for the most part, portions of long ranges or systems whose extremities run far into the temperate regions, so that there is little geographical isolation associated with them. This is so, for instance, in the case of the tropical Andes in the New World and in the case of the Malaysian mountains which connect up with the essentially temperate Himalayan mass. Only Africa is a marked exception. Here the mountains of the tropics, instead of being parts of a continuous zone, are isolated masses, so separated from one another and rising so abruptly out of the lowlands that they have gained for themselves the geographical term of "Inselberge." Each is, as it were, an island of elevation separated not only from its fellows but also, and more so, from any considerable mountain system of the temperate regions.

It is, no doubt, this circumstance that makes the flora of the higher levels of the African equatorial mountains one of the most remarkable and specialised in the whole world. Like other high mountains they have their "alpine flora," but this is very different from anything which corresponds to it elsewhere. Moreover, the difference is one of type as well as degree.

Like other high mountain floras, too, that of tropical Africa consists to a very great extent of genera familiar in temperate floras and often providing arctic-alpine species, but in Africa not only are the species quite distinct but they have usually an entirely different kind of growth-form (Plates 8, 13, 14), with the result that the flora in general of the upper levels of these African mountains can only be described as like nothing else on earth and by usual standards extremely bizarre.

This is, no doubt, related to a point which has frequently been made that the montane floras of the tropics generally consist, not of modified species from the lower zones, but of forms obviously related to the floras of more temperate and arctic regions. It is here that the African alpine floras are peculiar, because although there are in them many temperate types, they are for the most part related closely to the plants of the zones below them. The temperate types proper seem, as Taylor (546) has pointed out, to owe their presence to a different combination of circumstances and do not in fact form so definite an altitudinal *stratum* as in other continents. *Sanicula europaea*, for instance, which is a good example of a temperate plant on African mountains, is common often on the lower slopes and is by no means confined to the highest levels.

The mountains having this peculiar form of high alpine flora are widely scattered and fall into three groups, namely, the Abyssinian peaks; the group of east central Africa (Kilimanjaro, Kenya, Elgon, Ruwenzori and their associates); and Cameroon Mountain and Fernando Po. The general appearance of the vegetation has been described so often by travellers, especially in the case of Ruwenzori (288), that we can confine ourselves here to a consideration of some of the more prominent species and types comprising it.

By far the most outstanding and familiar of the African high montane plants are the so-called "tree Senecios" (250) and "tree Lobelias." Both belong to very widespread genera, but these mountain species have a most peculiar form. The Senecios have tall branched woody stems and may, according to some authorities, live for as much as 100 years, flowering and fruiting periodically. Their leaves, however, are not small and scattered as in ordinary trees but are large and more or less aggregated at the ends of the axes, and the branching is far less diffuse. These *Senecio* species are entirely confined to the tropical African mountains. The Lobelias are what may be called long-term monocarpic plants, that is to say they grow vegetatively for fifteen or twenty years, then flower and die. The word tree as applied to them is simply a rough indication of their unusual size, because in habit they are mostly tall and massive unbranched columnar woody herbs. In their most typical form they occur only on the African mountains, but a few similar species are known from Asia. They are also far less rigidly confined to the highest levels than the Senecios. It is interesting that the higher the situation of these plants the more restricted is their range, and Taylor has stated that of both genera no species among the highest-zoned is found on both sides of the Great Rift Valley. It is this very remarkable degree of segregation between the mountains that is perhaps the most interesting feature of their geography, and this cannot be better illustrated concisely than by quoting, in somewhat broadened form, a table given by Bruce (67).

Distribution of the Giant Lobelias on the mountains of Tropical Africa

	Fernando Po	Cameroons	Rhodesia	Virungas	Ruwenzori	Elgon	Aberdares	Kenya	Kilimanjaro	Ngongoro	Usambara	Uluguru	Utshungwe	Rungwe	Abyssinia	Totals
L. longisepala .	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	1
L. lukwangulensis .	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	1
L. milbraedii .	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	1
L. utshungwensis	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	1
L. rhynchopetalum .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	1
L. aberdarica	—	—	—	—	—	×	×	×	—	—	—	—	—	—	—	3
L. lanuriensis	—	—	—	×	×	—	—	—	—	—	—	—	—	—	—	2
L. lanuriensis var. ericeti .	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—	1
L. bambuseti .	—	—	—	—	—	—	×	×	—	—	—	—	—	—	—	2
L. usafuensis .	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—	1
L. volkensii .	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	1
L. giberroa .	—	—	—	×	×	×	×	×	×	×	—	×	×	—	×	10
L. bequaertii .	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—	1
L. burttii .	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—	1
L. deckenii .	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	1
L. keniensis .	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—	1
L. sattimae .	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—	1
L. elgonensis .	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—	1
L. telekii .	—	—	—	—	—	×	×	×	—	—	—	—	—	—	—	3
L. wollastonii	—	—	—	×	×	—	—	—	—	—	—	—	—	—	—	2
L. stricklandae	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—	1
L. columnaris .	×	×	—	—	—	—	—	—	—	—	—	—	—	—	—	2
L. conrani .	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	1

The giant Senecios are more restricted, in that they do not occur on the western mountain group. According to Cotton (112) and later records there are 18 species, all peculiar to one mountain or group, namely, 4 on Ruwenzori; 3 on Kenya; 2 on the Aberdares; 2 on the Virungas; 3 on Elgon; and 4 on Kilimanjaro and Meru.

The African high montane representatives of several other genera have also been revised, giving with some additional later records, the following results:—

Anagallis (188) has 15 species, mostly like *A. tenella* in appearance, and there are local species on most of the eastern mountains and in Abyssinia.

Swertia (189) of interest as a close relative of *Gentiana*, has 30 species; 8 of them in Abyssinia and most of the rest on the eastern mountain group.

Echinops (186) has 9 species, 2 in Abyssinia and 7 in the eastern mountains.

Sonchus (184) has about 30 tropical and South African species, of which several are on the eastern mountains and one on Cameroon Mountain.

Bartsia (187) has 11 species, of which 3 are in Abyssinia, one in Abyssinia and the eastern mountains, 6 on the eastern mountains and one on Cameroon Mountain.

Carduus (185) has 22 species, mostly on the eastern mountains and showing a high degree of segregation.

Alchemilla and *Hypericum* are other genera which contribute characteristic forms to the general montane flora.

A particularly interesting and characteristic element in the African montane flora is afforded by the members of the tribe *Ericeae* of the Ericaceae, and these plants have also been monographed (11, 12). *Erica* itself has some fifteen species in tropical Africa, including the more widely spread *E. arborea* (see p. 154), but most of them are from the south-east and few of them are really montane. In connection with their mention here it is interesting that Chevalier (96) concludes that the genus originated in tropical Africa and is a relic of the old xeromorphic Tertiary flora of that region. The genus *Blaeria* is actually discontinuous, because it occurs on the Cameroon Mountain and Fernando Po. It has in all about 20 tropical species in a special section (the others are at the Cape), and of these all but two are montane. Of the two species mentioned in West Africa, one, *B. tenuifolia*, is also on the Aberdares. *Philippia* has 40 species distributed widely in the tropics and in the Madagascar region. Of the tropical African species four are on the eastern mountains, one of them, *P. excelsa*, being on several peaks, and there are two species on the western mountains.

Because of its isolated position the Cameroon Mountain has attracted special attention and Chevalier (97) has made a floristic analysis of its vegetation, in which he recognises four important elements:—

1. Mediterranean and European,
   exemplified by *Cerastium triviale*, *Koeleria cristata*, and varieties of *Radiola linoides*, *Galium aparine*, *Umbilicus pendulinus*, *Senecio palustris*, and *Sibthorpia europaea*.
2. Species common to Cameroons and Abyssinia.
3. South African,
   including species of *Blaeria*, *Brucea*, *Gnidia* and *Helichrysum*.
4. Endemics,
   exemplified by the three genera of Melastomataceae *Afzeliella*, *Eugonia* and *Myrianthemum*.

The Madagascar Region

In general the flora of Madagascar and its neighbouring islands may be described as of African affinity with a strong Asiatic and Pacific element. This is well illustrated in Madagascar itself. The proportion of endemic species is high, perhaps 85 per cent., but many of them are related to African species and what has been called the African element in the flora is estimated to account for about one quarter of the whole (416). There are also said to be points of resemblance between the flora of some of the more elevated parts of Madagascar and that of the East African mountains (286). At the same time it may be doubted whether the floristic relation with Africa is as strong as should be expected from the proximity of the two areas and the presence in the island flora of so many non-African types raises problems of its history which are of great interest (221, 416).

Madagascar has not provided many economic or horticultural plants, but a few are familiar or characteristic, and one or two of them occasionally cultivated. Among these are *Angraecum sesquipedale*, *Aponogeton fenestralis*, *Cryptostegia grandiflora*, *Euphorbia fulgens*, *Kalanchoe uniflora*, *Raphia ruffia*, *Ravenala madagascariensis* and *Stephanotis floribunda*. The island is also said to have been the home of *Delonix* (*Poinciana*) *regia*.

In Mauritius and Réunion specific endemism appears to be about 50 per cent., and in the Seychelles it is about 40 per cent. (538).

Region of Ascension and St. Helena

Ascension Island had apparently, when first discovered, no vegetation except on the summit of Green Mountain, and even to-day is said to have only some eight indigenous species, of which at least two, *Euphorbia origanoides* and *Hedyotis adscensionis*, are endemic. *Wahlenbergia linifolia* occurs also on St. Helena.

To-day St. Helena has but the vestiges of the rich vegetation which it formerly possessed, and it is therefore difficult to arrive at any satisfactory statistics about its plants. Early visitors describe the island as covered with dense forests right down to the water's edge, but these same visitors left behind them asses, pigs and goats, and the last-named in particular have gradually devastated the original vegetation until to-day almost nothing remains. Melliss (381) gives a good account of the flora as it was in the eighteen-seventies. He enumerates some 900 species of flowering plants as occurring on the island, but considers only about 30 of them to be really native, all the rest being under suspicion of accidental or deliberate introduction. Of these 30 all but two or three are endemic. Some were even at that time very rare if not actually extinct, and the position is worse to-day. A recent paper by Turrill (562) gives the original indigenous flora as consisting of 39 species in 28 genera, of which 38 species (97 per cent.) and 5 genera were endemic, and on all counts it seems safe to assume that the aboriginal flora of the island was not large in number of species but very remarkable in being almost entirely endemic.

South African Region

The continent of Africa is unique in that it lies almost symmetrically astride the equator. It is true that owing to the actual shape of the continent the northern part is much larger than the southern, but in latitudinal extent there is little difference between them and in both hemispheres the continent stretches into extra-tropical regions. The plant life of Africa as a whole thus comes to include three perfectly distinct floras—a warm temperate northern, a tropical central or equatorial, and a warm temperate southern. At the same time the first and last of these are of that peculiar type known as "Mediterranean," and are not only rich but to a considerable extent specialised floristically.

It might be expected therefore that the flora of tropical Africa would show and include appreciable elements from these floras, and that there would be conspicuous zones of mingling or transition. In fact this is much less than might be anticipated, for the reason that on the equator side of each of the "Mediterranean" floras the climate is such as to produce desert conditions. In the north this desert belt—the Sahara—is so complete that there is no transition zone between the Mediterranean flora and the tropical African flora at all, but in the south conditions are not so extreme. The deserts there are more scattered and less arid on the whole, and along the east coast the climate is so favourable as to support the development of forest.

As a result of these circumstances there is, in southern Africa, what is not found in the north, namely, a very important floristic region where the tropical African flora and the southern "Mediterranean" flora, that of the Cape, mingle (2, 49, 51, 292). This transition region is of considerable size, but its flora is not exceptionally rich and is of interest chiefly in the way it illustrates (perhaps as well as any other flora in the world) how two floras may, by mutual intermigration, weld themselves into a kind of hybrid whole.

The South African region is, as has been suggested, easily divisible into a number of parts, and as floristic and geographical distinction here go hand in hand, it is appropriate to say something about these. The main constituents and floras number five, namely—the high veldt of the Transvaal and the Orange Free State; the Kalahari desert, or semi-desert, of Bechuanaland; the desert, or semi-desert, of South West Africa; the desert of the Karroo on the south; and the south-eastern coastal area that contains Natal.

As is only to be expected, this region has not contributed much either to gardens or to economic botany, and the importance of its flora is more theoretical, and on this account it is enough to mention a few of the more conspicuous and characteristic plants. Of the five areas mentioned the first three show comparatively little difference in vegetation and may be considered together. Among the noteworthy plants here are *Acacia giraffae*, *Acanthosicyos horrida*, *Carissa arduina*, *Dioscorea elephantipes*, *Elephantorrhiza burchellii*, *Euphorbia tetragona*, *Pachypodium namaquanum*, *Rhigozum trichotomum* and *Sarcocaulon patersonii*.

The flora of the Karroo is much more specialised, and indeed is one of the most striking examples of a xeromorphic flora in the world, a conspicuous feature of it being the "stone plants" (366) belonging to *Lithops* (399) and other genera (Plate 11), so called from their resemblance to the pebbles of the deserts in which they grow. The Karroo plants, which include also many species of *Mesembryanthemum* and related genera, *Crassula falcata*, *Crassula lycopodioides*, *Senecio articulatus*, *Rochea coccinea*, many Stapeliads, and species of *Gasteria* and *Haworthia*, have become increasingly familiar in recent years because of the fashion for their indoor cultivation, and it is worth while reminding readers that the flora also includes quite other kinds of plants, such as *Acacia karroo*, *Chrysocoma tenuifolia*, *Elytropappus rhinocerotis*, *Euclea undulata* and *Euryops tenuissima*.

The eastern coastal area is much less arid than the others. Over much of it the vegetation is savana or even forest, and it is here in particular that the transition between the tropical African and Cape floras is to be seen. Of its more familiar or characteristic species there may be mentioned *Albizzia fastigiata*, *Aloe candelabrum*, *Brachystegia spicaeformis*, *Buxus macowani*, *Erythrina caffra*, *Euphorbia cooperi*, *Hyphaene crinita* and *Strelitzia augusta.*

The Cape Region

The area occupied by the Cape flora proper, which, as has already been said, is one of the most remarkable in the world, is very small, consisting, roughly speaking, of the coast zone from Clanwilliam on the west to the neighbourhood of Port Elizabeth on the east. At the same time it is probably, in proportion to its size, the richest of all floras. It is not altogether easy to arrive at reliable statistics for the region as a whole because it does not fit in with any political area, but some measure of its wealth may be gained from the observation that the Cape Peninsula itself, which is little bigger than the county of Rutland, and of which a full-length study has lately appeared (4), possesses in all 2,500 species, of which about one third are Monocotyledons, a rather high proportion. This floristic richness is associated with a characteristic of the vegetation which is often commented upon, namely the lack of dominance in the plant associations, a feature which is often claimed to indicate age and long undisturbed settlement in a flora.

The Cape flora has few plants of economic importance, partly perhaps because the region had, before its European colonisation, a sparse and primitive human population, and the only ones which need be mentioned are one or two timber trees, including *Ocotea bullata* and *Olea verrucosa*, which come from the eastern part of the region where true forest is locally developed. This lack of economic plants is, however, more than balanced by the great numbers of garden plants which the flora has provided, and the botanical exploration of this country in the early days was a horticultural occasion of first importance, as the first volumes of the *Botanical Magazine* amply testify, and as the following selection will show:

Agapanthus africanus, *Amaryllis bella-donna*, *Arctotis stoechadifolia*, *Asparagus plumosus*, *Dimorphotheca* spp., innumerable species of *Erica*, *Freesia refracta*, *Galtonia candicans*, *Gazania* spp., *Gerbera jamesoni*, *Gladiolus* spp., species of *Ixia* and *Kniphofia*, *Lobelia erinus*, *Nemesia* spp., *Pelargonium acerifolium*, *Plumbago capensis*, etc.

It may also be noted that one of the commonest of all garden plants, Montbretia, whose proper name appears to be *Crocosmia crocosmiaeflora*, is an artificial hybrid between two wild South African plants. Besides all these there are many other native plants which although not generally cultivated are nevertheless more or less familiar or noteworthy, and among these may be mentioned:

Brabejum stellatifolium, *Disa grandiflora*, *Eriocephalus umbellatus*, *Euphorbia caput-medusae*, *Helichrysum vestitum*, *Leucadendron argenteum*, *Leucospermum conocarpum*, *Metalaisia muricata*, *Mimetes lysigera*, *Podalyria calyptrata*, *Priestleya villosa*, *Protea grandiflora*, *Protea mellifera*, *Rhus tomentosa*, *Satyrium carneum* and *Watsonia rosea.*

The position and other features of the Cape flora make it something of a key unit in relation to problems concerning the geographical history of the Angiosperms and the problems of the southern flora, and a great deal of attention has been paid it from these points of view. It would be too great a digression to consider this in detail but the reader will find the leading lines of thought well expressed by Levyns (340) and, at greater length, by Weimarck (583) who, in an extremely detailed geographical study of nearly five hundred of its species, concludes that the flora contains, in addition to the more obvious South African constituents, tropical African, montane African, antarctic, Mediterranean and north temperate, and cosmopolitan elements. The literature has also been admirably summarised by Adamson (3) who points out in particular that of these elements, the tropical and northern African is by no means negligible.

Indian Region

Political changes have tended to obscure the leading features of the flora of this region and in particular the inclusion, as parts of British India, of Burma and the Malay Peninsula, in Hooker's classic description of the plant life (276) gave an exaggerated impression of the floristic richness of the Indian region as defined on p. 30 above. It has also to be remembered that the more fertile parts of India have been so long and so densely inhabited by man that there is probably little of the original vegetation left. Nevertheless the Indian flora as a whole is an important and characteristic one. It contains many plants of value, among useful plants which appear to be native here being *Aegle marmelos*, *Artocarpus nobilis*, *Corchorus capsularis*, *Crotalaria juncea*, *Elettaria repens* (*cardamomum*), *Eleusine corocana*, *Gynocardia odorata*, *Indigofera tinctoria*, *Luffa aegyptiaca*, *Murraya koenigii*, *Nardostachys jatamansi*, *Pennisetum glaucum*, *Piper longum*, *Piper nigrum*, *Pterocarpus santolinus* and *Sesamum indicum*. A few of its species, among them *Cymbidium grandiflorum*, *Datura metel*, *Dendrobium nobile*, *Hibiscus abelmoschus*, *Jasminum grandiflorum*, *Vanda caerulea* and *Vitex negundo*, are sometimes grown in hot-houses, and among other interesting or conspicuous plants are *Bombax malabaricum*, *Butea frondosa*, *Calotropis gigantea*, *Corypha umbraculifera*, *Dorstenia indica*, *Ficus bengalensis*, *Ficus elastica*, *Humboldtia laurifolia*, *Ochlandra stridula*, *Oryza coarctata*, *Shorea robusta* and many species of *Strobilanthes*.

Naturally there is a high degree of community between the floras of India proper and of Ceylon, and many species, as for instance three of the large Asiatic Lobelias, *L. leschenaultii*, *L. nicotianifolia* and *L. trichandra*, are found in both, as well as some of those species already mentioned. The flora of Ceylon is more strongly Malaysian than Indian in affinity, and it has a high degree of endemism. Willis (596), who studied the flora in great detail in connection with his theory of Age and Area, estimated that there are over 800 endemics, and that these amount to about a third of the whole native flora. Most of the best-known plants of Ceylon, however, are found either in India or elsewhere also, but among the endemics *Diospyros ebenum* (the ebony), *Diospyros quaesita*, *Hortonia angustifolia* and *Schumacheria castaneifolia* may be noted.

The Laccadive and Maldive Islands, which are most appropriately mentioned at this point, are low coral islands, without endemic plants.

Continental South-east Asiatic Region

The difficulties of assessing this region and the paucity of larger endemic units has been stressed on p. 126 but the situation regarding species is probably very different and both the size of the area and the exuberance of much of its vegetation suggest that, could a reliable estimate be made, the proportion of endemic species would prove to be large and comparable with that in parts of Malaysia. Few of these species are, however, familiar.

Attention has been called to the fact that it is often very difficult now to say for certain where important crop plants had their original homes. This applies amongst others to rice, tea and the various *Citrus* fruits. To-day these are widely grown, but such evidence as there is suggests that most, and perhaps all of them, were natives of this region or at least of it and some of its bordering lands.

Among other species associated with this region are *Amherstia nobilis*, *Begonia rex*, *Cinnamomum camphora*, *Dipterocarpus turbinatus*, *Garcinia cochinchinensis*, *Liquidambar formosana*, *Melanorrhaea usitata* and *Torenia fournieri*.

Of the isolated parts of the region the flora of Formosa, which is largely a combination of continental and Malaysian types, is about 40 per cent. endemic, and the proportion in Hainan, which has a rich flora, is also high. The Andaman and Nicobar Islands, and the Riukiu Islands, each have a small proportion of endemics.

Malaysian Region

Probably nowhere else in the world, with the possible exception of parts of tropical America, does flowering plant vegetation attain such a richness and luxuriance as in Malaysia, where except for Timor and some of its neighbouring islands, conditions favour its fullest development in almost every way (see frontispiece).

Not only is the vegetation luxuriant, but the flora is very rich and contains many plants which have long been of value to man. Indeed, the "Spice Islands," as part of the archipelago was called in earlier days, have played no small part in the history of many nations (215). The nature of most of these economic plants is indicated by the name just quoted, but there are others as well, and as examples of the products of the region there may be mentioned the following, all of which are known or thought to have originated somewhere in Malaysia, *Arenga saccharifera*, *Artocarpus communis* (*incisa*), *Calamus draco*, *Canarium luzonicum*, *Colocasia esculenta*, *Curcuma zedoaria*, *Eugenia caryophyllata*, *Garcinia mangostana*, *Metroxylon rumphii*, *Musa textilis*, *Myristica fragrans*, *Piper betle* and *Zingiber officinale*. Besides all these the flora includes innumerable other noteworthy plants, among them being *Amorphophallus titanum*, *Antiaris toxicaria*, *Bulbophyllum grandiflorum*, *Coleus blumei*, *Croton lacciferus*, *Dendrobium superbum*, *Dendrocalamus giganteus* (Plate 22), *Dryobalanops aromatica*, *Hibiscus rosa-sinensis*, *Rafflesia arnoldi*, *Strychnos ignatii* and *Vanda tricolor*.

Specific endemism throughout Malaysia is undoubtedly very high (326), partly of course because of the insularity of the region. Merrill (386) states that in any large island or compact island group the primary vegetation, that is to say the vegetation which has never been cleared and which is thus not diluted by adventive plants, is likely to contain 75 per cent. of endemic species, and an even higher figure has been claimed for the Philippines (382, 383) which have a very rich flora, containing incidentally more than a thousand species of orchids. Phytogeographically New Guinea is probably the most peculiar and significant part of the region and when its immense flora is more completely known it will likely be found that it has a higher proportion of endemics than any other island. A partial count comprising but fifty odd of the native families even to-day reveals that some 85 per cent. of the species are endemic. The orchid flora is particularly remarkable and contains more than 2,500 species, practically all of which are confined to the island. Good accounts of the plant life have been given by Lauterbach (335), and, with interesting analyses of the floristic elements present, by Lam (328).

As for the region as a whole its degree of specific endemism is certainly to be compared with the figures just quoted, and almost every kind of distribution over the various constituent areas is, in addition, to be seen. At one end of the scale are such species as *Gnetum macrostachyum* and *Nepenthes ampullaria*, which range from the Malay Peninsula to New Guinea; at the other are the innumerable species confined to single islands; and in between are examples of almost every kind. Much

Plate 14. A giant Senecio (*S. keniodendron*) of the African mountains

(*from Karsten & Schenck, Vegetationsbilder*)

detail illustrative of these last will be found in the writings of Lam (326, 330, 331, 332) and van Steenis (528, 529, 531).

Particularly interesting are the ranges in Malaysia of some species belonging to groups which are characteristic of Australia, *e.g.*:

Stylidium inconspicuum	Java (511).
Stylidium javanicum	Java and Sumba.
Goodenia koningsbergeri	Java.
Eucalyptus deglupta	a rain-forest tree of the Philippines, Celebes, the Moluccas, New Guinea (and the Bismarck Archipelago).
Styphelia suaveolens	Borneo, the Philippines, Celebes and Timor.
Styphelia malayana	Malay Peninsula and Java.
Trochocarpa celebica	Celebes.
Trochocarpa learmonthiana	Borneo.

Much attention has been paid to the montane plants of Malaysia. Nearly all the islands are mountainous and bear, at high elevations, a well-marked "Malaysian Mountain Flora" containing, among other kinds of species, representatives of such familiar northern temperate genera as *Ranunculus*, *Rubus* and *Viola*. Wallace (569) gave a vivid picture of the vegetation of the summits of some of the Javanese mountains, and others have made further studies since. The most exhaustive and recent work on the subject is that of van Steenis (529), and from it it would appear that there have been three tracks by which the temperate forms so conspicuous in this flora, which is estimated to contain 800 species, have migrated into the Archipelago. One is by way of the Malay Peninsula, Sumatra, Java and the Lesser Sundas to S. Celebes and Timor; another is by the line Formosa and the Philippines to Celebes; and the third from Australia by way of New Guinea to Celebes, Borneo and the Philippines. Van Steenis' map shows that the first two cover the Philippines and most of Celebes in common, and that all three almost or quite overlap in southern Celebes, and the floristic relations of this key area have been discussed by Lam (330, 331).

Within the Malaysian region must be included the Cocos-Keeling atolls and Christmas Island which lie south of Sumatra and Java. The former have only a small flora of widespread species, but the latter (which is about the same size as Jersey) is a high island and had, when first studied (16), a flora of 130 species of Malaysian relationship, which included 16 endemic species.

Hawaiian Region

Geographically this is the most isolated of all the floristic regions, a fact which undoubtedly accounts largely for its most prominent botanical feature, the huge proportion of its flora which is endemic. Numerical estimates of this vary somewhat, but it has recently been stated (520) that more than 90 per cent. of the native Hawaiian plants are confined to the islands, and many of these are of marked and specialised types.

Several general accounts of the plant life (82, 352, 452) make mention of some of the more characteristic species such as *Acacia koa*, *Alyxia olivaeformis*, *Dianella odorata*, *Edwardsia grandiflora*, *Eugenia malaccensis*, *Freycinetia arnotti*, *Gunnera petaloides*, *Santalum pyrularium* and *Strongylodon lucidum*, but there are no particularly noteworthy economic or horticultural plants among the native species. In one of the earlier accounts, Wallace (570) draws attention to two of the many points of interest in the flora, namely the small proportion of Monocotyledons (less than one-fifth of the total and nearly all grasses or sedges) and the extraordinary development of shrubs and even trees in genera widely familiar as herbs, for instance, *Viola*, *Silene*, *Geranium*, and various Lobeliads and Composites. There is a well-marked montane flora which, like that of Malaysia, includes many temperate representatives (241).

To-day the flora contains so many introduced plants that it is becoming more and more difficult to sort out the original species. This influx of adventives has been going on for a long time and, as in some other islands of the Pacific, some species were doubtless introduced by the earliest inhabitants even before the islands were visited by Europeans. An interesting paper by Forbes (181) indicates that in the twenty-five years after 1886 more than sixty species came in, including even one of the "sea-grasses," *Halophila ovalis*, and there have been many additions more recently.

Thus the affinity of the total flora to-day is more with the New World than the Old but this is by no means generally accepted as expressing its history and derivation. In fact the problem of the origin of the Hawaiian flora is one of the most difficult in plant geography, and one which is not simplified by the circumstance that the islands are of comparatively recent volcanic formation. One view is that the flora is of American isthmian origin, that is to say that it is derived from Central America. Skottsberg, on the other hand, who has studied the flora for many years (497, 498, 500, 506), suggests that its most important relationship is with the south and that it is indeed a relic of a very old Pacific flora which has now almost entirely disappeared. In a more recent paper (508), he points out that while the largest floristic element is Malaysian and only a much smaller one without endemics is neotropical there is a considerable element of Australasian or even "Antarctic" affinity, and it is to this group that most of the more striking endemic forms belong. A third view is that the flora has had a "waif and stray" origin, having developed from a heterogeneous collection of plants which have reached the islands by all sorts of casual means. For this there seems little in the way of definite evidence, and some facts, such as the unusual poverty of the Hawaiian beach and strand flora, discussed at length by Guppy (241), are against it.

Region of New Caledonia

The main constituent part of this region, New Caledonia itself, an island not much larger than Yorkshire, in many respects exceeds even the Hawaiian Islands in the peculiarity of its flora (238), which has good claim to be considered the most remarkable in the world. It is very rich, with probably upwards of 3,000 native species, and of these well over 80 per cent. seem to be endemic, including some important whole groups. The island, which is composed partly of igneous rocks, including much serpentine (see p. 316), and partly of Permian and younger sedimentary rocks (109, 297) is even now far from perfectly known, and still yields surprises.

The proportion of more xerophilous woody plants in the flora is very high and because of this and of the prevalence of what are regarded as ancient types among the endemics Guillaumin believes (461) that the island has been an isolated land surface since the middle of the Tertiary. Another remarkable and related feature is that certain families (235), notably Rubiaceae, Myrtaceae, Orchidaceae and Araliaceae are particularly conspicuous while three others, usually among the best represented, the Composites, Grasses and to a less degree the leguminous families, have very few species. Indeed, there is said to be only one native Composite and only half a dozen grasses (109) and these facts again are thought to argue the antiquity of the island as a land surface.

The flora has been analysed and its origin discussed in detail by Guillaumin (461) and the conclusion is that it has a more or less equal affinity with Australia and with eastern Malaysia, a rather lesser relationship with the Pacific Islands, and a slight one with New Zealand. There are also some small but unmistakable evidences of affinity with the Madagascar region (221).

Schlechter (465) and Compton (109) have given useful accounts of the vegetation and the reader should refer to these and to the other works cited for the details of Angiosperm species, none of which is particularly familiar or of wide importance.

The flora of Lord Howe Island (259) has between 150 and 200 species, about 30 per cent. of them being endemic. Norfolk Island has rather fewer (325) and about 25 per cent. of endemism. The floras of both these islands have been described as intermediate between those of Australia and New Zealand (235), and several of their plants have already been or will be mentioned elsewhere, but almost certainly the most familiar is *Howea forsteriana*, the palm of Lord Howe Island which is now commonly grown for decoration.

Regions of Melanesia and Micronesia and of Polynesia

For present purposes it is best to combine these two regions, which together comprise all the islands south of Hawaii, east of the line Philippines—New Guinea—New Caledonia—Kermadecs, and between the Bonins on the north-west and Easter Island on the east, both inclusive, and to make only a few general statements, because the botanical facts about this area are so varied and complexing that to attempt to go into detail would almost certainly obscure what, in a general survey like this, is the main characteristic of the flora as a whole, namely that it is essentially a derived one, almost entirely Malaysian and Australasian in affinity and presumably in origin. Indeed, in comparison with other parts of the world it is no exaggeration to say that there is no real "Polynesian" flora and that all the plants within this great area, derive more of less directly, from adjacent floras. Merrill (386) and others have shown that this can be well demonstrated in the distribution of many genera whose species numbers rapidly diminish eastwards, the further they reach from Malaysia. This is particularly noticeable in the orchids (408), of which there are thousands of species in eastern Malaysia but scarcely any in the further Pacific Islands. It is also well seen in such genera as *Cyrtandra* and *Pandanus* (see p. 116 above) and in the Ericaceae, which are very few east and south of New Guinea.

This is not to deny that there is a considerable element of endemism in some of the islands, and especially in the larger western ones, but the species concerned mostly belong to widespread large genera. One of the major general sources of information about this point is the collection of figures by Guillaumin (235) and from this and confirmatory sources it would appear that Fiji has the highest proportion of endemic species, about 50 per cent. The New Hebrides (236, 237) and Tahiti (476) both have about 35 per cent. and Samoa rather less. Other main groups seem to have figures round about 25 per cent., as for instance the Solomons, the Carolines and French Polynesia, which consists of the Society Islands, the Tuamotus and the Marquesas. On the other hand Tonga and Rarotonga are quoted as having less than 5 per cent. each. Kanehira (310, 311) has studied the Micronesian flora in some detail and it would seem that the endemics in total over all these small scattered islands may amount to 50 per cent. but this is scarcely comparable with the other figures mentioned above. Brown (66) has dealt somewhat similarly with the flora of south-eastern Polynesia which he estimates to contain 339 native Angiosperms with a prominence of families similar to that seen in Hawaii. He considers that though the wide species of the flora are Malaysian and Asiatic, the total affinity of the flora is strongly American. Easter Island, which is the south-eastern outpost of Polynesia, has a native flora of only about 30 species, but is usually credited with one or two endemics.

One particular source of confusion in the study of the plant life of these two regions is the varied mixture of structure and, presumably, age in the islands. All types of oceanic island are represented and without any simple geographical segregation, except that the largest are in Melanesia and the adjacent parts of Polynesia. Generally speaking the mountainous volcanic islands have a considerable proportion of endemic species; the high coral-rock islands have a smaller proportion or may be almost without them (591); and the atolls have none at all (627). This last point is well illustrated by such a flora as that of Jaluit, an atoll in the Marshall Islands. Here in 1915 Koidzumi described the flora (318) as composed of 57 species, of which 38 had reached the island by natural means, without endemics. Since then it may be noted that the single species, or rather variety, of *Pandanus* mentioned by Koidzumi has been split into four local species.

There is also still some doubt, or at least some confusion of statement, as to which islands, if any, contain "continental" rocks (see p. 354). This and similar questions bear more upon the geological history of the Pacific basin than upon the plant life but the two are so intimately connected that they merit mention here. More especially in this sense is the problem of what has been called the Melanesian continent, a hypothetical land mass uniting such now scattered units as the Carolines, Solomons, Fiji, Tonga, Kermadecs and Chathams with Australia and New Zealand, and whose eastern margin is said to be represented by what is called the andesite line (see Chapter 20).

Caribbean Region

This is one of the most important regions, not only in the richness and luxuriance of its vegetation, but also because of the large number of valuable plants it has provided, and in these respects it may appropriately be regarded as the New World counterpart of the Malayan Archipelago. Geographically it rather is different, since it consists partly of an archipelago (the West Indies) and partly of a portion of the American continent (Mexico and Central America), and climatically also it is less constant, Mexico in particular having extensive desert areas.

It is not easy to say much about the degree of endemism in the flora of the region as a whole, but Willis (596) has stated that the continental part has 8,000 endemic species, a figure which certainly represents a very high proportion, and a recent estimate gives a figure of well over 2,000 for Costa Rica, including a great number of orchids. Cuba is generally credited with one of the richest floras in the world, and here also, as in most other larger islands of the West Indies, the endemism is undoubtedly high. Trinidad, on the other hand, has only about 7 per cent. Many species are common to both the constituent parts of the region, and among them are *Bletia purpurea*, *Calanthe mexicana*, *Epidendrum polybulbon*, *Prioria copaifera*, *Rhoeo discolor* and *Swartzia simplex*, but most of the other noteworthy plants either occur also beyond the confines of the region or are restricted to one or other part of it.

Central America in the wide sense has provided a number of economic plants (one very important) namely *Castilla elastica, Haematoxylum campechianum, Monstera deliciosa, Phaseolus multiflorus, Smilax medica, Vanilla planifolia* and *Zea mays* (see p. 3), but its contribution to gardens has been even greater and includes such well-known plants as *Beloperone guttata, Ceanothus caeruleus, Choisya ternata, Cosmos bipinnatus, Dahlia pinnata* (*variabilis*), *Echeveria* spp., *Euphorbia* (*Poinsettia*) *pulcherrima, Lycaste skinneri, Polianthes tuberosa* (actually not known wild but belonging to a Mexican genus), *Salvia fulgens, Tagetes erecta, Tagetes patula, Tigridia pavonia, Zebrina pendula* and *Zinnia elegans*. Other outstanding plants from here include *Achras zapota, Cordia gerascanthus, Deherainia smaragdina, Marcgravia nepenthoides, Neoschroetera tridentata* (*Larrea mexicana*), *Persea americana, Plumeria acutifolia* and *Theobroma pentagona*.

The West Indies, on the other hand, have contributed comparatively little to gardens, except perhaps *Lantana camara* and *Yucca aloifolia*, but are the home of many well-known plants of value, most of them tropical fruits, of necessity not very familiar in Europe but nevertheless of great importance in warmer countries. The actual home of many of these is lost but generally credited with a West Indian origin are *Annona muricata, Annona reticulata, Croton cascarilla, Grias cauliflora, Lagetta lagetto, Pimenta officinalis, Sapindus saponaria* and *Spondias mombin* (*lutea*). Besides these there are many other conspicuous species in the flora, as, for instance, *Myrica cerifera, Nectandra antillana, Ocotea leucoxylon, Pereskia aculeata* and *Sloanea jamaicensis*.

The Bermudas have a small flora of about 150 native species, and of these some 8 per cent. are endemic.

The little-known Revillagigedo Islands, of which the nearest is nearly 400 miles west of Mexico and rather less from the southern tip of Lower California, are of considerable botanical interest, and the flora has been described by Johnston (303). Each member of this scattered group of tiny islands is an isolated volcanic peak, and the largest of them, Socorro (50 square miles), has a flora of 93 native species, of which 31 are endemic. Two smaller islands have 11 and 6 endemics respectively. The great floristic affinity is with Central America and the West Indies but, most interesting, there is a distinct relationship with the Galapagos Islands, a relation typified by the occurrence of *Psidium galapageium*, previously known only from the latter islands.

Region of Venezuela and Guiana

The flora of this region is still far from well-known and it is therefore almost impossible to say what degree of endemism it possesses. Probably it is high, despite the close relationship of the flora with those of neighbouring regions. There are no very conspicuously important or valuable plants, and it must suffice here to mention from among the characteristic species of the vegetation, many of which are grasses or palms, *Arthrostylidium schomburgkii, Aulonemia quexo, Brosimum galactodendrom, Caryocar villosum, Copernicia* spp., *Curatella americana, Cusparia febrifuga, Dipteryx odorata, Duguetia quitarensis, Mauritia* spp., *Montrichardia arborescens, Nectandra rodioei* and *Paullinia cupana*.

Some of the mountains in southern Venezuela, notably Mt. Roraima (543) and Mt. Duida (544), have long attracted attention, not only because of their geological structure but also because of the peculiarities of their floras, which, as a result of recent explorations, are now much better known. Both are table mountains of sandstone and perhaps the remnants of a once much more extensive plateau.

Roraima, which rises almost sheer to its summit of 8,600 ft. from a rolling savana, has a summit of about 25 square miles, and a vegetation in which, in general, there is about 50 per cent. endemism, though a much higher proportion on the actual summit (94, 200). Duida rises to 6,000 ft. from a low plain and has a summit area of 250 square miles (201), and its flora has probably a similar degree of endemism. The same broad flora ranges over both, which are hundreds of miles apart, and shows a close relationship with that of the northernmost Andes.

The Amazon Region

The Amazon Basin has long been recognised as notably rich in species, especially of course, forest trees, and although it is not easy to arrive at a definite figure it would seem probable that the endemic species number at least three thousand and provide a considerable proportion of the total.

Two important economic plants are the Para rubber, *Hevea brasiliensis*, and the cocoa, *Theobroma cacao*, while among others of less significance are *Bertholletia excelsa*, *Paullinia sorbilis*, and certain species of *Smilax*.

Among the more characteristic plants, palms are outstanding and of them there may be mentioned, *Astrocaryum jawari*, *Attalea excelsa*, *Leopoldinia pulchra* and species of *Mauritia*. Other notable species are *Arundo saccharoides*, *Couma utilis*, *Pourouma cecropiaefolia* and *Psathyranthus amazonicus*. *Victoria amazonica* (*regia*), the giant water-lily is one of the best-known plants, but in all occurs a good deal more widely.

South Brazilian Region

The South Brazilian region is the largest and most varied in tropical America, and although no figures are readily available, it may be assumed that a very high proportion of its many thousands of species is endemic.

Among plants of considerable, and, in a few cases, of outstanding economic importance, which are regarded as having their origin here are *Ananas comosus* (*sativus*), *Arachis hypogaea*, *Cephaelis ipecacuanha*, *Copernicia cerifera*, *Ilex paraguayensis*, *Leopoldinia piassaba*, *Manihot glaziovii*, *Passiflora edulis* and *Quassia amara*. From this region come also a number of well-known garden and hothouse plants, among them *Aechmea fulgens*, *Begonia semperflorens*, *Billbergia nutans*, *Bougainvillea spectabilis*, *Datura suaveolens*, *Fuchsia coccinea*, *Neomarica northiana*, *Passiflora caeulea*, *Salvia splendens*, *Sinningia speciosa* and *Tibouchina semidecandra*.

Of other noteworthy plants (among which palms are prominent) there may be mentioned *Attalea compta*, *Bactris aristata*, *Bauhinia splendens*, *Caesalpinia echinata*, *Cattleya labiata*, *Chorisia ventricosa*, *Cocos coronata*, *Dalbergia nigra*, *Dinisia excelsa*, *Erythrina crista-galli*, *Euterpe edulis*, *Geonoma macroclona*, *Hancornia speciosa*, *Machaerium firmum*, *Manicaria saccifera*, *Mauritia vinifera*, *Melinis minutiflora*, *Oncidium papilio*, *Syagrus mikaniana*, *Utricularia nelumbifolia* and *Vellozia candida*.

Fernando Noronha and South Trinidad have several endemic species each. St. Paul's Rocks, which are still further away from the continent, have no Angiosperms.

Andean Region

This very extended region has been divided into a number of subordinate areas and floras, but the constituent parts which call for mention here are five, namely, the montane (tropical in the north), the tropical coast, the temperate coast, the eastern savanas or puna, and the Galapagos archipelago. The second of these is predominantly a desert area, and the third includes the Chilean "Mediterranean" vegetation and flora.

The region is above all remarkable for the number of its economic plants, which include many of the most important of all. These come chiefly from the more northerly parts of the montane zone and include *Annona cherimolia, Ceroxylon andicola, Chenopodium quinoa, Cinchona succirubra, Erythroxylum coca, Krameria triandra, Lycopersicon esculentum, Nicotiana tabacum, Phaseolus lunatus, Phaseolus vulgaris, Quillaja saponaria, Schinus molle* and *Solanum tuberosum.*

The garden plants, which are also very numerous, come naturally from the more temperate parts, especially the southern mountains and the Chilean coasts, but a number have their homes futher north. Among the former are *Alstroemeria aurantiaca, Berberis darwinii, Calceolaria integrifolia, Escallonia micrantha, Fuchsia rosea, Geum chiloense, Lapageria rosea, Lippia citriodora, Salpiglossis sinuata, Schizanthus pinnatus, Tropaeolum speciosum* and *Verbena erinoides*; and among the latter, *Browallia speciosa, Buddleja globosa, Ercilla volubilis, Heliotropium peruvianum, Tropaeolum majus, Tropaeolum peregrinum* and several orchids.

Other important or interesting species from the northern parts are *Aetanthus mutisii, Baccharis tola, Espeletia* spp., *Phytelephas macrocarpa, Puya raimondii* (Plate 7) and *Quercus humboldtiana*, while from the more southerly parts come *Azorella multifida, Drimys winteri, Eucryphia cordifolia, Gunnera chilensis, Jubaea spectabilis, Laurelia aromatica* and *Mutisia viciaefolia.*

The Galapagos or Tortoise Islands form a group of volcanic islands about 700 miles west of the coast of Ecuador, and have long been famous for the peculiarities of their animal life. The plant life is not so remarkable, although it contains many points of great interest. There are nineteen islands varying greatly in size and having a total area rather less than that of Devonshire, and the flora is not rich, amounting to about 350 species. According to Stewart (535), 40 per cent. are endemic, and the families Amaranthaceae, Euphorbiaceae and Rubiaceae are especially rich in endemic forms, while in view of the discontinuity of the genus *Pernettia* (see p. 389) the occurrence of an endemic species, *P. howellii*, is of particular interest (510). The relationship of the non-endemic species is almost entirely American, and especially Andean, there being but a very small number of more widely ranging plants. Kroeber (322) has studied in particular the distribution of the species among the islands. and concludes that there is little in it which cannot be explained on a combination of mathematical and geographical chance. Howell (280) states that of the 18 species of the endemic genus *Scalesia*, only 6 occur on more than one island and only one on more than two islands.

Pampas Region (71)

This region, which vegetationally contains one of the world's most important grasslands, contains no very important economic plants but has provided a small number of garden forms, including *Cortaderia selloana, Nicotiana affinis, Petunia* spp. and *Salpichroa rhomboidea.*

Characteristic species include *Acacia caven, Aspidosperma quebracho, Geoffroea decorticans, Larrea divaricata, Prosopis alba, Trithrinax campestris* and many grasses and composites, but not all these are entirely confined to the region and it is difficult to say what proportion of its total flora may be so.

Three of the plants most often commented upon are not natives, namely the ombu tree, *Phytolacca dioica*, of more tropical America; and the cardoon (*Cynara cardunculus*) and the milk-thistle (*Silybum marianum*) both of which were long ago introduced from western Eurasia. The two latter which are described as often growing to a great size, may in favourable seasons form an almost inpenetrable vegetation over wide areas (123, 282).

Region of Juan Fernandez

The Juan Fernandez group of three volcanic islands lying off the coast of Chile has a small but peculiar flora. According to Skottsberg (496, 497, 503), about 70 per cent. of the 142 species are endemic. Rather more than half the flora has a strong American affinity, but the remainder has an equally strong "Pacific," or western, affinity and in particular there is an appreciable relationship with Hawaii. There is considerable segregation of species between the two large islands, only 19 per cent. of the flora occurring on both. Of endemic species only 12 per cent. occur on both.

The flora of the Desventuradas Islands consists of twenty species (505, 626), of which about two-thirds are endemic. Most of them belong to widely distributed genera, and those which are not endemic are all found also in western South America.

North and East Australian Region

This region stretches in a wide coastal belt round the continent from the Kimberley District in the north-west to Tasmania. Vegetationally it is predominantly savana or savana-woodland, but there are considerable areas of forest, especially along the north-east coast, and also in the south-east and in Tasmania. The flora is almost entirely local and Australian in character except in the north where there is a considerable admixture of Malaysian, and especially New Guinea, types, but even here some groups notably developed in New Guinea, such as the palms and aroids, are poorly represented. The north coast has some 15 per cent. of species in common with Malaysia and on the east coast there is a notable relationship with the flora of New Caledonia. About 20 per cent. of the species in the flora of Tasmania are endemic to that island (453).

The flora of some of the mountains, particularly in Queensland, is of considerable interest to the plant geographer. For example, Mt. Bellenden-Ker (194) besides being the only locality of the one *Rhododendron* in Australia (see p. 153) has other noteworthy species, while on the mountains of New South Wales and Victoria there are two outlying species of Gesneriaceae (compare p. 136), *Boea hygroscopica* and *Fieldia australis*.

The forest areas contain a number of useful timber trees such as *Castanospermum australe*, *Casuarina torulosa*, *Dysoxylum fraserianum*, *Elaeocarpus grandis*, and *Eucalyptus pilularis*, but otherwise there are no notable economic plants. A few horticultural species are natives of the region, among them *Acacia dealbata*, *Grevillea robusta*, *Humea elegans*, *Nicotiana suaveolens*, *Trachymene caerulea* and *Viola hederacea*, and there is a good deal of evidence that *Acacia farnesiana*, now a wide species in warm countries, is also native here. Other notable species of the region are *Alphitonia excelsa*, *Atherosperma moschatum*, *Boronia serrulata*, *Brachychiton acerifolium*, *Brachycome linearifolia*, *Calamus australis*, *Ceratopetalum gummiferum*, *Doryanthes excelsa*, *Drimys lanceolata*, *Duboisia* spp., *Epacris longiflora*, *Eucalyptus marginata*, *Eucalyptus regnans*, *Nothofagus cunninghamii*, *Olearia nitida*, *Pandanus tectorius*, *Petrophila sessilis* and *Telopea speciosissima*.

South-west Australian Region (192)

Although small this region is floristically a very important one, containing the fifth and last of the world's "Mediterranean" floras. Like the others, and especially like the Cape flora, with which it has many interesting features in common, it is a rich flora showing a very high degree of endemism which may perhaps reach, or even exceed, 75 per cent. Its similarity with the Cape flora lies not so much in the actual number of forms in common, which are indeed few, but in the remarkable degree of parallelism between the leading characters of the two. In both the same families are frequently well developed, and the same types of growth form are common in each.

There are no important economic plants and it is surprising to find, in view of the large number of garden plants which have come from the other "Mediterranean" floras, that the horticultural representatives are also few—so much so that *Brachycome iberidifolia*, *Callistemon speciosus*, *Eucalyptus ficifolia*, *Helichrysum bracteatum* and one or two species of *Helipterum* practically exhaust the list.

The flora contains many very characteristic forms, and among these may be cited species of *Acacia*, *Banksia*, *Bauhinia*, *Chorizema*, *Dryandra*, *Eucalyptus* and *Hakea*, *Boronia megastigma*, *Chamaelaucium uncinatum*, *Kingia australis*, *Nuytsia floribunda* and *Xanthorrhoea preissii*, and many members of the Epacridaceae, Goodeniaceae and Stylidiaceae.

Central Australian Region

The flora of this great area which comprises most of the interior of the continent is comparatively limited, in correlation with the desert or semi-desert conditions which prevail over most of the region. It is also still incompletely known and studied, and it is therefore not possible to say much here about it. It is probably almost entirely endemic.

Among characteristic species, some of which give an important facies to wide areas of vegetation, may be mentioned *Acacia aneura* (mulga), *Acacia harpophylla* (brigalow), *Clianthus dampieri*, *Eucalyptus hemiphloia* (mallee), *Eucalyptus oleosa*, *Melaleuca acuminata* and *Swainsonia greyana*.

New Zealand Region

The flora of New Zealand (157) must always be of special interest to British botanists because of its antipodal geographical relationship, but comparison of the two is also revealing because, while the British Islands are continental islands, New Zealand is, and has presumably long been, separated from the nearest continent by over 1,000 miles of deep water (403).

Estimates of the size of the flora of New Zealand vary considerably but Cheeseman (95) and Oliver (405) recognise nearly 1,500 indigenous species, to which must be added several hundred groups of species hybrids and more than 600 introductions. Quite apart from the hybrids, which are one of its most remarkable features, the flora is thus seen to be considerably larger than that of Great Britain, and also differs markedly from it in that no fewer than 80 per cent. of the species are endemic.

There are about 100 native families and in three-quarters of these, comprising more than nine-tenths of the flora, 50 per cent. or more of the species are endemic. Of these endemics 40 per cent. are found on both the main islands; 15 per cent. in the North Island only; and 45 per cent. in the South (more temperate) Island. The total species population of the South Island is about one-third greater than that of the

North Island. The endemics are fewest in the Monocotyledons and most numerous in the sympetalous families of Dicotyledons and this again is specially noticeable in the South Island where practically all the latter species are endemic. At the same time three important families of this kind which might be expected (Plumbaginaceae, Asclepiadaceae and Acanthaceae) are entirely absent, while three others, Labiatae, Primulaceae and Solanaceae, are very poorly represented.

Another feature of the flora interesting to northern botanists is that of the 26 genera represented by more than 12 species, nearly half are familiar in the north temperate regions, while rather more than half are characteristic of the southern hemisphere only. Nearly all the former contain a high proportion of endemics and *Ranunculus*, *Epilobium* and *Veronica* (*Hebe*) are more strongly represented in New Zealand than anywhere else. Of the more characteristically southern genera the species are in nearly every case exclusively endemic.

Of the non-endemic species the great majority are found elsewhere in Australia, and especially Tasmania, only, as is shown particularly well in the Orchidaceae, but there are nevertheless great differences between the floras of the two dominions (403), as for instance between the Leguminosae of the two, in the absence of many characteristic Australian types such as *Eucalyptus* and *Casuarina* from New Zealand, and in the great development in the latter of some of the temperate genera mentioned above.

The vegetation is varied but is for the most part some kind of woodland, and there are several valuable timber trees, including *Beilschmiedea tawa*, *Hoheria populnea*, *Knightia excelsa*, *Metrosideros robusta*, *Nothofagus fusca* and *Plagianthus betulinus*. *Phormium tenax* is the only important economic plant.

The region has provided several good garden plants, among them *Clianthus puniceus*, *Fuchsia procumbens*, *Veronica* (*Hebe*) spp., *Olearia haastii*, *Olearia paniculata* and *Senecio greyii*.

Characteristic species include *Aristotelia racemosa*, *Celmisia coriacea*, *Corallospermum crassicaule*, *Cordyline australis*, *Coriaria ruscifolia*, *Haastia pulvinaria*, *Ixerba brexioides*, *Lagenophora forsteri* (found in all parts of the region), *Laurelia novae-zealandiae*, *Leptospermum scoparium*, *Pittosporum tenuifolium*, *Poa caespitosa*, *Ranunculus lyallii*, *Rhopalostylis sapida*, *Rubus australis* and species of *Veronica* (*Hebe*).

The region contains, besides New Zealand proper, four outlying islands or island groups, the Kermadecs 600 miles to the north-east; the Chathams 500 miles to the east; the Auckland and Campbell Islands to the south; and the tiny Antipodes Islands nearly 500 miles to the south-east. The flora of the Kermadecs (402) contains both Polynesian and New Zealand elements and consists of about 70 species with about 15 per cent. of endemism. The Chathams have some 140 species, of which about 20 per cent. are endemic. The Aucklands have about 110 species (10 endemic) and Campbells 85 (5 endemics). There are also about 20 species found on both the latter but not elsewhere. The Antipodes have a small flora of about 30 species including two endemics.

Patagonian Region

This small region is of some special interest because it is the only continental area in the southern hemisphere of latitude similar to that of north and central Europe. It divides up into three constituent areas: the woodlands of the west coast and of Fuegia; the southern tip of the Andes and the steppes of South Patagonia; and the Falkland Islands. The phytogeography has been discussed recently by

Cabrera (71) and Beetle (38) and there is a most interesting account of the country and the conditions of life there in a remarkable autobiography by Bridges (62).

The flora is small and none of the species is of value, although a few, such as *Fuchsia magellanica, Pernettia mucronata, Philesia buxifolia* and *Oxalis enneaphylla* (Falklands), are sometimes grown in gardens. Its most remarkable geographical feature is its relationship with the flora of New Zealand (147). Among other outstanding species are *Berberis buxifolia, Bolax glebaria, Empetrum rubrum, Gunnera scabra, Mulinum spinosum, Myrtus nummularia, Nothofagus betuloides, Nothofagus pumila, Opuntia darwinii* and *Poa flabellata.*

According to Skottsberg (495), the Falklands have about 170 species, of which some 10 per cent. are endemic. The remainder are all found in the continental part of the region.

Region of the South Temperate Oceanic Islands

Scattered far from land in the great ocean which surrounds Antarctica are a number of islands, very small in size and with but a slight vegetation, but, on account of the distribution and affinities of their tiny floras, forming one of the most interesting of phytogeographical regions.

These islands are, with their situations:

1. South Georgia.	54° S.: 36° W.
2. The Tristan da Cunha group	37° S.: 10° W.
3. Marion Island	46° S.: 38° E.
4. The Crozets	46° S.: 50° E.
5. The Kerguelen group	48° S.: 70° E.
6. Heard Island	52° S.: 72° E.
7. Amsterdam and St. Paul Island	37° S.: 78° E.
8. Macquarie Island	55° S.: 160° E.

Floristically belonging to this group are Antarctica and the South Shetland Islands, but the former has only two species of flowering plant, both South American, and the latter one, also South American, and they need not be considered further.

Considering the varied latitude of the islands their flora is remarkably constant and there is strong relationship between the islands. A compilation made by the writer from various sources shows that the number of species which may safely be regarded as native is 84, of which no fewer than 34 belong to the Cyperaceae and Gramineae. These latter, it is interesting to note, are appreciably less widely distributed over the islands than the rest, and their endemism is higher, namely 20/34 as compared with 17/50.

In the following analysis it saves a great deal of space and repetition if the various constituent parts of the region are referred to by the numbers attached to them above.

The floras of the constituent parts are:

1 has 10 species, of which 1 is endemic.
2 ,, 33 ,, ,, 19 are endemic.
3 ,, 8 ,, ,, none is endemic.
4 ,, 6 ,, ,, none is endemic.
5 ,, 21 ,, ,, 4 are endemic.
6 ,, 5 ,, ,, none is endemic.
7 ,, 17 ,, ,, 7 are endemic.
8 ,, 29 ,, ,, 1 only (?) is endemic.

Of the 84 species in total 37 species are endemic to the region as a whole, and 62 occur on one island or island group only, *i.e.* 3 on 1, 27 on 2, none on 3, none on 4, 6 on 5, none on 6, 9 on 7, and 17 on 8, this last number being no doubt influenced by the proximity of New Zealand.

Ten species occur on two islands or groups out of the eight in the combinations 15, 27, 27, 27, 27, 56, 57, 58, 58, 78, the endemics being underlined.

Five species occur on three islands or groups out of the eight in the combinations 145, 158, 278, 356, 458.

Three species occur on four islands or groups out of the eight in the combinations 1358, 3456, 3458, namely *Montia fontana*, *Pringlea antiscorbutica* and *Crassula moschata*.

Four species occur on five islands or groups out of the eight in the combinations 12378, 13458, 13568, 34568, namely *Ranunculus biternatus*, *Acaena adscendens*, *Callitriche antarctica* and *Azorella selago*.

Of the species which are not endemic to the region, the affinity lies, as might be expected, chiefly with Australasia and temperate South America. Thus there are:

Outside the region in Australasia only .	16
,, ,, ,, ,, South America only .	12
,, ,, ,, ,, both the above .	6
Remainder	13

The six which range from America through the islands to Australasia are:

Acaena adscendens, *Agrostis magellanica*, *Azorella selago*, *Callitriche antarctica*, *Crassula moschata* and *Juncus scheuchzerioides*.

The wider species include six variously distributed in the Southern hemisphere; three found in the northern temperate zone and in South America; and four more or less cosmopolitan. The distribution of these within the region is respectively:

2, 27, 2, 7, 27, 2: 1, 2, 5: 7, 8, 1358, 28.

It will thus be seen that only one species widely distributed outside the region is also widely distributed in it, and further that the six wide southern species, as they may be called, are found only on the Tristan group and/or on Amsterdam and St. Paul, that is to say, on the two equally most northern island groups.

CHAPTER 11

THE DISTRIBUTION OF SPECIES—IV

THIS chapter, which concludes the general survey of the geographical distribution of species, is devoted to certain particular aspects of the subject, namely: discontinuous species; species with very narrow ranges; vicarious species or species pairs; and, finally, the three types of Angiosperms which are particularly associated with marine and maritime habitats and which therefore differ fundamentally in geography from all the rest.

Discontinuous Species

Just as in families and genera, a proportion of all species have ranges consisting of two or more constituent and separate parts, and some have actually been mentioned in Chapter 8. There are, however, two reasons why it is impossible here to give more than a very brief account of these. In the first place they are very numerous and any attempt to deal with them critically and systematically would be far beyond the scope of this book; and, in the second place, the detailed account that has already been given of discontinuous genera applies in outline almost equally well to species. Indeed, genera often owe their discontinuity to that of one or more of their constituent species.

For these reasons no more is aimed at here than to demonstrate the great variation in the range of discontinuous species and the fact that they can be classified in the same way as discontinuous genera. It must also be pointed out that the different examples cited, though taken from reliable sources and authorities, have not been critically examined and verified in the same way as was done for the genera, and some of the details may well prove, on closer examination, to need qualification or correction.

It will be remembered that there are, in correlation with the major circumstances of world geography, four principal types of generic discontinuity, and species also are conveniently dealt with under these heads. The fifth, Hawaiian, category can here be ignored.

Discontinuous species of the north temperate zone
(see also pp. 161 *et seq.*)

A number of species are found discontinuously distributed throughout the northern temperate zone. *Potentilla fruticosa*, for example, is found in North America, in Europe, in Siberia and in the Himalayas, and among others with a rather similar type of range (though not all Himalayan) are *Anemone multifida*, *Arabis alpina* and several species mentioned in the analysis of the northern flora in Chapter 9.

The remarkable eastern North American—eastern Asiatic type of distribution, so well known among genera, is seen in various species, among them being *Acer rubrum*, *Cypripedium reginae*, *Ostrya virginica*, *Polygonum arifolium*, *Polygonum virginicum*, *Smilax herbacea* and *Symplocarpus foetidus*. Discontinuity between North America and Japan is particularly frequent and Gray (228) long ago listed the instances of three types, namely—eastern North America and Japan (17 species); western North America and Japan (15 species); and both eastern and western America and Japan (17 species), though whether all these are acceptable in terms of more modern taxonomy may be doubted (622).

Several "Bering" species (see p. 88) are discontinuous between eastern Asia and western North America across the strait, among them *Rubus spectabilis* and *Streptopus streptopoides.*

In the New World a number of species are found on the west and east sides of the continent, but not in between, including *Danthonia intermedia*, *Oxytropis foliosa* and *Senecio resedifolius* and a group discontinuously distributed between California and the south-eastern States (485).

Similarly in the Old World there are species such as *Betula humilis*, which occurs in Europe, Central Asia and eastern Asia.

Many examples of discontinuity on a smaller scale are afforded by the floras of Europe and the Mediterranean. The familiar *Rhododendron ponticum* grows on the south coast of the Black Sea, in parts of Palestine, and in the extreme south part of the Iberian Peninsula. *Potentilla apennina*, *Genista dalmatica*, *Althaea rosea*, *Phlomis lanata* and several others are found in Italy and Bulgaria only, while *Crocus veneris* and *Centaurea cretica* occur on the islands of Cyprus and Crete. *Androsace villosa* has recently been recorded from the Atlas Mountains, having long been familiar in the Alps and Balkans. On a still narrower scale *Pedicularis rosea* and *Saxifraga retusa* are discontinuously distributed within the Alpine mountain system.

Lastly, there may be mentioned here several north temperate plants which have been recorded, apparently wild, in one or more spots in the tropics, usually on mountains. *Drosera longifolia* is said to occur on one mountain in the Hawaiian Islands; the European *Luronium* (*Elisma*) *natans* has been collected in Java; *Scirpus setaceus* is known also from New Guinea; and *Sparganium simplex* has been found in Sumatra.

Discontinuous species of the tropical zone

The pan-tropical species which are, by the nature of the case, discontinuous, have already been dealt with, and there remain to be considered here those types of distribution which involve only parts of the warmer zone, and first to be dealt with are the several combinations among the three main sectors of the tropics.

A number of species have been noted as distributed over America and Africa and although it is, as with so many other categories of plant distribution, impossible to say exactly how far these plants are now native in one or other part of their area, there may be mentioned of them *Andira inermis*, *Dalbergia ecastophyllum*, *Drepanocarpus lunatus*, *Echinochloa crus-pavonis*, *Euclasta cordylotricha*, *Gossypium hirsutum*, *Hyparrhenia rufa*, *Hypogynium spathiflorum*, *Mucuna urens*, *Neurotheca loeselioides*, *Oplismenus hirtellus*, *Parinari excelsa*, *Paepalanthus lamarckii*, *Sauvagesia erecta*, *Sida linifolia*, *Symphonia globulifera* and *Tristachya chrysothrix*. *Eriocaulon bipetalum*, *Hibiscus diversifolius*, *Jussiaea erecta*, *Paratheria prostrata* and *Paullinia pinnata* are said to occur in the Madagascar region as well as on the two continents. Rather closely related to the foregoing are *Ludwigia palustris* found throughout America, Europe and Africa; *Hydrocotyle umbellata* of America, South Africa and the Madagascar region; and *Hydrocotyle verticillata* in America, South Africa and Hawaii.

A few species, among them *Arundinella hispida* and *Caesalpinia major*, occur in America and in Asia and the Pacific Islands, and in connection with these the reader may be reminded of one of the most remarkable of all discontinuous species, *Nertera depressa*, which is found in Central and South America, Hawaii, Tristan, Australia and New Zealand and south-east Asia and Malaysia.

Many species link Africa with Asia (and often the Pacific Islands) and the more widespread of these, such as *Dumasia villosa*, *Eragrostis aspera*, *Hibiscus lobatus*, *Hyptis lobata*, *Neyraudia madagascariensis*, *Sacciolepis curvata*, *Striga asiatica* and *Vahlia oldenlandioides*, relate closely to the wide species of the Old World tropics considered on p. 166. Among the species found in Africa and Asia only are *Abutilon pannosum*, *Albizzia lebbek*, *Asparagus racemosus*, *Canscora decussata*, *Gloriosa superba*, *Hibiscus micranthus*, *Mundulea sericea*, *Ormocarpum sennoides*, and *Phyllanthus reticulatus*. Some rather special cases are *Hypericum mysorense* from Socotra and India; *Trapa natans* in Europe, Africa and Asia; and *Sambucus adnata* in the East African mountains and in the Himalayan region. *Alectra arvensis*, *Apluda mutica* (also on Socotra), *Pipturus velutinus*, *Procris pedunculata*, *Thuarea involucrata*, *Tournefortia sarmentosa* and *Trichodesma indicum* occur in Asia and in the Madagascar region (but not on the African continent), while *Carex brunnea* is similar but extends to Australia and Hawaii.

In connection with Africa it may be noted that *Andropogon gayanum*, *Elyonurus royleanus* and *Panicum maximum* are said to link the Cape Verdes with the continent, and there are continental species which occur in other parts of Macaronesia, notably *Erica arborea*, which is found not only in eastern Tropical Africa but also in Madeira, the Canaries and the Mediterranean region.

Discontinuity on this smaller scale is, indeed, to be found everywhere, but it is, because of the mutual isolation of the land areas, perhaps most noticeable in, and best exemplified from, Asia and Malaysia, where the Asiatic-Australian montane flora in particular (529) affords many cases. Thus, *Melissa parviflora*, *Mosla dianthera*, *Neocinnamomum caudatum* and *Swertia bimaculata*, occur fairly widely on the Asiatic mainland and are also found in Sumatra. A number of species link India and the Himalayas with the Archipelago, among them *Alchemilla javanica*, *Craniotome versicolor*, *Hydrangea oblongifolia*, *Neillia thyrsiflora*, *Primula imperialis*, *Rhopalocnemis phalloides*, *Rubus lineatus*, *Schisandra elongata*, *Thalictrum javanicm* and *Valeriana hardwickii*, while others, including *Anotis wightiana*, *Damnacanthus indicus*, *Mitrastemon kawasasakii*, *Petrosavia sakuraii*, *Pirola japonica* and *Rubus niveus* link China and/or Japan with the Archipelago. At the other end of the axis *Trachymene saniculaefolia* is found on the mountains of Borneo and the Philippines and also in New South Wales.

Within Malaysia almost every possible kind of discontinuity is to be found and the proportionate relationships in this respect between the various constituent areas is a matter of great interest with regard to the history and population of the region, but it is too complex to be dealt with here and recourse must be made to the sources of information already cited on pp. 192, 193.

Discontinuity involving Australasia and the Pacific Islands again is naturally very varied, and it must suffice to illustrate it by the following random examples:

Stackhousia intermedia	Malayan Archipelago and Carolines.
Carex graeffeana	Philippines, Java, Fiji.
Alstonia plumosa	New Caledonia, Fiji, Samoa.
Cyathodes tameiameiae	Hawaii, Tahiti.
Gymnema stenophylla	Australia, Fiji.
Casuarina cunninghamii	Australia, New Caledonia.
Solanum aviculare	Philippines, New Guinea, Australia, New Zealand.

Didiscus procumbens	New Guinea, New Caledonia, Australia.
Geranium ardjunense	Malayan Archipelago, Australia, New Zealand.
Microlaena stipoides	Java, Philippines, Australia, New Zealand, Hawaii.
Gahnia gaudichaudii	New Zealand, Hawaii.
Carex uncinata	New Zealand, Chatham Islands, Hawaii.

Discontinuity in the southern extra-tropical regions

Because it has such a direct bearing on the history of the land masses of the southern hemisphere (263), this type of discontinuity is perhaps the most interesting and important of all, and has been studied by many plant geographers, notably by Skottsberg (498, 502, 504) and Oliver (403).

One of the commonest types of range is that between New Zealand and South America, as is shown by *Agrostis magellanica*, *Enargea marginata*, *Myosotis antarctica* and *Myosurus aristatus*. *Aristotelia peduncularis*, *Epilobium junceum*, *Lilaeopsis lineata*, *Selliera radicans* and probably *Tetragonia expansa* are discontinuous, among others, between Australia and New Zealand on the one hand and South America on the other. *Coriaria ruscifolia* is a notable species which is found not only in South America and New Zealand but also in the Kermadecs, Fiji, Samoa and Tahiti. *Oreomyrrhis andicola* occurs in Central and South America and from New Zealand and Australia to New Guinea and Borneo. *Lobelia anceps* is found in all three southern continents; *Papaver aculeatum* in South Africa and Australia; *Pelargonium acugnaticum* in South Africa and New Zealand.

On a rather smaller scale *Chevreulia stolonifera* is found on Tristan da Cunha and in South America; *Phylica nitida* on Tristan da Cunha and in South Africa; and *Oreobolus obtusangulus* has been reported from Juan Fernandez and the Falklands. In the Australasian region discontinuity on a smaller scale is also not uncommon and there are many species found in both Australia and New Zealand. *Disphyma australis* occurs in Australia, New Zealand and on the Chatham Islands; *Gaultheria depressa* in Tasmania and New Zealand, and *Acaena anserinifolia* in New Zealand, Tasmania and New Guinea. *Melicytus ramiflorus* ranges from New Zealand to Norfolk Island, the Kermadecs, Tonga and Fiji.

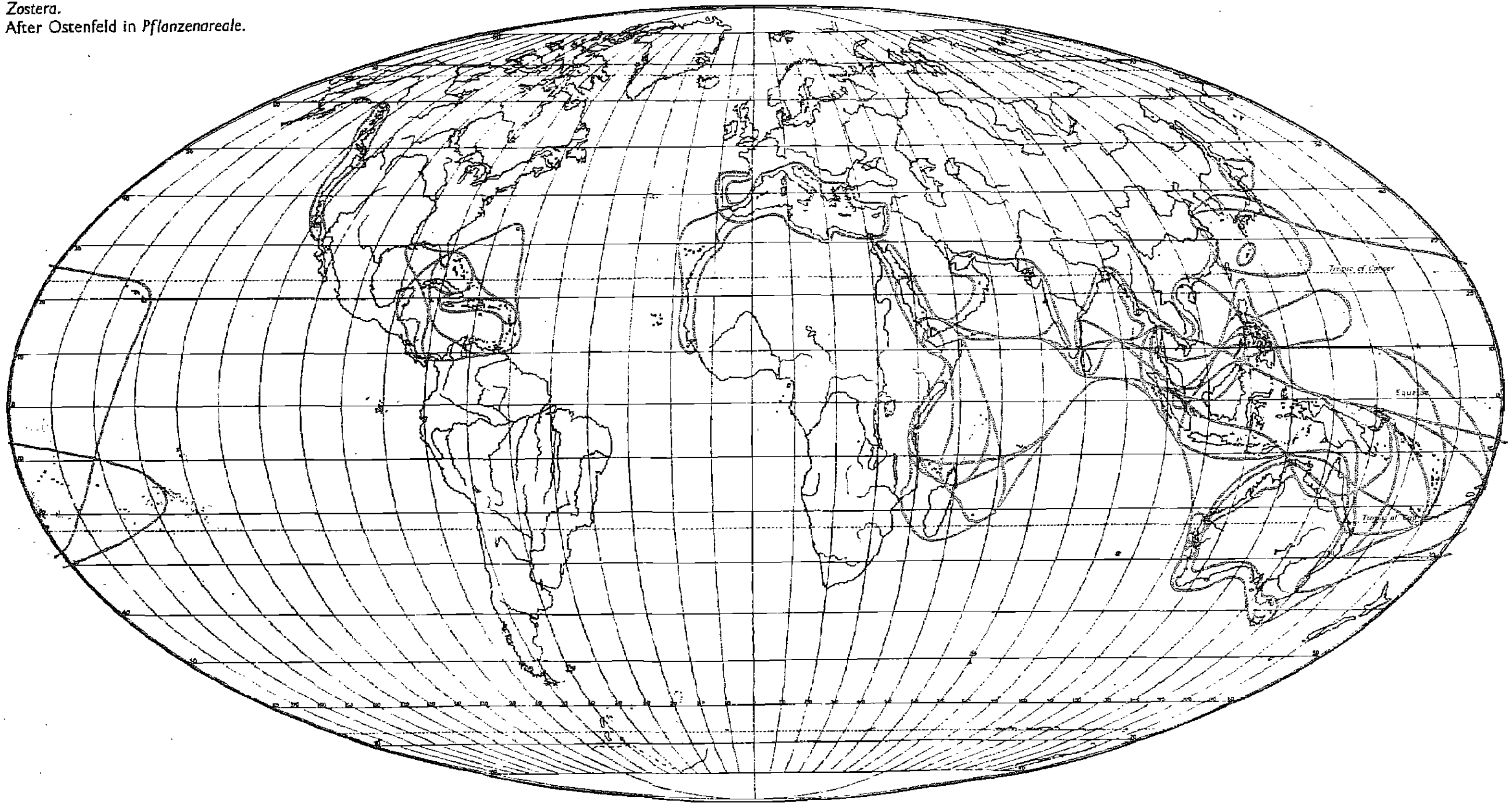
Discontinuity between the north and south temperate zones

This type of species distribution must be approached with great caution, because of the difficulty of saying, with any degree of certainty, that the occurrence of a northern plant in the south, and particularly in Australasia, is natural and not the result of accidental introduction in the course of human settlement. Quite frequently, for instance, such species have been recorded from Australia and New Zealand, but nearly always some suspicion attaches to their presence in these countries. Since it is manifestly impossible to consider all these cases critically here it is best to say as little as possible about them and to mention a few of the most authentic examples, referring the reader for any further details to papers by Du Rietz (146, 147) and Steffen (533) in which the whole subject of what are called bipolar distributions, and their possible explanations, are set out very fully.

Primula farinosa is one of the best examples, being fairly widely distributed in the northern temperate zone and occurring also in temperate South America (though in slightly different form), and others of the same sort, of which Steffen gives a useful list, are *Armeria vulgaris*, *Draba incana*, *Saxifraga magellanica*, *Gentiana prostrata* and several species of *Carex*, *Elatine americana* is reported from

Map of the World showing the distribution of the species of Marine Angiosperms, excluding the genus *Zostera*.
After Ostenfeld in *Pflanzenareale*.

PLATE 15



Areas correct. Distortion increasing towards border of map.
Approximate Scale 1:100,000,000 (1600 miles = 1 inch) along Equator
on Mollweide's Homolographic Projection

North America and from Australia and New Zealand, while *Epilobium tetragonum* is found in Europe and in the same two southern countries. *Ranunculus parviflorus* is said to occur in the southern United States, in the West Indies, in Europe, the Mediterranean region and the Canaries, as well as in Australia and New Zealand. Still other species generally regarded as discontinuous between some part of the north temperate and some part of Australasia include *Barbarea vulgaris*, *Geranium dissectum*, *Geum rivale* and *Geum urbanum*, but it is difficult to be sure that species of this sort have not been introduced in the south. Other rather different examples are *Lepturus cylindricus* in the Mediterranean and in South Africa; two or three species of *Anemone* are said to be discontinuous between the southern United States and temperate South America, and *Wahlenbergia gracilis*, which is found in India, New Caledonia, Australia and New Zealand. Finally the genus *Triglochin*, already briefly noticed on p. 109, is very remarkable in having no fewer than four species (156) which are, to a greater or lesser extent, discontinuous between the northern and southern hemispheres. These are the familiar northern species *T. maritima* and *T. palustris*, both of which are found in South America, *T. bulbosa* which is in the Mediterranean region and also in southern Africa, and, most remarkable of all, *T. striata*, which is found widely in North America, in Brazil and temperate South America, in Southern Africa and in Australia, Tasmania and New Zealand.

Two particular kinds of north-south discontinuity, although not so striking as any of the above and involving rather different problems are nevertheless of considerable interest. The first is the wide discontinuity of certain plants of arid regions, and three of the more notable here are *Aizoon canariense*, *Frankenia pulverulenta* and *Seetzenia prostrata*, all of which, while occurring fairly widely in the African-Indian desert region, and sometimes beyond it, are also recorded from South Africa. Rather similarly *Zygophyllum simplex* is recorded from the Cape Verdes, from East Africa to India, from the Aldabra Islands, and from South Africa. *Nitraria schoberi* is rather different in that its southern area is in south-eastern Australia.

The second kind of discontinuity is that between North American and temperate South America, which has been described by Bray (60), Campbell (84) and others. In the north the distribution is usually in the western states and Mexico but in the south it is more varied. The commonest condition is discontinuity between California and Chile-Argentina, of which *Calandrinia menziesii*, *Chorizanthe commissuralis*, *Gilia pusilla*, *Lastarriaca chilensis*, *Mentzelia albicans*, *Oxytheca dendroides* and *Prosopis juliflora*, have been quoted as examples. This kind of range presumably follows latitudinal movement along the mountainous western edge of the Americas and is of special interest in the demonstration it affords of the potential value of this route as a means of transtropical migration.

Vicarious Species or Species Pairs

In comparing the floras of two regions it is generally easy to see that certain species in one are perfectly distinct from any of the species in the other. Similarly, unless the floras are very different from one another there will generally be found some species that are common to both. In addition, however, to these well-marked differences and resemblances it will often be found that there are in the one flora certain species so closely similar to species in the other that it is difficult to say whether they should be regarded as identical or not. If the differences between them are very slight they will probably be considered no more than races or varieties of the same species, but if the differences are larger, they will generally be considered to be two distinct but closely related species. In these latter circumstances the two species are usually referred to as vicarious species or as a species pair. In each such pair one species is the geographical counterpart or representative of the other. Many such pairs are to be seen, for example, between the floras of North America and Eurasia. The American *Maianthemum canadense* represents there the Eurasian *M. bifolium*; *Epigaea repens* parallels *E. asiatica*; and there are instances in several other genera, including *Actaea* and *Scheuchzeria* (509). It is not however altogether easy to give an account of these pairs because their recognition depends so much on individual taxonomic conceptions. One authority may regard certain species of one region as identical with those of another, while a second may reckon them to form two distinct or vicarious species. In the northern hemisphere again the American form of *Hepatica triloba* is sometimes regarded as specifically distinct from the European plant and much the same is true of *Anemone quinquefolia* and *A. nemorosa*, *Oxalis montana* and *O. acetosella*, *Luzula saltuensis* and *L. pilosa*, *Vallisneria americana* and *V. spiralis*, *Ranunculus laxicaulis* and *R. flammula*, and *Scrophularia marilandica* and *S. nodosa*. The western European *Littorella uniflora* is sometimes regarded as distinct from the North American plant, and differences have been demonstrated between the representatives of the genus *Lysichitum* on either side of the Bering Strait. Nor need the isolation between the populations be a water one and there are pairs between the eastern and western sides of North America, such as *Carex misandroides* and *C. petricosa* and *Arenaria marcescens* and *A. obtusiloba* and the many instances quoted by Sharp in his study of the relationship between the floras of California and the South-eastern United States (485). Among Eurasian pairs are *Gentiana amarella*, in the west, and *G. acuta*, in the east, and this is a particularly interesting case because the latter species extends eastwards across the Bering Strait and right across temperate North America. Again, although we speak of pairs, there may be cases where more than two species are involved, as in one of the most notable of all, the *Chamaepericlymenum* section of the genus *Cornus*. This has been mapped by Regel (247) who claims that there are three species with the distributions shown in fig. 51. It will be seen that *C. suecica* and *C. unalaschkensis* are widely discontinuous, and that *C. suecica* and *C. canadensis* overlap in the Far East, in western America and in Greenland, *C. suecica*, it should be noted, has recently been reported by Kingdon-Ward from the mountains of Upper Burma (315).

But such pairs are by no means confined to the northern temperate regions. Skottsberg (500) mentions several between Java and Hawaii, including *Gahnia javanica* and *G. gaudichaudii*, and *Vaccinium varingiifolium* and *V. peleanum*. Similarly between Juan Fernandez and Hawaii there are pairs in *Cladium scorpoideum* and *C. angustifolium* and in *Plantago fernandezia* and *P. principis*. In the southern extra-tropical regions, too, there are interesting pairs. The New Zealand species *Donatia novae-zelandiae*, *Drosera stenophylla*, *Gaimardia setacea*, *Oxalis lactea* and *Pratia angulata* are represented in South America by *Donatia fascicularis*, *Drosera uniflora*, *Gaimardia australis*, *Oxalis magellanica* and *Pratia repens* respectively. Between New Zealand and Norfolk Island also there are pairs.

Still other miscellaneous examples are *Loudetia flammula* in tropical South America and *L. phragmitoides* in tropical Africa; *Ascolepis setigera* in West Africa and *A. gracilis* in south-east Asia; *Acacia sowdenii* and *A. loderi* (114) in South Australia, separated by the Flinders Range; the two sea-grasses, *Halophila decipiens* of the Indo-Pacific Ocean and *H. baillonis* of the Caribbean, and the various trans-equatorial instances in America such as *Allenrolfea occidentalis* in Western North

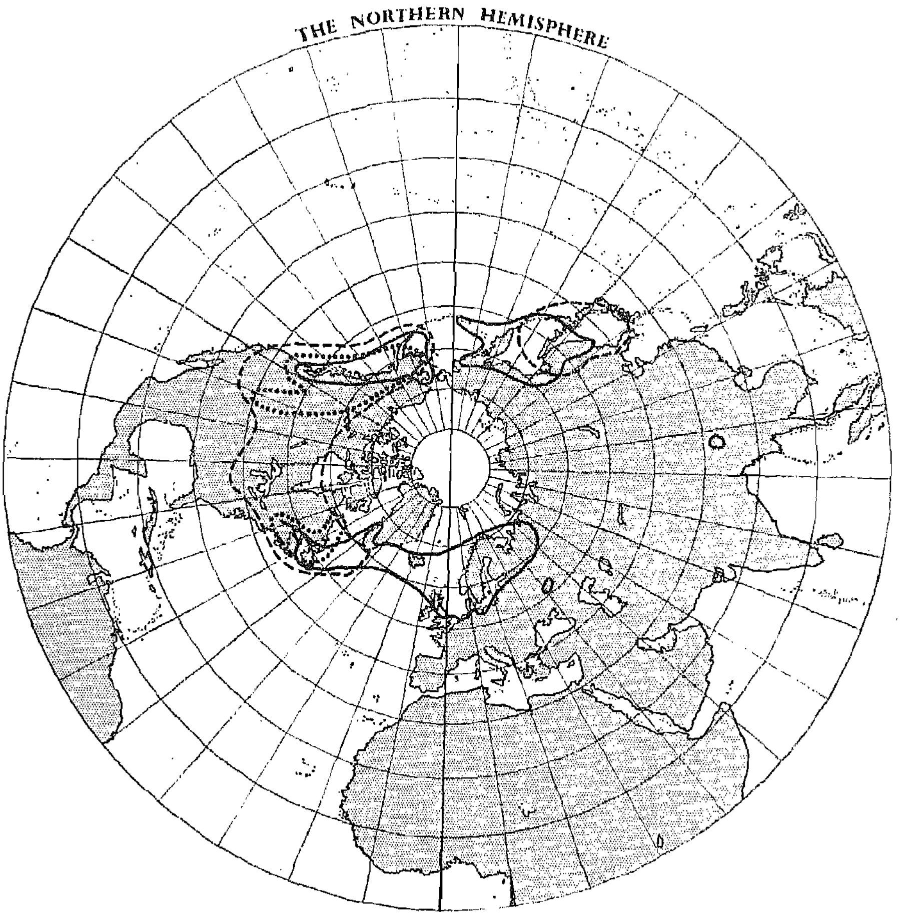


FIG. 51.—Map showing the distribution of the three closely allied species of the section *Chamaepericlymenum* of the genus *Cornus* i.e. *C. suecica,* continuous line (note the two outliers): *C. canadensis,* broken lines: *C. unalashkensis* dotted line. Mainly after Regel and Hultén.

America and *A. vaginata* and *A. patagonica* in temperate South America, or *Fagonia californica* and *F. chilensis.*

Simple or multiple vicariism of this kind is also commonly seen in connection with groups of islands. Skottsberg (506) has described several simple pairs between the two main islands of the Juan Fernandez group and even a case of three species on three different islands. He refers, too, to the palm genus *Pritchardia* in the Hawaiian Islands, which has thirty species distributed over eight islands, and here there is both water and land isolation, for the island of Oahu has nine species, each of which inhabits a separate valley. In some other genera of the Hawaiian flora also, such as *Viola* (see p. 152), much the same thing occurs. The genus *Scalesia* in the Galapagos Islands is another example (see p. 133).

The foregoing exemplify what may be called the classic conception of vicarious species, which is that they are, in the definition of Cain, who gives a useful survey of the subject (74), "allopatric species which have descended from a common ancestral population and attained at least spatial isolation," a definition which emphasises their essential and original interest namely that they are to be regarded as the incipient products of a divergent evolution in which geographical isolation has been an important factor, and hence that their frequency or otherwise may be used as some measure of the phyletic relationship between the floras involved. To-day however, the words vicarious and vicariism are applied much more loosely, and indeed to almost any binary species parallelism.

Thus Turrill (559) lists a number of species pairs between Spain and the Balkans, but some at least of these are species which, while representing one another in their respective floras, are not in fact of the closest relationship, and are rather the ecological counterparts of one another. For instance *Prunus lusitanica* in Spain is the counterpart of *P. laurocerasus* in the Balkans, and others are *Hypericum coris* and *H. empetrifolium*, and *Nonnea alba* and *N. ventricosa.*

Another kind of pair to which the word vicarious is scarcely applicable because the ranges of the two may be in part or wholly coterminous, is illustrated by those mentioned by Gates (193), among them *Clintonia borealis* and *C. umbellulata*, and *Ranunculus abortivus* and *R. allegheniensis*, in which the interest lies rather in the genetic relations between the pairs. Similar instances have recently been noted by Tutin (563) among the European grasses, in which one member of each pair is diploid and the other tetraploid.

Another particular kind of vicariism, which may be described as climatic, is illustrated very well by the two littoral species *Ipomoea pes-caprae* and *Calystegia soldanella.* The former is almost or quite pan-tropical, but the latter is more of less pan-temperate and the two meet at the Kermadecs and elsewhere in similar latitudes.

Then there is the widespread occurrence of ecological or edaphic vicariism in which, within the same general area two or more species are found in distinct types of habitat. One of the most familiar examples of this is afforded by the two "alpenrosen" of the Alps, *Rhododendron ferrugineum* and *R. hirsutum*, one of which occurs on granite rocks and the other on calcareous rocks, and there are other examples associated with the distribution of particular minerals such as is described in Chapter 17. In these cases there may be a good deal of real geographical segregation, on a small scale, but in others this may be scarcely discernible, as is to be seen in such pairs as *Lotus corniculatus* and *L. uliginosus* or in *Scrophularia nodosa* and *S. aquatica.* But in this direction the matter passes into the domain of plant ecology in the narrower sense and thus out of our province here.

Finally however there may be mentioned the occurrence in floras of pairs which seem to be duplicates of one another rather than substitutes or vicariants, as for instance *Reseda lutea* and *R. luteola* and *Drosera rotundifolia* and *D. longifolia.* It may be that this is no more than an expression of the laws of chance, but whatever the cause the result is sufficiently conspicuous to be worth mention.

Narrowly Restricted Species

It is inherent in the cycle of distribution described in Chapter 3 that an increase in the range of a species (or other unit) is usually associated with or accompanied by an increase in the number of individual plants comprising the unit and that the reverse is also true. A species is envisaged as increasing the number of its individuals up to a maximum and thereafter diminishing until none is left and extinction results. From this it follows that species which are either very young or very old will, for quite different reasons, consist of a comparatively limited number of individuals and that their ranges will be correspondingly small. This view has already been elaborated under the heading of endemism, but something more must be said about it here.

On this argument it is clear that species may in fact consist of any number of individuals, but it is equally obvious that there is a definite lower limit to the number because no species exists unless there is at least one individual of it. Thus the minimum range of a species is the area occupied by a single individual plant. The actual spatial value of this range will, of course, depend on the size and character of this individual.

It is not unnaturally almost impossible to maintain that any particular species does in fact consist of only one individual, but in some cases only one individual has ever been seen or recorded, probably the best known being that of *Franklinia alatamaha* (175) which has already received notice. Another is that of *Pharnaceum acidum* of St. Helena which in the time of Melliss (381) was known to survive only as one plant and which perhaps has entirely disappeared since. On a slightly different but clearly related point there is a good deal of evidence that species have actually become extinct. There are various plants of cultivation such as *Cryptostegia grandiflora* and *Delonix regia* of Madagascar and *Picrella trifoliata* of the West Indies which are no longer known in a wild state; three species of *Schizochlaena* are said (415) to have been collected once in Madagascar and not again, and Ridley (448) mentions several similar cases, such as *Didymocarpus perditus* and *Strophanthus maingayi* found, but never seen again, in Singapore, and several other species all or most of which seem to have been exterminated by modification or destruction of their only habitats. *Thismia rodwayi* (Tasmania) and *T. americana* (near Chicago) are also said to have been collected once only.

Since the one-individual condition is likely to persist, except perhaps in the case of true monocarpic annuals, longer if it comes about in the course of elimination than if it is the result of speciation there is a likelihood that such species will be species on the verge of extinction, and it is worth notice that there seems to be no instance in which a species first observed as a unique specimen has afterwards been observed to consist of many individuals clearly descended from the single ancestor. More often, as has been said, the original discovery has never been repeated.

It is therefore not difficult to believe that most of the examples just quoted at any rate were species in process of disappearance, but it is much more difficult to do this in what is probably the most extensive and puzzling of all such cases, some of the South African Stapeliads (585). Here, in these highly specialised genera, the number of species of which there is only one record is between one-third and one-half of the total, and a few of these are known only from single plants. Not only so but of 36 species discovered by one collector in the late eighteenth century, six have never been seen again, while others, by no means in the most remote districts, have only been rediscovered in late years. The actual status of some of these species, and especially whether they are hybrids, has yet to be decided but taking all the relevant circumstances into account it is difficult to resist the conclusion that they are young species and that such may persist exiguously for a considerable time. The case of *Notonerium gossei*, from the arid interior of South Australia, which has never again been seen since its discovery in 1873, may be a parallel and there are other Australasian species, too, which have been collected once only.

Passing from these extreme states of paucity and restriction to what may be called very local species, these can usefully be divided into three, those found in areas not much isolated geographically, those found on more or less isolated mountains, and those found on small islands. The first of these are most difficult to deal with here because the available information is seldom sufficiently exact and the following few instances must represent the category, namely *Shortia galacifolia*, *Neviusia alabamensis*, which is said to exist only as one small colony and *Caralluma winkleri*, which is described (585) as abundant over an area of a few acres, while others may be found in the flora of New Zealand (405). The work of Fernald and Marie Victorin on the floras of the shores of the Gulf of St. Lawrence (see Chapter 10) also includes references to a number of such plants, among them being *Cirsium mingaanense*, *Solidago victorinii*, *Solidago anticostensis* and several species of *Crataegus* and *Gentiana*.

Highly local montane species are more conspicuous and a number of good examples have been mentioned incidentally already, but a reminder may be given here of one or two which merit special comment. Willis (596) quotes the case of *Coleus elongatus*, which he says consists of a dozen or so plants on the mountain of Ritigala in Ceylon. This species is closely related to the more widespread *Coleus barbatus* which is also found on the mountain and there is an inference that it has been derived from it and that it is thus a good instance of a young species. Some of the isolated mountains in Malaysia and Australia, such as the Arfak Mts. in New Guinea (195) and Mt. Bellenden-Ker (194) in Queensland also have remarkable endemic species. Nor must the many peculiar facts about the tropical African mountains, described in Chapter 10 above, be forgotten. Finally of particular interest in this connection are some of the mountains in the south-eastern corner of Venezuela, such as Mt. Pacaraima, on which for instance there are three species of *Heliamphora*, and Mt. Roraima, which has a most remarkable flora including several endemic genera and many species, among them *Heliamphora nutans*. Mt. Itatiaya in south-eastern Brazil shows similar features.

Most familiar and prominent of all very narrow species are those from islands, because their bounds are so definitely and unmistakably laid down. It is perhaps this which gives rise to an impression that very restricted species are particularly associated with small islands but there seems no good evidence that this is so, and indeed some mainland species already noted are of almost the smallest possible area. There is of course the fact that species of small islands must, unless they can escape from it, be limited to its dimensions, but this is rather misleading because even the smallest islands with endemic species are much more extensive than the distributions of many continental species, and there is also the point that most islands with endemic species are not particularly isolated but are often the members of archipelagos where problems of dispersal between islands can scarcely be regarded as insuperable. There is also the question whether speciation, with its inevitable endemism, may not be favoured by narrowly insular conditions which are, of course, only one form of geographical isolation, but this is a question which is difficult to answer. It does, however, seem to be true that some comparatively small islands have numbers of endemic species greater than is usual for areas of similar size on continents, though the ranges of the individual species concerned are not themselves smaller. It also seems that certain families and genera already mentioned such as the Palmae and the genus *Cyrtandra* do seem to be specially characterised by the proportion of their species which occur on relatively small islands. Nor are these the only ones, and the genus *Weinmannia*, for instance, has among its species

W. camaguiensis from Camagui Island in the Philippines, *W. comoroensis* from Johanna Island in the Comoros, *W. vitiensis* and *W. spiraeoides*, each from one island in the Fiji group, *W. fraxinea* from Honimo Island in the Moluccas, *W. denhami* and *W. macgillivrayi* from a single island in the New Hebrides. Several comparable species of *Begonia* have already been mentioned in Chapter 8.

In fact practically all the more isolated small islands, even in archipelagos, except low coral atolls, have their own species, as for instance Christmas Island with sixteen endemics, and Easter Island with several, but there are many also on islands which are far from isolated, including *Cakile alacranensis* from the four islands of the Alacran Reef off Yucatan (391). In the Bahamas Taylor (549) has stressed the same thing, especially in the island of Inagua, which has no fewer than thirteen endemic species. Taking the archipelago as a whole also there are seven endemic species of *Agave*, four of them on one island only. *Coprosma* is another genus with some very narrow insular endemics and Oliver (404) includes two from the Kermadecs, one from Chatham Islands, two from Raiatau, and one each from Rarotonga, Pitcairn, Masatierra and the Tuamotus. Some of the tiny islands close to the shores of New Zealand, such as the Solanders, Herekopere and the Three Kings have endemic species (95), those of the last named including *Tecomanthe speciosa* and *Plectomirtha baylisiana* (407), both of which belong to families otherwise unrepresented in the flora of New Zealand. Rather similarly with regard to Norfolk Island three endemic species have been described from the closely adjacent Phillip Island (325). One of these, *Streblorrhiza speciosa*, which forms a monotypic genus, was among the species exterminated in early days by the importation of goats but which persisted in cultivation and is therefore in some ways comparable with *Franklinia*.

Still other examples of interest are *Maerua dupontii* from Aldabra Island, *Rapinia collina* from a tiny island off New Caledonia, *Aulacocarpus crassifolius* from Gorgona Island, *Rhipsalis megalantha* from San Sebastian Island near Rio de Janeiro, *Sesuvium distylium* and others from Fernando Noronha, *Campanula vidalii* from a rock in the Azores, *Dendrobium superbiens* from Thursday Island in the Torres Strait, *Latania loddigesii* and *Pandanus vandermeeschii* on three, and *Hyophorbe amaricaulis* on one, of the small islets just north of Mauritius.

Many of the species mentioned in the last few paragraphs may be described as very scarce and although it is not our purpose here to discuss the causes of rarity as such it is appropriate to draw the reader's attention to a paper by Griggs (233) in which many of the special features of these plants are commented upon with interesting suggestions.

The Distribution of the Marine Angiosperms, or "Sea Grasses"
(Plate 15)

There is one small group of flowering plants so different from all the rest in character and habitat that its geography merits very special attention in any general survey of plant distribution. This group consists of a small number of genera which live actually completely submerged in the shallow coastal waters of seas and which are popularly called the "sea grasses." The distribution of these plants has been described in detail by Ostenfeld in a number of papers, and the data have been collected together and illustrated by a series of maps (247). There are eight genera concerned, three of them, *Zostera*, *Phyllospadix* (fig. 52) and *Posidonia*, being found in temperate waters, and the rest in tropical seas.

FIG. 52.—*Phyllospadix scouleri*, about half natural size, after Engler.

The genus *Zostera* has been divided into eleven species distributed as follows:

Zostera marina . . .	northern temperate seas from the latitude of south-west Greenland almost to the tropics in eastern North America and East Asia (475).
Z. caespitosa . . .	Japan.
Z. asiatica	Japan and Korea.
Z. caulescens . . .	Japan and Korea.
Z. japonica	Japan and Sakhalin.
Z. nana	North Atlantic Europe.
Z. capensis	South Africa.
Z. capricorni . . .	Australia.
Z. muelleri	Australia.
Z. novazelandica . . .	New Zealand.
Z. tasmanica . . .	South Australia and (?) Tasmania.

Posidonia with two species shows great discontinuity, one species being Mediterranean and the other South Australian.

Phyllospadix has three species. Two of these overlap on the west coast of North America from California northwards, and one of them reaches to Alaska. The third species is on the Riukiu Islands on the opposite side of the Pacific.

The five tropical genera (fig. 53) comprise 23 species. It is unnecessary to describe their ranges in detail as these can be appreciated from the map (Plate 15), and it will be enough here to tabulate the leading points relating thereto which are not altogether apparent there. They are:

FIG. 53.—*Cymodocea ciliata*, a tropical marine Angiosperm, somewhat reduced, after Engler.

1. Only one species, *Thalassia testudinum*,[1] is in both the Old and New Worlds. It occurs in eastern America and in the Indian Ocean, so that even here there is complete oceanic segregation.
2. Seventeen out of the other 22 are found only in the Old World, a preponderance scarcely surprising in view of the immensely longer coast-lines there.

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[1] This is now often considered to consist of two species, one in each hemisphere, in which case there is no species common to both Old and New Worlds.

3. The other 5 species are all confined to America. All are east coast species and confined to the shores of the Caribbean, so that they have rather restricted ranges.

4. There is only a single species on the west coast of Africa, and this is a Mediterranean one which reaches down the coast to Senegambia.

5. Another species is confined to a very restricted part of Western Australia.

6. All the rest, 15 in number, inhabit the Indian and Pacific Oceans and divide into those which occur in East Africa and those which do not.

7. Of the 10 species which do so, 8 are found in some part of the Madagascar region.

8. Of the 5 non-African species, 3 reach from some part of Asia to Australasia or the Pacific Islands; one is found from Ceylon to Borneo; the other in the Riu-kiu Islands.

9. Of the 10 found in East Africa, 5 reach Asia, Australasia and the Pacific Islands; 3 reach Asia and Australia; one is discontinuous between Africa and Australia, and the last is confined to Africa and the Madagascar region.

Such are the more general features of the distribution of these plants, and much the most striking of them are the segregation in the hemispheres and the absence from the west coasts of the American and African continents. There are also the following minor features, which are partly shown on the map but which are more apparent in the original publications:

1. Of the 11 species which reach the Red Sea, 6 cover practically all of it; 3 cover only the southern half; and 2 only touch south-west Arabia or Aden.

2. Of 8 species in the Madagascar region, 5 occur only in the north of Madagascar; 2 in the north of Madagascar and on Mauritius; and one covers the Comoros and all Madagascar.

3. Of 6 species in India, 3 are only in Ceylon; 2 are only in Ceylon and south India; and one only is all round the coasts.

4. Of 13 species in Australia, 7 are confined to the north or north-east; 5 are local elsewhere, and only one is on all coasts.

5. Of 7 species in the Pacific Islands, 6 are restricted to the western groups; only one reaches further east, and there is none in Hawaii.

These latter points clearly reveal that, despite the differences in specific distributions, there are nevertheless certain prevalent range limits and the possible significance of these will be discussed later (p. 305). Meanwhile it may be said that the distribution of the sea-grasses in relation to water temperatures has been studied by Setchell (475), who divides the oceans into the following five latitudinal zones:—

Upper boreal	with a mean	maximum	temperature	of	0°–10° C.
Lower boreal	,,	,,	,,	,,	10°–15° C.
Temperate	,,	,,	,,	,,	15°–20° C.
Subtropical	,,	,,	,,	,,	20°–25° C.
Tropical	,,	,,	,,	,,	25° or more

He finds that of the 34 species under discussion, 18 are confined to the tropical zone, 8 to either the subtropical or temperate zones. Only *Zostera marina* is found in the boreal zone, and only one other species, *Halophila ovalis*, is found in more than two of the zones.

Mangroves
(Plate 16)

Mangrove forests are found in muddy tidal waters along much of the coasts of the tropics, and occasionally outside. The flora is a very specialised one, consisting of the mangroves proper, which are shrubs or trees belonging to about half a dozen genera, and a few associated species rarely or never found elsewhere. The number of species of mangroves and their most generally associated species is about thirty, and they are in general restricted to latitudes below 25°, though in places, as in Japan and the North Island of New Zealand, they reach much higher latitudes.

In many respects the distribution of the species is reminiscent of that of the marine Angiosperms, but as the following list shows, there are a number of other interesting points about them:

1. No species is at all completely distributed over the coasts of both hemispheres.
2. There is complete segregation between the species west of Africa and those to the east.
3. The species have been split somewhat recently, but *sensu latissime* there are only 4 in the New World, i.e. *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia nitida* which occur on both west and east coasts, and *Rhizophora racemosa*, which is only on the east coast. *R. racemosa* and *L. racemosa* occur also in West Africa, while *R. mangle* is found in the Pacific Islands.
4. Species of the East African coasts number about 8; 6 extend east to Australasia and the Pacific Islands; 1 to Malaysia (*Ceriops candolleana*); and the other, *Avicennia marina*, ranges from the Madagascar region to the Persian Gulf.
5. Of the rest no fewer than 7 range from India to some part of the Malayan Archipelago, and 3 from India to Australasia or the Pacific Islands. *Avicennia alba* and *A. sphaerocarpa* range from continental south-east Asia into Malaysia; *Sonneratia apetala* and *Avicennia lanata* are in continental south-east Asia only.
6. *Avicennia eucalyptifolia* ranges from Malaysia to Australia; *A. balanophora* is in Australia only; *A. resinifera* is in Australia and the Pacific Islands; and *A. tomentosa* is in the Malayan Archipelago.
7. No species occur in Hawaii or east of Samoa and Tonga.
8. The concentration of species in tropical Asia is more marked than in the marine Angiosperms, as the following tabulation into areas shows:

Western America	Eastern America	West Africa	East Africa	Madag.	India	S.E. Asia	Malaysia	Australia	Pacific Is.
2	4	3	8	9	18	23	23	10	12

The distribution of the mangroves thus follows in quite a number of ways that of the marine Angiosperms, and other points of resemblance could be noted did space permit. For instance, here again we find that nearly all the species in India are on the south coast or in Ceylon. Perhaps the main difference from the marine Angiosperms is the occurrence of species on both sides of the Atlantic and on both coasts of America.

The Distribution of Strand Plants

A number of flowering plants are found only on sea beaches or among the vegetation immediately associated with these beaches and such are generally referred to as littoral, or strand, plants. Some, such as *Cakile maritima*, *Calystegia soldanella* and *Salsola kali* are familiar inhabitants of temperate or even colder latitudes, but most are confined to the tropics, where they form a very characteristic and conspicuous feature of coastal vegetation, and it is to these in particular that the term "strand plants" is more narrowly applied.

It is not altogether easy to say what species properly compose this flora because there are many border-line cases especially with the mangroves, and for this reason no complete analysis of them is attempted here, but the number of species concerned is low and on most estimates is less than one hundred. The typical members show two particular features, buoyancy of seeds or fruits permitting their natural carriage by sea unharmed, and physiological specialisation enabling them to germinate and maintain themselves in close proximity to the sea, or to be more precise, where the sea is likely to have cast them, both these points being illustrated by the fact that the vegetation of low coral atolls is largely, and often entirely, composed of these plants (see p. 196).

For these reasons strand plants are of special interest to students of such subjects as plant dispersal and the historical development of tropical, and especially tropical insular, floras and it is mainly from these aspects that one of the most important accounts of them, that by Guppy (241), was written, This book deals with all manner of problems involving these plants and emphasises many points of great interest about them, as for instance the various structural conditions which may lead to buoyancy, the facts that Leguminosae are particularly conspicuous in the strand flora, that the strand flora of the Hawaiian Islands is notably meagre, that few strand plants are not somewhere or other found growing naturally inland, and that over much of the Pacific the spread of these plants seems to have been against the directions of the prevailing currents.

The distribution of tropical strand plants follows the same lines as that of the tropical marine Angiosperms and the mangroves, though it is rather more generalised than either, and the connection is strong with the latter plants, their main latitudinal limits being about the same (about 25° N. and S.) and the ecological distinction between them being indistinct. Some of the species occur apparently naturally on almost all tropical coasts wherever the substratum is suitable, among these being *Cassytha filiformis*, *Dodonaea viscosa*, *Hibiscus tiliaceus*, *Ipomoea pes-caprae* and *Thespesia populnea*. These species show little segregation between continents or between the opposite sides of continents, and this is also shown on a smaller scale by *Dalbergia ecastophyllum* and *Drepanocarpus lunatus*, which occur on both sides of the Atlantic, and by *Batis maritima* and *Hippomane mancinella*, which are found on both coasts of tropical America.

The majority of strand plants however, including some of the best-known, do not occur in the Atlantic, and it is the Indian and west Pacific Oceans which are especially the home of these plants (57, 462). These wide Old World species include *Barringtonia speciosa*, *Calophyllum inophyllum*, *Casuarina equisetifolia*, *Cordia subcordata*, *Guettarda speciosa*, *Pemphis acidula*, *Pongamia glabra*, *Scaevola koenigii* and *Tournefortia argentea*, and Merrill has given a useful survey of them (358). Some of these, including the first-named, reach far across the Pacific, but there is none on Juan Fernandez or the Galapagos.

Two groups of species with rather lesser ranges are those which are characteristically Asiatic, though often extending thence eastward, as *Crinum asiaticum*, *Samadera indica* and *Triumfetta subpalmata*, and the rather few distinctively New World species most of which are on the east side of America, and which include *Coccolobis uvifera*, *Euphorbia buxifolia* and *Omphalea triandra*. A few species which may perhaps claim mention here, notably *Nipa fruticans*, are even more local (see fig. 66).

CHAPTER 12

THE HISTORY AND DISTRIBUTION OF THE BRITISH FLORA

THE fossil history of the Angiosperms, which is described at some length in Chapter 14, shows clearly enough that the floras of to-day can be understood properly only if the past is also taken into account, and so, in discussing the distribution of the plants living in the British Isles to-day, due notice must be taken of their history. Much of this history is, however, so remote in time that it does not directly concern the actual species which now compose the flora, and it will be sufficient here to trace the story of these plants particularly from the time at which they became inhabitants of Britain. Fortunately this story of the British flora, that is to say of the assemblage of species which now forms the vegetation of the British Isles, starts at a definite point in geological time, beyond which it is not necessary to probe.

As will be seen in Chapter 14, the vegetation of the northern temperate latitudes remained more or less constant, presumably under the influence of equally constant climatic conditions, throughout the Cretaceous and most of the Tertiary epochs, but in the Pliocene period there began a rapid deterioration of climate, accompanied by marked floristic changes, and this deterioration culminated in the Ice Ages of the Pleistocene period. It so happens that one of the last stages before the oncoming of the ice, namely the Upper (later) Pliocene, has, in the British Isles, left behind it remains so clear that they give a good picture of the contemporary plant life. These remains are the fossils of the Cromer Forest bed and their outstanding feature is that they are almost the same species that are living in Norfolk to-day. It is possible to say, therefore, with some confidence that at the close of the Pliocene the flora of Britain was very much as it is to-day and that its subsequent history is that of the vicissitudes through which it has passed since that time.

The Cromer Forest bed contains remains not only of plants but also of animals, and these latter are in many ways the more striking. For instance, there have been described from among them no fewer than forty-six species of mammals, including such types as elephant, hippopotamus, rhinoceros, musk ox, glutton and a number of deer. Thirty of these were large animals and of these only six are known anywhere to-day, the remainder having become extinct, while of these six only three now inhabit the British Isles. It is, however, only in the mammals that there is any conspicuous difference between the past and present; the other vertebrates in the deposit are all species now living in the country, and the same is virtually true of the molluscs. Similarly with the plants, of which sixty-eight species have been identified, only some half-dozen, including *Trapa natans*, *Ranunculus nemorosus*, *Hypecoum procumbens*, *Najas minor* and an extinct species of *Corema*, are no longer to be found here. All the rest are species still familiar to British botanists, and these give ample evidence that the flora as a whole must have been very similar to that existing to-day (442).

What has been said about the mammals does not invalidate the comparison, because their disappearance can be explained by the difference in the distribution of land and sea as between the past and present. There are good reasons for believing that in Pliocene times Britain was part of the continent, joined to what is

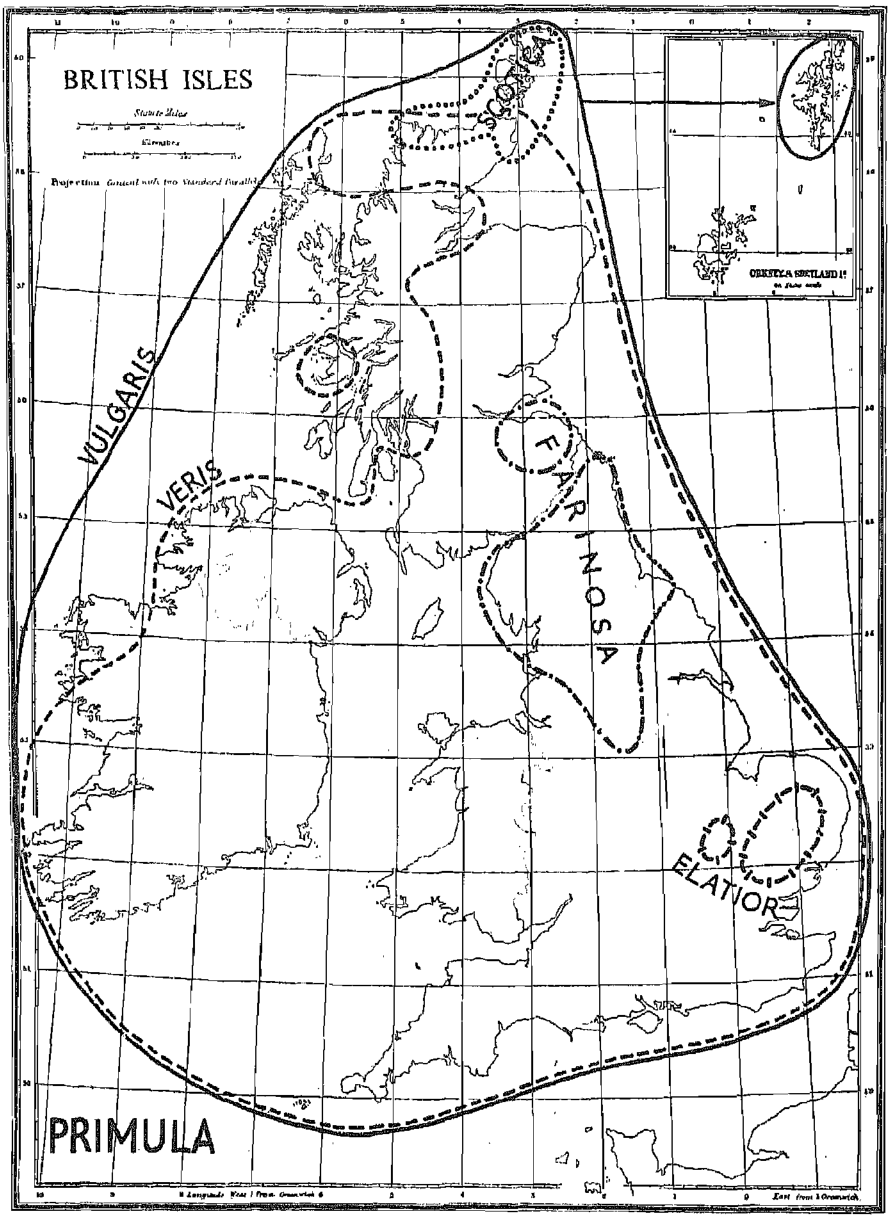

FIG. 54.—Map showing the distribution of the species of *Primula* in the British Isles.

now western Europe across the southern part of the North Sea, and that across this now water-covered area there flowed a greater and longer river Rhine of which in all probability the Thames was a western tributary. With the coming of the ice in the Pleistocene, the drainage of this great river to the north was dammed and the confined water escaped by cutting through what is now the Straits of Dover, thus completely severing Britain from the mainland. It is also supposed that at some later date this strait was again obliterated owing to the elevation of the land in relation to the sea, and that only comparatively recently, perhaps about 8,000 years ago (613), has the sea once more broken through to give Britain its insularity. That eastern England was indeed at one time part of the basin of the Rhine is supported by the observations of Stomps (537), who finds that some of the plants especially characteristic of East Anglia are equally characteristic of those parts of the continent which presumably formed part of the east side of the basin of this ancient Rhine. But, whatever the details, it is indisputable that considerable geographical changes have taken place, and the extinction of so many large mammals may be connected with this.

To return to the plants, what is said in Chapter 14 about the glaciations of the Pleistocene points strongly to the fact that, however much the Cromer Forest plants may resemble the present flora, it is impossible to imagine this similarity as due to the persistence of the flora unchanged ever since Pliocene times. During the maximum glaciation, for example, Britain suffered intense ice action, and there is little doubt that most of it, except the extreme southern part, was covered either by ice-caps or glaciers. In addition, there were other less severe glaciations and it seems clear that during some period of the Pleistocene a portion at least of the pre-glacial flora must have been driven south beyond the confines of the country, and hence that its presence here now must be due to subsequent reimmigration. This broad statement admits of little argument. What is uncertain is the extent to which the early flora was affected in this way, and in particular the proportion of it which was thus destroyed or driven out. On this question there is much controversy and the opposing points of view (603) must be considered with some care.

The problem really turns on two points, first, that of the real extent to which the country was glaciated, and second, the value as indications of climatic conditions of certain plant remains dating from the time of glaciation.

There is at the outset a difficulty in determining the actual extent of the ice at its maximum in that it is not easy to assign a limit to the effect of ice action. The limit of the ice as laid down in most geological accounts is a line joining the Thames and the Severn and passing south of Ireland and it is presumed that north of this line the ice was more or less continuous. But if this was the edge of continuous ice, it seems certain that much of the country further south must have contained numerous glaciers, and the size and number of these would obviously be of great importance. The thickness of glacial deposits but a little north of the Thames suggests that they must have been very extensive, and if so, then the effective limit of ice action must have been considerably further south. It is true that in general there are no glacial deposits in south England, but it is also to be noted that latterly the occurrence of something of the sort (in one case an actual boulder clay) has been recorded not only from the north coast of Devon (131) but even from the Scillies (34). Another deposit of southern England, the Coombe rock, is also believed by some to owe its origin in part to glacial conditions. All these remains, however, are slight and it may be accepted that south England was never covered by an ice-cap, although it may have been the site of numerous glaciers. This is the usual state of affairs on the margin of an extensive ice-sheet, as is seen in Greenland to-day (481), where near the coasts the marginal thinnings of the ice, together with the relief of the land, leads to a fringe of glaciers among and between which emerge the unglaciated summits known as "nunataks."

The theory that there were such nunataks not only in southern England but also further north, and that some of the flora found on them refuges in which it was able to survive the effects of the ice, has received considerable attention. Certainly there are considerable areas even in north England which, it is claimed, have never been covered with ice. One such large area is in the southern Pennines, and another is in Upper Teesdale. Many of these nunataks, it has been pointed out, are to-day remarkable for the number of rare plants to be found on them. Upper Teesdale, for instance, has several plants which are to be found practically nowhere else in Britain, and some of the British endemic forms (see below) are also restricted to such areas.

The possibility of the survival of members of the pre-glacial flora on unglaciated areas has been discussed with special reference to Great Britain by many geologists and botanists including Blackburn (54) and Raistrick (433), but the theory originated in connection with the investigations of Fernald and others into the flora of the shores of the Gulf of St. Lawrence in eastern North America (see Chapter 8). There occur here in certain places many peculiar species and forms often quite foreign to the region in general and most closely related to other species to be found many hundreds of miles away, and this has been explained on the view that they are ancient types which have persisted for hundreds of years, and throughout at least part of the glacial period, on the unglaciated regions. The theory is an attractive one, and that it is true to some degree can hardly be disproved, but it is only fair to say that both in North America and Britain the facts can be explained otherwise. In the former, Marie Victorin (364) believes, for instance, that the observed facts may be the result of divergent migration from one more northerly centre. In Britain it has been suggested that the rare and local plants mentioned above are to be regarded not as ancient survivors but as recent arrivals in their respective habitats. There is also another great objection to the theory of nunatak survival, namely, that if these unglaciated spots were, during the ice ages, peculiarly suitable for the plants concerned, they would almost certainly not be so now, and there seems no reason why they should still be restricted to them when the general conditions of the region have so materially altered. A somewhat similar opinion has been expressed by Deevey (126) in a stimulating new discussion of the nunatak theory.

Another argument used in favour of the view that a considerable proportion of the pre-glacial flora may have survived the glaciations is that to-day warmth-loving plants are often found growing in close proximity to glaciers. Hooker in his *Himalayan Journal* pointed out that the direct distance between the perpetual snows of these mountains and the tropical flora at their base was only about six miles, and more recently attention has been drawn to the occurrence in New Zealand of tree ferns equally near or even nearer to glaciers. These facts are undoubtedly striking, but they afford little indication of conditions in Britain during the Pleistocene. In both cases the ice concerned is the ice of mountain glacier systems and not the ice of continuous ice-sheets centred near the pole, and the difference is fundamental. The ice is present because of the elevation of the land and not because of the refrigeration at sea level of the whole latitudinal zone in which it is found, and on this account its influence on the climate is extremely local. Not only are polar ice-caps much more extensive but their very presence and persistence indicates minimum climatic values over wide areas, and their effects are felt far beyond their bound-

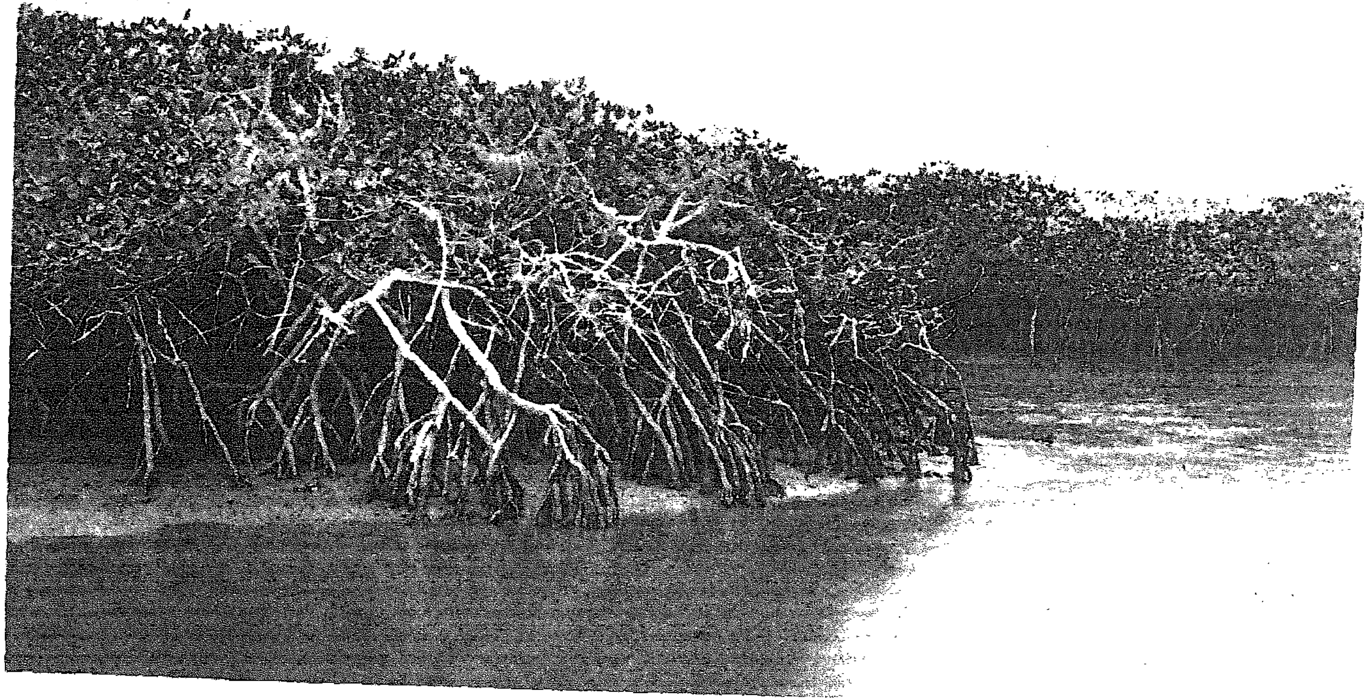

Plate 16. Mangrove vegetation on the coast of Lower California

(*from Karsten & Schenck, Vegetationsbilder*)

aries. To-day there is probably only one part of the world where conditions are at all parallel to those which must have existed in Britain during the Pleistocene. This is Greenland, which can, as a result, support only an arctic flora composed of cold-resistant types. There are neither tropical nor even warm temperate species within hundreds of miles of its shores. On this analogy, at any rate, it is difficult to believe that, if the conditions in Britain during the ice ages were as they have been pictured, the flora can have been anything more than an arctic flora with perhaps an ingredient of a few particularly hardy species of a more temperate character. At the same time it is to be remembered that southern England is at a much lower latitude than Greenland so that, as long as the pole remained in its present position, conditions would tend to be less rigorous, especially in summer, even if it was covered with ice to a comparable degree.

Let us now turn to the actual remains of the vegetation of the Pleistocene in this country. Unfortunately these are not very considerable, but there are some at least, and they have been the subject of much argument. This centres chiefly round certain so-called "arctic beds" the remains of which have been described from such different parts of England as East Yorkshire, East Anglia, Cambridgeshire (89), the Lea Valley (441), South Devon and the Isle of Wight. From these deposits there have been identified various plants which to-day are associated with arctic floras, such as some of the smaller willows, *Betula nana*, *Oxyria digyna*, *Arctostaphylos* and *Ranunculus hyperboreus*, and it has been argued that the presence of these species indicates arctic conditions at the time and place of their deposition, and as a corollary that plants of less arctic character must have had a home much further south. At first sight this seems a reasonable suggestion, but closer investigation reveals difficulties. According to Wilmott (600) the species mentioned are generally accompanied by others which are certainly not arctic in type, such as species of *Silene* and *Linum* in the Lea Valley flora, and in addition he regards some of the identifications as far from satisfactory. Indeed, if the total remains in these various beds are considered without special emphasis on particular species, their arctic character is open to doubt.

This point has been developed recently by Godwin (205) in an attempt to reconcile some of the opposing views regarding the nunatak theory. He claims that in one of these beds at least (the Lea Valley) the flora contains three categories of species—arctic-alpines such as *Dryas* and *Betula nana*; aquatic and marsh plants such as *Potamogeton* and *Filipendula ulmaria*; and various species, most or all of which are now generally regarded as weeds or at least species of disturbed ground, and he draws attention to the circumstance that these three types do in fact occur together to-day in Northern Scandinavia, under particular conditions which much be very similar to those of England during the Pleistocene. He suggests that the retreat of the ice laid bare areas which became colonised by this flora, but that in due course it became itself smothered almost to extinction by the later-spreading forest, so that many of its representatives occur in England to-day only in the artificially bared areas produced by man which are the nearest existing approach to their earlier habitats. On this argument Godwin suggests that the British areas referred to as nunataks served, not as pre-glacial refuges, but only as pre-forest period refuges in which these species were able to maintain a precarious hold until such time as they could spread into the later newly man-made habitats.

Nor are all the floras of the Pleistocene of the same character. In West Sussex, for instance, plants like oak, elder, dogwood and a now exotic maple have been recorded, showing that at some stage of the Pleistocene, presumably during the

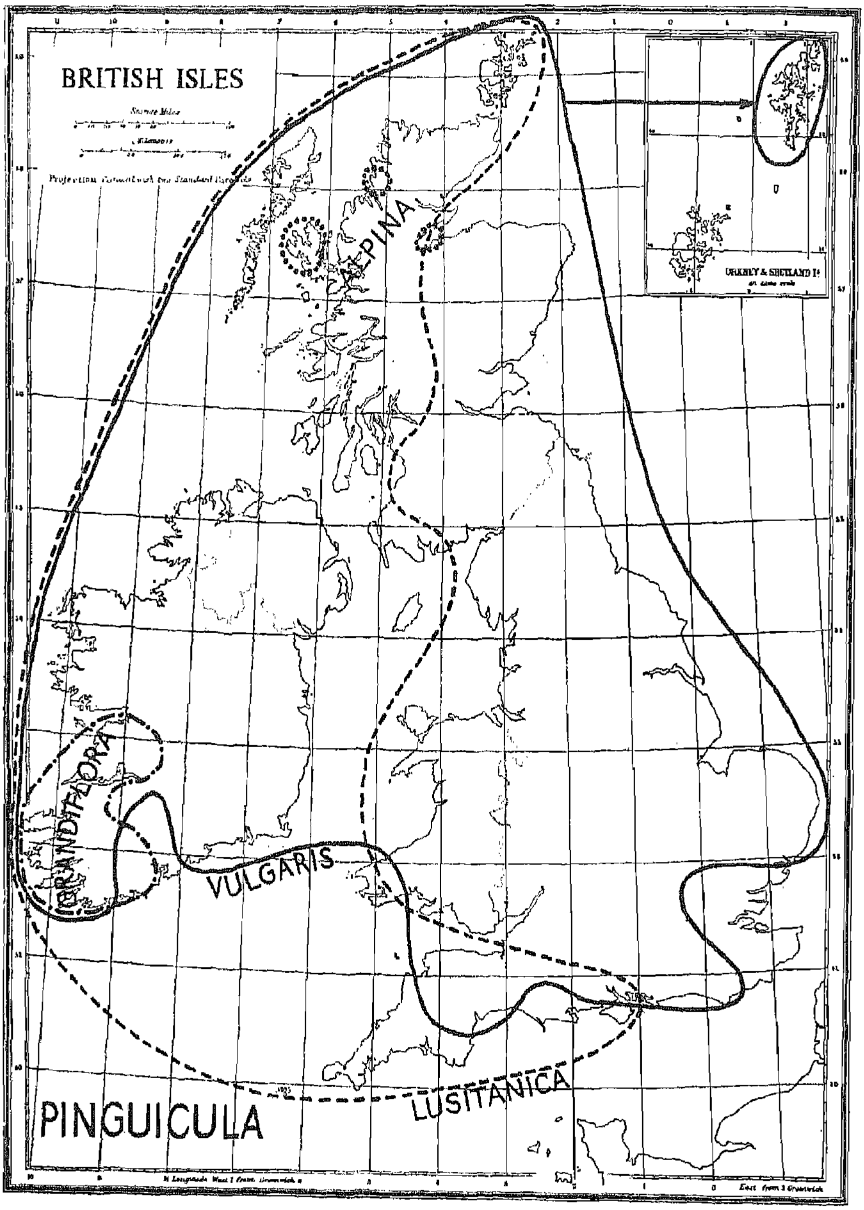

FIG. 55.—Map showing the distribution of the species of *Pinguicula* in the British Isles. It is doubtful whether *P. alpina* still occurs in any of its three areas.

inter-glacial period that followed the maximum glaciation, quite a temperate flora existed at least in the south of the country.

In short there seems no direct evidence by which the proportion of the pre-glacial flora which was able to persist unharmed in this country during the ice ages can be determined, and it is not surprising that there is a good deal of difference of opinion. Wilmott (603) some years ago expressed the view that in the main the present flora consists either of boreal and montane plants which would scarcely be affected by ice or of common central European plants which in his opinion might have survived south of the Thames, and other botanists have taken up much the same belief. On the other hand, Salisbury (603), Reid (439) and others believe that only the arctic and boreal types can have survived.

Both these views really concern only the commoner and more generally distributed British plants. As will be seen later, there are many species in the flora which are confined even to-day to the warmest and most southerly parts of the country, and there is no suggestion that these can have survived glaciation *in situ*. The statement that the British flora is to be regarded as essentially an immigrant or rather re-immigrant one is therefore certainly true in some measure. The difficulty is to determine exactly what that measure is.

The history of the flora *since* the latest glaciation is much better known, thanks to the results obtained from a careful study of the plant remains in post-glacial deposits, and particularly in peat, where the methods of pollen analysis (72, 203, 206) especially have proved of great value.

Woodhead (604) was one of the first to bring together in a single account much of the very scattered evidence concerning the course of events in the southern Pennines, and showed clearly that the sequence of deposits and events was very much like that described in Chapter 14 for Scandinavia. Immediately above the actual glacial horizons are the remains of a flora definitely arctic in character. This is followed by a sub-arctic late-glacial flora in which birch and pine occurred. Then comes a more temperate forest flora composed mainly of deciduous trees, and this in turn is succeeded by a thick deposit of peat indicating a climatic change from drier to more moist. Lastly there are indications of a cessation of peat formation and a return to forest conditions, and most recently of all, some recrudescence of peat formation which brings the record almost to the present day. This at any rate was the general outline for the Pennines, and later and more widespread investigations showed that the same sequence applies, with certain modifications, to the British Isles as a whole, and a useful summary of the subject is given (together with a wealth of other information concerning the British flora) by Tansley (542). For more recent discussion of a rapidly developing subject reference may be made to Zeuner (613) and from these together with certain other sources the table shown on p. 228, which is sufficiently detailed but not too complex for our present purpose, has been constructed.

The sequence of conditions shows, as is only to be expected, a series of increasingly temperate floras following the most recent retreat of the ice, and on the whole this gradual amelioration is unbroken except for the occurrence of a suggested climatic optimum (post-glacial optimum) somewhere at the end of the boreal period. This gradual amelioration is in itself evidence that the immigration and re-immigration of species into the country must also have been gradual, and the relatively great changes which were clearly necessary to re-establish the flora in the condition in which it existed before the ice ages is sufficient demonstration of the effects of the glaciation upon the plant life.

THE SEQUENCE OF POST-GLACIAL CHANGES IN SOUTHERN BRITAIN

Period	*Date*		*Climate*	*Vegetation*
	1950 A.D.			
Sub-atlantic			cooler, more oceanic, younger peat formation.	mixed oak forest contracting—beech, hornbeam, birch in fair amount.
	500 B.C.			
Sub-boreal			drier, more continental, peat formation checked.	mixed oak forest and alder, beech and hornbeam spreading.
	2500 B.C.			
Atlantic	? climatic optimum.		oceanic, humid, mild, peat formation.	mixed oak-alder forest with lime.
	6500 B.C.			
Boreal			continental, dry, warm.	pine and hazel, mixed oak forest spreading.
	7000 B.C.			
Pre-boreal			increasingly warm.	birch and pine.
Late-glacial	8000 B.C.	Dryas II	cold.	tundra.
	10000 B.C.	Alleröd oscillation.	temporary warmth.	birch and pine.
	15000 B.C.	Dryas I.	cold.	tundra.
Glacial				

But the building up of the present British flora has not been conditioned by climate alone. For several thousands of years now the country has supported an ever increasing human population, and a proportion of the flora certainly owes its presence to the intentional or accidental influences of human beings. Each of the human waves of invasion which constitute so much of British history has brought with it plants long associated with its peoples in their earlier homes, and each phase of history is reflected in the flora.

From the point of view of its influence on the natural vegetation the history of Britain may be divided into five periods, each of which has had its own effect on the plant life. For many centuries following man's first appearance on our shores the land was inhabited by a succession of relatively primitive communities which were able to make but little headway and impression against the forces of nature. Even agriculture, when it came to be practised at all, was practised on a very simple and restricted scale, and was almost certainly of necessity confined to the more accessible and amenable parts of the country like the chalk and limestones, where little natural vegetation had to be cleared to make way for it, and where on the other hand its effect on the general plant life was least.

This continued until, with the coming of the Romans shortly after the beginning of the present era, the second period began. The Roman occupation lasted for roughly 400 years, and there is no doubt that during that time the internal organisation of the country was raised to a level which it did not again reach for more than a thousand years.

The effect on the vegetation must have been profound, for the Romans brought with them or developed later the tools and technical knowledge which made it possible for them to subdue their environment almost completely. Forest clearance began; swamps were drained; roads were built; and indeed nearly all the activities calculated to modify the natural vegetation were in progress. Agriculture, too, was far more extensively and variedly carried on than before. It is difficult to visualise the condition to which all this must have brought the country eventually, but there is reason to believe that in the south of England, at any rate, the zenith of the Roman period, reached in the third and fourth centuries of our era, must have revealed a countryside not widely different from that of two or three hundred years ago.

Unfortunately for history, but perhaps fortunately for the flora, this standard was not maintained. The waning of the imperial power eventually necessitated the withdrawal of all the legions from Britain. With them went the hope of safety, and from that time the country sank under the plundering of its enemies into a state of collapse and chaos, during which it seems that the work of the Romans was virtually destroyed. Cities disappeared; drainage failed, and cultivated land degenerated into grassland, thicket and woodland.

This relapse continued, with no doubt some slow improvement, for a very long time. Not until the Norman period was there even any real political stability, and as far as the vegetation was concerned it can hardly have altered much again until the feudal system which the Normans established gave place, in the course of time, to the manorial system. This was based at least in part on agriculture, and as it became firmly established the vegetation must once more have undergone a slow but steady modification. Whether this was as marked as it had been in the Roman period is doubtful, but it was almost certainly more widespread, and it was probably now for the first time that some of the remoter parts of the country felt the real impress of man and his works.

Although the gradual growth of the population and the development of the country accelerated as time went on, there was no essential alteration that affected the vegetation until the middle of the eighteenth century. Up to that time Britain remained a purely agricultural country.

But about 1750 there was ushered in the period which was destined to see a greater revolution in almost every sphere than any that had gone before it—the age of industrialism and urbanism. Within a space of less than 200 years miles of what was hitherto largely fair and untouched country has become covered, to the utter exclusion of natural vegetation, with the products and achievements of man's hands and brain. The process still goes on. Every year more and more of the country disappears under the insatiable demands of the town and factory, and only in the last decade or two has there been any real indication that a long slumbering public conscience will at last awake and demand a cessation of what is partly senseless and unnecessary destruction.

This latest period is from the plant point of view unlike the rest in that it has been most entirely destructive. In earlier times what loss there may have been among native plants was probably more than balanced by the introduction of new species, but with industrialism there has been little such compensation except perhaps for a few garden plants which have established themselves among the wild ones. Modern farming does not encourage the weeds which, while a bane to the farmer, are often a joy to the botanist, and in addition there are the depredations of the plant collector who, it may or may not be significant to note, seems to have multiplied with the growth of industrialism.

An interesting attempt has been made to assess the changes which have taken

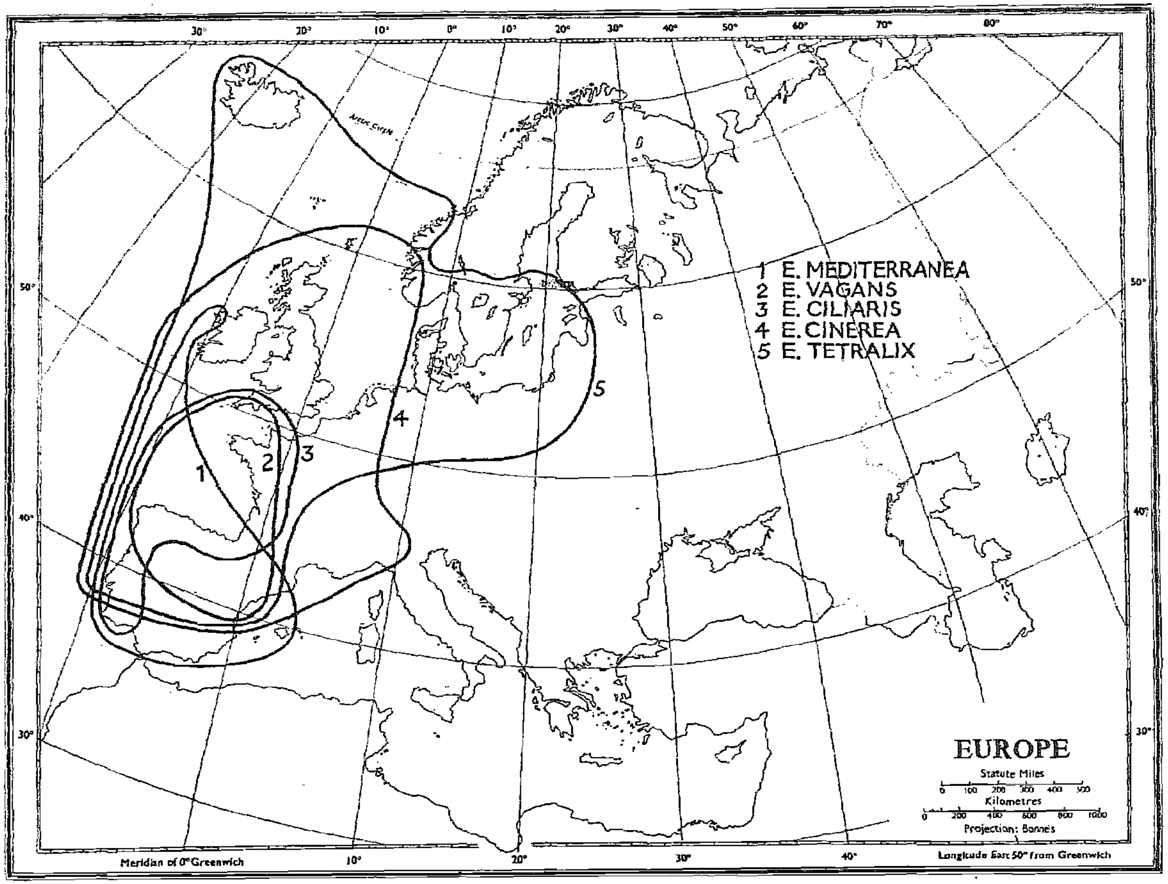

FIG. 56.—Map showing the distribution of the British species of *Erica* in Western Europe.

place in the British flora in the last fifty years (601) and from it, it would seem that while several species have become extinct more have been discovered by intensive study or collecting, so that the total number is slightly on the increase, and this is borne out by a rather earlier estimate (139) which suggests that less than a dozen species have become extinct since 1597. Nevertheless, it seems certain that many of the favourite wild plants are far less abundant than previously and are at least in danger of ultimate extinction, not by the processes of unaided nature but by the thoughtless or deliberate actions of their admirers.

Such is the story of the development of the British flora down to the present day. Its long and eventful history has been told in outline, and we have seen that it is now an assemblage of species moulded and modified in many different ways and by many different events and processes. This assemblage and the way in which it is distributed within the country must now be discussed.

The scientific study of the distribution of British plants may be said to date from the work and writings of Hewett Cottrell Watson, who devoted a long and active life to it. Certain earlier writers had touched upon the subject, but their writings were merely lists of the localities of some of the rarer species designed primarily for the convenience of collectors. Watson's first two works (574, 575) appeared in 1832 and 1835 respectively, but it was between the years 1847 and 1859 that there appeared his great four-volume work the *Cybele Britannica* (576), in which were brought together all the known facts concerning the geography of the species comprising the British flora. In the *Cybele* Watson analysed and arranged the British plants according to several methods which have ever since remained the basis for the geographical study of British plants, and they may therefore be properly considered here at some length.

He dealt first with the actual ranges of the species in Great Britain by dividing the region up into eighteen provinces and noting in which of them each plant occurred. The provinces were based chiefly on major topographical features and were:

1. Peninsula
2. Channel
3. Thames
4. Ouse
5. Severn
6. South Wales
7. North Wales
8. Trent
9 Mersey
10. Humber
11. Tyne
12. Lakes
13. West Lowlands
14. East Lowlands
15. East Highlands
16. West Highlands
17. North Highlands
18. North Isles

The actual limitation of the provinces was chiefly by counties.

Next he classified the species according to the altitude at which they grow, recognising and characterising six zones:

Super-arctic	*Salix herbacea* without *Calluna*.
Mid-arctic	*Calluna* without *Erica*.
Infer-arctic	*Erica tetralix* without *Pteridium*.
Super-agrarian	*Pteridium* without *Rhamnus*, etc.
Mid-agrarian	*Rhamnus* without *Clematis*, etc.
Infer-agrarian	*Clematis*, etc.

The arctic region was that above the limits of cultivation and the agrarian region the lower agricultural levels. This altitudinal classification although of considerable interest was not on the whole very satisfactory because of the innumerable complicating factors. It is still occasionally referred to, but is the one part of Watson's work which has virtually become obsolete.

A third classification is perhaps the most important of all, and marked a very definite step forward in the geographical conception of the British flora. This was the recognition of seven types according to the generalised distribution of the species within Great Britain (figs. 54, 55). Actually Watson had referred to such types in one of his earlier books, but here in the *Cybele* they were described in more definite fashion as:

1. British type	Plants occurring in all or nearly all the provinces of both England and Scotland.
2. English type	Plants predominantly English in distribution, especially southern and becoming rare towards the north.
3. Scottish type	Plants predominantly Scottish in distribution, especially northern and becoming rare towards the south.
4. Highland type	Plants confined to the mountain regions of England, Wales and Scotland.
5. Germanic type	Plants characteristic of the east part of England.
6. Atlantic type	Plants characteristic of the west and south-west parts of Britain.
7. Local or doubtful type.	

Mention must be made at this point of Forbes' (182) publication in 1845 of a very similar series of types or, as the author called them, "floras." We need not be concerned whether or not, as has been stated, this work of Forbes' was in fact a plagiarism of Watson's earlier work in which his types had first appeared. The important point is rather that Forbes not only listed his floras or, as we should call them to-day, "floristic elements," but also explained them on the grounds that they represented the stages and directions of the immigration of plants into this country following the ice ages. For this reason Forbes' work, even if not altogether original, cannot be ignored, and will be referred to again later.

To return to the *Cybele.* Watson next dealt with the British plants according to their status in the country, that is to say, according to their mode of origin. This question of status is a very thorny one, largely because in many cases the truth can never now be discovered, but it is also a very interesting one and helps very much in appreciating our flora properly. Here again, Watson's work has stood the test of time and his classification, which is as follows, is substantially that still in use to-day.

The first and most important category is that of the "native" species. These are the plants whose presence in the country has nothing to do with human action either direct or indirect. Many of them have no doubt existed in the country much longer than man himself and for this reason they have been described as botanical aborigines or, as the phrase goes, "aboriginal possessors of the soil." At the same time they certainly include some recent immigrants. It is to these native species that the natural vegetation of the country is almost entirely due.

The next category comprises all these species which owe their presence indirectly to man's activities. They are in short the weeds of cultivation which in absence of agriculture would find no home here. These plants Watson called "colonists."

Next come the plants which owe their presence to the direct action of man, that is to say, which have been introduced deliberately for purposes of cultivation but which have subsequently escaped from these surroundings and established themselves among the natural vegetation as a permanent feature of it. Such are called "denizens."

Lastly, there are the species which are constantly introduced by accident in the form of seeds and fruits, which grow for one or more summer seasons but which do not normally reproduce and whose presence is therefore transitory. They are found in disturbed ground and play no part in the natural vegetation. No doubt on the grounds of their foreign origin these plants were called "aliens," but the more recent terms "casual" and "adventive" are perhaps to be preferred.

Finally Watson classified the flora on what we should now call an ecological basis into the following groups according to habitat:

1. Pratal	Plants of meadows.
2. Pascual	,, ,, less rich pastures.
3. Ericetal	,, ,, moors and heaths.
4. Uliginal	,, ,, swamps and bogs.
5. Lacustral	Submerged or floating aquatics.
6. Paludal	Plants of marshy places.
7. Inundatal	,, ,, places liable to winter flooding.
8. Viatical	,, ,, disturbed ground.
9. Agrestal	,, ,, cultivated ground.
10. Glareal	,, ,, dry exposed ground.
11. Rupestral	,, ,, walls and rocks.
12. Septal	,, ,, hedges.
13. Sylvestral	,, ,, woods and shady places.
14. Littoral	,, ,, the seashore.

By the combination of these classifications Watson was able to give a very complete picture of the distribution of each British plant not merely in terms of its actual geographical range but in terms of geographical range, altitude, status and ecology, and a list of the British plants embodying this information is the main part of the *Cybele.*

In 1860 there appeared the first part of a supplement to the *Cybele* and in 1868–1870 the three volumes of the *Compendium of the Cybele Britannica.* In these works Watson made two further great advances in British plant geography. First he replaced or elaborated his eighteen provinces by dividing the whole of Britain into 112 vice-counties, and second he discussed for the first time the extra-British ranges of the members of the British flora. His system of vice-counties is still in full use, and more and more attention has come to be paid to the wider distribution of British plants.

Finally, in 1873–4, Watson published his last work, the two volumes of his *Topographical Botany* (577), which provided in tabulated form a summary of the known distribution of British plants. Its concise and convenient form has given to *Topographical Botany* a popularity which in comparison with the *Cybele* it scarcely deserves, and it has been kept up to date ever since by a second edition and by supplements. Most recently Druce's *Comital Flora* (141) is, as its author states, mainly a modern revision of *Topographical Botany* with Ireland also included. Regarding this latter point Watson did not deal with Ireland in either the *Cybele* or *Topographical Botany*, but this gap has long been filled by corresponding publications by Colgan and Scully (107) and by Praeger (426).

Any work which consists of the compilation and collection of records which are ceaselessly being made can never possess finality, and since Watson's day botanists have repeatedly revised or added to his work in detail, but it is a remarkable tribute to him that during a time of such rapid scientific advance the main outlines of his studies remain practically in the form in which he stated them. Some aspects have received more attention than others but the framework remains.

This sketch of Watsons' work has had two functions: it has given an account of the origin and development of the study of the geographical features of British plants, and it has also indicated the main ways in which that study has been conducted. With it as a background we may go on now to a brief consideration of the present position of these studies and to illustrate them by the examples which it would have been out of place to mention above.

Since Watson's time research into the distribution of British plants has continued mainly along three lines. The first is in fact the whole subsequent growth and development of the science of plant ecology or study of the plant in relation to its environment, and while it would be extravagant to hail Watson as the first plant ecologist there is, nevertheless, a clear forecast of the study of ecology in his classification of plants according to the kinds of habitat they occupy. Since his day ecology has developed so far and so wide that it has become a subject of its own, ranking with, and complementary to, the subject of plant geography in the narrower sense which deals with the spatial relations rather than with the physiological relation of plants to the earth that bears them. Since this book is devoted to plant geography in this narrower sense, plant ecology falls outside its scope and further information concerning this particular subject must be sought elsewhere. Nevertheless it must be borne in mind that this sharp demarcation of interests is largely made inevitable by the exigencies of convenience. It is not a natural separation, and the two subjects of plant ecology and plant geography are interrelated at almost every point.

The second line of development in British plant geography has been the further study of the classification of species according to their distribution *within* the country itself, an extension, as it were, of Watson's "types" and Forbes' "floras," and the third line has been the elaboration of the classification according to the distribution of the species *outside* Great Britain. The present position regarding both these must now be considered. In doing this it is necessary to write largely in terms of numbers. As was made clear earlier, numbers may mean little or much and must not be regarded too seriously, but without them it is almost impossible either to make comparisons with other floras or to demonstrate the comparative importance of different components. They also have another value in that they illustrate very vividly the extent to which our conceptions of the flora depend upon individual opinions, a limitation which cannot entirely be surmounted.

The differences which exist in the various estimates of the size, in number of species, of the British flora are chiefly due to two difficulties. The first lies in deciding to what degree the recognition of small species or "microspecies" should be carried and the second in deciding exactly what plants deserve to be considered as members of the established flora. As a general rule the more a genus is studied the more obvious become the differences between the individuals which comprise it, with the result that more and more species tend to be recognised in it, and these species to become smaller and smaller in value and distinction. For example, the blackberries to the everyday field botanist appear to belong all to one variable species but to the specialist who has particularly studied them this one variable species is regarded as comprising a large number of separate microspecies. Similarly, in the genus *Hieracium*, the non-specialist regards the British forms as representing about half a dozen species, but the specialist may recognise among them as many as 250.

The fact is that the species is not a standard measure and varies according to the conception of the individual botanist. It is therefore really impossible to determine how many species there actually are in the flora, and all that can be done is to arrive at some conclusion that will give a reasonable picture and estimate of the number of apparently different plants or, to use a scientific term, *phenotypes* present. How difficult even this is can be shown by a consideration of some actual estimates.

As regards status, it is with the casuals that the difficulty lies. Are any of them, and if so which of them, to be treated as definite members of the British flora? Although it is easy to define them as a class in general, it is not always easy to say exactly which species fall into this category. Some are more firmly established than others and some have almost the rank of colonists or denizens. For the most part, casuals are not regarded as members of the flora proper because they are not permanent and because they occupy no niche in the general vegetation, but some authorities include them and thereby increase the length of floral lists very considerably.

The effects of these two difficulties are best seen by referring to particular works on the British flora. One of the most satisfactory accounts of British plants is Hooker's *Student's Flora* (275) in which about 1,300 species are listed. Bentham and Hooker's *Handbook* (40, 177), which is perhaps the most familiar of all our Floras, gives about the same number. In both these works casuals are for the most part excluded. On the other hand Druce's *British Plant List* (140) includes these and enumerates no fewer than 4,250 species. In the latest Flora, that of Clapham, Tutin and Warburg (99) this total is again greatly increased by the inclusion of many planted species and garden escapes.

Fortunately we can resolve this disparity to some extent. There is practical agreement that the figures of Hooker and of Bentham and Hooker are too small, and that many worthy species have not been recognised in them, and this opinion has been implemented by the publication of what is in fact an appendix to these works enumerating some 500 additional species (69). Examination of Druce's list shows that no fewer than 1,750 casuals are included, and if these are cut out the total drops to something more than 2,500. Even this includes an extreme recognition of microspecies. Here we can gain assistance from various other Floras not yet mentioned, for Babington (27) and the *London Catalogue* (345), for instance, give 2,250 species including many *Rubi* and *Hieracia*, while Hayward (255) gives some 1,650 excluding microspecies of *Rubi* and *Hieracia*.

From this maze of figures it is possible to make some generalisation. It seems fairly clear that most authorities regard our flora as composed of about 1,750 species if certain microspecies and all casuals are excluded; as composed of about 2,250 species if the microspecies are included; and of anything up to 4,500 species if all possible casuals are included. For our present practical purpose then we shall be reasonably justified in regarding the flora as consisting of about 1,750 fairly well-defined species.

The next question is the proportion of the different status categories in this total. Here again it is difficult to reach conclusion, but, making a synthesis of various opinions, it would appear that of the 1,750 probably some 1,250 deserve to be regarded as natives, at any rate in some part of the country. About 250 are to be regarded as denizens, leaving a rather indefinite figure, not exceeding 250 and probably rather less, for colonists.

For statistical purposes only species are taken into account, but many species actually occur in two or more well-marked subspecies or varieties. In addition there

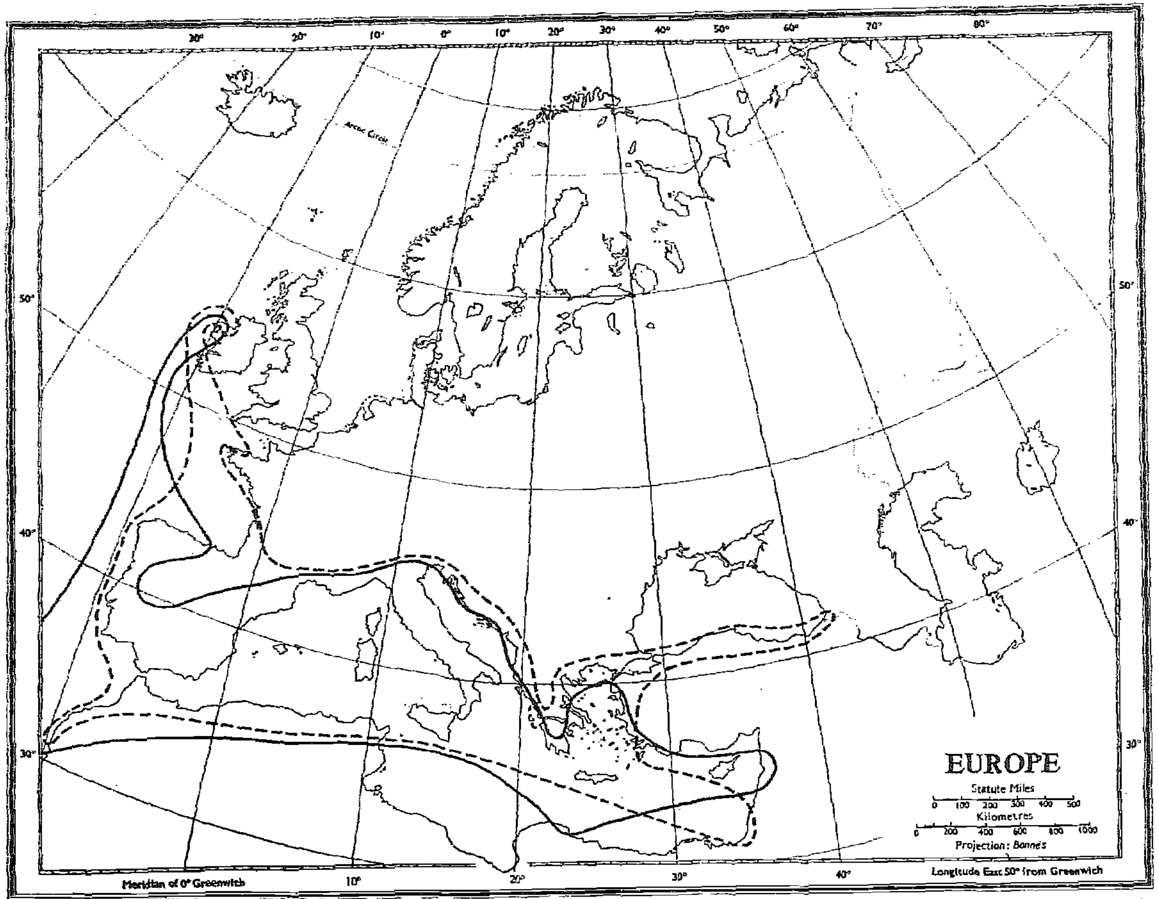

FIG. 57.—Map showing the distribution of *Neotinea intacta* (continuous line), mainly after von Soo, and *Arbutus unedo* (broken line), after Sealy.

is a considerable number of inter-specific hybrids, and certain genera such as *Salix*, *Rumex* and *Rosa* are particularly rich in them.

With regard to casuals, only one further point need be mentioned here. Fresh species are always being introduced into the country, and as there is no means of telling which of previous entrants still persist, the total number of recorded casuals is always increasing. This is the chief reason why every fresh estimate which includes such plants tends to contain more species. These estimates represent, however, not the condition of affairs at any one time but the total records over a long period.

The term British as applied to the flora includes not only Great Britain and Ireland but also the Channel Islands. The last named, however, are included solely on political grounds, the flora actually being far more French than British in character. They may therefore be excluded except for special mention. It may be noted that some twenty species are found in these islands only and not in the British Isles proper.

It happens that the distributions of plants in Britain and in Ireland respectively have nearly always been treated as two separate problems, and it is appropriate therefore to treat them so here, and it is convenient to begin with Britain. The distribution of plants in Britain is generally expressed in terms of the 112 vice-counties into which Watson ultimately divided the country, and this is probably as good a way of conveying their ranges as can be suggested. The *London Catalogue* (345), as well as one or two other works, summarises the information available in a convenient way, and the following table is taken from that work.

About	7	per cent.	of all	species	are	recorded	from	every one of the vice-counties.
,,	10	,,	,,	,,	,,	,,	,,	100–111
,,	5	,,	,,	,,	,,	,,	,,	90–99
,,	5	,,	,,	,,	,,	,,	,,	80–89
,,	5	,,	,,	,,	,,	,,	,,	70–79
,,	5	,,	,,	,,	,,	,,	,,	60–69
,,	5	,,	,,	,,	,,	,,	,,	50–59
,,	5	,,	,,	,,	,,	,,	,,	40–49
,,	6	,,	,,	,,	,,	,,	,,	30–39
,,	7	,,	,,	,,	,,	,,	,,	20–29
,,	12	,,	,,	,,	,,	,,	,,	10–19
,,	22	,,	,,	,,	,,	,,	,,	2–9
,,	6	,,	,,	,,	,,	,,	,,	only 1

The main fact which emerges from these figures is that the species in total show every degree of range from the minimum to the maximum. Actually the figures given are probably all on the low side, since our knowledge of plant distribution even in this country is still far from complete. For instance, many of those in the second line will probably be ultimately discovered in the one or few remaining countries. On the other hand, the comparatively large figures towards the bottom of the table are caused by recently recognised species whose ranges are still largely problematical.

The plants recorded from all vice-counties include, as might be expected, many of the commonest and most familiar, as, for instance, *Achillea millefolium*, *Bellis perennis*, *Capsella bursa-pastoris*, *Cerastium vulgatum*, *Cirsium arvense*, *Cirsium palustre*, *Cirsium vulgare*, *Hedera helix*, *Juncus conglomeratus*, *Juncus effusus*, *Lotus corniculatus*, *Prunella vulgaris*, *Ranunculus acris*, *Ranunculus repens*, *Rumex acetosa*, *Rumex acetosella*, *Rumex crispus*, *Rumex obtusifolius*, and *Taraxacum officinale*, together with such grasses as *Dactylis glomerata*, *Holcus lanatus*, *Lolium* *perenne*, *Poa annua* and *Poa pratensis*. Also included are various species distinctly less abundant but nevertheless thus completely distributed. Among these are *Achillea ptarmica*, *Alopecurus geniculatus*, *Galeopsis tetrahit*, *Hydrocotyle vulgaris*, *Linum catharticum*, *Lychnis flos-cuculi*, *Molinia caerulea*, *Myosotis versicolor*, *Oxalis acetosella*, *Ranunculus hederaceus* and *Thymus serpyllum*.

The species confined to only one vice-county each include, as has been indicated, a number of microspecies whose real distribution is still uncertain, but there are others about which there is no doubt. Not only so, but they are in some cases recorded only from one or two spots, or even from a single locality, as is true of *Cotoneaster integerrima* on the Great Orme; *Dianthus gratianopolitanus* (*caesius*) at Cheddar; *Saxifraga cernua* on Ben Lawers and in one other locality; *Arenaria uliginosa* on Widdybank Fell; *Scorzonera humilis* from one or two spots in Dorset; *Lloydia serotina* from a few rock faces in the Snowdon Range, and three species of *Trifolium* from the neighbourhood of the Lizard Point.

These species are to be regarded as among our rarest plants, but it is perhaps more accurate to call them local rather than rare. They may and sometimes do occur within their limited habitats in considerable quantity, while there are other species which, though more widespread, have been seen only in very small numbers and at long intervals of time. It is to these latter that the word rare more appropriately applies. An extreme instance of rarity in this sense is afforded by the orchid *Epipogium aphyllum*, of which in the last hundred years no more than about half a dozen individuals have been noted in three or four different and widely separated localities. Several other orchids are similarly but less conspicuously rare in this strict sense.

In view of what has just been said it would be interesting to arrange the vice-counties in order according to the total number of species recorded from each, but it is difficult to do this sufficiently accurately to be of value. It is clear, however, that the richest vice-counties are those in the extreme south-west and south-east of England, namely Cornwall, Sussex and Kent, and that from these points the richness decreases fairly regularly northward and westward. In short, there are most species in those parts of England nearest to the Continent, a feature which, in view of the glacial and post-glacial history of the flora, is only to be expected.

That even today there is much to be learnt about the British flora has been demonstrated in striking fashion by the discovery in Scotland in 1951 of no fewer than three additional species (348). These are *Diapensia lapponica* (624), never hitherto recorded from this country; *Koenigia islandica*, collected some years ago also but then not recognised; and *Homogyne alpina*, never previously confirmed.

The question of the comparative distribution of species over Britain can best be dealt with by reference to the types of Watson described above. The percentages of these types among British plants is roughly:

1. British type	44 per cent.
2. English type	30 ,,
3. Scottish and intermediate type	8 ,,
4. Highland type	5 ,,
5. Atlantic type	5 ,,
6. Germanic type	8 ,,

The British type obviously will include all the plants found in all the vice-counties as well as many not so completely distributed. The disparity between 2 and 3 is due partly to the fact that the majority of the plants found in a medium number of vice-counties fall under 2. It may also be said here that according to most estimates only some seventy species are found in Scotland and not in England. The Atlantic and Germanic types contribute largely to the greater richness of the flora in the extreme south which has already been noted.

The general nature of the flora of Ireland cannot be better described than by quoting the remarks in the introduction to the second edition of the *Cybele Hibernica* (107). The authors there say that "Viewed as a whole, the flora of Ireland may be regarded as an incomplete English flora, as this in turn may be regarded as an incomplete west European or French flora. It is in the species which it lacks that the Irish flora chiefly differs from the English; and the vast majority of the English plants which are absent from Ireland are common or widespread in western continental Europe."

According to most authorities the number of species in Ireland is about 70 per cent. of the number in England, but they include an appreciable group not found in the latter country. Praeger (429, 431) mentions the following as being definitely of this type, namely:

Arbutus unedo (fig. 57)
Arenaria ciliata
Daboecia cantabrica (*polifolia*) (fig. 58)
Erica mackaiana (*mackaii*)
Erica mediterranea (fig. 56)
Inula salicina
Neotinea intacta (fig. 57)
Pinguicula grandiflora (fig. 55).
Saxifraga hirsuta (fig. 58)
Saxifraga spathularis
Sisyrinchium bermudiana (*angustifolium*)
Spiranthes gemmipara

To these are perhaps to be added the following problematical and possibly endemic forms:

Arabis brownii
Orchis kerryensis
Orchis occidentalis (539)
Orchis traunsteinerioides
certain species of *Saxifraga* (578, 579)
three species of *Hieracium*

Species found in England but not in Ireland include:

Astragalus glycyphyllos
Chrysosplenium alternifolium
Convallaria majalis
Genista anglica
Helictotrichon (*Avena*) *pratense*
Lathyrus sylvestris
Ononis spinosa
Paris quadrifolia
Scabiosa columbaria

Among species commoner in England than in Ireland are:

Adoxa moschatellina
Calamagrostis epigeios
Corydalis claviculata
Filipendula hexapetala
Galium cruciata
Geranium pratense
Hypericum hirsutum
Ornithopus perpusillus
Teesdalia nudicaulis
Trollius europaeus

Conversely, *Lathyrus palustris*, *Pinguicula lusitanica* (fig. 55), *Rhynchospora fusca*, *Rubia peregrina* and *Utricularia intermedia* are more common in Ireland than in England.

For distributional purposes Ireland is divided into forty vice-counties which actually correspond more or less to the political counties. Considering the smaller size and greater homogeneity of Ireland, it is not surprising to find that the number of completely distributed species is proportionately much greater than in Britain. About 250 species are found in all the vice-counties and, also as might be expected, these include nearly all the species which are completely distributed in Britain. The additional species are chiefly of the sort that reflect one of the main ecological features of Ireland, namely, the prevalence of various kinds of aquatic habitats. This is well shown in the case of the genus *Carex* of which no fewer than fourteen species are completely distributed compared with only four so ranging in Britain.

On the other hand, the number of species occurring in only one vice-county is small, about forty in all, of which some seventeen are microspecies of *Rubus* and *Hieracium*. This figure gives a percentage of 4 as compared with 6 in Britain, but these figures have not much significance.

The concentration of species in the south-east of England and also several peculiarities of the Irish flora have been discussed and demonstrated by Matthews in a series of papers designed to throw light on the paths by which the bulk of the British plants re-entered the country after the glaciation. Matthews argues that the more or less completely distributed British plants, those which occur in nearly all the vice-counties, are not likely to reveal much in this direction, and confines his attention to those which have a markedly narrower range. In his first paper (372) he analyses that element of the flora consisting of species found only in England and Wales. These he estimates to number 266, and he shows very clearly that they are concentrated in the coastal counties from Dorset to Norfolk, and that this concentration decreases more or less regularly westward and northward. He further shows by inset maps that the area of greatest concentration of these plants outside Britain is in France, where over 90 per cent. of them are to be found. In a second paper (373) he deals with the 105 species found, in the British Isles, only in England and Scotland. These he finds fall into two almost equal groups, a boreal and a southern, concentrated respectively in Scotland and in the eastern half of England, especially the south-east. Outside Britain he finds the boreal group to be concentrated in Scandinavia, Germany and France, and the southern group in France and Spain. In his third paper (374) Matthews deals with the Anglo-Irish element of the flora. He refers first to the twenty or so species found only in Ireland, and shows that they belong almost entirely to a south European stock concentrated on the continent in northern Portugal and Spain. A second, larger, group of sixty-eight species occurring in Ireland and England he shows to have very much the same distribution as was the case of the English plants, namely, a concentration in the coastal counties from Devon to Norfolk together with a concentration in west and south-west Ireland. These plants again are like the English element in that their continental area of concentration is in France.

Taking the three papers together Matthews concludes that the non-boreal element of the British flora, which is the part with which the papers deal, may have begun to re-immigrate into the country directly from south-west Europe and that this was the oldest or first migration, but that very soon the centre of dispersal on the continent moved eastwards to the neighbourhood of France. The migration from this direction he considers to have been a very prolonged one and to account for the preponderance of French and central European species in our flora.

So far our attention has been confined to the distribution of species within the British Islands, but the members of the British flora must next be considered in the light of their distribution outside these countries.

This at once raises the question of British endemics. Are there any species occurring in the British Isles that occur nowhere else and which are therefore peculiar to them? The answer depends entirely on what we reckon as species. If by the term we mean units of the size, let us say, of those in Bentham and Hooker's

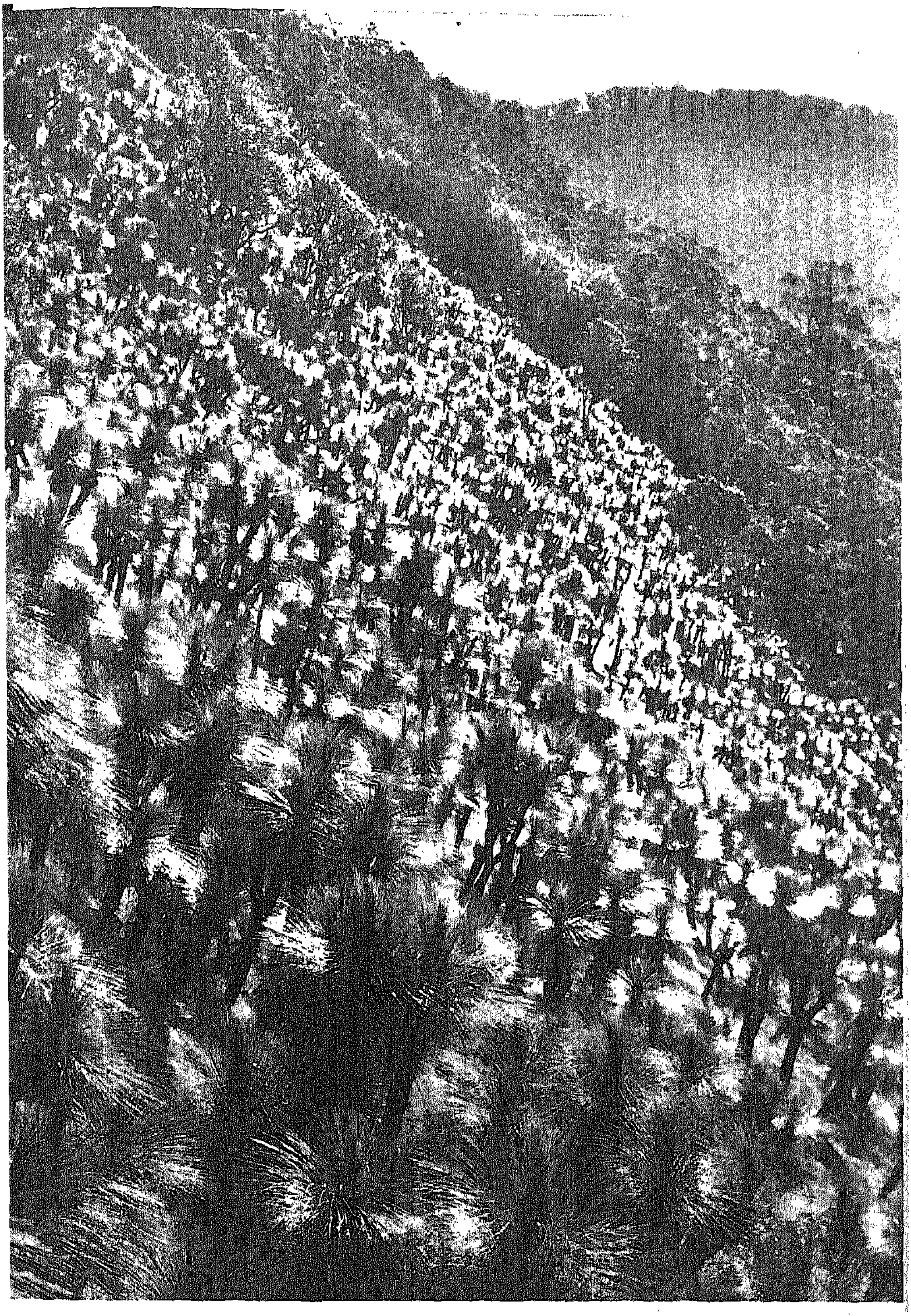

Plate 17. Grass-trees (*Xanthorrhoea sp.*) on the slopes of Mt. Mitchell, Queensland

(*Photo: F. Hurley*)

Handbook, namely, average or large species, then the answer is probably that there are none. If, on the other hand, we take into account small species, then the answer is that a small number are found only in the British Isles. This in one way is quite a sufficient statement, because it illustrates the main point, which is that the peculiar element in our flora is almost non-existent compared with the peculiar element in most other floras of the world. Wallace (570) gives one of the earliest and most lengthy surveys of endemic British plants. His list, which was compiled by Bennett, includes no fewer than seventy-two microspecies and varieties, but many of these must certainly be excluded. Indeed Hooker, in comments on this list, reduces it to one absolutely endemic species, *Potamogeton lanceolatus* (now known to be a hybrid), and some fifteen varieties. Wilmott (600) has discussed the matter at some length but does not give a definitive list. It would appear, however, from his remarks that the genera *Arabis*, *Cochlearia*, *Fumaria*, *Limonium* (*Statice*) and *Ulmus* all contain one or more endemic forms which have at some time or other received specific rank, and that in addition many microspecies of *Rubus*, *Rosa*, *Hieracium*, *Euphrasia* and *Thalictrum* are also unrecorded elsewhere. About a dozen small species of *Sorbus* have also been described as endemic (99). Salisbury (460) believes that there are fewer than twenty-five endemics, including varieties, and Matthews is of much the same opinion. As has been seen, some of these reputed endemics are confined to Ireland.

The first classification of British plants according to their ranges outside this country, and particularly on the continent, was made by Forbes (182) in 1846. He recognised five elements or sub-floras which he believed to represent as many distinct immigrations into the country subsequent to the Pleistocene. They were:

1. Iberian or Asturian:
   species found, on the continent, in the north of Spain.
2. Armorican or Gallican:
   species chiefly of the Channel Islands and western France.
3. Kentish:
   species found particularly in north and north-eastern France.
4. Scandinavian or Boreal:
   species representing northern and sub-arctic floras.
5. Germanic:
   species related to those of central and west-central Europe.

Since Forbes' day repeated attempts have been made to improve and amplify this classification, and it would be impossible to deal with these in detail. Matthews (375), however, has brought the whole subject more up to date in a single comprehensive paper, and we cannot do better than refer to this at some length.

Matthews treats the native or naturalised flora as comprising about 1,500 species, and divides them according to their extra-British ranges into fourteen groups or elements to which is to be added a small assembly of endemics. This classification is very detailed and can really only be properly appreciated in the original, but for our present purposes, and in order to facilitate a rapid survey, it may be condensed and rearranged as follows:

1. Wide element:
   Species found at least throughout the northern temperate regions . . . . . . 205 species.
2. Eurasian element:
   Species found generally distributed through Europe and temperate Asia . . . . . 480 species.

3. European element:
   Species generally distributed throughout Europe 130 species.
4. Southern element:
   Species whose continental range is predominantly more southerly than this country . . 315 species.
   a. Continental southern element:
   Species of south and central Europe 127 species.
   b. Oceanic west European element:
   Species found almost exclusively in western (Atlantic) Europe . . . . . . 76 species.
   c. Oceanic southern element:
   Species found chiefly in south Europe and western Europe, including the Mediterranean region 74 species.
   d. Mediterranean element:
   Species whose ranges are centred in the Mediterranean region . . . . . . 38 species.
5. Northern element:
   Species whose continental range is predominantly more northerly than this country . . 142 species.
   a. Continental northern element:
   Species whose main European range is central and north, but including some circumpolar species 91 species.
   b. Oceanic northern element:
   Species characteristic of north-west Europe, but some having a connection with north-east America 26 species.
   c. Northern montane element:
   Species of north Europe reappearing on mountains further south . . . . . . 25 species.
6. Continental element:
   Species characteristic of central Europe, generally extending east through Russia into Asia . 82 species.
7. Arctic-alpine element:
   Species characteristic of the arctic or sub-arctic regions or exclusively alpine . . . . 145 species.
   a. Arctic-sub-arctic element:
   Exclusively northern species . . 30 species.
   b. Arctic-alpine element: . . . .
   Northern species also on southern mountains 106 species.
   c. Alpine element:
   Species of the central European mountains 9 species.

Even in this somewhat simplified form the classification is complex, as is necessarily the case, and it is well to emphasise its more salient features.

It will be seen that the first three elements, comprising some 55 per cent. of the total flora, make up what may be called the expected proportion of the flora. That is to say they contain plants likely to occur merely by virtue of the country's position as part of the northern temperate continent of Europe.

The remaining elements are on most counts of greater interest, because it is in them that we are most likely to find indications of floral history. Matthews discusses them in special detail and brings out many important points, but attention may be concentrated on certain of them.

No portion of the British flora has received so much attention as that which comprises the species which are confined to the western parts of Britain and/or Ireland and which, outside this country, are more or less restricted to the Atlantic coast of south-western Europe and/or to the Mediterranean region. The fact that these do not all fall into one of the groups above simply indicates that their continental distributions vary, as Matthews has shown, so that they can be divided into three (4 *b*, *c* and *d*). They have in common one all-important feature, namely that the British part of the total range of each is much further north than the rest. As a whole these plants may be called "Atlantic," but the most noteworthy examples of them form an assemblage which is usually referred to as the "Lusitanian" element in our flora, for the reason that outside our boundaries the species are more or less restricted in range to that part of the Iberian Peninsula. For example, *Saxifraga hirsuta* is, outside Ireland, found only in the Pyrenean region, so that its occurrence in the former is far to the north of the rest of its distribution. Other species are less extreme in that they occur also on various parts of the west coast of France. These "Atlantic" species in general and "Lusitanian" species in particular have been studied by many botanists. Stapf (522, 523) has given a long account of them; Praeger (428, 431) has more recently resurveyed the facts and theories concerning them, and Drude's comparison of the British and German floras refers often to them (144).

The great question is how and when these plants, and especially the "Lusitanian" species proper, which number less than a dozen, reached our shores. They are to-day found only in those parts of these islands where the conditions are least rigorous, and it seems perfectly certain, in the light of present knowledge, that whatever may be true of other species, these at least cannot have survived the ice ages in their present positions. This being so they are presumably among the post-glacial immigrants. But whatever the changes in the distribution of land and sea may have been since the end of the Pleistocene, a period of only a few thousand years, there is no suggestion that they include any linkage of Ireland with Britain or of south-west England (and much less Ireland) with France, so that if these plants are indeed recent immigrants, they must have crossed considerable areas of sea.

This problem has been so often debated without conclusion that it seems almost presumptuous to suggest that its difficulties may have been overestimated, but this seems to be so, for the following reasons. The actual occurrence to-day of these plants in south-west England and Ireland proves that their climatic and edaphic requirements are different from those of the generality of British plants only in so far as the conditions of south-west England and Ireland differ from those of the rest of the country. That is to say they are present within our boundaries because there are spots herein in which they can find a congenial home and the conditions they need. Secondly, the separation of Ireland from Britain to the best of our knowledge antedates the last glaciation, during which most of Ireland is said to have been ice-bound, and hence the present Irish flora, except perhaps for a tundra element, must have re-immigrated since, and in doing so must have crossed the intervening sea. It would therefore seem clear that this expanse of sea has not proved a significant barrier to dispersal. Again, there is no reason to assume that the Straits of Dover have ever been wider than they are now, and on a similar argument they must therefore have always been a slighter obstacle to plant migration.

It is at this point that the argument usually becomes confused. Most of the

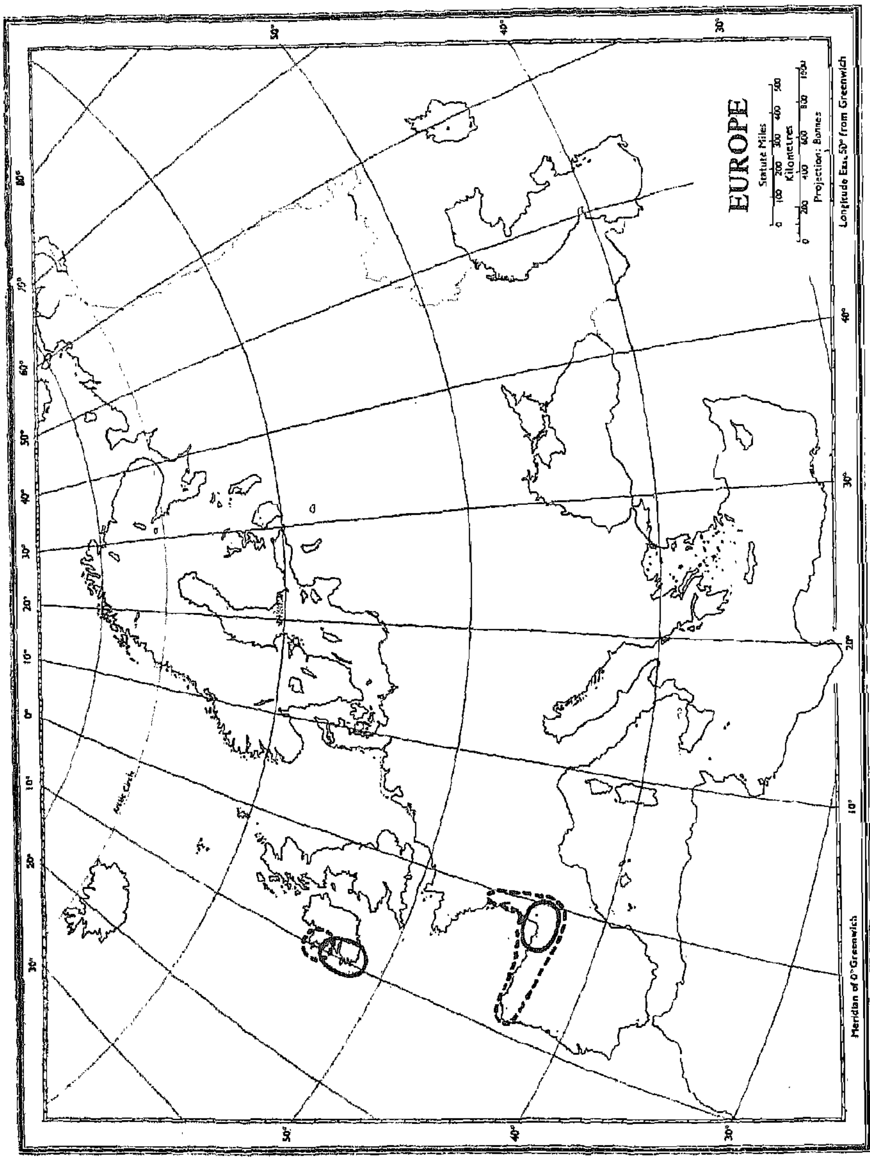

FIG. 58.—Map showing the distribution of *Saxifraga hirsuta* (continuous line) and *Daboecia cantabrica* (broken line). There is a closely allied species of *Daboecia* in Macaronesia.

"Lusitanian" plants are not found notably on the European coast north of Spain, and hence it has generally been concluded that they must, in order to reach Ireland, either have travelled direct from one to the other along land surfaces now submerged, or have been able to survive the ice ages in refuges also now submerged, as is postulated for instance in the view of Enquist, recently quoted sympathetically by Jessen (301), that there was during the last glaciation a forest refuge area south of the British Islands near the edge of the continental shelf, whence these plants again advanced into Ireland when the ice retreat allowed them to do so. There is, actually, no necessity to assume that either of these things has happened. Although the "Lusitanian" plants in the stricter sense do not by definition occur in France, there are species which differ from them only in the fact that they do so occur in France, and thereby show intermediate stations or "stepping stones" between Spain and south-west Britain. *Arbutus unedo*, *Erica ciliaris* and *Rubia peregrina* are such plants. From this it is clear that the conditions of western France are very close indeed to those required by "Lusitanian" plants in general, and this being so, very slight climatic changes, of the dimensions of those which we believe to have taken place since the end of the Pleistocene, would almost certainly permit the passage of species from Spain to Ireland by way of western France and England. In other words it is not necessary, in order to explain the presence of "Lusitanian" plants in Ireland and south-west England, to do more than to assume that some time since the end of the Pleistocene there have been such minor climatic fluctuations as would enable them to travel along the western shores of France and across the Channel somewhere in its narrower part, and the supposed post-glacial optimum might well have been that time. But even this last qualification is not strictly necessary, because the sea gap between Brittany and Cornwall is not very much wider than that of the Irish Sea, and need be regarded as but little more of a barrier.

On these facts and arguments it would seem that the "Lusitanian" and "Atlantic" species of the British flora do not present so much of a problem as is generally supposed, but that their presence can be explained by migration along the western shores of Europe during a period when climatic conditions were slightly higher than they are to-day, a conclusion it may be noted very similar to that recently arrived at by Sealy (471) in his special study of *Arbutus unedo*. It follows from this that the present populations of these species are comparatively recent immigrants to the Irish flora but that some at least of them were there in interglacial times has been shown by Jessen (300), who records *Erica mackaiana* (which is in Ireland to-day) and *Rhododendron ponticum* (which is not) from deposits of that age in Galway.

At the same time it should be made quite clear that this explanation of the presence of these species in the British flora is founded on the assumption that our present beliefs about the extent and effect of the Pleistocene glaciations in Britain and, particularly, Ireland, are correct. Should it ever transpire that they are erroneous in any major respect, then the whole problem of these plants will have to be reconsidered in the light of the new information.

Included in Matthews' oceanic northern element are six species found on the west side of Britain which outside this country occur only in North America. These are *Eriocaulon septangulare*, *Juncus dudleyi*, *J. tenuis*, *Sisyrinchium bermudiana*, *Spiranthes gemmipara* and *S. romanzoffiana*, the *Junci* in particular being of rather uncertain status. It would seem that the explanation of the presence of these plants in western Europe involves the difficult question of the distribution of land and sea in the past, and they should be recalled when this subject is dealt with in a later chapter.

The general northern element of the flora has an obvious and rather special interest, because it is the one most likely to have survived the Pleistocene *in situ*. Indeed, it may be accepted that practically all of it did so, and, this being the case, it may claim to be the oldest and most persistent part of the British flora.

It is obviously impossible in one short chapter to do justice to the many interesting features and problems of the British flora, and the very brief outline which has been given should be amplified by reference to some of the original works cited. It is to be hoped, however, that enough has been said to show how well the flora illustrates many of the fundamental aspects of plant geography, and that it must, for this reason, always be of special significance to the student of plant distribution.

First and foremost it shows in an unusual and perhaps unique way the stages by which a comparatively varied flora has been built up over a long period by immigration following serious and prolonged climatic upheavals. Secondly, it illustrates the extent to which a flora may be influenced and modified by contemporary human history. Thirdly, it epitomises the whole story of the northern temperate regions and their plant life since the Pleistocene. Indeed, it is perhaps no exaggeration to say that the British flora reproduces, in little, much of the whole story of the spread and development of Angiosperm floras, for what has overtaken the British plants in particular has almost certainly affected the whole world flora in more general and less drastic fashion.

CHAPTER 13

THE DISTRIBUTION OF PLANTS IN AN ENGLISH COUNTY†

IN the last few chapters the geography of the Flowering Plants has been surveyed with increasing precision by considering first the families, then the genera and the species, and then the distribution of a comparatively small number of species over one particular country—the British Isles. Throughout, however, attention has been directed almost exclusively to the *extent* of distribution, and little has been said so far about the almost equally important subject of the *intensity* of distribution. This chapter is intended to remedy this and to supplement the picture already drawn by describing in comparative terms the distribution of the species in the flora of a yet smaller area, as shown by a phytogeographical survey of one of the smaller English counties (220).

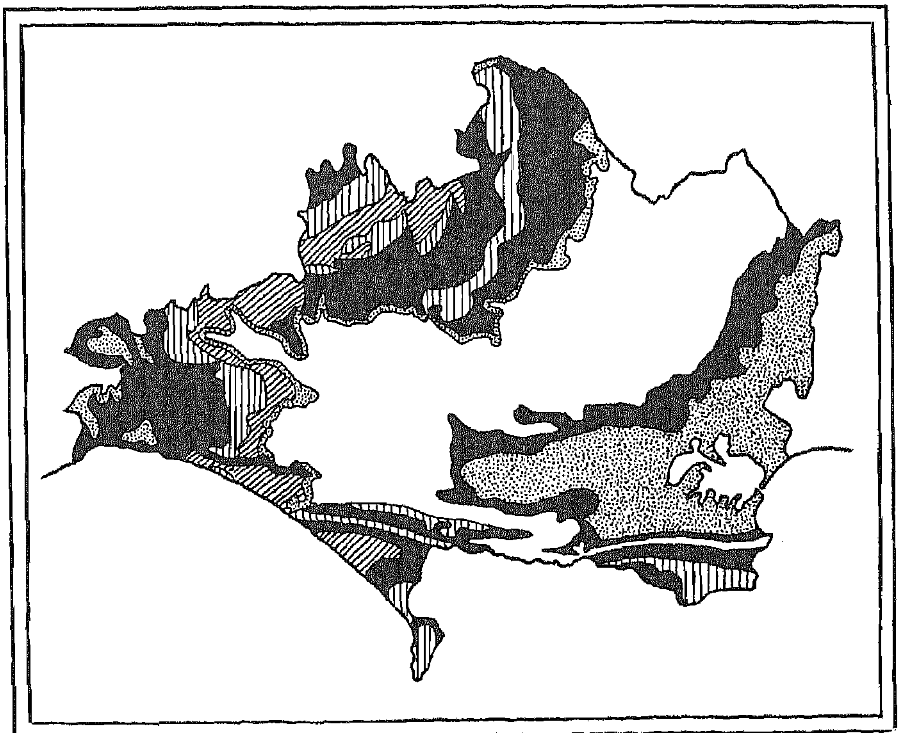

FIG. 59.—Map showing, slightly simplified, the distribution of subsoil types in the county of Dorset:—

dotted—sands.
white—chalk.
black—clays.
vertical shading—limestone.
diagonal shading—mixed clays and limestones.

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† The work of which this chapter is a condensed account has now been published as a book, *A Geographical Handbook of the Dorset Flora*, which is obtainable from the Secretary, County Museum, Dorchester, Dorset, price 20*s*., post free.

The county of Dorset, which was the area selected for study, is small but its topography and geology (fig. 59) are remarkably varied, affording an almost unrivalled series of plant habitats. In the east, round Poole Harbour, is a low-lying basin of Tertiary sands and clays; west of this is a wide extent of chalk uplands; while beyond this again are three distinct series of vales in which the rocks are mainly clays and marls interspersed with various kinds of limestones. Moreover, superficial deposits are very widespread, especially in the centre and west, adding greatly to the complexity of the surface geology. The relief is marked, though there are no heights of more than about 900 feet, and although the county is well watered, its rivers are, except perhaps for the Stour, little more than streams.

The distribution of climatic values in Dorset is still incompletely recorded in detail, but the leading facts are that the rainfall, which has a general average of about 35 inches a year, and is broadly correlated with elevation, generally increases towards the west and is least in the low-lying coastal areas; temperature lines run roughly parallel with the coast, values rising inland in summer and diminishing inland in winter; sunshine figures are very high, though they also fall inland, and on the whole the county is among the mildest; south-westerly winds prevail and are frequent and there is little fog.

When the ranges of the different species of its flora are plotted over the county, their chief geographical feature is quickly apparent, namely, that none of them is completely and evenly distributed. Even the commonest plants are absent from some small areas and are of more or less than usual frequency in many others, while at the other end of the scale there are certain rare species known only from a single spot and in very small quantity. In short, all show some geographical segregation, and the majority show it to a degree which, in fact, leads them to be absent from at least half the total county area.

It is also apparent that the distributions of individual species vary enormously, both in general character and in detail, and that, although it is true to say that most of them conform to a limited number of main types, it is equally true that no two are entirely alike.

The proportion of the county still bearing relatively natural vegetation is considerable, and it may therefore be assumed that this general segregation and localisation is not to be attributed primarily to man's actions or to other artificial circumstances, but is the consequence of the natural distribution of factors in the plants' environment, that is to say in the atmosphere and the soil.

In Dorset, as in most similar regions, there is one great difference between the distributions of climatic (atmosphere) and edaphic (soil) values. The former show a continuous range of variation or gradient—they wax or wane gradually in a given direction, but the latter, owing to the disorderly geological pattern, show a patchwork or discontinuous distribution. Moreover, in so far as such things can be compared, the differences among edaphic values are much greater than those of climate, and in consequence, while climate passes gradually from one condition to another, soil character may alter abruptly and completely within a very short distance.

It is, of course, a matter of everyday observation that most plants are found only in certain kinds of habitat, and that their distributions are indeed correlated with edaphic rather than climatic conditions is confirmed by the nature of their individual distributions, which are prevailingly of the second, discontinuous type. This is not to say that climatic factors are, in these cases, to be ignored altogether, and they are undoubtedly often of significance, if only indirectly, by controlling the value of certain edaphic conditions, but a geographical survey of the species within the county makes it clear enough that edaphic factors are paramount in determining not only their ranges but also their relative frequency. These edaphic conditions will be considered in more detail presently, but first it is desirable to discuss the apparent exceptions to the rule and to note particularly the instances in which a gradient type of distribution indicates that climatic rather than edaphic factors are of significance.

First of all among these there are some forty species whose Dorset records are marginal, that is to say, on the extreme edge, in some direction or another, of their total ranges. A very few of these are northern plants which reach towards the south or south-west only as far as Dorset, as for instance, *Gentiana pneumonanthe*, but most of them are the opposite, the Dorset records being among their most northerly or north-westerly occurrences. Some of these species are comparatively plentiful in the county, as, for instance, *Erica ciliaris*, though they are always localised, but most of them are rare and sporadic. As far as can be estimated none of them occur in peculiar kinds of habitats such as might be unknown elsewhere in England, and it may therefore be concluded that their appearance in Dorset is, primarily, at any rate, due to the existence there of certain particular climatic values. What these may be cannot be discussed here, but it may be hazarded that temperature is the main component concerned.

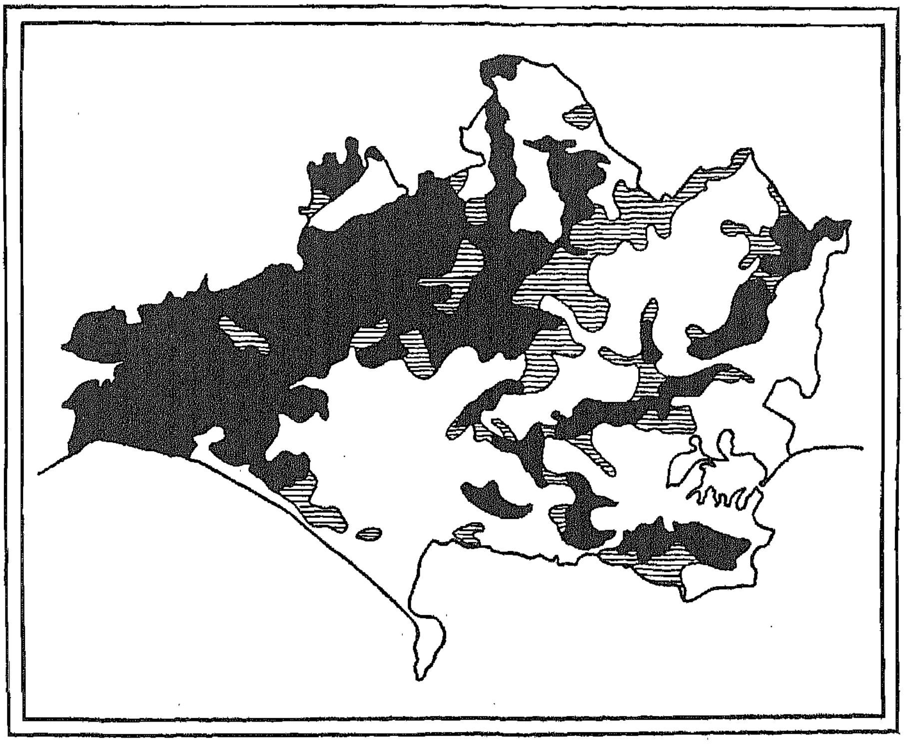


FIG. 60.—Map showing, slightly simplified, the distribution of the primrose (*Primula vulgaris*) in Dorset:—

black—present generally in both woods and hedges.
shaded—present generally in woods but not in hedges.
white—virtually absent from all habitats.

A second group comprises a handful of species (among them the primrose, *Primula vulgaris* (219)) which show increasing prevalence of occurrence from east to west, that is to say towards that part of the county where the rainfall is greater, and the result is that their distributions show so marked a gradient as strongly to suggest that some aspect of rainfall outweighs any correlation they may have with edaphic conditions (fig. 60).

A third and even smaller group comprises species which, within the county, are confined to the more northerly parts of the great chalk belt. The most striking of them is *Filipendula hexapetala*, which extends into the county from the north, with diminishing frequency, as far south-west as Dorchester. *Verbascum nigrum* is interesting, too, because it is almost confined to an area within a few miles of the Wiltshire border. There seems no good reason to suppose that these more northerly parts of the chalk are edaphically very different from the remainder, and it therefore seems clear that the localisation of these plants and their gradient distribution are due to climatic factors of some kind, and presumably that these are related in some way to the proximity of the sea.

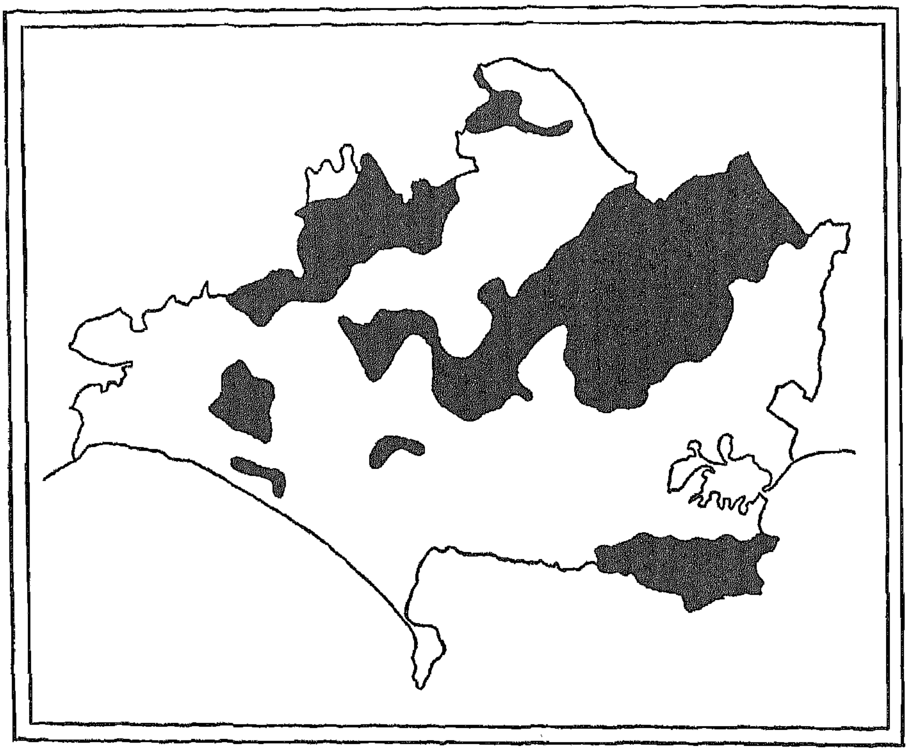


FIG. 61.—Map showing (black) the distribution of *Clematis vitalba* in Dorset.

One reason for this conclusion is that a considerable number of Dorset plants, forming a large fourth group, have just the opposite kind of distribution, being much more frequent in the vicinity of the coast than elsewhere. It must be made clear that we are not speaking here of those maritime species proper which occur in habitats which feel the direct influence of salt water and which will be mentioned later, but of what may be described as ordinary inland plants generally found fairly well distributed over England as a whole, and it is a remarkable fact that these latter number about a hundred, or roughly one-tenth of the total county flora.

Geographically these plants tend to be of three types: some being confined to a narrow coastal belt; some being chiefly so restricted but occurring sporadically, though less frequently, inland; and some ranging more or less all over the county but with notably greater frequency towards the south. The first include such extreme examples as *Vicia bithynica*, *Trifolium squamosum* and *Carduus tenuiflorus*, which are hardly ever found far from the immediate vicinity of the coast, but most of them are like *Rubia peregrina* and *Linum bienne*, which, though predominantly coastal, are not exclusively so. The second type includes *Picris echioides* (fig. 62), *Echium vulgare* and *Medicago arabica*, which occur not uncommonly far from the sea but which are peculiarly characteristic of the coastal belt. Notable examples of the third type are *Dipsacus fullonum* (*sylvestris*), *Allium vineale*, *Trifolium fragiferum* and *Anthyllis vulneraria*, but it includes also quite a number of common species such as *Rumex crispus*, *Lotus corniculatus*, *Anagallis arvensis*, *Daucus carota* and *Galium verum*, all of which increase in frequency towards the coast in a way which cannot be attributed solely to direct edaphic considerations.

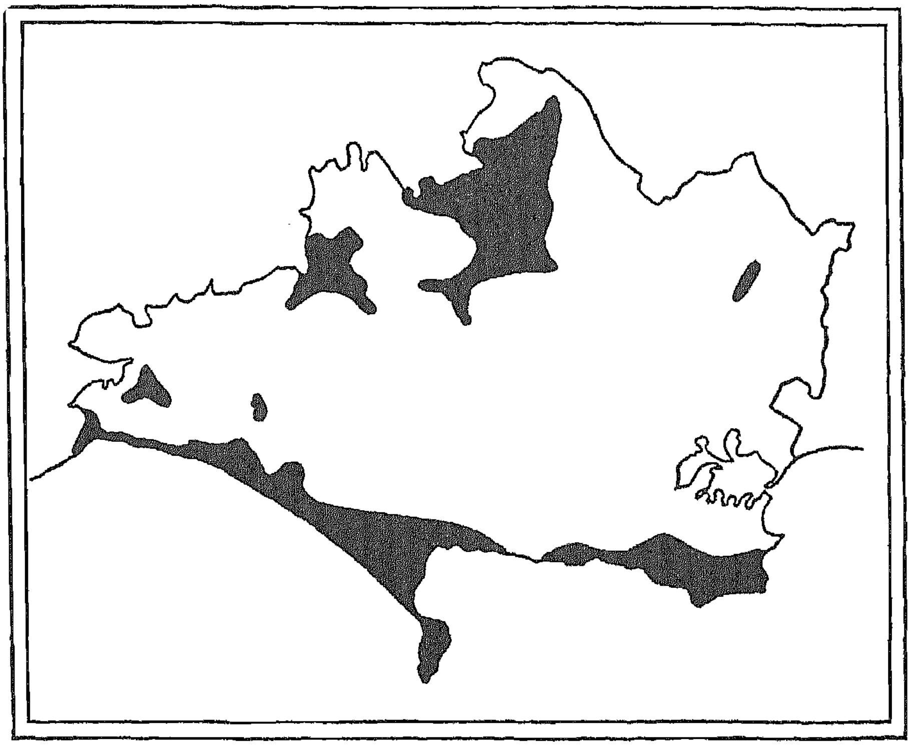


FIG. 62.—Map showing (black) the distribution of *Picris echioides* in Dorset.

It cannot, of course, be argued that the distribution of all these plants is exclusively determined by climatic considerations, but it seems clear that the increasing proximity of the sea is a matter of real importance to them in determining their frequency, and it is difficult to see how this operates unless it does so by modifying the climatic values locally. Only further careful investigation can show how this may come about, but it seems safe to assume that humidity and the presence of salt in the atmosphere have a good deal to do with it. That salt-laden winds from the sea do affect the vegetation inland is familiar enough when unusually strong gales blow inshore in early summer and the young expanding foliage of the hedges and woods becomes killed by the salt in the air. The nearer the coast the more these effects are felt, but they may be noticeable for many miles inland.

To sum up, there is every indication that climatic factors play a considerable, and it may be even an overriding, part in determining the distribution over the county of some proportion of its species, especially if their influences are reinforced by their effects in modifying edaphic conditions locally, but there is no evidence that climate is, in general, more than a subsidiary or secondary geographical determinant.

In the distribution of all the remaining species of the county flora, or at least all those that occur naturally, there is predominantly correlation with edaphic conditions of one sort or another. This is, of course, least obvious in the commonest and most widespread plants, but even here distribution is never quite complete, and the gaps are edaphic gaps, such as is their relative absence from wide areas of the barren sandy soils in the east. Nor do these species elsewhere all inhabit the same range of conditions, each tending to owe its exceptional frequency to particular circumstances, such as ability to flourish in disturbed or less hospitable ground or unusual powers of competition, which express themselves in terms of edaphic correlation. The question of shade and mutual protection is also of great importance, and even the commoner species are usually found either in sunny or shady situations, their comparative abundance being due to their occurrence in almost every variety of one or other of these conditions. A few species, while similar in the main, show also some soil preferences, as, for instance, *Senecio jacobaea*, *Galium mollugo* and *Sambucus nigra*.

The less common species, which form the great bulk of the flora, tend to show a more or less rigid restriction to one or other of a small number of major habitat-types, and the general importance of edaphic factors is here particularly clear. Soil conditions vary enormously, but, in the very broadest terms, it may be said that the main variable components are five, all of them related more or less directly to the physiological necessity under which plants live of absorbing water and nutrient salts from the soil, namely the absolute amount of water in the soil; the ability of the soil to retain moisture; the basicity of the soil; the acidity of the soil; and the salinity of the soil. The values of these components depend chiefly on the nature of the parent rocks of the soil, on the topography and on the effects of denudation, and the general effect is to produce six great series of habitats, which may be called, respectively, aquatic, impeded (clay soils), sandy, calcareous, acid and saline. To one or other of these the great majority of species are confined, and only a few show any appreciable ability to occur in more than one, though, naturally, the absolute degree of segregation depends in some measure on the closeness of relationship between the types, it being especially marked between the first two.

Furthermore, most species are less than completely distributed over any one of these. Thus among aquatic plants some, like *Epilobium hirsutum* or *Apium nodiflorum*, are found in almost all watercourses, but others favour certain kinds only, such as the more calcareous or silty or acid. Still others, like *Sagittaria sagittifolia* and *Butomus umbellatus*, find conditions to their liking only in the larger and deeper rivers, and others have different preferences again.

Circumstances combine to make heavier and less well-drained soils particularly plentiful in Dorset and there is every kind, from comparatively light loams to the stiffest and most water-logged clays. Some of the species associated with them are therefore very widespread, but most are much more limited. A very important point about this soil type is that it is especially the one on which dense thicket and woodland develops, and its plants therefore include most of the shade-loving species. Indeed plants of these heavier soils may be described as either woodland species or hay-pasture plants. Of the former a few are fairly widespread, but most are, by the nature of the case, more restricted, as Dorset is not an exceptionally well-wooded county. Among them they illustrate almost every kind of distribution over the woodlands of the area, and the ranges of some of the more local or uncommon, such as *Platanthera chlorantha*, *Melampyrum pratense* and *Ribes rubrum*, are particularly interesting and suggestive. A few species are characteristic of damp bushy places rather than of woodland proper, and presumably find therein conditions particularly suited to them. The distribution of the meadow plants varies a good deal, because some of them seem equally at home in more than one type of soil, and are thus by way of being exceptions to the general rule. *Chrysanthemum leucanthemum* and *Primula veris*, for instance, are found in calcareous grassland as well as in clay meadows, while *Deschampsia caespitosa* and *Serratula tinctoria* inhabit clays and certain other soils with a greater tendency to acidity. Of the plants more definitely confined to clay subsoils, *Silaum silaus* (*S. pratensis*), *Senecio erucifolius*, *Sison amomum* and *Hordeum nodosum* form a series peculiarly associated with the more calcareous clays. *Picris echioides* (fig. 62) and *Tussilago farfara* are frequently found on bare clay surfaces, and this may be partly the reason why they are conspicuously more frequent in the coastal zone.

The chief feature of sandy soils is the rapidity with which water passes through them, in consequence of which they easily become leached of mineral salts, and unless there is an impervious layer below them they are often very dry. On such soils two kinds of vegetation, dry heath and dry turf, generally develop, and each has its own particular plants. The former often covers wide areas and *Calluna vulgaris*, *Erica cinerea* and *Potentilla erecta* are prominent in its flora; the latter occurs more locally and its species are less familiar. Still other species are found in sandy places which are damp at certain times of the year.

When the normal drainage of water from sandy soils is impeded and they become water-logged, the soil water is usually acid because of the absence of neutralising bases, and when this condition is extreme a very specialised kind of habitat results which supports only a few particular species, but when, as in Dorset, there are considerable stretches of wet sand and gravel, almost all degrees of acidity are represented and there is a marked zonation in the distribution of species. In the less acid places several species of *Juncus* are prominent; in soils of medium acidity *Hydrocotyle vulgaris* and *Scutellaria minor* are among the characteristic species; while *Molinia caerulea* (fig. 63), *Myrica gale*, *Narthecium ossifragum*, *Pinguicula lusitanica* and the species of *Drosera* typify habitats of higher acid values.

The calcareous soils of Dorset comprise the chalk and a series of limestones and marls of varied calcium content, and in total cover a considerable part of the county, but the calcicolous species are by no means evenly distributed over them. The great majority of these are found not only on the chalk but also on some or most of the other calcareous formations (fig. 59), but certain species are much more restricted. *Asperula cynanchica*, *Campanula glomerata* and *Gentiana amarella* are among those found almost exclusively on the chalk, while *Cephalanthera damasonium* (*grandiflora*), *Monotropa hypopithys* and a few more are confined to it. On

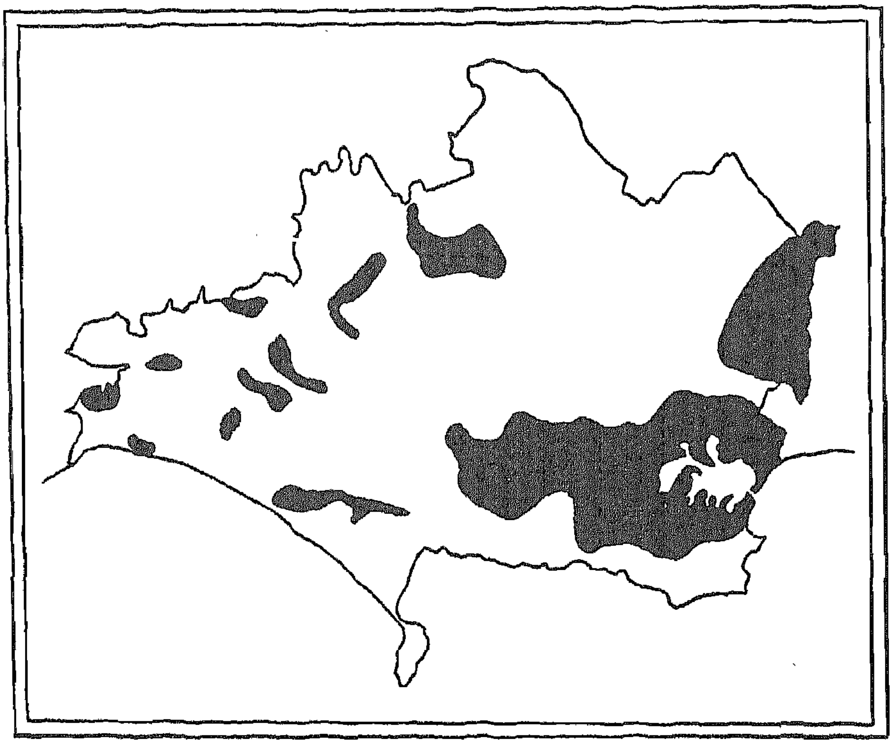


FIG. 63.—Map showing (black) the distribution of *Molinia caerulea* in Dorset.

the other hand, one or two species occur virtually only on certain limestones other than the chalk.

Although so many species are found only on one or other of these main soil types, there are a few which inhabit a considerably wider range of conditions, occurring not only on clays but in mildly basic as well as in mildly acidic soils. Presumably these plants find in all these soils some common factor of importance, but it is also well to bear in mind the possibility that the apparent wideness of distribution may be due to the fact that the species concerned is complex, with more than one ecotype.

The distribution of the halophytes is superficially rather different from the general scheme because of the naturally localised area of their habitats, but the same kind of edaphic segregation and zonation exists here also. This is specially noticeable in plants of tidal soil water such as occur widely in Poole Harbour and in the neighbourhood of Weymouth, but the more specialised habitats, like sand-dunes and shingle beaches, also have their characteristic species.

Only a few species do not fall easily into one or other of the edaphic classes just described, and therefore appear at first sight to be anomalous, but it seems clear that most of them are not really so but are unusual expressions of one or other of these types, their ranges being determined however by factors which, though similar, are peculiar and therefore less obvious.

Species which occur only in habitats which are the result of man's activities, such as cultivated ground and walls, conform to the same general scheme of things.

Since not only the habitats themselves but also their distributions are artificial, the ranges of the species inhabiting them are in most cases rather different from the normal, but this does not indicate any essential difference of plan, and examination shows that there is here just the same kind of segregation according to edaphic conditions and values.

So far we have been speaking chiefly about the extent to which the various Dorset plants occupy the county, but, as was pointed out at the beginning of the chapter, this is only part of the story, and we must consider also the question of the absolute frequency of the species' individuals. There are clearly four main possibilities. The area may be large and the occupation intense, the individuals being both widespread and plentiful; the area may be large and the occupation slight; the area may be small but the occupation intense; or the area may be small and the occupation slight. Such a fourfold classification is implicit in the usual procedure of describing species as "common," "frequent," "local," or "uncommon." It will be noted that the word rare is avoided, since it may refer either to area or numbers, and, indeed, the so-called rarities are plants either very restricted in range or which occur extremely sparingly, and to these the terms local and uncommon are best applied.

The commonest species are naturally those which occur in great numbers over a very wide area, and these have already been alluded to, but the more plentiful species in nearly all the main ecological categories may also be called common, and enough reference to these has also been made.

The term frequent is not quite so easily defined, because this condition may result from one or other of what appear to be two different circumstances, namely, the frequency with which particular kinds of habitat occur and the degree to which individuals may be discontinuously distributed over the range of one kind of habitat. Actually both these express the same fact, that the plants concerned are restricted to certain particular conditions, though in the one case this is more obvious than in the other. Many Dorset plants are frequent in the first sense, as for instance many aquatics which naturally tend to occur only here and there, but the second kind of frequency is on the whole the more interesting. Quite a number of woodland plants are far from general in that type of vegetation, and it is notable how much richer in less common plants some woods are than others. *Epipactis latifolia* and one or two other orchids illustrate this among woods on the chalk, while *Chrysosplenium oppositifolium* and *Ribes rubrum* are characteristic of a particular kind of damp woodland elsewhere. Then there are *Orchis fuchsii* and *Orchis ericetorum* (*elodes*), which not uncommonly grow together but which have quite different total distributions, in which the former is much more frequent. Again, many plants of calcareous grassland, such as *Hippocrepis comosa* and *Helianthemum nummularium* (*vulgare*) occur in only some of the apparently favourable places. In all these it is clear that the plants are confined to localities in which special conditions prevail.

Two other species deserve mention in this connection. *Linaria vulgaris* is often a hedgerow plant, but in these places grows only where it is well exposed and free from shading. It occurs over a wide area mostly on the chalk, and is often enough to be seen, but its occurrences are generally well spaced and it rarely grows in great quantity. *Hypericum androsaemum* is an extreme instance of the same thing. Its distribution, at least in the west of the county, takes the form of numerous but very isolated records in hedges, where the plant is seldom seen as more than a solitary individual, a state of affairs noted for other parts of England also.

The term frequent is peculiarly applicable also to many plants of unnatural status and habitat. Many cornfield weeds, such as *Specularia hybrida*, *Agrostemma* (*Lychnis*) *githago* and *Lycopsis arvensis*, are so, partly because their habitats are discontinuous and partly because each favours particular soil conditions. Similarly with the comparatively few species which normally grow almost exclusively on walls. These by no means occur on all walls but only where special circumstances pertain.

Just as many fresh-water aquatics are necessarily frequent, so the halophytic or maritime species proper are of necessity local in the sense that they are confined to the coast, but even here many have quite a narrow range. Among the salt-marsh species, for instance, *Althaea officinalis* is found only in the Fleet west of Weymouth, and among cliff plants *Brassica oleracea* is virtually confined to Purbeck.

Of inland plants all those which live in highly specialised habitats tend to be local because their situations are so, but this is only to be expected, and it is certain other species which are the most interesting of the locals. Outstanding among them are the two great treasures of the county flora, *Erica ciliaris* and *Pulmonaria longifolia.* The former is confined to a small part of the southern heathlands, and nearly all its records are from an area of about fifteen square miles, although here it is plentiful. The latter is a plant of certain woods towards the east of the county and also ranges mainly over only a few square miles, but here it is relatively much less plentiful. *Wahlenbergia hederacea* is, elsewhere on the heathlands, almost as restricted, and even more so is the calcicole *Ophrys sphegodes*, which is limited to a small part of Purbeck.

Viola palustris combines both the local and uncommon conditions. In the west of the county it occurs locally in connection with the Greensand, but otherwise it is uncommon, and is found only near the Hampshire border in the extreme east.

The uncommon species of Dorset naturally include all the great rarities. The extreme is seen in *Himantoglossum hircinum*, which for several years existed as only a single plant in the Weymouth neighbourhood. Several others have only one locality but therein are in larger numbers. *Melittis melissophyllum* has but one station, where there are two or three plants; *Cyperus longus* has two or three stations and is fairly plentiful in them, and the same is true of *Cladium mariscus.* Most of the uncommon species are, however, more plentiful than this and, like the members of other groups, can be classified according to the soils in which they occur. The following are interesting examples. Among shade plants *Platanthera chlorantha* is found in many woods and is widely scattered, but is always few in numbers. *Sedum telephium* has fewer stations but is rather more plentiful in each, and *Corydalis claviculata* is somewhat similar, though rather local in addition. *Calamintha ascendens* and *Nepeta cataria* occur very occasionally in hedges on the chalk. The rare orchids of chalk pastures, such as *Orchis ustulata* and *Herminium monorchis*, are also noteworthy, and on sandy soils there are other species, including *Moenchia erecta*, *Pulicaria vulgaris* and *Potentilla argentea.* There are still others among the aquatics, while among the plants of strongly acid soils *Hammarbya* (*Malaxis*) *paludosa* is outstanding.

In addition to all these, which except for the cornfield weeds or colonists may be considered native plants, there is a very interesting group of species which seem to have been introduced at some time or other and which vary greatly in abundance and range. Some are found only near human habitations, though the significance of this is not always clear. *Malva sylvestris* is generally found in hedges near villages and is seldom a constituent of more natural plant associations. Rarer and more

Plate 18. *Liriodendron tulipifera*

(from The Standard Cyclopedia of Horticulture by L. H. Bailey, by permission of The Macmillan Company, New York)

conspicuous examples of the same kind are *Chelidonium majus*, *Aegopodium podagraria* and *Smyrnium olusatrum*, the last very much favouring the coast region. *Ribes uva-crispa* (*grossularia*) is apparently wild often enough, but there is little doubt that this is due to bird-dispersal from gardens. The same is presumably true of the crab-apple of hedgerows, which is usually simply a wildling which has grown from the seed of a cultivated variety. The true wild crab does, however, also occur rarely.

More obvious denizens derived from shrubbery or garden plants are *Chrysanthemum parthenium*, *Vinca minor* and *Mimulus guttatus*, while *Linum usitatissimum* and *Onobrychis* are obvious relics of cultivation. *Sambucus ebulus*, sometimes seen in hedges, and *Inula helenium*, mostly found in orchards in the northern part of the county, are of similar but more remote origin. *Atropa bella-donna*, too, is of rather special interest. It is plentiful and frequent in one large private park and occurs occasionally in other parts of the same estate, but there is little doubt that it is directly or indirectly an introduction.

Particular problems are presented by a group of Monocotyledons which occur rarely in more or less natural surroundings and among natural vegetation, but whose native status is at least open to grave suspicion. They are *Narcissus biflorus*, *Leucojum vernum*, *Ornithogalum umbellatum*, *Fritillaria meleagris*, *Simethis planifolia*, *Acorus calamus*, *Tulipa sylvestris*, *Galanthus nivalis* and *Convallaria majalis*. All but the last three are almost certainly long-established denizens, and of these three at least the first has no good claim to recognition as a native.

This chapter may well close with an attempt to estimate the changes which have taken place in the constitution of the county flora in the 150 years or so since systematic records were first collected, because this will help to illustrate several other points of significance and interest in the distribution of Dorset plants.

The continued floristic study of any area tends inevitably towards an increase in the numbers of plants known therefrom, partly because more and more small species are recorded and partly because it is difficult to say what species become, in course of time, lost, and for these reasons there is little doubt that the Dorset flora is, in one sense, richer now than it has ever been. This is probably a fair picture of the balance of change, because it seems certain that additions have more than made up for losses. It is true that the former are mostly denizens or casuals and the latter are mostly native plants, but the general effect is certainly a net gain.

It is, of course, always difficult to be sure that any species has actually disappeared, but there are some which at least have not been seen for many years, and they may be regarded as lost. The most striking examples are *Parnassia palustris*, *Pinguicula vulgaris*, *Empetrum nigrum* and *Hottonia palustris*, all of which have been repeatedly sought for in recent years without result. The most remarkable fact about them is that three of them are markedly, and the last less conspicuously, northern species such as might be expected to disappear in the course of a gradual climatic amelioration, and that they are plants of this kind is highly suggestive.

On the other hand, the frequency with which certain plants continue to maintain themselves in the same stations is very notable. The first serious collection of county records dates from the end of the eighteenth century, and perhaps the majority of these early records can still be verified, showing that the plants concerned have persisted in the same place for at least 150 years.

Of change in relative abundance there is not much evidence except that some of the rarer plants have become even more uncommon, partly because they have been over-collected and partly because certain types of habitat are now much less frequent. For instance, many of the species of bogs and marshes have diminished with the passage of time owing to drainage, and for different reasons the same is doubtless true of some of the cornfield weeds.

Parentucellia (*Bartsia*) *viscosa* is perhaps the best example of a presumed native which is undoubtedly extending its range. Unknown in the county until fifty years ago it has now been recorded from a number of stations. Among adventives the most noteworthy is perhaps *Matricaria matricarioides* (*discoidea*). The first record of it seems to have been about the close of last century, but now the plant is abundant throughout the county. Several horticultural denizens are also gradually establishing themselves, among them the lilac (*Syringa vulgaris*), and Montbretia. The former is perhaps bird-dispersed into hedges and the latter is usually a garden outcast.

Finally, the innumerable miscellaneous problems of plant geography presented by even a county flora may be illustrated by reference to one which concerns two cornfield weeds. *Adonis annua* and *Centaurea cyanus* are both now very scarce in the county, and there is virtually only one persistent station for each. In both cases this is a single arable field and here the plants appear regularly, in the case of the latter often in quantity. Nevertheless this species never seems to spread from the one field, and the former is generally to be found in only one part of a single field, where it has been known, on good authority, for at least forty years.

It is to be hoped that enough has been said in this chapter to fulfil its purpose, which has been to show that the comparative and relative distributions of plants within one and the same area is an important aspect of plant geography, and in particular that two general statements are true. The first is that while climatic conditions may usually be regarded as primarily controlling the area which a species may occupy as a whole, the relative distribution of individuals within this area is, as usually, controlled chiefly by edaphic factors. The second is that a flora is dynamic rather than static, that is to say, that it is constantly undergoing some degree of change. Some species disappear, and others take their places; some become more plentiful, while others diminish. There are, in short, clearly to be seen indications of changes which, persisting over long periods, may eventually lead to marked and considerable floristic alteration.

CHAPTER 14

THE GEOLOGICAL HISTORY AND PAST DISTRIBUTION OF THE FLOWERING PLANTS

THE attention which was paid, in Chapter 3, to the evolutionary background to the study of plant geography makes it abundantly clear that few indeed of the problems presented by the distribution of plants to-day can fully be understood or appreciated without some knowledge of conditions and events, either actually within or in relation to the plant world, in the past. This being so, the second part of this book, which treats more particularly of the theoretical aspects of plant geography, cannot be appreciated without some preliminary outline of the history of the Flowering Plants and of the circumstances which have led gradually to the state of affairs which has been described in the preceding pages. This chapter is therefore devoted to a short account of their history and of their distribution in the past.

The Geological Time Scale

In the course of secular time the vegetation of the earth has gradually changed and developed by the processes of evolution. Little is known about the earliest plants of all, because they have left practically no traces behind them, but they were certainly gradually supplanted by new types. These newer types in turn gave way to others, each new development giving, for the time being, a particular character to the world vegetation.

This knowledge has come from the study of what is often called the "record of the rocks," that is to say, of the organic remains which, from time to time, have become imprisoned in sedimentary deposits, where they are familiar to us in the form of fossils. The story of fossil plants has been most graphically and admirably told by Seward in *Plant Life through the Ages* (483), and this, or the much shorter account of Reid and Chandler (445), should be consulted by those readers who wish to amplify the outline contained in this chapter.

It is believed that plant life began in the sea, and that plant evolution has been largely directed towards the attainment of the complicated and beautiful structural organisation which enables modern plants to colonise the land surfaces of the earth, and to exist as successfully in a subaerial medium as they did formerly and still do, to some extent, in subaqueous and particularly marine habitats. That is to say, it is, in a single phrase, the change from the kind of form possessed by such plants as the seaweeds to that exhibited to-day by the Flowering Plants. Coincident with these structural developments there have been equally great changes in reproduction and in life history.

The fossil record indicates that the history of each new group of plants has always followed much the same course (see also pp. 41 *et seq.* above). First, there appear a few isolated examples of the new type. Then gradually, but at a constantly accelerating speed, these new types multiply until in a comparatively short time they become the dominant vegetation of the world. This position of supremacy they hold for a while, and then, as rapidly as they rose, they tend to diminish before the competition of still newer plants until eventually they disappear entirely or persist merely as a few meagre survivors of a great but long-dead past. Not all newly evolved plants necessarily pass through the whole of this cycle. Many never succeed in establishing themselves; others may do so on a small scale but never develop into important elements in the vegetation. Nor must we think of this developmental cycle as something peculiar to plants. It is found in all aspects of life and even in the life of the individual. He is born; he slowly or more rapidly reaches maturity; he flourishes or the reverse; and he more slowly or rapidly declines, until he finally and inevitably passes away.

The whole sequence of the rocks that have been formed since the beginning of secular time is divided by geologists into five great eras based chiefly upon the kinds of fossils that the various formations contain, though it may be doubted how real some of these sharp divisions are (435). The first era consists of the oldest rocks, and these include no fossils, because they represent a time when life on the earth, if it existed at all, was of so simple a kind as to have left no traces. This is called the Archaeozoic era. Next comes the Proterozoic era, the rocks of which contain some evidence of life, but only of the most primitive sort. This is followed by the Palaeozoic era, and here, for the first time, the plant remains become abundant and unmistakable, though they all represent ancient groups of plants such as ferns, club-mosses and the very earliest and simplest kinds of seed-plants. Next comes the Mesozoic era, during which the vegetation consisted chiefly of ferns and Gymnosperms. Finally, there is the Caenozoic era, and this is generally described as the era of the Flowering Plants. Each of these eras is divided into shorter time divisions called periods. Of the Archaeozoic and Proterozoic eras no mention need be made here since they are so far in the distant past as to be outside our immediate consideration. The Palaeozoic era is divided into six periods called respectively, and beginning with the oldest, Cambrian, Ordovician, Silurian, Devonian, Carboniferous and Permian. The Mesozoic era consists of three periods, Triassic, Jurassic and Cretaceous, and the Caenozoic era of two periods, Tertiary and Quaternary. To-day we are living in the last named.

This short description of the geological eras and periods almost inevitably leads to the question of the length of geological time. Many answers have been given to this question but none can claim to be more than an estimate. That the total is to be reckoned in millions of years cannot be doubted, but how many millions it is impossible to say. Much depends on the method of estimation used, and readers may be referred to Holmes (268, 269, 270) for an account of these. It can only be said here that estimates range from something of the order of 20 millions to something exceeding 2,000 millions, but probably a space of some hundreds of millions is nearer the mark. As to the proportions of the whole occupied by the different eras, it is only natural that the remoter the time the more hazy are our ideas about it but the general opinion about the far-distant Archaeozoic and Proterozoic is that they probably accounted between them for at least half of geological time and perhaps considerably more. Of the total time which has elapsed since the beginning of the Palaeozoic there are close estimates (65, 613) and these agree that the figure is round about 500 million years, of which rather more than half, perhaps 275–300 million years, was occupied by the Palaeozoic itself. The Mesozoic is thought to have lasted about 120–150 millions; and the figure for the Caenozoic is in the neighbourhood of 70 millions. Of this last figure all but one million years are allotted to the Tertiary.

But millions and percentages convey little, and it is worth while putting the matter in more picturesque form. This can be done by imagining the whole of geological time to be represented by a vertical stick 36 inches long. On this stick the first two eras will occupy the bottom 20 inches or so; the Palaeozoic will cover the next 9 inches; the Mesozoic 5 inches; and the Caenozoic about 2 inches. Of this last era the Tertiary will account for all but about one-twenty-fifth of an inch. At this end of the scale the time divisions are more comprehensible and another illuminating statement can be made. If, working backwards from the present, the generous estimate of 10,000 years is allowed for the duration of human history proper, then this time, the time during which man has ruled the world, will on the scale be represented by something of the order of one-thousandth of an inch, that is to say, less than the thickness of the thinnest tissue paper. Fig. 64 is a

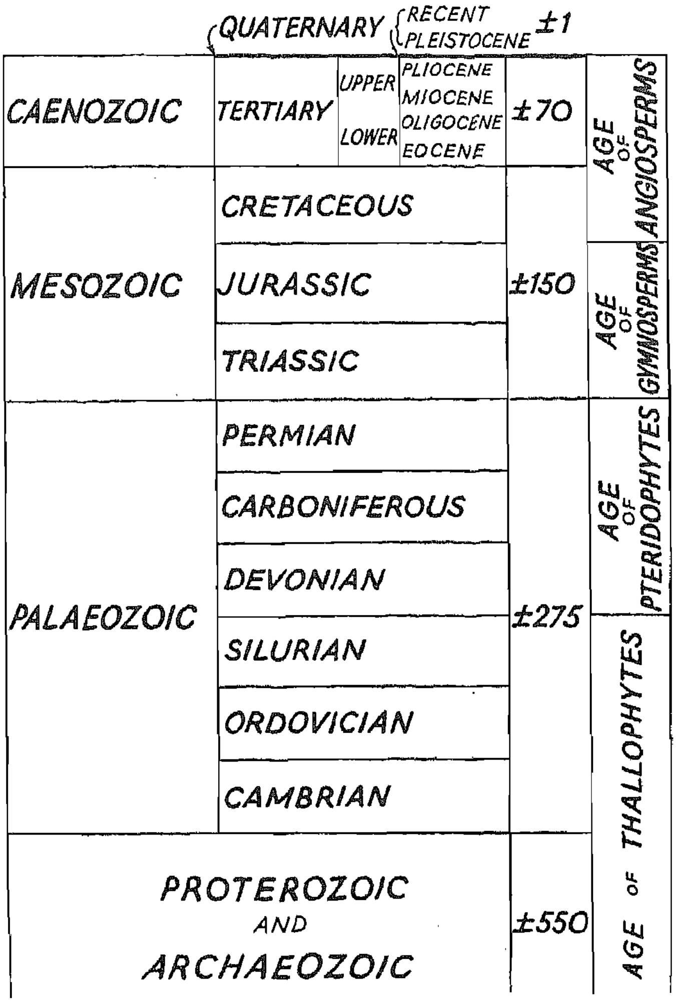


FIG. 64.—Diagrammatic representation of the *upper half* of the geological time scale.

The figures indicate the durations, in millions of years, of the four epochs, and also of the Quaternary which is more than represented by the thicker middle part of the top line. No attempt has been made to show the relative lengths of the other periods, a matter on which opinion is divided. Compiled from various sources.

diagrammatic representation of the upper half of the geological time-scale and shows most of the figures and divisions which have been mentioned.

The Caenozoic era was described as the era of the Flowering Plants, and an account of the history of these plants will therefore chiefly concern this time. This is not altogether so, however, because the Angiosperms certainly made their appearance some time during the preceding Mesozoic era, although it was not until the Caenozoic that they became abundant.

As was stated above, the Mesozoic era is divided into three periods, Triassic, Jurassic and Cretaceous, and the first of these contains no known fossils for which an Angiosperm nature can be claimed. In the Jurassic, on the other hand, there are several fossil types which, it has been submitted, represent very early and primitive kinds of flowering plants (618). Chief among these is a group of plants called the Caytoniales, described from the Jurassic rocks of the Yorkshire coast. They need not be discussed further here, but those who wish to know more about them may refer to the writings of their discoverer, Hamshaw Thomas (553), and to the more recent comment of Walton (572). It should be mentioned, too, that some of the Jurassic Cycadophyta are also thought to be the immediate ancestors of at least certain of the Flowering Plants. More recently Erdtman (162), has claimed that some tricolpate pollen found in early Jurassic shales in Scania is Dicotyledonous, and Simpson (491) has identified a pollen grain from the Jurassic of Scotland as that of a water-lily. Until these identifications are confirmed by other evidence, however, it remains that the first certain fossil Angiosperms are recorded from rocks of the Cretaceous period. For the most part they are the remains of leaves only, but they include a few fruits, notably those of a plane tree, and they are in general indistinguishable from modern Angiosperms.

This point brings us to one of the most curious features in the fossil history of the Flowering Plants, which is that the group appears almost suddenly and, as it were, ready made. There is scarcely a trace of any introductory types. In one series of rocks the plants are almost entirely absent; in the next they are present, not only in considerable numbers but apparently also in many of the forms which they include to-day. This sudden rise of the Angiosperms has long been an unsolved problem, and Darwin, indeed, refers to it as "an abominable mystery." One possible explanation is that a notable gap exists in the fossil record just at the time when Angiosperms were beginning to evolve, so that no traces remain of their earliest forms. There is something of a tacit assumption that the whole of geological time is represented by sedimentary rocks somewhere or other but the possibility that this is not so, and that long periods of years may have passed without leaving recognisable trace of themselves in the geological record, is a possibility. It may be argued that conditions adverse to the formation of sedimentary rocks would also be adverse to the existence of Flowering Plants but this is to dismiss the problem too easily for there are various circumstances in which an absence of normal deposits may come about, and the possibility that these plants did, in fact, arise at a time and at a place of which, now, there is no trace in the record must not be dismissed too summarily. Umbgrove (565), for example, points out that the rise of the Angiosperms is associated chronologically with one of the largest marine transgressions. This problem of possible breaks in the geological record deserves careful consideration and there is an interesting discussion of it by Heilprin (257), while Sahni, in a striking paper (458), has dealt with some of the larger theoretical implications of these supposed gaps. On the other hand, fossils of the earliest Angiosperms may yet await discovery in some remote, or for that matter even familiar, part of the world. Whatever the truth may be, however, the early history of the group is at present largely wrapped in mystery. All that can be said with safety is that they were well established by the latter part of the Cretaceous period and had by then become a conspicuous element in all contemporary floras. By the beginning of the succeeding Caenozoic era they had become the dominant plants of the world, a position they have retained ever since.

The Caenozoic era is divided into two, the Tertiary and the Quaternary, but this division is in many ways an artificial one, and from the botanical point of view there is little reason for it, because the same types of plants persisted through both. At the same time the division does mark and emphasise a very important stage in their history.

The Tertiary is divided into four sub-periods, named the Eocene, the Oligocene, the Miocene and the Pliocene, the first being much the longest. Throughout at least the first three of these the general conditions of climate in the world seem to have been fairly constant, and tropical or warm-temperate conditions seem to have been widespread, as indeed they also appear to have been during the later part of the Cretaceous. There was some change, it is true, in the main towards a lessening of temperature values, but these changes were comparatively small. By the beginning of the Pliocene, however, evidence of change increases, and in the course of this epoch the change became accelerated and almost catastrophic. For reasons which are not fully understood and which are doubtless complex (see chap. 19), the temperature, at any rate in higher latitudes, deteriorated very rapidly and finally sank to levels that resulted in widespread glaciation. For the first time for millions of years, conditions of ice and snow returned to the earth and there arose the kind of steep temperature gradient between the equator and the poles which is familiar to-day. It is this relatively sudden change of climate that is made the basis of the artificial division of the Caenozoic era into two parts, the Tertiary being considered to end with the oncoming of glaciation and to pass into the Quaternary, which comprises the whole of subsequent history. The Quaternary is itself divided into two, the Pleistocene period, which comprises the actual glacial ages, and the Recent period, which comprises the time which has elapsed since the latest glaciation, but this is an even more artificial separation, because this latter time is very short and affords no real evidence that the glacial ages have in truth ended, so that it may rather be but an interval between two of their more extreme manifestations.

The Identification of Fossil Plants

It was explained at the beginning of this chapter that our knowledge of plants in past ages is derived entirely from the fossils which are to be found in the various sedimentary rocks. At first sight this might seem a very simple and satisfactory source of information, and this indeed it would be were it not that the accurate identification of plant fossils, and especially those of Flowering Plants, is, for reasons which must be considered shortly here, a matter of great difficulty.

This difficulty arises from two distinct but related circumstances. The first is that the process of preservation in the rocks, or fossilisation as it may be called, is hardly ever so satisfactory as to reveal more than a small proportion of the characters of the plants involved. The second is that plant fossils rarely consist of more than a few small detached organs. Never is there found a fossil which comprises the complete whole body of any plant of appreciable size.

The actual methods by which fossils are formed are such as also to add to the problem. This is not the place to describe these methods in detail—fuller information about them must be sought in standard works on palaeobotany—and it is enough here to point out that by far the commonest and most abundant plant fossils are of the sort called "impressions." These, as their name implies, are in fact prints of the original tissues left from the pressure of their outline and relief on the texture of the sediment in which they became imbedded. These impressions are comparable with the "rubbings" by which such low reliefs as the designs of old brasses and old coins are reproduced, and they bear much the same kind of relation to the original. In short, they reproduce the outline and, to some extent, the surface relief of the tissues but do little else.

By certain other methods of preservation, such for instance as petrifaction, where the whole tissue becomes impregnated with silica, much more is revealed, and where portions of flowers, fruits or seeds are concerned even impressions are generally enough to allow of fairly trustworthy identifications, but where leaves only are involved the difficulty of accurate determination is very great. Unfortunately, as has been said, the great majority of Angiosperm fossils at least are the impressions of leaves only, and the problems involved in identifying these colour the whole picture of the fossil record of this great group of plants.

Let it be said at once that the plant geographer has always been and is likely to remain under a deep obligation to the palaeobotanist, and it would indeed be ungrateful to belittle this debt in any way. At the same time palaeobotanists themselves would certainly be the last to wish that this sentiment should hamper a critical discussion of the difficulties attending the identification of Angiosperm fossils.

This problem of identification can best be expressed in the form of two questions. How far can leaf form be accepted as diagnostic of different kinds of flowering plants? How far can the character and form of a whole large plant be deduced from the features of a few detached leaves?

As regards the first question it can only be pointed out that leaves are the most plastic and variable of all plant organs, and that the number of types and designs of leaves is infinitely smaller than the total number of plant species, so that there are many plants with almost identical leaf forms and designs. In some cases, of course, the foliage of a single plant species is characteristic, as, for instance, we assume to be the case in the tulip tree (*Liriodendron*) (Plate 18, fig. 65), which has

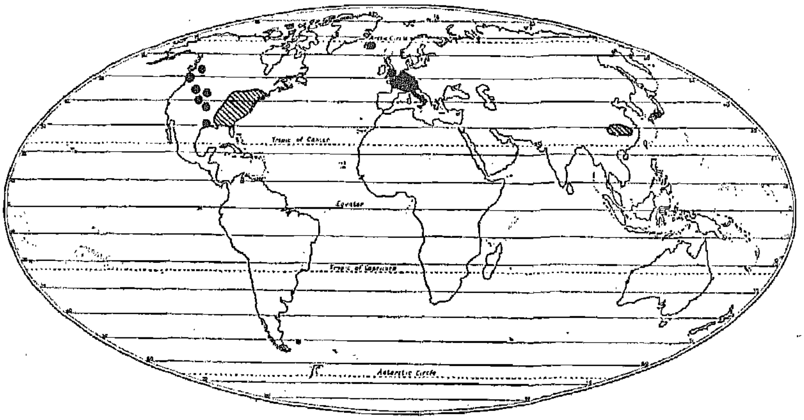


FIG. 65.—Map showing the past (black) and present (shaded) distribution of the genus *Liriodendron*, partly after Berry.

leaves unlike those of any other known tree; but even this is not quite enough, because it does not establish beyond doubt that this is equally true of the past and that every fossil leaf of this pattern belonged to this genus. Indeed, to suppose that all fossil leaves can be identified with plants which are alive to-day is demonstrably fallacious, since there are certain fossil leaves which bear no resemblance to those of any known living plant. These clearly cannot be identified with any modern plant, and it may well be that some other fossil leaves which superficially resemble those of known plants actually belonged to different ones. But the case of *Liriodendron* is quite exceptionally straightforward, and the great bulk of fossil leaves are of far more generalised types, such as are possessed to-day by numbers of distinct and unrelated plants, and in these cases identification is often difficult and sometimes well-nigh impossible.

The second question also admits of no ready answer. It is only necessary to pick and compare a number of leaves from different parts of the same plant to realise how difficult it is to say that any one is specially typical and characteristic of the species to which the plant belongs. There is nearly always variation among the leaves of any one plant, and more aberrant examples may often resemble the more typical leaves of a species other than that to which they in fact belong. Furthermore, individual detached leaves do not necessarily reveal all the characteristics of the foliage of the plants to which they belong. Such features as leaf-number and arrangement are generally far from clear, and it is even sometimes difficult to determine whether a fossil is really a complete simple leaf or only a portion of a compound one. Thus it will be seen that the identification of detached fossil leaves is full of pitfalls, and it is not surprising, therefore, that many attempts have been made to elucidate, by special methods of preservation, characters of the fossils which may not at first sight be readily apparent. For instance, minute details of cuticle structure have often been studied (31, 32) in the hope that they may substantiate determinations, either by their own virtue or in conjunction with other features; but the results have not been altogether satisfactory, since similar types of cuticle structure are frequently possessed by plants of quite different affinities.

In view of these difficulties it is generally admitted that identifications and records based solely on detached fossil leaves, that is to say, on leaves unattached to any axile structures and unaccompanied by other organs, must be regarded with caution and treated to a certain extent as provisional, requiring confirmation or correction as and when means of doing this become available. This is not, of course, to condemn all such records as unreliable. There is little doubt that many of them are correct, but it is only fair to say that these are generally those of least importance and tend simply to confirm what has been discovered from other sources. On the other hand, where fossil records have raised the greatest problems it will usually be found that the records and determinations must themselves be regarded as problematical. The problems may exist, but the evidence that this is so can only be called unsatisfactory.

It is worth while to illustrate this point by one of the most outstanding examples of it, namely the oft-reported occurrence as fossils in the northern hemisphere of genera and species now more or less rigidly confined to the southern hemisphere and generally considered characteristic of that zone. In particular, many fossils have been ascribed to *Eucalyptus* (now confined to Malaysia and Australia) and to the Proteaceae (almost entirely southern in distribution), the supposed fossils of which have been resurveyed lately by Kausik (313). If the determinations of these fossils are correct they may completely alter our whole conception of the origin and development of Angiosperms. Yet when the matter is further investigated and the specimens and illustrations examined, it can be said with perfect fairness that there is no single completely non-controversial fossil among them. In every case the identification is open to some reasonable doubt on purely morphological grounds, and this is the case even in the rare instances where the fossils are the remains of fruits rather than leaves. In short, these fossils may, as some authorities firmly believe, be the remains of the plants mentioned; but they may not be so, and there often seems little *prima facie* reason for their identification. While some authorities accept them others (17, 43) reject them, and they must certainly be regarded with an open mind. Lately, however, this particular problem of the past occurrence of southern plants in northern latitudes, has taken a new turn in the identification of such types from pollen grains, as in Simpson's studies, referred to by Godwin (206), of the earlier Mull flora. This use of pollen technique in this connection is of great interest but until there is a much more complete knowledge of the characters and specificity of pollen and of the changes which it may undergo in the process of fossilisation, it cannot be claimed that much progress has been made. It must also be remembered that unless the group with which the fossil pollen is identified has pollen which is unmistakably different from that of all other groups, any identification loses much of its value. Again it is not irrelevant in this connection to recall that when fossil Angiosperms were first recorded from the Antipodes they were commonly, and it is now generally admitted erroneously, identified with northern types (*e.g.* 164). To-day the sum of our knowledge of Angiosperm fossils outside the northern temperate suggests that they normally consist of plants very similar to those now living in the same localities.

Angiosperm fossil floras vary considerably in content, no doubt according to the actual circumstances or their origin, and fortunately not all consist exclusively of detached leaves. Some contain a few fruit or seed structures among numbers of leaves, and a few consist largely or entirely of reproductive structures. These latter are of special value and importance, not only because reproductive structures are actually more diagnostic than foliar structures but also because they are much less plastic and vary much less as a result of differences in the environments of the plants which bear them. At the same time it must be remembered that in theory at least there is no reason why two different species, one extinct and one recent, should not have fruits which are indistinguishable when one is in the fossil condition.

Apart from the difficulties of identification there is inherent in the fossil record the difficulty, amounting sometimes almost to impossibility, of correlating the geological horizons in different places and of synchronising the floras which they contain. Were it possible to be certain of the correspondence and relationship between strata widely separated in space, the advantages would be twofold. It would be possible to place the floras of the past in their proper chronological order and to see, without confusion, the succession in which the different kinds of plants flourished, and in addition, it would be possible to trace the variation over the world's surface among contemporary floras. At present it is often extremely hard to say which of two fossil floras is the older or whether two floras from distinct regions are of the same age. This particular problem is well illustrated in a paper by Chaney (91). In it the author begins by characterising each of a number of fossil floras as cool-temperate, temperate, intermediate or subtropical. He then plots the positions of these floras on a map of the world and, by joining together those to which he has given the same climatic description, draws lines, which he calls *isoflors*, from the distribution of which he comes to certain conclusions. These conclusions as to the former distribution of certain climatic values may in fact be entirely justifiable but it is clear enough that the proof of this by the use of isoflors can have validity only when there can be no room for doubt as to the exact contemporaneity of the fossil floras involved, and the paper makes it clear that this fundamental basis does not exist. Still another, somewhat allied problem, is the possibility that the remains of plants living far apart may occur together as fossils, and in this connection one is reminded of Guppy's observation (241) that sea-borne seeds of tropical species have been found semi-fossilised in Scandinavian peats.

It is chiefly because of these difficulties that no one can say exactly when in the course of geological history the Flowering Plants originated. The normal processes of evolution also militate against the recognition of a hard and fast date of first appearance. As far as our immediate purpose is concerned, therefore, it is best to place an arbitrary limit to the enquiry and to begin the story of these plants at the point when they first begin to form an appreciable proportion of the whole existing plant world.

There is unanimous agreement among palaeobotanists that the earliest fossil floras containing a considerable proportion of undoubted Angiosperms belong to the older part of the Cretaceous system, itself the last of the three great periods into which the Mesozoic era is divided. There also can be no doubt that the Angiosperms arose, by the processes of organic evolution, from some pre-existing group of plants, although what kinds of plants these ancestors were is uncertain. It is thus comparatively easy to answer two of the three leading questions relating to the origin of the group, namely how and when they came into being, but the third question of where this may have taken place is still very debatable. The reason for this resides in another of the limitations of the fossil record, but in this case it is a limitation which may eventually be removed.

It is that naturally enough the fossil plants of those parts of the world, North America and Europe, where scientific investigation has the longest and most important history, are vastly greater in number and much better known than those of other regions where the opportunities for their study have been fewer. Coupled with this is the fact that the actual land surfaces of the northern hemisphere are much greater than those of the south and may therefore be expected to contain a much larger absolute number of fossils. For all these reasons the fossil record is, to a great extent, the record only of the north, and we should be on guard against any assumption that the northern flora has therefore any exceptional inherent importance. Indeed, it is probable, for various reasons, that it is to the fossil floras of tropical and southern latitudes that we must look for the solution of many problems, and it is satisfactory that while the number of these is still comparatively small, the sum of information regarding them is steadily increasing. Moreover it is beginning to show more and more clearly an overall continuity of floras, namely that most fossil Angiosperm floras compare, within reasonable limits, with the present floras of the same region, rather than any evidence of profound change.

Thus it is true to say that the fossil record has as yet been of little assistance in elucidating the place of origin of the Flowering Plants, which still remains one of the most fundamental of our ignorances concerning the group. There are various opinions as to where this may have been, but these are generally based on deductions from the present distribution of these plants rather than from the past, and the fossil Flowering Plants known to-day scarcely support any particular view. The answer really depends upon another question which also cannot as yet be answered definitely, namely whether the Flowering Plants as a whole are to be regarded as having had a monophyletic origin or not. Are they all related by descent from a single common ancestor or small group of ancestors or have they originated from a number of relatively distinct ancestral types, their general similarity to-day being due to convergent, or at least parallel, evolution? If the former is true then they must have had a single place of origin, and in the face of the evidence from all kinds of sources it is difficult to resist the belief that this must have been somewhere in or near the equatorial regions (wherever these may have lain at the time), but if the latter is true they may have arisen in a number of different places and even, possibly, separately in both northern and southern hemispheres, as well perhaps as in the equatorial zone itself. At present all this is unrevealed. The fossil record alone may in time provide the necessary clues, but progress in many other branches of knowledge, such for example as palaeogeography and palaeoclimatology, may be of great assistance, and the botanist who is interested in this problem must keep well abreast of developments along these lines.

The Floras of the Past

The chief Cretaceous fossil floras are found in North America and in Greenland, though others of rather less importance have been described from many other parts of the world, including a number from Europe. Opinion about the age of the Greenland floras differs. Seward (480, 483) says, "It is probably true to say that in no other part of the world have familiar types of Angiosperms been described in rocks as old as those of Greenland." Knowlton (317), on the other hand, considers them to be of Upper Cretaceous age. These floras are very rich and include such genera as *Artocarpus*, *Platanus*, *Ocotea*, *Cinnamomum* and *Magnolia* (483). Apart from Greenland, probably the oldest flora containing a considerable number of Angiosperms is the Potomac flora of Maryland and Virginia. There are also several rich Upper Cretaceous floras in North America, including the Raritan of New Jersey, the Dakota flora, the Tuscaloosa flora of Carolina and Alabama, and various floras in Alaska (266).

Regarding the constitution of Cretaceous floras in general, Berry (42, 44) has emphasised the fact that they contain a mixture of what would be called to-day tropical and temperate genera such as is now found in southern Chile, south Japan and New Zealand. That is to say, they may be described as indicating the occurrence in their time of a warm-temperate or subtropical climate.

The question of the extent to which fossil floras are evidences of climatic conditions is a very important one. There is in general no doubt that deductions based on the nature of fossil plant remains are sound, provided of course that the determinations of the fossils can be relied upon. This is particularly well illustrated in some of the earlier descriptions of floras from the arctic regions. Many of the fossils in these were originally attributed to genera of a tropical or subtropical character, and on the strength of this there grew up the belief, still widely held, that during the earlier stages of Angiosperm history the climate was of corresponding value up to the highest latitudes. More careful comparison of these fossils with modern plants, however, seems to show, as Berry (47) has pointed out, that these "tropical" identifications are unsound and that the plants must rightly be attributed to more temperate genera. Chaney (90) has similarly thrown doubt on the determination of many North American fossils, and in particular records his belief that of the 150 fossil species of *Ficus* described therefrom, the majority belong to other and "less romantic" genera. It would seem therefore that the opinion formerly held that a tropical or, at least, subtropical climate extended in the Cretaceous and early Tertiary almost or quite to the North Pole must be modified. That there was a well-developed vegetation there is evident enough, but that it was anywhere in these high latitudes of more than temperate facies and relationship is very doubtful. But whatever may be the exact truth about this, the impression left by the Cretaceous floras is that in their time the temperature gradient from the equator to the poles was much less steep than at present and that floras were more widespread and generalised in character. This state of affairs seems to have persisted into the Tertiary, and the actual passage from the Cretaceous reveals no marked floristic change, so that the distinction between the two is, on this count, rather an arbitrary one.

By the end of the Cretaceous the Flowering Plants had attained that predominance in the plant world that they have ever since maintained, and the fossil floras of the Tertiary, which are innumerable, all show the same general constitution that is to be seen in living floras. Much the greater part of the whole Tertiary era was occupied by the Eocene, and fossil remains of this time are abundant. The coastal plain of eastern North America (48) has revealed thousands of fossils and seems to have been inhabited successively by three rather distinct floras—the Wilcox flora, the Claiborne flora and the Jackson flora, all of which contain some markedly tropical types, indicating a considerably warmer climate than had prevailed in the Cretaceous. Further west in North America the Raton flora from Colorado and New Mexico was probably contemporary with the Wilcox; the Fort Union flora extended far to the north; and in the coastal region the Puget flora may be of the same age as the Fort Union. Particularly, in thinking of these latter floras it should be remembered that the Rocky Mountains did not then exist, at any rate in anything like their present form (46). The early Tertiary floras of Alaska are also considerable (267).

In Greenland the Eocene floras are generally thought to date from the latter part of the period. They are especially abundant and well known in the neighbourhood of Disco Island on the west coast, at a latitude of nearly 70° N. They contain many forms which to-day are characteristic of the north-eastern United States.

In Britain there is a small flora, presumably of early Eocene date, from the island of Mull, but far more extensive and important is the great fossil flora of lower Eocene age from the London Clay of what is now the London Basin. Not only is this flora very rich but it consists almost entirely of well-preserved fruits and seeds so that the identifications of its constituents are unusually reliable. This great flora has been re-studied and monographed on a monumental scale by Reid and Chandler (446). Practically all the specimens are illustrated in a series of fine plates, and the result is a singularly convincing volume whose conclusions permit of little or no difference of opinion. The flora consists of about 250 species, and these include the palms *Nipa* (Plate 19, fig. 66) and *Sabal*, as well as *Cinnamomum*, *Endiandra*, *Hugonia*, *Iodes*, *Lannea* (*Odina*), *Leucopogon*, *Litsea*, *Magnolia*, *Meliosma*, *Ochrosia*, *Olax*, *Oncoba*, *Spondias*, *Symplocos*, *Tetracera*, *Tinospora*, *Toona* and *Vitis*. Although the list of determinations is rather different, the flora is on the whole like the other Eocene floras mentioned, the difference being largely due to the fact that the well-preserved fruits and seeds permit an exceptional accuracy of determination and discrimination. Reid and Chandler's monograph does not confine itself merely to the description of the fossils but discusses this and other Eocene floras in a most interesting way. The authors reach a number of conclusions of which the most important to note here are that the flora is of the tropical

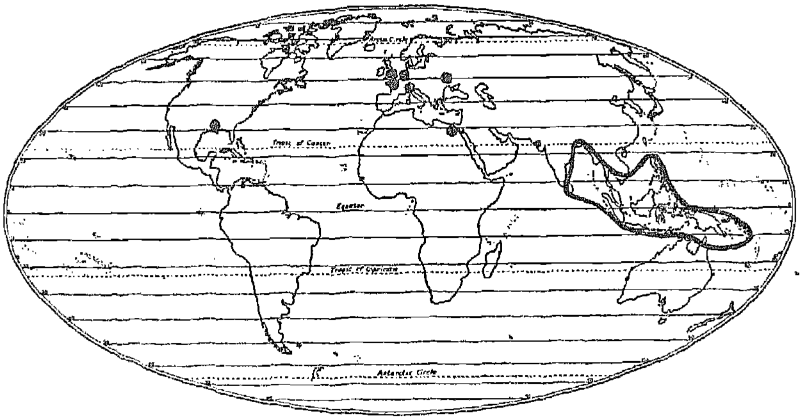


FIG. 66.—Map showing the past (black dots) and present (heavy outline) distribution of the genus *Nipa*, partly after Berry.

rain-forest type; that it has a marked affinity with the present flora of Indo-Malaysia; and that it probably reflects a mean annual temperature of about 70° F.

The impression given by the Eocene floras serves to emphasise that derived from Cretaceous remains. There was no considerable break between the two periods either in plants or in climate, although the climate of the Eocene seems to have been warmer, and the latter was, so far as the vegetation is concerned, more or less an extension of the Cretaceous. The two together suggest strongly that there may have been something in the nature of a single extensive and generalised flora over much of the whole world or at least over the northern hemisphere, though there cannot have been any complete elimination of the latitudinal climatic zonation. Chaney, indeed, in an interesting summary of the North American Eocene floras (92) recognises a Neotropical-Tertiary flora which ranged northward to 49° in the west and to 37° in the east, a Madro-Tertiary flora which occupied parts of south-west North America and an Arcto-Tertiary which occupied the land north of the first, up to the highest latitudes. Both the first and last of these at least moved gradually southward later in the Tertiary as the climate became slowly less genial. In addition to all these there was a Palaeotropical-Tertiary flora in the Old World and an Antarcto-Tertiary flora in the southern temperate regions.

The Oligocene sub-period which succeeded the Eocene left comparatively few fossils. It is fairly well represented in Europe, including the south of England, and in North America, but there is only one flora that calls for special mention here. This is the Bembridge flora from the Isle of Wight, which like that of the London Clay has been monographed by Reid and Chandler (444). It is not a very large flora, and in general somewhat resembles the Eocene Wilcox flora except that there are rather more herbs. Its special interest is the resemblance and affinity that many of its plants bear to types at present found only in North America and Asia, and there is an inference, if no more, that these plants may, in Oligocene times, have been part of a completely circumboreal flora, the greater part of which has since been destroyed, leaving only two widely separated remnants. Although the Oligocene floras are scanty, they are sufficient to show that here again there was little real change accompanying that from the Eocene to the Oligocene. That there is some change is true, but the comparison of the Bembridge flora with the Wilcox is enough to suggest that it was relatively slight.

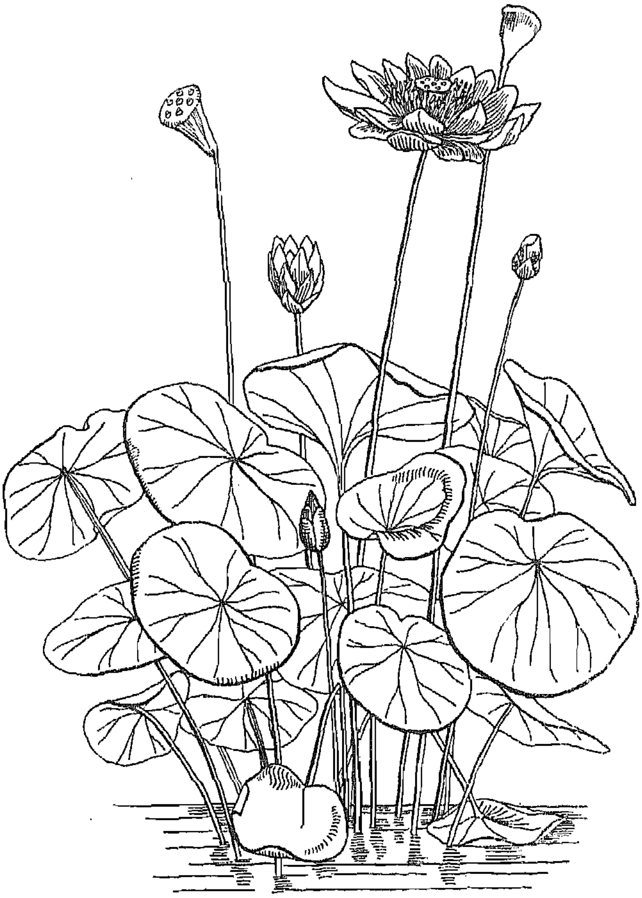


FIG. 67.—*Nelumbo nucifera*, much reduced, after Baillon.

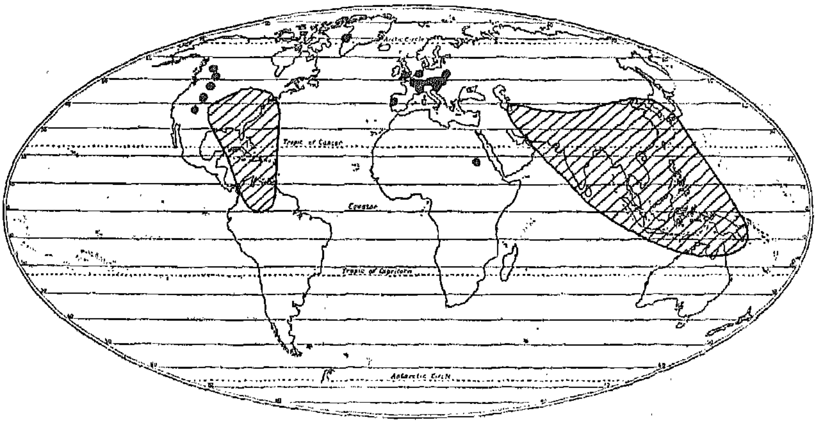


FIG. 68.—Map showing the past (black) and present (shaded) distribution of the genus *Nelumbo*. The evidence for the occurrence of the genus in Greenland is scarcely convincing.

The Miocene sub-period is, like the Oligocene, short compared with the Eocene and has correspondingly fewer remains, and the important floras of the time are found chiefly in western North America and in Europe. One at least from each region needs special mention. The first is the Florissant flora from Pacific North America (105), which is actually one of several floras closely related in time and space. It contains about 250 species, among them being many plants familiar in similar latitudes to-day. The second outstanding flora is that from Oeningen in the neighbourhood of Lake Constance and should perhaps be reckoned as partly Oligocene and partly Miocene. It, again, is but one of a number of floras which together have been described by Knowlton as "probably the richest plant deposits known anywhere in the world." The total number of species described approaches a thousand, but the flora of Oeningen itself contains about 500, some quarter of which are herbs. Most of the fossils are beautifully preserved and enhanced by the fineness of their details. They include, moreover, a good proportion of flowers and fruits. The identifications of the Oeningen fossils show that the flora was in general very much of the same kind as the Florissant or, at any rate, consisted of plants which are associated with similar conditions of climate. Both, however, differ appreciably from any preceding floras in that they indicate a climate rather, and perhaps much, colder. It would appear, therefore, that during the Miocene the climate and flora, which had been comparatively constant for so long, began slowly to change, and that in the direction of more temperate conditions. But this is not the only way in which the Miocene indicates change. It was a time of great earth movements and of intense volcanic action and mountain folding, and it is from this period that the greatest mountain ranges of the world date.

The last of the Tertiary sub-periods, the Pliocene, is generally considered to have been shorter than any of the others, and remains of it are scarce. They are widely scattered but nowhere abundant, and it is fortunate that those of Europe are complete enough to give a fairly good picture of the period as a whole, because the Pliocene provides some most important links in the history of the Flowering Plants. The outstanding feature of the period is that, unlike what has been seen before, it illustrates conspicuous floral changes, and these are best realised from a description of successive Pliocene floras. Particular reference may be made to three fossil floras closely related in space but usually assigned horizontally to the Lower, Middle and Upper Pliocene respectively. The first and oldest of these is the Reuverian flora from the Dutch-Prussian border in the neighbourhood of the Rhine. It contains some 300 species which are of distinctly warmer affinity and type than those now living in the locality, and which suggest a flora not unlike that of the Miocene. There is also, as was noted in the Oligocene, a very marked relationship with plants to-day living in eastern North America and eastern Asia. The second or Teglian flora also comes from the Dutch-Prussian border and differs from the first chiefly in having more herbs and aquatics and much less affinity with the American-Asiatic flora. The third or Cromerian flora comes from East Anglia and belongs to the end of the Pliocene. All but about 5 per cent. of its species are identical with those now living in eastern England, and the American-Asiatic affinity is almost gone. Conversely this flora may be described as practically that of the same region to-day. These floras contain many seeds and fruits and have been carefully studied by the Reids (442), whose work on this kind of plant fossil is so well known.

The correlation of other Pliocene floras is too uncertain to make possible any real comparison with those just mentioned, but most of them reveal floras very like those of the same regions to-day. The comparatively rich fossil floras of Japan,

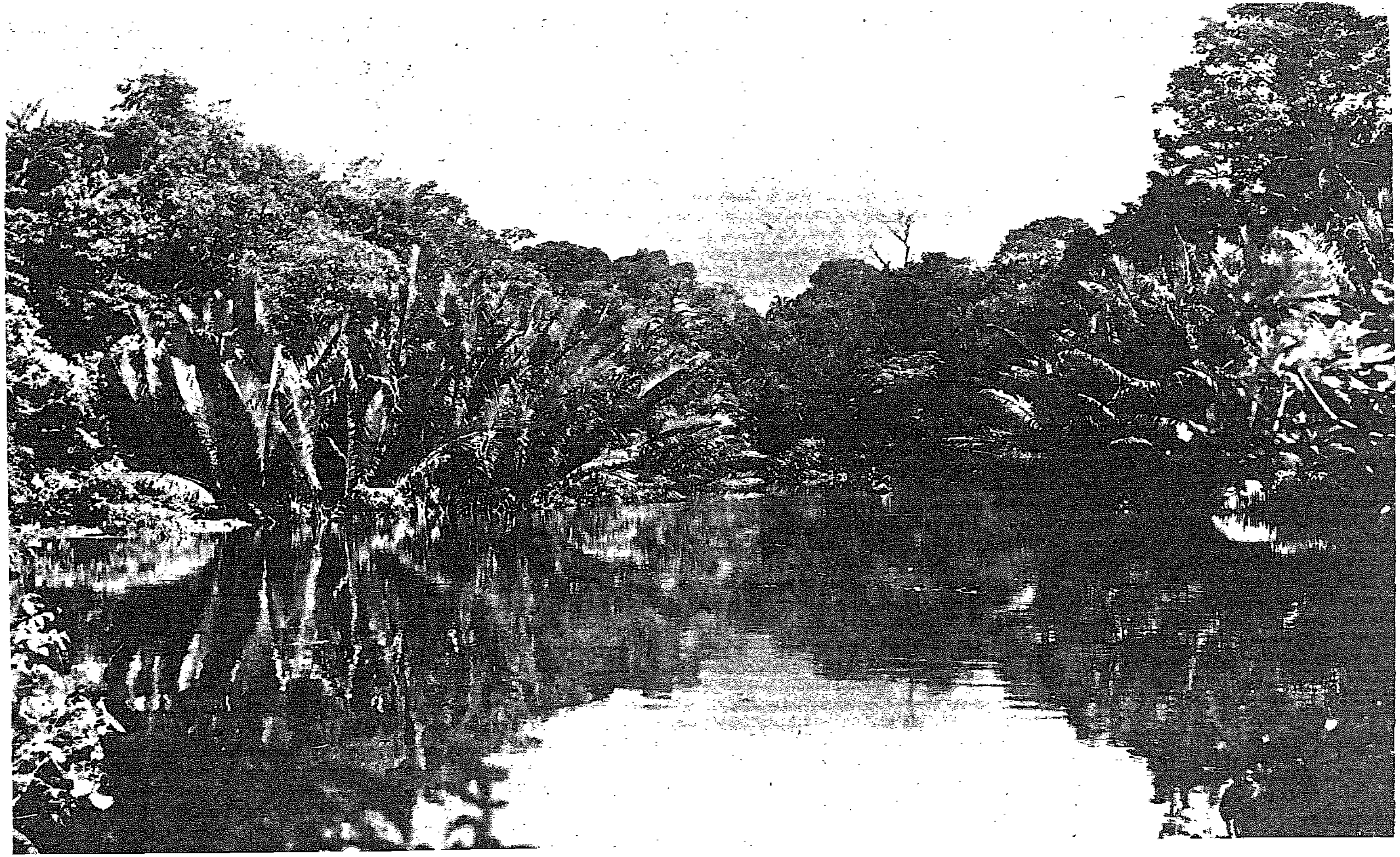


Plate 19. *Nipa* palms along the banks of a river in the Malay Peninsula

(Photo: E. J. H. Corner)

however, seem to be rather different in that they indicate somewhat cooler conditions, as appears to be true also of certain other Asiatic floras. Poor as it is compared with earlier periods, the fossil record of the Pliocene is, nevertheless, sufficient to reveal the most important feature of the time, namely, the comparatively sudden and rapid change in climatic conditions. At the beginning of the period the vegetation, and, by analogy, the climate, remained much as they had been for a very long time and perhaps ever since the Cretaceous. By the end of the period the plants, of north-west Europe at least, were practically as they are to-day, conforming to a temperate or even cool-temperate climate. In short, in many parts of the world the age-old and generalised warm-temperate or subtropical flora had given place in a relatively very short space of time to one of a kind not previously recorded in the history of the Flowering Plants, and perhaps representing climatic conditions equally unprecedented.

This alteration marked the beginning of the catastrophic change and deterioration in world climate which culminated in the extensive glaciations or "Ice Ages" of the immediately succeeding Pleistocene sub-period, but before considering this very important phase in the history of the Flowering Plants it is worth while to summarise what has so far been said.

All the available evidence points to the fact that the Flowering Plants, from the time that they are first recognised somewhere in the earlier part of the Cretaceous right down to the middle or end of the Pliocene, pursued the even tenor of their way without encountering any serious problems or difficulties in the nature of rapid environmental changes. Throughout this long period their history seems to have been that of a group of organisms gradually broadening and differentiating by the multiplication of forms, in the course of secular time, and coincidentally attaining a more and more dominant position among the vegetation of the world as a whole. Environmental or, at least, climatic differentiation, with its attendant morphological differentiation, seems to have been at a minimum, and the fossil record certainly suggests that, at any rate in the higher latitudes of the northern hemisphere, there was one almost ubiquitous flora, which has been called the Arcto-Tertiary flora, reaching, it may have been, even to the highest latitudes. Then quite rapidly at some time during the Pliocene this idyllic sequence was broken by a drastic deterioration in the climates of the higher latitudes, culminating in widespread glaciation and presenting to the world of flowering plants problems of environmental harmony which it had never before encountered.

The foregoing brief survey of fossil Angiosperm floras has been almost entirely concerned with the northern extratropical regions and only one brief reference has been made to those floras, comparatively few in number, which are known from the southern hemisphere, this being for the purpose of showing that these floras on the whole reveal a plant life similar to that of the same places to-day. There is, however, one southern fossil flora which, from almost every point of view, is of outstanding interest and importance. This is the fossil flora found on Seymour Island at latitude 64° S. and longitude 57° W. in the antarctic, and described by Dusén (149) who identified it as in character very like the present floras of New Zealand and Fuegia. Skottsberg (508) has stressed the significance of this Antarcto-Tertiary counterpart of the Cretaceous and Eocene floras of the north, especially with regard to the problem of the relation between the northern and southern temperate floras, and the evidence it affords for the autochthonous origin of the latter.

The Ice Ages

By far the longest part of Angiosperm history has been covered in the last few pages, and what remains is almost infinitely shorter, but this is more than compensated for by its exceptional interest and significance. This may be expressed by saying that the first part is a history of prosperity, and the second a history of adversity, and with the Flowering Plants, as so often with other things, it is the latter which is the more revealing.

The study of the Pleistocene and its Ice Ages is so complex, and there is so great a literature about it, that it can be dealt with here only in the merest outline, and then only so far as it directly concerns the subject of plant geography. Much of all the available information is to hand in the writings of Wright (606), Antevs (19), Zeuner (612), Flint (179) and Deevey (126) and these have been the sources of much that follows here.

As a preliminary it is of value to distinguish between the two most striking effects of glaciation, the formation of glaciers and of ice-caps, because although the difference between them is one of degree only, it is a matter of some importance here. Glaciers are commonly to be observed to-day in elevated regions at almost all distances from the poles and may be described as frozen rivers filling the upper valleys between the mountains. They are usually more or less distinct entities, and are normally overtopped by uncovered mountain peaks. Where and when, however, the effects of intense cold are sufficiently accumulative, the individual glaciers tend to lose their identity and to coalesce into huge masses or caps of enough bulk to over-ride and cover all land elevations and to form great ice-fields, which are known as ice-caps. In their typical form they are found only in the polar regions. To-day there are in the world only two major ice-caps, one in the north covering Greenland, and one in the south covering the whole of Antarctica. The latter is much the greater and its magnitude may be gauged from the statement that the summit of the ice dome is estimated to be 15,000 ft. above the sea (358). There are certain other minor ice-caps, especially in the north, but the polar area here is sea. Glaciers, on the other hand, occur to-day wherever the altitude is enough. They are present even on the summits of high equatorial mountains, and are increasingly plentiful in higher latitudes. When for any reason the temperature of the world falls, the ice-caps increase in size and area and the glaciers become not only more numerous but extend down to lower levels, often coalescing in the process. Conversely, with a rise of temperature the area covered by ice contracts. The measure of the intensity of glaciation at any time is thus the size of the ice-caps, namely the latitude to which they extend, and the level to which glaciers descend. Since it is only natural to regard the present state of affairs as a norm or mean, the term Ice Ages has thus become applied to such times as the caps and glaciers extended appreciably beyond their present limits.

It is now known that the Pleistocene consisted of more than one glaciation, that is to say that the amount of ice increased and diminished more than once in accordance with climatic oscillations, but there is some doubt still about the exact sequence of events in the different parts of the world. There are evidences of extensive glaciations in the southern hemisphere as well as in the north, (fig. 69) but there is, in particular, much variance of opinion as to whether these glaciations were synchronous with those of the north. On the whole the evidence seems to suggest that

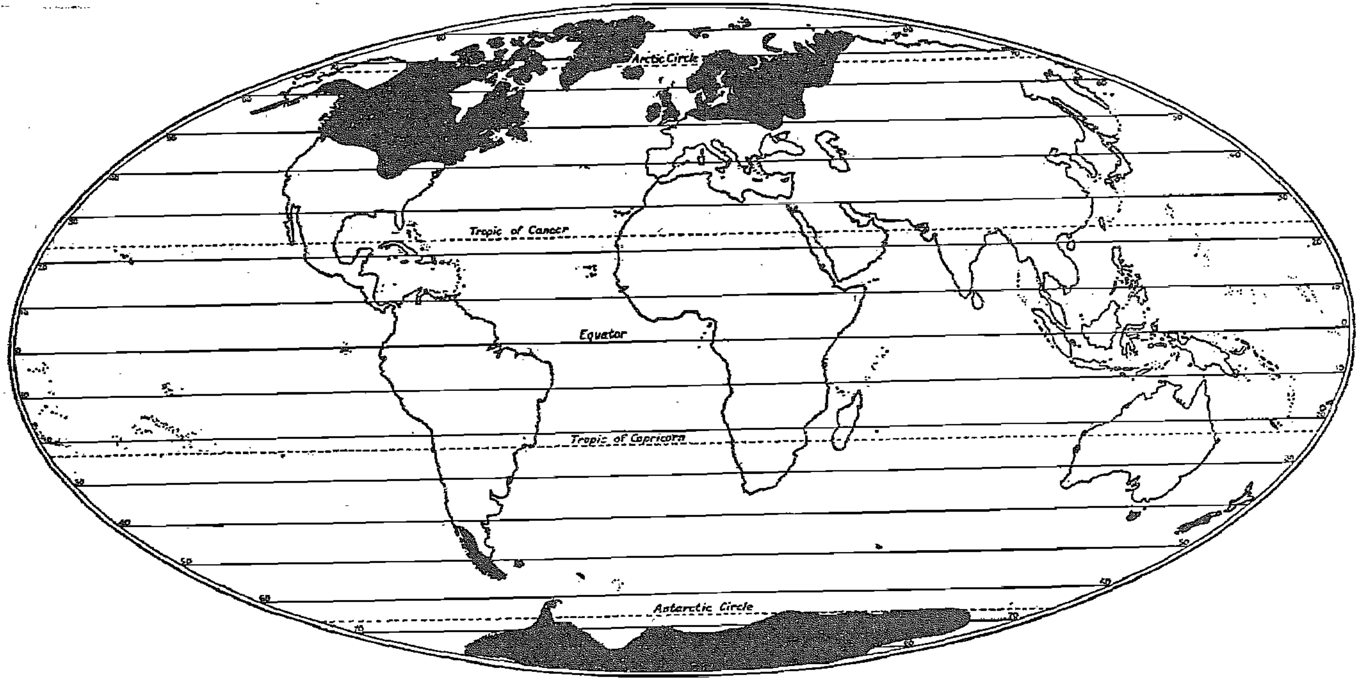


FIG. 69.—The Pleistocene Glaciation.

Map of the world showing, in general terms, the maximum extent of the main northern and southern ice-caps (black) during the Pleistocene. It must be remembered that the snow-line was everywhere considerably lower at that time, so that at all latitudes there were, in addition, some larger or smaller local accumulations of ice at higher altitudes. Compiled from various sources.

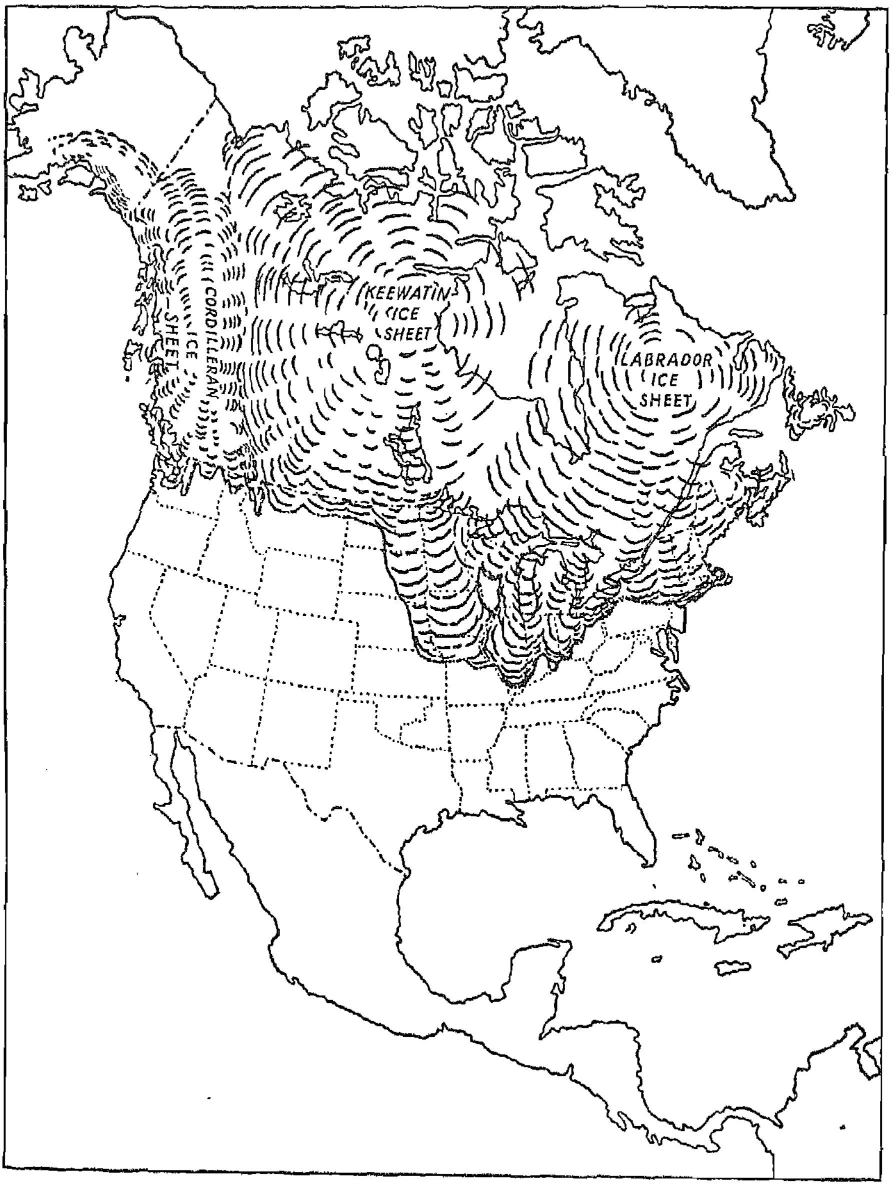


Fig. 70.—Map showing the extent of the ice advance in North America during the maximum glaciation, after Chamberlin and Salisbury.

they were. There is also evidence that at lower latitudes there were contemporaneous pluvial periods.

In any case the distribution of land and sea in the two hemispheres and the remoteness of Antarctica have made the traces of glaciation much more conspicuous in the north, and there is an inevitable tendency to regard the effects of glaciation as being much more marked in the north than in the south. This is probably quite unjustified, and Skottsberg (497) has corrected the impression graphically when he says "the disappearance of the Tertiary antarctic flora during the ice ages is of fundamental importance and has been greatly underestimated by plant geographers. No catastrophe of such dimensions and of such consequences has ever befallen the Tertiary flora of the northern hemisphere."

The course and sequence of the Pleistocene ice ages have been particularly studied in the Alps by Penck and Brückner (414), and it appears that here at least there were four successive glaciations of different intensities and that these were separated by interglacial periods during which the climate returned to more genial values, such as are familiar to-day (472) (fig. 72). During the glaciations the glaciers crept down the valleys, and during the interglacials they retreated. Fortunately glaciation leaves behind it, in the form of striated rocks, moraines, eskers and drumlins, fairly clear evidences of its course, and from these it is possible to learn a great deal about the different ice advances.

The first advance of the ice is called the Günz glaciation and was of medium intensity. It was followed by an interglacial during which the climate probably reached values rather higher than those of to-day. The second glaciation is the Mindel, and this again was followed by a similar but much longer interglacial. During the Mindel the ice probably reached its maximum extent. The third glaciation is called the Riss and seems to have been of lesser extent than the one preceding it. It, again, was followed by a third interglacial period, from which several interesting fossil floras are known, indicating a climate slightly warmer than the present. Finally there was the Würm glaciation, less intense than any of its predecessors, and this was followed by a gradual improvement of climate to the condition that we know to-day.

The question next to be considered is whether the sequence of events in the Alps occurred also elsewhere. It can only be said here that while the fourfold classification and nomenclature just described were made with special reference to the Alps, there is reason to believe that a similar if not exactly synchronous series of glaciations occurred in other parts of the northern hemisphere.

In the Alps the glaciations concerned a relatively small complex of glaciers, but in higher latitudes it was the polar ice-cap itself that waxed and waned, and what in the former case was but a local lowering of the snow line, in the latter took the form of great latitudinal extensions of the ice-cap. During the first glaciation the spread of this ice south was relatively small, covering Europe only in its most northerly parts. It was in the second glaciation that the polar ice attained its maximum extent, and the limits of this must be discussed in some detail.

It might be anticipated that the ice would extend in all directions south from the present poles, but for reasons which are not altogether clear this was not so, and the actual centre of the northern ice-cap during the maximum glaciation lay somewhere near the middle of Greenland. Because of this the glaciation most affected North America, and here the cap's southern edge (fig. 70) followed approximately the present frontier of Canada in the west and the latitude of 40° N. in the east. Passing to Europe (fig. 71), the edge was so situated that the whole of Ireland was

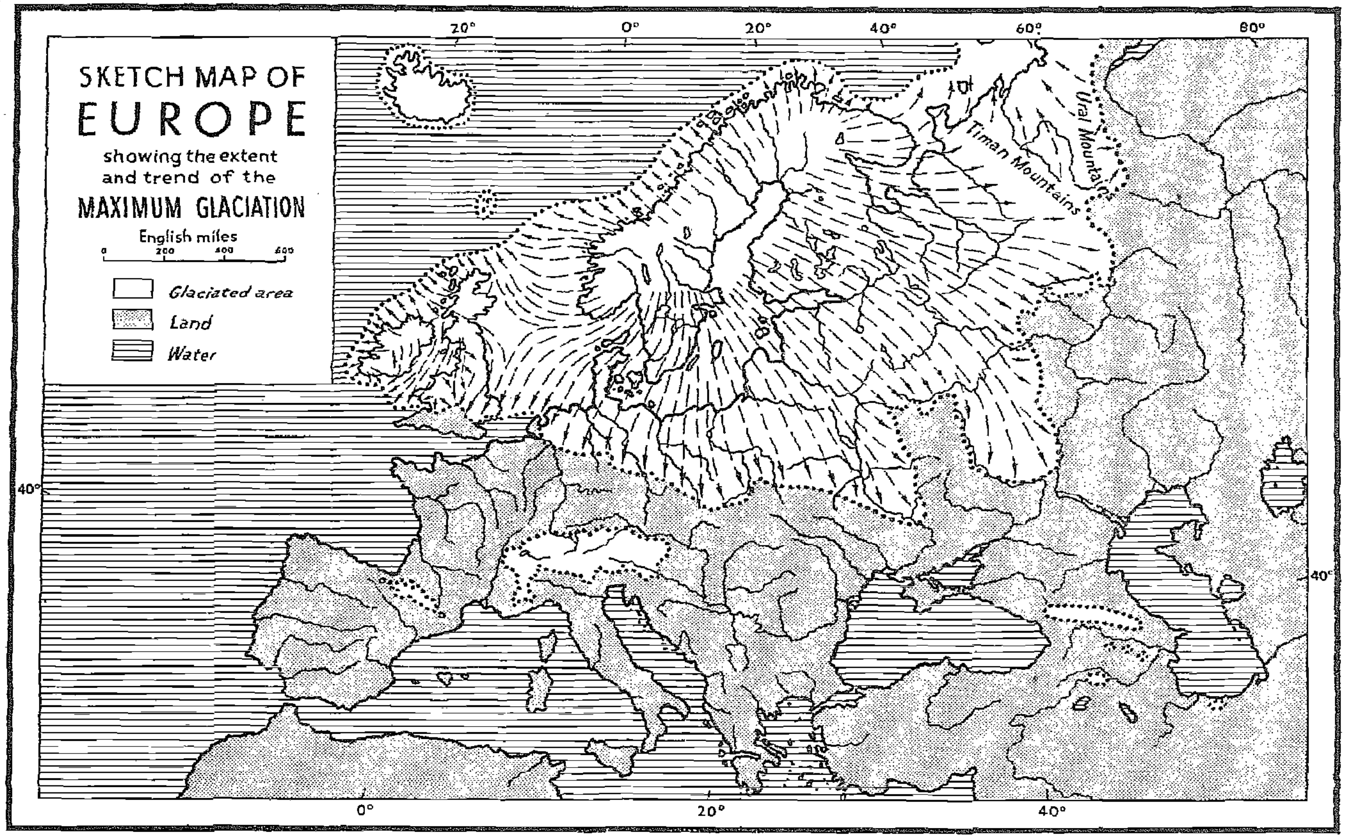


FIG. 71.—Map showing the extent of the ice advance in Europe during the maximum glaciation, after Chamberlin and Salisbury.

covered and all Britain as far south as a line joining the Severn and the Thames. Thence the edge extended almost straight across the continent to a point some distance north of the Crimea, and from here it ran, with certain marked indentations, to pass out into the Arctic Ocean along a line somewhat east of the Ural Mountains. Thus scarcely any part of Asia was covered by the cap, but the glaciation of the mountain masses in that continent was much greater and there may, locally, have been an approach to ice-cap conditions (113, 179).

The greater extent of this maximum glaciation obscures to some extent the details of the others, but it is thought that the third glaciation was comparable to the first in extent. The fourth, which is the most problematical, was apparently markedly smaller than the others. As in the Alps, the glaciations were separated by interglacial periods of improved climatic conditions, but the details of these periods are not yet very well defined.

It will be readily appreciated that the amount of ice contained in the caps during the glaciations must have been enormous, not only in bulk but also in weight, and that with variation in the caps there must have been corresponding differences in the weight of the ice resting on the surface of the earth. It is probable that mainly to this must be attributed the many changes in the relative level of land and sea so often found associated with glaciation. But besides the actual effect of weight, a single glacier or arm of an ice-cap may often have had the effect of damming up the normal drainage of an area and causing the imprisoned waters to rise to a much higher level than would otherwise have been the case. Changes of these sorts have doubtless played an important part in plant geography.

For a long time after their recognition it was supposed that the ice ages of the Pleistocene formed an isolated phenomenon in geological history, but it is now known that this is not so. There have been, in the whole course of geological history, several glacial epochs, but these have been separated by immense periods of time and they are for the most part so remote that little is known of their details. References to a Cretaceous glaciation are not infrequent in the literature but this is very hypothetical and it is generally accepted that the glacial epoch before that of the Pleistocene was as far back as the Permian period, many millions of years before the Flowering Plants came on the scene at all. Here, therefore, we need take notice only of the Pleistocene glaciations, although the fact that there have been others is of considerable theoretical importance.

What the cause or causes of these long intermittent ice ages may have been is still very problematical (302) and there is fortunately no necessity to discuss the matter at length here. Suffice it to say that opinion to-day, which is set out in considerable detail by Zeuner (612), tends towards the view that whatever the actual contributory causes may have been, and they were probably many, they are likely to have become effective only in some rare combination of circumstances and values.

One of the most important recent developments in the study of glaciology has been the success attending some of the attempts to arrive at an actual chronology of the Pleistocene, and especially of the latter part of it. In the case of the Alps, for instance, actual figures, compiled from many sources of evidence have been mentioned with some confidence. Penck (414) has made a curve to a time scale for the whole period (fig. 72), also indicating the rise and fall in the snowline, that is to say in the general level of the ice. According to this curve something like half a million years have elapsed since the end of the Pliocene, and nearly half of these are occupied by the long interglacial period between the Mindel and Riss. Twenty

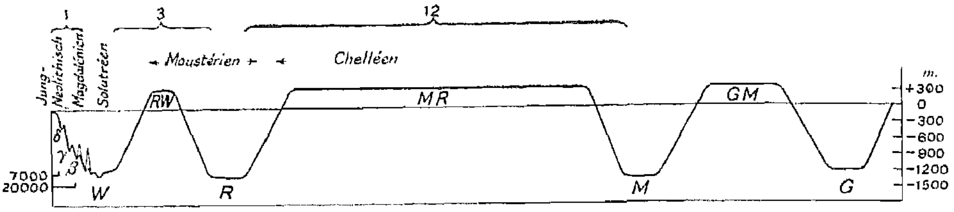


FIG. 72.—Graph showing the variation in temperature in the Alps during the Ice Ages, after Penck and Brückner.

thousand years is suggested as the time covering what is called the post-glacial period, that is, the time since the latest (Würm) ice-cap began to retreat. It will be noted that this last rise of the curve is shown as a number of steps. Probably all the curves should be drawn in this way with minor oscillations, but it is only in this latest phase that these are sufficiently well known to be recorded. The shortness of the post-glacial period is one of the most interesting features of the curve. Twenty thousand years is a long enough period, but compared with the usual measures of geological time it is scarcely appreciable and brings the fourth glaciation almost within sight, as it were, of the present.

This chronology is supported in general by other and different estimates. One of the best-known is the rate of movement upstream of the Niagara Falls, which have existed only since the retreat of the fourth ice-cap. Here the figure is about 25,000 years. The most striking figures, however, are those obtained by De Geer (127) and others from their studies of the laminated clays or *varves* of southern Scandinavia. Details of these studies may be sought elsewhere and particularly in the recent work of Zeuner (613), but it can be said here that from them it would appear that a period of some 14,000 years has elapsed since the southernmost part of Sweden began to be uncovered by the retreating ice, and that about 9,000 years have passed since the neighbourhood of Stockholm was uncovered.

The study of these laminated clays (128) is but one instance among many of the way in which Scandinavian scientists have taken advantage of the features of their country to make themselves pre-eminent in the study of problems relating to glaciation. Another line of research that has attained great proportions far beyond the land of its birth is in the investigation of post-glacial and, to a lesser extent, other floras by pollen analysis (72, 203, 206). Peat, which may be called a peculiar sub-fossil state of plant remains, normally contains great numbers of pollen grains of the plants which lived during, and contributed to, its formation, and by treating samples of peat in a special way it is possible not only to examine this pollen but to identify it. Peat has been forming for much of post-glacial time, and this method, correlated with others, has enabled a good account of the vegetational changes consequent upon the retreat of the ice to be drawn up. Recently, it is of some interest to note, it has been suggested that this chronology has been confirmed by the occurrence of cold and warm kinds of Foraminifera in the deposits on the bed of the Caribbean Sea (417, 613).

It appears, as might be expected on other and less direct evidence, that there followed in the wake of the retreating ice a series of floras and vegetation states each more temperate in character than the one before it. In Scandinavia in general five main stages are recognised in this gradual re-immigration of the flora (15) namely preboreal, boreal, Atlantic, sub-boreal and sub-Atlantic (compare p. 228) and the last four of these stages constitute what is generally called the Blytt-Sernander scheme, from its original authors. The first plant-cover after the actual departure of the ice was an arctic one, giving rise fairly soon to a flora in which birch was prominent. This in turn gave place to coniferous forest, which was itself followed by deciduous forest in which oak and hazel were outstanding constituents. At a later stage beech became prominent. After that there seems to have been a slight return to earlier conditions and a final recovery to the present state. These stages have been recognised in whole or in part in many parts of the glaciated regions (see Chapter 12). In Ireland, for instance, a very important point was first brought to light, namely the existence of a post-glacial optimum, that is to say of a time when climatic conditions were actually rather better than they have ever been since. This optimum has also been particularly well demonstrated in Scandinavia in the distribution of the hazel.

These post-glacial changes have now been much studied, especially in north-western Europe, and the summary of his own investigations, as well as those of others, by von Post (425) gives a most valuable picture of the present state of knowledge on this subject, from which the idea of a post-glacial optimum, followed by climatic deterioration, similar probably to the sequence of events in the earlier, interglacial periods of amelioration, clearly emerges. The sequence comprises three main phases ; that of the approach of the warm period, with increase of the more temperate kinds of trees ; that of the culmination of this forest vegetation ; and that of its contraction and change to the conditions observable to-day. Nor are these fluctuations observable only in temperate latitudes, and that a parallel course of events has occurred in the warmer parts of the world has been indicated by many observations, such as those of Selling in the Hawaiian Islands (473).

Most recently of all an entirely new method has been applied to the estimation of post-glacial chronology, that of calculating the age of organic remains by estimating the proportion of radio-carbon, a radioactive isotope of carbon, in them. It is too early to say much as yet about the results, but a recent account of the method by Flint (180) claims that it shows first that the date of the final glaciation is more recent than has been supposed, and second, that subsequent climatic changes have been synchronous in the northern temperate regions of both the Old and New Worlds.

Brief as the foregoing account of the Pleistocene is, it is enough to show what a profound effect this period must have had on the vegetation of a great part of the world. Whether or not, previously, there was local glaciation on the summits of high mountains is a question which will be discussed in a later chapter, but there can be little doubt that the arctic conditions (widespread glaciation at sea level) which characterised the period were conditions never previously experienced or encountered by the Flowering Plants, and that many of these were, as a result of them, faced with the necessity of adjusting themselves to influences of a quite novel kind. Further than this, the effects of the ice were greatly intensified by the catastrophic speed at which it came and by the series of oscillations that accompanied it. The significance of the speed of glacial onset in particular requires to be fully realised. Previous to the later part of the Pliocene the speed of morphological evolution in the Angiosperms may be pictured as being faster than and perhaps unrelated to climatic change, or, to put it differently, the plants may be pictured as changing by the processes of evolution more rapidly than their surroundings, so that quite possibly the problem of "adaptation," as the term is understood to-day, did not arise. With the coming of the Pleistocene glaciations this relationship was entirely altered. Climatic change was accelerated to such a pitch that by no stretch of imagination can it be supposed that evolution was able to keep pace with it, and there thus arose a situation in which the environment was changing much more rapidly than its inhabitants. Again, in somewhat different phrase, environmental change completely outran evolutionary change. The result in many parts of the world was a state of stress between organism and environment such as may never have occurred before. In short, if these suppositions be correct, the effect of the ice ages on the Flowering Plants was completely to upset, over much of their range, the balance between plant and habitat. Since there has not been, in the time which has elapsed since the fourth glaciation, any appreciable restoration of the long-term pre-glacial conditions, the botanists of to-day are studying a world vegetation but lately subjected to a devastating disaster. The study of the geography of the Flowering Plants is peculiarly the study of the consequences of this disaster, and this being so, the outstanding importance of the Pleistocene in relation to the general story can scarcely be overestimated.

Note.—The above account of the Pleistocene glaciation is written in the usual terms of the waxing and waning of ice-caps in response to major temperature oscillations, but it should be remembered that some, at least, of the facts and effects described can be explained otherwise by supposing that the ice-caps themselves moved from time to time while the temperature gradients of the world remained relatively constant.

PART TWO

CHAPTER 15

THE FACTORS OF DISTRIBUTION—I. GENERAL REVIEW

THE first part of this book described the facts of Angiosperm geography: the purpose of this second part is to consider their possible explanation. The present chapter therefore gives a general preliminary survey of what are usually called the "factors controlling plant distribution," and the five following chapters discuss how far and in what manner the more important of these may, in combination, be considered to provide a general explanation of the distribution of these plants as it is to be observed at the present time.

In the widest sense the distribution of plants to-day is the effect not only of natural causes but also of artificial ones, namely those which operate as a result of the intentional or unintentional activities of human beings. With these human factors this book is not, to all intents and purposes, concerned, although it is necessary on occasion to refer to some of them incidentally. Its theme is rather the natural distribution of plants, and for this reason the influences of man, though often intense and widespread, receive little or no attention except in so far as they can be made to illustrate or explain more natural process. At the same time the extent and degree of man's influence on the plant life of the world must never be underestimated. Obvious as much of it is there is to-day a growing belief that many of the apparently more natural vegetational states are in fact the less direct consequences of man's activities, and it has even been suggested (23, 530) that he has played a not inconsiderable part in hastening the spread of desert conditions. Those who are interested in this relation between man and his environment should read the classic account of it by Marsh (367).

One natural factor of distribution is so fundamental that it underlies all others. This is the evolutionary factor, which arises from the circumstance that the plant world of to-day has gradually developed from pre-existing forms of plants by those manifold processes which are called "organic evolution." The basic characteristic of nature as a whole is that its history has been one of slow evolution over an immense period of time, and a proper understanding of the effects and implications of this is so essential for the consideration of any biological problem that the matter was referred to as early as Chapter 3, even before the facts of plant geography had been cited. It is necessary here, therefore, only to emphasise once again the degree to which the evolutionary factor is, as it were, a master-factor, determining in one way or another the operations and results of all those others that have now to be reviewed. Evolutionary factors may be regarded as inherent or predisposing factors. The more direct factors next to be discussed may be regarded more as potentials or as variables which may or may not influence plant distribution. They represent variable conditions under which plants live and which may become decisive in determining the range of species.

The ordinary flowering plant lives its whole independent life with its roots in the soil and with its remaining parts exposed to the atmosphere, and that it is incapable of movement during this long phase of its existence must always be remembered as one of the main factors in phytogeography and one of the chief ways in which it differs from zoogeography. In fact this immobility is far more fundamental than is usually admitted, and indeed ranks next to those inherent evolutionary factors just mentioned. The reason is clear. Whatever our views may be about the actual origin of new species, such forms when they first arise must occupy an extremely limited area, perhaps no more than the space covered by a single individual, and their attainment of any appreciable range must be a matter of the actual movement of individual plants. This being so, the likelihood of any range being attained depends upon the ability of the plant to move at some stage or another in its life history. The question of the average ability of plants to move will be discussed more appropriately later. Here we are concerned only with the axiomatic statement that if the individuals of a species have no mobile phase, the species itself cannot attain a range, no matter how favourable other factors may be. There are not likely to be many plants without the power of mobility, for the reason that such a disability will function very much as a lethal factor, and we may therefore assume that all plants which do attain an appreciable range possess at some stage in their lives some degree of mobility. What that degree may be will be seen later.

Plants are normally in contact with their environment in two rather distinct directions. Their aerial parts are in contact with the free atmosphere and their terrestrial parts are in contact with the soil, but the latter is really a complex, since it comprises not only the solid constituent of the soil, but both the water and air in the soil. Even this is a simplification of the position, though it is sufficient for immediate purposes. The conditions of the atmosphere and of the soil vary greatly from place to place and are indeed rarely constant over any considerable area, so that climatic as well as soil conditions are variables obviously likely to affect the distribution of plants in ordinary circumstances. Naturally if all plants were capable of existing under all known conditions, then the effect of these conditions as factors in distribution could at least be no more that secondary, but as far as is known no plants are capable of such existence, and hence these variables are normally direct factors of distribution.

The complex of atmospheric conditions which is usually called climate is generally classified with regard to plant distribution into four components. Most fundamental among them is heat, that is to say the temperature of the air, because it is a direct function of the shape of the earth and its position with regard to the sun. Its actual value from place to place is controlled by various secondary considerations, but these, which will be referred to in due course, have seldom more than a local influence. Next in importance to temperature comes moisture, most familiar in the form of precipitation or rainfall, but expressed also in the form of humidity, dew and snow. The distribution of moisture values differs essentially from that of temperature, in that it is local rather than general and depends upon local combinations of circumstances rather than upon world-wide conditions. That is to say, moisture conditions are not necessarily bound up with heat but tend to vary widely at all temperatures. Besides these two primary climatic variables there are at least two others which are important secondarily. These are light and wind, and they are to be regarded as secondary because they exert their influence by modifying the two primary variables of temperature and precipitation. This relation is clearly seen in the close correlation between light and heat, both being directly due to the influence of the sun. Similarly there is the relation between heat and humidity of the air, which in turn controls the likelihood of precipitation. Finally, both temperature and precipitation are controlled to some extent by wind or air-movement, since this influences both the accumulation of temperature and the accumulation of humidity. Actually light is probably the least important component in relation to the *distribution* of plants, since, except in the highest latitudes, its mean value and duration seem sufficiently great to preclude it from acting as a limiting factor in plant life. Locally, however, and especially when itself controlled by still more minor conditions, it may be of some importance. The potentiality of wind as a factor in distribution lies chiefly in the manner in which it may modify other climatic values, and its effects upon temperature and precipitation have already been mentioned. Besides these, however, it may have a more direct influence by facilitating or impeding the proper functioning of the plant at certain particular phases of its life history, or by militating against the attainment of normal growth-form.

In contrast to climatic factors, the variables influencing the plant either potentially or actually through its physical contact with the soil in which it grows are usually described as edaphic factors, and here again there is considerable complexity and interrelationship—so much so that it is not easy to arrange these edaphic factors in any very definite order of importance, and the sequence in which they are mentioned here does not imply any such relative value. Generally speaking, edaphic factors are regarded as comprising three components—the physical nature of the soil, the chemical nature of the soil, and the topographic or physiographic character of the habitat. The first two may be regarded as absolute features, but the third is chiefly of importance as a modifying influence, conditioning not only the first two but also at least some of the climatic factors mentioned previously. Almost all physiographic conditions may affect a locality as a potential plant habitat, but in the main the two important considerations are altitude and exposure. The effect of altitude has already been dealt with fairly adequately in the chapter on world geography, and it is sufficient to remind readers here that it has a very important influence not only on temperature but also on precipitation, and in fact tends to influence these values in the same kind of way in which they are influenced by latitude. Exposure is important owing to the way in which it may intensify or diminish the influence of other factors. For example, the detailed relief of an area may profoundly influence the effect of climatic and edaphic factors upon the area according to the degree in which it provides shade or shelter. Slope is also important, since it may obviously influence the effect of precipitation or the effect of insolation. The prevalence of cloud also is often a matter of topography and may lead to a considerable modification of temperature values.

It is seen, therefore, that in so far as the life of the plant is passed in contact with the atmosphere and the soil, variations in the values of these surroundings must almost inevitably react upon the life of the plants exposed to them, and therefore that climatic and edaphic factors must always be among the chief factors in distribution. How far this is true and the general effect of it on the total picture of plant distribution will be seen later, but meanwhile the reader may be referred to a general discussion of the problem by Pearson (413).

We are justified in assuming for the purpose of studying plant geography that every species possesses some powers of extending its range in the sense of being able, when circumstances permit, to multiply the number of its individuals and thereby to cover a greater superficial area. Granted this, it follows that there must be for every species a maximum potential area of range representing that proportion of the world's surface which it may hope to cover in the course of time and by means of its powers of mobility. This conception is a very important one, because it clearly indicates the part which climatic and edaphic variability may play in determining this potential area. If we imagine a species to be entirely uninfluenced by climate or soil, it is obvious that it is potentially of cosmopolitan range as regards them. There may, of course, be other factors which will restrict its potential area, but they will not be climatic or edaphic. Thus the main rôle of these variables must be to determine the potential maximum area of a species. Suppose, for instance, that a species is unable to maintain itself in presence of frost, then clearly the potential range of that species consists only of those parts of the world where frost does not occur. Whether it will in time come to inhabit all such places depends on many other considerations, but its relationship to frost does lay down a range beyond which it cannot extend. Thus the rôle of what have been called the climatic and edaphic factors of distribution is primarily that of determining the potential areas of species, that is to say, how much of the world's surface each species may come to occupy in the course of time if its spread is unopposed. At any rate this is the most convenient way in which to regard these factors and to fit them into the general scheme of plant geography. The convenience lies in the fact that it points the way towards a useful understanding of other factors which also play a part in determining the distribution of plants, and which in terms of what has been said clearly do so by influencing the ability of plants to attain their potential areas as determined by their relation to climatic and edaphic factors.

Since the attainment of range can only be brought about by the mobility of individuals, it follows that no range at all will be achieved if the individual is completely immobile, and mobility must therefore clearly be the primary factor, at any rate in the facility with which a species will attain its maximum range. As a broad generalisation it may be said that no flowering plants are capable either of transporting themselves from place to place or of being so transported during their active vegetative life, because their physiology necessitates a permanent association with the substratum in which they grow. The only exceptions are certain plants in which this does not prevail, or rather where it is of a very special character, as, for instance, among small free-floating aquatic plants. Except for these, flowering plants may be regarded as completely immobile during their active vegetative phases.

How then is their movement accomplished? The answer is that in all normal circumstances the reproductive processes of the Flowering Plants incorporate a phase during which the offspring of one generation can survive separation from their parents and during which their physical attachment to their habitat is severed. This is the seed phase, during which the dissemination or scattering of offspring from the point occupied by the parent occurs. In some plants the production of seed is replaced by the production of such small vegetative parts as bulbils, but these possess the essential feature of seeds, the ability to pass through a dormant period during which they are capable of being spread over the surface of the ground. This process of "dispersal," as it is more shortly termed, is thus of supreme importance in the distribution of plants and must rank as one of the fundamental factors (392, 450). It is appropriate therefore that we have already found place for it as a general process, but here we are considering more particularly its relative value in assisting species to attain their maximum distribution, and thus it is really to be regarded as a factor of distribution in two rather different senses. In the one sense it is quite fundamental, since without it no extension of range can take place; in the other sense its relative value as between different plants is also of great importance and must be regarded as one of the main factors in determining how easily and rapidly extensions of range may take place.

The actual means by which plants achieve adequate dispersal will be surveyed later, but mention of the process in general is essential here because it bears directly upon the importance of the next factor to be considered. This may, for the sake of a brief title, be called the factor of "barriers." If dispersal is the only means by which range can be attained, much obviously depends upon the facilities with which such dispersal can operate, and there are likely to be factors which will react either beneficially or harmfully on the process. We need not concern ourselves with the former, because they can only intensify existent powers of dispersal, and we may therefore confine ourselves to recognising what causes are likely to result in an opposite effect. In other words, what are likely to be the obstacles to effective dispersal?

First it is necessary to try to gain some impression of what is meant by the phrase, which has just been used, "adequate dispersal." It is a well-known fact that species differ very much among themselves in the degree to which their seeds and fruits possess characters calculated to facilitate dispersal. We must, of course, be cautious in approaching this subject, because at best we have only a human estimate of these characters, but it is usual to regard certain structural features in seeds or fruits as providing their possessors with what are called "dispersal mechanisms," which increase their dispersal potentialities. There is no doubt that some seeds and fruits possess features which habitually cause them to be dispersed over greater distances than others, and it is tempting to assume that these plants have an absolute superiority in the matter of dispersal, but this view is based upon a quite unwarranted assumption and its truth is not borne out by observation in the field. The false assumption is that wide dispersal is in a biological sense superior to, or more valuable than, narrow dispersal. It cannot, of course, be denied that there may be occasions in which wide dispersal may be of enormous importance, and examples of this will be mentioned later, but to assume it is certainly unjustifiable. Indeed, there is one consideration which is strong presumptive evidence to the contrary. This is the fact that wide dispersal must have a general tendency, not present with restricted dispersal, to carry the disseminules (to use a convenient term comprehending seeds, fruits or vegetative parts) into regions where the conditions of climate and habitat will probably be very unlike those from which the parent plant came. In other words, wide dispersal will take the disseminule further but it is very likely to increase the chances against its survival and establishment when it arrives at its destination. This "useless" dispersal, as it may be called, is discussed by Guppy (241) and similar comments have been made by Setchell (476).

As to the value of specialised dispersal mechanisms, it need only be said here, and it can be said quite categorically, that there is no real evidence that species possessing such mechanisms are more widely distributed, that is to say, have more extended ranges, than those without such advantages, and there is nothing to show that exceptional dispersal methods result, in general, in exceptional ranges.

Confusion of thought on this point seems to arise from a mistaken conception of the purpose of dispersal. It is perfectly true that dispersal leads to the attainment of range and is in fact the only means towards that end, but it by no means follows that this is necessarily its only purpose, and, indeed, from a biological view it is difficult to imagine that this can be so. Its primary purpose must surely be something more intimately connected with the successful maintenance and survival of the individual plant which in due course will reproduce, and it is not difficult to see what this may be. The immobility of a flowering plant means amongst other things that its offspring will, unless subjected to some degree of dispersal, fall to the ground more or less vertically from their points of origin and will thus come to lie in the shadow of the parent. In some cases, and especially with some types of growth-form, they may not even reach the ground but will be intercepted by the lower parts of the parent. Such hazards are least apparent in ephemeral annuals where the whole parent tends to disappear almost as soon as the ripe seeds are borne, but these plants are by no means conspicuous in range or abundance of individuals, and do not alter the view that in most plants this problem of what may be somewhat picturesquely called "botanical overlaying" is a very real one. May it not, therefore, be that the primary object of dispersal is not to spread the species in the sense of appreciably extending its range but to give the disseminules the best chance of survival by scattering them outside the immediate shadow of the parent? Whether this is so or not, it is certain that we must regard many of the most widely distributed of flowering plants as having attained their ranges in the course of repeated but comparatively restricted dispersal.

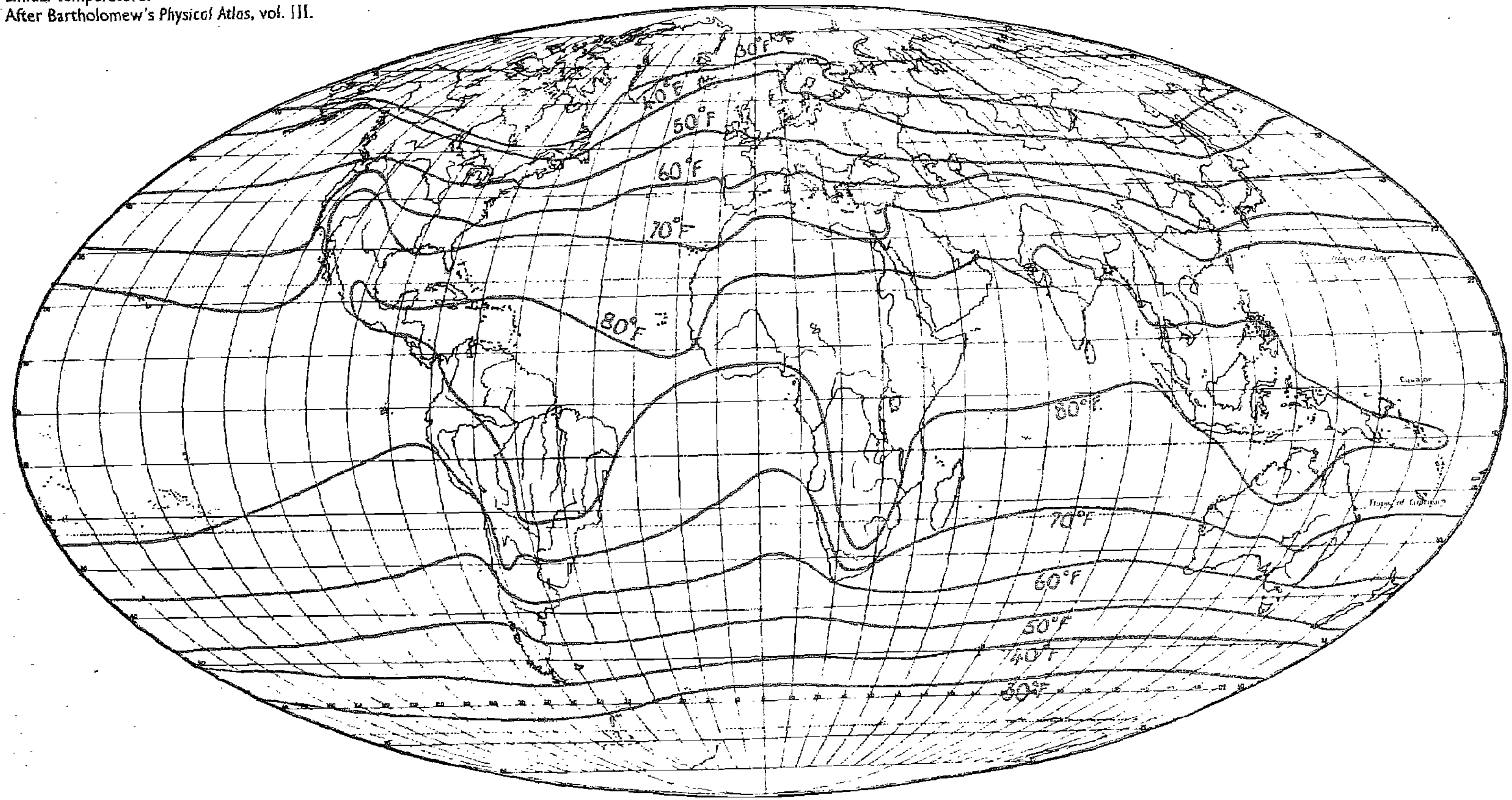
This view leads to what is certainly an important consideration in the total efficacy of dispersal, namely the frequency with which it is repeated. Of two plants with similar dispersal potentialities the one with the greater frequency of reproduction will obviously, other things remaining equal, attain a given range more rapidly than the other. That is to say, the shorter the generation in the species the more frequent will be dispersal and the greater the total area covered in a given time. Contrast, for instance, a plant of chickweed with an oak. There is no need to attempt to estimate their relative powers of dispersal, but it is perfectly certain that the oak will have to be dispersed a very long way at its first reproduction to make up for the large number of generations of chickweed which have passed while the oak was attaining its reproductive condition. At first sight it may be supposed that in cases of this sort, involving large perennial plants, when once the reproductive age is attained the annual or more frequent production of seed will remove much of the disparity. This is, of course, not so, because in such perennials the seed is produced each time at the same spot and dispersal is not accumulative. It will in fact not be appreciably increased until the offspring of the original tree have themselves reached a reproductive stage.

Another very significant consideration in dispersal is the length of time that the disseminules remain viable and capable of germination, because it is obvious that the longer a seed remains alive the more time will the various dispersal factors have in which to make their influence felt, and the greater therefore will be the likelihood of wide dissemination. Viability, especially in relation to seeds, is a large subject, and readers who desire further information about it may refer to a summary in which most of the relevant information is considered in one fairly short article (115), but it is worth while noting that the life of many seeds is considerably shorter than is generally supposed, and that the oft-reported germination of seeds from ancient tombs and similar situations has never been substantiated.

We must now return to the question of "barrier" factors, but our digression has not been without value, because it will help us to estimate what may or may not constitute a barrier to dispersal. It will be remembered that we were concerned to discover what might be meant by "adequate dispersal," and it will now be seen that there is good reason to regard it as anything which scatters the disseminules so effectively that they can begin their germination unhampered by the presence of the parent. How does this affect our conception of barriers?

PLATE 20

Map of the World showing the distribution of mean annual temperature.
After Bartholomew's *Physical Atlas*, vol. III.



Areas correct Distortion increasing towards border of map.
Approximate Scale 1:100,000,000 (1600 miles = 1 inch) along Equator
on Mollweide's Homolographic Projection
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By a barrier (using the term in its phytogeographical sense) is clearly meant something which cannot be surmounted by the only process of movement open to plants, namely dispersal, and it is possible to imagine one or two very different kinds of such barriers. For instance, it is conceivable that purely local conditions might be such that the ordinary methods of dispersal would be unable to operate, as might easily happen to an individual in such a position that its disseminules are actually and physically prevented from scattering sufficiently to allow them to germinate. Here the normal dispersal of the individual is interfered with.

Much commoner and indeed the usually accepted type of barrier is one which, rather than interfering with dispersal, simply tends to make it nugatory. In short, "barriers to dispersal" are considered in a general sense as comprising areas of such a kind and extent as cannot be crossed by the spreading species in the ordinary processes of its dispersal. Two components are obviously involved, the one being the nature of the area and the other its size. Potential barriers of this kind are therefore provided by any areas where conditions are so unsuitable for a particular species that its disseminules, when scattered into the area, cannot germinate. This is a general statement, but clearly the actual barrier value of any area to any given species must depend upon the dispersal potentialities of that species.

This leads to what is perhaps the most important general conception with regard to barriers, that they are seldom to be regarded as complete barriers to the dispersal of every plant. It is true that the very largest areas will tend to be so, but even here one has to reckon with the possibility of accidental dispersal across them, and in usual terms barriers should be recognised as likely to be of very varied significance according to the different plants in whose path they lie.

In the present circumstances of world geography potential barriers may be either land surfaces or water surfaces. These differ rather fundamentally in relation to the Flowering Plants, in that the nature of the obstacle presented by the former will tend to depend upon a variety of circumstances, while the latter will tend to be absolute obstacles in almost all circumstances except in the case of accidental circumvention.

Hence the distribution of land and sea in general must also be regarded as one of the important factors of distribution. As regards land barriers, these may be of very varied nature according to the plants associated with them, and, what is most important, they tend to have a marked segregating effect. Many areas, for instance, may act as barriers to the dispersal of some species while permitting the dispersal of others, while some barriers will be complete obstacles to most if not all species. It is therefore almost impossible to generalise about them, and each must be considered as a law unto itself. It can, however, be said that the more homogeneous an area the smaller or fewer the barriers it will present, while the more heterogeneous it is the more complete and numerous the barriers it will contain. For example, if two regions with very different climatic or edaphic values adjoin one another, it is probable that each will be a serious barrier to species belonging to the other, because neither is likely to provide the conditions required by species from the other. On the other hand, where the passage of environmental conditions is gradual, so much the less complete are the barriers likely to be. Again, areas in which conditions are extreme in whatever sense are likely to be more serious barriers than areas where the conditions are of more medium values. This is why mountain ranges and deserts are among the most obvious barriers to dispersal. But these are only extreme cases, and it is to be remembered that any area is a potential barrier to the disseminules of species inhabiting places where the conditions are appreciably different.

Nor must it be forgotten that though one geographical arrangement may place barriers in the way of dispersal, a different arrangement of external conditions may facilitate dispersal. This is a very important consideration, because the latter effect is likely to be a focusing of plant movement along certain lines, and there will develop what may be regarded as lines of least resistance along which extensions of range will be especially easy. This point can be nicely illustrated with reference to mountain ranges. A mountain system running athwart the direction of dispersal of a species is likely to provide a very serious obstacle to its further spread, because the conditions at the higher levels will tend to be very different from those on the plains below, but mountain ranges or systems lying in the direction of dispersal are likely to be valuable stepping stones or pathways, because conditions will tend to maintain themselves throughout the length of the mountains, and even if this is not so, the flanks of mountains usually exhibit so wide a range of conditions in a comparatively confined space that they are almost certain to provide some niches or footholds by which dispersal can be continued. The most striking instance of this is afforded by the Rockies and Andes of western America but there are lesser examples in many parts of the world.

The question of water barriers, although of even greater absolute importance than that of land barriers, is simpler for two reasons. Except for a few comparatively unimportant exceptions water barriers to dispersal are sea barriers. Large areas of fresh water are nowhere in the world to-day very conspicuous, and none is so situated as to present a barrier of first-class importance. Moreover, the Flowering Plants are, except for the small number that inhabit tidal waters, all land or fresh-water plants to which any considerable width of sea water is almost inevitably a complete obstacle. Certainly there are quite a number of species whose disseminules can withstand prolonged immersion in salt water and which are therefore liable to be transported widely by sea currents, but these are mostly highly specialised strand plants occurring only in the immediate vicinity of the sea shore and do not bulk largely in the constitution of inland vegetation. As a matter of fact these plants afford an indirect but none the less interesting confirmation of the views on the significance of wide dispersal given above. In their case dispersal by currents is effective not in virtue of the wide distances which may be covered but because the correlation of these plants' requirements with the conditions on sea beaches enables them to germinate and establish themselves successfully there after they have been so dispersed. On the contrary, inland plants are not likely to benefit by current dispersal, first because their disseminules are not likely to reach the sea, and secondly because even if they do so they will not be carried to spots where they can germinate.

Opinions vary considerably as to the extent to which areas of open sea constitute barriers to the dispersal of species living in ordinary inland situations. It may be greatly influenced by the structure of the disseminules themselves, and it is particularly in this circumstance that many so-called "dispersal mechanisms" may possess real and absolute values. With regard to this problem generally, the case of the island of Krakatau is of much interest and importance, as affording at least a small amount of definite fact. It lies 40 miles west of Java in the Malayan Archipelago, and in 1883 was the scene of a devastating volcanic eruption, as a result of which two-thirds of it was destroyed, the part which remained being generally supposed to have been completely sterilised of living things by lava and ashes. In 1886 visiting botanists found on the island 15 species of Angiosperms, most of them strand plants; at the present day there are 271 species, and Docters van Leeuwen (136) expresses the opinion that, of these, 40 per cent. owe their origin to dispersal by wind, some 30 per cent. to dispersal by ocean currents, and 25 per cent. to carriage by animals; only a handful are the result of man's introduction. This work of Docters van Leeuwen is of special interest because it seems to dispose finally of the suggestion (28) that part of the vegetation existing before the eruption survived it. On the contrary, it seems reasonably certain that the present vegetation is entirely new, and hence that in the last fifty years some 250 species have succeeded in crossing at least 40 miles of sea by the ordinary methods of dispersal, and that the island has been restocked with vegetation by this means in a comparatively short time. It is dangerous to argue from the particular to the general, but it seems safe to conclude on this evidence that sea distances of the dimensions noted do not in fact present any considerable obstacle to dispersal. It is of interest to note here that Erlanson's account (163) of the colonisation of two new islands in Cochin harbour, India, shows a parallel with the earlier stages of colonisation on Krakatau.

It was pointed out in introducing this discussion on the factors of distribution that these result from and depend upon the fundamental consideration of the development of the organic world by the processes of evolution, and this led to the recognition that time itself must be one of the most basic factors. In that reference to age we were concerned only with its possibilities as determining the actual size of the range of species and other units, and it was regarded chiefly from the point of view of the concepts embodied in the theory of Age and Area, but age, or rather the passage of time, has another most important bearing on plant distribution in that it affects the operation of other factors. It may be expressed as a general assumption that the *status quo* in nature is never maintained for very long, and indeed the whole developmental conception of the cosmos incorporates the fundamental idea of constant if slow change. What the direction of that change may be does not concern us, but the fact of change itself does so intimately. In relation to our immediate subject it means that factors of distribution must be regarded not as something static and unchangeable, but as something subject to the same influences of time as other aspects of nature. Hence any particular factor must be looked upon not only from the point of view of the present but also of the past, and particularly there must be taken into account changes which the passage of time may have brought about in it, while for each of the factors already mentioned there must be added a subsidiary or supplementary factor incorporating the possibility of changes in the operation of the factor or since at an earlier time. This influence of the past is not of equal importance with regard to all factors. Dispersal, for instance, or rather facility for dispersal, is a character of the species more often than not associated with morphological features and is not subject to change by the mere passage of time unaccompanied by evolutionary change in the organism. The morphology may in time so change as to influence the dispersal potential, but this will be presumably accompanied by such a change of shape and structures as may constitute the characteristics of a new species, in which case it begins to establish a distribution of its own. Again we need not concern ourselves especially with changes in edaphic conditions in the past, because these changes are almost exclusively the result of the operation of other factors. Thus changes in climate and changes in topography will usually be the cause of changes in habitat, although there are doubtless many other minor factors on which the nature of the substratum will depend, but there is no particular sequence or series of edaphic changes which is the result of the secular passage of time alone except, perhaps, those resulting from gradual denudation.

There remain the two main factors of climate and barriers, and in both of these the time conception is of such importance that we must regard changes of climate and changes of geography in the past as among the leading factors of distribution. Changes of climate mean alterations in the distribution of climatic values over the surface of the world. In so far, then, as the potential area of species is determined by climatic considerations it will change in response to any change in climate distribution. To put the matter rather differently, if there is accepted the view that the distribution of climate has changed in the past, then there must also be accepted the view that potential areas of distribution have also changed to a greater or lesser extent and therefore that such climatic changes must be a factor in the present distribution of plants. The possible importance and significance of geographical changes in the past in relation to plant distribution are even more clearly demonstrated. These geographical changes may be visualised as affecting two geographical features (the outline of land and sea and the distribution of relief), which may be described as geographic and orographic. But these features of geography are, as has been seen, the very features which produce barriers to dispersal, and so it is clear that changes in outline and relief in the past may effect plant distribution very considerably, at least in so far as they may accentuate or diminish the effects of barriers.

Still one factor remains to be discussed, and it is interesting to observe that, like the first one mentioned (the evolutionary factor), it is one which resides in the very nature of the plants themselves and is not directly a factor of the environment, although environmental features may condition its operation. This factor is the factor of competition, as it is usually called. Competition is not altogether a satisfactory term and it might be better to say the "struggle for existence" which is more nearly what is really meant. The existence of a disparity between the potential number of individuals and the means for their support has long been a biological axiom. It was first demonstrated in scientific form by Malthus in his famous essay on human population (356), but the phrase is most familiar to-day in connection with the doctrine of "natural selection," which is the belief that, given such a disparity, there must be a struggle between individuals for the limited supplies, and that victory will go to those best equipped for the battle, a conclusion which is expressed by the further biological conception of the "survival of the fittest." Whatever validity such conceptions may or may not have and whatever justification there may or may not be for the use of such anthropopathic terms as "competition" and "struggle," it is undeniable that in normal circumstances only a proportion of newly produced offspring survives. Hence there must always be, as a general concomitant of evolution, that particular process of elimination which, in the plant world at any rate is usually termed competition. The important point is to realise that in the circumstances this factor must, by whatever name it goes, be the final and decisive one.

It is easy to see the reason for this. The variation in climate over the world's surface is much less than the multiplicity of species which have to live within it, and the same is true of the range of edaphic conditions. It follows, therefore, that there is no possibility of species sorting themselves out geographically in such a way that each will occupy its own niche in space untroubled and unaffected by others. It is true that the degree to which the presence of others will be felt varies greatly according to the circumstances, but it may be accepted that most areas will be open to occupation by more than one species, and more often than not by a large number. The ultimate constitution of the vegetation must therefore depend upon what happens to the different potential constituents, and to what extent each is able to maintain itself against and among the others. If one cannot do so at all it will be absent from the area, and thus its total range must depend ultimately on the result of what we call for convenience competition. In no common circumstances can the absence of this be visualised, and hence it must be the ultimate factor in determining the detailed distribution of plants.

The operation of competition is best illustrated by the stages in the gradual colonisation by plants of an open and suitable piece of ground such as may be provided by a landslip, by an eruption, by rainwash or by the retreat of ice. Sooner or later the first colonists will make their appearance on the uninhabited area by dispersal from the surroundings, and at first at any rate the number of immigrants will be so small that each to which the habitat is suitable will germinate and grow without any interference from the rest except in so far as accident of position may cause it. Gradually numbers will accumulate until the space available is full and the plants are in actual contact, forming a complete covering. The vegetation is then said to pass from the open to the closed condition. This passage is an important one because it means that henceforth competition in some degree will be the prevailing condition. The mere process of dispersal into the area will not normally bear much relation to the suitability of the immigrants to the habitat, and hence competition is likely, in the earlier stages, to take the form of the gradual elimination of some species by those more suited to the conditions. At a somewhat later stage the competition will become more and more competition between relatively equally suitable species. Those plants whose claim to position is simply based on the act of dispersal will tend to give place to others more in harmony with the actual conditions, until there develops an association of species more or less characteristic for the habitat. Hereafter the competition will take the rather different form of a struggle between the individuals of a comparatively small number of species, and on the outcome of that will depend the relative abundance and frequency of the different species concerned.

Usually the competition between species as opposed to the competition between individuals of the same or of a few species will not entirely disappear, because with the development of the vegetation there will usually go minor changes in the habitat brought about by the effects of continued plant growth. For instance, decaying vegetable matter will accumulate from the generations which are gone and the soil will tend to become different in a variety of ways. For this reason there is generally a gradual development of the vegetation in the sense that new combinations of species grow up in addition to the competition between individuals of the same species. The whole process moves towards an equilibrium which will ultimately be established provided no serious disturbing factors such as climatic or other changes intervene. This equilibrium is reached when the association of species becomes such that the entry and establishment of fresh species from outside diminishes to vanishing point. Thereafter competition will become entirely a matter of struggle between the progeny of the individuals of the species which form the vegetation. This equilibrium vegetation is called the climax vegetation and represents the highest grade of vegetational development which is possible in the general conditions of the environment. Where the climate is suitable the climax vegetation is usually some kind of forest, and the gradual stages by which it is attained can roughly be described as the replacement of small and herbaceous species by larger woody species, but there are many factors which modify the process and which induce certain degrees of equilibrium short of this condition.

Such is but a very bare account of what is in fact the whole of one very important aspect of the study of plant ecology. Its purpose is merely to show that competition is not one simple process but may take very different forms in varied circumstances. To summarise still more what has been said, the earlier stages of development and plant succession may be likened to the more active and chaotic stages of struggle from which there gradually emerges the victory of a comparatively small number of forms, which thereafter may be regarded as having attained a working degree of harmony between themselves. It is not supposed that when this is attained competition ceases. It is rather that competition comes to have the rather more limited objectives of maintaining the occupancy of species and of maintaining an appropriate balance between the different species. So long as any appreciable number of species are present there will tend to be some degree of competition between them, and apart from this the struggle between the individuals of any one species will always continue. The point to be remembered is that it is this competition that must be the ultimate deciding factor in determining the actual range and abundance of any particular species.

It is very natural that the human conception of competition tends to be of an active physical struggle between plants of various kinds and between the individuals of a species, but a moment's consideration will show that by its very nature the plant (and particularly the land plant) is debarred from such active means of expressing itself. It is, therefore, of some interest to try and picture the way in which competition between plants may actually occur.

Perhaps the most obvious form of competition and the nearest to an active struggle is that between individuals, often in the seedling stage, for room in which to develop. It is, for instance, especially in this connection of competition for space that we picture the "struggle for existence." Actually, of course, this form of competition is not restricted to seedlings and obtains between plants at all stages of growth, particularly perhaps at the stage of maturity, where the size and robustness of individuals must be of great importance. For instance, the growth-form of heather and other ericoids is such as to make difficult or impossible the presence of other plants where they grow and in such cases as these it is the physical contact or proximity of individuals which causes and controls the competition.

But, as Brenchley (61) and others have pointed out, space competition is not the only kind and indeed is not infrequently absent, as is the case for instance with the open vegetation such as is characteristic of desert regions. There may also be competition for other essentials in short supply, such as food in the soil, water, or light. Not only this but there is good reason to believe that competition may take a rather more active form in the way in which different species may react mutually upon one another. The many problems involved here have as yet received less attention than they deserve, but indications of the importance of this as a promising line of investigation are accumulating.

It is probably fair to say that no one studies the detailed distribution of species and individuals over a limited area without being impressed by the way in which there is association between certain forms and dissociation between others. The whole arrangement of vegetation into edaphic types is based upon the facts of such association, and the question almost inevitably arises whether there may not be some factor or factors which favour close association between certain plants and preclude it between others. That is to say whether there may not be certain factors inherent in certain plants which favour or inhibit the growth of others in close proximity. The actual edaphic requirements of plants must, of course, primarily control their presence in any particular spot, but as between two species with similar edaphic needs the ultimate competition between them may sometimes perhaps be determined by factors inherent in the plants themselves.

Many years ago Pickering (420) called attention to the effect of grass on fruit trees, and Fletcher (178) also discussed the subject of toxic excreta in plants, and since then many other experiments (353, 354, 393) have shown more or less satisfactorily that if certain species are grown together or in close proximity they may sometimes have a very considerable effect on one another. Different pairs of species belonging to distinct genera or families have been grown together, and it has been reported that with different combinations the relative growth of the components varies greatly. The hemp, *Cannabis sativa*, if grown with spinach, *Spinacia oleracea*, does very badly while the spinach does very well. This is also the case, to a varying extent, when the spinach is replaced by *Secale cereale*, *Vicia sativa* or *Lepidium sativum*. On the contrary, the hemp does exceptionally well compared with its companion when the latter is *Beta vulgaris*, *Brassica oleracea*, *Lupinus luteus* or *Zea mays*. The same thing has been shown markedly in *Atropa bella-donna*. When this plant is grown with *Sinapis alba* its growth is far below normal, but if grown with *Artemisia vulgaris*, or particularly with *Galega officinalis*, its growth is appreciably above the normal. Again, when *Vitis vinifera* and *Euphorbia cyparissias* are grown together in the same pots, the former's growth, and especially its fructification, is much lessened. Another very interesting instance is that of the relation between the rye (*Secale cereale*) and *Viola tricolor*. Only in the presence of rye is it possible to obtain anything approaching a 100 per cent. germination of the *Viola*, and this is particularly significant because these two species may occur together naturally in the relation of crop and weed. Similar observations have been made by Funke (190, 191) with different species and by Varma (566). Shull (488) has commented, from a rather different point of view, on a somewhat similar association of species and Osvald (411) has shown that an aqueous extract of the roots of *Agropyron repens* may have different effects on the germination of rape and oats according to its concentration, and that the substance concerned is probably an acid belonging to the phytohormones or hormone derivatives.

As just indicated the suggested explanation of these facts is that many plants produce some sort of chemical emanation or secretion which is inimical to the development of certain other plants. These secretions are visualised as of three kinds, namely gaseous emanations from the aerial parts of the plant, as is well known in *Dictamnus*, and perhaps also in *Rhus toxicodendron*; liquid or solid secretions from the leaves which tend to be washed down into the soil by rain (20); and secretions direct into the soil from the roots. It is the last which is presumably concerned in the cases mentioned above.

That at least something of the kind occurs is indicated by quite other observations, such as the intolerance of some plants to the presence of certain Crucifers, and especially the mustards. Here there seems little doubt that some biochemical substance characteristic of these plants has some sort of toxic reaction towards other plants. Apart from the direct toxic effect of such secretions they may have a marked effect in determining the value of the habitat. It is well established, for instance, that acid or alkaline root secretions may seriously alter the hydrogen ion concentration of the soil water. Still another observation bearing on the same point is that of the liberation into the soil of ethylene from organic sources (306).

However these results may be modified (and it is only fair to say that some of them are inconclusive) and their interpretations altered by further research, it seems reasonably clear at present that competition is to be regarded as something more complex than has been generally supposed in the past. Probably actual physical factors are the chief considerations involved and must almost of necessity be so normally, but there are at least indications that other factors and particularly chemical factors may play an important part. It is also important to remember that the issue of competition may be decided at various stages in the life of the individual. For instance, the danger of overcrowding to species of large plants is usually marked only in the early and seedling stages, and once these have been passed the danger is generally over. Similarly the copious growth of ephemeral annuals may produce a temporary condition of danger which will pass in the course of a few weeks.

This rather lengthy discussion of competition may perhaps leave the reader with the impression that the relations between plants are naturally and always relations of antagonism. They may naturally be so but they are not always. One type of plant life may in fact provide the essential conditions necessary for the presence of another type or species, as is seen, for example, in plants which require to live in the shade of others as in woods or hedges, and in lianes and epiphytes. The continued growth of one species may also actually affect the substratum in such a way that it becomes colonisable by other species, as for instance in plants which inhabit the deep leaf-mould found in long-established beech woods. Sometimes the relationship is even closer, and this is particularly the case with parasitic or epiphytic plants whose ranges are determined by those of their hosts. Often-quoted extreme examples of this are certain species of *Utricularia* which live exclusively in the water which accumulates at the base of the leaves of certain tropical American Bromeliaceae, and whose range is thus always correlated with that of the species they inhabit.

The conclusion therefore is that competition is itself but one aspect of a wider and more generalised factor of distribution, which is the influence of one kind of vegetation (or by analogy one kind of life, whether animal or plant) on the distribution of other plants. This general influence is often called the biotic factor, and at least in its aspect of competition must be regarded as of great importance.

This somewhat informal approach to the subject of the factors responsible for distribution has been made quite deliberately, in order to emphasise that these factors are only those that might be expected in the circumstances of the nature, life and history of the Flowering Plants. In order to arrive at what these factors are there is no necessity to possess any very profound botanical knowledge, because they will, to a large extent, become apparent in the course of such a discussion as has just been completed. It has, however, been rather lengthy, and we must now summarise the conclusions we have reached and go on to see how they compare with the conclusions reached on this matter by others.

In making this summary it is convenient to arrange the factors more in accordance with their mutual relations than was done above, where the main consideration was a cursive presentation of them. When this is done, what has already been said may be restated in the form of the following table of factors concerned in the distribution of plants:

1. Place and time of origin.
2. Distribution of climatic values (temperature, rainfall, light, wind):
    a. in the present.
    b. in the past.
3. Distribution of edaphic values (physical, chemical, physiographic):
    a. in the present.
    b. in the past.

4. Potentialities for dispersal.
5. Configuration of land and sea:
    - *a.* in the present.
    - *b.* in the past.
6. Influences exerted by other plants:
    - *a.* direct competition.
    - *b.* indirect influences.
7. Human influences (not considered in detail).

These conclusions accord well with those of others. Hayek, for instance (254). recognises:

1. Climatic factors;
    i.e. light, temperature, atmospheric pressure, precipitation and wind.
2. Edaphic factors;
    i.e. soil.
3. Biotic factors;
    i.e. influence of the animal world, influence of man.

Thomson, J. A.,† comprehending the distribution of both plants and animals, arranges the factors in three pairs thus:

a. The physical peculiarities of the region under discussion, and the constitutional peculiarities of the living creatures.
b. The original headquarters of the stock (usually uncertain), and the means of dispersal in each case.
c. The physical changes of climate, earth-movements, etc., in the region, and the changes brought about in the struggle for existence between the various living tenants of the country.

Both these authorities point out that there are also many minor additional factors, and also that those mentioned interact so as to produce a very complex state of affairs.

Du Rietz (145) gives a rather more elaborate classification, especially in regard to biotic factors, which is of interest as incorporating the essential factor of time, not mentioned in the above two schemes, namely:

A. Actual factors—
    I. Abiotic:
        a. climatic.
        b. edaphic.

    II. Biotic:
        a. non-antropeic—not influenced by man—
            1. phytobiotic:
                a. climatic—such as shadow, wind, shelter, etc.
                b. edaphic—such as humus, soil, humidity, etc.
                c. pyric—effects of fire.
            2. zoobiotic—presence of excreta, carcases, etc.
        b. antropeic—due to man's influence—
            1. direct.
            2. indirect.
B. Historical factors (with all the same groups as "actual").

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† In Mill, H. R. (ed.) *The International Geography.* 3rd ed., London, 1903.

He also gives a classification in which he sets out the factors influencing "the distribution of species upon a certain spot during a certain period." They are six in number, namely:

1. Nature of habitat at beginning of period.
2. Distribution of species upon or near the spot at the beginning of the time factor.
3. Supply of dispersal units.
4. Strength of each species in competition.
5. Interference of animals, man and plant parasites.
6. Time elapsed.

Here there is recognised as a separate edaphic factor an effect which has not previously been specifically mentioned, namely fire. Fire may often be due to human action, but in certain parts of the world it is a normal occurrence at certain seasons, and in response to it certain peculiar features of the vegetation in these regions have been developed. The subject will be dealt with more fully later.

These specimen classifications of factors show two things—that the differences between them are mainly due to difference of opinion as to what may justifiably be termed a factor, and that the arrangement arrived at above incorporates, within the limits of its detail, all the relative types of factors. It does not, however, mention all the aspects of these factors, and we must therefore pass on now to the more particular consideration of those factors which have most bearing on those theoretical aspects of plant geography which are the subjects of the two final chapters, namely climatic factors, edaphic factors, dispersal, changes of climate and geographical changes.

Before doing this, however, there is one more subject to be mentioned. This is the migration of species or of floras, and it is rather a consequence of the interaction of the factors outlined above than a factor itself.

It cannot be doubted that if the factors which have been described have all played a part in controlling plant distribution—and it is the purpose of the next few chapters to demonstrate this—plant distribution must be regarded as something in more or less constant flux and rarely if ever constant for more than a short period. The fluctuation may be visualised as of two kinds, first in respect of the floristic constitution of any flora, and secondly in respect of the position of various floras. That the latter and more important type of change has taken place is demonstrated wherever there is evidence that a particular area has been occupied at successive periods by different assemblages of plants. Unless it can be assumed that each successive flora developed *in situ*, it must be believed that the later ones in turn displaced those that went before, and such an assumption being out of the question, if on no further grounds than those of time, this belief is justified. Again, if an earlier flora is found at a later date in a different position and contemporary with the flora which replaced it in its original site, we may assume that very extensive movements of floras over the surface of the world must have occurred. The evidence of migration is thus chiefly palaeobotanical, and it is very copious and unmistakable. There are repeated examples of superposed floras of different types, as well as of similar floras changing position with the passage of time.

We need not go beyond the bounds of Great Britain to demonstrate this and to see how even one small country has been the home of a succession of floras one after the other. Almost every geological horizon has revealed a different type and constitution of native flora.

Particularly is migration revealed in the special geological matter of glaciation, and we need only remind readers of the later history of the British flora and particularly of the changes which have taken place between the earlier Pliocene and the present day. At the former time the flora was much as we know it now, but in the interim much of it was undoubtedly forced out of the country, to return once more at a later stage. In North America the degree and extent of the floral movement were almost certainly even greater, as is illustrated by Core's account (111) of the successive migrations and movements of the flora in the Appalachian region which have left it as it is to-day.

In this particular instance of the effect of glaciation it is fairly certain that the result of the climatic change was to telescope up the floristic and climatic zones rather than to eliminate the higher values, and the lowlands of the equator do not seem to have been appreciably colder than they are now. At the same time the spread of the ice must have diminished the total area open to plant growth very considerably. In these circumstances it is impossible to deny the probability not only of floral migration but also of increased floral mixing, and so these same geological evidences afford examples of the first kind of fluctuation mentioned above, that of the constitution of different floras.

But this kind of migration, the movement by which independently originating floras become mixed so as to consist of or show elements derived from various directions, is shown even better and more generally in the present world flora. Perhaps nowhere in the world to-day can it be said that the flora consists entirely of plants which have originated locally. Almost always the flora contains some proportion of foreign ingredients. Clearly there must be some kind of differential movements of floras to produce this effect—there must be an infiltration of forms from the frontiers or from distant lands, and where, as in many cases, this infiltration seems to have taken place from many directions, its effect is even more striking.

The same thing is seen in the difficulty which exists in defining certain floristic areas or regions, and a brief reference back to Chapter 2 is sufficient to show how real this sometimes is. The difficulty arises simply because particular parts of the world's surface have become focal points at which streams of migration or infiltration from various directions meet. One of the most important of these is in eastern Malaysia, where there is a conspicuous mixture of Asiatic and Australian floras, and the problem of just where the line of demarcation between the two is to be drawn has puzzled many investigators. The fact of the matter is that in passing from Asia towards Australia the change in floral constitution as between Asiatic and Australasian plants is so gradual and the mixing so complex that it can hardly be sorted out. Similarly, but on a lesser scale, the more southerly parts of the East African coastal belt are a notorious transition region where the northern parts of the South African flora and the southern parts of the tropical flora have met and mingled (51). The flora of the high alpine region at the junction of Tibet, China, Burma and India is another very marked instance, and the flora of this general region contains elements of the flora of each of the neighbouring countries, a fact that is reflected in the degree to which the flora as a whole can be divided in geographical detail.

Migration and mingling of this kind is perhaps least seen in America, and the presumptive reason for this is interesting. When two moving societies begin to mix in the way that has been indicated it is only a matter of time before the mixing is complete, and the result is a homogeneous one with, as time goes on, an increasing character of its own. Hence where this mixing is most conspicuous and localised, as in the instances given above, it is reasonable to suppose that it has not been going on very long. This, of course, will depend on the length of the opportunity for such mixing. In America the indications are that there have been opportunities for the mingling of at least most of the floral elements of the continent for a very long time, and indeed that such prolonged mingling has been in progress. As a result it is far less in evidence than in the Old World.

In terms of the present world flora it is perhaps not too much to say that floristic mingling caused by this kind of migration is one of its most general features, but, whether this is a fair statement or not, the instances which have been mentioned in conjunction with the geological examples of wider migration are ample to show that actual movements of assemblies of plant species over the world in various directions have taken place as a more or less direct consequence of the distributional factors outlined above.

CHAPTER 16

THE FACTORS OF DISTRIBUTION—II. CLIMATIC FACTORS

CLIMATE may be described as the physical state of the atmosphere and may be regarded as the result of the sun's influence on the layer of gases that covers the surface of the earth. This total physical state of the atmosphere is composed of a number of different constituents which it is convenient to term the elements of climate. Of these temperature and moisture are the most important, but there are a number of others of secondary significance. Most of these do not call for any extensive treatment in this chapter and it will be sufficient for our immediate purpose if climate is regarded as consisting essentially of four aspects, temperature, precipitation, light and wind. It would be difficult to maintain that this is invariably their order of importance, but, as will be seen, it represents their general relation and it is convenient to deal with them accordingly.

The problem of the influence of climatic factors on plant geography has been discussed by many writers and it is not possible to refer here to all the important sources of information on the subject, but the reader will find much of interest in publications by Livingston and Shreve (344) and by Zotov (614), and a comprehensive source of further information in Schimper and Faber (464).

Temperature

(Plates 20, 21)

It is believed that the interior heat of the earth, although considerable, contributes but negligibly to the heat of the atmosphere, which is derived almost entirely from the sun. At the same time it must be remembered that the heat of the atmosphere is not the only direction in which temperature affects plants, and that the heat of the soil, which is itself derived from the heat of the atmosphere, has also an important influence. For our present purposes, however, the latter may be regarded as generally proportional to and determined by the former.

The basic consideration determining the distribution of temperature on the earth is the shape of the globe, and its inclination to the direction of light and heat coming from the sun. In equatorial regions the incident rays from the sun not only reach the earth almost perpendicularly but thereby pass most directly through the atmosphere. Progressively away from the equatorial regions the curvature of the earth not only causes the incident rays to strike more and more obliquely but also causes them to pass less directly through the atmosphere, until at the poles they may be said to be almost parallel with the earth's surface.

For these reasons the basic distribution of temperature value is a latitudinal one showing a gradual and considerable diminution between the equator and the poles (see Plate 20). At the same time the obliquity of the ecliptic causes a seasonal variation in the gradients alternating in the two hemispheres, so that they are least steep in the summer and most steep in the winter. The latitudinal zonation of temperature must therefore be regarded as in a state of regular oscillation.

Since the two main factors of the position of the sun and the thickness of the atmosphere are to all intents and purposes constant, it might be expected that the latitudinal distribution of temperature would be perfectly regular and symmetrical on both sides of the equator. There is no reason to suppose that this would not indeed be the case were the surface of the earth exactly the same in all places—if, for instance, the surface were entirely land and that land were of constant height. As it is, neither of these states prevails. The distribution of land and sea is very complex and irregular, and in addition the relief of the land is extremely varied. Both these features influence temperature to a considerable extent. The general effect of large areas of sea is to tone it down and to reduce extremes, and it may also have a secondary effect through the influence of warm or cold currents. Elevation of the land has the general effect of reducing the normal latitudinal values of temperature. It may be expected, therefore, that the actual distribution of temperature will be a latitudinal one modified by these two considerations, and a glance at a temperature map of the world will show that this is indeed the case. As a result the world can be divided into a series of rather irregular latitudinal zones on the basis of temperature, as is, of course, perfectly familiar in such terms as "tropical," "temperate" and "arctic," the irregularity depending on the degree of variation in the distribution of land and sea and of altitude. In this distribution the equatorial values tend to remain more or less constant throughout the year, but elsewhere they oscillate between maxima and minima according to the season, the hemispheres alternating in this respect. These circumstances lead, on the land surfaces of the earth, to the occurrence of two rather distinct types of climate based chiefly on their temperature features. Away from the influence of the sea, that is to say towards the interior of the larger land masses, the climate is "continental" and characterised by comparative extremes of heat in summer and of cold in winter. On the edges of large land masses and on islands there is an "oceanic" climate characterised by more moderate variation and less extreme seasonal values.

The effect of altitude is much less generalised and more localised, in accordance with the irregular distribution of elevated regions. It is true that a great part of the world's land surface is raised considerably above mean sea level and that therefore the temperature values tend to be widely modified, but it is only in the regions of great elevation in the more temperate latitudes that the modification becomes strikingly apparent. Especially is it noteworthy in the huge plateau system stretching north from the Himalayas, and on a smaller scale in the areas occupied by the great mountain systems of western America, but it is seen to some extent in practically all the mountains of the world.

Ocean currents, by bringing either colder water into warmer seas, or *vice versa,* tend to effect the distribution of temperature wherever they occur except when their direction is parallel to the equator, but in fact there are only two regions of the world where the effect on a world-wide scale is marked. These are in the north Atlantic and north Pacific oceans, where the Florida and Gulf Streams and the Kuro Siwo current respectively cause the isotherms to deviate far to the north by the influence of the warm waters which they bring from the tropics.

The main features in the distribution of temperature are shown in Plates 20 and 21, but they may conveniently be summarised here. Annual isotherms, that is lines of equal mean annual temperature, are basically latitudinal, when reduced to sea-level values, but they are distorted northwards by warm currents in the northern hemisphere and southwards over the land masses of the southern tropics.

The average minimum temperature varies from — 76° F. in the north-east of Siberia to over 68° F. in Guiana and parts of Malaysia. It is below — 40° F. in much of northern Canada and Siberia. In Spitzbergen the mean summer temperature is little above freezing and the growing season lasts only about six weeks. In the north part of Ellesmere Land, where the figures are somewhat similar (385) the temperature hardly ever reaches 60° F., and there is very rarely a month without frost, circumstances which may make this area, in terms of accumulated temperature, one of the coldest parts of the world.

The average maximum temperature varies from below 68° F. in parts of North America and north Asia to over 113° F. in parts of the south-west U.S.A., in the African-Indian desert and in parts of Australia, and is above 104° F. over a considerably wider area.

The annual mean range of temperature varies from under 10° F. in most of the tropics to over 120° F. in part of Siberia.

The annual extreme range of temperature varies from about 20° F. in parts of the tropics to 170° F. in parts of north-east Siberia.

Constancy of temperature throughout the year is very important in plant distribution and is perhaps to be regarded as the essential character of climate in the tropics.

A last general point about the distribution of temperature, and indeed of other factors too, is to remind readers once more that the northern hemisphere is a land hemisphere and the southern a water hemisphere, so that great caution must be used in comparing conditions and values in the two.

The correlation between plant distribution and climate is shown more clearly in the case of temperature than anywhere else (*e.g.* 321), and indeed is so obvious that it scarcely needs demonstrating, as our common application of such words as "tropical," "temperate," "hardy," "tender," to plants shows. It is here, however, important to draw the proper distinction between flora and vegetation, because it is especially in the limitation of the range of species and other units that temperature is important. It has already been seen how few plants are anything like cosmopolitan in range, and what a marked distinction there is between tropical and temperate forms. Indeed, it is fairly true to say that the reason why there are not more completely distributed plants is that most wide species are ultimately limited by considerations of temperature.

This is to be seen almost everywhere. Our own flora affords many instances in which species occupy the more southerly part of the country but do not range far north. Similarly with the question of casuals: the factor which prevents them from establishing themselves is temperature—not, it will be noticed, temperature at all times, or they would clearly not occur at all in the country, but the temperature at some season of the year, that is to say at some stage in their development.

The way in which temperature acts as a limiting factor of distribution seems to be twofold. In the first place a low temperature may not provide that combination of heat quantity and quality which is necessary for the production of seed and fruit, as is the case with the casuals just mentioned, but there is generally also a temperature minimum below which even the vegetative life of the plant cannot continue. This will actually determine whether a species can occur in a given area, and clearly the higher the temperature needed for growth the narrower will the potential area of the species be. It would seem, however, that most plants can live vegetatively over a fairly wide range of temperature provided that this does not fall below freezing point. This is not to say that they can reproduce, but they can exist, and this is shown by the innumerable examples of garden plants from warmer countries which are hardy in this country except in very extreme conditions.

The question of frost raises quite a different problem, because it involves the possible injury of tissues by the expansion of their juices when they freeze. It is significant that there are no Flowering Plants which pass the whole of their life history in a temperature below freezing, and there is probably none capable of doing so. Indeed, very few can survive serious freezing during the time that they are in full vegetative vigour. Naturally the lower the temperature the greater is its effect likely to be, but there is reason to suppose that very often the duration of freezing is more important than the actual degree of coldness, and Shreve (487) has shown this to be the case with certain cacti, one of which (*Opuntia missouriensis*) successfully resisted 375 continuous hours of frost, while others were destroyed by much shorter periods at the same temperature. In this connection it may be noted that another cactus (*Mammillaria vivipara*) extends to above 50° N. in Canada and normally endures much longer periods of continuous frost.

Indeed the frost-line, in one or other of its many possible definitions, is probably the most important of all climatic demarcations in plants, and in very general terms it seems to be true that many plant groups, especially genera, are either frost-sensitive or not, the former being restricted to the "tropical" parts of the world. It is at all events noteworthy that the number of truly cosmopolitan genera (see p. 81) is small, and that there are very few large genera which can be described as characteristically sub-tropical in the sense that they have a balanced distribution on both sides of the frost-line.

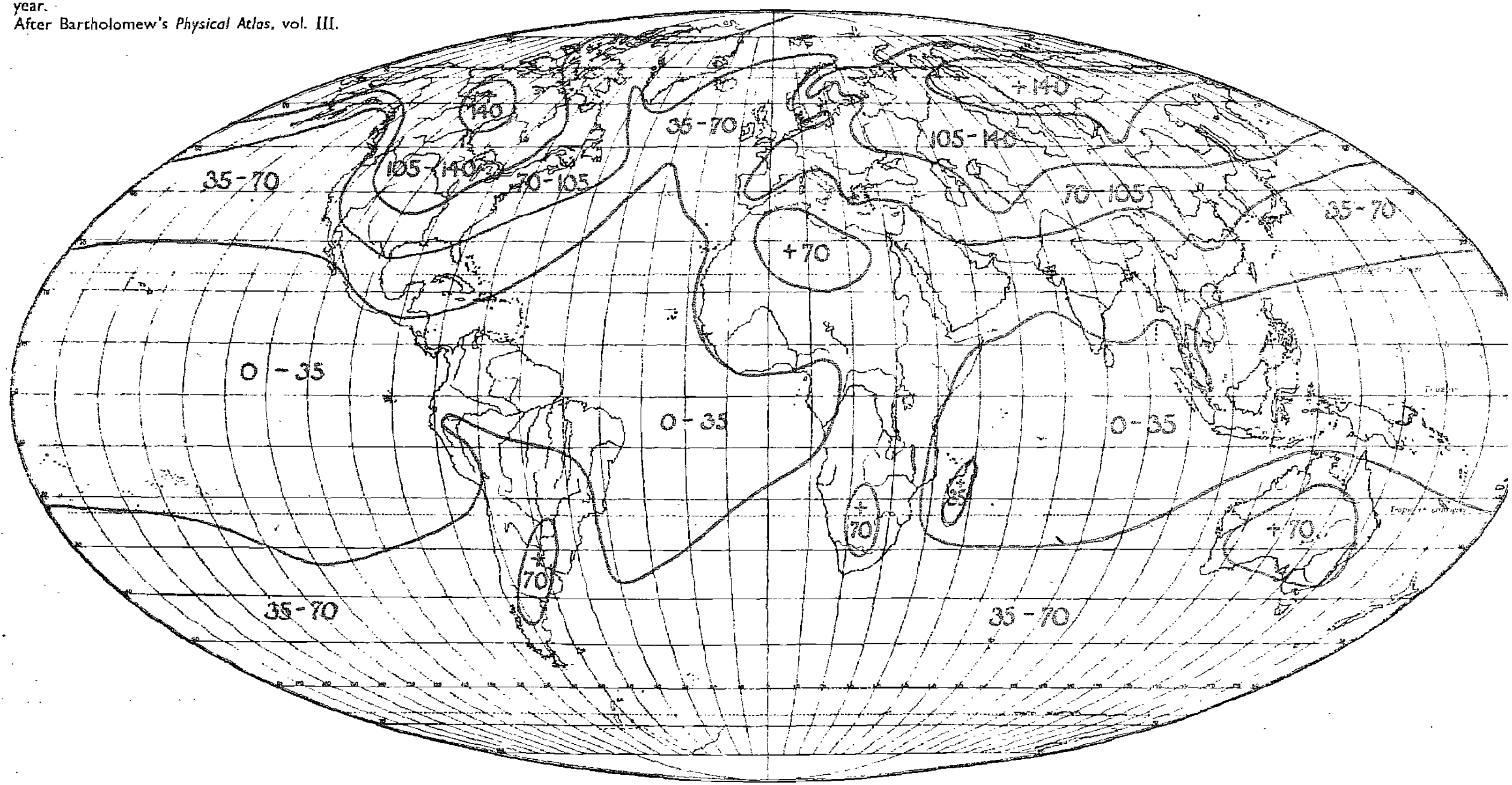
This point has been nicely illustrated recently by Hartley (253) in a study of the world distribution of the six largest tribes of the grasses in which he shows that, with the exception of one which is probably not a natural group, each is either characteristically tropical or characteristically temperate. He also demonstrates a correlation in their distribution with the line (isocheim) for 50° F. mean temperature for the coldest month, a line which "delimits, in a very general way those parts of the world in which severe winter frosts are normally experienced."

Plants which inhabit regions where frost is general during the winter season normally spend that period of the year in some condition which protects them from the dangers of freezing. This process of self-protection against winter rigours is called perennation and is carried out in a variety of ways such as the restriction of life to buried organs only, the loss of leaves during autumn, and so on. The winter may also be passed in the seed condition, where the plant is not only dormant but protected by various resistant structures. This indeed seems to be the normal process in ephemeral annuals. Some seeds may germinate in the autumn and endeavour to pass the winter as young seedlings, and may, if the conditions are not too bad, succeed in doing so, but there are always many seeds which do not germinate till the following spring, when it may be presumed safe to do so.

It is in relation to temperature as a geographical factor that the subject of growth-forms is most appropriately mentioned. It has long been recognised that plants can be classified according to their general form, and many people have published such schemes, but the study of growth-forms (75, 122, 436) is especially associated with the Danish botanist Raunkiaer. He recognises the following main forms, each of which he further classifies in detail. The names used are for the most part indicative of the chief features of the types.

PLATE 21

Map of the World showing, in degrees Fahrenheit, the range of extreme temperature variation during the year.
After Bartholomew's *Physical Atlas*, vol. III.



Areas correct. Distortion increasing towards border of map.
Approximate Scale 1:100,000,000 (1600 miles = 1 inch) along Equator
on Mollweide's Homolographic Projection

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Phanerophytes	Plants whose size is not appreciably diminished in cold or dry seasons. It includes all woody perennials of erect habit and also many epiphytes and succulents. At least a dozen minor types can be recognised.
Chamaephytes	Subshrubs or herbs which partially die back in winter or which grow closely adpressed to the surface of the soil. This includes cushion plants.
Hemicryptophytes	Plants which lose practically all their aerial parts in winter and are visible above the surface only as rosettes or offsets.
Cryptophytes	Plants which disappear entirely to below ground (geophytes) or water (helophytes and hydrophytes) during winter and which perennate by rhizomes, bulbs and corms, or by under-water buds.
Therophytes	Plants which pass the winter in the seed, as most annuals.

This classification might be paraphrased as one which is based on the degree to which plants find it necessary to protect themselves against winter conditions. In these terms the phanerophytes include the plants which are under no such necessity, as well as those in which the method is least obvious. In the other groups the degree of protection, which is usually the reverse of exposure, becomes progressively more marked until it culminates in perennation in seed form, which may be regarded as the last resource.

One slight complication needs to be explained here. In some parts of the tropics, where temperature conditions are always more or less at an optimum, growth continues all the year round, but in other parts there is an unfavourable period because of an uneven distribution of rainfall in time. In other words, here the winter cold unfavourable season is replaced by a dry season where the danger is desiccation instead of refrigeration. This point will be returned to later, but it is worth noting here that the two distinct dangers are met by plants in much the same way.

As to the absolute temperature values which flowering plants can stand, two general statements seem to be true: first, that little or no development goes on at temperatures below freezing; and second, that there are no parts of the world where the temperature is too high for growth and reproduction. As will be seen, there are regions where the plant life is very scanty, and some where it is virtually absent, but this is not due solely to temperature values.

The relation between plant distribution and temperature alone is perhaps most clearly seen in the case of aquatic plants, and especially in the marine Angiosperms, because here many of the complicating related factors such as other air conditions, precipitation and so on are absent. Plants living in the sea may, it is true, be affected by the chemical constitution of the water and also by the movement of the water in the form of currents, but the former is reasonably constant and the latter does not seem to be a decisive factor in the determination of range, and it is fairly safe to say that the one really important consideration must be temperature. With this belief the account of the distribution of Angiosperms in the sea in Chapter 11 and as illustrated by Plate 15 is very significant. Above all, the occurrence of prevalent latitudinal distribution limits will be noticed, and it can scarcely be doubted that these are due to the temperature relation of the species concerned. Moreover, it is clear that this relation must be a very exact one, because the latitudinal temperature gradient in the sea is very gradual.

The importance of the modification of the general latitudinal distribution of temperature by elevation as a factor in distribution can scarcely be overestimated. In rising vertically above the mean sea level there is a fall of temperature of approximately 3° F. for every 1,000 feet, so that all mountains reproduce, according to their height, a temperature range corresponding to that between certain latitudes at sea level, and any mountain which has permanent ice and snow epitomises the whole temperature gamut at sea levels between the latitude in which it is situated and the nearer pole (fig. 1). Thus a mountain on the equator which is high enough to have permanent snow reproduces on its slopes the temperature gradient of a whole hemisphere. For this reason mountains provide habitats, as far as temperature goes, for plants characteristic of quite different latitudes, and thus afford a series of stepping stones in range which is often of the greatest value. It has been seen that many plants occur in the temperate regions of both hemispheres, and are therefore to be regarded as having crossed the tropics in the course of their spread. This they have certainly done by way of mountains, which, for the reason mentioned, afford a pathway for their movement.

It is often not sufficiently realised how widely distributed in the tropics are mountains of great elevation, but actually they are of common occurrence. Most obvious is the great range of the Andes, which, while indeed of least magnitude in the north parts of the tropical zone, does in fact provide a more or less continuous line of peaks between north and south. Less noticeable, but none the less serviceable, are the mountains which stretch in an almost unbroken line from the Himalayas down the Malay Peninsula and through Malaysia to New Guinea, whence the step to Australia, which has itself an elevated eastern border, is short. Only in Africa is the situation rather different, not only because there the heights are less continuous but because a particularly wide break of desert regions cuts them off from the northern temperate mountains of Europe. Also, at present at least, there is enormous oceanic discontinuity south of Africa.

In view of these facts the occurrence of bipolar plant types is almost certainly due to the fact that they have succeeded in crossing the tropics by passing along mountain chains, and this they have been able to do because of the peculiar temperature relations which the mountains afford. Incidentally it may be added that Du Rietz (146) and others have shown that some species have probably crossed the tropics by the New World mountains, some by the Malaysian route and some by both means.

This view is supported too by the present occurrence on nearly all tropical mountains of types which are either identical with or very closely resemble those of the temperate regions and especially those of the north. Allusion has already been made to northern genera with extensions into the tropics along the mountains, and this is specially notable in America, though only less so in Malaysia. Van Steenis (529) has made a careful study of the mountain flora of Malaysia and has shown how many northern forms there are in it, and also the routes by which they apparently came.

In Africa too the same is true, except that here, owing to the peculiar distribution of the mountains, the relationship with the north is more discontinuous. Time and again, however, the prevalence of northern types on the African mountains has received comment, and indeed many of our familiar British plants occur there, as, for instance, *Sanicula europaea* and *Epilobium hirsutum*, while *Linnaea borealis* has been reported apparently growing wild on the slopes of Ruwenzori.

Precipitation

(Plates 23, 24)

Under this term are included all forms of atmospheric moisture, but it will simplify the discussion if we consider it in terms of rainfall only, remembering nevertheless that such other forms as snow and dew are sometimes of great importance.

The distribution of rainfall is essentially different from that of climate in that it is not regularly latitudinal. It is true that the heaviest rainfall tends to be in parts of the equatorial, or at least tropical, zone, but the main feature of its distribution is that nearly all values tend to occur in nearly every latitude. This alone is sufficient to show, bearing in mind the general distribution of plant life already described, that of the climatic factors rainfall is to be regarded as secondary in effect to temperature.

It is particularly with the relative importance of heat and rainfall that we can illustrate the difference between floristic and vegetational distribution. It has been seen that floristic distribution, that is to say the distribution of taxonomic units, is predominantly a latitudinal one. The distribution of vegetation types, on the other hand, is predominantly one of precipitation. That is to say, such vegetation types as forest and grassland tend to occur at any latitude in certain rainfall values, while deserts are similarly distributed where rainfall is inadequate. To put the matter from a rather different point of view, it may be said that in matters of plant geography temperature is more fundamental than rain; in matters of plant ecology, in the sense of vegetational development, rain is more important than heat.

At the same time there is an intimate relation between temperature and rainfall because of the influence which the former may have in determining the humidity of the air and thereby the effectiveness of the precipitation, and many attempts have been made to arrive at some combined formula or equation by which the correlation of the distribution of vegetation and floral units with these factors may be more accurately expressed. Among these there may be mentioned, for purposes of illustration, the precipitation-evaporation ratio or P/E used by Thornthwaite (556, 619); the Meyer ratio, which is the ratio of the precipitation to the saturation deficit of the air, and which has been applied in an interesting way to the vegetation of Western Australia by Gardner (192); and such particular rainfall-temperature equations as those used by Miller (390) in his attempt to express the climatic lines of separation between forest, grassland and desert.

Owing to the absence of any basic latitudinal zonation, rainfall, even more than temperature, is correlated with the distribution and relief of land and sea. This is because winds coming from the sea will be moisture-laden, and also because elevated regions may protect inland areas from the influence of these winds. Rainfall must therefore be considered as very directly related to wind, and reference should be made to the discussion of that subject below.

As it is, the simplified distribution of rainfall is roughly as follows. Regions of maximum rainfall are nearly all equatorial, namely the lowlands of Brazil, parts of west Africa, and the whole of Malaysia and the Pacific. In all these the total annual rainfall is above 80 inches. Other more localised regions with similar values are the east coast of Brazil, parts of the west coast of South America, the east coast of Madagascar, the Himalayas and Burma, parts of south India, New Zealand and a small area in Alaska. The highest annual figures recorded (about 450 inches) are from single stations in Burma and the Hawaiian islands. Regions of exceptionally low rainfall, under 10 inches a year, are in the arctic, parts of western North America, parts of temperate South America, North Africa and Arabia, Central Asia, South Africa and the interior of Australia. Elsewhere the distribution of rain varies from 10 to 80 inches annually. The two main features are undoubtedly the practically continuous area of high rainfall from the Himalayas through Malaysia and far across the Pacific, and the almost continuous range of low rainfall, leading to desert conditions, which stretches from the west coast of North Africa practically to China.

The general correlation of species distribution with this distribution of rainfall will be apparent from the close correspondence of some of the floristic regions with it, but reference to total annual rainfall is not enough to show this correlation fully. Obviously the absolute amount of rainfall must be of primary import, but except where this is definitely inadequate a much more significant aspect is the distribution of the rain during the year, that is to say during the various phases of the plant life. In brief the following conditions are to be found :

1. Heavy rainfall all the year round.
2. Moderate rainfall always, becoming heavy at certain times.
3. Moderate rainfall throughout the year.
4. Moderate rainfall concentrated in the summer.
5. Moderate rainfall concentrated in the winter.
6. Low rainfall spread over the whole year.
7. Low rainfall concentrated in one season.
8. Relative absence of rain.

A rather different classification, of which Plate 24 is a somewhat simplified edition, recognises six types, as follows:

1. Constant drought:
    N. Africa to India, C. Asia, California, western S. America, S. Africa and C. Australia.
2. Periodic rains:
    a. summer rain, dry winter and spring—
        especially in the monsoon regions of Asia, western Africa and parts of tropical America.
    b. winter rain, summers dry—
        Mediterranean, western N. America, Cape, western S. America and S.W. Australia.
3. Rain at all seasons:
    a. maximum in summer—
        tropical S. America, eastern N. America, Europe and W. Asia, parts of Malaysia.
    b. maximum in winter and autumn—
        W. Europe, parts of Malaysia, N. Pacific coasts, Fuegia and New Zealand.
4. Continuous rain, no month with less than fifteen rainy days:
    occurs only in parts of certain oceans.

Light

As Hayek (254) and others have pointed out, light must, in one sense at any rate, be the fundamental climatic factor in relation to plants, because the chemical process, photosynthesis, which is the basis of the whole of their physiology, is, as its name implies, one which goes on only in the presence of light, so that in its absence plant life as we know it to-day could not continue. This is, of course, perfectly true, but our concern here is rather with the effects of various climatic factors in limiting the actual distribution of plants, and in this respect light is of comparatively minor importance.

Owing to the shape of the earth the insolation of the equatorial regions is stronger or at least more direct than that of the latitudes further south and north, but there are no data to indicate that tropical plants require stronger light than temperate ones. On the other hand, many plants protect themselves from extreme insolation by some structural or chemical means. Nor is the value of insolation at any spot always constant. It may be greatly modified by the degree of cloudiness, and this being so, it may be assumed that ordinary sunlight provides appreciably more light than plants actually require, and that nowhere, during summer months at least, is it deficient. The main effect in the distribution of light values seems, on the other hand, to be the length of time of illumination. In the equatorial regions the day is about the same moderate length all the year round, but towards the poles the day becomes longer in the growing season and shorter in the winter, until in the arctic and antarctic there is more or less continuous light for six months and a corresponding length of darkness.

The effect of length of day on plants and particularly on their flowering has been much studied and there is available a useful summary of the subject (589). There are now generally recognised to be "short-day plants," "long-day plants" and "day-neutral plants," the first including essentially those of the tropics and the second those of temperate latitudes. In temperate lands the short winter day does not affect the question because the plant is dormant during this season of the year.

If this distinction is indeed operative in nature, that is to say if the generality of plants are either "short-day" or "long-day" and are therefore segregated geographically, length of day, which is an expression of the obliquity of the ecliptic, must be a fundamental distributional factor, but the matter may not be quite so simple as this. For instance many tropical plants which in nature live under short-day conditions can be made to flourish and flower without difficulty in glasshouses in long-day latitudes, provided the necessary warmth and moisture are supplied. Conversely it would seem to be very much more difficult to make long-day plants flourish in lower latitudes where short-day conditions prevail (447, 529), though here the results might be different if the local temperature and other factors could be modified by some sort of refrigeration. The whole subject is made more interesting to the plant-geographer because of its special association with problems of Angiosperm history and because of the light it promises to cast on climatic change in the past, and for these reasons it will be discussed shortly again at the end of Chapter 19.

Wind

Broadly speaking, wind, that is to say air in motion, is the result of local variations in the pressure of the atmosphere, and we must therefore, in discussing the effect of wind on the distribution of plants, keep in mind its relation to barometric pressure. This latter alone, however, has not received much attention as a direct factor nor does it appear to be important as such, though it has been suggested that there may be optimum pressures for certain plants.

Wind may be regarded as of potential effect in plant geography in three ways, namely:

1. By its physical influence on the growth-form of plants, as in restricting or preventing the growth of trees. In the Falkland Islands, for instance, wind seems to have exerted a considerable influence on the nature of the vegetation in this way.

2. By its effect on dispersal. Here a distinction must be drawn between land winds and oceanic winds. The latter have a fairly simple distribution, but the former are very complex and variable, depending on all sorts of extraneous factors, and, although there are prevailing winds, it is probably true to say that in most land areas wind direction varies greatly. This is obviously of great potential significance in dispersal, which normally occurs only at certain seasons of the year.

3. By its effect in determining other climatic values. Two climatic elements are especially liable to be varied by wind, namely temperature—which becomes lowered by the increased evaporation that results—and rainfall. Indirectly the absolute amount of this latter may be affected, but wind chiefly controls it by determining its direction and the areas over which it will fall. The monsoon of the Indian ocean is perhaps the best example of this.

As has been indicated, it is almost impossible concisely to describe the normal distribution of wind over the continents, but the general planetary circulation of the atmosphere, particularly over the oceans, is fairly simple. Extending for some distance on both sides of the equator is a belt, the doldrums, where the pressure is low and winds are very light. North and south of the doldrums are the two great belts of the trade winds, strong steady winds blowing, in the northern hemisphere, from the north-east, and, in the southern hemisphere, from the south-west. Between the latitudes 30° and 40° are the northern and southern horse latitudes, which are regions of high pressure and comparative calm. Between the horse latitudes and the poles are the westerlies, strong winds predominantly from the south-west and from the north-west respectively in the northern and southern hemispheres.

Bush Fires

Apart from their direct effects upon the distribution of plants, climatic factors often exert their influence in indirect ways, and as one striking example of many such the case of bush fires may appropriately be mentioned.

The deliberate and periodic burning of vegetation is a feature of many systems of agriculture, especially in the tropics, but in certain parts of the world the combined features of climate and vegetation are such that seasonal fires are a normal and more or less natural occurrence. This is true, for instance, in parts of the savana zones of tropical Africa, where there is a prolonged dry season, and it is believed by many that these periodic fires actually help towards the establishment and maintenance of savana conditions (23). How such fires start is not always apparent, but both lightning and incandescent volcanic materials are known to be among the causes (451).

In Angola, where much of the vegetation is a patchwork of dry forest and grassland, the latter is regularly burnt during the dry season. Associated with the grasses are many perennial plants, and these are characterised by exceptionally well developed and peculiar underground rhizome systems by which they are able to survive even when their aerial parts are burnt. Equipped thus such plants are able to exist where others would almost certainly be destroyed. Exell (166) cites, as good examples of these fire-resisting plants, species of *Tetracera*, *Combretum*, *Annona*, *Eriosema*, *Geissaspis*, *Aeschynomene* and various Rubiaceae. Other plants of the same kind, including species of *Parinarium*, *Pachystigma*, *Lannea*, *Elephantorrhiza* and *Dichapetalum* have been recorded from the Transvaal (338).

Climatic Regions

It is evident from what has been said in the foregoing pages that the surface of the earth can be classified into regions or areas according to the values of any one of the climatic elements that have been mentioned. But it is possible to go further than this and to divide the world up into what may be called general climatic regions with regard to which all the major climatic elements and values are taken into account.

Classifications of this sort have been made by Koppen (320), Supan (540), and many others, and to illustrate them an arrangement attributed to Supan, in which the world is divided into thirty-four climatic provinces, has been used as the basis for Plate 5. The names of the various regions are more conveniently given with the plate and need not be repeated here, but the main purpose of the plate may well be emphasised once more. It is to demonstrate, by comparison with Plates 2 and 4, the remarkable degree of similarity existing between the general distribution of floras, of vegetation and of climate. These three maps, in particular, show more graphically than any words can describe the close correlation between plants and climate, and the truth of the statement that climatic factors are among the most important of all the forces controlling plant distribution.

CHAPTER 17

THE FACTORS OF DISTRIBUTION—III. EDAPHIC FACTORS

IT was shown in Chapter 15 that the ordinary flowering plant lives in contact with its environment in two directions, its aerial parts being surrounded by the air and its subterranean parts by the soil, so that environmental factors may be divided into climatic and edaphic. The former having been discussed in the last chapter it remains here to say something of the latter. This subject of edaphic factors is, however, a very complex one and only the briefest outline of it can be given here, and this should certainly be supplemented by reference to standard books on plant ecology, in the province of which this subject especially lies, and in particular to works like Daubenmire's *Plants and Environment* (125).

As regards the Flowering Plants it may be said that some amount of soil is a primary necessity for their growth and that none can live on the bare surface of rock. Soil may be described as the product of the disintegration of rocks, both sedimentary and igneous, by the process and effects of weathering, that is to say by the action of various climatic influences. To take but one of the more conspicuous instances, frost is a very potent rock breaker. All but the hardest rocks tend to become more or less soaked in times of rain; this contained water expands when it freezes and in doing so splits the rock in varying degree. The mere physical action of prolonged rain too will in time wear away even the hardest rocks. As a result of this weathering the surface layers of rocks sooner or later become broken up so that three distinct layers can be recognised. On the actual surface where the effects of weathering are greatest there is a thickness of soil proper where the rock has become more or less completely disintegrated. Below this for a varying thickness is the subsoil, where the weathering has begun the process of breaking up the rock but has not carried it very far. Below this again is the solid rock or parent material itself as yet unchanged. Thus, much may be learnt about a soil and its genesis by the study of vertical sections through it, and the consideration of such soil-profiles as they are called is an important aspect of modern pedology.

The physiological processes of the plant are such that it can make little use of and take little from disintegrated rock unless the process of its breakdown has proceeded far, and hence its soil relations are almost entirely with the actual soil layer, although to varying degrees the subsoil may be of importance. Since soils are the products of weathering it is not surprising that there is a close correlation between climatic conditions and certain kinds of soil, the two most important factors being temperature and rainfall. Generally speaking the higher the rainfall and the lower the temperature the greater the amount of organic matter in the soil and *vice versa*, while at any given mean temperature the type of soil tends to vary according to the annual rainfall. These relations have been expressed in a simple diagram by Lang (333), and this is reproduced, after Brooks (65), in fig. 73.

In the normal course of events weathering will result in the development of soil *in situ*, that is to say immediately over the rocks from which it is derived, and such soils are called local soils. On the other hand, circumstances will sometimes result in the washing away or other transportation of the soil from its point of formation, and its subsequent deposition elsewhere. Such soils are called transported soils. The main influences producing them are wind action, such as causes the accumulation of blown sand; glacial action and the movements of glaciers, as is illustrated by boulder clays and other morainic deposits; and rain and river action such as can be observed in any delta. It is worth noting that all three are capable of producing areas of soil where there would otherwise be water, and especially of producing bare soil areas open to plant colonisation. For instance, much of Holderness, in Yorkshire, would be beneath the surface of the sea were it not for vast accumulations of boulder clay and other glacial deposits. Similarly in tidal rivers fresh surfaces of alluvium are constantly being formed and may become permanent. In the case of both tidal mud and sand-dunes, however, subsequent action often tends to remove and redistribute accumulations of this kind.

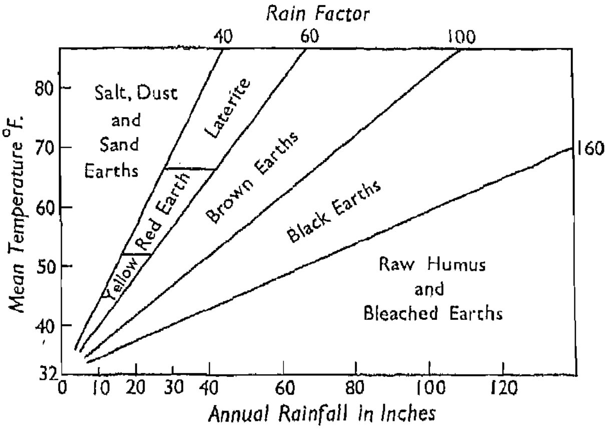


FIG. 73.—Diagram of Lang's Rain Factor. (Redrawn from Brooks, *Climate through the Ages*, E. Benn, Ltd.)

The rooting of plants in soil has a twofold function. Chiefly it enables the plant to absorb such food materials as it requires from the soil, but in addition to this it serves as an anchorage and provides the base upon or from which the aerial parts may grow up into the atmosphere. Generally speaking, the larger the plant the firmer and deeper the anchorage it will require, and so the absolute amount or depth of soil is a primary factor, in the sense that no plants can flourish unless there is a sufficiency of soil for the proper development of their underground parts.

Another very important point about soils in general is that the continued growth of plants in them tends to add greatly to their depth and bulk. Generation after generation plants grow and die and the products of their decay are washed down into the soil, and in certain circumstances the upper layers of the earth's surface may indeed come to be composed of little else than organic matter. This organic constituent of the soil is known as humus and is sometimes very conspicuous, as in the deep layers of leaf-mould in beech woods or as in peat. On very hard rocks it sometimes happens that the growth of flowering plants is only possible by reason of this accumulation of humus, and it is one of the great dangers of fire that its effect is not only to destroy living plants but also to destroy much of the soil in which they might regenerate. This is particularly serious in that the soil so lost cannot quickly be replaced, and the whole immensely long development of the accumulation of a humus soil has to be gone through again before large plants can become established. This occurs, for instance, in parts of Canada where the underlying rock is very hard.

Except in some new soils and desert soils there will always tend to be some proportion of humus, and this constituent is of the greatest importance not only for the substratum it may provide but in determining the characteristics of the soil as a whole. Newly deposited transported soils are often exceedingly poor in many of the more necessary minerals and may contain no humus at all, so that their rapid colonisation by flowering plants is sometimes difficult to understand. New sand-dunes in this country, for instance, are often colonised almost from their inception by at least one Angiosperm, though analysis may show them to be composed of silica and carbonate of lime without measurable quantities of anything else. Yet in this apparently inhospitable medium *Ammophila* will flourish, and is soon joined by other species.

This outline of the methods by which soils are formed is sufficient to indicate the general differences which will be found between them. The most obvious and direct of these are in physical and chemical constitution, but to these must be added a third, the biotic factor, depending upon the living inhabitants of the soil, and to-day there is a growing appreciation of the importance of this factor.

The physical condition of the soil itself depends on three considerations, all of which are more or less intimately related to climatic conditions. First is the question of depth, which has already been mentioned. It will be obvious that many factors will control the depth of soil and, conversely, many of the physical features of the soil will depend upon its depth. Most important here is the influence of depth on water content. Shallow soils always tend to be lacking in water, not only because evaporation to the air dries them out quickly but also because water is not easily held. On the other hand, exceptional depth of soil may affect plant distribution by allowing the proper growth of the larger forms of life. Some of the very largest trees, for instance, seem to be restricted, as might be expected, to regions where the soil is particularly deep.

The second physical feature of soils and that which causes the most obvious differences between them is their texture, by which is meant the size of the particles of which they are composed. In local soils the process of weathering will tend to produce particles or masses of almost every size from stones downwards, and such soils are generally characterised by this heterogeneity. In transported soils, as well as in some kinds of local soils, this is much less marked and they are characterised by homogeneity. This is obviously true of sand-dunes and alluvium, for instance, where there is in the process of transport a gradual gravitational sifting. It does not, however, prevail so widely in glacial deposits, as the very name boulder clay testifies. The importance of the nature of the rock in local soils is clear in clays, which are themselves only hardened and ancient alluvial deposits and which thus tend when weathered to produce a homogeneous soil. Some substrata consist entirely of masses of stone dimensions, as, for instance, the detritus sometimes seen on the tops of mountains and in such situations as pebble beaches. Conventionally, however, these are not regarded as soils and from the plant point of view at any rate may be regarded as discrete rock surfaces. In so far as they form a substratum for the growth of plants it is by virtue of small quantities of finer material which in course of time accumulate within them but which may be foreign to their constitution.

The three ingredients which in fact control, by their proportionate representation, the physical constitution of the soil are sand, clay and humus. Each of these plays a considerable part in determining the two main structural features of soil, its texture and tenacity. Their effect, however, is nearly always intimately connected with the water relations of the soil and can scarcely be divorced from them. The presence of much sand, by which is meant here particles of medium size, leads to a loose and easily broken soil. The presence of much clay produces a dense, stiff, tenacious soil. Humus, which is itself essentially heterogeneous since it is composed of more or less decayed organic tissues, has in general a moderating effect and, while binding sandy soils, loosens and opens clays. Apart from the fact that loose soils provide a less satisfactory anchorage for plants, texture affects plants chiefly in relation to water and air. Sandy soils with little or no humus allow water to percolate through at a maximum speed and with a minimum retention, and such soils are therefore more or less physically and physiologically dry. Clays, on the other hand, not only hold large quantities of water because of the surface effects of their small particles, but are often actually impervious to its passage. Thus unless there is considerable evaporation clay soils easily become water-logged. Similarly the coarser a soil the more adequate is likely to be its aeration.

The way in which water is actually held in soil offers a very difficult problem and can be considered here only in relation to the absorption of water by the plants. On this basis it is customary to recognise the water in soil as of three categories. First, there is the continuous liquid water or free water which actually forms the water table. Second, there is capillary water which adheres to the soil particles and which tends to move gradually by capillarity to wherever the soil is drier (normally towards the surface). Third, there is hygroscopic water which clings to the particles so closely that it does not travel by capillarity and which in fact can only be removed by such processes as boiling. To these three there may be added a certain amount of water which is chemically combined with certain compounds in the soil. Soil in which there is a great deal of free water may be described as water-logged. Soil in which there is little or no free water but a reasonable supply of capillary water may be called moist, and it is the gradual loss of this capillary water which marks the change from moist to the condition which we call dry. This ordinary conception of dryness however is but a relative one, and when a soil appears dry to the human senses it normally still contains an appreciable amount of capillary water. This is demonstrated by the fact that it is in general only the capillary water which is availabe for plant use and absorption, and it is a matter of common observation that plants can continue to live for varying periods in soil which appears to be "dry." It must not be supposed from this that plants make no use of other water, but on a simple view the water easily available to the plant may be considered to be the capillary water only. The free water will, of course, provide a great reservoir of this. It is particularly in regard to water that humus plays a part. The very structure of small masses of vegetable matter is such that they act as minute sponges and retain, by capillarity, water which otherwise would easily be lost. So the presence of humus in the soil adds greatly to its water-retaining power, and in sandy soils this is often a very important point.

The impermeability of clay soils has been mentioned. One rather special effect of this is that in basins of such soils standing water may accumulate readily as ponds or lakes, and thus produce locally an entirely new kind of habitat open to occupation by species very different from those characteristic of clay soils.

The third important physical feature of the soil is its temperature. This may be considered for all practical purposes as due entirely to solar radiation, except for the possible occurrence of exothermic chemical reactions in the soil. Soil temperature is becoming more and more recognised as a factor in distribution, and this is almost entirely in relation to the absorption of water by the plant. The process by which this is actually accomplished is too complex to be described here, but it can be said that it appears to be strictly conditioned by soil temperature. As a result of this, soils in which the temperature is low may, although holding copious supplies of water, be to the plant as if they were deficient in water. In other words, the water is there but is not available to the plant, which suffers as a result from what is called "physiological drought." This state of affairs must almost necessarily obtain where the water of soil is actually frozen, as it is more or less permanently in very high latitudes, but since the optimum temperature for water absorption in the plant may normally be regarded as appreciably above freezing point, this limiting factor has a much wider application in practice.

The chemical constitution of soils is a most intricate subject because of the immense range of chemical compounds or minerals that occur in nature. All the solid elements as well as many of the gaseous ones occur in the crust of the earth, and hence often in the soil, and many of these in a variety of combinations.

A review of the detailed facts of plant distribution shows that a great many minerals react favourably or unfavourably on the presence or absence of various plant species, and Hayek (254), among others, has given a long account of plants whose distribution is correlated with the occurrence of definite chemical compounds, particularly some of the metals, in the soil. One of the most remarkable examples of this is afforded by what has been called serpentinomorphosis, which may be described as the morphological change which certain plants undergo when growing on serpentine. This is a metamorphic rock, derived from basic eruptive rocks, in which magnesium compounds are plentiful, the magnesium/calcium ratio is greater than unity, and there is an absence of chlorides (401). Pichi-Sermolli (419) gives a list of the modifications so caused, such as glabrescence, glaucescence and nanism, and recognises three kinds of species: typical serpentinophytes, which occur only on serpentine; preferential serpentinophytes, which occur especially on serpentine; and serpenticolous relics which now survive only on that substratum. The operative factor appears to be the magnesium in the rock, and similar morphoses occur in respect of calcium and of zinc (463). Novak (401) draws attention to the fact that these three elements are closely related.

But in general there are in soils four chemical constituents of special importance in this direction, namely quartz, of which sand is largely composed; aluminium silicate, which is the chief constituent of clay; calcium carbonate, which contributes largely to the formation of chalk and limestone; and humus, which comprises a wide range of organic compounds. These are the most widespread of all chemical soil constituents, and their proportional representation is the chief chemical distinction between soils, on which is based the broad classification of soils into sandy soils, clay soils, calcareous soils and organic soils. Each of them may occur almost to the exclusion of others, but more often soils show a combination of two or more and a preponderance of one or other. The correlation between this broad classification and the distribution of plants is very marked. The species of sandy soil are in general different from those of clay or limestone, as are these from one another. Similarly, where the humus constituent is preponderant still other species occur. Where, as in many soils, the constituents are well mixed, there is a similar admixture of species in the flora. Innumerable instances of these conditions might be given, but they formed a particularly important part of the chapter on the distribution of plants in Dorset (Chapter 13), and reference may be made to that account for particular examples.

It must not be supposed, however, that the physical and chemical features of soil are necessarily separate conditions. Indeed there are strong indications that they are intimately connected. In particular it seems clear that the importance of certain chemical features of the soil lies, from the point of view of the plant, in the physical conditions which they produce. It is familiar to find species that occur exclusively either on limestone or on sandy soils, but there are many which inhabit both. The common harebell, *Campanula rotundifolia*, is an instance of this. It is a normal constituent of the flora of many chalk or other limestone grasslands, but is also common on some soils of almost pure sand, and it is difficult to explain this except on the view that these two types of soil tend to provide the same physical conditions. This is true also of certain other species commonly associated with chalk pastures.

In turn the physical state of the soil influences its water relations and its temperature, and the general conclusion is that chemical and physical conditions must not be regarded as essentially distinct but rather as contributing equally to the general character of the substratum (22).

The question of humus is rather different, and is of great interest and significance. The waters of ordinary inorganic soils are in themselves either neutral or slightly alkaline in reaction. On the other hand, humus is to a greater or lesser extent acid in reaction. This is due partly to the secretion of acids from living plant roots and partly to the production of acids in the course of the decay of dead plant tissues. As a result the presence of considerable quantities of humus, especially in association with less alkaline mineral soils, tends to change the water reaction of the soil from alkaline to acid. This again is a very complicated chemical matter which can only be expressed here in very simple terms. The reaction of soil water in this way is due to its ionisation and to the resultant concentration of hydrogen ions. Where this concentration is low the general reaction will be alkaline; where it is high the reaction is acid. The hydrogen ion concentration is denoted by the letters *p*H, and the values are given mathematical expression in such a way that the greater the alkalinity the higher the *p*H figure, and *vice versa*. Neutrality is roughly indicated by the value 7, so that reactions of value above this are alkaline and below this are acid.

In practice the result will be an expression of the amount of humus and the natural reaction of the soil minerals, and in fact these considerations lead to a very wide range of *p*H values in different soils. Particularly, however, is this the case where humus is plentiful and the modifying effects of minerals are slight, as, for instance, in some peat soils and here the acidity may be very high. On the other hand there are some peaty soils, such as those of the Cambridgeshire fens, which receive drainage water rich in basic minerals and which may, in consequence, be alkaline. As a practical issue in plant distribution it appears that the correlation of species with the *p*H of the soils in which they grow is very close, and that the segregation of species on this basis is very clear-cut. This point is well illustrated by reference to the British flora.

The great majority of British plants grow in situations where the soil reaction is either about neutral or slightly on the acid side. A comparatively small number live only where the reaction is much more definitely and sometimes markedly acid. So clear is this distinction that it is no exaggeration to say that it is by far the most conspicuous example of segregation according to habitat. It is true that the bulk of the species of the flora vary greatly in the degree to which they can stand acid conditions, and in places where the values fluctuate about neutrality or where there is but slight acidity many of these plants will occur, but no more than a handful of species can stand conditions where the acidity is high, and these never occur except in such conditions. In Britain high acidic values are to be found chiefly if not only in water-logged humus soils lacking in modifying minerals, namely in peat-bogs, and it is here that the acid-loving plants are found to the exclusion of all others. So obvious is this that it suffers from the familiarity that breeds contempt, and it is important to emphasise its interest. In any attempt to classify the facts of plant distribution in terms of the habitat such as was made in Chapter 13, the extreme segregation of these acid plants will be one of the most obvious features, and indeed it is not too much to say that only here is there to be found any invariable and unmodified correlation between habitat and range. It would seem indeed as if species, at least in Britain, can be divided into two groups most easily according to their relation to soil acidity, and no other basis seems to give so clear a segregation.

The explanation appears to be that these exceptionally acid habitats are essentially extreme and apart and are characterised by certain very particular and peculiar features. For this reason they are inhabited only by certain equally peculiar and specialised species which by reason of that specialisation find there, and there only, the conditions necessary for their growth. As illustrating the sort of conditions which this specialisation may entail, it is significant that many of the so-called insectivorous plants of our flora, species of *Drosera*, *Pinguicula* and *Utricularia*, are restricted to acid habitats. Just in so far as this specialisation may fit species for extreme conditions, so it normally may be expected to unfit them for more ordinary conditions, and this is certainly indicated by the edaphic restriction of these acid-loving species.

To some extent the marked observed segregation in terms of soil reaction is due to the fact that the point of neutrality is by no means in the centre of the whole gamut of conditions. That is to say there is a wider range of values on the acid side than on the alkaline. Associated with this it might be expected that more species would be able to exist throughout the whole alkaline range than throughout the whole acid range, and that there would be less likelihood of visible segregation in terms of alkalinity than in terms of acidity. This is supported by the fact that while it is very difficult to arrange species in terms of what may be called "alkalinity tolerance," it is comparatively easy to arrange many species in terms of their acidity tolerance. In rather different terms, it is easy to find species which are rough guides to acidity of the soil, but it is not easy to find species which are equally trustworthy guides to alkalinity.

Extreme values of alkalinity are, however, associated with a special soil condition which does markedly affect the distribution of plants. These are the soils in which sea-salt attains a considerable concentration. The plants able to live in such soils are called halophytes and they do not normally occur in other habitats. They are in fact specialised in much the same sense as the acid plants mentioned above, but perhaps in a lesser degree. They habitually show the morphological characters associated with an inadequate water supply, and are xerophytes because the concentration of the salt in the soil interferes with the absorption of water by the roots, so that these plants live in a state of physiological drought. Most halophytes can to some extent live in habitats of ordinary salt values, and to that extent their occurrence in maritime situations is facultative rather than obligatory. It is interesting to note that they occur also commonly in inland salt deserts or pans, and this suggests that it is indeed a matter of the soil salt that controls their distribution and not any other factor connected with the proximity of the sea. They are thus to be sharply contrasted with those species, mentioned in Chapter 13, which appear to owe their distribution partly to the distribution of salt in the atmosphere.

Biotic edaphic factors comprise all influences of other organisms on the habitat, though they chiefly concern in practice the activities of the bacteria of the soil, which control the rapidity or slowness with which humus may be formed as well as such chemical reactions as nitrogen fixation. The bacterial content of soils indeed is a very important measure of their general fertility, and the lack of this proper content is certainly the cause of the failure of many species to maintain themselves in the lighter, and what are generally called the poorer, soils.

Under biotic factors must also be included mycorrhiza, which is the name given to the symbiotic relation between certain flowering plants and fungi. In some plants the fungus permeates even the tissues of the seed and thus is kept in readiness for its germination, but in others the seed does not carry the fungus and successful germination depends upon the presence of the latter in the soil, whence it may come into association with the seedling at an early stage. In such cases as these the distribution of the species may easily be limited by the absence of the appropriate fungus in the soil. Some of the terrestrial orchids illustrate this condition.

In addition to these two main types of biotic factor many others will no doubt suggest themselves to the reader. Earthworms, as Darwin pointed out, play a great rôle in mixing and aerating the soil and altering its physical condition, and other animals do the same thing on a slighter scale. There is also the question of animal excreta. At least in the south of England certain plants tend to be associated with rabbit-burrows and warrens in a way that strongly suggests that it is the result of the locally enhanced nitrogen values in the soil. Such plants include *Bryonia dioica*, *Myosotis arvensis*, *Urtica dioica*, *Cynoglossum officinale* and *Verbascum thapsus*. Similarly the flora of manure heaps and of chicken runs is generally very characteristic.

Chapter 18

THE FACTORS OF DISTRIBUTION—IV. THE DISPERSAL OF PLANTS

An enormous and very scattered literature has grown up round the subject of dispersal, and Ridley (450) has done botanists, and indeed all biologists, a great service by collecting together and publishing in one volume almost all the available information on the subject. This work is the source of much of what has to be said on the matter here.

The chief theoretical aspects of plant dispersal have already been dealt with, but it is desirable to review shortly at this point the various actual methods by which it is brought about, and the best way of doing this is to give first a tabulated list of them and then to make what further comments may be necessary about each.

Ridley classifies the main methods of dispersal as follows:

1. Wind—
    - A. Without special direct structural modification:
        - *a.* tumble weeds;
        - *b.* dust seeds;
        - *c.* jactitation.
    - B. With special structural modification:
        - *a.* winged disseminules;
        - *b.* plumed disseminules;
        - *c.* woolly disseminules.
2. Water—
    - A. Rain-wash.
    - B. Ice, rivers, floods.
    - C. Sea.
3. Animals—
    - A. Internal carriage.
    - B. External adhesion:
        - *a.* simple adhesion;
        - *b.* special adhesive methods;
        - *c.* viscid adhesion.
    - *a.* mammals;
    - *b.* birds;
    - *c.* other animals.
4. Mechanical—
    - A. Explosive fruits.
    - B. Elongated stems, etc.
5. Human Agency.

Tumble weeds.

Normally the seed falls from the parent plant when ripe either separately or in small groups contained in fruits, but occasionally the whole plant comes loose from the ground and is capable of being blown along the surface carrying its disseminules with it. Such plants are called tumble weeds. It is interesting to note that they occur especially or entirely in steppes and other open situations. *Psoralea argophylla* of the North American prairies and *Anastatica hierocuntica* of the North African-Indian deserts are good examples.

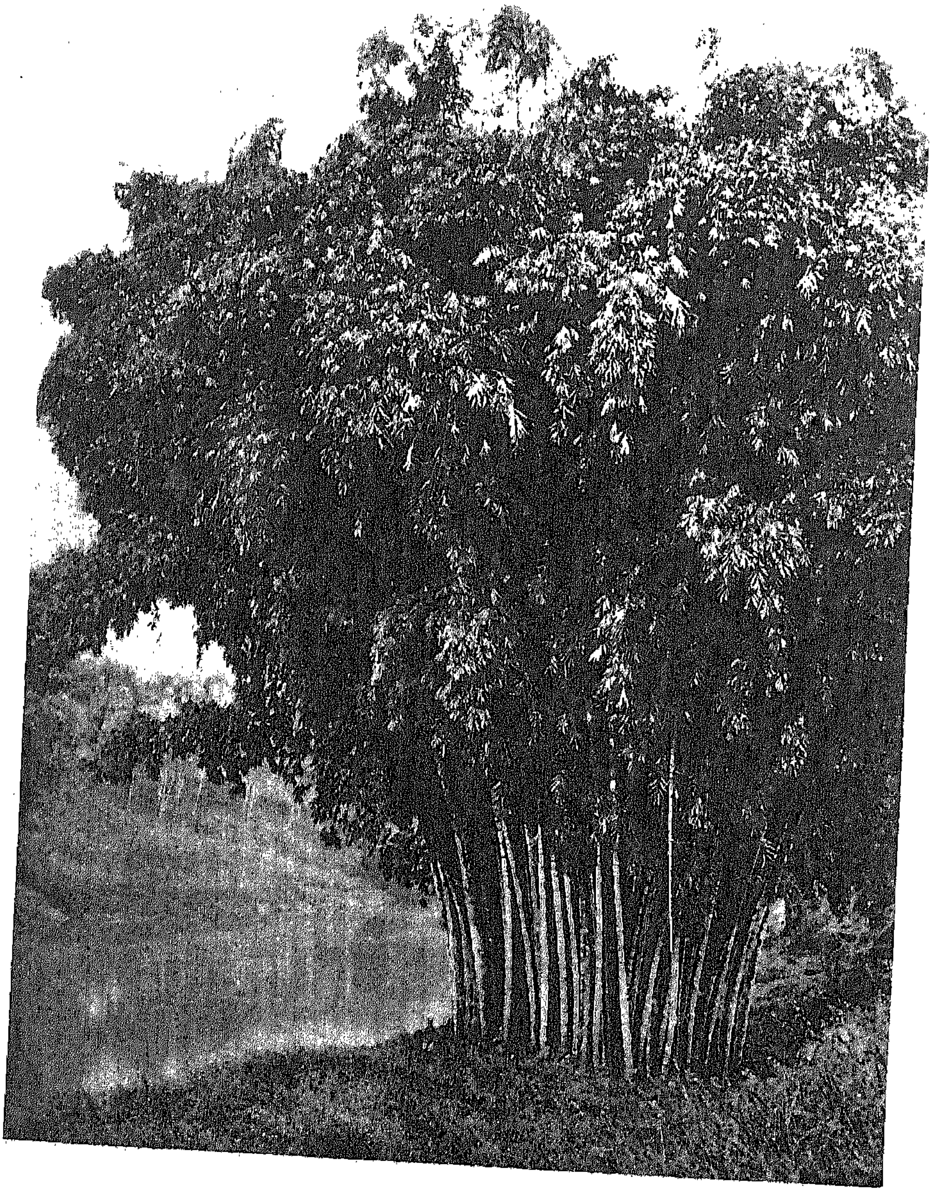


Plate 22. An Asiatic giant Bamboo (*Dendrocalamus giganteus*)

(from Karsten & Schenck, Vegetationsbilder)

Dust seeds.

Given the occurrence of wind, it must follow that many plants will tend to be dispersed by this means, merely by virtue of the small weight of their seeds, especially if their shape also is such as to favour this.

Small light seeds occur in a number of families, but they are particularly characteristic of the orchids. Some idea of their size may be given by the statement that some species may produce as many as several hundred million on one plant, and that individual seeds may weigh as little as two-millionths of a gramme. Ridley gives an interesting account of the occurrence of orchids on remote islands, but it is noteworthy that there are quite a number of islands in which no species occur, and one obvious possible explanation of this is in the direction of the wind. This point is of some interest in relation to the general opinion expressed earlier that the possession of good dispersal means does not necessarily lead to effective dispersal in all directions.

Jactitation.

This is the term given by Ridley to the process by which seeds are scattered by being shaken out of the parent plant under the influence of wind. It is perhaps more popularly known under the phrase "censer mechanism." It may be said to occur to some extent in all plants which have dry dehiscent fruits and which are without any more definite methods of dispersal, and it is of special interest in view of the earlier discussion because it is a restricted method of dispersal whose chief effect is obviously to spread the seeds outside the shadow of the parent. It is seen in a number of very familiar plants, as, for instance, *Melandrium* (*Lychnis*) *dioicum*, *Scilla non-scripta* and many species of *Papaver*.

Winged fruits.

Ridley points out that the presence of wings on fruits is not always associated with dispersal, and instances *Begonia*, where the fruit is winged but in which dispersal is related to the minute size of the seeds. Nevertheless in most winged fruits the wings serve as dispersal mechanisms, and the following types can be recognised.

In bladder fruits the carpel walls become thin and papery so that the whole pod can be blown about and, incidentally, will usually float. The bladder senna of gardens, *Colutea arborescens*, is a good example. In some plants the calyx develops into a thin bladdery covering to the fruit. Winged or angled fruits are common. Conspicuously four-winged fruits occur in *Combretum* and in *Terminalia*, but the number of wings may be anything from two to a dozen. In the genus *Pentace* the number of wings is a useful specific character. Fruits in which only a single wing is developed are usually called samaras, and this type is well represented among British plants. Everyone is familiar, for instance, with the "keys" of the sycamore and maple, and others are found in the ash and the elm. Sometimes, as in the first two, the fruit as a whole is really two-winged but splits into two disseminules each with one wing. Samaras are also common in tropical plants. Nearly allied to the last in function are the bract wings which occur in a number of fruits such as those of the hop, the hornbeam and the lime. In some species of *Scabiosa* the involucel-like bract, in which each individual flower is set, is expanded above into a circular wing. A rather particular condition is seen in members of the grasses and sedges, where the special type of bract associated with the flower often acts as a fruit wing in dispersal. Rarely the pedicel is flattened out into wings, this condition being particularly associated with the genus *Brunnichia*.

A fairly common condition is for the sepals of the flower to become enlarged and more or less membranous in fruit, and thus to provide wings of value in dispersal. This is particularly well seen in the family Dipterocarpaceae, where the wings and fruit are sometimes of great size, so much so that it would seem that the function of the wings can be no more than to control in some measure the fall of the fruit to the ground, and it is significant in this view that many of the members of this family are very tall forest trees. The same thing, however, occurs often in climbing or herbaceous plants and is no doubt associated with wider dispersal. The much rarer condition of petaline wings occurs chiefly in tropical plants, but is found to some degree in many species of *Erica*. Finally, it must be remembered that any organ, if sufficiently light and extensive, may assist in the dispersal of fruit or seeds.

Winged seeds.

These are in general not so common as winged fruits, perhaps, as Ridley has pointed out, because the only structure which can easily become winged is the seed coat. There are, however, many beautiful and well-developed instances, some of the finest being associated with the family Bignoniaceae. This is a tropical family, but *Catalpa*, which shows the condition excellently, is frequently grown in gardens. The genus *Dioscorea* also has well-marked seed-wings. Among British plants the genus *Spergularia* is interesting as showing various stages in the development of seed-wings. It should also be mentioned that in many plants with minute seeds these latter are often winged (e.g. *Rhododendron* spp.), and it is a question whether lightness or the presence of wings is the more important in dispersal.

Plumed fruits.

In many grasses pluming, that is the presence of long silky hairs, is associated with the fruit or its related structures. *Phragmites communis*, which is often described as one of the most widespread Angiosperms, has such hairs well developed on the axis of the spikelet. On the other hand, Ridley comments on the fact that while such grasses are widespread on continental areas they are surprisingly rare on islands.

Plumed styles are not uncommonly developed and are conspicuous in a number of temperate plants, especially those of mountains. *Anemone* and *Dryas* exemplify the latter, and the genera *Geum* and *Clematis* are other conspicuous instances.

The subject of plumed sepals is almost entirely that of the pappus of the Compositae, which is so familiar and often-quoted an example of dispersal mechanisms. In these plants the calyx lobes are modified into bristles which may or may not be plumed, and the whole arrangement, as in the dandelion, is often very specialised. It should be pointed out that there are many Composites without this pappus development, and there is no evidence that their dispersal suffers in consequence. *Matricaria matricarioides* is an interesting example of this. A native of North America, it was introduced, presumably accidentally, into Britain in the latter half of the last century. It possesses no pappus at all, but it has by now spread to practically every corner of the country. The Composites are, however, by no means the only plants with plumed calyx lobes, and the Proteaceae, especially the well-known silver tree, have them extremely well developed.

Plumed seeds.

Ridley points out that plumed seeds are always borne in capsules or follicles, and that they are specially characteristic of herbs or climbers rather than trees. Above all, they are to be found in the Asclepiadaceae and Apocynaceae, where they perhaps attain their greatest development in *Strophanthus*, but they are also well developed in the more temperate genus *Epilobium*.

Woolly seeds.

It is sometimes difficult to draw the line between plumed and woolly seeds as, for instance, in the seeds of the willows and poplars, but the condition is really characteristic and well developed in certain Malvales, where it provides some at least of the economic value of the cottons and the kapok.

Rain-wash.

Ridley, it is interesting to note, is of opinion that this is more important than is generally supposed because of the part which it may play in carrying the fallen seed further away from the mother-plant. It must in ordinary circumstances be of comparatively little general significance, and it is difficult to visualise any extensive carriage by this means. It seems likely to have particular application in the colonisation of newly formed land.

Ice, rivers and floods.

It is clear that moving water in whatever form will tend to have the same effect on disseminules as it may have on other objects, and hence that it must be a dispersal means to some extent. In the case of ice it has long been suggested that icebergs may transport disseminules, but this is an instance of a theoretical conception whose practical application can scarcely be regarded as other than very slight and, indeed, can hardly be more than accidental in occurrence.

Rivers will certainly assist plant dispersal in one direction and floods will tend to assist it less directionally. In these there is a general tendency to dispersal merely by the power of water movement irrespective of whether the disseminule can float or not, and there is also the particular aspect of dispersal of aquatic plants in the vegetative form of pieces of stems or buds, a method not generally applicable to land plants. The question of what may be called special water dispersal mechanisms involves the problem of flotation, and there is no doubt that many seeds and fruits are capable of floating in fresh water for a considerable time. Often this effect is produced by structures which are properly to be associated more particularly with other means of dispersal, as is the case with many of the winged and plumed disseminules, which by their nature will also tend to float, but there are several directions in which structure seems directed solely to flotation. Such, for instance, is the nature of the pericarp in fruits and of the testa in seeds. Broadly it may be said that where the texture of these is such as to hold much air the disseminule will float for a longer or shorter period. It may also fairly often happen that in falling into water some air may be inevitably imprisoned in the cavities of fruits and thereby cause flotation. Ridley gives many examples of these things and also a survey of flotation in different families. The general conclusion is that freshwater dispersal by flotation is comparatively common, but must also, by the nature of the case, be of but comparatively local importance.

Carriage by sea.

The obvious possibilities of sea carriage have made this one of the most studied of all aspects of dispersal, and readers will find the work not only of Ridley but also of Guppy (241, 242, 243) of great interest here.

At first sight sea dispersal looks a most promising way of explaining many otherwise inexplicable distributions and especially of many wide discontinuities, and so before going into any details it is important to emphasise certain general limitations inherent in the method.

In the first place, sea carriage differs fundamentally from freshwater carriage in that the actual medium of transport is more or less toxic to most disseminules. In other words, most seeds are killed by anything like prolonged immersion in sea water. Cases of great resistance to this danger are often mentioned, but these exceptions only prove the rule. Secondly, sea carriage must be correlated almost entirely with currents and hence will tend to be in certain directions only, and these are by no means the ideal theoretical directions. Again, most currents tend to have at least some north and south direction, and thus will tend to transport disseminules into different climatic zones. Thirdly, only a very small number of plant species are likely to disperse their disseminules into the sea, and, most important of all, sea carriage is very unlikely to deposit disseminules in spots where they can germinate and establish themselves. For instance, a plant growing on the slopes of a continental mountain is not likely to disperse its seeds into sea water. Still more unlikely is it that sea will disperse those seeds to the slopes of a mountain.

As Ridley's very long and detailed account shows, there are undoubtedly many species of plants which are, by various peculiarities of structure and resistance, capable of floating unharmed for long periods in sea water (241, 462), and which therefore may suffer transport over vast distances by the action of sea currents. It is not surprising that the plants so widely spread on tropical beaches or throughout small tropical islands, such as the so-called strand plants, possess in greater or lesser degree such features. The coconut (*Cocos nucifera*), for instance, can float unharmed in the sea, and may do so for a length of time permitting it to drift 3,000 miles in favourable circumstances (37, 152, 378). It is also not surprising that the strand plants are very widespread, because they inhabit places to which the action of the sea can bring their disseminules. On the other hand, it is very significant that these strand plants are in general either tropical or (more rarely) temperate. There are few, if any, subcosmopolitan strand plants. In this connection the family Palmae is of peculiar interest. As described in Chapter 4 it shows an unusually high degree of insular endemism and very few transoceanic distributions, and this may doubtless be associated with the fact that the coconut, already mentioned, and *Nipa fruticans* are almost the only members of the family which can be sea-dispersed (450). True, the huge fruits of the double coconut, *Lodoicea*, which grows nowhere but in the Seychelles, have been found floating and not infrequently cast up on the shores of Asia, but this is only when their specific gravity is reduced by the decay of its contents and they are no longer capable of germinating (148).

In short the case of sea dispersal more than any other puts the general potentialities of dispersal in their right perspective. Where all the associated factors are favourable it may be of immense importance and allow a species to cover enormous distances, but this optimum condition is likely to be rare. In the first place the disseminule must reach the sea, in the second it must be capable of floating, in the third it must resist the action of salt water, in the fourth it must be deposited, at the end of dispersal, in a suitable climate, and lastly in a suitable habitat for germination and establishment. It may be left to the reader to conclude how often all these conditions are likely to be fulfilled, and a reference back to the distribution of marine and semi-marine Angiosperms may be of assistance (Chapter 11). The distribution of the mangroves is particularly illuminating in this connection, in the way that they indicate that there are many considerations besides mere passage by sea transport which limit their ranges. These observations must not be interpreted as belittling the interest of many aspects of sea dispersal. The structures which enable disseminules to float or which protect the embryo are often intricate and beautiful, and Ridley gives a most interesting account of them.

So far attention has been drawn only to plants whose disseminules are capable of independent flotation. It has often been suggested that many seeds, especially if small, may be transported more or less accidentally in drifting wood or in pumice. The possibility of this in special cases must be borne in mind, but enough has been said to show that it is likely to be but very rarely efficacious.

It may also be remarked in relation to the mention of the coconut above that the exceptionally wide area of this plant to-day is certainly largely due to the influence of man.

Dispersal by animals.

As was indicated in the table on p. 320, animals tend to disperse disseminules in three ways, by swallowing them, passing them through and out of the digestive tract, by carrying them attached to their outer surface, or by carrying them in mud adhering to their feet, and, as Ridley points out, all animals thus may disperse plants to some extent. The primary consideration must naturally be the movement of the animals themselves, and this must always be borne in mind in gauging the importance of such dispersal. Locally restricted animals, or animals relatively immobile, will not play a large rôle. Generally speaking the problem involves mammals and birds, and the latter are of vastly greater potential importance because of their greater range of action. Grazing mammals, on the other hand, are probably responsible for a more intensive type of dispersal, because their food will always contain a certain number of disseminules and these will be almost continuously passed out of the body.

The structure of disseminules is correlated with animal dispersal in two main ways. On the one hand there is the development of the fruits so as to make them attractive to animals, which in consuming them will also consume the seeds, and on the other there is the development of special structures which will enable the disseminule to adhere to the surface of the animal.

Attractiveness to animals in turn is generally due to one or both of two features, namely colour and palatability. Colour may be in the fruits themselves, or in associated structures such as parts of the inflorescence axes, or in or about the seeds, as for example in arils.

Bird dispersal.

Dispersal by birds is generally associated with brightly coloured fleshy fruits such as form the main diet of many birds, but small dry seeds and fruits such as those of grasses are also commonly eaten, and no doubt dispersed to some extent.

As with sea carriage, so also has bird dispersal received great attention because it promises to provide an explanation of much in plant distribution which is otherwise difficult to understand, but it seems doubtful whether it is capable of doing all that is sometimes claimed for it. There are many factors which will decide the value of bird dispersal, and these must be taken carefully into account. One, the active range of the birds concerned, has already been mentioned. Attention has rather naturally been focused on birds which are known to fly long distances, but these are comparatively few and most birds have a comparatively limited range of flight. This is especially the case with those in which territoriality is strongly developed. Migrant birds usually have very definite routes and these routes are generally north and south, that is to say between widely different climatic zones. This is probably the most important point of all, because there must always be the possibility that long-distance bird flight may, at least on rare occasions, have taken place in almost all directions, but unless such flight can result in the deposition of the disseminules in conditions suited to their development it must necessarily be of no account. Again, in some parts of the world, as for instance in much of the tropics, there is little or no migrationary movement.

Another very important consideration, especially in relation to possible wide transoceanic carriage, is the speed of flight and the time that a disseminule takes to pass through the body. In general this time is probably very short, perhaps at most a few hours, and whether birds can and do retain their intestinal contents for a longer period when in flight is still doubtful.

It has been stated that migratory birds habitually travel on an empty stomach, but this has been contradicted, and it would at any rate be difficult to maintain that they never do so. It is also important to note that most isolated oceanic islands are not visited to any great extent by migrant birds. Related to this also is that many of the most wide ranging sea birds are not fruit eaters. In Tristan da Cunha, for instance, the only frugivorous land birds are endemic species.

In short, it seems that dispersal over wide areas by birds is very much on a par with wide dispersal by sea. There is a great potentiality in it provided that all the subsidiary factors are favourable, but the details of the process are such that it is difficult to imagine that such totally favourable conditions can be anything but very occasional. It may be argued that even very rare wide dispersal will be sufficient, but here there is the overriding consideration already emphasised that dispersal must be followed by germination and establishment, and this is something quite apart from the mere question of transport.

There is, however, one direction in which bird dispersal has probably had a paramount effect on plant distribution. This is the case of certain freshwater aquatic plants such as the duckweeds (*Lemna*). As was shown earlier, these plants are tiny free-floating aquatics, some with an extremely wide geographic range. They have no dispersal mechanisms in the ordinary sense of the word, but their form is such that they can easily be transported by simple adhesion. At the same time they are no better equipped for this than many seeds and fruits, and their wide distributions are to be attributed not to any specially valuable dispersal potentiality but to some other factor. It is not difficult to imagine what this may be. Free-floating aquatics live in a habitat quite different from that of land plants, the essential distinction being the elimination of many of the most stringent climatic influences. For instance, fresh water normally shows a much narrower range of temperature values than neighbouring land surfaces, and, more obviously still, the amount of precipitation is likely to be of much less consequence. In view of this it seems reasonably certain that the wide range of *Lemna* (and what applies to it applies also to some other aquatics) is due to the greater similarity between its habitats the world over and the absence of space competition in open water, with the consequent greater chances of survival and establishment after dispersal. Birds carrying *Lemna* will tend to rise from one sheet of water and to come down on another which, however far away, is likely to be fairly similar to that from which the bird came. Here, it will be seen, the chance of deposition in an unsuitable spot which is so likely in the case of land plants is almost eliminated.

Carriage on the feet of birds.

The researches of Darwin (124) on this subject have ever since made it a somewhat classic example of dispersal, but all that we need say about it here is that it is in fact very parallel with the carriage of disseminules inside birds, and in particular is controlled by those same general considerations concerning bird carriage which have been noted there.

Other animals.

As regards dispersal by animals other than mammals and birds, attention chiefly centres round the activities of ants, whose relation to plants in general and to dispersal in particular is a subject of great interest. All that can be said here is that while in certain circumstances almost any animal may be instrumental directly or indirectly in dispersing seeds or small fruits, the result can scarcely be considered to contribute appreciably to the general distribution of plants.

Special adhesion mechanisms.

Perhaps the most noteworthy feature of these is that they parallel very completely the structural modification associated with wind dispersal, the difference being that, instead of wings and plumes, hooks are developed.

Rarely adhesion may be by branches of the inflorescence, as has been noted in certain grasses and Cyperaceae.

Adhesion by armed bracts is commoner and particularly associated with Composites, where *Xanthium* and *Arctium* provide two excellent examples. Here the hooks by which the disseminule clings are developed on the phyllaries.

The glumes of grasses are often so furnished with hairs and hooks that they cling readily, and several of our British grasses have these, although there are more striking examples in the tropics. In addition to mere attachment the structures in some grasses are such that the fruits actually bore into the skin of the animal and become absolutely fixed. Presumably in this case, if it is indeed a dispersal mechanism, the seeds cannot germinate until the death of the animals. The genus *Stipa* affords several examples of this, and the writer has seen joints of imported mutton so thickly penetrated by the fruits that they have been condemned as unfit for human consumption.

Adhesive perianth segments, such as are found in some of the Amaranthaceae, are not uncommon, and, in particular, adhesive calyces are familiar. They are found, for instance, in many Composites, where the bristles of the pappus are modified into hooks, the genus *Bidens* being notorious in this respect. *Myosotis* is also a good instance, as anyone who has walked through a wood where *M. arvensis* is in fruit will know. The Labiatae furnish many examples too. Here the teeth of the calyx are variously recurved so as to form hooks.

Hooked styles are also frequent, as in *Geum*, *Anemone* and *Ranunculus*. A special form of this method is also seen in the stiff-haired awns of the stork's bill (*Erodium*).

It is, however, particularly in fruits that special adhesion methods are developed and they are very common, sometimes attaining great development and specialisation. Indeed, almost every type of dry fruit may be found furnished with hooks of one kind or another. Most of our familiar native examples of special adhesion belong here, and among them *Sanicula europaea*, *Circaea lutetiana* and *Galium aparine* may be cited, all three of them being exceptionally and irritatingly efficient. Extreme conditions are best seen in the so-called grapple plants belonging to the genera *Harpagophytum* and *Martynia*. In the former the fruit is several inches long and furnished with robust long-hooked processes. In the latter one end of the fruit is produced into a pair of very long curved hooks.

Viscid adhesion.

In much the same way as with plumes, wings and hooks, many parts of the flower or associated structures may become sticky by exudation from glands, but most of these variants are too rare to need mention here and our attention may be confined to viscid fruits and viscid seeds.

In some fleshy fruits the pulp is so sticky that the seeds adhere to anything they touch. This is particularly well known in the mistletoe, but it occurs also in a number of exotic plants.

Another form of adhesive fruit is where dry fruits of various kinds, chiefly achenes, are furnished with sticky glands. Several Composites, including *Adenostemma*, illustrate this well.

Quite a number of seeds become viscid when wet by the development of mucilage from their surface cells (see p. 332). This condition has been noted in several British plants, and the best example is certainly *Plantago major*, in which the secretion of mucilage is very copious. Many of the species of *Juncus* and *Luzula* show the same character.

Explosive fruits.

In all the cases so far discussed the fruit has been a relatively passive agent in dispersal, but there must now be mentioned some instances where it takes a more active part. In all of them dehiscence of the fruit, instead of being gradual, is so sudden that the contained seeds are shaken out more or less violently, sometimes to a considerable distance. The exact method by which this is accomplished varies a good deal, but is in all cases due to unequal strain set up in the ripening fruit, a strain which is ultimately relieved by the explosive rupture of the fruit wall.

One of the best known though not one of the most striking is the gorse. On hot summer days the popping of the ripe pods is very noticeable. The genera *Oxalis* and *Impatiens* also furnish many instances, the familiar name "touch-me-not" given to a species of the latter being a well-earned tribute to the sensitiveness of its ripe capsules.

Hura crepitans, a tree of the Euphorbiaceae, and the squirting cucumber (*Ecballium*) are other very remarkable examples.

Other mechanical dispersal.

In his chapter on mechanical dispersal Ridley refers to the fact that many plants possess rhizomes, soboles or runners which do in fact play a kind of subsidiary rôle in dispersal because they give the plants some kind of mobility, in that they enable new fruiting branches to arise at some distance from the parent axis.

From the theoretical point of view it must be emphasised that this is not really a method of dispersal at all, because no actual spatial discontinuity is involved, but a method by which the parent plant extends its own body over the surface of the ground. In no case, as far as the writer is aware, does such a vegetative spread replace dispersal by seeds or fruits, at least under natural conditions. Its function also seems to be quite distinct from that of dispersal. The latter, as has been shown earlier, is designed to scatter the species and to be a method at least by which increase of range can be accomplished, and it is intimately bound up in conception with the protected resting stage of the seed. Creeping stems on the other hand, while they may in fact increase the area occupied by a species, would appear to have, as their main function, the occupation of soil at the expense of other species, often together with the secondary function of perennation. Hence it seems justifiable to regard the process of spreading by vegetative means as related more closely to the problems of competition rather than to the problems of dispersal, and on these grounds it is not considered necessary to go further into the matter here. It may, however, be worth noting that in some cases exceptional powers of vegetative spread are associated with exceptional powers of dispersal, as is the case with *Chamaenerion* (*Epilobium*) *angustifolium*, and this may perhaps be evidence in favour of the view expressed above.

Dispersal by human agency.

This is perhaps the most convenient place at which to consider shortly the whole question of the introduction of plants into new countries by the agency of man. As has been said, we are chiefly concerned in this book with the natural distribution of plants, but their accidental or deliberate introduction by man is now so widespread and so much vitiates the picture of natural distribution that some account of it is necessary. It has, moreover, a very definite bearing on many theoretical aspects of our subject.

In general it may be said that there is scarcely a country in the world where human activities have not led to the introduction and establishment of species foreign to that country, and the intensity of this introduction is roughly proportional to the extent of man's influence on the country. The subject is therefore largely the story of the emigration of man from European countries and his colonisation of distant parts of the world, but this is not the whole of the story and introduction of one kind or another has accompanied almost every human movement. For instance, many tropical plants, especially those of Asia and Polynesia, have been carried far and wide by the migratory movements of the native races of the region, and the wide range of many such plants and the uncertainty of their place of origin are generally due to this. This type of introduction extends over a long period of time and many of its early stages are now beyond elucidation. The other aspect of the subject, that of introduction by the migrating and colonising activities of white peoples, has a much shorter history and is more or less coincident with the great colonial expansions of the last two or three hundred years.

This in turn has two aspects which illustrate in themselves the two main types of introduction, namely deliberate and accidental. The first of these is mainly associated with outward movements of the more advanced races from their centres in the northern temperate regions, and the second is generally the reverse. The former also tends to provide some of the more conspicuous examples of introduction, although the latter probably accounts for the larger bulk of species transference. That is to say, deliberate introduction usually concerns a fairly narrow range of species, while accidental introduction may be contributed to from a very great number of species.

Although introduction into the more distant parts of the world may be regarded as a fairly recent process, more localised transfer of plants has been going on ever since mankind first began to move freely about the world. The status of plants in Great Britain illustrates this point well. Species have been entering the country for hundreds, and perhaps thousands of years, and many of them have now become so integral a part of the vegetation that it is almost impossible to determine their real status. In relation to this particular point, however, it must be remembered that introduction has been over comparatively limited distances and from areas not too widely different. Where transference is over much wider areas, and more particularly across the equator, there is not the same difficulty in distinguishing between native and adventive species.

Except for the doubtful cases just mentioned, the adventive species in such a country as Great Britain, for instance, are generally to be recognised because they inhabit only unnatural habitats, that is to say habitats which exist only by virtue of man's actions. Arable fields, roadsides, waste places, buildings and walls are the special homes of adventive species, and it is generally only in particular cases and after a long time that introduced plants succeed in establishing themselves as constituents of the apparently aboriginal vegetation. This is an important point which has been emphasised by many writers (7, 607), and there seems little doubt that the struggle of introduction *versus* native (exotic *versus* indigene) is much less in favour of the former than is generally supposed. The point already mentioned, that introductions tend to be restricted to disturbed ground, is very generally true and is indeed probably the reason for the idea that introductions prevail, because it leads to their appearance just where they will be most conspicuous to the human observers. This has been demonstrated very distinctly for New Zealand (104), and the conclusion is that exotics have scarcely entered at all into the primitive vegetation. It is pointed out that they are nearly always plants of the lowland belt, and also that their growth forms tend to be different from those of the indigenes and to militate against their successful competition. At the same time it must be remembered that the history of introduction, at least of northern plants, is for the most part very recent. New Zealand has been the subject of a great deal of study in relation to introduction, and Thomson (554) has collected an enormous amount of interesting information, which will be reviewed in a moment.

The reason why introductions are mainly confined to disturbed ground is apparently that there the vegetation is open and the question of competition with existing plants does not arise, or only does so in lesser degree. In these circumstances of freedom from opposition the introduced species may flourish and multiply to an amazing extent, as for instance the Opuntias when introduced into Australia. Open water too provides the same freedom, and there are many examples of introduced freshwater plants luxuriating greatly. Two of the best-known examples are *Elodea canadensis* in England and *Nasturtium officinale* in New Zealand. Such plants, however, tend after a time to settle down to a more reasonable scale of existence.

Human dispersal of plants is of two kinds, deliberate and accidental. The former may obviously take all kinds of forms and there is nothing to be gained in analysing it further here, but in the latter certain circumstances are of special importance. These may be tabulated as follows :

1. Dispersal by accidental adhesion to moving objects:
    a. Adhesion to man's person.
    b. Adhesion to moving vehicles:
        e.g. mud on cart-wheels, dust carts, trains, etc.
2. Dispersal among crop-seed:
    e.g. many cornfield weeds.
3. Dispersal among other plants:
    e.g. fodder and packing materials.
4. Dispersal among minerals:
    e.g. soil export, ballast, road metal,

5. Dispersal by carriage of seed for purposes other than planting:
    e.g. this includes a whole range of possibilities. One mentioned by Ridley is the spread of drug plants from the seeds escaping from druggists' shops.

So much for some of the more qualitative aspects of introductions. An idea of the quantitative side of the question is best conveyed by a reference to some particular country, and in view of Thomson's work just mentioned New Zealand may well be selected. The reader may also be reminded that the introduction of plants into Great Britain was dealt with at some length in Chapter 12.

The Naturalisation of Plants in New Zealand

According to Thomson (554) more than 600 species have been introduced into New Zealand and have become more or less truly wild in the sense that they reproduce habitually by seed and have become permanent features of the vegetation there.

A great many of these have become abundant or common throughout the country (8, 9). They include many well-known weeds but also a few others, and the following is a list of some of them:

Ranunculus repens
Nasturtium officinale
Cardamine hirsuta
Capsella bursa-pastoris
Silene quinquevulnera
Cerastium vulgatum
Stellaria media
Sagina procumbens
Spergula arvensis
Hypericum androsaemum
Malva rotundifolia
Ulex europaeus
Sarothamnus scoparius
Trifolium pratense
Vicia sativa
Foeniculum vulgare
Arctium lappa
Cirsium arvense
Cirsium vulgare
Chrysanthemum leucanthemum
Bellis perennis
Senecio jacobaea
Senecio vulgaris
Hypochoeris radicata
Crepis capillaris
Sonchus arvensis
Anagallis arvensis
Centaurium umbellatum
Digitalis purpurea
Mentha pulegium
Prunella vulgaris
Verbena officinalis
Plantago lanceolata
Plantago major
Rumex acetosella
Rumex crispus
Rumex obtusifolius
Chenopodium album
Euphorbia peplus
Phalaris canariensis
Anthoxanthum odoratum
Phleum pratense
Polypogon monspeliensis
Holcus lanatus
Dactylis glomerata
Cynosurus cristatus
Poa annua
Poa pratensis

Of these *Hypochoeris radicata* is often considered the most ubiquitous of all. *Nasturtium officinale* and *Verbena officinalis* have occurred or still often occur in very large forms. *Trifolium pratense* (red clover) is of exceptional interest because its abundance is directly associated with the presence of humble-bees, which seem to be the only insects capable of pollinating it. These bees were deliberately introduced into New Zealand, and before their advent the red clover rarely if ever set seed. All the species mentioned are common European plants, and the only other species which has become widely established appears to be *Eschscholzia* *californica*, which, as its name implies, is a native of western North America. Some species have become so completely established and form so intimate a part of the natural vegetation that they have often been considered to be native. They are, however, almost certainly introductions and include *Geranium molle*, *Sonchus oleraceus*, *Plantago coronopus* and *Polygonum aviculare*.

On the other hand a number of species are much less common than might be expected. Among them are:

Papaver rhoeas
Geranium robertianum
Daucus carota
Centaurea cyanus
Cichorium intybus
Calluna vulgaris
Convolvulus arvensis
Lamium album
Lamium purpureum
Urtica dioica
Urtica urens
Arrhenatherum elatius
Agropyron repens
Brachypodium sylvaticum

Others have become firmly established locally as garden escapes, as *Pelargonium zonale* and *Tropaeolum majus*. The peach, *Prunus persica*, is of interest here too. In the earlier days it established itself freely, but now it does so far less frequently and seems to be restricted by the occurrence of certain diseases from which it suffers.

Perhaps more interesting than any of these are the plants which have never been able to establish themselves, even with the repeated help of man. *Viola odorata* and various species of *Primula* such as the primrose, cowslip and polyanthus are noteworthy examples of this, and the reason seems in some measure at least to be the absence of the normal pollinating insects. In the case of the Primulas the plants refused even to seed before the introduction of bees. They now do so in gardens but have never become established. Heaths of various kinds also have never been naturalised. Other species which, fortunately or unfortunately, have never become established are *Linum usitatissimum*, *Pisum sativum*, *Lathyrus odoratus*, *Petunia parviflora*, *Opuntia vulgaris* and *Scilla non-scripta*.

A group of species has become widespread only since the introduction and subsequent multiplication of such fruit-eating birds as thrushes and blackbirds. The prevalence of the blackberry, *Rubus fruticosus*, which is perhaps the worst of all weeds in New Zealand, is a case in point, and others are *Berberis vulgaris*, *Rosa rubiginosa* (which incidentally is far more widespread than *R. canina*), *Crataegus*, *Ribes uva-crispa*, *Sambucus nigra* and *S. racemosa*, *Leycesteria formosa* and *Phytolacca*. There are, of course, native fruit-eating birds, but presumably their natural diet is in general confined to native species.

In the course of his remarks Thomson refers frequently to the dispersal mechanisms of the various plants, and it is interesting to note that in the following species the seeds or fruits become sticky when wet: *Capsella*, *Lepidum sativum*, *Viola tricolor*, *Artemisia absinthium*, *Senecio vulgaris*, *Gilia* spp., *Glecoma hederacea*, and species of *Plantago*.

Finally there are a few cases of special interest. *Brassica oleracea* was planted by the earliest visitors to the country, and the progeny of this stock has gradually reverted to the wild type, which now inhabits sea cliffs in various parts of the dominion as it does in Europe. *Matricaria matricarioides*, which has been referred to before in another connection, was locally abundant as early as 1882 and has since spread almost everywhere. *Verbascum thapsus* is especially common where there are big populations of rabbits, a feature which is noticeable in its distribution in England also. The broad bean, *Faba vulgaris*, has been noted sprouting from the skeleton of a pigeon, the inference being that germination was possible only after the body of the carrier had decayed. Some people think that many seeds are distributed in this particular way.

Certainly the most conspicuous feature of the long list given above is the fact that practically all the plants mentioned are what may be called common European weeds belonging to what has been distinguished as the Scandinavian floristic element. The great prevalence of these as adventives not only in New Zealand but in almost all countries (see Chapter 4) has been commented on again and again from the time of Hooker, who in his *Introductory Essay to the Flora of New Zealand* (271) discussed the matter at length. So impressed was he by what he considered to be the aggressive colonizing power of the Scandinavian flora that he foresaw the gradual extermination of indigenous floras by these adventive species. This extreme point of view was no doubt connected with the fact that at first sight these adventive species appear much more ubiquitous than they really are, because they follow so closely in the footsteps of man, and it is fairly certain now, as Thomson and others have shown, that there is no strong likelihood of this eventuality. It would seem that it is not so much the inherent aggressiveness of the species in question as the advantages which their association with man confers on them. Man's actions tend to provide a series of habitats, those of disturbed ground, which are specially the domain of these plants and which do not occur in nature. This certainly leads to local destruction of the native vegetation and some native species inevitably become rare in the process, but Thomson has stated definitely, in respect at least of New Zealand, that he knows of no case where a native species has been completely exterminated by adventives, and his general opinion, as it is also that of others, is that when man's influence is removed the native flora can everywhere hold its own.

But there is also another very interesting aspect of this problem. The northern hemisphere generally and Europe in particular has been the stage of man's development for vastly longer than any southern countries, and the kinds of artificial habitats which this development produces have in the north been available for local plants for much longer. May it not be then that the common northern weed species are in fact species or strains peculiarly fitted for these habitats, and in fact slightly different from the corresponding forms which grow in more natural situations? If this is so, then it might be expected that these weeds would flourish in all artificial habitats no matter where they might be, and would tend to produce the effect of aggressiveness observed. In this connection it is not without significance that a few plants such as *Festuca ovina* and *F. rubra* and *Cardamine hirsuta* occur in New Zealand not only as adventives but also as natives, and that in these cases the exotic is generally more prominent than the indigene.

CHAPTER 19

THE FACTORS OF DISTRIBUTION—V. CHANGES OF CLIMATE

THE belief that climatic values have in the past fluctuated greatly with the passage of time is now so generally held as to have become almost axiomatic, but it is nevertheless desirable here to consider shortly the reasons that have given rise to it. For more complete presentations of the subject the reader may refer to the work of Simpson (489, 490), Brooks (63, 65), Huntington and Visher (289) and Russell (456).

The direct and indirect evidences for climatic variation in the past are of five kinds, namely mathematical and geodetic, geological and topographical, botanical, archaeological, and meteorological.

The first need not detain us long because it is rather remote in all senses of the word from our present subject. It comprises the relations between the earth and other heavenly bodies, and also the question of the mode of formation of the earth and its subsequent vicissitudes, these being such that it is impossible to suppose that the present conditions of climate can have existed unchanged for any considerable part of secular time or of the earth's history. Indeed, there is reason to believe that for long after the formation of the world no climate in the modern sense existed.

Geological and topographical evidence of climatic change is of three chief kinds, the first being that afforded by the appearance and texture of certain rocks. Thus some sandstones appear to be formed of dune sand, while some Tertiary granites show signs of having been weathered by sand blasts, both suggesting that contemporary conditions were very arid (483). On the other hand many clay deposits can scarcely have been formed except under pluvial conditions. Not only are these rocks found where now the climate is very different from that indicated by their origin, but the various types may be found superposed or intermingled, showing that the climate of their region of deposition must have undergone considerable changes. Indeed a vertical section through almost any series of geological beds will show a variation of type that can only be explained by an equal variation of climate. Moreover, freshwater deposits will be found among and between marine deposits, indicating at least geographical changes such as are unlikely to have been without effect on climate.

The second kind of geological evidence of climatic change, and perhaps the most familiar one, relates to glaciation. Ice-sheets and glaciers scour and mark the surface of the earth where they occur in ways which leave unmistakable evidence of their former presence long after they have disappeared. The nature of these traces has already been described and it need only be remembered here that they are found over wide areas of the world where now the climate is far from polar. Glacial conditions are now generally supposed to have been more or less widespread on the earth on a number of occasions during geological history, that is to say it is believed that there have been in the past a series of glacial epochs or ice ages. These were, however, separated by vast periods of time. Only two (if we ignore the debatable indications of a Cretaceous or early Eocene glaciation) have occurred since the beginning of the Palaeozoic, and of these only the latter involves the Angiosperms and is therefore of more than passing interest to us here. As will be seen, these glacial ages are to be regarded as long intermittent catastrophes in the general story of climate, and as such are perhaps the most striking evidence of the fact that climatic values have not always been as they are to-day.

The nature of the changes which accompanied the Pleistocene glaciation, and their far-reaching effects on the existing vegetation, have already been described, but it is well to stress again here that the climatic change at this time was both great in its degree and vast in its significance and that it has been the main influence in moulding the world flora into its present state. Nor, it is now generally held, was this change confined to those parts of the world which were actually covered with ice, but expressed itself widely elsewhere, particularly in many parts of the tropics, as a corresponding series of pluvial and dry periods, which in all probability, as has been suggested by Gilliland (197) and many others, caused plant migrations of a similar though perhaps less drastic kind. If, indeed, as many now believe, high precipitation values are an essential feature of glacial periods, then we may expect comparative dryness to be an equally characteristic feature of non-glacial conditions like the present, and this falls satisfactorily in line with the growing evidence that there is generally increasing dryness now at lower latitudes, or in other words that aridity is spreading in many parts of the tropics.

This problem of what has been called the "désertification" of tropical regions is a most interesting and important one. That semi-desert or desert conditions are, in many places, spreading, as Aubréville has admirably demonstrated for tropical Africa (23, 24), seems indisputable, but whether this is to be attributed solely to natural causes is more debatable. Hitherto this has been generally assumed to be the case but the work of Aubréville and others has thrown considerable doubt on this view and suggests that the spread of desert conditions may often be caused by human rather than natural factors. Van Steenis (530) goes even further and believes that man has in many cases actually converted his areas of settlement into deserts and has consequently been obliged to abandon them.

A third direct line of geological and topographical evidence is afforded by the occurrence, in regions now comparatively arid, of physiographic features obviously caused by the action of large bodies of water. Empty gorges and dry, or almost dry, river beds are the commonest of these and may be seen in many parts of the world. Among striking instances are some of the tributary valleys of the lower part of the Orange River in southern Africa, and the great wadis in parts of the Sahara and in Arabia, which, presumably not so long ago, must have carried rivers capable of watering great tracts of land.

Among the more indirect evidences of climatic change caused by geological and topographical factors two may be mentioned here. Mountain ranges are one of the most potent influences in determining local climate in many parts of the world, because they intercept moisture-laden winds from the sea, thereby causing on their leeward sides not only conditions of drought but also many consequent climatic changes. It is fairly clear that mountain building on the grand scale has been particularly the characteristic of certain times, as for instance the later part of the Tertiary when most of the present high ranges were elevated, and that at other periods relief was much less marked. This cannot fail to have had an enormous effect on the distribution of climatic values, and hence the very presence of mountain ranges of different ages is evidence of appreciable climatic change in the past. This point may be illustrated by the often-quoted case of North America (46) where there is abundant evidence that the elevation of the western mountain line radically altered the climatic values of almost the whole subcontinent.

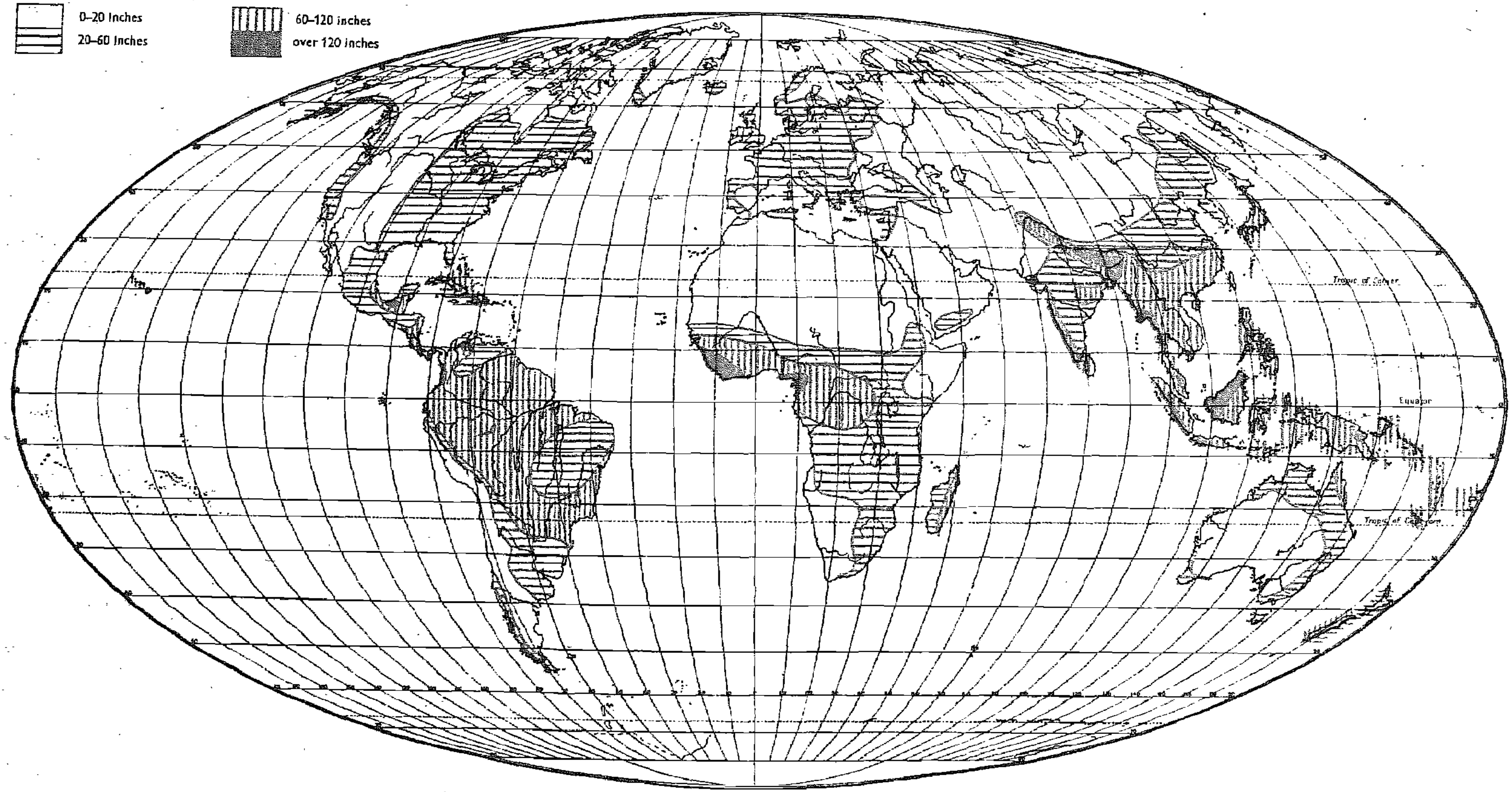
In much the same ways any considerable alterations in the relative outlines of land and sea are likely to lead to changes in climatic values by increasing, diminishing or diverting oceanic effects. Something of this kind will doubtless have happened following alterations in relative level, with its consequential broadening or narrowing of seas, but the point is of much greater importance in relation to ideas of continental drift (see next chapter) for it is almost impossible to imagine that this can have occurred on any appreciable scale without causing climatic changes of a profound character, and it is particularly necessary to bear this in mind when theories involving continental movement are under discussion.

The botanical evidence is similarly twofold, but by far the more important aspect is that afforded by the nature and characteristics of fossil plants. The question of the extent to which fossil floras are tests of climate has already been discussed in Chapter 14, and it is clearly dangerous to push conclusions too far, but it cannot be denied that in a broad sense the general appearance and structure of plants do to a large extent indicate the types of climate under which they flourish. To take the most obvious example, it is contrary to all experience to associate highly succulent plants such as the cacti with any but very dry climatic conditions. Unfortunately the problem of fossils is not so clear-cut as this, but they may nevertheless be very significant indicators of climatic values, and at least it seems certain, on their evidence, that temperate or warm-temperate conditions were formerly much more widespread latitudinally than they are to-day. In particular they indicate that conditions of this kind must once have prevailed much further towards the poles than they do now, and indeed that they may have extended far into the arctic and antarctic. On matters of detail there is still a good deal of difference of opinion, but that this is true of both the northern and southern hemispheres seems beyond doubt. Fossil floras from the tropics, in so far as they have been studied, also add to the picture, for they appear to be very like the floras in the same places to-day, and thus indicate that changes of climate in the past probably largely concerned the temperature gradients between equator and poles rather than absolute differences in world values.

The second and minor type of botanical evidence is that afforded by the annual rings of certain large and long-lived trees, especially the sequoias of California (202). The width of the annual rings in trees is a rough measure of the amount of growth which the tree has achieved season by season. This in turn is generally supposed to be a function of the climatic conditions, and especially of the precipitation. Developing this argument, it may be suggested that variation in width of ring will reflect and correspond to variation in rainfall from year to year. Examination shows that the rings of a large tree do in fact vary greatly in width, and also that this variation is a fluctuating one, the rings over one series of years being small and over another series being large. They tend in fact to wax and wane through the years, and this is generally interpreted as indicating a corresponding oscillation in climatic values. Naturally the length of life of any single tree is negligible in terms of geological time, but some of the big trees mentioned live for some thousands of years and thus cover comparatively long periods. This subject of the correlation of ring growth and climate has received much attention, especially in the work of Douglass (138), and the general conclusion that there is something approaching a persistent fluctuation in climatic values is inescapable. Actually investigation on these lines has been pursued very intensively, and there have been built up on the basis of ring-size climatic curves for the area in which these trees live extending back for hundreds of years. These curves, as has been said, seem to show beyond

PLATE 23

Map of the World showing the distribution of annual rainfall. Slightly simplified from various sources.



Areas correct Distortion increasing towards border of map.
Approximate Scale: 1:100,000,000 (1600 miles = 1 inch) along Equator
on Mollweide's Homolographic Projection

doubt that rainfall at least has varied almost continuously during the period concerned and, also, that there is a relation between tree-growth, climate and the sunspot cycle (613).

It will be noticed that these various lines of evidence have gradually brought the problem of climatic change more and more towards the present time, and the next type of evidence, the archaeological, is almost entirely concerned with changes in recent, and especially in historical, time. In many ways this evidence is the most interesting of all, because the earlier ones concerned periods and events so remote that they necessarily seem a little unreal. With the archaeological evidence the question of climatic change becomes more tangible and realistic. On the other hand, the changes themselves are naturally smaller, though not for this reason of any less interest.

At this point it is desirable to draw a careful distinction between climatic changes and climatic fluctuations, as there is some ambiguity in the use of these terms. The geological and botanical evidence has shown that there has been considerable long-term alteration in the climate of the world, and that this has included a series of catastrophic alterations. It is to these secular alterations and oscillations that the word change can be best restricted. Other botanical evidence has shown, and the archaeological evidence will also show, that in addition to these there have been constant minor variations, variations superposed, as it were, on the general trends of change. Major change seems never to have been quite smooth and unbroken but to have progressed in the form of irregularities. It is to these minor irregularities and variations that the word fluctuation is best applied. For instance, the general trend of climatic *change* since the end of the Pleistocene has been a gradual amelioration of condition, and this process has been sufficiently noted in Chapters 12 and 14. At the same time there have been almost constant *fluctuations* and advances and retreats in the main process of amelioration, and it is with these that we are now concerned. It must be emphasised that, although these fluctuations are minor compared with the main changes, they are nevertheless more than adequate to influence plant distribution, and indeed this may be the more normal way in which this influence makes itself felt. It must also be remembered that there is a close relation between change and fluctuation, and that the accumulation of the latter may and no doubt does often produce the former.

The archaeological evidences of climatic variation are very numerous but for the most part inferential rather than direct. That many of them represent indeed some measure of change can scarcely be doubted, but the nature and extent of that change are often matters of considerable argument. We are not, however, concerned here with details, but rather in demonstrating that change of one kind or another has occurred, and for this purpose deductions on archaeological grounds are valuable and important.

These indications of climatic fluctuations are really of four types. The first concerns the relatively minor oscillations that have taken place in the north polar ice-cap during the historical period. In the Norse period settlements were established on both the western and eastern coasts of south Greenland, and there is evidence that a fairly well-developed agriculture was carried on there. Now the region is permanently glaciated and even habitation by Europeans is out of the question. Of special interest are the excavations which have been made in a burial ground attached to the settlement near Cape Farewell because the details and methods of burial here clearly point to a gradual oncoming of severe conditions leading eventually to the disappearance of the whole settlement. Like changes are evidenced by the oscillations of ice-advance and retreat in the glaciers of the Alps and other European mountains. Some of these are comparatively modern and Brooks (65) notes particularly the great outburst of mountain glaciation which began about 350 years ago and which was so remarkable as to gain the name of the "Little Ice Age." This was followed by a retreat, a re-advance, and in the last hundred years a more rapid retreat.

A second general indication of climatic fluctuations, and especially of rainfall, is seen in various directions where changes in the level of bodies of water can be estimated. The best known of these is the record of the annual level of the Nile which is known from about A.D. 600 and which shows almost continuous fluctuation superposed on a gradual and steady rise. Similar variations have been observed in the Caspian and in parts of North America, especially in the old lakes associated with the Pleistocene glaciations. In Africa there is the well-known shrinking of Lake Chad.

Another more general inference is that afforded by the distribution of some of the great city civilisations of the past, an aspect of the subject which is of special interest in view of the growing belief already referred to that the actions of man himself has made no small contribution to the ultimate results. Thus, in the familiar case of Mesopotamia, where there are many vestiges of civilisations which could scarcely exist there to-day because of the general dryness of the country, it is known that there formerly existed water storage and irrigation systems which were destroyed in the course of human warfare. Again, in one of the most striking cases, that of the Syrian deserts, once so densely populated but now abandoned, so vividly described by Butler (70), the conclusion is that the vital changes have taken place in not much more than a thousand years, and though partly no doubt due to natural causes, were in large measure the results of bad government. Much the same is suggested by the remains of the once flourishing Roman cities of North Africa which to-day stand in regions so arid that it is difficult to see how any very considerable population could be supported there, and also by the remains of the earlier civilisations of the Indus plain where conditions seem formerly to have been much moister than now. All these give evidence of change which, though it may have been greatly intensified by man, can scarcely have been entirely due to him. The Kharga Oasis on the eastern edge of the Sahara illustrates a related state of affairs. In earlier historical times the oasis was a lake which gradually degenerated into a swamp, since when the water in the oasis has varied greatly and the human population with it. The extraordinary local changes which may be caused by a few seasons or even a single season of abnormality have lately been most strikingly demonstrated by Lake Eyre in South Australia. This is part of the drainage basin for much of the country to the north-east of it but for very many years it has contained no water and its affluents have been dammed by sand, but recently the rainfall in Queensland has been sufficient to form rivers capable of overcoming the sand obstacles and at one period† the lake had become a sheet of water more than 3,000 square miles in extent.

The reverse condition, of ancient cities now lying buried in dense tropical forests, and which seem to have been overwhelmed by an increase in precipitation, is seen well in the country of the Mayas in Central America. Here the cities appear to have been at their zenith about the first few centuries of the present era. Now, as Brooks says (65), "this country is at present covered by almost impenetrable forests, the climate is hot, moist, and enervating, while the inhabitants are idle and uncultured." A less familiar example is furnished by Angkor, the great abandoned city now buried in the tropical jungle of Cambodia. It was founded about

† The lake is expected to be dry again by March or April 1953.

A.D. 600 and flourished for the next 500 years or so, and at one time is estimated to have had a million inhabitants. It is thought to have been abandoned in about A.D. 1200.

This brings us to the last and most detailed evidence, that afforded by actual meteorological observations during the last 200 years or so. All such observations go to show that in most respects, and perhaps particularly as regards rainfall, climatic values tend to fluctuate more or less continuously, a series of years below the norm being followed by a series of years above the norm. This at any rate is a general conclusion, and it can be substantiated in detail and particularly from many meteorological records.

One aspect of this fluctuation and its effect on plant distribution has been studied in some detail (217). The lizard orchid, *Himantoglossum hircinum*, has an interesting geographical history in Britain, of which the main features are its fairly regular occurrence locally up to about the middle of the nineteenth century, its decline and virtual disappearance between that date and 1900, and its marked increase in numbers and range during the present century (or at least to 1933 when the study was made). So conspicuous is the last feature that enquiries were made to discover whether there was any meteorological explanation of it and the result showed that the facts correlated well with a general climatic change in the direction of winter temperature amelioration which became notably accentuated after 1900 (53, 64, 341, 359).

That this fluctuation has not been confined to Britain has been shown by the work of Ahlmann (5) and others (278, 468), and Lysgaard (351) concludes that in the thirty years, 1911–1940, compared with the thirty years, 1881–1910, both temperature and rainfall have been *higher* in temperate latitudes and *lower* in the tropics. On a still shorter scale the fluctuations of climate from year to year are in everyone's experience, and it is necessary only to mention the markedly hot and dry summers of 1933–1935 and the frequent cold winters between 1940 and 1947 as instances of this.

The combined effect of all the lines of evidence which have just been reviewed has been sufficient to demonstrate beyond doubt the two main facts that climate has suffered changes both great and small, and that these have been reflected directly in the distribution of plants. We may now go on to see whether it is possible to give a more general picture of climatic change during geological time, and especially during the history of the Angiosperms.

This has actually been done with a wealth of evidence and detail by Brooks (65), and we cannot do better than describe shortly the conclusions to which he comes. Put very concisely, these are that the climate of the earth has normally been a genial climate interrupted only at long intervals and for short durations by glacial periods, "as at long intervals a passing cyclone disturbs the peaceful life of a tropical island." The long genial or warm periods were all times during which the relief of the world's surface was low and during which, as a result, shallow seas encroached more or less extensively over the land surfaces. These periods too were characterised especially by comparatively small and gradual differences between the equator and the poles. On the other hand, the glacial periods seem to have followed periods of active mountain building and were characterised by steep and extensive temperature gradients from equator to poles.

One of these long warm periods apparently persisted from the glaciations of the Permian to those of the Pleistocene, and it was during this long time that the Flowering Plants were evolved. As regards these plants then, they originated during a long warm period, and these conditions continued to prevail for millions of years after they had appeared. Only comparatively recently, from a geological point of view, did these optimum conditions give place almost suddenly to one of the catastrophic periodic glaciations whose vibrations still persist.

This conception throws much light on the geographical development of the Flowering Plants. Arguing from it we are justified in regarding this great group of plants as developing in response to and in correlation with more or less constant and optimum climatic conditions, and perhaps as having reached, towards the end of this period, what may be described as something approaching an equilibrium. With the onset of glaciation this equilibrium was suddenly and rudely disturbed. An almost completely new range of climatic conditions arose in the higher latitudes at any rate, conditions to which the Flowering Plants were quite unaccustomed, and their subsequent history has undoubtedly been the story of their attempts to exploit this new environment. It is to this more than any other factor that many of the more puzzling details in the present distribution of plants are due.

This point of view can be conveniently illustrated by a consideration of certain aspects of arctic plants. From the various evidences available it is an almost inevitable conclusion that during the long warm period of the Cretaceous and earlier Tertiary temperate or warm-temperate conditions must have been the rule throughout the upper latitudes, and that arctic conditions, that is to say glacial conditions at sea level, were unknown anywhere in the world. Apart from the circumstantial evidence afforded by fossil plants, there is, according to Brooks, definite meteorological and mathematical evidence for this view. He shows, for instance, that even to-day a comparatively small rise in mean annual temperature of the order of 5° F. would be sufficient to cause the gradual melting of the polar ice-caps and to prevent them re-forming, and the temperature of the warm periods was certainly above this figure. Moreover, once the ice-caps disappeared their effects on the climate would be removed and almost certainly an even warmer climate would be the rule.

As regards the Angiosperms then the essential feature of the glacial period of the Pleistocene was to produce, for the first time in their history, what we now call arctic or polar conditions, that is to say glacial conditions at sea level, and these over a comparatively wide area. This being so, and there seems little reasonable doubt about it, several consequences follow, the chief of these being that cold temperate and arctic plants must be regarded as among the more recent in origin, and this element as one of the youngest in the world flora. But the problem of the actual source of this cold flora is not so simple. At the present time the snow line is nowhere so high that there are not some snow-capped mountains, even on the equator, as in East Africa and in the Andes. On the other hand there are high mountains so far north and so far south, as for instance in Alaska where there are elevations of over 20,000 feet and in Antarctica, that they are virtually entirely above the snow line. Thus a temperature change which would suffice to raise the snow line above the tops of all the mountains at all latitudes would have to be enormous and indeed theoretically quite inconceivable. It would therefore seem that although arctic conditions may be recent alpine conditions must have existed somewhere much longer and these places would afford an obvious source from which the polar flora could have developed.

On the other hand the long genial period of the Cretaceous and earlier Tertiary is pictured as one of low relief and least continental area (65) and if this is a true representation then it may well have been that until the orogeny of the later Tertiary there were in fact no elevations sufficient to bear ice and snow, at all events in the north, where there is polar sea, though it is not so easy to visualise the possible conditions in the south where there is a land pole. All that can be inferred with profit is that alpine conditions must have existed since the Miocene and Pliocene and may have been present in some form much earlier, especially on some of the more ancient mountain systems. Bearing in mind that there was a considerable time gap between the Miocene and Pliocene orogeny and the Pleistocene glaciation to which it contributed it seems clear enough that alpine vegetational conditions are older than polar conditions and hence that the relationship between the arctic and alpine floras expresses the origin of the former from the latter rather than the reverse, a conclusion which is fully in agreement with the distributions of their respective constituents.

Finally let us turn to the vegetation of the low-lying tropics. There are no indications either from fossil or other evidence that the maximum or equatorial world temperature has, since the rise of the Angiosperms, ever been much greater than it is to-day. Indeed on astronomical grounds there are *a priori* reasons for the view that it has not. The difference between the climate of a genial or warm period and that of the Pleistocene was therefore, as has been already said, essentially the difference between a generalised latitudinal climatic zonation and a steeper zonation. In other words, the tropics in the warm periods were probably not much warmer, but the higher latitudes in the glacial periods were much colder. Nor does it appear likely that the equatorial values were very greatly diminished during glaciation. In floristic terms then it may be said that while, in the warm periods, circumstances favoured the development of a few widespread and generalised plant types, of which some of the present tropical flora are probably good examples, circumstances in the glacial periods produced not only a tendency towards the production of more specialised types in correlation with the more specialised conditions, but also brought about a world-wide telescoping of the climatic zones, so that, if nothing else, there must have been an intense competition for space, although this may have been offset to some degree by the relative greater elevation of the continents and their consequent greater areas. This in turn doubtless led to further and more local specialisation, and thus the whole effect of the glaciation appears to have been to hasten the conversion of a generalised world flora into a number of more or less specialised floras. Certainly this specialisation is one of the leading features in the world flora to-day, and it would seem that this is at least a partial explanation of it.

Attention has often been called to the fact that on oceanic islands where there is a high degree of endemism, the endemics are commonly mesophytic woody plants. This is not surprising in view of the oceanic climates of most such islands but it has been suggested that it has a greater significance than this and that these floras are relics of older, moister world conditions like those indicated above for the genial periods. Wallace (570), for instance, expresses the view that every island represents the flora and fauna of the period when it was last separated from the adjacent continent, while Guppy (244) has put the matter even more plainly when he says, "islands appeal to me more as registers of past floral conditions in the continents than as representing their present state. Their marked peculiarities bear the impress of the past on the continents, whilst their common features tell the story of the present."

On the other hand in continental floras where there is much endemism, as for instance at the Cape and in south-western Australia, the endemics are notably associated with the more arid kinds of habitat and this raises the very interesting and important question of how far arid conditions or "desert habitats" have existed in the past, and whether the existent floras of such regions are to be regarded as of recent or of more remote origin. The undoubted facts that mountain building tends, by excluding rainfall, to produce desert conditions and that the extension of continental areas intensifies similar aridity towards their centres, suggests that arid habitats are now much more prevalent than in the early stages of Angiosperm history, and hence that most desert floras are young floras, but it is well to be cautious in accepting the validity of this conclusion. It must be remembered that rocks of desert origin are frequent in the geological record and are by no means always associated with periods of mountain building or glaciation. Also the long genial periods of the past which constitute what is called by Brooks the normal climate of geological time, are described as warm and dry. This does not of course necessarily mean aridity everywhere and always, and the Eocene, which is of special importance in Angiosperm history is admitted to have been more than usually moist, but it does suggest that desert conditions are not so modern as might at first be thought. In short it permits the view that the present deserts of the world, and their floras, are not all of the same age, a view which may go far to explain the several notable differences, both qualitative and quantitative, between these, and in particular the curious fact that the largest desert area of all, the North African-Indian region has a less specialised flora and fewer characteristic forms than almost any other.

But when all due allowance has been made for the possibility that certain extreme environmental conditions, such as those of mountain snows and those of deserts, have existed since the Flowering Plants first appeared, it seems reasonable to regard the changes of climate during the history of these plants as having led gradually to a more and more specialised series of local climates, particularly during and since the Pliocene, with consequent differentiation in the vegetation. This point has been well put by Bews (52), who says, "the evidence from phylogeny . . . affords convincing support to the view that climatic differentiation has been responsible for the production of plant forms adapted to more open grassland conditions, to scrub, semi-desert and also, though this began very early, to the temperate floras as well."

This view involves the belief that the earlier Angiosperm flora was of a generalised forest type and very widespread, and that the development of the vegetation as we see it to-day has been in the various directions of specialisation from this original condition. This is differentiation, and this particular aspect of Angiosperm history is, as we have seen, an important basis of Guppy's Theory of Differentiation.

So far in this chapter we have been concerned chiefly with the more definite evidences of climatic change in the past, and the point has now been reached at which there can be most properly discussed certain contingent conditions and their possible consequences which have a direct bearing on the subject of climatic change and which may, indeed, be a strong pointer towards an explanation of it. This is the subject of the variable elements in the earth's movement and orbit which are called inequalities or perturbations and which are known to have certain periodicities. Although to discuss these at length here is impossible the general nature of the possibilities can be sufficiently explained by a consideration of the one of these perturbations with which problems of plant geography would seem almost inevitably to be most closely related, the obliquity of the ecliptic.

It is well enough known that the axis of rotation of the earth is not at right angles to the plane of its orbit or path round the sun, but it may not be so generally realised that this obliquity is the cause of seasonal differences, which become increasingly marked from the equator, where conditions are almost constant, to the poles. In consequence also of the obliquity, and constituting a leading element in seasonal change, there is an increasing variation pole-ward in the length of day and night throughout the year, so that while, at the equator, day and night are each of about twelve hours all through the year, at the poles the year consists of one "day" of six months and one "night" of six months. The change in this respect with latitude is not, however, constant and whereas from the equator to latitude 45° or so the variation in length of day is comparatively small, it becomes greatly accentuated above 45°. The present distribution of plants is plainly correlated with this matter of length of day, as was shortly stated in Chapter 15, and any serious alteration in its values would be likely to have a profound effect on plant geography.

It is not surprising therefore that the perturbations of the earth have been much considered by those who seek an explanation of the major climatic changes of the past, and a useful summary of the position in relation to one particular change of this sort, the Pleistocene ice ages, has been given by Zeuner (612) in a discussion of the Astronomical Theory of Glaciation. He considers four perturbations—the length of year, which he concludes has been virtually unchanged since the Palaeozoic; the eccentricity of the orbit, which fluctuates with a period of 92,000 years; the precession of the equinoxes, with an effective period of 21,000 years; and the obliquity of the ecliptic, which at present fluctuates within narrow limits with a period of about 40,000 years. Doubtless major alteration in any perturbation would gravely affect plant distribution, but the last has particularly interesting possibilities in this connection.

Were there no obliquity of the ecliptic there would be, at all latitudes, a condition of perpetual equinox, in which, although the shape of the earth would still cause a temperature gradient from equator to poles, there would be no seasonal variation. Since equinoctial conditions are to-day characteristic of equatorial regions it might at first be thought that this would ameliorate the climate of temperate regions, but this is not so, and the meteorologists conclude that a *decrease* in obliquity, while diminishing seasonal differences, would increase the distinctness of the climatic zonation, so that the climate would tend to be less clement than now at high latitudes. Conversely, any *increase* in obliquity would intensify seasonal variation but diminish the climatic zonation, and Zeuner quotes Milankovitch in Koppen and Geiger (320) for the proposition that if the obliquity reached an amplitude of as much as 54° (it is now about 23°) the annual total of radiation would be the same for each of the poles as for the equator, and the general climatic conditions would be much alike all over the world and characterised by very marked seasons.

It would take too long to deal here with all the botanical implications of such hypothetical changes in the obliquity of the ecliptic and the reader should consult the interesting summary of these by Allard in Murneek and Whyte (397), from which it is clear that changes of this sort, if appropriate in scale and in time, might explain not only many problems of plant geography but also many puzzling aspects of Angiosperm history, such for example as the development of the great herbaceous element in the northern flora. But on the broader general issue of climatic change in the past which has been the subject of this chapter, it would certainly also seem that further knowledge of what we have called the earth's perturbations may well make plain much that is still obscure to-day.

CHAPTER 20

THE FACTORS OF DISTRIBUTION—VI. GEOGRAPHICAL CHANGES

THERE are few clearer illustrations of the bearing of the evolutionary conception on problems of plant distribution than that of the importance of the distribution of land and sea. On the assumption that species were created in or near the situations in which they occur to-day, discontinuity is not necessarily of any great significance, because it can be explained on the assumption that creation took place on more than one occasion and in more than one place, but if an evolutionary origin of species is assumed with its generally accepted premise that species are monophyletic, then clearly the discontinuity of species becomes a matter of much greater interest and importance. It is not surprising therefore to find that the pioneers of the idea of evolution realised almost from the first that discontinuity was a subject likely to hold the key to many riddles. More remarkable is the fact that in those early days, and actually antedating the *Origin of Species*, there was a widely held view that the present distribution of living things could not be explained on the present distribution of land and sea, and that changes in this feature must be a potent factor in plant and animal geography. For instance, Hooker (271) quotes Lyell as saying: "As a general rule species common to many distant provinces, or those now found to inhabit many distant parts of the globe, are to be regarded as the most ancient . . . their wide diffusion shows that they have had a long time to spread themselves, and have been able to survive many important changes in Physical Geography," and Hooker himself (272), in his *Introductory Essay to the Flora of Tasmania*, writes: "These and a multitude of analogous facts have led to the study of two classes of agents, both of which may reasonably be supposed to have had a powerful effect in determining the distribution of plants; these are changes of climates, and changes in the relative positions and elevations of land." The final phrase of this statement is especially interesting because it distinguishes between the spatial relations of land surfaces, that is to say the distances between them, and their relief and outline, and it is important before going further to amplify this.

That Hooker's remark is true and that neither the distribution of the land nor its elevation has remained unchanged during the past is shown by a glance at any stratigraphical map of the world or of any one continent, for it will be plain that marine and freshwater sedimentary deposits cover many parts of the surface, and hence that these areas must at one time have been below the sea (though not necessarily all at once) and many maps purporting to show the state of world geography at different geological epochs such as those of Mathew (371), Grabau (226), Arldt (21) and others have been constructed on this basis. At the same time the problems involved in the circumstances, dates and intensities of these changes are many, and certain of them must be considered with some care here. In particular must an attempt be made to come to some conclusion about the last of these, the *degree* to which there has been change.

An enquiry of this kind, which can be made to include almost every aspect of earth history is fascinating but liable to lead all too easily into realms beyond the scope of this chapter, and the following observations are therefore confined as strictly as possible to some of the matters which especially concern the distribution of plants, and for further information on other topics the reader should consult such general works as those of Arldt (21), Umbgrove (565), Daly (119), Shepard (486) and Gutenberg (246).

With regard to the minor and less controversial kind of change, that which merely involves elevation, a perusal of geological maps also shows that in all the larger land masses of the earth there are great areas where very ancient Archaean (pre-Cambrian) rocks are exposed at the surface, and that in general these areas are central rather than peripheral. Furthermore, these ancient rocks, which represent the original materials of the land masses, normally extend widely beneath the sedimentary deposits already mentioned. In short a continent or subcontinent is to be regarded as composed of a core or base of these Archaean rocks on parts of which, from time to time, sedimentary younger rocks have been laid down. Such ancient rock surfaces, or Archaean shields as they are often called, are conspicuous in Canada, in eastern South America, in Scandinavia, in India, in Manchuria, in Africa, in Arabia, and in Western Australia, but they are also represented on a smaller scale in many of the larger islands.

There is also good geological reason for believing that all or nearly all of the superposed sediments are deposits formed under comparatively shallow water in which the Archaean shield lay not far below the surface, and on this evidence it is generally supposed that the sedimentary deposits of the larger land masses were formed during times when certain of their parts were shallowly submerged. These sediments vary greatly in age and it is therefore unnecessary to assume that any land mass was submerged to the total extent of such deposits at any one time. Rather may we visualise the successive shallow submergence of different parts of the continents in different periods, the various sediments being laid down accordingly. We may therefore also imagine that the seas around the masses have encroached upon them locally and at different times according to changes in the relative levels of land and water. This conception raises the question whether the present extent of the continents is a maximum one or whether in fact some parts of them are even now invaded by shallow seas. The question is whether or not the present land outline of the continents actually represents the boundaries of their Archaean bases.

To answer this it is necessary to consult a map showing the submarine relief. Here it will at once be noticed that the shallower submarine contours closely follow the outline of the land, but that as depth increases so they become more irregular. This means in effect that round most land surfaces there is a narrow edging of very shallow water beyond which the sea becomes rapidly deeper. The details of this distribution leave no room for doubt that the line where the sea passes from shallow to deep represents the real edges of the continents, but that these are in general at present slightly encroached upon by the sea. Such submerged edges of the continents are called continental shelves, and one of the most striking is in western Europe, where the true edge of the continent runs west of Ireland, so that the British Isles are islands rising from the surface of the continental shelf which elsewhere forms the beds of the shallow seas which separate them from what is generally called the "continent." Seas of this kind, which are clearly intrusions over the land surfaces of the continents, are called epicontinental seas (see Chapter 1), and by a justifiable extension of the phrase, sedimentary deposits formed on their beds may be called epicontinental deposits. Although the British Isles have been cited for their familiarity they are by no means the best example of such conditions, and far greater areas of shallow waters, which are presumably also epicontinental, are to be found in south-east Asia, where they extend over much of Malaysia. Specially notable is the occurrence of shallow water between Australia and New Guinea. On the other hand many parts of the world are conspicuously without these epicontinental seas, and here the shore edge is more or less exactly the real continental edge. The west coasts of Africa, America and Australia are perhaps the best instances of this.

A point of considerable interest as well as of great theoretical importance is whether or not the real edges of all the continents are at about the same level or whether some are more deeply invaded by water than others because their general level is lower, but this is a difficult point which can only be answered rather inferentially here. Returning to our examination of submarine contours we shall notice that one of those most generally depicted is the 200 metre or 600 ft. contour. There is no inherent virtue in this figure, except perhaps that it is also 100 fathoms, and its repeated use is partly based on the fact that it serves particularly well to reveal vividly the salient points of under-water relief, and that it does usually mark the point at which a gradual deepening of the sea round a continent becomes suddenly and intensely accentuated. On this account it is a reasonably fair inference that this depth broadly represents that to which in present circumstances the true edges of the continent are submerged, and since the depth is equally significant for all, that these have more or less the same common level, a conclusion which, it may be added, accords with that reached by entirely different lines of reasoning. We may, indeed, for present purposes, be allowed to regard the 600 ft. submarine contour as giving a generalised if not an exact impression of the actual outlines of the chief land masses of the globe.

This enables us to gain a much clearer picture of what changes in the relative levels of land and sea, and especially of what, to coin an ugly word, "epicontinentality" may mean, because by following this particular contour there can be drawn an outline of the continents as they would presumably appear if they were at such an elevation that they were free from the encroachment of epicontinental seas. Plate 3 is such a map and it is illuminating. It will already have been realised that Great Britain and Ireland would be joined to the continent, but this is a minor aspect of the whole. Taking the continents in order we should see that in Europe there is not much other change except that the narrower straits of the Mediterranean disappear. That sea as a whole survives but in diminished form. In Africa, too, the only change of note is the joining of the Canaries to the mainland. In America the changes are much greater. Working from north to south, the Arctic Archipelago would disappear and become a continuous extension of the northern mainland, and the North Atlantic would be almost bridged; Newfoundland would be united to Canada; the Bahamas and Cuba would be practically continuous, not only with Florida, but also with Yucatan; the rest of the West Indies would be much enlarged; and the Falklands would be connected up with Fuegia. Extensive as these American changes would be, they are slight compared with what would happen in Asia and Australia. Here, once more starting in the north, the Bering Strait would disappear; Japan and Sakhalin would be joined to the mainland; the Philippines, Borneo, Java and Sumatra would all be united to the continent of Asia by way of the Malay Peninsula and Siam; and New Guinea would be joined to Australia. All this would happen were there an effective lowering of the sea level by 600 ft., but much of it would follow even if the change was much less than this. For instance, a difference of 150 ft. would connect Asia and America by a belt of land nearly 200 miles wide (284); a similar difference would be effective in western Malaysia; and one as slight as 65 ft. would unite Australia and New Guinea (565).

Conversely it is just as interesting to note, a relative lowering of the land by the same amount of 600 ft. would, except in western Europe and central Asia, have but comparatively little effect, and would put but few new obstacles in the path of plant migration.

Is it justifiable to believe that changes of this kind of dimension and especially a relative rise in the land of such degree that, for example, with few quite minor exceptions almost all the islands of the northern hemisphere would be replaced by continuous land surfaces and the only major discontinuity would be that of the ocean basins, have indeed occurred during the history of the Flowering Plants?

There are several lines of evidence which go to show that the present state of affairs is not extreme in either direction. The distribution of Tertiary epicontinental deposits shows clearly that the continents must, as wholes or in part, have been much more submerged than now at some period since the Angiosperms became widespread and the same is true of somewhat earlier times, the great Cretaceous transgression being a striking case in point. Turning to more recent times there are in many parts of the world raised beaches far above present sea level. On the other hand a mass of evidence shows that there must have been much relative elevation. The British Isles are generally supposed to have been joined, on one or more occasions, to the continent and also to one another, and evidences of like elevation are considerable in mid-America and in parts of Malaysia (36, 512). All these would presumably involve changes of the order of magnitude described above and there seems no reason to doubt that they have occurred.

There is no sure means of judging how much the land surfaces of the world may have been reduced and their isolation increased at times of greatest depression but some idea can be obtained by tracing their outlines from a geological map as they would appear if the deposits of Tertiary or of more recent times are excluded as if they were in fact below the sea. It would take too long to go through the whole world on this basis, but the case of Europe and Asia for instance will show the sort of degree of change that might be expected. Great areas of north-east Siberia are covered with Tertiary deposits, as is also much of the interior of Asia. Similarly in Europe, Asia Minor, Arabia and parts of North Africa, and at least it can be said that an appreciable proportion of the whole might well have been simultaneously submerged at a time of maximum relative depression. There are also considerable Tertiary deposits in other continents, but they are least perhaps in Australia, where the Eocene is lacking.

We cannot here discuss all the possible causes of depression and elevation but they are of two main sorts (35), eustatic changes which are due to alterations in the overall sea level and which therefore make themselves felt equally all over the world, and orogenic and epeirogenic changes due to deformation of the land masses by such agencies as mountain building, which are usually of comparatively local significance only. Both these may be illustrated by a short reference to one sequence of events in which both are concerned, and which because of its unusually accurate time relation is of special interest to the plant geographer.

During the Pleistocene glaciations (see Chapter 14), great quantities of water must, from time to time, have been locked up in the enormous polar ice-caps and the amount of water in the oceans must have been correspondingly less, resulting in a world-wide (eustatic) lowering of sea level. What this lowering may actually have amounted to is controversial and estimates range from one hundred feet or so to many times that figure but even at its lowest it is generally believed to have been sufficient to have eliminated many of the shallower sea-water barriers. True, it is believed also that the actual weight of the ice-caps must have depressed those parts of the land surfaces on which they rested (119) so as to compensate to some degree for the general lowered water level, but this effect would not have been eustatic and would have affected only the land areas under or near the ice and would have been without significance further afield, and, with the melting of the ice these depressed areas are thought gradually to have risen again as the weight lifted. The Pleistocene glaciations thus illustrate both kinds of relative elevation and also demonstrate that as recently as this many of the shallow-water epicontinental areas were dry land and open to plant migration. It may be too that the evidence of the tilting of Great Britain along a north-south axis, which, from a study of raised beaches, seems to have taken place comparatively recently (440), is associated with these times.

But whatever the actual details may have been, it is certain that we must think in terms of considerable epicontinental changes during the lifetime of the Angiosperms, and, moreover, that these changes must at one time or another have affected the distribution of these plants in three ways. First, they must have controlled plant movement and dispersal by the formation or elimination of barriers. Second, they must have led to tremendous changes in the actual amount of land available for plants. Third, they must have caused correspondingly great alterations, not only in the zonation of climate, but also, and as a consequence, in the prevalence of habitat types.

So far we have been concerned only with changes in the level of the land masses. Certainly, changes of this sort may, by submerging some parts and raising others above the sea, cause considerable alterations in superficial geography, but they do not involve modifications of either the basic area of the continents or their relative positions in respect of one another. Thus, the changes already described, important though they may be, are not of the magnitude required to explain the larger problems in the distribution of plants. We must therefore now enquire what evidence there may be of geographical change on this much greater scale. Here again there are two aspects of the matter and it is convenient to deal first with the smaller, which concerns the subject of mountain building.

The fact that certain geological epochs, and especially the Miocene and Pliocene, were periods of intense mountain elevation has already been referred to more than once. Mountain building on a large scale may be described as a corrugating of the earth's surface widely or locally according to its extent. This can be illustrated in a familiar way by compressing a flat surface such as a sheet or pile of paper laterally. In so doing, not only is the surface thrown into folds but the ends of the paper are brought closer together, so that the horizontal distance between the ends is decreased. That such compression folding has indeed been the mode of formation of many mountain systems has been shown conclusively in the case of the Alps for instance (108), where it appears that part of North Africa has actually been pushed into south Europe. The difference between the model and the real is that in the paper the folds are hollow, but in the earth they are solid, so that mountain building must mean a considerable redistribution of the material of the land mass concerned, not only in order to provide for the thickening caused on the surface by the folding but also to provide for the compensation on the underside of the mass required to bring about isostatic equilibrium and, as it were, to buoy up the increased local load. This material can come only from more outlying parts of the land mass and hence it may be expected, on quite general grounds, that mountain building will cause some contraction of area, which in turn means that the distance between land masses so affected will increase. By how much will of course depend on the amount of folding and overfolding in the mountains and may be very great, as for instance has been suggested in the case of the Himalayan systems, which, it is thought, may have caused such a contraction that India may have been drawn away from the neighbourhood of Africa across the western part of the Indian Ocean. Similarly the width of South America may well be a good deal less now than before the Andes were uplifted.

We see then that geographical changes may be brought about in at least two ways, by relative elevation and depression of land surfaces and by changes in their actual areas and that in the latter particularly the amount of alteration may be considerable. But it is still not of sufficient dimension to explain many of the problems and we must now consider a fresh possibility which would be sufficient in this respect, namely the possibility that there have been major changes in the relative positions of the continents.

The brief mention above of isostatic compensation was made because it served two useful purposes. Not only was it appropriate to the more restricted question there under discussion but it was a valuable introduction to the wider question of continental position now to be discussed, because it clearly indicates that what may be regarded as the normal idea of continental structure and behaviour may have to be radically revised. To the ordinary man in the street a continent or other large land mass is symbolic of all that is solid, rigid and unchangeable, but the geophysicist has quite a different conception, because to him such attributes as solidity and rigidity have a more precise meaning. On his criteria very few kinds of matter merit these descriptions, and a continent is certainly not one of them. How then is it to be regarded? The best way of explaining this point is to pass straight into a simple account of the crust of the earth as it is believed to exist in the light of modern physical ideas.

In brief, the outer layers of the earth's core are pictured as being of the consistency of a very viscous liquid, "solid" by all ordinary standards but essentially fluid in the more strictly scientific meaning of the term. On the outermost layer of this fluid core the continents, themselves more rigid though far from absolutely so, float, like a series of rafts, partially immersed. The layer of the core in which they float is called the "sima," because it is composed of more basic material containing much silica and magnesia, and the continental slabs themselves are composed of a material called "sial" which is more acidic and contains much silica and alumina (fig. 74). The continental slabs are regarded as of the same average thickness but their absolute thickness varies locally, of course, according to their relief and to compensation on their undersides in accordance with isostasy. Between the continents, over the beds of the oceans, the surface of the sima is nearly everywhere in direct contact with the water. The continents are thus pictured as isolated slabs of one sort of material floating partially immersed in another sort of material.

With this picture before us we shall at least be partially equipped for an enquiry into one of the most topical of such subjects to-day—the question of whether or not the continents have always occupied the same relative positions as they do now.

There seems little doubt that the idea of continental movement, for which other names now current are displacement, drift and shift, has been vaguely in the minds of men for many years, but the whole conception is so revolutionary and so opposed to traditional teaching that it was not put forward as a definite hypothesis until the present century, and it was not indeed until Wegener (580) published his book *Die Entstehung der Kontinente und Oceane*, in 1915, that the theory came into full prominence. Because this was the first really illustrative attempt to put continental drift into words Wegener's name has become rather too exclusively linked with the general theory, and it should be remembered that he was but one of a number of apostles. His theory is as follows. During the early part of the Palaeozoic the continents of the world as we know them were all joined together in one huge land mass or Pangaea, but subsequently separated and drifted apart until they have come to reach the positions they now occupy (fig. 75). This movement centred on Africa, which, with the main part of continental Asia, has retained its original position more or less unchanged. The theory also postulates a movement or wandering of the poles, in order to account for considerable alterations in the distribution of the climatic zones. Since the publication of Wegener's book the Theory of Continental Drift has received a great deal of attention (*e.g.* 83, 150, 151, 265, 347, 457, 617), and many improved forms of it, correcting or modifying some of the more obvious weaknesses of Wegener's ideas, have been put forward. Du Toit (150) in particular has brought together in one volume much of the relevant matter relating to these theories, to which he has added many of his own beliefs, and it is to this work that the present writer is most indebted in the following discussion.

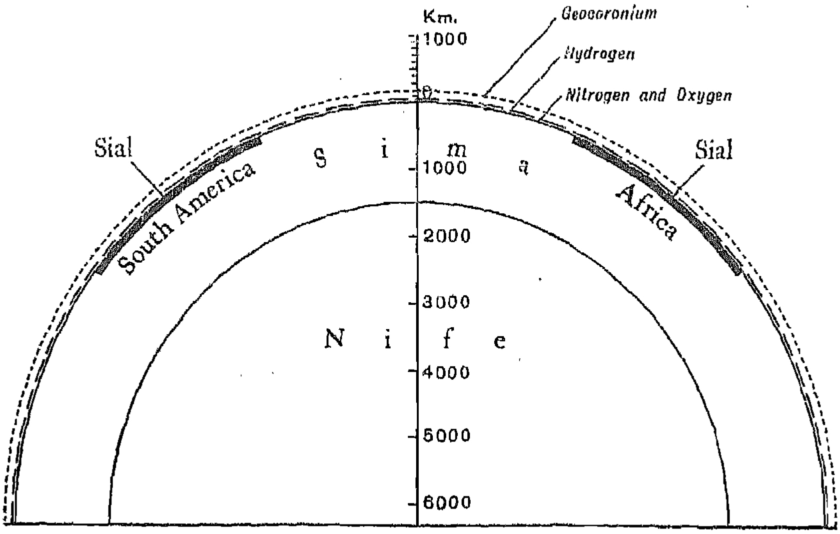


FIG. 74.—Diagram of a section of one hemisphere to show the position of the sial and sima. (Redrawn from Wegener, *Origin of Continents and Oceans*, Methuen & Co.)

It would be out of place to consider here the many very controversial aspects of this subject, but it is essential to survey very shortly the evidences on which the idea of drift is based, and these Du Toit has usefully summarised as the "criteria of drift," and a much simplified presentation of them is as follows:—

1. Physiographic:
   The general similarity in shape of many opposed coast-lines such, for instance, as those of eastern South America and western Africa.
   The correspondence of physiographical features in lands now widely separated.
   The occurrence of various submarine features producible by drifting blocks.

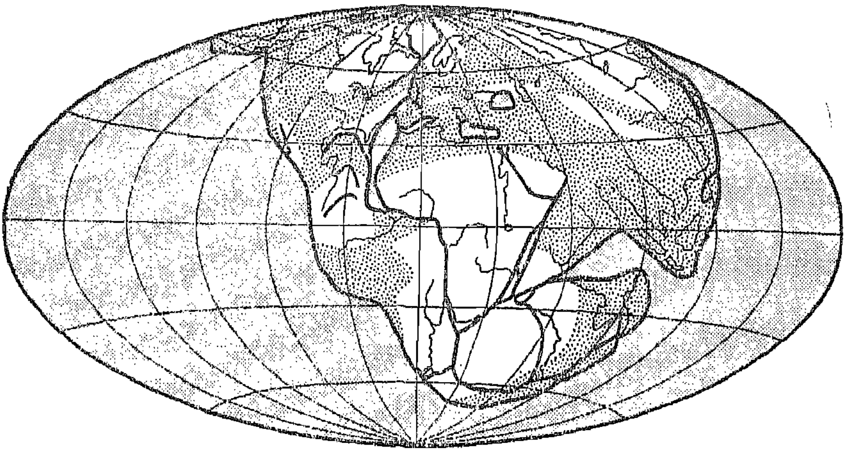
2. Stratigraphical:
   - The occurrence of similar geological formations on opposite coasts.
   - Other geological resemblances on separate masses.
3. Tectonic:
   - The occurrence of comparable geosynclines, fold systems, fault systems, and rift valleys on different continental masses.
4. Volcanic:
   - Similarities between the volcanic geology of separated masses.
5. Palaeoclimatic:
   - The peculiar distribution of glacial deposits and of other extreme climatic types of deposits over the different continents.
6. Palaeontological:
   - These may be comprehended in the single statement of the difficulty or impossibility of accounting for the present distribution of organisms on the assumption that the major distribution of land surfaces has been constant. It involves in detail a great many important special aspects, as for instance the floral relation between America and Africa, and between the widely sundered lands of the southern hemisphere. The distribution of marine organisms also presents many very difficult problems on such an assumption.
7. Geodetic:
   - This may be interpreted as the evidence afforded by the actual measurements of longitudinal and latitudinal values.

For further details of these criteria the works of the authors cited should be consulted, but it is well to say here that while these show considerable differences in detail there are no essential discrepancies between them. For example, there are differences of opinion about the course of continental drift and also about the condition of the world at the time it began (in contrast to Wegener's Pangaea Du Toit postulates two primaeval continents, Laurasia in the north and Gondwanaland in the south) but these do not affect the general theory.

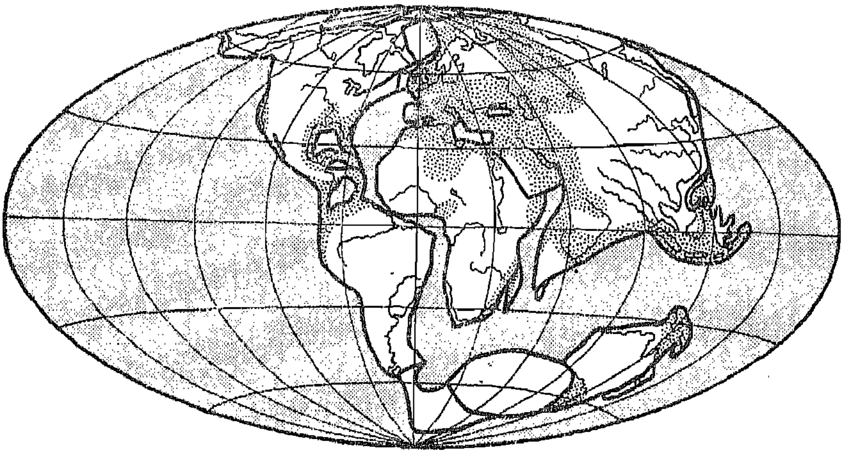
The last two of the above criteria, however, call for further comment and we may dispose of the final one first. It is particularly important here because to those who are not expert geologists or geophysicists it is by far the most easily understood evidence, and even to them it must if substantiated be the most conclusive. In brief, has actual astronomical and mathematical measurement shown that the continents have moved or are moving? Du Toit, who considers the evidence at some length, concludes that a positive shift of crustal matter has been instrumentally demonstrated, but Longwell (346) and others do not agree, and the evidence on this most crucial point must unfortunately still be regarded as uncertain.

The evidence based on the distribution of organisms, and especially of plants, is obviously of special relevancy here but we need not repeat it because it has already been set out in the earlier part of this book and more especially in those pages dealing with discontinuity, and has also been summarised elsewhere (222). The theoretical importance of that aspect of plant geography is largely in relation to this question of continental drift and the chief facts about it are stated both in Chapter 6 and in Appendix B.

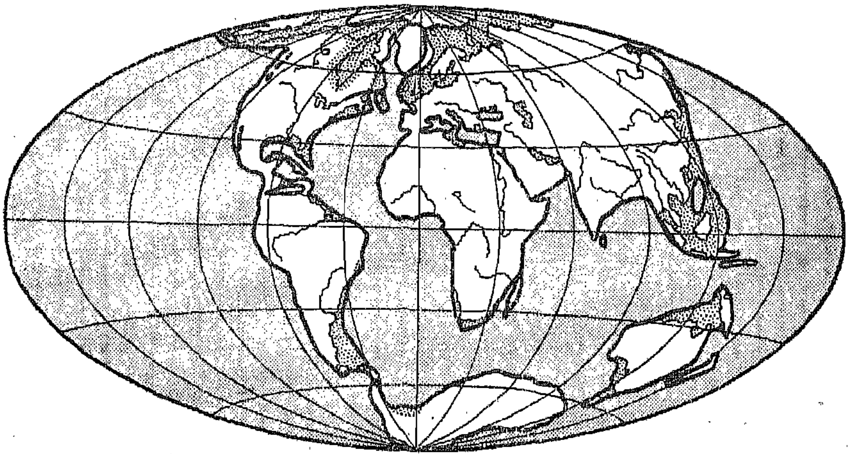
From what has already been said it might be supposed that the more or less unanimous opinion that the distribution of plants cannot properly be explained on the present distribution of land and sea which has already been commented upon implies acceptance of the theory of continental displacement, but this is not so, for there is an alternative view which, until recent times, held the field unchallenged.



Upper Carboniferous



Eocene

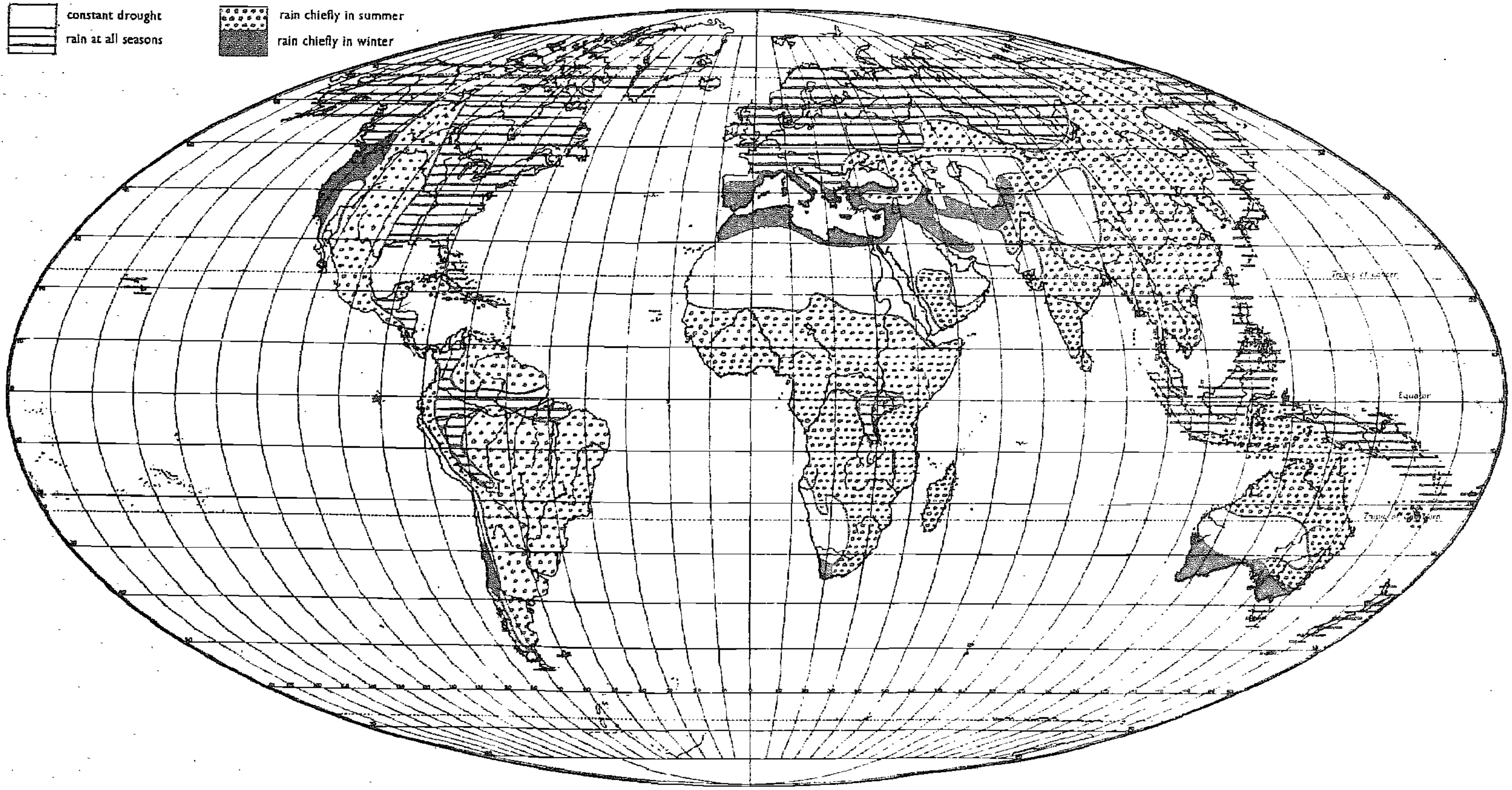


Older Quaternary

FIG. 75.—Reconstruction of the map of the world at different periods in geological history, according to Wegener's Theory of Continental Drift.
(Redrawn from Wegener, Origin of Continents and Oceans, Methuen & Co.)

PLATE 24

Map of the World showing the seasonal distribution of rain. After Bartholomew's *Physical Atlas*, vol. III.



Areas correct   Distortion increasing towards border of map.

Approximate Scale 1:100,000,000 (1600 miles = 1 inch) along Equator

on Mollweide's Homolographic Projection

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There are obviously two possible methods by which in theory sundered units may be joined. The first is by the movement of both towards one another, the second is by throwing a bridge across the gap between them (470). The first is in effect, as regards continents, the displacement theory, and the second is the Theory of Land-bridges, which supposes that there have existed in the past great additional land surfaces which served to unite the now-severed continents in various ways, and to this we must now turn our attention.

As regards direct evidence the land-bridge theory, which postulates that former huge land areas have now vanished and foundered beneath the sea, is in no better position than the theory of continental drift, for of this foundering of land masses there is no satisfactory evidence, and it would seem clear that the theory must have originated as a theory *faute de mieux*, that is to say as the only conceivable explanation of other facts. But this makes the criterion of it largely that of what can or cannot readily be conceived by the human intelligence. Until the coming of the idea of evolution human thought in general and scientific thought in particular were bounded by conceptions of cosmogony of so ponderous a traditional weight that only exceptional intelligences could become free of them. It is therefore not surprising that the idea of continental drift was not seriously entertained earlier, and in its absence the theory of land-bridges was inevitable. Even to-day tradition is by no means dead and it is the freshness of thought in the displacement theory which arouses at the same time the strong antagonism of some and the enthusiastic support of others. Unfortunately these circumstances gave to the theory of land-bridges a long freedom from criticism, and it became established so firmly that its overthrow became exceedingly difficult, though by no merits of the theory itself. Indeed it is in many respects a weak theory and there is much weight against it. The nature of this evidence has been discussed elsewhere (213, 484) and need only be summarised here in a general way.

The occurrence of marine deposits on what is now land, and the occurrence of land or freshwater deposits where there is now sea, might be taken at first sight to afford evidence of the former existence of bridges or at least of the sort of geographical changes which might produce them, but the earlier part of this chapter has sufficiently shown that the first have been the work of epicontinental seas and have no relation to the actual shapes and areas of the continents. The second, however, requires more attention since it is in fact the crux of the land-bridge theory.

There are two likely sources of evidence for the former existence of now-vanished land surfaces, the structure of oceanic islands and the nature of the ocean floor. With regard to the first it is difficult to imagine the existence of shallow water sedimentary deposits except as a consequence of the subaerial denudation of land surfaces over a comparatively long period, and hence the presence of such beds on more or less isolated islands would indicate that these were once parts of larger land masses. From time to time the discovery of deposits of this kind has been claimed but none has been substantiated and it appears to be true to say that there is still no knowledge of the existence of such beds on any islands which can properly be described as oceanic in the strictest sense. Certainly some of the high coral islands bear sedimentary deposits but these have been formed from the denudation of parts of the coral material of the islands themselves during periods of different relative elevation.

The study of the nature and formation of the ocean floor, which involves very complex problems of geophysics and geology is the most promising source of evidence for or against various theories of geomorphology and it is therefore not surprising that it is receiving special attention to-day and is itself in a state of very rapid development (119, 486, 565). In consequence only the briefest reference, to one or two of its aspects most relevant to plant geography, will be made here.

The main point is that sedimentary rocks of the sort just discussed are not the only kind of rock formations which are regarded as of a "continental" rather than an "ocean floor" nature, that is to say which are found especially associated with the floating continental blocks. All the rocks which are comprised within the term *sial* are of this kind, as well as certain related others, being derivable either directly or indirectly from the more or less sialic materials of which the primaeval continents were formed. Therefore if the presence of sialic or sialic-related rocks can be detected on the ocean floor the presence there of continental material may be inferred. It is therefore of great interest that granite (which is a sialic rock) is present in certain oceanic islands, notably in the Azores, on Ascension Island, and in the Seychelles, and that related rocks are found on Fiji and some of its neighbours. The first two of these instances arise from a long bottom elevation which runs almost exactly centrally down the middle of the north and south Atlantic, and which is called the mid-Atlantic swell. The Seychelles rather similarly arise from a less well-defined ridge which underlies part of the Indian Ocean between Madagascar and India. The case of the south-western Pacific is a little different. Here Fiji and many other of the islands contain andesite, which though not strictly sialic is nevertheless regarded as associated with continental formations, and on this basis it has been argued that the islands concerned mark the eastern edge of a once great Melanesian continent which would in effect have extended the great Australian land mass far to the east (see p. 196 above). There are thus at least three areas in which there seems to be continental material on the floors of the oceans but how far these can be regarded as traces of former land surfaces of the land-bridge sort in these positions is very doubtful. The mid-Atlantic swell for instance runs down the ocean and not across it, while the situation with regard to the south-west Pacific is still largely hypothetical. Only in the Seychelles does the case look stronger, but here the land-bridge explanation is least required because of the direction and fair proximity of the East African and Arabian coasts. Indeed it seems more reasonable to suppose that these areas, if indeed they are extensive areas of sialic rocks, are thin residual patches torn or thinned away by stretching from a continental block according to one or other of several modern theories of crustal behaviour, and if this is so the view that this may have occurred in connection with some kind of horizontal rather than vertical displacement of the continents would seem a very reasonable one.

But apart from all this the actual idea of land-bridges is less promising than would appear at first sight. To begin with the phytogeographical problems which land-bridges are particularly called to explain are mostly those of Angiosperms, and hence any bridges must be of Cretaceous or later date to be effective. Again, the list of discontinuities in Appendix B shows that in this period since the Cretaceous it would be necessary to postulate bridges in almost every direction, between America and Africa, between Africa and Asia, linking the scattered lands of the south, joining oceanic islands with some mainland, and stretching across the Pacific. In short, it is necessary largely to cover the oceans with land-bridges, and more or less contemporary ones at that. Such an assumption is unwarrantable on any grounds, including geophysical arguments, and it is no small point in favour of the idea of drift that it avoids postulating such enormous and unlikely increases in the land surfaces of the globe.

It must not be supposed from this that no land-bridges can have existed in any circumstances or time, nor even that faith in them has been entirely abandoned (231, 232) and it has already been shown that comparatively small elevations would serve to link what are now some quite widely separated areas, but land-bridges proper are tacitly meant to be land areas crossing the main oceans, and for such it can only be said that the evidence is in no case adequate. It is fair to say that many of these difficulties are realised and attempts have been made to meet them, and that few geologists would accept the bare land-bridge theory to-day without saving clauses. For instance, one view supposes that there was in the Palaeozoic a huge mainly southern continent, and that this, to use the current phrase, "broke up" in the Mesozoic, the breaking up being pictured as a differential sinking of its constituent parts so as to produce a discontinuous series of land masses. The interesting point about this is that it takes liberties with the stability of continents which are not always allowed to the protagonists of drift. There are other reasons too why land-bridges are far from being the universal remedy that they appear. One in particular is that the submergence of great extents of land will not necessarily produce the phytogeographical results actually to be observed. For instance very wide discontinuity of types will follow only if those types are completely distributed throughout the bridge before it founders and, moreover, in very constant form. Otherwise the subsidence of the bridge would have to take the most peculiar and special course to produce the observed discontinuity. These difficulties have indeed been realised often enough, and frequently, it should be noted, by some foremost authorities on distribution. Wallace (570), for instance, believed firmly in what he called the permanence of continents and would not admit the possibility of land-bridges. Unfortunately he knew not continental drift and was thus faced with the necessity of explaining the awkward facts of discontinuity largely on the basis of dispersal, and this, to say the least, is a very uneasy standpoint.

As the last few paragraphs have implied it is in relation to the problem of oceanic islands and the processes by which they may have become populated that the land-bridge theory appears in the most favourable light because of the easy opportunity it affords of regarding them as the remnants of foundered continents, from which, of course, their biota will have been derived, though as has been shown there is little or no evidence of this. It must be admitted that the theory of continental drift cannot provide so simple an explanation as this of the formation and population of isolated islands but one view is that the elevation of many of them was associated with the disturbed crustal conditions which would be expected to occur immediately in the wake of a drifting continent, from which their biota would have been derived at a time when it was still comparatively near at hand. An explanation of this sort may certainly be feasible enough for some islands, such for instance as those of the north and south Atlantic, but for others, among which the Hawaiian Islands are particularly prominent, it will hardly do, though neither, it should be made clear, will the theory of land-bridges. In these more difficult cases it may well be that the solution of the puzzle depends on knowledge not yet at our disposal.

Turning now once more to the theory of continental drift, it is not unfair to say that many of the criteria mentioned by Du Toit—that is to say the direct evidences of the theory—are very compelling. It would be presumptuous to make further comment on the inorganic arguments but it is permissible and indeed desirable to refer once more to the evidences afforded by plant geography, and of this it can be said, in the writer's opinion without fear of rebuttal, that the theory of continental drift explains the peculiarities and leading features of Angiosperm distribution more simply than any other hypothesis. By this is meant that not only is drift more likely than bridging on phytogeographical evidence, but that drift can explain the details and sequence of distribution in a way quite beyond the power of any reasonable theory of land-bridges or of the theory of distribution entirely by dispersal. The writer also believes that few will read the early chapters of this book dispassionately without coming to the same conclusion.

Nor, despite the fact that discontinuity has been so particularly mentioned, is the botanical evidence restricted to this. On the contrary there are other features in the geography of the Flowering Plants which are even more difficult to explain otherwise and it is worth while to stress these at this point. Paramount among them is the remarkable degree of underlying similarity and community between the floras of all parts of the world, which, because differences are often so much more obvious than resemblances, is seldom commented upon. There are Angiosperm floras in all the plant-habitable parts of the globe and no one of them is significantly distinct from any of the others, or so unlike them as to suggest some quite peculiar history. Naturally some have greater degrees of particularity than others, as for instance the flora of Australia, but this peculiarity is superficial compared with the degree of basic similarity, so that even in Australia we find the more prevalent families in much the same order as in other places. Even in what is perhaps the most distinctive of all floras, that of New Caledonia, the difference in this respect is comparatively little. Again, as Chapter 4 has shown, there are practically no large endemic groups of Angiosperms such as would surely be inevitable if the continents had always been as isolated from one another as they are now. And finally there is the extraordinary circumstance of the Monocotyledons, which compare almost completely with the Dicotyledons in distribution and which are almost everywhere present in the same minor proportion to them. In short the Angiosperms have spread all over the world with a degree of completeness and constancy which it may well be argued is inconceivable if the continents had never been more closely adjacent than they are now. Indeed taking all these facts into consideration it seems an almost inescapable conclusion that the Angiosperms must have achieved a great part of, and even perhaps nearly all, their distribution during a period prior to the sundering of a super-continent into its constituent parts (222).

But why, it may be asked, in view of this biological evidence, is the theory of continental drift not more widely accepted? The reply is that there are at least three important objections to it. Important at least in theory though it is to be noted that each is peculiarly unsatisfactory in some way. The first is the purely psychological objection to something which not only breaks entirely new ground but which in doing so does violence to long-established opinions. If the theory of drift is true, then much that has been written on all kinds of other topics is untrue, and there is thus an enormous inertia against the theory. Du Toit has expressed this so vividly that we cannot do better than quote his words (the italics are his), in which he says:

". . . it must frankly be recognised that the principles advocated by the supporters of Continental Drift form generally the antithesis of those currently held. *The differences between the two doctrines are indeed fundamental and the acceptance of the one must largely exclude the other.* Indeed, under the new hypothesis certain geological concepts come to acquire a new significance amounting in a few cases to a complete inversion of principles, and the enquirer will find it necessary to re-orient his ideas. For the first time he will get glimpses—albeit imperfect as yet—of a pulsating restless earth, all parts of which are in greater or less degree of movement in respect to the axis of rotation, having been so, moreover, throughout geological time. He will have to leave behind him—perhaps reluctantly—the dumbfounding spectacle of the present continental masses, firmly anchored to a plastic foundation yet remaining fixed in space; set thousands of kilometres apart, it may be, yet behaving in almost identical fashion from epoch to epoch and stage to stage like soldiers at drill; widely stretched in some quarters at various times and astoundingly compressed in others, yet retaining their general shapes, positions and orientations; remote from one another throughout history, yet showing in their fossil remains common or allied forms of terrestrial life; possessed during certain epochs of climates that may have ranged from glacial to torrid or pluvial to arid, though contrary to meteorological principles when their existing geographical positions are considered—to mention but a few such paradoxes!"

This extract illustrates a point which should be stressed, namely that the conceptions of continental structure described above, such as the sial and the sima, floating blocks and isostasy, are not peculiar to the theory of drift, but rather quite generally accepted views of modern geomorphology. That they are so apposite in view of possible drift is then distinctly in favour of that theory. This emerges in an interesting way from the consideration of the other general objections to the theory. The second of these, and the only one which approaches the scientific, is that there is not known any force which could possibly be regarded as sufficient to move the continents in the way suggested. That is to say, there is no satisfactory explanation of their movement. This objection has all too often been accepted as final, but it must be realised that at best it is only negative, and it would surely be untenable to suppose that there *cannot* be any such force. It is simply that no such force is known at present. The ordinary observer is not likely to be much impressed by such negative evidence and it has also been most appropriately pointed out (434) that this is exactly the position also with certain other geological beliefs which have been generally accepted on their circumstantial evidences, such as the sinking of land-bridges and the occurrence of the ice ages. There is no properly understood physical explanation of them either.

The third objection or series of objections is based on weaknesses in the presentation of the drift theory by earlier writers, and especially by Wegener. He, for instance, painted much too detailed a picture for the contemporary state of the theory and laid both himself and it open to criticism on matters of really unimportant detail. Probably no one among even the most fervent advocates of drift is prepared to accept the theory in the precise form of Wegener, but this cannot be considered to be evidence against the broad conception underlying it. Again, he made his chronology so definite that it is easy to pick holes in it, but this has no real bearing on the absolute likelihood or otherwise of drift. Similarly he pictured more or less constant movement of land masses over very long periods of time and the possibility of this again is controversial. He also postulated displacement of the poles, though it is not essential to the basic geophysical argument, and in doing so gave his adversaries a valuable weapon, since there are powerful arguments against this idea.

As a matter of fact this very abstruse problem of polar change is, from the botanical point of view, of some special interest in relation to the light requirements of plants, and calls for further notice on that account. It is generally agreed on the evidence available that in Tertiary times Antarctica sustained a flora of temperate *facies* (see p. 273 above) probably similar to the present floras of New Zealand and Fuegia. To-day, Antarctica, because of its position in relation to the polar axis of rotation, has very long days, and even, according to latitude, continuous daylight in summer, and very short days, or even continuous darkness, in winter. It is difficult to believe that the kind of flora which has been described could have existed in these circumstances and there would seem inevitably to have been a subsequent change of some considerable degree. There are two leading possibilities—either the length of day relation at high latitudes has altered through some such cause as a variation in the obliquity of the ecliptic or these values have remained constant. If the latter it must be supposed that Antarctica is not now in the position, *relative to the pole*, which it occupied during that part of the Tertiary, and this may be due to polar movement, or to continental movement or to a combination of the two. The more unlikely the former, the more likely the latter. In this connection it is interesting to notice the opinion, recently re-expressed by Joyce (307), that the form of the Scotia arc of islands between South America and Antarctica may be the consequence of some such movement of the latter.

Although many geophysicists and geomorphologists have felt themselves unable to accept the theory of drift some of them seem to have appreciated the weakness of their position and to have put forward theories of their own to rationalise it. These may be illustrated by references to one of them, Joly's Theory of Climatic Cycles, which to the present writer seems to indicate very clearly the direction in which a synthesis between opposing views about drift is likely to be achieved eventually, an opinion already expressed by Bews (52) who looks forward to a combination of the views of Wegener and Joly. Joly (304) supposed that in the course of time the internal heat of the earth accumulates as a result of radioactivity, and that the effect of this is to melt the sima progressively outwards till that layer of it supporting the continents and oceans becomes molten. This has two consequences—a reduction in the density of the supporting sima and a resultant sinking of the continents, with some inevitable transgression of the seas, and a rapid conduction away of the heat of the sima by the oceans and continents, so that the molten layer soon resolidifies and there begins a new cycle. This theory was propounded to account for certain major features of geological history, and especially for the repeated but long-separated periods of climatic catastrophe (glaciation), epicontinentality and mountain building. Joly supposed, in the theory, that these are the inescapable consequences of the stages at which the outer layer of the sima becomes molten. Strangely enough, however, he did not admit the possibility of continental movement to any great degree in these circumstances, despite the fact that they might on general grounds be supposed to be exactly the conditions to favour it. Because of the association of glaciation and mountain building the latest melting of the sima must have occurred, as Joly postulated, some time since the beginning of the Tertiary, so that any drift it might involve is likely to have been more or less of similar date, and this it will be noticed accords very well with the requirements of the botanical evidence which favours the view that drift was not marked or continuous till well on in the Tertiary. Thus Joly's theory, if it permitted the conception of continental displacement or drift as a consequence of one of the cyclical revolutions described, would provide an almost ideal geomorphic theory from the point of view of the plant geographer. It is therefore significant that some recent regional studies of crustal movement, such as those of Smit Sibinga in Malaysia (512) as quoted by Lam (328), clearly suggest circumstances which might have led to drift, and even to intermittent drift, at a comparatively late date. On the other hand some believe that during the Pleistocene the position of the continents was much as it is to-day (565), which suggests that had drift occurred it would have effectively ceased by that time. Holland, too, (265) has stressed the evidence that some 50–70 million years ago, a date presumably in Tertiary times, there was a widespread physical revolution and thinks that this was of a kind which might well have facilitated continental drift, while Seymour Sewell (265) believes that the Indian, Atlantic and Arctic Oceans may have been formed during the Tertiary.

To summarise, the theory of continental drift would explain plant distribution to-day to a remarkably complete degree if it could be substantiated in the following terms and made to incorporate the following points:

1. That at least at some time between the Cretaceous and the middle or later Tertiary the continents were, more or less, joined into one and were fixed in position.
2. That as a consequence of a thermal reaction of the kind pictured by Joly the sima became molten in the latter part of the Tertiary.
3. That continental drift resulted, first, perhaps, at a rapid rate and then as the sima cooled, more slowly.
4. That an immediate result of this drifting was the uplifting of mountain ranges on the forward sides of the moving masses.
5. That a later consequence of the rapid loss of heat was the onset of the glaciations of the Pleistocene.

If, as is said, a theory incorporating these points could be put forward, then it would not only explain most points of plant geography but would also reveal the main outlines of the sequence of events by which the Angiosperms have attained their present development and distribution in the world. Each point in the above summary is provided for by one hypothesis or another, and if these at present apparently divergent details could be welded into a whole, it would be a very satisfactory theory of historical plant geography.

To conclude a chapter which has in places taken us far from this subject, let us describe the position (in respect of the matters which have been discussed) as it appears to be to-day:

1. Many features in the present distribution of plants, and especially those associated on the one hand with the overall similarities of floras and on the other with the particular phenomenon of discontinuity, cannot easily be explained.
2. Three general explanations are possible:
   (*a*) That they are due solely to dispersal factors.
   (*b*) That the now separated continents were once joined by land-bridges.
   (*c*) That the continents have changed their relative positions.
3. All three of these have probably had some effect, and the question is to decide which has been of paramount importance.
4. The inadequacy of dispersal has been particularly demonstrated in Chapter 18.
5. There are grave objections to the theory of land-bridges.
6. The idea of continental drift affords a satisfactory explanation but the theory is not yet generally accepted.
7. The obstacles to the acceptance of the idea of continental drift are gradually being removed and there is a reasonable prospect that the theory will, in some final form, not only receive general support but will provide the desired explanation of many problems in the geography of the Flowering Plants.

In the latter part of this chapter attention has been concentrated upon the subjects of land-bridges and continental displacement not solely because these have a particular appeal to the plant geographer but also because they illustrate in a specially vivid way the necessary relation that exists between plant geography and these theories of earth structure and geochronology, and it is therefore very desirable to make clear here that these are by no means the only hypotheses of this kind. Certainly, as far as can be seen at present, these seem to be more directly applicable to problems of phytogeography than any others but they should not be regarded as the only conceivable explanations or allowed to exclude the consideration of many other aspects of the matter such as are conveniently summarised in a single chapter by Gutenberg (246). Nor is this all. One of the most perplexing things about Angiosperm geography is its inherent chaos, which expresses itself in the difficulty of accounting satisfactorily for any appreciable proportion of the total facts by any one single theoretical explanation of the more detailed sort. It is, indeed, as if there still remains to be discovered the key to knowledge which will convert this discordance into harmony, and while this state of affairs continues plant geographers will be wise if they are as receptive as they can be to the implications and possibilities not only of such hypotheses as have been the subject of this chapter but even perhaps of some of the more fantastic theories of cosmogony and earth-history.

CHAPTER 21

THE THEORY OF TOLERANCE

IN the last six chapters the factors of distribution were first reviewed in general and then discussed in particular. The purpose of this chapter is to consider how far and in what manner they can be made to provide a theoretical explanation of the geography of the Flowering Plants.

What has already been said makes it clear that there are certain general statements which can be made regarding the causes of plant distribution, and that these are so incontestable that they may rank as general principles of plant geography. These principles are fundamentally six and may be expressed most concisely as follows:

1. Plant distribution is primarily controlled by the distribution of climatic conditions (see Plates 2, 4 and 5).
2. Plant distribution is secondarily controlled by the distribution of edaphic factors.
3. Great movements of species and of floras have taken place in the past and are apparently still continuing.
4. Plant movement, especially in its larger aspect of plant migration, is brought about by the transport of individual plants during their dispersal phases.
5. There has been great variation and oscillation in climate, especially at higher latitudes, since Angiosperms became prominent.
6. At least some, and probably considerable, variation has occurred during the same period in the relative distribution and outline of land and sea.

Although in the light of what has been said earlier these principles need no further demonstration, there are one or two points connected with them which have not yet been adequately noted. The first is the relation between the first two principles. The facts of plant geography everywhere show that the first of these is the more fundamental and that plant distribution is basically a climatic distribution. Edaphic factors can have but a secondary rôle, if for no other reason than that they themselves are often controlled by climatic considerations. Moreover, edaphic factors tend to be distributed without much regard to latitude, whereas plants are normally correlated in range with latitude unless the factor of altitude, which is itself a climatic effect, comes into play. Actually the difference between the two factors is best expressed by saying that while climatic factors control the extent of distribution, edaphic factors control its intensity. On climatic factors will depend whether a given species shall be a potential occupant of a given area; on edaphic factors will depend whether it will in fact occupy it, and if so in what relative abundance. Climatic factors must decide whether an area is open to colonisation by a species in view of its general atmospheric requirements; its eventual presence will depend on whether or not there are habitats suitable for it. Usually the more numerous and larger such habitats are, the more plentiful within this area will the species be. Naturally other factors may also be involved, but this is a fair general statement.

Except for the third, each of the six principles comprehends one of the main factors of distribution already discussed at length, and one of the most important points is that they and the factors involved in them are of two kinds. The first two and the fourth can be distinguished from the rest as being *internal*, in the sense that they concern the inherent constitution of the plant. In the first two the aspect of constitution concerned is the physiological, and in the fourth it is the structural. Numbers five and six are *external* or extraneous, in the sense that they are no more than guides controlling the direction of effects resulting from the inherent conditions of plants. The relationships between the six principles are fairly clear and generally accepted. That between the first two has just been dealt with; that between the third and fifth is believed to be one of effect and cause; the fourth explains the mechanism of the third; and the sixth will control to a greater or lesser extent the result of the third. Indeed, taking the whole six principles together, they clearly indicate what is in effect a theoretical explanation of plant distribution, namely that it is the result of complicated plant movement or migration under the influence of climatic change, this movement being achieved by dispersal and being modified by contemporary topography, and this, with or without minor modification, is the view generally held to-day by those who are familiar with the facts and history of plant geography.

At first sight this view, which is at least one hundred years old and which may be called for convenience the Theory of Climatic Migrations, appears to be all that is to be desired, but on close examination it will be seen to be deficient in one very important and fundamental respect. It visualises plant movement; it indicates exactly how such movement may be made; it indicates the primary cause of such movement, but what it does not do is to explain why the cause (climatic change) should actually result in the movement or migration of plants. How the result can be achieved is clear, namely by dispersal. As to *why* the cause should have this particular result there is no indication. There is no conception of how and why climatic change is able to bring about plant movement by the agencies of dispersal. As it stands the theory is like a locomotive which lacks connecting rods. Climatic change may be compared with the steam power generated in the boiler, and plant movement, by means of dispersal, may be compared with the mechanical movement of the locomotive by means of its wheels, but just as without the connecting rods the first cannot be converted into the second, so the theory cannot be made to explain plant movement without some definite provision which, as expressed above, it lacks.

This deficiency is met by the tacit and therefore to such extent unsatisfactory assumption of what is in fact the conception of specific tolerance, namely the view that each and every species can exist only within a given range of external conditions, and that this tolerance to environmental values does not and cannot change so rapidly as to "adapt" itself to change in external conditions. On this assumption the species can only survive in so far as its dispersal methods are able to keep pace with the changing external conditions in such a way that its range is always that of the conditions which it requires for its development. On this assumption the necessary connecting rod is provided in the form of a rigid relation between the species and the conditions under which it can exist. This relationship prevents the species from staying where it is and modifying its existence to the new surroundings which the movement of climatic values (climatic change) has brought about.

Let it be said at once that no criticism of this assumption on the score of its probability is possible. It may be that in the early days of the Flowering Plants climatic changes were so slow and gradual that species were able to adapt themselves to them by the processes of evolution, but at any rate in more recent times climatic changes have been so rapid and so drastic as to make this suggestion in general quite untenable, and it is to these rapid and recent changes that are undoubtedly to be attributed the major features of plant distribution to-day. The point at issue is that this all-essential part of the Theory of Climatic Migrations has grown up without proper presentation and without the standing which would be its due as a properly expressed and tested hypothesis.

To remedy this deficiency the present writer published some twenty years ago a paper reconsidering the conception of tolerance and expressing it in the form of a definite theory (214). In that paper the six principles enumerated above were first dealt with, and there was then enunciated the Theory of Tolerance in the following terms:

> "Each and every plant species is able to exist and reproduce successfully only within a definite range of climatic and edaphic conditions. This range represents the tolerance of the species to external conditions.
>
> The tolerance of a species is a specific character subject to the laws and processes of organic evolution in the same way as its morphological characters, but the two are not necessarily linked.
>
> Change in tolerance may or may not be accompanied by morphological change, and morphological change may or may not be accompanied by change in tolerance.
>
> Morphologically similar species may show wide differences in tolerance, and species with similar tolerance may show very little morphological similarity.
>
> The relative distribution of species with similar ranges of tolerance is finally determined by the result of the competition between them.
>
> The tolerance of any larger taxonomic unit is the sum of the tolerances of its constituent species."

This enunciation was followed by a long discussion of the meaning and application of the theory, and, because they serve to illustrate many points of general interest to the student of plant geography, the main features of this discussion may appropriately be summarised here.

According to the theory there must be a total area which a species can, in virtue of its tolerance, occupy, and this may be termed its "potential area." Its ability to cover this area depends first upon its dispersal over the area and then upon the result of the competition it may encounter in the process. If the potential area is large, competition will tend to vary in intensity in different parts of it so that establishment will not be equally easy everywhere. A species never can or will, under natural conditions, become established outside the potential area, and the size and position of the potential area will tend to vary with change in external conditions. If tolerance is a specific character amenable to the laws of evolution and genetics, it may change in the same manner and from the same causes as structural characters, and since these latter are normally more or less closely correlated with conditions of life, some distinct relation between morphology and tolerance may normally be expected.

It is important to note that the theory as a whole visualises three kinds of changes, each with its own particular speed. First, there is the rate of evolutionary change; secondly, there is the speed of change in external conditions; and, thirdly, there is the speed of movement of the species by means of dispersal. It is a fundamental postulate of the theory that the first speed (evolutionary) is nowadays immeasurably slower than the other two, and that these (external change and dispersal) are normally comparable.

The tolerance of a species will be composed of many ranges of tolerance to individual conditions, but in practice one of these will usually become a distributional limiting factor. A narrow range of tolerance as regards one condition—say, for instance, rainfall—will control the distribution even though the tolerance to other conditions, perhaps to soil constitution, is much wider. If tolerance to a particular condition or factor is so wide as to include the whole existing world gamut of this factor, the tolerance may be described as complete in respect of it. In the theoretically conceivable case of a species exhibiting complete tolerance to all factors and conditions, its potential area will also be complete, namely cosmopolitan, but there are no species which can be cited as possible examples of this. The world gamut of most external conditions is relatively small, and, taking into account the great number of plant species, it must be presumed that many species will tend to have very similar tolerances, especially as regards one or a few factors. This is in accord with the observed facts of competition and affords a possible explanation of it. The result may be anything from the complete supremacy of one species to a balanced deadlock between two or more.

Many detailed studies in plant distribution (220, 224) suggest strongly that within any range of tolerance as a whole there are minimum, optimum and maximum conditions. Existence, in absence of competition, will be possible within the whole range, but the species will only be at its strongest, in relation to competition and also to vigour, within certain optimum figures. It also seems certain that minute differences in tolerance between species, such as are imperceptible to the ordinary human observer, may be quite critical and decisive in determining the issue of competition. Conversely, very minute differences in external conditions may be vital to the plant.

The assertion that the tolerance of a larger unit is the sum of the tolerances of its constituent species needs no elaboration except to point out that these specific tolerances need not form a continuous range of values for any or all factors. Thus the tolerances of the species of a genus towards temperature, for instance, may have wide limits but they may not cover all values between these limits. As there is usually continuous variation in climatic values, this may well lead to the potential area of the genus being discontinuous, that is to say composed of spatially separated parts. This obviously has a direct bearing on the subject of discontinuous distribution, and is only one example of the way in which the conception of tolerance impinges on all sorts of geographical problems.

The corollary to this final phrase of the theory is that the tolerance of a species will, in its turn, be made up of the tolerances of its constituent individuals, since (as the third sentence of the statement says) these individuals will vary in tolerance among themselves much as they vary in form, and it is important for several reasons to appreciate this fully. For one thing it follows that the tolerance of a species will depend on what individuals are included within it, that is to say on the taxonomic conception of it, and there is thus no necessity in connection with the theory to attempt any definition of what a species may or may not be. Any population of individuals will have its own tolerance and this will be unaffected by what taxonomic rank may or may not be given it. Again, the conception of individual tolerance is consistent with many of the results observed in the study of geographical races and ecotypes, and with much of what is now often called cytogeography (see pp. 35, 161 above). It would be out of place here to attempt any detailed appreciation of these lines of work but the reader will find a useful guide to them in three papers by Clausen, Keck and Hiesey (100, 101, 102) of which the most recent contains a summary of other investigations of the same kind. Most of all, however, the idea of the variation of tolerance among individuals is important because of the way in which it affords to populations a means of protection against the effects of alterations in external conditions. Were all the individuals of an assemblage rigidly similar in their tolerances then a serious change in some environmental value might, even if it were no more than a short-term fluctuation, have the most serious consequences, since a transgression of this rigid tolerance limit might easily result in total elimination. Individual differences of tolerance on the other hand, diversified as they are likely to be by a multiplicity of components, provide a buffering or damping effect which serves to spread the harmful effect of external fluctuation so widely over the population that only from an exceptionally severe or prolonged change is there real danger of the extinction of every member of the population even if the change is so widespread as to affect the whole of the population distribution. Some may perish but not all, the incidence of mortality depending upon such factors as the nature and direction of the external alteration, degree of exposure, stage of development, and so on.

This conception of individual tolerance may indeed be looked upon, without undue exaggeration, as one of the most vital aspects of the theory because it provides an explanation of an obvious difficulty, namely the fact that the occurrence of temporary exceptional environmental conditions does not produce an immediate wholesale effect. True, it is possible to conceive of circumstances in which this might be the result, as for example the sudden occurrence of severe frost in an area hitherto without it, but all experience shows that environmental fluctuation is, even in its most extreme form, something of a much less drastic order than this, and that individual tolerance variation is sufficient to meet it to a considerable degree. Thus a single exceptional season is not often observed to have, under natural conditions, a widely destructive effect, though some proportion of individuals may suffer. Indeed it may well be that the measure of individual variation in tolerance has become, in the course of ages, generally attuned to the amplitude of environmental fluctuation and its distribution over the different portions of the world's surface as a whole.

The Theory of Tolerance bears also on the conception of Age and Area (see Chapter 3). A species or genus may be very restricted in range for one or other of two totally distinct reasons. It may be because the unit has such a tolerance that the area occupied is in fact its whole potential area, in which case it is in at least a temporary state of equilibrium, or it may be because the unit has not succeeded in occupying more than a part of its potential area. Lack of time must always be a probable explanation of this, and thus area may be a matter of age, but only in certain circumstances. For instance, where a potential area is discontinuous, failure to occupy it may be attributable to such difficulties as those of crossing the space between the parts of the area, and this may have little or no relation to age, except that the longer a species exists the greater the chances of a successful crossing. Where the range of a unit is complete, that is to say where the whole of the potential area is occupied, area obviously can give no indication of age. It is practically impossible to say which of these circumstances prevails in any given case, and hence from the point of view of tolerance there seems little hope of deducing age from area.

It must always be remembered that change in external conditions is independent of change in tolerance except in so far as the latter is the result of the former. Hence potential area must not be regarded as something fixed but as something that fluctuates according to the distribution of external conditions. Supposing, for instance, that a species is able to exist only within certain precipitation values, its potential area at any time will be the area over which these values pertain. This clearly will vary in one way or another with the passage of time. This is no doubt a partial explanation of the well-known cases where a genus is known to have had in former geological periods a range much greater than it has to-day. Both the former extensive and the recent restricted areas may represent its potential area at the respective times. To this, of course, must be added the possibility that the constitution of the genus has altered by the extinction of species.

These are some of the points which arise in the consideration of tolerance, and there must now be considered exactly how tolerance works, that is to say, exactly how it makes movement inevitable if the species is to survive.

Imagine a species which is tolerant to a range of mean annual temperatures between 50° and 55° F. (the figure is purely illustrative), and suppose that the area over which these figures prevail, that is to say the potential area of the species, is continuous. Also suppose that its distribution is complete and that the range of the plant and the range of these temperature values are the same. Every generation, if the species is monocarpic, and every reproductive season if the species is perennial, the individuals composing it will produce dispersal units (usually seeds or fruits), and these will tend to be disseminated in all directions from the parent plants. Except along the edges of the species area, dispersal, unless very wide, will cause the units to come to rest at a point within the existing area of the species. Along the edges of the area, however, the result will be different, since, if dispersal is in all directions from the parents, some at least of the dispersal units from the outer individuals will fall beyond the specific limits, that is to say outside their necessary temperature conditions, and will therefore be unable to develop successfully. This process will continue at reproductive intervals of time as long as the specific tolerance and the distribution of temperature remain unchanged, some disseminules each time failing to develop. Now suppose that a climatic change associated with general lowering of temperature begins. Other things (such as topography) being equal, the temperature area of 50°–55° F. will move towards the equator. What will be the effects on the individuals of the species? On the northern edge of their area there will be, as climatic movement begins, the equivalent of a contraction of potential area so that some of the disseminules, not only of the outermost plants but also of those slightly further in, will fall outside the necessary conditions. Before very long the parents which were originally the outermost will be themselves outside the potential area and will therefore perish. As the climatic movement continues the belt of destruction in its wake will widen. On the southern edge of the specific area the circumstances will be exactly reversed. After a time none of the disseminules of the outermost individuals will any longer fall outside the potential area, but within it, and will mature successfully, producing disseminules in their turn. These new parents will at first disseminate themselves partly outside the area, but very soon, with the continuance of climatic change, their disseminules, too, will fall within the necessary conditions, and this process will be repeated in succeeding generations. The combined effect on the southern and northern edges of distribution, together with the similar but modified effects on other parts of the periphery, will in fact be such that correlation is maintained between climatic and specific area, and hence, since the former moves, so also does the latter.

But this movement will only result if tolerance remains unchanged while climate alters. This is the most crucial part of the whole theory, and the reason for the comparison, in the enunciation, of tolerance and morphology in relation to evolution. It is essential to remember that the rates of climatic change and evolutionary change are in present conditions unlike, and that this disparity has prevailed for a long time past. The great climatic changes which have occurred since the Pliocene period, that is to say, have occupied an almost negligible portion of evolutionary time and are entirely out of phase with the normal slow changes of evolution. That is to say, it is inconceivable that during this time evolutionary change and climatic change have continued *pari passu* but unrelatedly. Climatic change may have been the *cause* of evolutionary change, that is of the production of new forms, but these will, if they are indeed distinct forms, have by the Theory of Tolerance their own ranges of tolerance.

Actually the theory is of considerable interest in regard to the possible mechanism of species production. In the simple case described above there is a very great difference between the individuals in the van of movement and those in the rear. In the van the correlation between climate and area is never seriously upset; there is simply a gradually unfolding space into which dispersal can be effective. In the rear the conditions are quite different. Here the potential area is continually diminishing and the possibility of successful dispersal is, for many individuals, becoming increasingly small, so that the plants are constantly in incomplete harmony with their external conditions. They are, in short, in a state of environmental stress. There is still no perfect understanding of the causes of the changes in genetic constitution which are the heralds of new morphological forms, but there is plenty of experimental evidence that such changes can be induced by external means and it at least seems possible that the conditions of stress outlined may do this. This conception is a very important one. It was seen in Chapter 19 that climatic changes during the history of the Flowering Plants have been of two kinds, or rather of two degrees. There have been first of all the long-term gradual secular changes which appear to be inseparable from the circumstances of cosmogony, and there have also been the rapid and catastrophic changes associated with periods of glaciation. These may well be reflected in two kinds of species formation, an equally gradual and inherent production of new forms in which time is the main factor, and the more rapid production of forms induced by the stress of catastrophic changes. This is in good accord with the view, frequently expressed, that the families of flowering plants are of two kinds, ancient and generalised, and modern and specialised, and may indeed be the explanation of this difference.

Although, as mentioned above, many species must have generally similar ranges of tolerance, any exact similarity between species in this respect is, if only on account of the number of factors involved, likely to be improbable, and even very slight differences may be of great significance. This being so, the influence of the tolerance relation will tend to be a selective influence, so that there is a sifting out of the species affected. As a result of this a climatic change need not be visualised as leading to equal movement among all of a large number of species, but as acting differentially, so as to increase the intermingling of floristic elements. Some species will be moved at a maximum rate while others will, to a more or less marked extent, lag behind, and hence there will tend to arise the blurring of floristic boundaries which is so characteristic a feature of plant distribution in many parts of the world.

The Theory of Tolerance also provides support for the views concerning the essentially limited real function of dispersal as described earlier. In terms of the theory, exceptionally wide dispersal is likely to be ineffective, because it will tend to deposit the disseminules in regions outside their potential areas, and they will therefore not establish themselves. Moreover dispersal, as a means of increasing geographical range, will probably be of appreciable value only in cases where the species has already occupied but part of its potential area. On the other hand, the minimum powers of dispersal required by the theory are no more than will suffice to enable the movement of species to keep pace with the movement of climatic zones, and there is every reason to suppose that even the smallest degree of dispersal is sufficient to do this.

It will, of course, be evident that in the attainment of the potential area barriers of various kinds must exercise a considerable influence. The symmetrical distribution of climatic values on both sides of the equator suggests that the potential area of many temperate species may in fact consist of two parts, one in the northern hemisphere and one in the southern, and that many of the plants confined to one or other have incomplete distributions. No doubt two causes contribute to this. First, there is the barrier presented by the tropical latitudes, a barrier across which the only obvious passage is by north-and-south mountain systems. Second, there is the constitution of the floras in the two temperate regions. The flora of each has probably developed more or less completely in isolation from the other owing to the barrier just mentioned, and thus there tend to be corresponding plant forms occupying the corresponding niches in the vegetations of the two. As a result of this, competition to an intrusive species must almost certainly be exceptionally severe.

Two common observations bear directly on these points. Where a temperate genus is found in both hemispheres it will generally be noted that there are connecting species along one or other of the trans-tropical mountain systems; and southern temperate species commonly grow well in the north in circumstances where the factor of competition is eliminated and *vice versa*.

Although the paper enunciating the Theory of Tolerance and discussing its application to problems of plant geography appeared only in 1931, the conception on which the theory is based is implicit at least in many earlier writings. This has been pointed out by Wulff (608, 610), who gives several references, and especially one to the work of Engler (154). Certain more recent writers have expressed themselves even more definitely. Thoday (552), for example, writing of the genus *Passerina*, says, "the distribution of the species . . . indicates that each has a distinct physiological constitution and is specialized to a definite range of environmental factors." Salisbury, in a particularly important paper (459), makes frequent and direct allusion to the conception of tolerance, actually employing the phrase "climatic tolerance." He considers that a species has three zones of distribution: one where reproduction in full can take place; one where only vegetative propagation is possible; and one of cultivation where purely artificial reproduction is necessary. Thus he introduces the interesting subsidiary point that tolerance may not be the same in respect of all aspects of a plant's life and that, while certain conditions may suffice for ordinary vegetative growth, more particular values are necessary for reproduction. Since reproduction is the crucial stage of life, it is of course these latter values which will actually determine the distribution of the

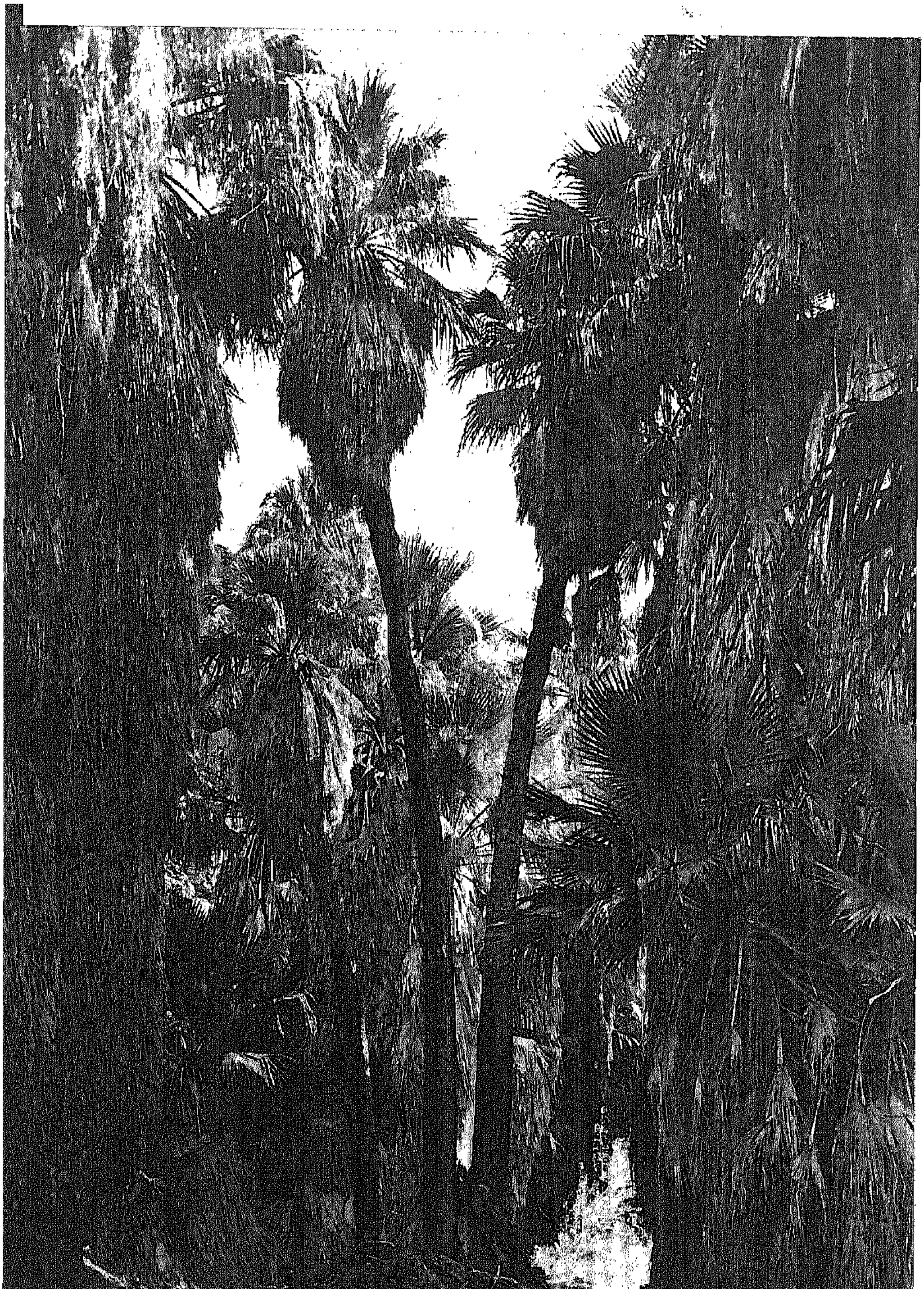

Plate 25. A grove of palms (*Washingtonia filifera*) in California

(*Photo: Josef Muench*)

species. He mentions, too, the well-known fact that many garden plants do not flower because the special conditions necessary for this process are lacking, and also states that *Ranunculus ficaria* reproduces by vegetative means near its northern limits of range. Even more interesting is his reference to *Stratiotes aloides*, of which he says that the male plants have a more northerly distribution than the females. Where they overlap there is seed production, but otherwise reproduction is vegetative. Setchell (475) records the rather similar circumstance that the marine Angiosperm, *Halophila ovalis*, has not been found fertile in the wide southern extension of its range in Australasia.

Another noteworthy reference to tolerance is that of Hutchinson (290) in a paper with the significant title "Limiting factors in relation to specific tolerance of forest trees." He refers to Schimper's statement (463) that "*the differentiation of the earth's vegetation is thus controlled by three factors—heat, atmospheric precipitation (including winds), soil.* Heat determines the flora, climatic humidity the vegetation; the soil as a rule merely picks out and blends the material supplied by these two climatic factors, and on its own account adds a few details." He goes on to discuss the distribution of many tree species in North America with special reference to their southern limits, and shows that many of these are coincident, while others intersect. In some precipitation seems clearly to be the determining factor, but others are also involved. He finally discusses various species particularly in relation to their tolerance, and gives several valuable diagrams illustrating the different points which emerge in the discussion.

The presentation of the Theory of Tolerance by the present writer (214) has been discussed at length by Wulff (608, 610), who deals with the history of the conception involved and emphasises a number of facts which in his opinion serve to support it. He also stresses the importance, not perhaps made sufficiently explicit in the original presentation of the theory, of the fact that climatic changes cause not only horizontal but also vertical plant movement, an effect that may lead to significant floristic mingling. The theory has also received lengthy consideration by Mason (369), who, working with special reference to the flora of California, has reviewed the general principles therein set out and, in addition to making them more precise in their application, has increased their number to ten by including four based upon the acceptance of the Theory of Tolerance. In so far as these afford an amplification of the earlier exposition they may well be quoted in full here. They are, as the author points out, "organized under four headings. The first deals with the general subject of the environment in a dynamic sense, including the factors of the environment and the physical basis for their modification and control. The second group deals with the responses of the plant as governed by the Theory of Tolerance and the Principle of Limiting Factors. The third group is concerned with migration and establishment, and the fourth group deals with the perpetuation of vegetation, and the evolution of floras."

A. The Environment of the Plant.

1. Plant distribution is primarily controlled by the distribution of climatic factors, and in any given region the extremes of these factors may be more important than their means.
2. Plant distribution is secondarily controlled by the distribution of edaphic factors.
3. There has been great oscillation and variation in climate, especially in the higher latitudes, during the geological past.

4. At least some, and probably considerable, variation has occurred in the relative distribution and outline of the lands and seas in the geological past.

B. THE RESPONSES OF THE PLANT.

5. The functions governing the existence and successful reproduction of plant species are limited by definite ranges of intensity of particular climatic, edaphic and biotic factors. These ranges represent the tolerance of the function for the particular factor.
6. In the life history of the organism there are times when it is in some critical phase of its development which has a narrow tolerance range for a particular factor of the environment. The distribution of this intensity span of the factor during the time the plant is in this particular phase limits the area in which the function can operate, and hence governs the distribution of the species. The narrower the range of tolerance, the more critical the factor becomes.

C. THE *MIGRATION* OF FLORAS.

7. Great movements of floras have taken place in the past and are continuing to take place.
8. Migration is brought about by the transport of individual plants during their motile dispersal phases and the subsequent establishment of these migrules.

D. THE PERPETUATION AND EVOLUTION OF FLORAS.

9. The perpetuation of vegetation is dependent first upon the ability of the species to migrate, and secondly upon the ability of the species to vary and to transmit the favourable variations to their offspring.
10. The evolution of floras is dependent upon plant migration, the evolution of species, and the selective influences of climatic change acting upon the varying tolerances of the component species.

More recently the theory and, particularly, the principles of plant geography associated with it have been made the subject of an introductory chapter by Cain in his *Foundations of Plant Geography* (74), the remainder of the book consisting, to quote the author's own words, "in part, of an amplification of these principles with illustrative data and discussion, and such additional materials as compose the framework of plant geography . . . conceived as an explanatory science which attains its unity and justification by abstracting and synthesising from the contributions of more specialized sciences."

Cain begins with a further statement of principles, which besides incorporating all those of Mason's extended presentation, increases the total number to thirteen by expressing more explicitly, and thereby rightly emphasising, certain points which hitherto were more or less implicit, namely, that biotic factors may be of importance; that the environment is holocoenotic; and that tolerances have a genetic basis. The first of these is extracted from the principle that edaphic factors play a secondary part in plant geography. Biotic factors are not capable to any appreciable extent of influencing climatic conditions, but they may have a profound effect on the substratum and thus become, at second hand, edaphic factors. By the statement that the environment is holocoenotic is meant that its various factors react upon the plant life in concert and not independently, that is to say they react upon or qualify one another at the same time. From the discussion accompanying this statement it seems clear that its main purpose is to emphasise the dangers of deducing causes and correlations on insufficient grounds, and to this end it is valuable, but it involves very complex problems as yet far from fully understood, and it is doubtful whether the clarity of the presentation of principles is enhanced by its particular mention. The principle that tolerance has a genetic basis, which, as Cain states, is due to Mason, is of special interest here because it is the essence of the Theory of Tolerance, and indeed its statement is very close to that of the third sentence of the theory. Besides these additions Cain's presentation of principles makes much more clear the point that the different ontogenetic phases of a plant may have different tolerances. This is a very important conception closely related to the subject of phasic development noticed on p. 375 and is valuable because it adds an extra variable, namely the age of the individual, to the interaction of plant and environmental factor, and this in turn gives a time component of great theoretical significance and capable of widely spreading the incidence of harmful factors.

The Evidences of Tolerance

The Theory of Tolerance, it has been clearly shown, is intimately related to various evolutionary theories and shares with them the inevitable limitation that because of the immense time values involved no direct experimental proof is possible, and evidence must be circumstantial.

Actually the onus of proof is but a light one. The theory is built up on a generally accepted assumption of standing, and it may therefore be said that the reasons for the assumption may rank as evidence for the theory. These reasons are no more and no less than the observed facts of plant distribution as a whole and the impossibility of explaining them on any other basis, and the main thesis of the theory may therefore be considered to be upheld by the whole array of facts contained in the earlier chapters of this book.

As enunciated, however, the theory particularises the general assumption in various ways, and it is desirable to deal shortly with certain facts which support these more detailed opinions.

There is first the case of garden plants. These are habitually classified as hardy, half-hardy or tender, and there are no known instances of a plant departing from the behaviour which such terms imply. By half-hardy is meant roughly a limited tolerance to conditions of severe cold such as must be met by protection in the winter in such latitudes as those of Britain, or by germination in artificial heat of some kind. The point is that this half-hardiness is obviously a specific character, and a plant with such tolerance relations does not lose them on being transplanted from its native place to some other country. Moreover, this is a general character of the individuals of the species, and we do not find there is appreciable difference in tolerance between different plants. It may be that under cultivation some individuals may seem more resistant than others, but this can always be explained either by individual tolerance variation or on the grounds that the conditions under which the species is growing are slightly different.

What is true of individuals may, however, not be true of the different strains of a species. Cultivated strains vary greatly in their tolerance, some being much more resistant than others to cold or other unfavourable conditions, and it is but one aspect of the art of gardening to realise which are the appropriate strains to grow in varying circumstances. This, however, is exactly what might be expected according to the theory, because the strains are genetically distinct from one another and may be compared with incipient species, and their differences in tolerance are almost certainly reflected in their gene complement.

It may be urged that reference to cultivated plants is undesirable because of the artificial conditions in which they grow, but this really only increases their value as evidence, because the essential feature of cultivation is the removal of competition, a factor which always tends to obscure the relation of plants to external conditions in nature. In addition cultivated plants illustrate most vividly the way in which new forms can be induced by external means. It is true that cultivation may lead to an evolutionary change which in nature would have taken immeasurably longer, but this again is only in accordance with the theory.

What is true of the climatic portions of a plant's tolerance is also true of its relation to edaphic factors, and this also is commonly illustrated in horticulture. Every gardener knows that different plants need certain soil conditions and will tolerate no others, and that to grow plants otherwise is to court disaster. Here, again, closely related species may differ in requirement, but the individuals of the same species or strain do not do so, except, of course, within the limits of their tolerance variation.

Both aspects of tolerance are combined in the general difficulty which is experienced in cultivating certain plants. Many most desirable garden plants either will not grow in gardens or glass-houses or only do so clearly under protest, and the explanation of this can hardly be other than that the resources of the cultivator are insufficient to provide the plant with the conditions which it needs. The greater the number and variety of plants to be cultivated, the greater the variety of facilities required for doing so. The scope of the ordinary outdoor gardener is comparatively limited compared with that of one who has a whole range of glass-houses, each reproducing some special condition, at his disposal.

One special aspect of this is of particular interest. Practical growers often believe that in the special circumstances of their work it pays to obtain the seed of a given species from a particular source because this seed suits their special conditions and place of cultivation better than any other—that is to say that this seed produces plants more in harmony with the conditions available. At first sight this may seem to cut across the thesis that all the individuals of a species have the same general tolerance, but it actually affords one of the most interesting confirmations of it. As has been shown by experiment, the state of affairs described is generally due to the fact that the "species" comprises two or more strains, indistinguishable by visual characters but having definitely distinct ranges of tolerance, exactly the situation envisaged in paragraphs three and four of the theory (see p. 363).

Another important line of evidence is afforded by the subject of "acclimatisation." This, again, appears at first sight to be against the theory, but it can actually be explained quite simply in accordance with it. Species which do well in cultivation under conditions different from those in which they are found in a wild state are often supposed to have modified their external relations in conformity with their new surroundings. This is an unnecessary explanation. It has been shown that many species do not, for various reasons, occupy in nature the whole of their potential areas, and this means, in terms of the theory, that their tolerance to certain external conditions may be much wider than appears from a study of their natural ranges. If this is so, then species may be grown artificially, especially in absence of competition, under conditions which do not exist in their natural habitats, because such conditions may be well within their tolerance, although this fact is not apparent in nature. For instance, many South African plants can be cultivated out of doors in Britain. This does not necessarily imply that these species have altered their tolerances to accord with conditions in this country, but is explained on the assumption that such conditions are within the tolerances of the plants in question, although for reasons of topography or competition this is not apparent from their distributions in their native countries.

It is probable that many and perhaps all the supposed examples of acclimatisation are of this kind, and it is significant that many authorities have expressed the view that there is no such thing as real acclimatisation in the sense in which it is popularly meant. Hooker (271), for instance, says, "the fact now universally conceded by all intelligent horticulturists, that no plant has been acclimatized in England within the experience of man, is a very suggestive one. . . ."

It is perhaps natural to think of acclimatisation as primarily a process by which plants may be grown in countries in which conditions are more rigorous than their own, but it is important to remember that the reverse is also true. Van Steenis, in the second part of his study of the Malaysian mountain flora (529) has brought together a great deal of scattered information about the results of plant introduction and transplantation in that region, including a lengthy quotation from two papers by Ridley on acclimatisation (447). This makes abundantly clear that the responses of the plants concerned to their changes of circumstances are, as would be expected in terms of the Theory of Tolerance, extremely varied. Some northern temperate plants, such as *Digitalis purpurea,* will do well in Malaysia, provided they are planted at sufficient altitude, and some local montane species will grow well, at least for some years, when transplanted to the lowlands, but in the great majority of cases the change is detrimental, and the plants either fail to hold their own, or persist in a reduced and unreproductive state. Two points of special interest in relation to the discussion on the true function of dispersal, in Chapter 15, are that certain mountain species which are habitually and normally dispersed downwards do not become established below certain altitudes, and that among the temperate plants which do less than usually well are some familiar northern weeds, and many well-known northern garden plants.

Although considerations of hardiness and acclimatisation usually involve cultivated plants, there is an increasing amount of work on these problems in relation to wild plants. We have already mentioned one such (487), and another is the paper of Dexter and others (132) in which an interesting attempt to estimate frost resistance quantitatively is described. Of particular interest and importance, in that they bear very directly on the conceptions of the Theory of Tolerance, are also two papers by White, the second being largely a reprint of the first (586, 587).

White begins by referring to the common horticultural practice of using seeds collected from towards the northern limits of specific ranges to give the most cold-resistant seedlings, and instances the case of the black walnut (*Juglans nigra*). In this plant the individuals native to the southern States like Texas and Alabama are said to be incapable of living in such northern States as South Dakota and Minnesota. There are other cases of the same thing too, and there is distinct evidence favouring the belief that varieties, strains and geographical races, within species, vary considerably in their ability to resist cold (that is to say, in their tolerance to that external condition). White refers to de Candolle (87) in this connection, who finds no indication that perennial species have become adapted to greater cold and have thus extended their ranges northwards within the historical period, despite the fact that their seeds are continually being carried northwards. He quotes de Candolle's own words in which he says, "Periods of more than four or five thousand years . . . are needed apparently to produce a modification in a plant which will allow it to support a greater degree of cold."

White himself believes that the walnuts from the northern States may differ from those from the southern States by a gene, or perhaps a series of genes, that determines their ability to withstand different winter temperatures but in no other way expresses itself, at least so far as external characters are concerned. In other words, he supposes there may be two or more walnut genotypes indistinguishable at sight but restricted geographically by the nature of their tolerance to cold, and thus visualises exactly one of the conditions postulated in the enunciation of the Theory of Tolerance. He thinks it probable, moreover, that many tropical and warm-temperate species give rise, by mutation, to individuals much more cold-resisting and that these remain for the most part unrecognised because they occur and grow under conditions where the character in question could not be expressed. If this is so, then the Pleistocene glaciation would have a sifting effect, some genera being able to continue living in what would appear to be more rigorous conditions, while others would be destroyed there, only later re-immigrating from the south as they produced more hardy genotypes by mutation (361, 362). He mentions a number of plants which, having a wide north-south range, are known to have hardy and less hardy forms, and also points out that if a species is restricted in its range by conditions other than temperature it may in fact be much more resistant to cold than its natural range indicates. Also, since some wide-ranging species are apparently without different forms, species may clearly be of two types as regards their resistance to temperature. In one type all the individuals can exist over a wide range of temperature, but in the other the species is composed of numerous groups, each with its particular temperature range, although these groups are indistinguishable morphologically. Finally he refers to a number of species which occur over a wide range of temperature, such as *Tillandsia usneoides*, *Asimina triloba* and *Nymphaea odorata*, and to species which are tropical in natural range but which on cultivation prove to be unexpectedly hardy. Among these latter he cites *Leitneria floridana*, *Gleditsia aquatica*, *Lavandula spica*, *Yucca filamentosa*, *Maclura pomifera*, *Magnolia grandiflora*, *Hamamelis vernalis* and *Nymphaea mexicana*.

In a more recent paper White (588) takes his conception of tolerance to temperature, or cold and heat susceptibility, which he believes has been proved to be hereditary, rather further. He considers that mutation towards increased cold resistance has taken place in many plant groups irrespective of their geographical or climatic locations, and that in consequence many units will be mixtures as regards cold and heat tolerance. Temperate as well as tropical species give rise to temperature tolerance mutations in either direction, but in temperate regions those towards cold susceptibility tend to perish. Hence, one would expect to find, outside the tropics, only mutations of greater cold resistance, while within the tropics there would be cold-resistant as well as cold-susceptible individuals, although these would be indistinguishable. His paper ends with several tables incorporating experimental observations on cold resistance, including one of species which are known to have strains and varieties differing in this respect.

What is usually looked upon as incomplete acclimatisation is also explicable in terms of the Theory of Tolerance. There are various exotic species for example, such as the myrtle (*Myrtus communis*) and the bay (*Laurus nobilis*) which maintain themselves successfully in cultivation in various parts of Britain until some particularly severe climatic condition destroys them. One explanation at least of this is that conditions in these places are, in general, within but only just within the tolerance ranges of the species concerned, so that any excessive departure from the mean will pass outside them, and since the conditions in which the plants are living are so marginal, their individual variations of tolerance (see p. 364) will be insufficient to meet the crisis, and they will, unless protected by some particularly favourable circumstance of local situation, perish.

But the conditions under which the plants referred to are in cultivation are not widely different, except possibly for the absence of space competition, from the natural environments of many individuals on the edges of wide distributional areas, and there is much evidence that life for these plants is something rather different and more rigorous than that of their fellow plants in the more central parts of the range. For many of these latter conditions are sufficiently near the centres of their ranges of tolerance to allow for a good deal of oscillation in one direction or the other without much risk to the plants, but for the former the crucial environmental values are so near one end of the tolerance gamut that much less oscillation is likely to result in a situation which is insupportable.

The conception of ecesis, or "adaptation to environment," also infers the application of the Theory of Tolerance. Many species have a peculiar and particular morphological structure which, so far as can be seen, enables them to inhabit certain equally definite types of habitat or to live under equally definite conditions. It is generally believed that these structures have the effect of thus restricting the species possessing them. This is tantamount to saying that these species can exist only in these special habitats or conditions, at least while their peculiar morphology persists, and this in turn is equivalent, in fact at least, to an acceptance of the main thesis.

Next, the early researches of Klebs on phasic development in plants, and their subsequent great elaboration by Lysenko and other Russian workers (616) in connection with the vernalisation of seeds, have a very direct bearing upon the conception of tolerance. Lysenko's work and views have now been presented in the form of a theory of which the most important and apposite portions are as follows. Lysenko believes that the growth of a plant is not a single and simple process of increase in quantity but is in fact made up also of a series of stages at each of which changes of a qualitative nature occur. These two he distinguishes as "growth" and "development." The two may go on dependently or independently and plants may show rapid growth but slow development, slow growth but rapid development, or rapid growth and rapid development. The culmination of the life of the plant is the production of ripe fruit, and this particularly is believed to be achieved only by the fulfilment of each of a number of developmental stages. Moreover, these stages always proceed in one order and no stage can be initiated until the proper preceding one has been completed. Finally, the most important postulate from our point of view is that different stages of development of the same plant require for their completion different external conditions.

For any detailed account of vernalisation the reader must refer to other works, of which perhaps the most convenient are the Bulletins of the Imperial Bureaux of Plant Genetics (376, 590, 615, 616) and the symposium by Murneek, Whyte and others (397) in which reference to much other literature will be found, and to the excellent review of the subject of phasic development in plants by Whyte (589), but a very brief account is of sufficiently direct relation to geographical problems to warrant inclusion here.

The time that it takes for an individual plant to pass from the condition of a dry seed to that of producing ripe fruit—that is to say, the time which must elapse between sowing and reaping—obviously depends (on the old view) upon the rapidity of growth, but according to the theories just described it depends more accurately upon the time occupied by each of the developmental stages through which the plant has to pass during its life. In the ordinary way much of the time is occupied by the period between sowing and the emergence of the seedling above ground. According to the modern view this period is in fact one of the developmental stages and during it the seed must be provided with certain definite conditions, and until these are fulfilled it will not proceed to the next stages of development. In theory, then, if the seed's requirements at this stage can be discovered, it should be possible to provide the seed with them before it is sown. In other words, it should be possible to make the seed pass through this initial stage in development before it is put in the ground, so that when it is so planted it will almost immediately germinate. This has actually been done with a number of crop plants, especially some of the cereals, and is the process known as vernalisation. Vernalised seeds therefore take a shorter time to come to fruition after they are sown, and it need hardly be said that this is a consideration of the utmost importance. Especially is it so in countries where the latitude gives so short a growing season that many crops cannot reach maturity in the time available. If the growth period can be shortened, then many crops may be grown that would otherwise be impossible. This state of affairs prevails over much of Russia, and this is the reason why vernalisation and related problems have received so much attention from Russian scientists. It should perhaps be emphasised that vernalisation does not in any way alter the developmental necessities or stages of the plant. Its value lies in the fact that it permits the first stage of development to be carried out when and where required and before external conditions allow of ordinary sowing in the field.

The importance of these theories and of vernalisation to the Theory of Tolerance is the very important supporting evidence they provide that the individual plant and also each species as a whole require certain perfectly definite external conditions for their development, and that without those particular conditions they cannot mature. There are, of course, plenty of other indications that this is so, and the special importance of Lysenko's work is in the demonstration it affords that the life of the plant is divided into a number of stages each of which not only requires exact external conditions but more often than not quite different external conditions. This means that different external conditions will be crucial to the plant at different stages in its history, and its tolerance must be something even more detailed and exact than appears at first sight. For instance, according to the researches described, the first stage in development is intimately connected with temperature and moisture values, while the second involves more deeply than anything else the factor of light.

Finally, there is the belief widely held by palaeobotanists, and the basis for much of their hypothesis and determinations, that the occurrence of fossils similar to or identical with living plants indicates that the conditions under which they existed were similar to or identical with the conditions under which their modern counterparts exist to-day. This opinion has already been mentioned, not only in Chapter 14 but also as one line of evidence for climatic change in the past. It is true that there is little direct evidence for the view, but it is nevertheless generally accepted in broad outline. It is important here because tacitly, if not admittedly, it is based upon the primary postulate of the theory, namely that the relation of a species to external conditions is a character of that species and that it may persist unaltered as long as morphological features persist. Actually it will be realised that this belief involves an even more rigid outlook than is required by the theory, in that it does not allow due latitude for the *possibility* of tolerance change without morphological change during time of evolutionary magnitude.

Summary

From the discussion of the Theory of Tolerance in the foregoing pages the following three major conclusions emerge.

First, the main thesis, that any species shows a definite range of tolerance to external conditions at any given time is scarcely to be denied, because the whole picture of plant distribution is so intimately related to the distribution of external factors that no other view can reasonably be maintained.

Second, supporting evidences of this, if they are needed, are furnished by the behaviour of plants in cultivation; by the non-occurrence of "acclimatisation"; by the whole conception of "adaptation to environment"; and by such matters as phasic development and vernalisation.

Third, certain more detailed aspects of the application of the theory are more debatable. In particular the value of the theory as an *explanation* of phytogeographical facts stands or falls by the subsidiary hypothesis which postulates that environmental change has, at least during the more recent past, been more rapid than change in tolerance or morphology, or, in other words, by the view that progressive adaptation to external change has not had time to occur *in situ*.

Clearly the problem here involves the past as well as the present, and it is to palaeobotany that we must turn in search of evidence. This is not far to seek. The history of the British flora since the latter part of the Tertiary period amounts, by itself, to almost conclusive evidence in support of this thesis. It shows clearly that since Pliocene times species have altered but little morphologically, yet in the same period there have been drastic changes in climate and environment. It is surely beyond the bounds of reasonable probability to suggest that tolerance has varied coincidently with and proportionately to these changes, but has been virtually entirely unaccompanied by morphological change. Were this indeed the case it would inevitably be betrayed, either rarely or more commonly, in the habits and habitats of living plants. In fact all these, as has been demonstrated in the last few pages, point to the reverse, and this being so, this second and more particular postulate of the Theory of Tolerance may also be claimed to be the truth.

But it is this particular part of the general theory which converts the whole, at least as regards plant geography, from a mere conception to a means of elucidation, because, if it is accepted, it is possible to construct in the way indicated in the earlier pages of this chapter a general explanation of the facts of plant geography and, as will be done in the next and final chapter of this book, to weave into one single pattern the many diverse and separate threads of the subject.

CHAPTER 22

CONCLUSIONS

It is the task of this final chapter to attempt a synthesis of all that has gone before and to present to the reader a brief but comprehensive summary of the processes and events which have led to that state of plant distribution observable to-day. On first considerations such a task may, with reason, seem almost impossible, so great and multifarious is the mass of fact and theory to be taken into account. But by carefully sorting and sifting the material a gradual outline emerges, and this outline becomes clearer with every increment to our knowledge. The form which that outline takes has been made sufficiently apparent by the discussions which form so large a part of Chapters 15 to 21, and from these, reinforced by the innumerable facts cited in earlier chapters, it is possible to paint a picture which may claim at least some degree of completeness.

First and foremost we must visualise the constant production of new forms (the taxonomist's species) by the processes of evolution. This is as it were the primary determinant of the picture; it is the medium in which it is painted. This must be so because the very appearance and development of the great group of the Flowering Plants is an expression of it. It is the fundamental cause of the geographical facts which we observe. The picture must therefore have as its background the historical development of these plants, and this, in so far as it has been revealed, can be described fairly shortly.

Some time in the middle or later parts of the Mesozoic epoch there arose, presumably from some already existent type of seed-plant, a group of plants characterised by possessing special closed structures known as carpels, and having other associated features. Thus there came into being the group of plants—the Angiosperms or Flowering Plants—destined to become the dominant vegetation throughout the land surfaces of the globe. Of this actual origin very little is known. There are indications here and there in the rocks of what may be regarded, with varying certainty, as forerunners or ancestral types, but the Flowering Plants proper appear with bewildering suddenness in the deposits of the later Cretaceous. In the horizons below this they are few; in this and succeeding horizons they predominate to a greater or lesser extent and indeed almost at once attain that position in the general vegetation that they hold to-day. The reason for this sudden appearance is not clear, but it is enough to know that the Flowering Plants have been the dominant world group since the end of the Mesozoic era. For the reasons which have been explained in Chapter 14, caution must be exercised in making deductions from the fossil record, but this and other evidence certainly suggests that the earlier Flowering Plants were mostly woody plants living under fairly moist and rather warm conditions. The great herbaceous families of to-day, associated as they so often are with extreme climatic conditions, such as lack of water and severe cold, are practically unrepresented in the earlier parts of the fossil record of the Angiosperms, and on this ground at least may be considered as a later development, though we must not forget that their absence from the record may be due to causes other than their non-existence.

This is in accordance, moreover, with what is known of the climates of the past. There are cogent reasons for believing, and it is generally accepted to-day, that the later Cretaceous and all but the latter part of the Tertiary period were a time of relatively constant or but slightly fluctuating climates, characterised by genial, moist conditions varying little with the passage of time and associated with a minimum of relief on the world's surface. The Angiosperms, then, may be pictured as originating and slowly diversifying for millions of years, comparatively little affected by changes in their external circumstances, and it is believed that during this period the main outline of the group as it is seen to-day was determined. It was, as has so frequently been said, an age of generalisation—an age of natural evolution by the inherent processes of change with time.

During this period there is little doubt that the distribution of the Flowering Plants was also far more generalised than it is to-day. Temperature and other climatic gradients were everywhere more gradual, and there is reason to think that what are now called temperate conditions, with their accompanying vegetation, reached almost if not quite to the poles. In terms which have been frequently used above, potential areas were probably much larger, much more extensive, and their attainment was much less impeded by barriers. Mountains were lower and their climatic effects less pronounced. In addition there is a general belief that the land surfaces of the globe were less scattered. As to this last belief, it is only the explanation which is contentious. An older school believes in the former existence of connecting land surfaces which have now disappeared. A more modern belief is that the continents have drifted away from one another. Whichever is correct—and there is an ever-increasing movement towards the latter view—it is generally accepted that geographical isolation, which is the direct result of the separation of land-masses, has increased to what may be regarded as a maximum to-day. With this increasing isolation came, inevitably, local specialisation by the effects of segregated and isolated evolution, and this was probably the first kind of specialisation superposed on the earlier generalised distribution of the Flowering Plants. All this time the distribution of plants was being attained almost entirely by spread in all directions by means of dispersal, this dispersal being directed and controlled by external factors only to a minimum extent. It may, indeed, be described as essentially a period in which this newly evolved group of plants multiplied, and in doing so established something like a geographical equilibrium with the fairly constant external conditions. It was a period of steady and widespread colonisation of the land surfaces of the globe by a new and superior type of vegetation.

It is no exaggeration to say that towards the end of the Tertiary epoch the picture changed in almost every respect. At that time causes of which little is known brought on one of the periodical catastrophic periods which there seems little doubt have been an intermittent feature of all past time. The catastrophe effectively consisted of a drastic and, in a geological sense, sudden alteration in the temperature relations of the world's surface, a change which brought in its train all kinds of minor and secondary variations. It culminated in what is called a glacial period during which, probably for the first time in the history of the Angiosperms, glacial conditions developed at sea level near the poles. It is possible that equatorial temperature values were but little affected, but, whether this is so or not, it is certain that the main result of the change was to telescope up the latitudinal zonation of climate. That is to say the gentler gradient from the equator to the poles was replaced by a steep gradient culminating at higher latitudes in what are now called arctic and antarctic conditions. From the point of view of the vegetation this meant a marked diminution in the areas available for the different sorts of plants and the diminution nearly everywhere of the average size of potential areas. It is unlikely that the effects were felt everywhere equally. In some parts of the northern hemisphere, for instance, the effects of the polar ice-cap were felt far less than elsewhere, but it is safe to say that nowhere was its influence entirely negligible.

This great climatic change was heralded or anticipated by a period of intense mountain building such as has also been an intermittent feature in world history. This process is generally associated more particularly with the Miocene period, and from it date practically all the great mountain systems of the world to-day. Their effect on the climate also was, quite apart from the subsequent glaciation, immense. Not only were appreciable areas of the earth's crust raised into colder layers of the atmosphere but, even more important, the newly elevated mountain ranges intercepted the moisture-laden winds from the oceans and condemned many parts of the interior of the continents to aridity. These changes in turn brought alterations in all sorts of other climatic aspects, such as those of pressure and wind, and every kind of external condition for plant life suffered some modification. It may well have been in direct association with these orographic and climatic changes that changes in the distribution of land and sea were especially notable, and there is even some reason to suggest that continental drift and displacement may have been an essential feature of this period, and even perhaps was initiated then rather than earlier.

The effect of all this on the Flowering Plants was profound. Everywhere their long-familiar world and surroundings were changed, and survival in the face of such disasters became the main theme and problem of their life. Those, for instance, living at the higher latitudes were faced, very likely for the first time, with the problem of frost, a danger which it can scarcely be doubted they were unequipped to meet. Moreover, their potential areas were everywhere being moved under the influence of climatic change. Rarely could this movement be unaccompanied by change in area, and with the general shrinking of the more genial parts of the world there was an almost inevitable general tendency to shrinking of their potential areas. More than this, some of them no doubt were completely eliminated. Everywhere conditions of stress as between plant and environment became inevitable. These were least, no doubt, in the equatorial regions, and it is noteworthy that it is the vegetation of this zone which to-day is considered on quite other grounds to be the most primaeval, but they must have been felt to some degree almost everywhere.

There can be little doubt that this had a profound effect not only on the results of evolution in the Flowering Plants but also, it may be, on the processes of evolution themselves. No longer can evolutionary change be pictured as something inherent and perhaps unrelated to external conditions. No doubt this type of evolution continued, as indeed it must, but the changes which it produced were henceforth to be judged by the stern test of practical success. Such changes as contributed appreciably to increasing the correlation between plant and environment were effective; those which had no such value, or which, owing to external conditions, may have had an opposite import, were ineffective. There thus arose quite a different conception of evolution: the conception of something which was capable in certain circumstances of meeting the dangers to which the plants involved were exposed. Similarly the factors of distribution took on new rôles and new values. The potentiality for dispersal became, with the increasing heterogeneity of external conditions, of less significance. Range of tolerance, on the other hand, must have increased in importance. Distribution of land and sea became a matter of great moment, determining as it did the directions of possible retreat from danger. Changes of climate not only enforced migration but also partly at least determined its direction.

It is perhaps permissible to summarise what has been said by asserting that while in the pre-glacial portion of their history the Flowering Plants were the masters of their environment, in the sense that they were probably, to some extent at least, in equilibrium with it, their post-glacial history saw the development of the reverse state of affairs. No one general feature of plant development and distribution since the Pliocene is so prominent as the marked lack of equilibrium between vegetation and its environment. This must not be taken to mean that many plants are not peculiarly and beautifully in harmony with their surroundings. This fact is rather to be emphasised as indicating how far from general correlation of this kind is.

Returning to the difference in evolution mentioned above, there is ample evidence that mutation, which is so often the physical basis of new forms, can be induced at unusual rates by the application of certain external factors, and especially by changes in external factors. It can scarcely be denied that the changes consequent upon the Pleistocene glaciation constituted such influences and that they may thus have greatly accelerated the production of new forms by this method. The species constitution of some genera, especially, be it noted, those living in what were once glaciated regions, can indeed hardly be explained on any other basis.

But no matter what the aspect, the constitution of groups as well as their distribution everywhere reflects the disastrous result of the ice ages. The extraordinary development of many herbaceous types, and especially of those with well-marked methods of perennation, seems clearly to be correlated with a distribution of climatic conditions such as would put a premium on the possession of these features. In particular, perhaps we may mention many semi-desert families and genera, as well as many constituents of the more northerly temperate or subarctic zones. Again, it is probable, as has been shown, that the arctic flora and to a certain extent the alpine flora as known to-day are to be regarded as a consequence of the glacial ages. Yet again, there is clear evidence that this time brought in its train extensive annihilation of plants in many parts of the world. That, for instance, is the generally accepted explanation of the poverty of the European flora (as distinct from the purely Mediterranean) compared with that of eastern North America and eastern Asia, and there are many other examples.

No longer then is the development of the Flowering Plants something that is proceeding with a slow, stately, and inevitable progress scarcely modified by the more detailed aspects of environment. On the contrary, to-day this development must be visualised as something everywhere controlled by factors beyond the response of the plants themselves. As with evolution, so with distribution. The distribution of plants to-day gives every evidence that it is in a state of almost complete flux. The movement of species and of floras over the world is everywhere being forced upon them by the exigencies of environmental change, and everywhere the plants can survive only by keeping pace with this movement, or by giving place to new forms less critically affected by these conditions. As has been said, all these influences appear, as might be expected, to be expressed least in the equatorial regions and, conversely, are most marked in the higher latitudes, and this is in accord not only with the story which has been outlined here but also with the assumptions of plant relationship and phylogeny based upon and derived from other sources.

In a word, the distribution of plants to-day unquestionably suggests that the Flowering Plants are recovering from a catastrophe, and that they are actively in process of reconstituting that generalised balance or equilibrium between vegetation and environment which has been pictured above as the outstanding feature of pre-glacial plant geography. So far the period of recovery (if, indeed, it is one of absolute recovery) has been very short and one can only be amazed at the progress which the plants have made in the course of it. Whether it will continue at its present rate to its culmination without setbacks or whether fresh disasters are still to come cannot and will not be revealed, but that eventually, though perhaps only after the passage of enormous time, such result will be achieved can scarcely be doubted. Whether the Angiosperms will still be recognisable or whether they will, before then, have given place in the process to some still more highly developed group is a question which admits of no answer now.

APPENDIX A

Statistics of the World's Land Surfaces

If the latitudinal and altitudinal zonations described in the early pages of Chapter 2 are modified, for statistical purposes, into simpler and rounder figures, it is possible to obtain from a paper by Murray (398) a useful and reasonably accurate mathematical impression of the proportionate distribution of the more important climatic types of vegetation at different latitudes.

Let it be assumed then for this purpose that latitudinal zonation is expressed sufficiently accurately as follows:

0°–20°	Tropical;
20°–40°	Subtropical and warm temperate;
40°–60°	Temperate;
60°–80°	Arctic and antarctic;

and that altitudinal zonations may be set out in the following scheme:

In the tropical zone	0– 3,000 ft.	bears	tropical vegetation.
	3,000– 6,000 ft.	,,	subtropical vegetation.
	6,000–12,000 ft.	,,	temperate vegetation.
	12,000–18,000 ft.	,,	arctic-alpine vegetation.
In the subtropical zones	0– 3,000 ft.	bears	subtropical vegetation.
	3,000– 6,000 ft.	,,	temperate vegetation
	6,000–12,000 ft.	,,	arctic-alpine vegetation.
In the temperate zones	0– 3,000 ft.	bears	temperate vegetation.
	3,000– 6,000 ft.	,,	arctic-alpine vegetation.
In the arctic zones	0– 3,000 ft.	bears	arctic-alpine vegetation.

On the basis of these classifications the relevant figures from Murray can be arranged in a series of three tables.

Table 1.

Total Land Surfaces of the *Latitudinal* Zones, in Thousands of Square Miles.

80°–90° N.	112
70°–80° N.	1,379
60°–70° N.	4,767
50°–60° N.	5,300
40°–50° N.	6,225
30°–40° N.	6,436
20°–30° N.	5,773
10°–20° N.	4,278
0°–10° N.	3,832
0°–10° S.	3,973
10°–20° S.	3,630
20°–30° S.	3,550
30°–40° S.	1,659
40°–50° S.	408
50°–60° S.	87
Antarctica	3,565 (virtually no flowering plants)

TABLE 2.

Total Land Surfaces of the Main *Vegetation* Zones, in Thousands of Square Miles.

North arctic-alpine	6,146
,, temperate	11,525
,, subtropical	12,210
,, tropical	8,110
South tropical	7,605
,, subtropical	5,208
,, temperate	495
,, antarctic-alpine	——

Or, combining the equivalent zones in each hemisphere:

Arctic- and antarctic-alpine vegetation zones	6,146
Temperate zones	12,020
Subtropical zones	17,418
Tropical zones	15,715

that is to say, in rough proportion:

arctic-alpine 1; temperate 2; subtropical 3; tropical 2·5.

The next table shows the figures further analysed and segregated according to altitude as well as latitude:

TABLE 3.

Areas open to the several Vegetation Types at different Latitudes.

	No Vegetation	Arctic-alpine	Temperate	Subtropical	Tropical	Total
80°–90° N.	112	—	—	—	—	112
60°–80° N.	729	5,417	—	—	—	6,146
40°–60° N.	895	2,137	8,493	—	—	11,525
20°–40° N.	921	1,487	2,318	7,485	—	12,211
0°–20° N.	1	24	326	1,188	6,571	8,110
0°–20° S.	17	193	261	1,583	5,551	7,605
20°–40° S.	110	180	652	4,266	—	5,208
40°–60° S.	28	63	404	—	—	495
60°–80° S.	—	—	—	—	—	—
80°–90° S.	—	—	—	—	—	—
Totals	2,813	9,501	12,454	14,522	12,122	51,412
Northern hemisphere	2,658	9,065	11,137	8,673	6,571	38,104
Southern hemisphere	155	436	1,317	5,849	5,551	13,308

Finally it is worth while to show the proportion of the land in each zone which, *on account of elevation*, is not occupied by the type of vegetation characteristic of the zone at sea level. The figures are:

North temperate	0·26 or about one-fourth
North subtropical	0·39 ,, ,, three-eighths
North tropical	0·19 ,, ,, one-fifth
South tropical	0·27 ,, ,, one-fourth
South subtropical	0·18 ,, ,, one-fifth
South temperate	0·18 ,, ,, one-fifth

The chief points emerging from the foregoing tables are:

1. Excluding the arctic and antarctic, there is two and a half times as much total land in the north as there is in the south.
2. There is virtually no available land south of 60° S.
3. Land sufficiently high to bear arctic-alpine vegetation occurs in all zones, but by far the smallest proportion is in the north tropics.
4. The total area of temperate vegetation in the northern hemisphere is between eight and nine times as great as in the southern.
5. The total area of arctic-alpine vegetation in the northern hemisphere is more than twenty times as great as in the southern.

APPENDIX B

Discontinuous Genera

The following is a third edition of the list of widely discontinuous genera which first appeared in the *New Phytologist* (210). As there, authorities for the names are given; genera which are to be considered *in sensu stricto* are indicated by asterisks; and certain pairs of genera are combined. In addition the comparable figures in each of the two latest editions are given at the end of each major and minor category.

The main differences between this and the last edition are: the exclusion here, for various reasons, of the following genera or pairs of genera—*Anisophyllea*, *Astephanus*, *Halenia*, *Pelea*, *Stephanotis* and *Jasminanthes*, *Triantha*, *Trymatococcus*; the inclusion here of *Asclepias* and *Gomphocarpus*, *Cedrela* and *Toona*, *Citronella* and *Chariessa*, *Couthovia*, *Criosanthes*, *Cyrtandra*, *Dyerophyton*, *Edwardsia*, *Erisma* and *Erismadelphus*, *Foetidia*, *Haloragis*, *Hippuris*, *Humblotidendron*, *Lebetanthus* and *Prionotes*, *Orites*, *Paratheria*, *Petersianthus*, *Santiria* and *Santiriopsis*, *Symphoricarpos*, *Tetrachondra*, *Zizania*; and a few transfers from one category to another. This gives an overall increase in the list of 16, bringing the total to 758.

The chief purpose of the names and, particularly, the authorities given being to define the groups of species intended, as unmistakably as possible, for those readers who may not be expert taxonomists, I have, in general, used those which seem most likely to achieve this aim, even if they are not those which, according to the strict letter of the Rules of Nomenclature, should be cited.

A. Genera found entirely or predominantly in the North Temperate Zone.

a. Discontinuous over the whole North Temperate Zone.

Aesculus L. and *Hippocastanum* Rupp., *Apocynum* L., *Bifora* Hoffm., *Carpinus* L., *Cercis* L., *Epimedium* L. and *Vancouveria* C. Morr. et Decne., *Fagus* L.*, *Gleditsia* Clayton, *Harrimanella* Cov., *Hypopitys* Dill., *Liquidambar* L., *Narthecium* Moehr., *Ostrya* Scop., *Paeonia* L., *Philadelphus* L., *Pistacia* L., *Staphylea* L., *Tilia* L. 18 (17)

b. Europe and/or W. Asia and E. Asia.

Bosea L. and *Rodetia* Moq., *Forsythia* Vahl, *Leontopodium* R. Br., *Ligustrum* L., *Meconopsis* Vig.*, *Parrotia* C. A. Mey. and *Fothergilla* Murr. p.p., *Pterocarya* Kunth, *Theligonum* L., *Wulfenia* Jacq., *Zelkova* Spach 10 (10)

c. N. America, Europe and W. Asia.

Ammophila Host, *Arbutus* L., *Cakile* Mill., *Cinna* L., *Comandra* Nutt., *Corema* D. Don, *Datisca* L., *Douglasia* Lindl., *Eurotia* Adans., *Heberdenia* Banks, *Helianthemum* Tourn., *Hottonia* L., *Loeflingia* L., *Lupinus* L., *Peganum* L., *Platanus* L., *Spartina* Schreb.*, *Specularia* Heist. . . . . 18 (19) *d.* N. America (especially or entirely in the West) and in Central and/or E. Asia.

Achlys DC., *Boschniakia* C. A. Mey., *Boykinia* Nutt., *Chamaesaracha* A. Gr., *Clintonia* Raf., *Dicentra* Bernh., *Echinopanax* Decne. et Planch., *Enemion* Raf., *Glehnia* Schmidt, *Mahonia* Nutt., *Mitella* L., *Monotropa* L.*, *Nephrophyllidium* Gilg, *Phyllospadix* Hook., *Stenanthella* Rydb., *Thermopsis* R. Br., *Tiarella* L., *Trillium* L. 18 (17)

e. Eastern N. America (especially or entirely) and both continental and insular E. Asia.

Apios Moench, *Buckleya* Torr., *Caulophyllum* Michx., *Cladrastis* Raf., *Cryptotaenia* DC., *Diarrhena* Beauv., *Diervilla* Mill. and *Weigela* Thunb., *Diphylleia* Michx., *Hamamelis* L., *Houttuynia* Thunb. and *Anemopsis* Hk. et Arn., *Kraunhia* Raf. and *Wisteria* Nutt., *Menispermum* L., *Pachysandra* Michx., *Panax* L., *Penthorum* L., *Phryma* L., *Podophyllum* L., *Pogonia* Juss., *Saururus* L., *Shortia* Torr. et Gr., *Stewartia* L., *Symplocarpus* Salisb., *Tipularia* Nutt., *Trautvetteria* Fisch. et Mey., *Triosteum* L., *Zanthoxylum* L.,* *Zizania* L. 27 (25)

f. Eastern N. America and continental E. Asia only.

Aletris L., *Calycanthus* L. and *Chimonanthus* Lindl., *Campsis* Lour., *Chionanthus* L., *Criosanthes* Raf., *Decumaria* L., *Gymnocladus* Lam., *Halesia* L., *Jeffersonia* Barton, *Liriodendron* L., *Pyrularia* Michx., *Stylophorum* Nutt., *Symphoricarpos* Juss. 13 (10)

g. Eastern N. America and Japan only.

Amsonia Walt., *Arethusa* L., *Chiogenes* Salisb., *Croomia* Torr., *Epigaea* L., *Hydrastis* Ellis and *Glaucidium* Sieb. et Zucc., *Mitchella* L. . . . 7 (11)

h. Eastern N. America and E. Asia, with extensions southward in one or both hemispheres.

Abelia R. Br., *Aralia* L., *Astilbe* Buch.-Ham., *Berchemia* Neck., *Catalpa* Scop., *Disporum* Salisb., *Gelsemium* Juss., *Gordonia* Ellis, *Hydrangea* L., *Illicium* L., *Itea* L., *Magnolia* L., *Nyssa* L., *Photinia* Lindl.*, *Schisandra* Michx. . 16 (18)

B. Genera found entirely or predominantly in the tropical regions, but excluding pantropical genera.

a. America, Africa and/or the Madagascar region.

1. America, Africa and the Madagascar region.

Asclepias L. and *Gomphocarpus* R. Br., *Ascolepis* Steud., *Bertiera* Aubl., *Caperonia* St. Hil., *Carpodiptera* Griseb., *Cassipourea* Aubl. and *Weihea* Spreng., *Eichhornia* Kunth, *Elaeis* Jacq. and *Corozo* Giseke, *Eulophidium* Pfitz., *Hirtella* L., *Landolphia* Beauv.; *Loudetia* Steud., *Mostuea* Didr. and *Leptocladus* Oliv., *Paepalanthus* Mart., *Paratheria* Griseb., *Paullinia* L., *Pentodon* Hochst., *Piriqueta* Aubl., *Raphia* Beauv., *Sabicea* Aubl., *Savia* Willd., *Symphonia* L., *Trachypogon* Nees, *Trichilia* L., *Tristachya* Nees, *Vellozia* Vand. and *Barbacenia* Vand. 26 (25)

2. America and continental Africa only.

Amanoa Aubl., *Andira* Lam., *Anthephora* Schreb., *Antrocaryon* A. W. Hill et B. L. Burtt, *Aptandra* Miers, *Bartsia* L.*, *Bouchea* Cham.*, *Brachypterys* A. Juss. (?), *Buforrestia* C. B. Cl., *Cacoucia* Aubl., *Chlorophora* Gaudich., *Chrysobalanus* L., *Conocarpus* L., *Copaifera* L., *Corrigiola* L., *Drepanocarpus* G. F. Mey., *Eriochrysis* Beauv., *Erisma* Rudge and *Erismadelphus* Mildbr., *Euclasta* Franch., *Genlisea* St. Hil., *Guarea* Allem., *Heisteria* Jacq., *Heteranthera* R. et P., *Heteropteris* H., B. et K., *Hoffmanseggia* Cav., *Hydranthelium* H., B. et K., *Hypogynium* Nees, *Laguncularia* Gaertn. f., *Lindackeria* C. Presl, *Macrolobium* Schreb., *Malouetia* A. DC., *Maprounea* Aubl., *Mayaca* Aubl., *Melasma* Berg.*, *Microtea* Sw., *Neurotheca* Salisb., *Ochthocosmus* Benth. and *Phyllocosmus* Klotzsch, *Olyra* L., *Parkinsonia* L., *Pentaclethra* Benth., *Pitcairnia* L'Hérit., *Prevostea* Choisy, *Priva* Adans., *Ptychopetalum* Benth., *Quassia* L., *Renealmia* L.f., *Saccoglottis* Mart., *Schaueria* Nees, *Schultesia* Mart., *Sclerocarpus* Jacq., *Sparganophorus* Crantz, *Sphaeralcea* St. Hil., *Symmeria* Benth., *Syngonanthus* Ruhl., *Talinum* Adans., *Tapura* Aubl., *Thalia* L., *Thamnosma* Torr. et Frem., *Trianosperma* Mart., *Tristicha* Thou., *Vismia* Vand., *Voyria* Aubl. and *Leiphaimos* Ch. et Sch. 62 (62)

3. America and the Madagascar region only.

Pedilanthus Neck., *Ravenala* Adans. and *Phenakospermum* Endl., *Rheedia* L., *Turnera* L. 4 (4)

b. Africa, the Madagascar region and Asia.

1. Africa and Asia (often extending into Australasia and the Pacific Islands).

Adenanthera L., *Adina* Salisb., *Adinandra* Jack, *Aegle* Corr. and *Afraegle* Engl., *Alstonia* R. Br., *Ancistrocladus* Wall., *Anogeissus* Wall., *Antiaris* Lesch., *Aphania* Bl., *Argostemma* Wall., *Artanema* D. Don, *Baissea* A. DC., *Bowringia* Champ., *Brachylophon* Oliv., *Brackenridgea* A. Gr., *Brucea* J. F. Mill., *Bryonopsis* Arn., *Cajanus* DC., *Calamus* L., *Capillipedium* Stapf, *Centotheca* Desv., *Clausena* Burm. f., *Cleistachne* Benth., *Coccinia* Wight et Arn., *Combretodendron* A. Chev., *Ctenolophon* Oliv., *Cyanotis* D. Don, *Cyrtococcum* Stapf, *Dalhousiea* R. Grah., *Dichanthium* Willemet, *Dovyalis* E. Mey., *Droogmansia* De Wild., *Elatostema* Forst., *Elsholtzia* Willd., *Elytrophorus* Beauv., *Englerastrum* Briq.*, *Epithema* Bl., *Erythrophleum* Afzel., *Fingerhuthia* Nees, *Firmiana* Marsigli, *Flacourtia* L'Hérit., *Flemingia* Roxb., *Fluggea* Willd., *Ganophyllum* Bl., *Geissaspis* Wight et Arn., *Halopegia* K. Sch., *Harrisonia* R. Br., *Heritiera* Ait., *Holarrhena* R. Br., *Hunteria* Roxb., *Hymenocardia* Wall., *Illigera* Bl., *Kaempferia* L., *Kedrostis* Medik., *Lasianthus* Jack, *Lecanthus* Wedd., *Lepistemon* Bl., *Leptonychia* Turcz., *Limonia* L. and *Citropsis* Swingle et Kellerm., *Mallotus* Lour., *Manisuris* L., *Mansonia* J. R. Drum., *Microdesmis* Hk. f., *Millettia* Wight et Arn., *Mitragyna* Korth., *Monochoria* C. Presl., *Musa* L., *Naregamia* Wight et Arn., *Neuropeltis* Wall., *Opilia* Roxb., *Oropetium* Trin., *Orthanthera* Wight, *Ottochloa* Dandy, *Oxytenanthera* Munro, *Parochetus* Buch.-Ham., *Perotis* Ait., *Petalidium* Nees, *Petersianthus* Merrill, *Platostoma* Benth. et Hk., *Pterolobium* R. Br., *Pterygota* Schott et Endl., *Pygeum* Gaertn., *Pyrenacantha* Wight, *Quisqualis* L., *Ranalisma* Stapf., *Remusatia* Schott, *Rothia* Pers., *Roureopsis* Planch., *Sansevieria* Thunb., *Santaloides* Schellenb., *Santiria* Bl. and *Santiriopsis* Engl., *Sarcocephalus* Afzel., *Sauromatum* Schott, *Schoenefeldia* Kunth, *Sesamum* L., *Shuteria* Wight et Arn., *Stephania* Lour., *Strombosia* Bl., *Telosma* Cov., *Tenagocharis* Hochst., *Thelepogon* Roth, *Tiliacora* Colebr., *Tinospora* Miers, *Vossia* Wall. et Griff. 104 (101)

2. Africa, the Madagascar region and Asia (often extending into Australasia and the Pacific Islands).

Achyrospermum Bl., *Acridocarpus* Guill. et Perr., *Acrocephalus* Benth., *Adenia* Forsk., *Alangium* Lam. and *Marlea* Roxb., *Albizzia* Durazz., *Alloteropsis* Presl, *Alysicarpus* Neck., *Amorphophallus* Bl., *Apodytes* E. Mey., *Aponogeton* L. f., *Arduina* Mill. and *Carissa* L., *Artabotrys* R. Br., *Asteracatha* Nees*, *Asystasia* Bl., *Azima* Lam., *Baphia* Afzel., *Blyxa* Nor., *Borassus* L., *Bothriochloa* Kuntze, *Bridelia* Willd., *Bruguiera* Lam., *Canarium* L., *Canscora* Lam., *Centipeda* Lour., *Ceriops* Arn., *Ceropegia* L., *Cheirostylis* Bl., *Cirrhopetalum* Lindl., *Cleistanthus* Hk. f., *Cnestis* Juss., *Coffea* L., *Commiphora* Jacq., *Corymbis* Thou., *Crossandra* Salisb., *Cryptolepis* R. Br. and *Ectadiopsis* Benth., *Deeringia*

R. Br., *Dichrostachys* Wight et Arn., *Dicoma* Cass., *Disperis* Sw., *Dumasia* DC., *Ecbolium* Kurz., *Emilia* Cass., *Enhalus* L. C. Rich., *Enteropogon* Nees, *Ethulia* L. f., *Exacum* L., *Filicium* Thw., *Flagellaria* L., *Gaertnera* Lam., *Garcinia* L., *Gastonia* Comm., *Gelonium* Roxb., *Geniosporum* Wall., *Gerbera* Cass., *Giseckia* L., *Gloriosa* L., *Gnidia* L. and *Lasiosiphon* Fres., *Grangea* Adans., *Grewia* L., *Gymnema* R. Br., *Gynura* Cass., *Helinus* E. Mey., *Hemarthria* Munro, *Holmskioldia* Retz., *Hugonia* L., *Hydrilla* L. C. Rich., *Hydrophylax* L. f., *Hymenodictyon* Wall., *Hypoestes* Soland., *Iodes* Bl., *Iphigenia* Kunth, *Laggera* Sch.-Bip., *Laurembergia* Berg., *Lepironia* L. C. Rich., *Lumnitzera* Willd., *Macaranga* Thou., *Maesa* Forsk., *Medinilla* Gaudich., *Memycylon* L., *Mezoneuron* Desf., *Micrargeria* Benth., *Micrococca* Benth., *Microglossa* DC., *Moschosma* Reichb., *Mundulea* Benth., *Mussaenda* L., *Myrsine* L., *Neyraudia* Hk. f., *Nothosaerva* Wight, *Oberonia* Lindl., *Ochna* L., *Odina* Roxb., *Olax* L., *Olea* L., *Orthosiphon* Benth., *Osbeckia* L., *Paropsia* Nor., *Pavetta* L., *Pedalium* L., *Pemphis* Forst., *Peristrophe* Nees, *Phaius* Lour., *Phaylopsis* Willd., *Pleurostylia* Wight et Arn., *Pollia* Thunb., *Polyalthia* Bl., *Premna* L., *Pseudarthria* Wight et Arn., *Rhamphicarpa* Benth., *Rhinacanthus* Nees, *Rungia* Nees, *Saccolabium* Bl. and *Acampe* Lindl., *Satyrium* Sw., *Scolopia* Schreb., *Sebaea* Soland.*, *Secamone* R. Br. and *Toxocarpus* Wight et Arn., *Smithia* Ait., *Sopubia* Buch.-Ham., *Sphaeranthus* L., *Stereospermum* Cham., *Streblochaete* Hochst., *Striga* Lour., *Strophanthus* DC., *Tarenna* Gaertn., *Thunbergia* Retz., *Toddalia* Juss., *Tricalysia* A. Rich., *Tristellateia* Thou. and *Hiptage* Gaertn., *Turraea* L., *Tylophora* R. Br., *Uraria* Desv., *Urophyllum* Wall., *Vangueria* Juss., *Ventilago* Gaertn., *Vepris* Comm., *Voacanga* Thou. and *Orchipeda* Bl., *Wiesneria* M. Mich., *Woodfordia* Salisb., *Xylia* Benth. 140 (142)

3. The Madagascar region and Asia (often extending into Australasia and the Pacific Islands).

Actinoschoenus Benth., *Agrostophyllum* Bl., *Agyneja* L., *Anacolosa* Bl., *Apluda* L., *Atylosia* Wight et Arn., *Balanophora* Forst., *Barringtonia* Forst.*, *Bleekrodea* Bl., *Byrsophyllum* Hk. f., *Carallia* Roxb., *Cephalostachyum* Munro, *Cerbera* L., *Cipadessa* Bl., *Cymbidium* Sw., *Ellertonia* Wight, *Erythrospermum* Lam., *Euodia* Forst. and *Melicope* Forst., *Foetidia* Lam., *Geniostoma* Forst., *Givotia* W. Griff., *Hedychium* Koenig, *Melastoma* L., *Nepenthes* L., *Ochlandra* Thw., *Ochrocarpos* Thou., *Paederia* L., *Pongamia* Vent., *Pothos* L., *Samadera* Gaertn., *Sandoricum* Cav., *Soulamea* Lam., *Strobilanthes* Bl., *Thuarea* Pers., *Tropidia* L., *Vateria* L. *Wormia* Rottb., *Zoisia* Willd. 38 (37)

4. Africa and/or the Madagascar region and Australasia.

Adansonia L., *Athrixia* Ker-Gawl., *Caesia* R. Br., *Cunonia* L., *Hibbertia* Andr., *Keraudrenia* J. Gay, *Rulingia* R. Br., *Triraphis* R. Br. 8 (8)

c. America and Asia (often extending into Australasia and the Pacific Islands).

Anaxagorea St. Hil., *Bocagea* St. Hil., *Callicarpa* L., *Capsicum* L., *Cedrela* P. Br. and *Toona* M. Roem., *Citronella* D. Don and *Chariessa* Miq., *Engelhardtia* Leschen. and *Oreomunnea* Oerst., *Enydra* Lour., *Gilibertia* R. et P., *Helicteres* L., *Ichnanthus* Beauv., *Inocarpus* Forst., *Klugia* Schlechd., *Laplacea* H., B. et K., *Lespedeza* Michx., *Linostoma* Wall. and *Lophostoma* Meissn., *Mappia* Jacq., *Meliosma* Bl., *Microtropis* Wall., *Mitreola* R. Br., *Nelumbo* Adans., *Oxybaphus* L'Hérit., *Physurus* L. C. Rich., *Roucheria* Planch., *Sageretia* Brongn., *Sapindus* L.*, *Saurauja* Willd., *Schoepfia* Schreb., *Sloanea* L. and *Echinocarpus* Bl., *Spathiphyllum* Schott, *Symplocos* Jacq., *Talauma* Juss. *Thismia* W. Griff., *Turpinia* Vent. 34 (32)

d. America and Australasia only.

Atkinsonia F. Muell. and *Gaiadendron* G. Don, *Distichlis* Raf., *Lindenia* Benth., *Nicotiana* L., *Orthosanthos* Sweet, *Trichocline* Cass.* . . . . . 6 (5) *e.* Discontinuous over a considerable part of the Tropical Zone.

Arundinaria Michx., *Byttneria* Loefl., *Calliandra* Benth., *Campnosperma* Thw., *Carapa* Aubl. and *Xylocarpus* Koenig, *Clethra* L., *Cochlospermum* Kunth, *Diplanthera* Thou., *Halophila* Thou., *Hermannia* L., *Hernandia* L., *Kalanchoe* Adans., *Lochnera* Reichb., *Lonchocarpus* H., B. et K., *Mimulus* L., *Omphalea* L., *Passiflora* L., *Protium* Burm. f., *Rhizophora* L., *Schrebera* Roxb., *Styrax* L., *Suriana* L., *Syringodium* Kütz., *Ternstroemia* Mutis., *Thalassia* Banks, *Weinmannia* L. 26 (28)

f. Anomalous genera of the Tropical Zone.

Aldrovanda Monti, *Brasenia* Schreb., *Buxus* L., *Canarina* L., *Cohnia* Kunth, *Cossinia* Comm., *Cytinus* L., *Dyerophyton* O. Ktze., *Fagonia* L., *Hydrodea* N. E. Br., *Kissenia* R. Br., *Nesogenes* A. DC., *Pelargonium* L'Hérit., *Pharnaceum* L. and *Hypertelis* E. Mey., *Phylica* L., *Pilostyles* Guill., *Ruthea* Bolle . 17 (16)

C. Genera found entirely or predominantly in the South Temperate Zone.

a. America and Australasia, some reaching Malaysia and Asia.

1. America, Australia and New Zealand, some reaching the Pacific Islands.

Abrotanella Cass., *Amphibromus* Nees, *Aristotelia* L'Hérit., *Carpha* Banks et Soland., *Colobanthus* Bartl., *Discaria* Hook., *Donatia* Forst., *Drapetes* Banks, *Haloragis* Forst., *Hebe* Comm., *Libertia* Spreng., *Lilaeopsis* Greene, *Muehlenbeckia* Meissn., *Nothofagus* Bl., *Oreomyrrhis* Endl., *Ourisia* Comm., *Pernettia* Gaudich. and *Gaultheria* L., *Phyllachne* Forst., *Schizeilema* Domin, *Selliera* Cay., *Uncinia* Pers. 21 (17)

2. America and Australia, some reaching the Pacific Islands.

Drimys Forst., *Eucryphia* Cav., *Lebetanthus* Engl. and *Prionotes* R. Br., *Lomatia* R. Br., *Oreocallis* R. Br., *Orites* R. Br. 6 (4)

3. America and New Zealand, some reaching the Pacific Islands.

Azorella Lam.*, *Enargea* Banks, *Fuchsia* L., *Gaimardia* Gaudich., *Griselinia* Forst., *Jovellana* R. et P., *Laurelia* Juss., *Marsippospermum* Desv., *Pseudopanax* C. Koch, *Rostkovia* Desv., *Tetrachondra* Petrie 11 (12)

b. Africa and Australasia.

Anacampseros L., *Arctotis* L. and *Cymbonotus* Cass., *Australina* Gaudich., *Bulbine* L., *Bulbinella* Kunth, *Chrysitrix* L., *Dietes* Salisb., *Helipterum* DC., *Hypolaena* R. Br., *Restio* L., *Villarsia* Vent., *Wurmbea* Thunb. . 12 (12)

c. Anomalous genera.

Carpobrotus N. E. Br., *Chevreulia* Cass., *Leptocarpus* R. Br., *Pringlea* Anders., *Tetragonia* L. 5 (5)

D. Genera found in both North and South Temperate Zones.

a. North Temperate Zone, and S. America, S. Africa and Australasia.

Erodium L'Hérit., *Frankenia* L., *Geum* L., *Koeleria* Pers., *Myosotis* L., *Myosurus* L., *Thesium* L., *Triglochin* L., *Viola* L., *Zostera* L. 10 (10)

b. North Temperate Zone, S. America and Australasia.

Calandrinia H., B. et K., *Caltha* L., *Coriaria* L., *Daucus* L., *Eryngium* L., *Euphrasia* L., *Gentiana* L., *Glycyrrhiza* L., *Montia* L., *Myrtus* L., *Scleranthus* L. 11 (10)

c. North Temperate Zone, S. Africa and Australasia.

Emex Neck., *Kochia* Roth., *Limonium* Mill., *Papaver* L., *Trigonella* L., *Zygophyllum* L. . . . . 6 (6) *d.* North Temperate Zone and S. Africa.

Althenia Petit*, *Cryophytum* N. E. Br., *Herniaria* L., *Oligomeris* Cambess. *Pityranthos* Viv., *Seetzenia* R. Br., *Sium* L.* 7 (7)

e. North Temperate Zone and Australasia.

Angelica L., *Damasonium* Mill., *Nitraria* L., *Posidonia* Koenig, *Saussurea* DC., *Sparganium* L., *Veronica* L.* 7 (7)

f. North Temperate Zone and S. America.

Adenocaulon Hk. f., *Antennaria* Gaertn., *Armeria* Willd., *Chrysosplenium* L., *Cicendia* Adans., *Drusa* DC.*, *Empetrum* L., *Hippuris* L., *Honkenya* Ehrh., *Hymenolobus* Nutt., *Lardizabala* R. et P. and *Parvatia* Decne., *Lepuropetalon* Elliott, *Littorella* Berg., *Phippsia* R. Br., *Primula* L., *Saxifraga* L., *Sibthorpia* L. 17 (16)

E. Genera of various distribution but all with outlying species in the Hawaiian Islands (excluding cosmopolitan and pan-tropical genera).

a. Entirely or predominantly Old World.

Alectryon Gaertn., *Alphitonia* Reissek., *Alyxia* Banks, *Antidesma* L., *Byronia* Endl., *Canthium* Lam., *Claoxylon* A. Juss., *Coprosma* Forst., *Cordyline* Comm., *Couthovia* A. Gr., *Cyathodes* Labill., *Cyrtandra* Forst., *Dianella* Lam., *Dracaena* L., *Embelia* Burm. f., *Exocarpus* Labill., *Freycinetia* Gaud., *Gahnia* Forst., *Joinvillea* Gaudich., *Korthalsella* van Tiegh, *Metrosideros* Banks, *Myoporum* Banks et Soland., *Ochrosia* Juss., *Osteomeles* Lindl., *Pandanus* L., *Pipturus* Wedd., *Pittosporum* Banks, *Plectranthus* L'Hérit. and *Coleus* Lour., *Santalum* L., *Schizostachyum* Nees, *Strongylodon* Vog., *Suttonia* Hk. f., *Tetraplasandra* A. Gr. 33 (31)

b. Entirely or predominantly New World.

Cuphea P. Br., *Hesperocnide* Torr., *Nama* L., *Sicyos* L., *Sisyrinchium* L., *Sphacele* Benth. 6 (6)

c. Both Old and New World.

Acaena L., *Astelia* Banks et Soland., *Edwardsia* Salisb. (see special note, p. 117), *Eurya* Thunb., *Gunnera* L., *Lagenophora* Cass., *Lysimachia* L., *Nertera* Banks et Soland., *Oreobolus* R. Br., *Osmanthus* Lour., *Perrottetia* H., B. et K., *Pritchardia* Seem. et Wend., *Urera* Gaudich., *Xylosma* Forst. f. . . . 14 (12)

Numerical Summary

A	127	(127)
B	465	(460)
C	55	(50)
D	58	(56)
E	53	(49)
	758	(742)

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